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Review

Turning heads: The biology of solar tracking in sunflower

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ABSTRACT

Solar tracking in the common sunflower, *Helianthus annuus*, is a dramatic example of a diurnal rhythm in plants. During the day, the shoot apex continuously reorients, following the sun's relative position so that the developing heads track from east to west. At night, the reverse happens, and the heads return and face east in anticipation of dawn. This daily cycle dampens and eventually stops at anthesis, after which the sunflower head maintains an easterly orientation. Although shoot apical heliotropism has long been the subject of physiological studies in sunflower, the underlying developmental, cellular, and molecular mechanisms that drive the directional growth and curvature of the stem in response to extrinsic and perhaps intrinsic cues are not known. Furthermore, the ecological functions of solar tracking and the easterly orientation of mature heads have been the subject of significant but unresolved speculation. In this review, we discuss the current state of knowledge about this complex, dynamic trait. Candidate mechanisms that may contribute to daytime and nighttime movement are highlighted, including light signaling, hormonal action, and circadian regulation of growth pathways. The merits of the diverse hypotheses advanced to explain the adaptive significance of heliotropism in sunflower are also considered.

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Contents

Introduction	20
A history of back and forth	21
Solar tracking is not solely driven by the movement of the sun	22
Candidate molecular mechanisms	22
Directional light perception	22
Differential stem growth	23
Nocturnal reorientation	23
Cessation of solar tracking	24
Ecological function(s) of solar tracking and mature head orientation	24
Conclusions	25
Acknowledgements	25
References	25

Introduction

Plants live in continuously, but in many ways predictably, changing environments. The availability of resources and the

prevalence of stresses oscillate over each 24 h period. Plants have evolved adaptations that synchronize growth, development, and metabolism to these daily cycles, fostering survival and reproduction in such fluctuating conditions. These rhythms may be driven by the cycling external factors themselves, such as light, water availability, and temperature. However, many diurnal traits are also governed by interactions between internal, or endogenous, rhythms often powered by the circadian clock and non-autonomous, exogenous rhythms driven wholly by cycles of environmental cues [e.g., 1,2].

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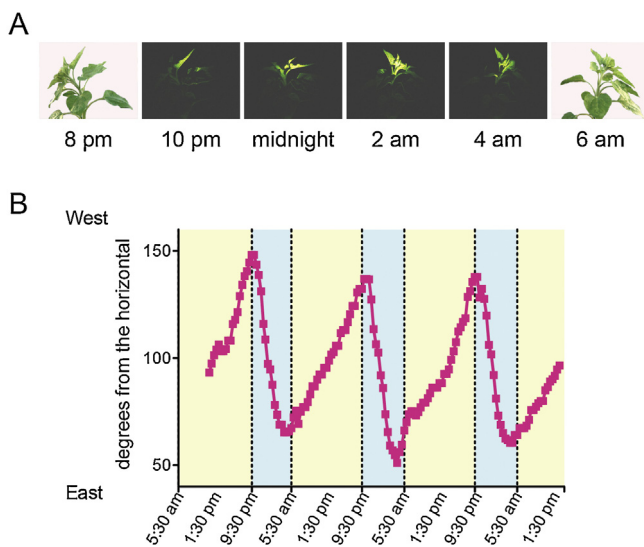


Fig. 1. The sunflower shoot apex tracks the sun during the day and reorients at night, facing east well before sunrise. (A) Stills from a time-lapse photography series taken every 30 minutes using a consumer camera and a dim-solar powered light to enable photography (West = left). Plants were grown in pots in the field in Davis, California, and images were taken when the plants were ~2 months old. (B) Daily cycles of the stem angle relative to the horizontal plane (90° = skyward orientation) measured at first node below apex.

Source: S. Harmer.

