

VIEWPOINT

Phototropic solar tracking in sunflower plants: an integrative perspective

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Received: 11 June 2015 Returned for revision: 21 July 2015 Accepted: 30 July 2015 Published electronically: 29 September 2015

- **Background** One of the best-known plant movements, phototropic solar tracking in sunflower (*Helianthus annuus*), has not yet been fully characterized. Two questions are still a matter of debate. (1) Is the adaptive significance solely an optimization of photosynthesis via the exposure of the leaves to the sun? (2) Is shade avoidance involved in this process? In this study, these concepts are discussed from a historical perspective and novel insights are provided.
- **Scope and Methods** Results from the primary literature on heliotropic growth movements led to the conclusion that these responses cease before anthesis, so that the flowering heads point to the East. Based on observations on 10-week-old plants, the diurnal East–West oscillations of the upper fifth of the growing stem and leaves in relation to the position of the sun (inclusive of nocturnal re-orientation) were documented, and photon fluence rates on the leaf surfaces on clear, cloudy and rainy days were determined. In addition, the light–response curve of net CO₂ assimilation was determined on the upper leaves of the same batch of plants, and evidence for the occurrence of shade-avoidance responses in growing sunflower plants is summarized.
- **Conclusions.** Only elongating, vegetative sunflower shoots and the upper leaves perform phototropic solar tracking. Photon fluence response and CO₂ assimilation measurements cast doubt on the ‘photosynthesis-optimization hypothesis’ as the sole explanation for the evolution of these plant movements. We suggest that the shade-avoidance response, which maximizes light-driven CO₂ assimilation, plays a major role in solar tracking populations of competing sunflower plants, and an integrative scheme of these growth movements is provided.

Key words: Phototropic solar tracking, photosynthesis, phototropism, plant movement, shade avoidance, solar tracking, sunflower, *Helianthus annuus*.

INTRODUCTION

In the USA and European countries, the common sunflower (*Helianthus annuus*) is not only a popular garden plant, but also a field crop of considerable economic importance. As the species name indicates, it is an annual herb, characterized by coarsely hairy stems and leaves, as well as large, terminal circular heads composed of numerous, small yellow flowers. In the centre, these flowers can develop into seeds (disc florets), whereas the outer, petal-bearing and non-seed-producing florets (ray flowers) form a yellow wreath that attracts potential pollinators, such as bees and butterflies (Fig. 1) (Heiser, 1976).

Sunflower seeds are a major source of vegetable oil worldwide, and commercially available varieties of the species *H. annuus* (Asteraceae) contain up to 50 % oil in their seeds. Accordingly, the growth of large populations of sunflower plants as an oilseed crop, which began in Russia in around 1860, has developed into an international agricultural business. Currently, the extracted oil accounts for approximately four-fifths of the value of these crop plants (Heiser, 1976; Schneiter, 1997).

In addition to gardeners and agriculturists, botanists have long been interested in the anatomy and physiology of these large, rapidly growing dicotyledonous angiosperms. The founding father of experimental plant physiology, Julius Sachs (1832–1897), used *H. annuus* individuals to analyse root exudation and sunlight-dependent dry matter accumulation within the

leaves (Sachs, 1882, 1884) and, during the 1930s, sunflower seedlings served as important model organisms for the study of blue-light-dependent organ development (see Briggs, 1963; Briggs and Baskin, 1988). More recently, *H. annuus* has been used to study root development (Josten and Kutschera, 1999), cell wall architecture (Kutschera, 2008), C₃ photosynthesis (Kutschera *et al.*, 2010), the biophysical basis of stem elongation (Kutschera and Niklas, 2013), the adaptive significance of the timing of seedling emergence (Mercer *et al.*, 2011), speciation (Levin, 2013) and as a representative genome of the family Asteraceae (Gill *et al.*, 2014).

However, one aspect of growing sunflower plants, the heliotropic movements of the stem and leaves, has sometimes been ignored or misrepresented in the recent literature. For instance, Whippo and Hangarter (2006), Holland *et al.* (2009), Christie and Murphy (2013), Hohm *et al.* (2013) and Liscum *et al.* (2014) reviewed the literature on shoot phototropism in seed plants, but none of these authors mentioned sunflower. Vandenbrink *et al.* (2014) reviewed some aspects of solar tracking in sunflower plants, but they did not address a number of issues, such as the relative photosynthetic activity of the upper leaves, or consider any possible role for a shade-avoidance response.

