P-wave delay method is based on a number of assumptions and cannot resolve details in the velocity-depth profile, it does lend support to the type of interpretation we have presented. For example, the Carder model (with a 30-km crust in which velocities are 6.1 km/sec), considered in the context of the Press and Biehler study, would be associated with a P-wave delay of at most 0.3 second, relative to Pasadena, whereas the observed delay was 0.8 second.

Of course, many uncertainties about the nature and structure of the crust of the Sierra Nevada remain, but we believe that we have demonstrated that the root of the Sierra Nevada exists and that it projects downward to a depth of about 55 km beneath the highest mountains of the range, as proposed by investigators as far back as Lawson (*1*). Our preferred model of the root of the Sierra Nevada (Figs. 5A and 6A) is compatible with modern principles of plate tectonics.

Most of the remaining ambiguities and uncertainties about the structure of the root of the Sierra Nevada could readily be resolved by analysis of travel times from local and distant earthquakes, by detailed seismic profiling across and along the axis of the range, and by application of the latest techniques of modeling to seismic record sections.

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15. The delay of time of P_n waves caused by propagation through the crust is the additional time for waves to travel any segment of the P_n path over the time that would be required to travel the horizontal component of that segment at the velocity of P waves in the uppermost mantle. Variations in delay time are directly proportional to variations in the thickness of the crust.
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20. We thank W. H. Jackson, Sedalia, Colo., who supervised the reflection recording and the explosions in Mono Lake; personnel of the U.S. Geological Survey who participated in the field work; personnel of the Seismological Laboratory at California Institute of Technology who helped install and operate the stations for the Sierra profile; A. Ryall, of the University of Nevada, who supervised the recordings of the Truckee earthquake aftershocks; C. Archambeau, of the University of Colorado, who helped in the early stages of the analysis of the Sierra profile; A. Griscom, W. Hamilton, A. Lachenbruch, and H. Oliver, of the U.S. Geological Survey, for valuable discussions of the data and conclusions; and J. Eaton, A. Espinosa, D. Hill, P. Lipman, W. Spence, and D. Warren, of the U.S. Geological Survey, for helpful reviews of the manuscript.

Solar Tracking by Plants

James Ehleringer and Irwin Forseth

Leaf movements in higher plants have been recognized for many years. Perhaps the most widely known examples are rapid leaf closure in *Mimosa* and the circadian sleep movements in beans and other leguminous species in which leaves move from a horizontal to a vertical position at night (*1*). The movements of leaves fall into three categories: nyctinastic (sleep movements), seismonastic (movements in response to shaking), and heliotropic (*1-3*), which is the subject of this article. As the name implies, heliotropism is the movement of leaves following the sun and is of two types: diaheliotropism and paraheliotropism. The movement of blades of diaheliotropic leaves is such that they remain perpendicular to the sun's direct rays throughout the day. The movement of blades of paraheliotropic leaves is such that they remain parallel to the sun's direct rays. In effect then, heliotropic leaves are solar trackers (Fig. 1). The heliotropic leaf movements may be accomplished in several ways. The two most commonly observed means involve petiole twisting and pivotal movement of the pulvinus, a turgor-dependent structure located at the base of the leaf blade (*1, 2*). These leaf movements are rapid and reversible tropic responses and should not be confused with or considered as growth responses.

Physiological aspects of leaf movements and the morphological mechanisms for achieving them have been studied extensively (*1-3*). However, there has been little discussion of the adaptive value of either of these types of leaf movements and the environmental regimes in which natural selection should favor them. In this article, the heliotropic leaf movements in arid land plants, the potential consequences to metabolic activity, and the probable adaptive value to native plants and agronomic species are discussed.

Diaheliotropism will have a tremendous impact on the daily rate of net photosynthesis because it allows a sunlit leaf to experience high solar irradiances and to operate at maximal rates throughout the day (*4*). This trait could be of particular value to ephemeral or annual vegeta-

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tion that must complete its life cycle in a brief period before the onset of long periods of unfavorable conditions such as drought or high temperatures. Paraheliotropism would be of value in allowing annual vegetation to survive intermittent unfavorable periods that occur before the end of the growing season. Thus, we might predict a high frequency of solar tracking in plant species of arid lands. Heliotropic leaf movements are known to occur in several species in the families Asteraceae, Fabaceae, and Malvaceae (3-8), but the extent of its distribution in other families is unknown.

Fig. 1. Leaves of *Lupinus arizonicus* orienting to track the sun.