Solar tracking, or heliotropism, of developing sunflowers is one of the most conspicuous diurnal rhythms observed in plants (Fig. 1). The term heliotropism was first introduced by Augustin Pyramus de Candolle [3] and later used by Charles Darwin [4] to refer to any form of plant movement in response to incident light. However, today we recognize distinct categories of plants movements in response to light. By far the best-studied phenomenon is phototropism, typically described as a growth-mediated movement in response to unilateral light that is integrated with gravitropic responses, producing a sustained curvature [5]. In contrast, heliotropism is a more dynamic and oscillatory form of plant movement by which some or all of an individual's aerial tissues continually shift their orientation throughout the day, following or avoiding the ever-changing position of the sun or, in experimental conditions, another steadily moving source of photosynthetically active radiation. Often this is accompanied by a nocturnal reorientation, the movement under complete dark of the tracking organs back to an easterly orientation prior to dawn. All of these movements are distinct from circumnutation, a spiraling or elliptical movement that is observed in many plants, including sunflower. Circumnutation is driven by endogenous rhythms so that the movement occurs with an ultradian period, though parameters of the movement can also be modulated by circadian rhythms [6].

Both heliotropism and phototropism can be growth-mediated or turgor-mediated. The physiological mechanisms that govern turgor-mediated heliotropism of leaves have been intensively studied and reviewed in detail elsewhere [5]. In these plants, reversible changes in cell turgor involving specialized organs called pulvini are responsible for the heliotropic movement [5]. Pulvinus-driven movements can be exceptionally rapid. For instance, a moving experimental light source can drive *Lavatera cretica* leaves to reorient as rapidly as 40° per hour [7]. However, many heliotropic plant structures, especially the stems and peduncles subtending inflorescences and floral organs, lack pulvini. Heliotropism is mediated in these organs through localized patterns of growth by irreversible cell expansion [5,8]. The physiological mechanisms governing this form of movement have received limited study, and

whether the same processes drive growth-mediated heliotropism of shoot apices and growth-mediated phototropism of seedlings is a major open question. Here, we examine what is known and what remains to be learned with respect to growth-mediated heliotropism, specifically focusing on the dramatic heliotropic movements of sunflower heads.

In the common sunflower, *Helianthus annuus*, leaves, apical buds, and developing inflorescences are diaheliotropic, changing their position and facing normal to the sun throughout the day. This is in contrast to paraheliotropism, which results in movement to maintain a parallel orientation to incident light. At night, sunflower organs undergo movement not mediated by light, reorienting to an easterly orientation by dawn (Fig. 1). Although phototropic bending can be elicited in the hypocotyls of young sunflower seedlings [9,10], heliotropic movement of the shoot apex does not begin until later developmental stages [10,11; B. Blackman, S. Harmer, unpublished data], indicating fundamental differences exist that distinguish these two processes. Notably, and contrary to conventional wisdom, solar tracking of sunflower inflorescences slows to a halt by anthesis, and then the mature blooms maintain an easterly orientation until senescence [10,12].

Although solar tracking of sunflower apical buds and inflorescences has long been observed, it would not be an exaggeration to say that it has been the inspiration for more poetry [e.g., 13,14] than scientific publications. Investigators have largely focused on sunflower leaf heliotropism [e.g., 15,16]. Early, detailed studies of the movement of the inflorescence date back over a century [11,17], but this trait largely has not been studied in the context of major advances in our understanding of plant growth or with modern techniques. Consequently, many aspects of the physiology, development, and ecological function of solar tracking remain unexplained. Recent genetic and genomic advances [e.g., 18–20] poise sunflower to be a strong, tractable model system for revealing the basic mechanisms underlying growth-mediated heliotropism. Here, we review the state of our knowledge regarding solar tracking in sunflower with the purpose of highlighting open questions and raising hypotheses to be addressed by future efforts that take advantage of these new experimental resources.

A history of back and forth

Fascination with solar tracking dates back at least to the time of ancient Greece, and the Roman poet Ovid penned the myth of the nymph Clytie in his *Metamorphoses* [21]. After being jilted by her lover, the sun god Helios, the languishing Clytie stared at the sun from the same outcrop for nine days, after which she transformed into a rooted, heliotropic plant. Ovid could not have drawn his inspiration from sunflower because *H. annuus* and its relatives are native to North America, and he most likely had a member of the genus *Heliotropium* in mind. Many other plants have similar forms of inflorescence or floral heliotropism, including *Chrozophora tinctoria* (Euphobiaceae), *Xanthium strumarium* (Asteraceae), and diverse arctic and alpine species [5,22].

