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Review

Following the star: Inflorescence heliotropism

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ABSTRACT

Plant movements in response to directional solar radiation, known as “heliotropism” are frequently observed in nature. Although there is a considerable amount of literature on these movements in vegetative organs, knowledge about heliotropic responses in flowers and inflorescences is relatively limited. Here we comprehensively review studies on this topic, profile the diversity of responses encompassed under the term “heliotropism” and propose a conceptual framework for their classification. In addition, we discuss the mechanisms underlying different types of heliotropism in two species commonly used as model systems: Arabidopsis and sunflower. Finally, the ecological consequences of floral heliotropism are elaborated with an emphasis on the effects on plant reproductive success, and the potential agricultural implications of manipulating heliotropic responses are addressed as well. We conclude that inflorescence heliotropism appears conserved in many plant species that depend on pollinators, and consists of an auxin dependent response to solar radiation.

1. Introduction

Life on the Earth’s surface is exposed to solar radiation, which constitutes a crucial source of energy for photosynthesis, heat for the regulation of metabolic processes and information from which plants can detect spatial and temporal features of their environment. In this context, plants in the field can be spotted frequently with flowers facing the sun (Fig. 1), and in many studies, researchers have asked how and why such orientation occurs.

The movements of plant organs in response to the incident solar light are encompassed under the term “heliotropism”, which derives from the Greek “helios” (sun) and “tropos” (turn). Although there is a large body of literature about plant movements in response to light, knowledge on movements of flowers or inflorescences is limited compared to that on the responses shown by vegetative organs. Both heliotropic and phototropic responses of vegetative organs have been extensively reviewed elsewhere (Whippo and Hangarter, 2006; Pedmale et al., 2010; Koller, 2011; Hohm et al., 2013) and will not be considered in the present article. The main objective of this paper is to critically review the existing literature on flower and inflorescence orientation in response to directional light. We review studies in which

heliotropic responses in flowers have been assessed, and attempt to produce a general framework organizing the existing literature on the topic. We then present our current knowledge of mechanisms involved in inflorescence and flower orientation, and assess the ecological and potential agronomic implications of flower heliotropism.

2. Conceptual framework for the classification and understanding of heliotropic responses

An important issue that arises when trying to compare studies on inflorescence heliotropism is that no specific criteria are established to discriminate between different types of heliotropic movements and no protocol exists to standardize the way of measuring and quantifying the response. Because of that, many studies use the same term “heliotropism” to describe different responses, or conversely, describe the same response using different terminology. Therefore, it is necessary to establish clear definitions of heliotropism and related terms (see Box 1).

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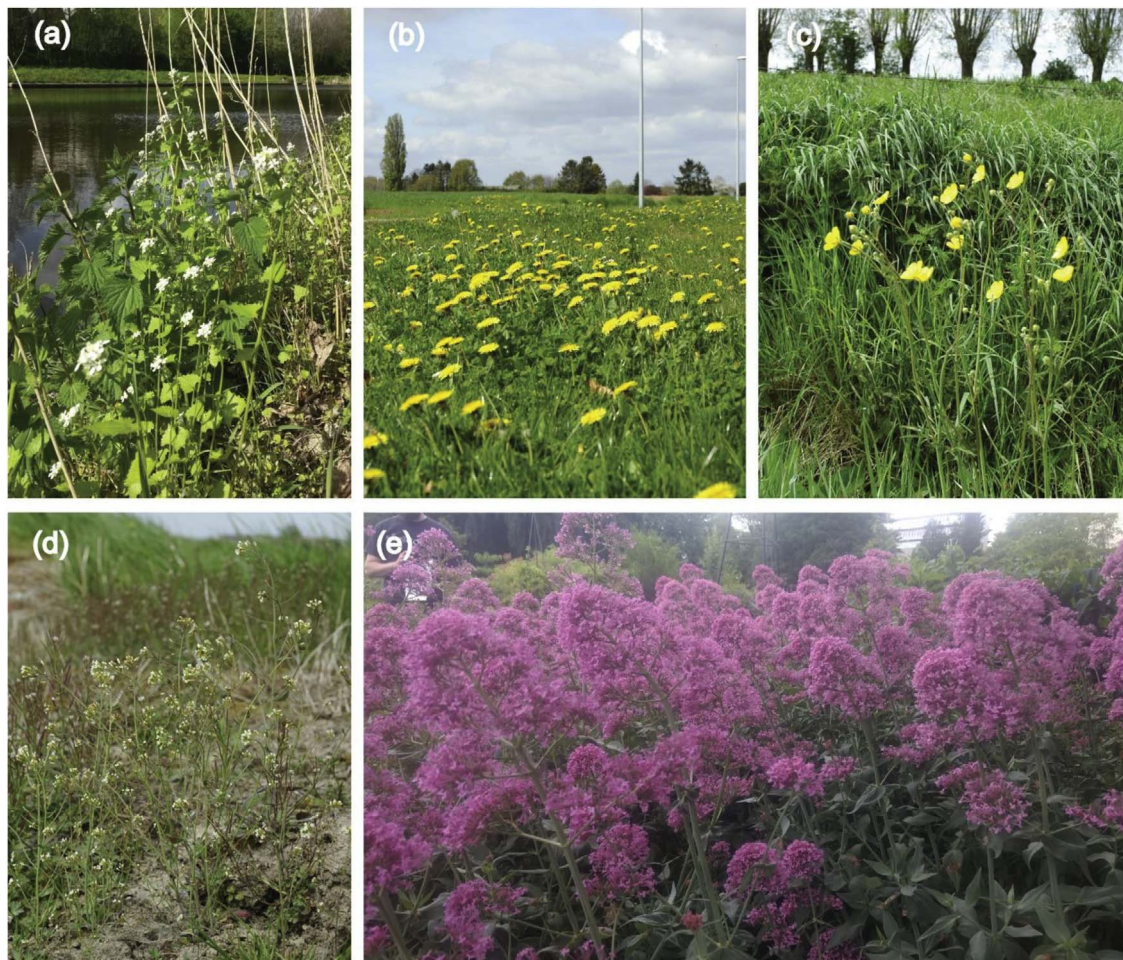


Fig. 1. (a)–(d) Examples of flowers oriented toward the sun in and around Merelbeke and Oosterzele (Belgium). (a) *Alliaria petiolata*, (b) *taraxacum officinale*, (c) *Ranunculus acris*, (d) *Cardamine hirsuta* and *Arabidopsis thaliana*. (e) Inflorescences of *Centranthus ruber* oriented toward the sun in the Ghent University Botanical Garden.