In this article, we first provide some basic definitions. Then, we summarize the pertinent literature on solar tracking, discuss misconceptions on the behaviour of *H. annuus* shoots, and present an integrative hypothesis on the possible adaptive

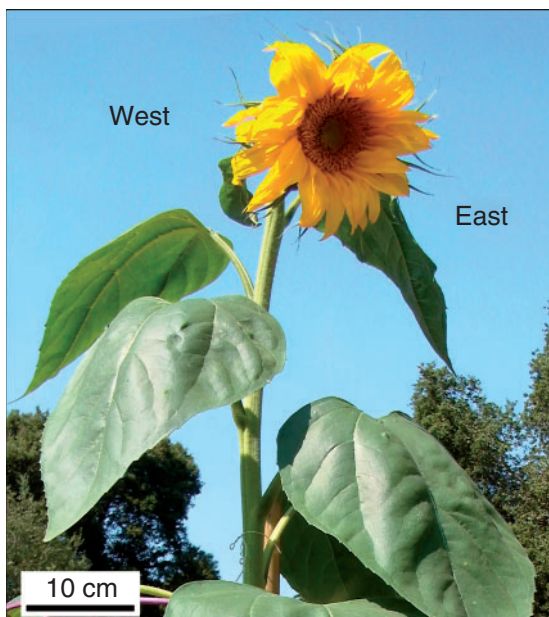


FIG. 1. Upper part of a mature sunflower plant (*Helianthus annuus* L., 'Sunspot'), height approx. 2.2 m, with the flowering head facing East (original photograph, Stanford, CA, USA; September 2013).

significance of this striking physiological process based on our own unpublished results.

TERMINOLOGY: CIRCUMNUTATION VS. SOLAR TRACKING

The early literature on solar tracking (heliotropism) in land plants (embryophytes) often uses the terms 'circumnutation', 'nutate' and 'nutating' when referring to the physiological phenomena under investigation (see, for instance, Schaffner, 1898, 1900). However, nutation occurs without any change in the direction of the light source and is driven by an internal signal (see the recent review by Vandenbrink *et al.*, 2014). Circumnutation, a term coined by Darwin (1881) in his book *The power of movement in plants*, also functions strongly in a microgravity environment in the absence of a moving light source (Brown *et al.*, 1990). Solar tracking, on the other hand, is driven by an external signal (changing light direction), although an internal process prompts nocturnal re-positioning (Vandenbrink *et al.*, 2014).

Some years ago, Galston (1979) reported that unilateral blue light did not alter the circumnutation of etiolated seedlings of garden pea (*Pisum sativum*), although it modified the growth rates of proximal and distal sides of the stem to develop curvature. He also reported that dim red light induces an increase in circumnutation some hours later, while bright white light completely damped circumnutation for several hours, followed by enhancement over dark-control seedlings. These experiments demonstrated that, although light signals could clearly alter circumnutation, the response was not directional. Here we use the terminology 'solar tracking' as distinct from circumnutation *sensu* Darwin (1881). However, as we have retained the



FIG. 2. Two versions of Athanasius Kircher's 'sunflower clock'. The famous drawing of 1643 shows a sunflower plant with the stem fixed to a floating disc (ACB), which is growing on water (A). The inset shows a second 'ABC version' of the same alleged phenomenon, with a plant growing in soil, published in 1667 (B) (adapted from Athanasius Kircher at Stanford www.stanford.edu/group/kircher/cgi-bin/site/, accessed 24 February 2014).

nutation terms in quotations and titles of articles, we want to alert the reader to this source of possible confusion.

SOLAR TRACKING: FROM KIRCHER 1643 TO KOLLER 2011

The most popular misconception is that flowering *H. annuus* heads (Fig. 1) track the moving sun across the sky. This belief can be traced back to the writings of the German Jesuit polymath Athanasius Kircher (1602–1680), who has been described as 'the last man who knew everything' (Breidbach and Ghiselin, 2006). In a monograph published in 1643, Kircher depicted a 'sunflower clock', which purported to inform humans about the time of day via continuous movements of the mature, flowering head, driven by a mysterious cosmic magnetic force (Fig. 2A). Today, we no longer take this example of early 17th century natural magic seriously, but in Kircher's time the standards were different. In a subsequent book of 1667 entitled *Regnum Naturae Magneticum*, Kircher depicted a more realistic version of his 'sunflower clock', which is reproduced here (Fig. 2B). This drawing shows a mature sunflower plant the

head of which tracks the sun during the day, from 0600 h (6 am), through 1200 h (noon), to 1800 h (6 pm).

