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Journal of Arid Environments 60 (2005) 697–707

Journal of Arid Environments

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Desert vegetation and timing of solar radiation

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Received 11 December 2003; received in revised form 20 July 2004; accepted 26 July 2004
Available online 5 October 2004

Abstract

Timing and amount of solar radiation were examined as factors influencing the distribution of seven perennial plants on a small mountain located in the Chihuahuan Desert. Average direct beam solar radiation fluxes at differing times throughout the day and year were estimated with computer calculations. Principal components analysis was used to reduce the number of solar radiation parameters and include the maximum available information with a manageable number of variables. The remaining solar radiation parameters were compared to plant distributions using redundancy analysis and generalized additive models. Unimodal, bimodal, and monotonic responses were all found depending upon the species and solar radiation parameter. Niche separation at this location depends upon the timing as well as the amount of solar radiation.

Keywords: Solar radiation; Water stress; Evapo-transpiration; Chihuahuan desert

1. Introduction

The importance of slope, aspect, and topographic variations to the distribution of terrestrial plant and animal communities has been noted by many authors (Cantlon, 1953; Yeaton and Cody, 1979; Lieffers and Larkin Lieffers, 1987). Mapping of vegetation spatial patterns at large scales based upon moisture and calculated solar

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0140-1963/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2004.07.016

radiation has been attempted with remote sensing technology (Dymond and Johnson, 2002). Vegetation patterns as affected by slope and aspect in the Chihuahuan desert were investigated by Mata-Gonzalez et al. (2002). They concluded that topographic variations were an important influence on plant distributions. Weiss et al. (1988) examined solar radiation influence on the life cycle of Euphydryas butterflies. Theoretical modeling of the amount and timing of solar exposure was combined with experimental and observational studies of the phenologies of life stages and host plants. The study found a correspondence between life cycles, senescence and solar radiation timing.

In many ecosystems, especially in semi-arid climates, soil moisture deficit is often the most important stress factor for vegetation. Heat stress, e.g. is most important after the cooling effect of transpiration has been reduced by moisture deficit. Stephenson (1998) explains climatic variation in plant distributions in terms of actual evapo-transpiration and moisture deficit. Porporato et al. (2001) and Rodriguez-Iturbe et al. (2001) have developed models of the interaction of soil moisture dynamics and plant response under conditions of water stress. Goldberg and Novoplansky (1997) explain the two-phase resource dynamics hypothesis which predicts that critical conditions for desert plants correspond to periods of water stress and the timing of water stress. In both models timing of precipitation and evapo-transpiration are predicted to be primary predictors of plant niche separation.

One of the primary variables influencing evapo-transpiration and thus soil moisture in semi-arid regions is the amount of solar radiation (Monteith, 1973). Veera (2004) calculated potential evapo-transpiration (PET) for 230 sample sites located on two small volcanoes in the West Potrillo Mountains, NM located in the Chihuahuan Desert. He found that solar radiation and PET were highly correlated and both offered essentially the same prediction of plant distributions. Qiu et al. (2001) found a positive correlation between the cosine of the aspect (shows north–south trends) and soil moisture content in a semi-arid region of China.

Sunlight is more complex on a small mountain than generally appreciated. Fig. 1 shows the path of the sun at different times of the year at the location of the study site. The zenith angle is the angle between vertical and the sun, azimuth is the compass direction to the sun with North = 0°, East = 90°, South = 180°, and West = 270°. Slope and azimuth (aspect) must be considered in combination with shading. For example, a flat or south-facing site could be located just to the north of a cliff. This occurs, e.g. near a subsidiary peak on the south side of the study site. Flat sites can occur at a mountain top, with no shading, or at the base of a mountain or cliff where shading reduces radiation during some times of the day and year.