Box 1

Glossary

Heliotropism: any type of process that modifies an organ orientation in response to the sun position (Kevan, 1972; Ehleringer et al., 1980; Koller, 1986; Hart, 1990; Stanton and Galen, 1993; Thanisawanyangkura et al., 1997).

Orthoheliotropism: those cases of heliotropism in which the organ orients orthogonally to the sun rays. <http://www.encyclo.co.uk> (May, 2017)

Apheliotropism: those cases of heliotropism in which the organ bends away from the sun rays Darwin (1880).

Paraheliotropism: those cases of heliotropism in which the organ orients parallel to the sun rays. (Ehleringer et al., 1980; Koller, 1986; Thanisawanyangkura et al., 1997; Habermann et al., 2011).

Diaheliotropism: those cases of heliotropism in which the organ orients perpendicular to the sun rays. (Ehleringer et al., 1980; Koller, 1986; Thanisawanyangkura et al., 1997; Habermann et al., 2011)

Diurnal Heliotropism: when the adjustment of the orientation of the heliotropic organ occurs in periods of about 24 h. (Defined in the present article)

Seasonal Heliotropism: when the response happens only once and the orientation acquired by the organ remain essentially constant. (Patiño et al., 2002)

Horizontal Heliotropism: when plant tracks the compass (or azimuthal) orientation of the sun (along the horizontal plane) (Defined in the present article)

Vertical Heliotropism: when plant tracks the variation of the sun elevation from the horizon (along the vertical plane). (Defined in the present article)

2.1. Mechanistic specification of heliotropism: growth-mediated, turgor-mediated, and circadian controlled movements

Closely related to heliotropism is a process known as phototropism, from the Greek “phos” (light; genitive “photos”) and “tropos” (turn). As it

has been stated by Sherry and Galen (1998), the difference between both concepts is often difficult to establish. This is shown in several examples, where phototropism is considered indeed as a special case of heliotropism, in which the light source is fixed in space (Kevan, 1972; Hart 1990; Zhang et al., 2010). The term “phototropism” often refers to

the differential growth or expansion of plant tissues in response to the direction of incoming light, which generates an orientation response. Furthermore, on many occasions the phototropism concept is constrained to movement toward the light, induced by light of wavelengths shorter than 500 nm (UV-Blue) and its mechanism has been mostly associated to the action of a transmissible substance, auxin (Whippo and Hangarter, 2006).

In contrast to phototropism, the use of the term heliotropism is not linked to any particular mechanism. Therefore, the term “heliotropism” is often applied to any kind of plant movement that leads to orientation of an organ in response to the direction of the sun, regardless of the mechanism that drives that movement. In literature one can frequently encounter studies that use the term heliotropism to refer to movements that are driven either by differential growth or by turgor changes in specialized cells at the base of the leaves (pulvini).

Circadian rhythms can also take part in the mechanism of heliotropic responses. For example, in sunflower, a circadian mechanism re-orientates the inflorescences during the night (Atamian et al., 2016), essentially generating a heliotropic response when the sun is not visible. In the particular case of the movement of sunflower heads, it has been recently demonstrated how phototropic and circadian processes contribute to the full heliotropic response of unopened flower heads (Atamian et al., 2016).

2.2. Spatial specification of heliotropism: vertical and horizontal heliotropism

- When describing quantitatively heliotropic movements, it is necessary to determine to which extent the organ tracks the sun; in other words, the magnitude of the heliotropic response is associated with the angle between the direction of sun rays and the direction to where the organ points. There is a high variability among studies regarding the criteria applied to choose parameters for quantifying heliotropism (Fig. 2). Below we suggest a series of terms to distinguish between the aforementioned criteria.
- Horizontal deviation from the sun: the angle between the flower and the solar position measured in the horizontal plane parallel to the earth surface (Kevan, 1972; Luzar and Gottsberger, 2001; Fig. 2a). The use of this variable is advisable when elevation of the sun is rather stable, like for studies in the arctic.
- Vertical deviation from the sun: the angle between the flower and the solar position measured along the vertical plane, parallel to the gravity vector (Stanton and Galen 1993; Zhang et al., 2010; Fig. 2b). This variable is suitable for studies where the light source is not too variable in trajectory, like for example, phototropic movements towards a fixed light source.
- Absolute deviation from the sun: a three dimensional magnitude that integrates both vertical and horizontal components of the angular deviation from the sun. The angle is calculated from the shadow projected by a heliotropometer consisting of a white disc and a stick normal to the corolla (Stanton and Galen, 1989; Totland, 1996; Fig. 2c). This approach is useful when there is no need to specify the azimuthal (horizontal) or elevation (vertical) components of the angle.
- Horizontal deviation from the east: the angle between the flower orientation and the geographic east measured along the earth surface (horizontal plane), (Stanton and Galen, 1989; Zhang et al., 2010; Fig. 2d). This is used as an alternative to the horizontal deviation from the sun, when there is an intention to trace the trajectory of the flower throughout the day as a continuously increasing magnitude and it is easily translatable to the horizontal deviation from the sun for comparison purposes.
- Vertical orientation toward the east/west: consists in measuring the elevation angle of the flower above the horizon, applying a distinction between east and west orientation using either a positive or negative criterion (Lang and Begg, 1979), or values lower or higher

than 90° (Vandenbrink et al., 2014) (Fig. 2e). This procedure is only advisable in low latitudes where the apparent trajectory of the sun goes from east to west passing close to the zenith at noon

The above descriptions illustrate the variety of perspectives from which heliotropism is analyzed, and highlights the importance of being cautious when making comparisons between different cases of heliotropism.

2.3. Temporal specification of heliotropism: diurnal vs. seasonal

It is generally assumed that heliotropism implies a daily movement of plant organs tracking the solar trajectory in periods of approximately 24 h. In 2002, Patiño et al. described the floral movement of two tropical convolvulaceous species and noted that the short lived flowers preferentially oriented toward the north before the equinox and toward the south after the equinox. Although these flowers did not show daily east to west movements, they were considered heliotropic because their orientation followed the predominant position of the sun in each part of the year. Therefore, Patiño et al. (2002) called this type of heliotropism “seasonal heliotropism”, in contraposition to more familiar “diurnal heliotropism”. It is possible that plants that have this type of heliotropism may have been considered as non-heliotropic or simply ignored in previous studies.

In Fig. 3, we summarized the data available in literature on horizontal heliotropism for several species (Kevan, 1972; Stanton and Galen, 1989; Totland, 1996; Luzar and Gottsberger, 2001; Patiño et al., 2002; Zhang et al., 2010), and compared their observed behavior with that of ideal flowers showing perfect daily and perfect seasonal heliotropism. Heliotropic responses were quantified as the absolute value of the deviation of flower orientation from the azimuthal position of the sun during the day. Perfect daily heliotropism (of an ideal plant) consists of a situation where there is an absolute alignment of the flower and the sun (values equal to zero) at all times, while an ideal, perfect seasonal heliotropism was recognized as a case where a flower points to the equator, at a fixed angle throughout the photoperiod.