Sunflower derives its name in many languages from its reputation for solar tracking (Spanish: girasol is a compound of “to spin” and “sun”; French: tournesol is a compound of “to turn” and “sun”). Nonetheless, due to the common misconception that heliotropism continues past anthesis, the status of sunflower as a solar tracking plant has frequently been questioned. This dates back as early as European herbalists' descriptions of New World plants in the 1500s: “some have reported it to turn with the sun, the which I could never observe, although I have endeavored to find out the truth of it” [23]. In the late 1800s, several reports claimed that sunflowers did not track the sun and argued that the name was instead derived originally from the resemblance of the flower's disk and

rays to the sun [24,25]. This debate was settled by two seminal studies that, along with other evidence, provided photographs detailing the daily east to west movements of the developing heads of domesticated sunflower, wild *H. annuus*, and additional wild relatives [11,17].

Solar tracking is not solely driven by the movement of the sun

The majority of studies focusing on solar tracking by sunflower inflorescences have been at the organismal level, focusing on the environmental signals that drive the behavior, the tissues that interpret those cues, and how asymmetric growth alters stem curvature over the course of diurnal cycles and across developmental stages. One major cue is obvious: solar tracking requires a moving light source. Plants grown in greenhouses or growth chambers with consistent overhead lighting do not display heliotropic movement, indicating that the behavior is dependent on a dynamic, directional light source [12].

The sun is below the horizon at night, however, suggesting that other signals are responsible for the nocturnal reorientation of the shoot apex from west to east. This nighttime movement is not completely synchronized with the progress of west-to-east reorientation by leaves, and it is much more rapid than the daytime tracking, with angular velocities twice as high the rate of daytime head movement (Fig. 1) [11,26]. Furthermore, the full heliotropic cycle continues, though sometimes with diminished amplitude, through cloudy days, suggesting that an entrained, endogenous rhythm maintains the movement in the field in the absence a strong directional light cue [10,11]. Experimental evidence also supports the existence of regulation by endogenous signals. Sunflower plants rotated 180° in the field during the night maintain the original trajectory of their oscillation and only reverse their movement, re-coordinating rhythmic bending of the stem with the direction of sunrise and sunset, after several days in the new orientation [10]. Reorientation experiments have yielded analogous results for leaf heliotropism in *Malva neglecta* [27].

An optimal level of water availability is also necessary for sunflower to move robustly. Wilting in drought-stressed plants arrests solar tracking. Less obviously, rainy weather that saturates the ground prevents solar tracking, and this inhibitory effect is maintained under clear skies until the soil dries to permissive moisture levels [11].

The leaves, rather than the heads or stem, may be the organs that receive the stimulus that results in solar tracking of sunflower stems. While decapitation or lateral wounding of the stem along the curving area does not stop the diurnal movement, delamination does [10,11]. A developmental component to the involvement of leaves as the source of the behavioral stimulus has been described [11]. Removal of portion of the shoot with young leaves (<4 cm in length) prevented tracking only after the passage of several days. Removal of mature leaves (>4 cm) halted tracking, though tracking resumed as young leaves reached maturity [11]. Although these observations suggest that mature leaves are critical for the induction and maintenance of the rhythmic stem movement, these results do not distinguish whether the mature leaves function as the location of light reception, the source of a diffusible signal, and/or the source of energy to support the movement. Disentangling these possibilities will require further experimental studies that manipulate light interception physically or genetically in an organ-specific manner. A role for non-foliar structures in phototropism or heliotropism is not unprecedented. Reception for the light stimulus driving floral heliotropism in snow buttercups (*Ranunculus adoneus*) occurs in the peduncles subtending moving flowers [8], and phototropic movements by de-etiolated sunflower

seedling hypocotyls occur even when the shoot tip and cotyledons are covered with foil or removed [9].

If the mature leaves do perceive the arc of the sun's movement throughout the day, how they do so is unknown. The mechanism may be similar to that governing the phototropic curvature of young seedlings, where differential interception of irradiance by illuminated and shaded organs on opposite sides of a plant sets up a gradient that when translated at the molecular level drives differential growth [10]. However, a model of light interception parameterized with positional information taken on growing sunflowers found no difference in the irradiance upon leaves growing on the eastern and western sides of plants [12]. Alternatively, changes in orientation could result when incident light is oblique to the leaf surface but not when light is normal to it, a mechanism known as vectorial excitation that is well described for leaf heliotropism in *L. cretica* [5].