In a classic monograph on Asteraceae of the genus *Helianthus*, Heiser (1976) summarized quotations from poets in which Kircher's 'sunflower dogma' had been praised. He referred to the English botanist John Gerard (1545–1611), who was the first to dispute the old misconception of the 'moving sunflower heads' (Gerard, 1597), as depicted by Kircher in 1667 (Fig. 2B). Heiser argued that 'green plants are phototropic and respond by growing toward the source of light. Thus many plants, particularly at early stages, bend toward the east in the morning and toward the west in the evening. The common sunflower shows this tendency more strikingly than most plants, but, once the flower head opens, it no longer bends toward the source of light. Interestingly enough, in my gardens the heads of the giant sunflowers always end up facing the east' (Heiser, 1976, p. 28).

Despite this and other more recent clarifications (see, for instance, Iino, 1990, 2001; Vandenbrink *et al.*, 2014), Kircher's alleged 'sunflower head-movements' persist in the popular literature. A recent book by Koller (2011) describes the most important plant movements and their biophysical bases (reviewed by Kutschera, 2011). Specifically, Koller (2011) summarizes growth-mediated solar tracking (heliotropism) in angiosperms, a topic on which he had published extensively (e.g. Koller, 1986, 1990; Koller *et al.*, 1985). The author acknowledges that 'the domestic sunflower . . . is the most familiar and conspicuous manifestation of . . . growth-mediated solar tracking'. With reference to a schematic drawing, he described the old 'sunflower clock-dogma' (Fig. 2B) in the following words: 'The apical bud and its cluster of young leaves, and eventually its disc-shaped developing inflorescence, keep moving to remain facing the sun with high fidelity during the course of each day. They do so by growth-mediated positive phototropic curvature of the young, growing part of the subtending stem. Solar tracking is kept up as long as the stem grows, throughout reproductive development, until fruit set' (Koller, 2011, p. 136).

Koller's description is not entirely correct. As mentioned by Heiser (1976), the growing vegetative shoot is the solar tracking organ, and tracking ceases at some early time during flower development (Vandenbrink *et al.*, 2014). Mature *H. annuus* heads are themselves not solar trackers, nor are the flowers of at least one other sunflower relative, *Rudbeckia laciniata* (W. R. Briggs, pers. obs.). In both cases, tracking ceases as the flowers mature and open, and the mature heads cease tracking the sun and face doggedly east. However, the mature flowers of many species do indeed follow the sun (e.g. *Ranunculus adoneus* and other alpine flowers, see Sherry and Galen, 1998; *Viola pedunculata*, W. Briggs, pers. obs.). In the case of the alpine *R. adoneus*, the interior of the flowers reached temperatures several degrees Celsius above the ambient air temperatures. When flowers were prevented from tracking, their internal temperatures were several degrees lower than their tracking counterparts, and both insect visitation and seed set were significantly reduced (Sherry and Galen 1998).

Koller (2011) summarizes that 'The developing leaves (of *Helianthus annuus*) play a role in the diheliotropic response of the stem, as their excision results in partial loss of the response. However, the site of perception of the solar signal remains unknown' (Koller, 2011, p. 136). In another chapter of his book,

he writes 'Throughout the day, . . . (the vegetative shoots) track the sun with high fidelity. At the end of the day, they are oriented toward the direction of sunset. Sometime after sunset, they start reorienting in the opposite direction and end (well before daybreak) by facing in the anticipated direction of sunrise . . . Nocturnal reorientation is more rapid (ca. $26\text{ }^{\circ}\text{C h}^{-1}$) than tracking the sun (ca. $15\text{ }^{\circ}\text{C h}^{-1}$)' (Koller, 2011, p. 143). In the next section, we describe this process in more detail, with reference to the history of sunflower research.

THE MOVEMENTS OF SUNFLOWERS: FROM KELLERMANN 1890 TO GROWTH-MEDIATED SOLAR TRACKING 2014

Prior to Kellerman (1890), there was little literature on heliotropism, a term that was coined by the French botanist Augustin Pyramus de Candolle (1832). Although Sachs (1882) referred to 'heliotropism' on several pages of his classic monograph, and depicted a sunflower plant in the context of root exudation, he only briefly mentioned solar tracking in *Helianthus*. The reasons for this are unknown. There is evidence to suggest that *H. annuus* seeds were not readily available in Germany during the 19th century (Heiser, 1976). Hence, the founding father of experimental botany may not have planted sunflowers in his botanical garden where he made so many key discoveries on the growth and behaviour of seed plants (Morton, 1981; Kutschera and Briggs, 2009, 2012). One year before Sachs's death, Rothert (1896) published a comprehensive review on heliotropism in seed plants (in German). However, the author mentioned the species *H. annuus* only with reference to hypocotyl development.