To date, with the exception of *Ipomoea pes-caprae* (Fig. 3c), studied by Patiño et al. (2002), most species have been considered heliotropic in the traditional, diurnal sense. Nevertheless, a careful analysis of the movements shown by these plants reveals that most of them may be considered being seasonally- rather than diurnally-heliotropic. For example, the curves describing the movements of *Dryas integrifolia* and *Ranunculus acris* in the Arctic (Fig. 3a) are much closer to the reference line corresponding to seasonal heliotropism than to the curve representing diurnal heliotropism. In mountainous areas, *Anemone rivularis* constitutes another example of seasonal heliotropism and *Ranunculus montanus* a case of diurnal heliotropism with an average lag of 30° (as can be inferred from a rather flat distribution of points around an angle of 30°) (Fig. 3b). *Ranunculus adoneus* shows an intermediate response, i.e. tracking the sun in the morning (until 10 a.m.) and staying in a fixed position during the afternoon.

3. Biological diversity of the inflorescence heliotropic responses

In vascular plants, heliotropism and phototropism of vegetative organs has been described in hundreds of species (Ehleringer and Forseth, 1980; Sailaja and Rama Das, 1996; Iino, 2001), while floral heliotropism has been reported in 94 species, belonging to 28 families occurring in extremely different biogeographical areas, i.e. from cold Arctic (Kevan, 1973; Mølgaard, 1989; among others) to temperate and warm equatorial regions (Smith, 1975; Patiño et al., 2002; among others) (Table S1 in Supplementary material). Moreover, among the species that are currently documented to be heliotropic, detailed quantification of the response is only available for 12 of them in terms of the duration of the sun-tracking behavior, and for 7 of them in terms of the orientation angle of the flowers (Table S1).

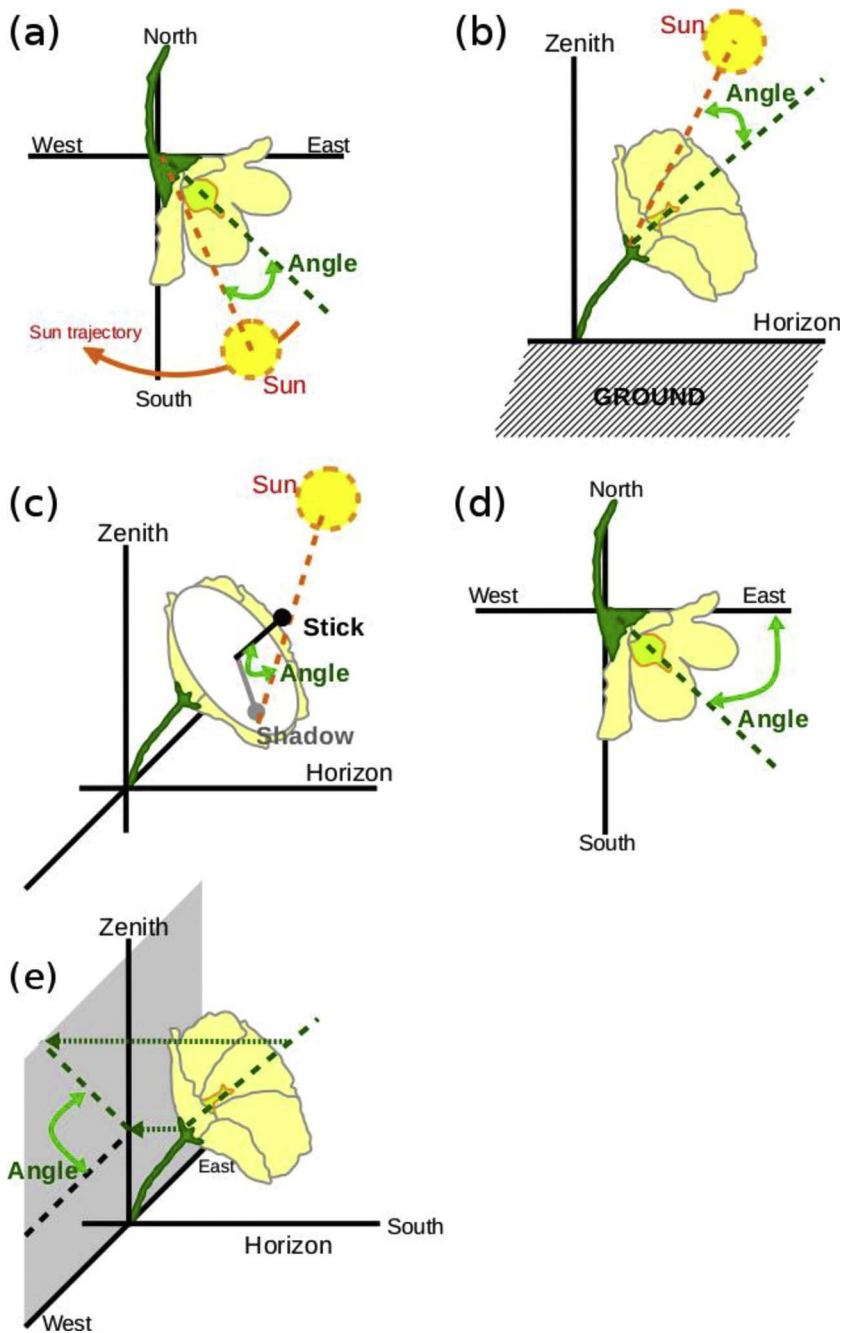


Fig. 2. Description of the different flower movements adopted as a measure of heliotropic response by different authors: (a) the horizontal component of the angle between the flower and the sun, measured on a plane perpendicular to gravity vector (Kevan, 1972; Luzar and Gottsberger, 2001) (b) the vertical component of the angle between the flower and the sun, measured on a plane perpendicular to the Earth surface (Stanton and Galen, 1989; Zhang et al., 2010). (c) a tridimensional combination of both angles (Stanton and Galen, 1989; Totland, 1996; Zhang et al., 2010). (d) the compass orientation (on a plane perpendicular to gravity vector) relative to the east. (e) the elevation angle (vertical) incorporating an east/west discrimination. The short spaced dotted arrow indicates direction of projection against an east-west oriented plane (Lang and Begg 1979; Vandenbrink et al., 2014).