There has been no detailed examination of the developmental or cellular basis for differential lateral stem growth. Still, a few reports partially address these questions. As mentioned above, no pulvini specialized to generate turgor-mediated movements have been described in the sunflower stem. Moreover, the rhythmic movement of heads ceases at anthesis when leaf cell expansion is also complete, and this coincident timing has led several authors to conclude that the movement is growth-mediated [5,12]. However, direct observations of localized growth rates and cellular dynamics [e.g. as performed in 8] on both sides of the curving stem throughout a diurnal cycle remain necessary to confirm this inference.

Candidate molecular mechanisms

Even considering this modest set of insights from previous work, it is clear that heliotropic movement by the developing sunflower inflorescence is a complex, cyclical process that is likely orchestrated through the action of multiple intrinsic and extrinsic signaling pathways. Given the features discussed above, one can posit that some or all of the following mechanisms may be involved: (1) from dawn to dusk, perception of a directional light source; (2) initiation of differential growth of lateral stem segments, paced to the east-to-west movement of the light source throughout the day; (3) a light-independent and likely entrained driver involved in the reversed differential lateral stem growth during the night that reorients the shoot apex from facing west to facing east before sunrise; and (4) a molecular signal or structural change that slows and stops the movements at anthesis. None of these putative mechanisms have been determined. However, a consideration of other growth responses in sunflower or heliotropic movements in other taxa suggests several candidate mechanisms, which we discuss in turn below.

Directional light perception

The steady change of stem curvature throughout the day that characterizes solar tracking may be driven by the ongoing stimulation of the mechanisms that generate permanent curvature of young sunflower hypocotyls as a phototropic response to persistent unilateral light [28]. These mechanisms have received a significant amount of study in sunflower, and considering their details is instructive [29–32]. For instance, when one cotyledon is shaded, directional growth occurs toward the illuminated cotyledon [10,29]. Notably, hypocotyls of de-etiolated seedlings bend toward direct illumination by blue light, but the same phototropic response is not observed with red light [33]. Bending of etiolated seedling hypocotyls is similarly dependent on light quality [9]. Notably, the precision of heliotropic leaf and floral movements is maintained with fidelity under blue light illumination but not

under red light illumination in many species [e.g., 22,27,34], and exposure of one mature leaf to weak blue light results in the bending of the stem in juvenile sunflower plants [35].

The hue-specificity in sunflower seedling phototropism implicates blue light photoreceptors, possibly cryptochromes or members of the *ZEITLUPE* gene family but most likely proteins homologous to the phototropins commonly involved in similar responses in higher plants [reviewed in 36]. For instance, the leaves, petioles, and inflorescences of *phototropin 1* and *phototropin 2* double mutant *Arabidopsis thaliana* plants fail to reorient when a unilateral blue light source is moved to a new fixed position [37,38]. Notably, in wild-type *Arabidopsis* plants, these movements are reversible, and a subset of these movements occur with angular velocities comparable to those seen for leaf heliotropism in other plant species in field environments [5]. However, whether phototropins function directly as “heliotropins” that provide a capacity to follow the transit of a continuously moving light source has not been confirmed in any system and is a clear direction for further investigation.

Although bending does not occur in response to red light alone in many systems, red light may still play a secondary role in light-driven movements [5,36]. For example, the effect of a unilateral blue light source is accentuated under ambient red light, leading to significantly more rapid morphological and electrophysiological responses by young sunflower stems [35]. How red-light sensing phytochromes interact with the blue-light receptors to facilitate these movements is another key area for future research.

Differential stem growth

Though the signals regulating differential stem growth during heliotropism have not been described, the molecular signals that regulate phototropic bending of the sunflower hypocotyl in response to unilateral illumination have been subject to substantial investigation and may provide some insight. Auxin-mediated processes have received the most attention. For instance, initial work in other systems, most notably the oat coleoptile, led to the formulation of the Cholodny–Went hypothesis, which proposes that the bending of growing plants toward a light source is caused by differential transport of auxin from illuminated areas into shaded areas of plants [39]. Consistent with this hypothesis, an early study reported an asymmetrical release of auxin in exudates obtained from the illuminated and shaded sides of sunflower seedlings split into longitudinal halves, as determined by an oat coleoptile curvature bioassay [29]. Contrary to the Cholodny–Went hypothesis though, this difference was shown to result from increased production of auxin by shaded cotyledons rather than differential lateral auxin transport.