Instantaneous versus daily averaged radiation may be important. The sun follows a curved arc across the sky with the arc being most noticeable in the summer. Fig. 1 is calculated for the latitude of the study site. A steep south-facing slope receives sunlight throughout the day in the winter and is at a favorable angle (normal) to the sunlight angle during the winter. At the spring and fall equinox the sun rises and sets exactly to the east and west but spends the rest of the day to the south, but to a lesser degree than in the winter. Around the summer solstice the sun rises in the north-east, moves slightly to the south at solar noon, and in the afternoon moves westward and

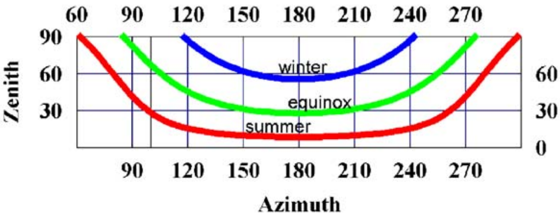

Fig. 1. Path of the sun at winter solstice, summer solstice, and equinox.

northward, setting to the north-west. In the winter, the sun rises in the south-east, remains to the south at solar noon, then sets in the south-west. Steep north-facing slopes receive no sunlight in the winter but can receive direct sunlight in the morning and evening hours during the summer. The extent of these trends depends upon latitude and is reversed in the southern hemisphere.

Integrated daily radiation reflects this solar path. Flat and slightly sloping areas receive the most sunlight during the summer solstice. North-facing slopes may receive no solar radiation in winter and extended day lengths in the summer. At winter solstice, south-facing slopes receive the most radiation. Interestingly, south-facing slopes receive low solar radiation at the summer solstice and high radiation during the winter, leading to lower seasonal changes in solar radiation.

This work examines the hypothesis that timing, and not simply total amount of solar radiation is an important predictor of plant dynamics as predicted by Porporato et al. (2001) and Rodriguez-Iturbe et al. (2001) and the two-phase resource dynamics hypothesis (Goldberg and Novoplansky, 1997). The study was performed on a small mountain located at the Indio Mountains Research Station in the Chihuahuan Desert. The limited distances and changes in elevation make solar radiation with its influence on evapo-transpiration a primary differentiating factor in micro-habitats. Based upon slope, aspect, and shading from the local topography, an annual history of solar radiation at each sample plot was calculated. Solar radiation at different times of the year as well as annual average solar radiation were calculated and statistically related to plant distribution. The study plants were limited to long-lived shrubs, whose distribution is more likely to reflect long term or average climate. To be more parsimonious solar radiation rather than PET was used in this paper.

2. Methods

2.1. Study site description

The study was performed on Flat-Top within the Indio Mountains at the University of Texas at El Paso Indio Mountains Research Station (30°44′50″N, 104°59′50″W). The Indio Mountains are located within the Chihuahuan Desert in southern Hudspeth County, Texas. Flat-Top is composed of relatively uniform Oligocene volcanic deposits and offers a wide range of topographic and shading sites. The research station is protected from livestock grazing. The soil is an undifferentiated regolith.

2.2. Sampling

Seven perennial plants were chosen for the study. Perennial plants were desired because the study considered only calculated direct beam solar radiation. Long-lived plants are more likely to show predictable responses to average conditions. The seven study plants were: *Verbenaceae Aloysia wrightii* (Oreganillo), *Ephedraceae Ephedra aspera* (Mormon Tea), *Asteraceae Parthenium incanum* (Mariola), *Boraginaceae Tiquilia greggii* (Plume Tiquilia), *Asteraceae Viguiéra stenoloba* (Skeleton Leaf Goldeneye), *Fouquieriaceae Fouquieria splendens* (Ocotillo), and *Agavaceae Yucca treculiana* Carrierre (Palmilla). All of the plants are small to large shrubs.

A grid was defined with an origin at the top of the mountain. Sampling transects ran in each of the eight cardinal directions from the top. Sampling plots were separated by 15 m. Each sampling plot was circular and 3 m in diameter. The number of each of the seven study plants in each plot was counted. Slope, aspect, and angle to the horizon in the eight cardinal directions were recorded at each plot. A total of 2310 plants were recorded in 177 plots. The raw data set consists of 177 rows with columns containing the number of each species per plot, slope, azimuth, and angle to the horizon in eight cardinal directions.