Summary. Leaves of many desert and agricultural species have the ability to move diurnally, orienting perpendicular or parallel to the sun's direct rays. This phenomenon is widespread in many plant families and occurs in both C_3 and C_4 photosynthetic pathway plants. In the annual flora of desert communities, solar tracking becomes more frequent as the length of the growing season decreases. Leaves that are perpendicular to the sun's direct rays for tracking appear to have high photosynthetic rates throughout the day, whereas leaves parallel to the sun's rays have reduced leaf temperatures and transpirational water losses.

Solar Tracking in Desert Plants

In the arid regions of the southwestern United States, the vegetation is usually dominated by perennials, primarily shrubs and succulents (9). After winter or summer rainstorms, however, an ephemeral vegetation appears and at times carpets the soil surface (10). We have surveyed this ephemeral vegetation for solar tracking by leaves in three types of plant communities with short growing seasons of differing lengths (11). The plant communities chosen were coastal sage scrub, which grows during a winter precipitation period of 20 to 30 weeks; Mohave and Colorado desert scrub, which grow in winter during a precipitation period of 15 to 20 weeks; and southern Arizona desert scrub, which grows during a summer precipitation period of 5 to 15 weeks (12).

In the annual floras surveyed, the frequency of solar tracking increased as the length of the growing season declined. The winter coastal sage vegetation has the longest growing season, and only two genera, *Lupinus* (Fabaceae) and *Malva* (Malvaceae), comprising 11 percent of the annuals in the genera sampled, showed diaheliotropic movements (13). Nine genera of annuals, or 28 percent of those sampled in the desert's winter annual vegetation, tracked the sun (14). These included *Abronia* (Nyctaginaceae), *Astragalus* (Fabaceae), *Coldenia* (Boraginaceae), *Dicoria* (Asteraceae), *Lotus* (Fabaceae), *Lupinus* (Fabaceae), *Malvastrum* (Malvaceae), *Palafoxia* (Asteraceae), and *Sphaeralcea* (Malvaceae) (14). In the summer annual vegetation with the shortest growing season, 12 genera, or 75 percent of the annuals in the genera sampled, tracked the sun. These genera were *Allionia* (Nyctaginaceae), *Amaranthus* (Amaranthaceae), *Boerhaavia* (Nyctaginaceae), *Euphorbia* (Euphorbiaceae), *Helianthus* (Asteraceae), *Kallstroemia* (Zygophyllaceae), *Portulaca* (Portulaceae), *Proboscidea* (Martyniaceae), *Solanum* (Solanaceae), *Tidestromia* (Amaranthaceae), *Trianthema* (Aizoaceae), and *Tribulus* (Zygophyllaceae) (15). Although our survey was not comprehensive, it is rather indicative of a pronounced trend in the vegetation sampled.

Our studies indicate that solar tracking is much more widespread than has been reported. We have identified heliotropic leaf movements in plants from 16 different families (16). The tracking ability is independent of photosynthetic pathway and taxonomic affinity, since species representing both C_3 and C_4 photosynthetic pathways and families from diverse plant orders demonstrated solar tracking. Leaf movements for solar tracking are even more general than our investigations of annuals indicate, as they also occur in some desert perennials that have deciduous leaves (17).

Paraheliotropic or leaf cupping movements were observed late in the growing season in both annual and perennial genera including *Astragalus*, *Cassia*, *Kallstroemia*, *Lotus*, *Lupinus*, *Stylosanthes*, and *Tribulus*. All of these genera have compound leaves and the paraheliotropic movements occurred primarily along leaf midribs.

Solar tracking ability can be related to solar irradiance by determining the fraction of the sun's direct rays that are intercepted. The angle between the leaf blade and a perpendicular to the sun's direct rays is termed the cosine of incidence of the leaf (18). In a plant with leaves that track the sun perfectly, this angle will be 0° (that is, the leaf blade is perpendicular to the sun's rays) or a cosine of incidence of 1.0. Winter and summer desert annuals track the sun closely throughout the day (Fig. 2) by changing leaf azimuth and leaf angle. Slight deviations in the cosine of incidence may occur at dawn and dusk in some species because of constraints on leaf movement that prevent full vertical extension of the leaf.