Subsequent work has disputed the importance of a lateral auxin gradient in sunflower phototropism. The difference in auxin content between illuminated and shaded sides of sunflower seedlings has not been replicated despite repeated efforts and use of direct measures of auxin molecule content [9,30,31]. More recent evidence from sunflower and several other species supports an alternative model in which phototropic stem curvature is caused by the generation of auxin inhibitors in illuminated tissue [40], and a series of elegant studies has specifically implicated the auxin inhibitor 8-epixanthatin in sunflower. This compound occurs in higher concentrations in the illuminated side of sunflower seedlings, and these levels are significantly correlated with differences in growth rates and the amount of stem bending toward a unilateral light source [32,41].

Electrophysiological signaling may act as part of or in parallel to auxin signaling. In young sunflower plants, targeted blue light illumination of one leaf in a pair under ambient red light causes the epidermal pH of adjacent stem tissue to decrease within minutes,

coincident with stem bending [35]. These more acidic conditions may promote the activity of proteins called expansins that increase the plastic extensibility of cell walls. Because illumination also causes hyperpolarization of leaf cell plasma membranes [35], protons extruded from mesophyll cells and transported to the stem may be the direct cause of the stem acidification. However, further experimental manipulations are required to demonstrate that these two phenomena are causally related and not driven by different processes stimulated by the same combination of blue and red light conditions.

Gibberellins and hydraulic signaling have also been implicated in phototropism in sunflower. Unilateral light induces release of $\sim 8\times$ greater quantities of diffusible gibberellin from the shaded side than from the illuminated side of a sunflower shoot tip bisected with a glass barrier [42]. A water potential difference is also transmitted from illuminated and shaded cotyledons to the peripheral hypocotyl tissues below them [43], but the mechanistic significance of these phenomena to the bending of the stem is an open question in need of further exploration by experimental manipulation. Nonetheless, auxins, gibberellins, and their inhibitors remain prime candidates for mediating the differential lateral stem growth that characterizes heliotropic movement of the sunflower inflorescence. Characterizing and genetically or biochemically manipulating the daily dynamics of their synthesis and transport is likely to be a promising avenue for further understanding the regulation of this spatially and temporally complex growth-mediated movement.

Nocturnal reorientation

The mechanisms underlying nighttime movements of heliotropic organs are less well studied and less conserved in other species, leaving the signals responsible for the nocturnal reorientation of sunflower heads back from west-facing to fully erect to east-facing as a source of great speculation. The more rapid speed of the nighttime movement has led some to hypothesize the involvement of mechanical signals that manifest themselves as the release of an endogenous ‘spring’ [26]. The energy invested by actively winding the spring during the day is proposed to translate to an unhindered release during the night.

A more concretely rooted hypothesis asserts a major role for the circadian clock. The circadian clock influences most aspects of plant physiology, gating the timing of many daily growth and metabolic functions so that they occur in rhythmic anticipation of the optimal activity period during a diurnal cycle [1]. The nighttime movement that positions the shoot apex to face east at dawn (Fig. 1) and the delayed reset to solar tracking following an 180° rotation are both hallmarks consistent with an entrained circadian rhythm [10]. Evidence for ‘memory’ of previous movements or positions in other solar tracking species is variable however [e.g., 27,44]. For instance, snow buttercups (*R. adoneus*) fail to achieve a morning eastward orientation in the absence of directional blue light at sunrise [22]. Consequently, more thorough experimental manipulations (e.g., extension or reduction of diurnal cycle length) or genetic studies (e.g., generation of sunflower clock mutants) remain necessary to confirm a role of the circadian clock in this aspect of solar tracking behavior. In addition, studies are sorely needed to determine whether the endogenous rhythms driving nocturnal reorientation act through the same or unique hormonal and electrophysiological means as those that are used for daytime tracking in response to directional light cues.