Phototropic behavior of reproductive organs is widespread, and occurs even in fungi and lower plant taxa such as *Phycomyces* (Fungi, Mucoraceae) sporangiophores (Denisson, 1965), *Pellia epiphylla* (Bryophyta – Pelliaceae) sporophyte setae (Thomas et al., 1987), *Aplodon wormskioldii* (Bryophyta – Splachnaceae) sporophytes (Steere, 1973) and conchosporangia of the marine red macroalga *Pyropia yezoensis* (Rhodophyta – Bangiaceae) (Takahashi and Mikami, 2016).

A special case of seasonal heliotropism can be found in columnar cacti native from desert and semi-arid lands of South and North America and is called stem tilting. Many species of columnar cacti show a conspicuous bending of their upper section toward the equator (i.e. to the South in North American deserts and to the north in southern regions). This case of differential growth in the stem results eventually in an orientation toward the sun of the part of the plant where flowers develop. In some species of the genus *Copiapoia* which grow in the cold Atacama desert, this apical part of the body is covered by a waxy

reflective layer and a dense hairy area in the central meristematic region, corresponding with the location of the flowers. As a result of this stem tilting, the well protected apex of the column becomes the warmest part of the cactus, minimizing the lateral, glabrous surface exposed to solar radiation during the dry and warm part of the year. At the same time, the flowers are heated during the cool months when flowering occurs (Ehleringer et al., 1980). In a warm desert in an intertropical region of Mexico, the same equatorial tilting can be observed, but in this case, the south oriented apices of the columnar *Echinocactus platyacanthus* provide protection from overheating to the flowers that develop in the warm summer when the sun shines slightly from the north, while during the rest of the year, light interception is maximized (Herce et al., 2013). In contrast, negative stem tilting has been reported in *Cephalocereus columna-trajani*, a giant cactus of Zapotitlán, Mexico (Zavala-Hurtado et al., 1998), but due to the south orientation of the sun during the flowering season, the same double

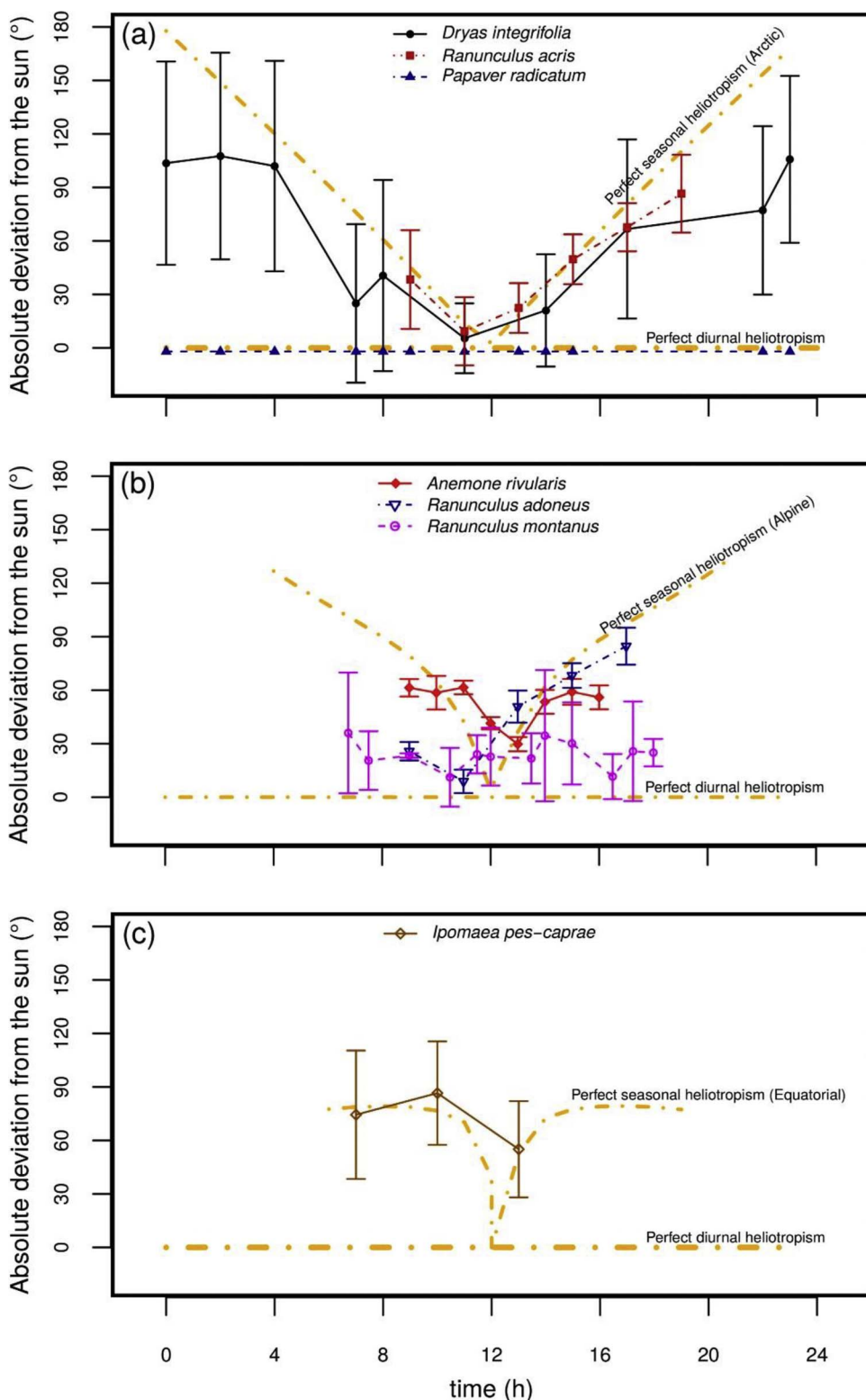


Fig. 3. Heliotropic responses (in terms of horizontal deviation from the sun) of seven species for which quantitative data is available in literature, contrasting their behavior with ideal plants (orange dash-lines) showing perfect seasonal or daily heliotropism in arctic (a), alpine (b) and equatorial (c) regions according to the place where the measurements were taken. It is noteworthy that only *Papaver radicatum* (a) and *Ranunculus montanus* (b) show diurnal heliotropism. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consequences of protection of reproductive structures against heat load, and maximization of annual radiation interception is achieved.