Canopies were relatively sparse in the species observed, and all leaves, not just a small fraction, tracked the sun. *Boerhaavia annulata*, *Lupinus arizonicus*, and *Kallstroemia grandiflora* demonstrated this for both winter and summer desert annual species (Fig. 3). Generally, leaf azimuths were within 15° of solar azimuth, slightly ahead in the morning hours and slightly behind in the afternoon hours. In contrast, nonsolar tracking desert annuals such as *Phacelia calthafolia* were observed to have random leaf azimuth distributions (Fig. 3).

Diaheliotropism and Irradiance

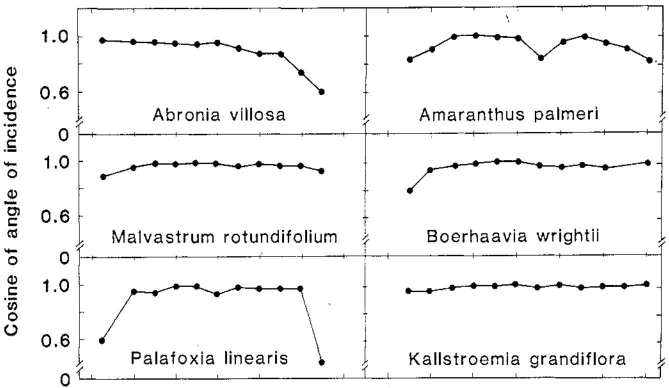
One immediate consequence of diaheliotropism is that leaves experience a high and relatively constant solar irradiance (Fig. 4). Solar irradiance incident on these leaves is attenuated below the solar constant only by changes in the air mass along the optical path. In contrast, the solar irradiance on leaves with fixed leaf angles is lower because it depends additionally on the geometric orientation (angle and azimuth) of the leaf relative to the sun. For example, consider the solar radiation received on a clear day (*19*). The daily total of incident photosynthetic quantum flux (400 to 700 nanometers) on the leaf that tracks the sun will be 8.09 millimoles per square centimeter and on the leaf with a fixed angle of 0° it will be 5.85 mmole/cm^2. The enhancement of total incident quantum flux in diaheliotropic versus flat leaves will increase far beyond this 38 percent as the leaf angle of the nontracking leaves increases. When fixed leaf angles are vertical (random azimuth and 90° from the horizontal), the enhancement by solar tracking will be 167 percent. Diaheliotropic leaves have more quanta available for photosynthesis, and if physiologically able to use the high irradiances (*4, 20–24*), a greater potential daily photosynthetic gain than nontracking leaves (*4, 8, 25*). Thus diaheliotropic leaf movements may give a competitive advantage in mixtures with nontracking species. Energy and heat balance equations point out a possible disadvantage of diaheliotropism in that the leaves are under a greater heat load, resulting in increased leaf temperatures and increased rates of water loss (*18, 26, 27*). Plants with dense canopies may experience a second disadvantage from solar tracking since it will benefit only the outermost leaves and may greatly reduce the photosynthetic quantum flux available to leaves lower in the canopy.

Solar Tracking as a Component of Productivity

Many morphological and physiological factors affect photosynthesis and interact to determine rates of plant productivity (*28*). Three important aspects of plant productivity are canopy and leaf morphology, physiological and biochemical components, and solar tracking ability. We expect that the extent to which these factors will affect primary productivity in native annual vegetation should change as a function of the length of the growing season (Fig. 5). In habitats with long growing seasons, there will be ample time for annuals to develop extensive canopies and some shading will occur. This would lead to an environment in which leaves compete for light and in which canopy and leaf morphology characteristics such as leaf angle, leaf area distribution within the canopy, internodal elongation capacity, and the number of palisade cell layers per leaf would be most influential in determining the rate of primary productivity. Because of the reduced irradiance on the average leaf within the canopy, the rate of photosynthesis should be less sensitive to physiological factors that determine the intrinsic maximum photosynthetic capacity of a leaf.

In shorter growing seasons, less time is available for canopy development, and the mean solar irradiance on a leaf will be relatively high. Selection for physiological factors affecting productivity will be greater in these environments. Factors such as photosynthetic enzyme concentrations, chlorophyll photosynthetic unit size, and stomatal conductance for carbon dioxide transfer should increase so that the intrinsic photosynthetic capacity of the leaf is greater. There is a limit, however, to the extent to which physiological components of the intrinsic photosynthetic capacity can be increased. This limit in conversion efficiency would occur when individual leaves operate at maximum quantum yield capacities (*29–31*); the limit appears to be fixed in higher plants at approximately 0.053 mole of CO_2 per mole of quanta (*31*). At this point, the rate of primary productivity will be determined by the solar irradiance incident on the leaf. With further reduction in the length of the growing season, solar tracking is a means of increasing primary productivity and may be essential if annual plants are to grow to the minimum size necessary to reproduce and complete their life cycles.