Sunflower is a crop species that originated in the Americas, where seeds were available during the 19th century (Blackman *et al.*, 2011). This may be one reason why the scientific study of the 'solar tracking of *Helianthus*' commenced in the USA. To the best of our knowledge, it was Kellerman (1890) who gave the first account of heliotropism in sunflower plants that were cultivated in Kansas (USA), which, incidentally, uses this plant species as its state flower. Kellerman's account is not very revealing. Despite some valuable observations, the author concluded that 'It is likely that nutation is more marked in the head previous to anthesis, but this question was not regarded' (Kellermann, 1890, p. 141). Based on observations on wild/cultivated sunflower plants grown in Clay county (KS) and Columbus (OH), Schaffner (1898, 1900) summarized heliotropism in this angiosperm. According to Schaffner (1900), growing sunflower (cultivated variety) 'nutate from 60° to 90° west in the evening and from 50° to 70° or more, east in the morning'. At night, the leaves droop and the tips point downward. When anthesis begins nutation ceases and the heads are tilted toward the east or northeast' (Schaffner, 1900, p. 197). In addition, the author pointed out that only growing shoots display heliotropism, which ceases when the adult plant reaches anthesis. According to Schaffner (1900), the flowering heads generally are oriented toward the east.

Six decades later, the Japanese botanists Shibaoka and Yamaki (1959) documented essentially the same mode of heliotropism in 9-week-old (growing) cultivated sunflower plants (although they failed to cite Schaffner, 1898, 1900). In addition,

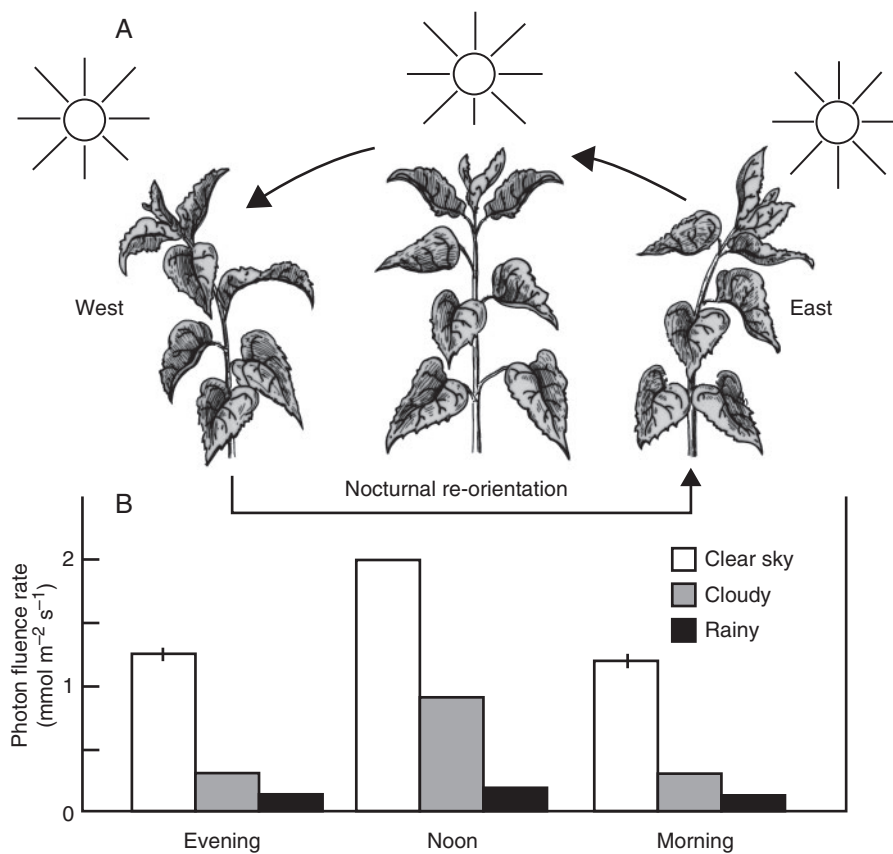


FIG. 3. Growth-mediated solar tracking of the stem and upper leaves in a sunflower plant (*Helianthus annuus* L., 'Sunspot'). The drawings were plotted from observations on a 10-week-old plant (A). Photon fluence densities of sunlight on the surface of the upper leaves were measured as described by Pieruschka *et al.* (2011) in the morning (0700 h), at noon, and in the evening (1900 h) under three different weather conditions (7–25 September 2013; means \pm s.e.m. of nine measurements each) (B).

their description includes the nocturnal re-orientation response. Vandenbrink *et al.* (2014) published data on the daily cycle of the stem angle, measured at the first node below the apex of 8-week-old sunflower plants. These results are consistent with earlier observations (Schaffner, 1898, 1900; Shibaoka and Yamaki, 1959).