In the above mentioned datasets, most reports on flower and inflorescence heliotropism describe orientation toward the light. However, in certain species, inflorescences bend away from the light, thus displaying negative heliotropism. For instance, in the vines *Cymbalaria muralis* (*Linaria cymbalaria*) (Schmitt, 1922) and *Tropaeolum majus* (Oehlkers, 1922) the negative phototropism occurs after

fertilization and this has been interpreted as an adaptation to increase the chances of the seeds to fall on rocks or wall surfaces, which are suitable places for seedling establishment (Junghans and Fischer, 2008). Change in tropic direction of the inflorescence appears somewhat more general, as it was also observed in *Cyclamen persicum* (Darwin, 1880). The latter system was investigated more thoroughly in *Cyclamen*, and in accordance with the observations in *Cymbalaria* and *Tropaeolum*, young inflorescence stems are positively phototropic, while

older, fruit bearing stems, display negative phototropism (Kiendl, 1940; Zinsmeister, 1960 Zinsmeister, 1960).

4. Candidate physiological mechanisms for the different heliotropic responses

Our understanding of the mechanisms that underlie tropic responses in vegetative organs is substantially greater (especially in hypocotyls or coleoptiles of young seedlings) than in flowers or inflorescences. To date, two classes of mechanisms for tropic movements have been described for plants, irrespective of the organ: hormone (auxin) based, and turgor (pulvinus) based responses. The pulvinus is a specialized structure typically found on leaves, leaflets or petioles, and to date no turgor-based mechanism has been described for inflorescence or flower heliotropism. Current knowledge indicates that heliotropism of flowers is the result of differential growth of pedicel, peduncle or the entire stem of the plant.

Few studies are available that reveal details on the mechanism of inflorescence movements. Most of our mechanistic understanding is derived from work with two model systems: sunflower, where solar tracking of the unopened flower heads has been studied in detail (Atamian et al., 2016; Kutschera and Briggs, 2016), and Arabidopsis, in which multiple molecular genetic tools have been used to unravel the mechanisms of phototropism in inflorescence stems (Kumar and Kiss, 2006; Kagawa et al., 2009; Kumar et al., 2011; Sato et al., 2014).

4.1. Sunflower buds: a model for diurnal heliotropism

Solar tracking in sunflowers depends on differential elongation of the stem. During the day the east-facing side elongates faster than the west-facing side, and this pattern of differential elongation is reversed during the night (Atamian et al., 2016). The diurnal differential growth persists in free running conditions, indicating that it is under control of the circadian clock (Fig. 4a). An “east-west” moving blue light source, with 16 h light/8 h dark containing periods, is sufficient to mimic the response in the field, while this is not the case for a 30 h (20 h blue light/10 h dark) period. Hence, directional blue light photoreceptors, like phototropins, are believed to act in concert with the circadian clock to control downstream growth regulating processes (Vandenbrink et al., 2014; Atamian et al., 2016). It is of note that the circadian clock itself can be under the control of multiple photoreceptors (Millar, 2003), which all may have an effect on the outcome of solar tracking. The differential growth pattern is associated with differential expression of distinct auxin response genes at the faster elongating side, which points to the necessity of auxin signaling in the elongating tissue. Furthermore, elongation in sunflower stems depends on the presence of the plant hormone gibberellin. In view of the reported interactions between auxins and gibberellins in other species (Ross et al., 2003; Weston et al., 2009; Willige et al., 2011), a similar interplay may cause bending in differential growth of sunflower stems. Both hormones are necessary for a correct elongation of cells, and often have synergistic effects. Older sunflowers lose the ability to elongate in a western direction, resulting in east facing heads. The mechanism behind this appears to depend on a combination of circadian gating conferring a higher sensitivity to phototropic signals in the morning, and a gradual cessation of elongation growth of the stem (Atamian et al., 2016).

4.2. Arabidopsis: a model for seasonal heliotropism?

The Arabidopsis inflorescence has no record of tracking the sun in the diurnal way sunflower buds do, but rather classifies as seasonally heliotropic (Serrano and Arana, unpublished). However, a substantial amount of mechanistic data is available on the response of inflorescences to artificial light sources in controlled conditions. Multiple photoreceptors appear to be involved in the phototropic response of Arabidopsis inflorescence stems toward blue light (Fig. 4). Analogous to

the situation in seedlings, the blue light photoreceptors phototropins induce the movement of inflorescence stems of Arabidopsis toward blue in a very sensitive manner (Kagawa et al., 2009). Interestingly, in similar blue light conditions, the red-far red photoreceptor phytochrome E (phyE) has been suggested as an additional important photoreceptor for phototropism in inflorescence stems (Kumar and Kiss, 2006). Auxins appear involved in inflorescence phototropism, as the dominant Arabidopsis *AUX/IAA7* mutant *axr2*, which shows an auxin resistant phenotype, lacks positive inflorescence phototropism and even tends to show negative phototropism (Sato et al., 2014). This suggests that correct auxin signaling is of utmost importance to achieve the inflorescence phototropic response. Furthermore, auxin efflux carrier *abcb19* (*mdr1*) mutants have enhanced phototropism towards blue light (Kumar et al., 2011).

Current models indicate that ABCB19 is responsible for the downward flow of auxins from apical meristem to base, in both seedlings and inflorescence stems (Noh et al., 2001). Inferring that a similar model applies to both seedlings and inflorescence stems, it is tempting to speculate that apically derived auxin diminishes the capacity of inflorescences to respond in a phototropic manner. Since auxin signaling is necessary for bending, it is likely that with diminished downward auxin transport, the eventual auxin available in the bending zone becomes closer to the thresholds necessary for efficiently generating an auxin gradient and consequent differential growth (Vandenbussche et al., 2014). In such a case, the locally available transport machinery for generating a lateral auxin gradient (Cholodny–Went theory) may be more effective than when a strong downward auxin flow is present (Fig. 4).