When predicted trends (Fig. 4) in the components of productivity are applied to the observations of annual vegetation in arid lands, it appears that canopy development is most extensive in the coastal sage annuals, which have the longest growing season (*32, 33*). Intrinsic photosynthetic capacities of the coastal sage



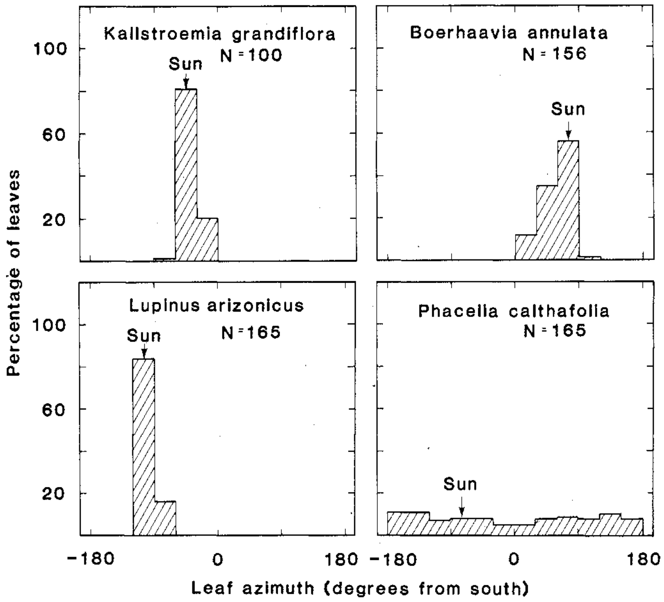


Fig. 2 (left). Representative diurnal courses of the cosine of incidence for leaves of desert winter annuals (left) and summer annuals (right). Sample size for each data point is nine. Cosine of incidence was measured with an inclinometer and compass and calculated according to (*18*). Fig. 3 (right). Frequency histograms for the orientation of leaves of three solar tracking species, *Boerhaavia annulata*, *Lupinus arizonicus*, and *Kallstroemia grandiflora*, and a nonsolar tracking species, *Phacelia calthafolia*. The sun's azimuth at the time of the measurement is indicated.

annuals are the lowest of the three types of annual vegetation studied and range from 20 to 40 micromoles of CO_2 per square meter per second (*33*). Photosynthetic capacities of winter and summer annuals are comparatively high, ranging from 35 to 60 and 35 to 55 μmole per square meter per second, respectively (*4, 21, 24, 30, 33*). The solar tracking data for leaves are also consistent with our expectation that solar tracking ability is rare among coastal sage annuals, which have the longest growing season of the three plant communities, and occurs most frequently in the desert summer annuals, which have the shortest growing season. It is possible, however, that part of the decreased frequency of solar tracking in coastal sage annuals results because that habitat is somewhat cloudier than the other desert habitats. This cloudiness would reduce the possible selective advantages for solar trackers.

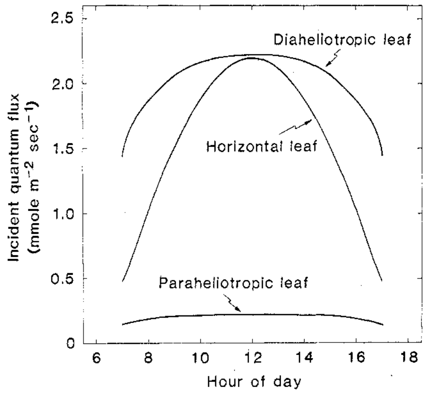


Fig. 4. Photosynthetically useful solar radiation between 400 and 700 nm incident on three leaf types over the course of the day (*19*): a diaheliotropic leaf (cosine of incidence = 1.0); a fixed leaf angle of 0°, the horizontal leaf; and a paraheliotropic leaf (cosine of incidence = 0.1).