A general scheme of growth-mediated heliotropism in developing *Helianthus* plants, based on our observations on 10-week-old *H. annuus* individuals that were raised in an open field in Stanford, CA, is shown in Fig. 3A. The characteristic movements, i.e. diurnal East–West oscillations of the heads (before anthesis) and the upper leaves, are depicted in relation to the position of the sun. It is apparent that the phototropic bending both of the upper part of the stem and of the petiole/midrib of the 3–4 youngest leaves contributes to the movements of the sunflower plant. The East–West oscillations of the upper fifth of the stem, and the nocturnal re-orientations, ceased as the flower head opened and anthesis commenced, so that the heads finally faced to the east, exactly as reported by Schaffner (1898, 1900) over a century earlier. This observation was confirmed by Shibaoka and Yamaki (1959), Heiser (1976) and, more recently, by Vandenbrink *et al.* (2014) and Harmer *et al.* (2015).

In a series of investigations carried out during the 1970s, it was shown that (a) the heads and leaves reach their original

position at night, well before sunrise (between 0300 and 0600 h) (Shell *et al.*, 1974; Shell and Lang, 1975); (b) leaf movements lag behind the azimuthal movement of the sun by 12°, corresponding to approx. 48 min (Shell and Lang, 1976); and (c) the easterly direction of the flowering heads has the advantages of reducing the heat load at noon, and provides a larger irradiation during early morning. This may speed up drying of the developing seeds and may decrease the likelihood of fungal attack (Leshem, 1977; Lang and Begg, 1979). These investigators also noted that the East–West oscillations of young plants (Fig. 3A) do not occur on cloudy or rainy days, when the heads remain in an upright position, although they do occur in older plants as long as stem growth persists (Shibaoka and Yamaki, 1959). Moreover, in a growth chamber, under a 16 h daytime overhead illumination (approximately one-third full sunlight), no heliotropism occurs in populations of growing sunflower plants (Shell and Lang, 1976). These facts, consistent with our own observations, suggest that an endogenous rhythm may not be the primary driver of daytime solar tracking in sunflower plants. However, more recent studies indicate that the daytime heliotropic response in sunflower is, at least in part, regulated by the circadian clock (Atamian, 2014; Harmer *et al.*, 2015; S. L. Harmer, pers. com.), as originally suggested by Shibaoka and Yamaki (1959).

Schaffner (1900) proposed that heliotropism in *Helianthus* is an adaptation for the optimization of leaf photosynthesis. This hypothesis is discussed in the next section.

PHOTON FLUENCE AND LEAF PHOTOSYNTHESIS

It was proposed long ago that the East–West oscillations in sunflower plants (Fig. 3A) result in an improvement of photosynthetic activity of the upper leaves (Schaffner, 1900). Shell and Lang (1976) provided more recent evidence. From field measurements of leaf position, they calculated that, at clear skies, ‘heliotropism of the sunflower head leaves throughout the day could result in an average increase of 9.5 % in photosynthesis compared to the optimum arrangement of fixed leaves, and 23 % increase relative to a (hemi-) spherical distribution. Average daily photosynthesis would be only 14 % less than for leaves which were always aligned perpendicular to the sun’s beam. Therefore, heliotropism could cause an important increase in photosynthesis, particularly in the early morning and late afternoon’ (Shell and Lang, 1976, p. 169). These values were inferred from their calculations, but they are not accompanied by actual measurements of photosynthesis *per se*.

In a more recent study, heliotropic sunflower plants were compared, under open sky conditions, with modelled ‘non-moving (static)’ controls with respect to light interception throughout the day. The calculations for the amount of photosynthetically active radiation absorbed by the leaves indicated that this parameter was largely identical in both groups of plants. Thus, heliotropic movements apparently had no significant positive effect on light capture (Rey *et al.*, 2008).

In these studies, no direct photosynthetic photon flux density measurements on the surface of the upper leaves on clear, cloudy or rainy days were provided, with respect to the corresponding CO₂ assimilation rates. Moreover, the recent finding that, in sunflower leaves, the rate of water loss by transpiration changes in proportion to the radiation load at half to full sunlight (Pieruschka *et al.*, 2011) has not been taken into account.