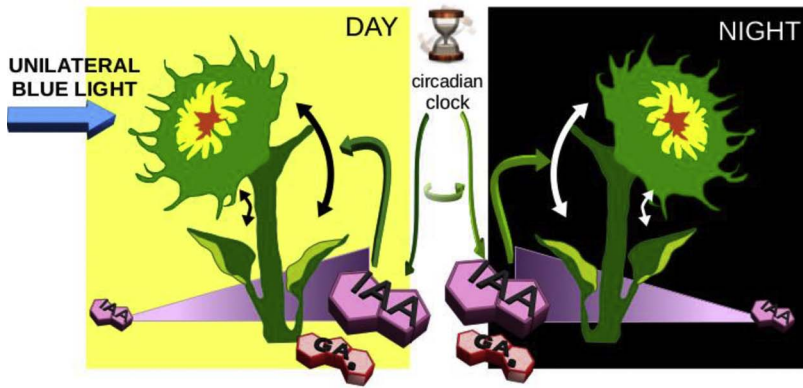
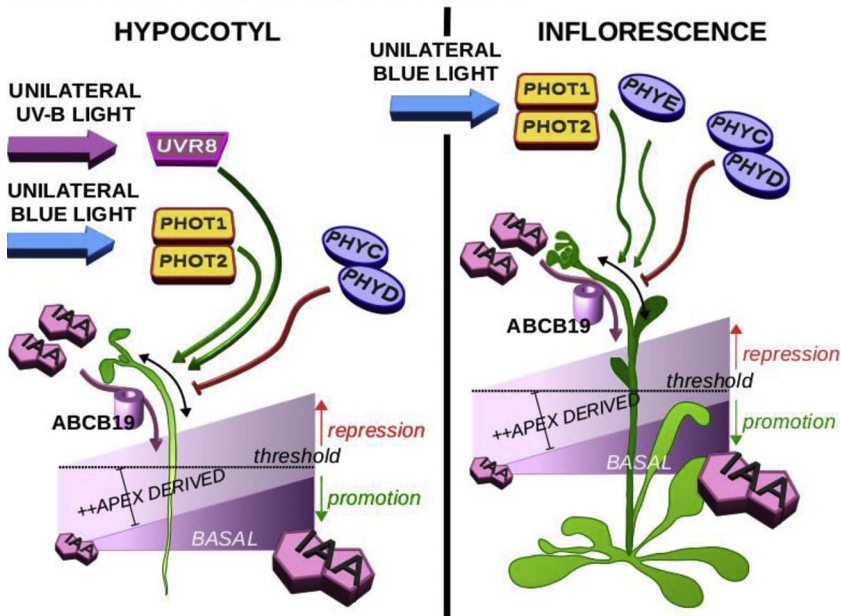
Similarly to what is known for *Arabidopsis*, blue light has been shown more effective than light of higher wavelengths for inducing heliotropism in other species such as *Ranunculus adoneus* (Stanton and Galen, 1993) and *Anemone rivularis* (Zhang et al., 2010). Furthermore in both studies it was shown that a mechanism based on differential growth rates between shaded vs. illuminated sides of the peduncles is responsible for the bending response.

Finally, different floral organs have been identified as important components of the heliotropic mechanism in plants growing in the wild. For example, flowers of *Dryas integrifolia* lacking the gynoecium lost the response (Krannitz, 1996) while petals and tepals are required for heliotropic movements of *Papaver radicum* and *Anemone rivularis* (Corbett et al., 1992; Zhang et al., 2010).

Future challenges to unravel the mechanistic differences between diurnal and seasonal heliotropism lie ahead. In this respect, the investigation of differential involvement of components of the circadian clock in diurnally versus seasonally heliotropic species, with the help of currently available targeted mutagenesis strategies, will be of key importance.

5. Ecological significance

Solar light provides not only energy for photosynthesis but also information about the characteristics of the environment, mainly associated to competition and interactions with the animal kingdom. In addition, the infrared portion of the solar spectrum constitutes a source of heat. In this context, phototropism of vegetative organs allows plants to orient their photosynthetic tissues according to incoming light, increasing light interception in photosynthetic organs. However, the same phenomenon taking place in organs of which the primary task is not photosynthesis related, like flowers, cannot be explained by the same principles of light capture with a subsequent increase in photosynthetic metabolism and growth. In spite of the aforementioned diversity of plant heliotropic responses, ecological studies indicate that heliotropism has a major and unique consequence in the plant kingdom; the increment of reproductive success. This is reflected in different processes that extend from the maturation and development of sexual structures to the success of pollination and the contribution to the

(a) Diurnal heliotropism: *Helianthus annuus* unopened heads(b) Seasonal heliotropism: *Arabidopsis thaliana*

number/weight of the seeds (Table S2).

5.1. Effects of flower heliotropism on floral characteristics and its relation with entomophilous pollination

Most of the ecological studies point to a positive effect of floral heliotropism on entomophilous pollination. From a general point of view, orientation of flowers towards the light may help in displaying them for pollinators, thus generating more contrast with the background vegetation. Flower color itself may also be influenced by the position of the flower vis à vis the light. Although in many species much of the floral pigmentation is developmentally regulated, and patterns are formed in the bud (Schlangen et al., 2009), the color of flowers is affected by environmental cues (Griesbach, 1987). The presence of sufficient light is necessary for pigmentation of petals of some *Rhododendron* species (Halligan, 1988), or for intensifying color of flowers of species such as *Paeonia lactiflora* (Zhao et al., 2012) and *Eustoma grandiflorum* (Griesbach, 1992; Zhao and Tao, 2015). The latter species has been reported to have a clearly phototropic flowering stem (Scace, 2001), but for other species the correlation between heliotropism and light induced color changes has not been investigated. It is plausible that such promotion of color intensity or pattern by light, influences the visiting behavior of pollinators that are attracted by the pigment based floral characteristics (Chittka and Raine, 2006). For instance, bees use the contrast of flower color versus a green background to detect flowers

(Spaethe et al., 2001; Chittka and Raine, 2006) and for attracting pollinators numerous plant species rely at least in part on light absorbance or reflectance (Chittka et al., 1994; Horth et al., 2014; Koski and Ashman, 2014; Peterson et al., 2015). Within a species, floral color can vary and differences occur in the patterns that serve as guide to pollinators (Yoshioka et al., 2005; Horth et al., 2014). In this context it is noteworthy that wild bees prefer exaggerated large size floral guides, suggesting benefits for pollination (Horth et al., 2014). Nevertheless, despite these possible influences on floral display, in most cases entomophilous pollination was found predominantly associated with an increment of the temperature in heliotropic flowers with a consequent creation of a favorable environment for insect activities and has led to the adoption of the so-called heat reward hypothesis. This might represent a plant-pollinator co-adaptation, of particular relevance in cold arctic and alpine ecosystems (Kevan, 1975; Smith, 1975; Stanton and Galen, 1989). On the other hand, the increment of floral temperature increases the production of nectar (Petanidou and Smets, 1996) or other botanical characteristics (Cooley, 1995) that might promote the visiting by pollinators. It has been demonstrated that an increase in flower temperature as well as the light irradiation itself also enhances the release of volatile components (Jakobsen and Olsen, 1994; Hu et al., 2013; Borghi et al., 2017) and influences the relative abundance of the different floral scent constituents (Farré-Armengol et al., 2014) by modifying several plant physiological processes involved at different stages of the biosynthesis of volatile components and

their emission or release (Niinemets et al., 2004), or by affecting the physicochemical properties of the substances (volatility, diffusivity, etc). However, the release of floral scents decays after an optimal temperature is reached. This optimal temperature for volatile compound emission varies across plant species according to the conditions that are predominant during flowering time; i.e. winter-flowering species show the lowest optimal temperature while summer-flowering species have the highest (Farré-Armengol et al., 2015). For this reason, it was proposed that extreme warming such as predicted for global average temperatures at the end of the century may cause a significant disruption of this kind of plant-pollinator communication.