Implications for Agriculture

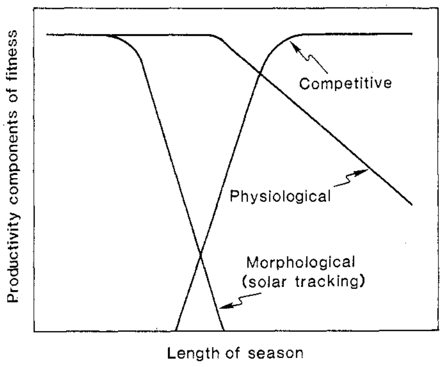
Diaheliotropic leaf movements have been reported in various crop and pasture species including cotton (*5*), sunflowers (*7, 8*), Townsville stylo (*34*), cowpeas (*27*), lucerne (*6*), soybeans (*35*), and to some extent beans (*7*). The supporting data generally take the form of diurnal frequency changes in leaf azimuth of canopy leaves; however, where measurements of the cosine of incidence are reported, values approach 1.0. Isolated plants have been shown to track the sun better than plants growing in rows, and solar tracking appears to have some effect on competitive ability (*36*). Solar tracking ability declines within the plant canopy and is affected by both row arrangement and planting density (*5, 23, 36*). The extent to which solar tracking appears in the leaves of agricultural species or even within varieties of the species named above is largely unknown. Findings suggests that varieties of cotton (*5*) and soybeans (*35, 37*) differ in their solar tracking abilities.

A few studies that have addressed the question of diaheliotropism and plant productivity (*4, 8, 25*) showed that the average daily interception of direct sunlight was 30 to 40 percent higher in leaves that track the sun than for fixed leaves with random azimuths. This agrees with Fig. 4. Comparing rates of photosynthesis among C_3 dicot crop species, we find that those with solar tracking ability tend not to be saturated at midday irradiances; thus maximum rates tend to be higher than for those species that do not track the sun (Fig. 6A). As a consequence of solar tracking, daily productivity increases proportionally as sunlight interception increases. Photosynthesis is enhanced particularly in the morning and afternoon hours when the solar elevation is lower and plant-water relations are more favorable (Fig. 6B). Small differences in daily productivity compounded over the length of a growing season could lead to large differences in biomass and convey a competitive advantage on solar tracking species. However, more studies of productivity at the individual leaf and canopy levels are required before a definite statement of the advantages of solar tracking can be made.

Indirect evidence to support the notion that solar tracking conveys a competitive advantage in agricultural situations comes from an analysis of weed species in the Southwest. Among all the major winter and summer weed species in the Arizona crop systems (*38*), a remarkable 53 percent of these species are solar trackers.

The extent to which solar tracking will increase plant productivity and yield is still unclear, although our present knowledge strongly implies that the effect will be significant. There are two additional consequences of heliotropic abilities that relate to plant performance and are of significant adaptive value. Both establishment and survival of drought stress are enhanced by solar tracking. Developing seedlings (with two to four leaves) of some winter and summer desert annual species whose leaves do not track the sun show daily stem movements similar to solar tracking (*24*). Such a response would increase incident photosynthetic quantum flux and enhance productivity. If this phenomenon also occurs in seedlings of crop species, it could be quite important in seedling establishment.

In response to drought, a number of solar tracking species show paraheliotropism, the active sun avoidance response in which the leaf blade is oriented parallel to the sun's rays (*2, 26, 27, 34, 39*). The consequence of this movement is that during periods of drought stress, leaves minimize absorption of solar radiation through the day rather than maximizing it (Fig. 4). Leaves with para-



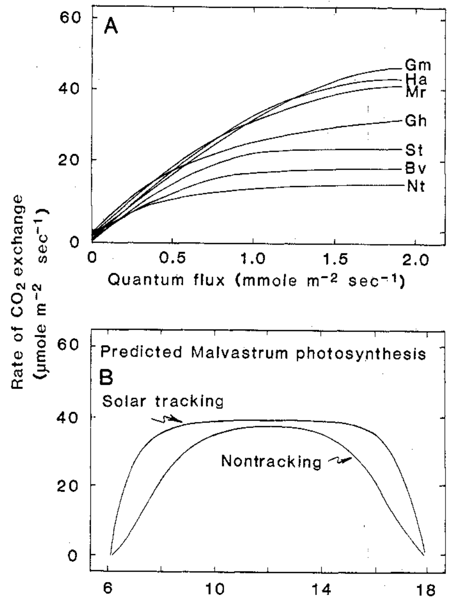


Fig. 5 (left). Hypothetical relation of three components of productivity of plant fitness in annual plants plotted as a function of the length of the growing season. Fig. 6 (right). (A) Rates of net photosynthesis versus incident quantum flux (400 to 700 nm) for solar tracking and nonsolar tracking C_3 dicot species. *Glycine max* (*Gm*), *Helianthus annuus* (*Ha*), and *Gossypium hirsutum* (*Gh*) are solar tracking crops. *Malvastrum rotundifolium* (*Mr*) is a solar tracking desert annual. *Solanum tuberosum* (*St*), *Beta vulgaris* (*Bv*), and *Nicotiana tabacum* (*Nt*) are nonsolar tracking crops. (B) Predicted diurnal photosynthetic rates for *Malvastrum rotundifolium* with solar tracking leaves and a hypothetical situation with leaves not tracking. Data from several sources (*4, 20, 22, 23, 42*).