Using our methods for quantification of photon fluence and photosynthetic CO₂ exchange in sunflower leaves, as described recently (Kutschera *et al.*, 2010; Pieruschka *et al.*, 2011), we generated the data set shown in Figs 3B and 4A, B. In Northern California, with clear skies, average photon fluence densities increased from approx. 1200 (morning) to 2050 (noon) $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and, in the evening, reached values similar to those in the morning. On cloudy days, the respective values were approx. 300, 900 and 290 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and, on rainy days (dark-grey sky), only 115, 180 and 110 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively, were recorded on 9–12 September 2013 (Fig. 3B). If we compare these data with the average rate of photosynthesis (i.e., net CO₂ assimilation), measured on the upper leaves (Fig. 4A), the following conclusions for vegetative *H. annuus* 70 d post-germination can be drawn:

1. Under clear skies (i.e. half full sunlight providing approx. 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$): leaf photosynthesis is >98 % saturated, so that the erect position (at noon) does not further enhance photosynthesis, compared with the morning and evening positions. However, it might confer an advantage in the early springtime when days are shorter and fluence rates overall

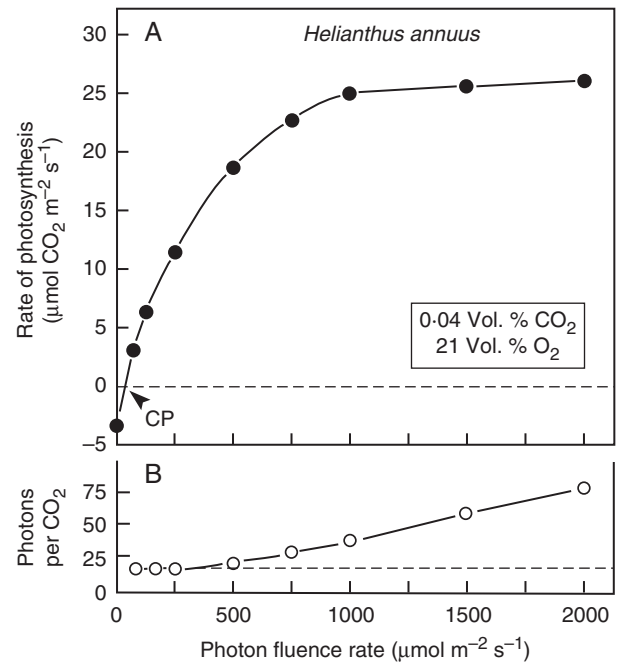


FIG. 4. Representative light–response curve of net photosynthesis (CO₂ assimilation) rate, measured on an upper, fully expanded leaf of a sunflower plant (see Fig. 1), as described by Kutschera *et al.* (2010). The light compensation point (CP) is indicated (approx. 40 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) (A). The calculated ratio (photons per CO₂ assimilated) indicates the growing inefficiency of photosynthesis with increasing irradiance (B).

lower, and in geographic areas where sunflower plants are grown under sub-optimal light conditions.

2. Under cloudy skies, in theory, the rate of photosynthesis might be significantly enhanced by phototropic solar tracking, but, in this medium light environment, the movements of these 70-day-old plants are only weak or absent. Shibaoka and Yamaki (1959) also report relatively weak heliotropism on rainy days for 70-day-old plants, but a somewhat stronger response for 100-day-old *H. annuus*.

3. In sunflower leaves, the light compensation point is approx. 40 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (i.e. 2 % of full sunlight) (Fig. 4A; for details, see Kutschera *et al.*, 2010). In rainy weather, under these limiting-light conditions, net assimilation rates are very low (<5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). No heliotropism was observed under these environmental conditions. Based on the fact that, in sunflower seedlings, root respiration reaches values of approximately one-third of that of the entire organism (Kutschera and Niklas, 2012), chances are that the plant as a whole may be heterotrophic during the daytime. In other words, photosynthesis is insufficient to compensate for the respiratory CO₂ loss of this C₃ species. Heliotropism would make no difference, because, even at noon, net CO₂ assimilation of the leaves would probably not compensate for the respiratory CO₂ loss of the root system, plus that of the entire above-ground plant body.

Finally, it should be mentioned that our photosynthesis measurements, which are in accordance with those of other investigators on the leaves of *H. annuus* (e.g. Demming-Adams *et al.*, 1989), document that above photon fluences of 500 μmol

photons $\text{m}^{-2} \text{s}^{-1}$ the efficiency of light-driven CO_2 assimilation decreases drastically (Fig. 4B). Our data are in accordance with the much more detailed measurements of Björkman and Demming (1987).