Observations by Kevan (1970) at Hazen Camp (North Canada) indicated that mosquitoes and dance flies may rise their body temperature up to 14 °C above ambient air by resting for long periods inside flowers of *Dryas integrifolia*. Smith (1975), Stanton and Galen (1989) and Luzar and Gottsberger (2001), also measured the time spent by pollinators inside heliotropic versus non-heliotropic flowers and observed that insects spent more time in heliotropic ones. Studies in sunflower heads showed that heliotropic inflorescences facing east in the morning attracted five times more pollinators than inflorescences artificially oriented to the west. This effect was correlated with higher temperatures in east oriented heads. Moreover, artificially warmed inflorescences pointing west, also attracted more pollinators than non-heated inflorescences, when both groups of inflorescences were equally oriented (Atamian et al., 2016). However, the authors could not fully explain the effect of inflorescence temperature in the number of visits, since artificially warmed heads facing west indeed received more visits than cooler ones, yet less than naturally east-oriented heads, suggesting additional plant-pollinator interaction mechanisms play a role.

Other examples of flowers that become more attractive for pollinators as a result of their heliotropic response include *Oritrophium limnophyllum* (Smith, 1975), *Ranunculus montanus* (Luzar and Gottsberger, 2001), *Ranunculus adoneus* (Stanton and Galen, 1989) and *Adonis ramosa* (Kudo, 1995). Interestingly, in the tropical species *Merremia bornensis*, heliotropic flowers are colder than non-heliotropic ones. Notwithstanding this, heliotropic flowers receive more pollinator visits. Here heliotropic orientation of flowers and transpiration are proposed to prevent high temperatures of the gynoecium (Patiño et al., 2002), and may be a variation on the theme of achieving the optimal temperature conditions for pollinators. On the other hand, no significant effects in pollination of flower heliotropism of *Drosera filiformis* flowers have been detected, suggesting an evolutionary anachronism that no longer has a function (Wilson, 1994).

5.2. Effect of flower heliotropism on plant physiological processes related to reproductive success

In addition to its effect on the attraction of pollinators, changes in floral temperature due to heliotropism may create a favorable thermic environment for the development of plant physiological processes related to sexual reproduction. For example, the duration of meiotic division of pollen mother cells, pollen maturation, pollen transfer, stigmatic receptivity, pollen germination, pollen tube growth, double fertilization and ovule and seed development are all processes regulated by temperature (Pigott and Huntley, 1981; Kjellberg et al., 1982; Young, 1984; Corbett, 1990; Stephenson et al., 1992; Kudo, 1995; Delph et al., 1998; Hedhly et al., 2003; Li and Huang, 2009; Whittle et al., 2009) and might be affected by thermic environments created by heliotropism. In accordance with this, flower heliotropism of *Anemone rivularis* increased flower temperature, seed size and number and it was suggested that flower heliotropism enhances the pollen viability and seed production, resulting in higher reproductive success (Zhang et al., 2010).

Heliotropism has been shown to increase seed set in *Papaver radicum* (Corbett et al., 1992), *Anemone rivularis* (Zhang et al., 2010) and *Ranunculus adoneus* (Stanton and Galen, 1989). In addition, heliotropic

flowers of *Papaver radicum* and *Dryas integrifolia* produced heavier seeds than non-heliotropic flowers (Corbett et al., 1992; Krannitz, 1996). Such effects may relate to the light reaching the embryo during seed filling. Although to date not (yet) associated with heliotropism, light stimulates photosynthesis in embryos of Brassica, and thus affects oil content in oilseed rape (Asokanathan et al., 1997; Goffman et al., 2005). Furthermore, in soybean, seed filling and thus yield are dependent on the light regimes reaching the developing embryo (Allen et al., 2009).

On the other hand, within the frame of global warming, it is important to consider that some heliotropic flowers, particularly those growing in warm environments, may become damaged if temperatures rise to stressful conditions. For example, it has been proven that heat stress reduces fruit number and weight in tomato and seed number per fruit (Peet et al., 2002). Moreover, solar-tracking flowers of *Ranunculus adoneus*, experience higher rates of water loss due to transpiration, and absorb a larger amount of water from the soil than non-heliotropic flowers (Galen, 2006). Hence it was suggested that flower heliotropism rises the water cost of reproduction, meaning that a potential trade-off relation between water use and flower behavior as that of heliotropism may shape the reproductive success of the plant.

As has been discussed above, the most common effect of heliotropism in flowers is the heating of reproductive structures, resulting in diverse advantages in terms of fitness. This is especially true in the case of diurnal heliotropism, and hence it is tempting to hypothesize that this phenomenon is more common at higher latitudes, where the ecological advantage on increasing flower temperature is likely to be more important. The graph in Fig. 5a shows the geographical distribution of the studies surveyed in this article. Most of the species reported to exhibit diurnal heliotropism belong to arctic and mountainous areas, while the plants studied in equatorial and tropical regions are mainly seasonally heliotropic (Fig. 5a). Nevertheless, among the species that show diurnal heliotropism there is no correlation between the relative heliotropic time (the proportion of the day that the flowers tracked the sun) and the latitude (Fig. 5b), and many of them occur in both mountainous and lowland habitats.

It is important to note that these geographically isolated observations do not represent all habitats where the species exist, and there are some habitats that are under-represented. For instance there must be a number of species also endemic to lowland regions or to countries of the southern hemisphere, which have received less attention for scientific research.

It is important to remark that although the studies cited above indicate that the main rewards of heliotropism appear to be caused by consequent beneficial changes in irradiance and/or temperature, it remains elusive which processes or organs are responsible for increased fitness. Experimental studies are needed to investigate a possible association of the plant's increase in reproductive success with the male or female reproductive parts, or other floral aspects. Furthermore, unraveling the relative importance of both irradiance and temperature for fitness as a consequence of heliotropism, warrants an in depth study. This may involve analyzing developmental regulation of reproductive organs and seeds, and production of volatiles and a suitable physical flower environment for optimal interaction with pollinators, in a range of temperatures and irradiances.