2.3. Solar radiation calculation

Direct beam radiation was estimated with the Solpos code (NREL, 2000) developed by the National Renewable Energy Laboratory (NREL). The C language source code was converted into *Mathematica* language and modified to allow for shading. The angle to the horizon at the eight cardinal directions was interpolated to make a continuous function. The result of this function was compared to the position of the sun at each time step to determine the presence or absence of sunlight. When the sample plot is not shaded, the direct beam radiation (total energy from all wavelengths) is estimated at each point in time taking account of slope, aspect, and atmospheric path length. The code is time stepped through a full year period at each of the 177 sampling plots with summation of the solar radiation from a list of potentially relevant time periods. The original list of solar radiation variables is presented in Table 1. Since diffuse radiation differs very little by topography we considered only direct beam radiation. Direct beam radiation focuses on differentiation between sites since diffuse radiation is independent of direction.

Table 1
Initial solar radiation variables

Annual average radiation ($MJ\,m^{-2}$)
Summer solstice, fall equinox, spring equinox, and winter solstice radiation ($kJ\,m^{-2}$). All four were calculated for a 10-day period centered around the appropriate solstice or equinox
Morning and afternoon radiation ($J\,m^{-2}$) morning was defined as sunrise to 10 a.m. and afternoon was defined as 2 p.m. to sunset. A time gap must be left between morning and afternoon to ensure that all the variables are statistically independent
Maximum and minimum daily radiation ($kJ\,m^{-2}$)
Maximum instantaneous radiation ($W\,m^{-2}$)
Day of the year for minimum daily, maximum daily, and instantaneous radiation (Julian day). On south-facing slopes, e.g. the maximum solar radiation period is not during the summer solstice

2.4. Statistical calculations

Three statistical techniques were applied to the data and solar radiation modeling results. The number of solar radiation variables was reduced from 13 to 5 based upon Principal Components Analysis and scatterplots. Redundancy analysis (RDA) was used to obtain an overall picture of the results, and Generalized Additive models were used to portray the species response to individual environmental gradients. Statistical analyses shown in all the figures were performed with the CANOCO Version 4.5 software package (ter Braak and Smilauer, 1998).

3. Results

3.1. Reduction of number of variables

The initial variable list was reduced in number using correlation matrices, scatter plots, and principal components analysis. The correlation matrix indicated that, for the sampling area, total annual radiation, fall equinox radiation, and spring equinox radiation are all highly correlated and thus provide the same information.

Principal components analysis of the solar radiation variables at the 177 sample plots gave three principal components. The first principal component corresponds to winter solstice radiation and the difference between maximum and minimum daily radiation at a plot. The results inspired us to define a combined variable, *seasonality*, as the difference between the peak and minimum daily radiation. The second principal component was dominated by summer solstice radiation. The third principal component can be summarized as the difference between afternoon and morning radiation. A new variable was defined as this difference. The resulting variables chosen for further statistical analysis were: equinox, winter solstice, summer solstice, seasonality, and afternoon–morning radiation (Table 2).

Table 2
Final environmental radiation variables

Environmental variable	Potential connection with plant growth
Equinox and total annual radiation ($MJ\,m^{-2}$)	Equinox and total annual radiation were highly correlated at the site and thus represent the same information. High solar radiation is associated with moisture and heat stress
Seasonality ($kJ\,m^{-2}$) = maximum daily–minimum daily	Low seasonality occurs primarily on south-facing slopes. Low seasonality (in general) means both lower heat stress during the summer solstice and less cold stress in the winter. High seasonality is associated with colder soil temperatures and lack of direct sunlight in winter
Winter solstice ($kJ\,m^{-2}$)	Winter solstice radiation is associated with the amount of cold stress in the winter. Low solar radiation in the winter provides an opportunity for storage of soil moisture. Some plant pests may be winter killed
Summer solstice ($kJ\,m^{-2}$)	At the study site, the hottest time of the year is only about 1 week after the summer solstice. High summer solstice radiation is associated with greater heat and moisture stress during the most critical time of the year
Afternoon–morning ($J\,m^{-2}$)	A high absolute value of this parameter indicates the opportunity for a shorter exposure to sunlight during the day; this may provide more recovery time for moisture transport from soil to plant roots