The circadian clock has been implicated in other forms of periodic growth mediated by rhythmic cell expansion [45,46], and as noted above, the differential regulation of lateral cell expansion at different times of day is a plausible mechanism for the generation of stem curvature and directional growth. This could be due either to oppositely-phased coupling between central clock and growth

pathways, or oppositely-phased entrainment of the central clock on the east and west sides of a stem. Either finding would be a paradigm-shifting result, since differential circadian phase regulation within a single organ has been reported in the mammalian brain [47] but no similar finding has been reported in plants or other non-neural tissues.

Cessation of solar tracking

It is currently unknown what mechanistic changes result in the reduction in apical heliotropic movement with age as sunflowers approach anthesis, and unlike the other aspects of solar tracking, few inferences based on analogous movements within sunflower or other species suggest themselves. For instance, foliar heliotropism in sunflower continues past anthesis, albeit at a dampened amplitude, after apical heliotropism stops [10,12,16]. Several possible, non-mutually exclusive developmental mechanisms may contribute to the cessation of solar tracking. First, the signals promoting general vegetative growth may cease. As noted above, aerial leaf expansion also trails off at anthesis, the developmental stage at which the plant begins investing its resources in seed production. Second, new and unknown mobile signals, possibly produced by the mature head, may actively repress lateral stem growth in the afternoon and evening. Finally, mechanical stress from the increasingly weighty head could elicit changes to the composition of cell walls in the subtending stem such that these cells provide better support but are less easily and flexibly expanded.

Ecological function(s) of solar tracking and mature head orientation

Although the ecological function of solar tracking is well-studied for sunflower leaves [15,16] and the flowers of some species [48,49], it has not been examined for developing sunflower inflorescences. This gap is surprising given that abundant hypotheses have been advanced proposing that solar tracking has adaptive effects through (i) increased light reception and/or (ii) altered head temperature. The former possibility has been addressed in the context of leaf heliotropism. Photosynthesis in plants with solar-tracking leaves has been estimated to be 9.5% greater than photosynthesis with an optimum arrangement of fixed leaves due to increased light interception [15]. Solar tracking by the inflorescence may similarly allow for more efficient capture of incident light and, consequently, production of photosynthate by the young leaves that subtend the shoot apex. These leaves may be constrained from independent heliotropic movement by their short petioles and tight clustering prior to internode elongation. Likewise, heliotropism may also increase light capture by the green involucre bracts that envelop developing sunflower heads during the period between budding and anthesis. The photosynthetic contribution of bracts is an order of magnitude smaller compared to the contribution of leaves [50]. Nonetheless, this may be biologically significant for supporting the growth of energetically costly reproductive structures in stressful and changing environments. Indeed, subtending foliar structures make important contributions to grain filling and harvest yield in other species [51]. Estimates of light interception at the crop canopy level obtained through 3-D simulation modeling with or without leaf and stem heliotropism are only marginally different, however [52].

Shoot apical heliotropism may generally serve an ecological function in maintaining higher and more constant heat loads throughout diurnal cycles. Potential advantages of higher temperatures may include greater pollinator recruitment to open flowers, the hastening of seed development, or improved seed set. Some evidence in support of these hypotheses has been amassed. For

instance, exposure of plants to temperatures below 20 °C during the period of floret differentiation decreases the number of flowers per disk that develop pericarps and dehiscent floral organs at maturity [53].

More targeted physiological characterization and experimental manipulations are needed to fully test these proposed ecological functions, particularly involving wild sunflower. An important and common oversight in these adaptive stories is that they have been predominantly advanced and evaluated from the perspective of the cultivated plant even though solar tracking evolved in wild progenitors that possess extremely different branching architectures. Unlike the unbranched cultivated oilseed or confectionary forms that yield a single large or exceptionally large head with large seeds, wild *H. annuus* are highly branched plants with many small heads that produce many, though often fewer, small seeds. As a consequence, minor advantages in light interception that result from leaf and stem heliotropism in cultivated sunflower [15] may have much stronger physiological impacts in highly branched, small headed wild species with greater opportunity for self-shading. Likewise, a more convincing case for the role of heliotropism in pollinator recruitment can be made in the context of wild plants: the proposed higher heat load of developing buds may provide pollinator warming stations proximate to stationary, open disks that have matured past anthesis. Because branching architecture and head number vary among species [54], a wider taxonomic survey for solar tracking may identify phylogenetic patterns that yield further insight into the ecological function of this trait.