These facts, combined with the enormous latent heat flux from a leaf in full sunlight (and the associated water loss through transpiration), indicate that the erect position of the sunflower plant in full sunlight at noon is of questionable adaptive significance. Numerous studies have shown that green photosynthetic organisms must cope with what can be severe light stress, when absorption of solar radiation exceeds photosynthetic capacity ($>1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in the case of *H. annuus*), so that the photosynthetic apparatus must be protected from photodamage (Takahashi and Murata, 2008).

Clearly, solar tracking of leaves can provide a significant improvement in photosynthetic carbon gain in some species. Ehrlinger and Forseth (1980) reported that photosynthesis of the desert annual *Malvastrum rotundifolium* was only saturated at photon fluence rates above the mid-day maximum. They conclude that tracking the sun provides a significant advantage to this species, and it is highly likely that it does so for many other species with solar-tracking leaves. In this sense, the solar-tracking response of *H. annuus* vegetative shoots, and perhaps other composites, may be an exception.

HELIOtropISM AND SHADE AVOIDANCE

Based on numerous experimental data, Shirley (1929) concluded that sunflower plants ‘needed more light for survival, more for flowering and fruiting, more for maximum height growth, and more for attaining maximum dry weight’ than other angiosperms raised under the same environmental conditions. Decades later, other investigators corroborated this hypothesis (Wilson, 1966; Sinclair and Muchow, 1999). Moreover, Shirley (1929) documented that, in small populations of 6-week-old *H. annuus* plants, the stems are longer when the organisms were grown under 48 and 21 % of full sunlight, respectively, compared with unshaded controls. These observations suggest the presence of a photomorphogenic, phytochrome B-regulated shade-avoidance response in populations of sunflower plants (Smith, 1995; Kutschera and Briggs, 2009, 2013). Without reference to Shirley (1929), Shell and Lang (1976, p. 169) concluded that, with respect to ‘more mature and denser plantings, where the tendency for mutual shading of leaves would be greater’, . . . ‘the main advantage of heliotropism of sunflower plants would be in the early stages of growth, when heliotropism may improve their competitive position.’

The fact that the shade-avoidance responses, i.e. the elongation of the stems and petioles as a result of a lack of red light in dense populations, occurs in *H. annuus* is obvious. Usually, individual *Helianthus* plants that grow at the margin of a field are smaller and sturdier than their conspecifics in the centre of the group, which are considerably taller. This observation has been corroborated experimentally. Garrison and Briggs (1972) covered portions of the internodes of growing sunflower plants with foil and found that they were significantly longer than those of untreated controls. The

data indicated that light on the internode itself was required to suppress stem elongation. They then showed that direct irradiation of the internode itself with far-red light was sufficient to allow for an increase in growth, although far-red irradiation of the entire plant allowed for a greater increase (Garrison and Briggs, 1975). Subsequently, Morgan *et al.* (1980) demonstrated that localized irradiation of internodes of growing *Sinapis alba* seedlings with far-red light elicited a substantial increase in the growth rate of the internode within 10–15 min, whereas similar irradiation of leaves had no effect. These results clearly document the occurrence of a phytochrome-mediated shade-avoidance response in the growing internodes in both sunflower and *S. alba*, and probably in other angiosperms (Kutschera and Briggs, 2009, 2013). They are also in accordance with the well-characterized far-red enrichment of photosynthetically active radiation under high population density conditions, which results in a promotion of basal leaf senescence (Rousseaux *et al.*, 1996).

In a comprehensive analysis of phototropism in angiosperms, Iino (2001) concluded that, with reference to work on sunflower, shade avoidance is the key process behind heliotropic movements. Our observations and measurements on stem and leaf phototropism in sunflower plants (Figs. 3 and 4) do not add new insights on this topic. Nevertheless, we conclude that a photomorphogenic, phytochrome-regulated shade-avoidance response is a major biological function of the heliotropic growth movements in sunflower plants, and not optimization of photosynthesis *per se*.

CONCLUSIONS AND OUTLOOK

The annual sunflower, a plant first domesticated about 5000 years ago in a region that is now the South-eastern USA, has been used by indigenous Americans as a symbol of their solar deity (Blackman *et al.*, 2011). More recently, selected strains of sunflower with an enhanced oil content have been employed as a major crop, and this large annual herb is also planted by gardeners as an ornament (Heiser, 1976; Schneiter, 1997). However, despite its economic importance and popularity, the most conspicuous feature of this fast-growing angiosperm, its striking heliotropism, has not yet been fully characterized (Vandenbrink *et al.*, 2014).

