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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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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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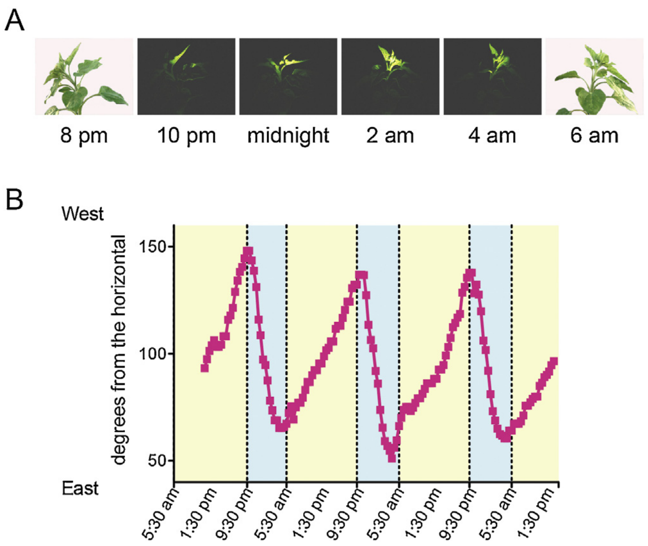

Fig. 1. The sunflower shoot apex tracks the sun during the day and reorients at night, facing east well before sunrise. (A) Stills from a time-lapse photography series taken every 30 minutes using a consumer camera and a dim-solar powered light to enable photography (West = left). Plants were grown in 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 ultraradian 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