3.2. Redundancy analysis

RDA accounted for 34.4% of the variance and was statistically significant at $p<0.0001$. The first three axes accounted for 29.0%, 3.8%, and 1.2% of the variance, respectively. Polynomial RDA (Makarenkov and Legendre, 2002) accounted for 38.5% of the variance. The results for the linear RDA are shown in Fig. 2. Eigenvalues and percentage of variance explained of the species data dropped from PCA to RDA. The total of the constrained eigenvalues explained 34.4/95.3 = 36.1% of the total unconstrained eigenvalues.

The correlation between environmental variables is approximately equal to the cosine of the angle between the arrows. The length of the arrows represents the explanatory importance of the environmental variable, and how well a species is explained by the environmental variables. Summer and winter solstice radiation contain different information. A steep north-facing slope receives relatively low amounts of solar radiation in both summer and winter whereas a steep south-facing slope receives relatively little solar radiation in the summer and the highest solar

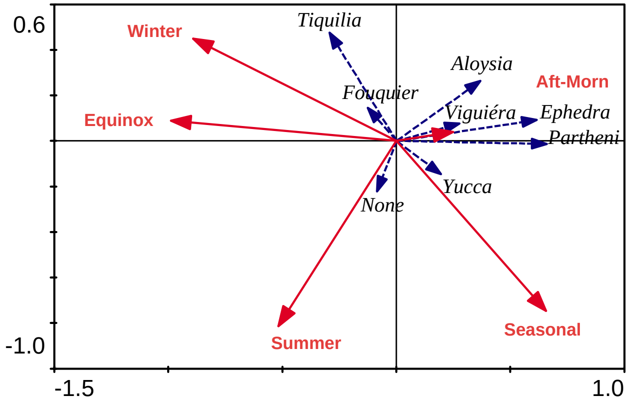

Fig. 2. Redundancy analysis.

radiation in the winter. Peak summer solstice radiation tends to occur on relatively flat unshaded plots. The steep south-facing slopes have a low seasonality and steep north-facing slope have high seasonality. Most of the plants have greater abundance with low equinox and winter radiation. *Tiquilia* and *Fouquieria* are exceptions with a preference for high winter solstice radiation and a low degree of seasonal variability. "*None*" representing plots where none of the study plants were present is aligned with high summer solstice radiation indicating that all the study plants are negatively associated with summer solstice radiation.

3.3. Generalized additive models

Generalized additive models represent an advance in regression analysis appropriate for studies of species distributions (Austin, 2002; Guisan, et al., 2002). Species response curves to each of the environmental variables were calculated using the Poisson error model and two degrees of freedom to predict the number of plants per plot. Only statistically significant results ($p < 0.05$) are included. Response to winter solstice radiation is shown in Fig. 3. *Tiquilia* and *Fouquieria* have a positive response to winter solstice radiation. *Viguiéra* and *Aloysia* have a bimodal response, while the other plants have a negative response. "*None*" was not statistically significant. Species response to equinox radiation (effectively the same as total annual radiation) is illustrated in Fig. 4. *Tiquilia* and *Fouquieria* have positive responses and the other plants have a negative response. Seasonal change in radiation gives a very strong statistical response as illustrated in Fig. 5. All responses are monotonic. Summer solstice radiation provides the most interesting result (Fig. 6). Two species (*Viguiéra* and *Partheni*) have a unimodal response and the others are associated with low summer radiation. Only *Yucca* does not show a significant response to summer solstice radiation. The "*none*" category is associated with high summer solstice radiation. The "*none*" category was entered as a binary zero or one plant count. Fig. 7 is the response to afternoon minus morning radiation. Bimodal