Here we confirm that only growing, vegetative shoot apices and immature flower buds perform growth-mediated heliotropic movements, accompanied by leaf bending responses (Fig. 5A). Mature flowering heads point in a fixed, easterly direction throughout a sunny day, although wind and rain can turn the heads and modify their position. After anthesis, fruiting heads bend downwards (Fig. 5B). In our experience, on cloudy or rainy days, and in a growth chamber with fixed light bulbs, the stems/leaves of growing, juvenile sunflower plants do not change in position. Hence, for these plants, any endogenous rhythm appears to be dominated by the growth-mediated organ movements that occur in the field. However, recent reports provide growing evidence for a role for the ‘internal clock’ in modulating heliotropic movement during the day and driving the reorientation movement at night (Harmer, 2009; Atamian, 2014; Harmer *et al.*, 2015). It was the seminal study of Shibaoka and Yamaki (1959) that first suggested that an

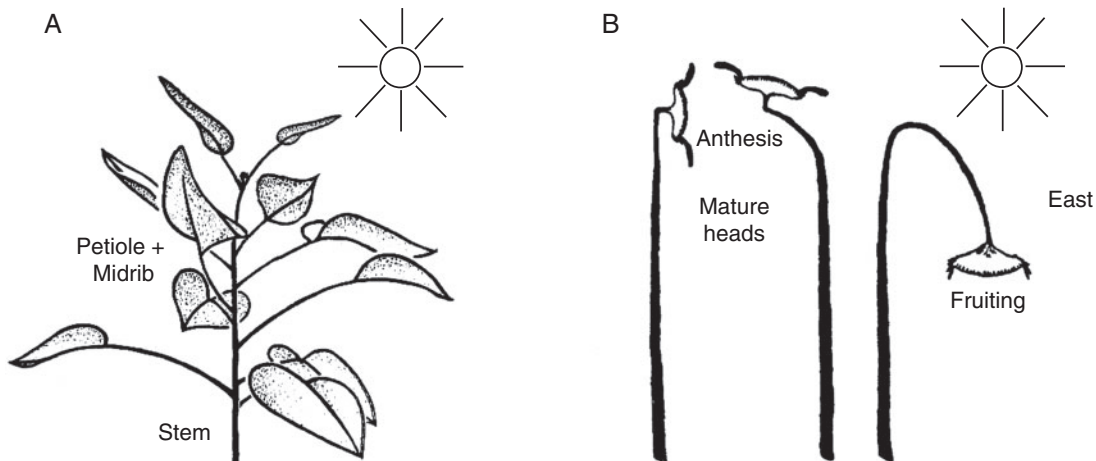


FIG. 5. Schematic summary of phototropic solar tracking in a growing sunflower plant (A), and position of the mature head at anthesis, and during fruiting (B). Note that, in the younger, solar-tracking plant, both the stem and the upper leaves turn towards the sun (adapted from Shibaoka and Yamaki, 1959).

endogenous rhythm is involved in the regulation of phototropic solar tracking in *H. annuus*. The role of the circadian rhythm during the daytime evidently increases as the growing seedlings become older.

Finally, our data show that the classic ‘photosynthesis-optimization hypothesis’ (Schaffner, 1900; Hart, 1990; Schneider, 1997; Li *et al.*, 2012) as sole explanation is questionable. We suggest that the shade-avoidance response may play a major role, but acknowledge that, by this means, the rate of light-dependent CO₂ assimilation in the upper leaves of solar-tracking plants may be optimized. However, many open questions as to the physiology and adaptive significance of heliotropism in developing sunflower plants (Fig. 5) are unanswered. (1) How is the nocturnal re-orientation regulated? (2) Are the light-dependent shoot and leaf movements independent reactions or co-ordinated processes? (3) Is heliotropism in sunflower a blue light (phototropin)-mediated process, or are other photoreceptors involved (Deng *et al.*, 2014)? (4) Which phytohormones (auxins, brassinosteroids or gibberellins) are causally involved in the re-distribution of growth leading to organ bending (Kurepin *et al.*, 2007, 2012)? (5) What are the sites of photoperception? (6) Are the heliotropic movements of the stem and upper leaves true irreversible growth processes (phototropisms) or, at least in part, turgor-driven nastic bending responses?

These and other questions must be answered before we fully understand one of the most popular physiological processes in the plant kingdom.

ACKNOWLEDGEMENTS

This article is dedicated to our colleague Dov Koller (1925–2007), a pioneer in the field of experimental plant physiology. We thank the Alexander von Humboldt-Stiftung (AvH, Bonn, Germany) for financial support (AvH-Fellowships Stanford 2013/14 to U.K., Institute of Biology, University of Kassel, Germany).

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