Many adaptive hypotheses have been ventured to explain the ecological function of the final eastward orientation of blooming sunflower disks as well. It is clear that facing one of the cardinal directions rather than skyward is adaptive, as the narrower perch reduces seed depredation by birds [55]. However, the question of “Why east?” has been the target of much unresolved speculation.

Most hypotheses consider the influence of orientation on diurnal cycles in head temperature. For instance, it has been proposed that the eastward orientation permits greater reception of radiation in the morning, thus allowing the more rapid drying of morning dew and reducing the opportunity for fungal establishment [12]. Warmer morning temperatures may facilitate pollinator recruitment during the period of initial anther emergence and pollen presentation [56]. Alternatively, some have suggested eastward orientation reduces heat load especially during afternoon periods of high irradiance [55]. Maintaining cooler floret temperatures may boost yield or fitness by preventing reductions in pollen viability and fertilization (pollen sterility increases at temperatures >30 °C) or improving grain filling during seed development [55,57]. None of these advantages are mutually exclusive, but some of these functions may be an incidental byproduct rather than the original adaptive function. It is also possible that eastward head orientation is not an adaptation at all but instead a pleiotropic consequence of the interaction of endogenous and external signals during developmental cessation of heliotropic movement.

Limited evidence bearing upon these hypotheses has been collected. Head temperatures are always elevated relative to ambient daytime temperature. More critically, the heat load of the faces of eastward oriented sunflowers has been shown to be 3–8 °C lower than the faces of heads constrained to face skyward at midday [12,56]. Manipulations of head reflectance and vertical vs. horizontal orientation have also suggested that higher temperatures are associated with more rapid seed maturation and reduced grain filling [57]. Although these findings are suggestive, teasing apart the various hypotheses advanced regarding the ecological function of the specifically eastward head orientation will require temperature monitoring over complete diurnal cycles along with a joint assessment of impacts on the performance of wild and cultivated plants manipulated to face various orientations.

Conclusions

Solar tracking by sunflower stems is a fascinating, developmentally and environmentally dynamic trait about which much is left to discover. Many open questions remain about its phenomenology, underlying mechanisms, and environmental significance, and we have endeavored here to specifically highlight key avenues for future research in each of these areas. The complex regulation of the movement over both daily and ontogenetic time scales by putative endogenous cues as well as light and perhaps other environmental signals suggests that understanding their respective roles will yield novel insights into how plant growth is continuously and adaptively tuned to changing environments. In addition, understanding the mechanisms that regulate shoot apical heliotropism and the ecological advantages provided by the behavior may help identify new pathways or genetic variants that can be utilized for improvement of sunflower and other crop plants.

One central question that particularly needs to be addressed in the future is whether or not the mechanisms governing phototropism in sunflower seedlings and heliotropism by inflorescences are fundamentally different. Detailed characterization of the anatomical, ionic, and hormonal changes associated with stem bending under a series of light conditions (fixed vs. moving, blue vs. red, varied diurnal cycle lengths, etc.) and at multiple developmental stages will be necessary to address this problem. If the dichotomy is trivial, then a number of candidate pathways suggest themselves, and the phenomenon may be more tractably studied under controlled conditions. To the extent that the processes differ, either in the daytime interpretation of directional light cues or in the nighttime incorporation of endogenous rhythms, mechanistic insight into sunflower heliotropism may shed new and unique insights into the ways that intrinsic and extrinsic signals are integrated to regulate plant growth.

The new genetic and genomic resources being developed for sunflower promise to greatly accelerate such work. A draft genome has recently become available (www.sunflowergenome.org), and the assembly is currently being anchored to dense genetic and physical maps and annotated with extensive transcriptome sequencing datasets [18]. These resources will foster candidate gene identification through transcriptomic comparisons of lateral stem sections in tracking and top lit non-tracking plants. Recent advances facilitating reverse genetics through targeted induced lesions and germline transformation will allow targeted alteration of candidate genes [19]. In addition, recently generated germplasm resources – including advanced generation recombinant inbred lines and association mapping panels [18,20] – will provide powerful tools for connecting natural allelic variation to phenotypic variation in solar tracking.

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