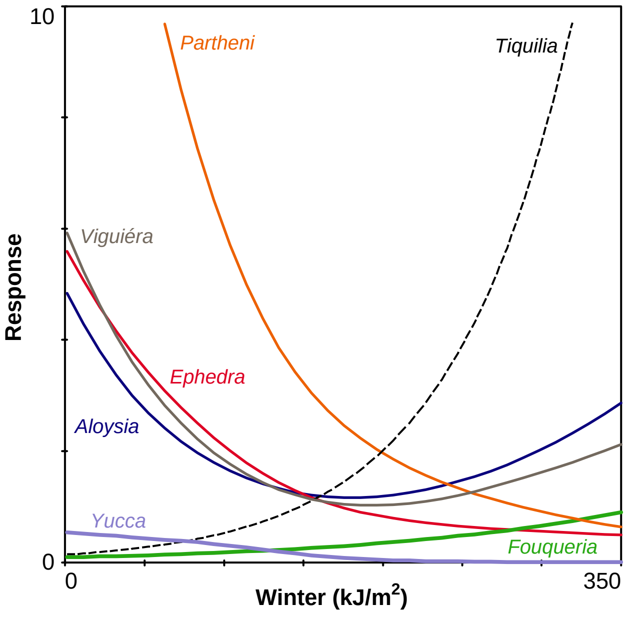

Fig. 3. Species response curves to winter solstice radiation.

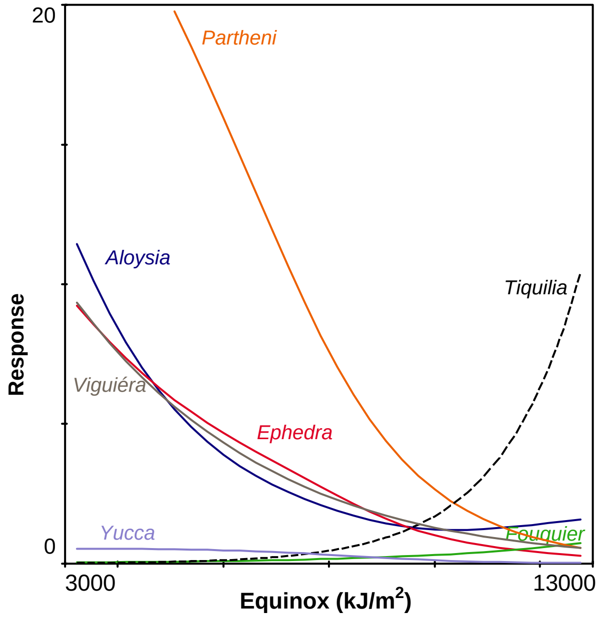

Fig. 4. Species response to equinox radiation.

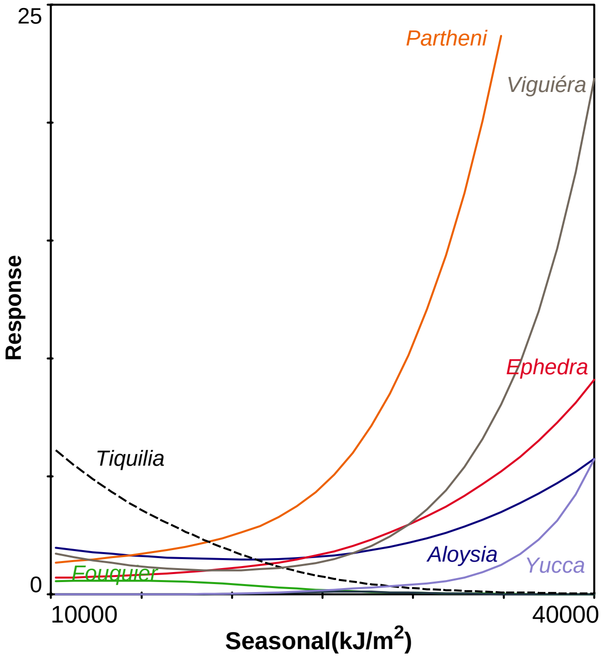

Fig. 5. Species response curve to variability in solar radiation during the year.