6. Conclusions and perspectives

Heliotropism of reproductive structures is a widespread response in the plant kingdom, and it is even present in fungi and algae. Despite the interesting advances on this topic, many questions that comprise different areas of knowledge (i.e. evolutionary, ecological up until the molecular scale) remain open. For example, from an evolutionary point of view we still ignore the phylogenetic origin of the heliotropic responses in the plant kingdom. We lack evidence of the existence of this phenomenon in reproductive structures and fruits in gymnosperms, and

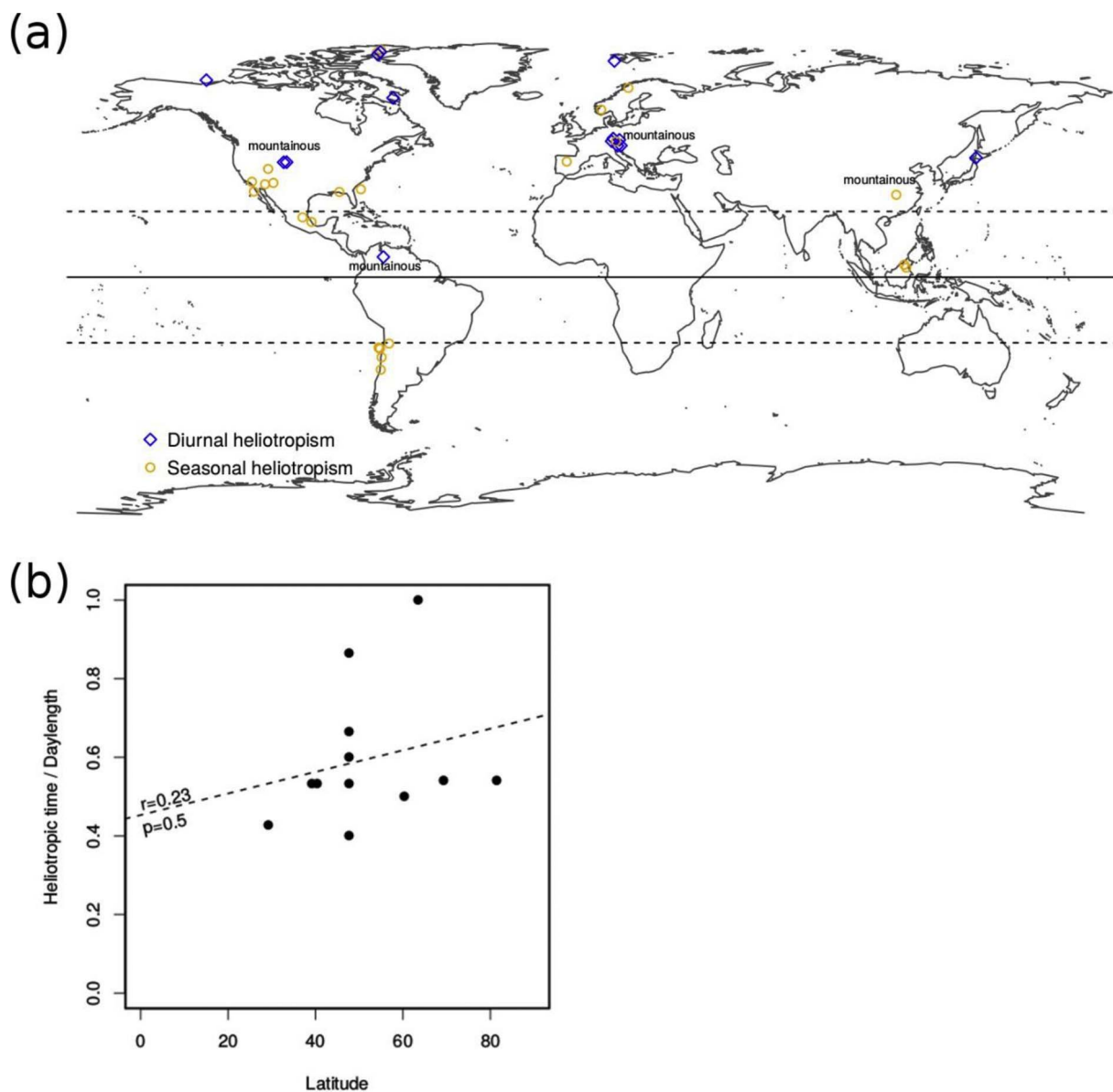


Fig. 5. (a) Geographic distribution of the reported cases of diurnal and seasonal heliotropism. (b) Relation between the heliotropic time (the proportion of the day during which the flower tracks the sun) and the latitude where the study was performed. A Pearson's product-moment correlation test was carried out yielding no significant correlation between variables (Pearson's coefficient $r = 0.23$). The p -value yielded by a linear regression analysis is 0.479, indicating no effect of latitude on heliotropic time.

there is a shortage of information about the possibility of heliotropic responses in “primitive” angiosperm clades. Detailed characterization of this phenomenon in genera such as *Amborella*, *Nuphur* and *Illicium*, which are clades at the base of the flowering plant lineage, could provide interesting insights into the evolutionary aspects of inflorescence heliotropism of vascular plants. An additional question is whether seasonal and diurnal heliotropism share similar origins, or if they arise from different evolutionary pathways. For this last subject, once the mechanistic details are established, molecular studies might shed light on possible common signaling pathways of both responses. The availability of new molecular tools and next generation sequencing techniques open new opportunities for advances in this area.

In spite of the diversity of the heliotropic response of flowers and inflorescences and its occurrence in a wide variety of plant species and families, there is a common ecological significance: a positive impact on reproductive biology, in terms of size and/or quantity of seeds. Up until now, the benefits of heliotropism in reproductive organs have been mainly associated with the regulation of the temperature environment during fertilization/fruit development, and with positive effects on

entomophilous pollination. It is noteworthy that a temperature optimum for seed growth rate exists and deviations from this optimum strongly influence the yield of many crops such as wheat, common bean, soybean, sorghum, rice and barley (Chowdhury and Wardlaw, 1978; Egli and Wardlaw, 1980; Siddique and Goodwin, 1980; Campbell et al., 1981; Kiniry and Musser, 1988; Porter and Gawith, 1999). In cold areas, the modification of the temperature of the inflorescence during seed maturation by the use of genetic lines with stronger heliotropic responses after pollination might mean an agronomical opportunity for the improvement of yield of crops. On the other hand, high temperatures can be harmful for flower development and seed production. For example, heliotropic flowers of plants native from cold areas (like *Papaver* species) may become damaged when grown in warm regions, especially when managed inside greenhouses where cooling systems are costly. In addition, high temperatures during the period of flowering reduce the success of fertilization and the seed growth rate (Egli and Wardlaw, 1980; Ferris et al., 1998; Wheeler et al., 2000). In such conditions, the capacity to generate lines developing paraheliotropic or aphilotropic flowers (or leaves) may constitute an economical

improvement. Furthermore, the process described by Patiño et al. (2002) constitutes a unique case where a combination of heliotropism and floral morphology (bell-shaped corollas of *Convolvulaceae* species) causes a cooling rather than a heating effect. This can inspire alternative ways to generate a cooling solution to growing heliotropic flowers in warm environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.envexpbot.2017.11.007>.

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