heliotropic capabilities seem able to rapidly change or reverse the cosine of incidence between 0 and 1, depending on the degree of plant-water stress (*26, 27, 34*). Paraheliotropic movement reduces heat load on the leaf and decreases leaf temperature and transpiration rate (*26, 27, 40*). Paraheliotropism should be of tremendous adaptive value in allowing plants to maintain favorable water relations and avoid thermal damage during brief, intermittent periods of drought. Another possible benefit of paraheliotropism may be an enhanced water use efficiency (the ratio of photosynthesis to transpiration). This aspect of paraheliotropism has apparently not been examined. Sun avoidance responses in water-stressed plants are known to occur in a few crop species (*27, 34, 39, 40*) and in desert annuals (*24, 26, 41*), but the extent and distribution of paraheliotropism is poorly understood.

As demands on agriculture increase, it will become necessary to increase the efficiency of food production and to extend agricultural activity onto arid lands. To grow crop plants successfully on arid lands, we must know what physiological and morphological traits to incorporate in them. Native annual plants of arid lands should possess the adaptations needed to produce the most effective photosynthetic systems and to mature quickly before the onset of drought. Heliotropic leaf movements occur frequently in desert plants and may be one of these desired traits. Thus, studies of this phenomenon and of native plants may be of considerable benefit to agriculture. Diaheliotropic and paraheliotropic leaf movements, which appear to be independent of both photosynthetic pathway and taxonomic limitations, occur widely in desert annuals, crop weeds, and agricultural species, suggesting that selection for these traits might well be feasible. The capacity of diaheliotropism and paraheliotropism to enhance plant productivity during periods of water availability and to enhance survival during intermittent periods of drought may be significant for increasing agricultural productivity on arid lands.

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12. We studied coastal sage communities at Irvine and Point Mugu, California; the Mohave and Colorado desert scrub communities at sites in Death Valley and Anza Borrego State Park, California; and southern Arizona desert scrub communities at Gila Bend and Tucson, Arizona. All annuals found at each site were included in the survey. Sites with a high diversity of annuals were chosen, but no attempt was made to include all annuals known to occur in these habitats in the survey.
13. The solar tracking species included *Lupinus truncatus* and *Malva parviflora*.
14. The solar tracking species included *Abronia villosa*, *Astragalus lentiginosus*, *Coldenia nuttallii*, *Dicoria canescens*, *Lotus saluginosus*, *Lupinus arizonicus*, *Malvastrum rotundifolium*, *Palafoxia linearis*, and *Sphaeralcea coulteri*.
15. The solar tracking species included *Allionia incarnata*, *Amaranthus palmeri*, *Boerhaavia wrightii*, *Euphorbia abramsiana*, *Helianthus annuus*, *Kallstroemia grandiflora*, *Portulaca oleracea*, *Proboscidea parviflora*, *Solanum rostratum*, *Tidestromia lanuginosa*, *Trianthema portulacastrum*, and *Tribulus terrestris*.
16. Since our initial surveys we have observed solar tracking in the following desert genera: *Cleome* (Capparidaceae), *Dalea* (Fabaceae), *Eriogonum* (Polygonaceae), *Melilotus* (Fabaceae), *Oxystylis* (Capparidaceae), *Trifolium* (Fabaceae), and *Xanthium* (Asteraceae).
17. Winter active solar tracking perennials include *Abutilon parvulum*, *Boerhaavia annulata*, *Croton californica*, and *Sphaeralcea ambigua*. *Acacia angustissima*, *Boerhaavia coccinea*, *Cassia bauhinioides*, *Cercidium microphyllum*, *Dalea emoryi*, *Marina divaricata*, *Prosopis juliflora*, *Sida lepidota*, and *Stylosanthes viscosa* are summer active solar tracking perennials.
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