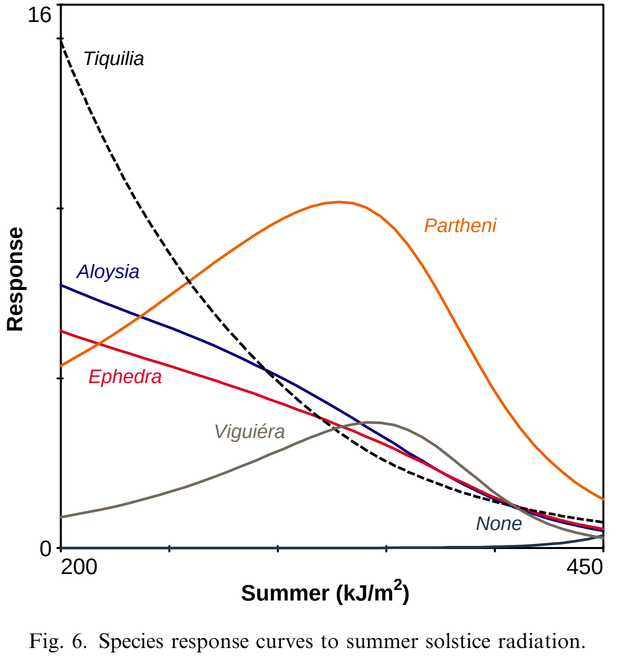

Fig. 6. Species response curves to summer solstice radiation.

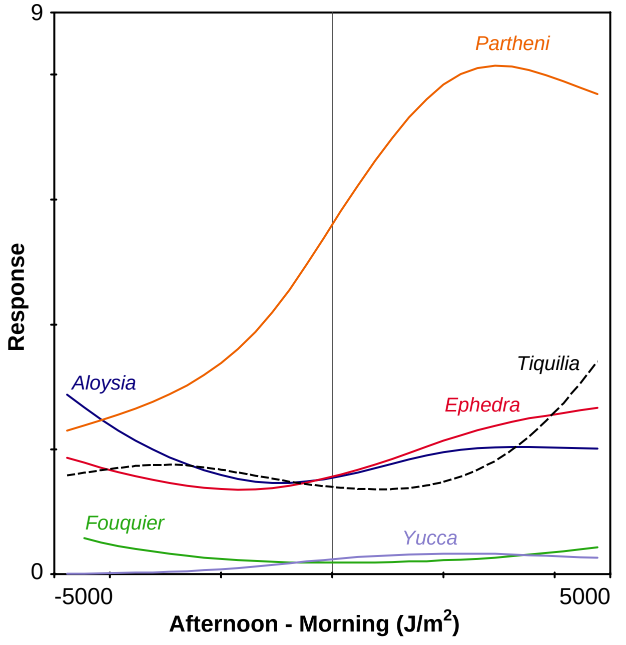

Fig. 7. Species response to afternoon minus morning radiation.

responses appear to be the norm with the exception of *Yucca*. This suggests that a location with shading during either the morning or evening may be a strategy for reducing peak daily radiation during the summer solstice. Yucca, which has a rosette growth form, has a unimodal response suggesting a preference for flat areas.

4. Discussion

In the Chihuahuan Desert climate solar radiation is highly correlated with PET making solar radiation an excellent analog for water stress (Veera, 2004). Based upon historical meteorological date for Van Horn, Texas the summer solstice is the hottest and driest time of the year at the study site. All of the seven study plants except Yucca had a lower density at locations having high solar radiation during the summer solstice. Summer solstice radiation is lower on steep slopes facing in any direction, including south and/or at locations partially shaded from more complex topographic features.

Tiquilia and less definitively, *Fouquieria* associated positively with high winter solstice radiation. The rest of the plants grew preferentially where winter solstice radiation is low. Low winter solar radiation allows for accumulation of soil moisture during a dormant period. The positive association of *Tiquilia* with winter radiation could indicate lower cold tolerance and/or competitive pressures.

The research results clearly demonstrate the timing of solar radiation is an important factor in the topographic distribution of vegetation. Solar radiation alone was able to predict 38.5% of the variation in plant distributions. The statistical observations support the hypothesis of Porporato et al. (2001) and the two-phase resource dynamics hypothesis that dynamic water stress is an important factor in plant distributions in the desert.

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