Coordination of branch orientation and photosynthetic physiology in the Joshua tree (Yucca brevifolia)

Kaylie E. Rasmuson  
*Idaho State University, Pocatello, Idaho*

Jay E. Anderson  
*Idaho State University, Pocatello, Idaho*

Nancy Huntly  
*Idaho State University, Pocatello, Idaho*

Follow this and additional works at: [https://scholarsarchive.byu.edu/gbn](https://scholarsarchive.byu.edu/gbn)

**Recommended Citation**

Available at: [https://scholarsarchive.byu.edu/gbn/vol54/iss3/2](https://scholarsarchive.byu.edu/gbn/vol54/iss3/2)
COORDINATION OF BRANCH ORIENTATION AND PHOTOSYNTHETIC PHYSIOLOGY IN THE JOSHUA TREE (YUCCA BREVIFOLIA)

Kaylie E. Rasmuson¹, Jay E. Anderson¹, and Nancy Huntly¹

ABSTRACT.—Despite the profusion of light in deserts, morphological adaptations to increase light interception are common among desert plants. We studied branch orientation and related physiological parameters in the Mojave Desert Joshua tree, Yucca brevifolia (Agavaceae). Azimuth and inclination were measured on all leaf rosettes of 44 Y. brevifolia trees. Interception of solar radiation was modeled for leaves in hypothetical rosettes facing due south and due north in December, March, and June. Carbon isotope discrimination, nitrogen content, and conductance to water vapor were measured in leaves from north- and south-facing rosettes. Rosette azimuths were nonrandom; rosettes predominantly faced southeast. North-facing rosettes were more steeply inclined than those facing south. The preponderance of south-facing rosettes reduces self-shading and increases interception of solar radiation during the winter–spring growth period. Stomatal conductance was higher for leaves in south-facing than in north-facing rosettes. Nevertheless, discrimination against 13C was less in leaves of south-facing rosettes, indicating that average intercellular CO₂ concentration was also lower. South-facing whorls had higher leaf nitrogen content. Greater allocation of nitrogen to leaves in south-facing whorls probably results in those leaves having a greater photosynthetic capacity than their north-facing counterparts. Orientation of rosettes to increase interception of sunlight during the period most favorable for photosynthesis, coupled with allocation of nutrients to maintain a higher photosynthetic capacity in those rosettes, should significantly increase whole-plant carbon gain in Y. brevifolia.

Key words: Yucca brevifolia, Joshua tree, carbon isotope discrimination, photosynthetic capacity, branch orientation, rosette azimuth, morphological adaptations.

Morphological adaptations to the light environment are common among desert plants (Ehleringer and Werk 1986). The angle and inclination of leaves (Ehleringer 1988, Neufeld et al. 1988) or cladodes (Nobel 1980, 1981, 1982) may increase interception of solar radiation when air temperatures and evaporative gradients are moderate (e.g., early in the day or during winter months) and reduce incident solar radiation during hotter parts of the day or year. Neufeld et al. (1988) reported that foliage clusters in creosote bush (Larrea tridentata), a long-lived evergreen shrub of the Mojave and Chihuahuan deserts, are inclined from 33° to 71° and oriented predominantly toward the southeast. They suggested that such architecture would tend to minimize self-shading and maximize carbon gain during periods most favorable for photosynthesis, which could result in improved water-use efficiency. We wondered if similar morphological adaptations might be found in the Joshua tree (Yucca brevifolia), a long-lived arborescent monocot with evergreen leaves.

Yucca brevifolia is restricted to the Mojave Desert, where it often occurs with L. tridentata. Its tough, fibrous leaves grow in symmetrical whorls forming cylindrical rosettes at the end of branches (Fig. 1A). The axis of newly expanding leaves at the top of a rosette is parallel with that of the rosette. As leaves mature and become photosynthetically active, they reflex away from the branch axis so that the adaxial surfaces of the youngest fully expanded leaves are at about 55° from the rosette axis. This angle gradually increases along the rosette axis so that the oldest photosynthetically active leaves are nearly perpendicular to the rosette axis (J. Anderson unpublished data; cf. Smith et al. 1983).

Rosettes vary from about 0.2 to >1.5 m in length and typically contain 200–1000 leaves. Young trees possess a single vertical rosette of leaves. Older trees have multiple branches that result from dichotomous branching at the apices of rosettes (Fig. 1B). Old trees can have over 100 branches and grow to >5 m in height (J. Anderson and N. Huntly unpublished data).

¹Department of Biological Sciences and Center for Ecological Research and Education, Idaho State University, Pocatello, Idaho 83209.
Yucca brevifolia is a C$_3$ species with modest photosynthetic rates (Smith et al. 1983). Photosynthesis is light saturated at a relatively low photosynthetic photon flux density (PPFD) of 400–600 $\mu$mol m$^{-2}$ s$^{-1}$; the nonoverlapping leaf arrangement results in a relatively even distribution of light throughout the rosette. Smith et al. (1983) found that stomatal conductances are highest during the winter–spring wet season and predicted that 80% of the annual photosynthetic productivity would occur from January through May. During the dry season, conductances are reduced to a very modest peak early in the morning. Thus, like L. tridentata and most aridland plants, Joshua trees live in an environment where opportunities for carbon gain are constrained, both seasonally and diurnally.

We tested the hypothesis that leaf rosettes are distributed nonrandomly within crowns of Y. brevifolia. After documenting a strong tendency for southeasterly orientation of rosettes, we compared leaf nitrogen content and carbon isotope discrimination ($\delta$) of rosettes on south vs. north sides of trees. Finally, we used porometry to explore the significance of differences in nitrogen allocation and $\delta$. We show that nonrandom orientation of photosynthetic leaf rosettes in Y. brevifolia is closely integrated with physiology.

**STUDY AREA**

The study was conducted at Lytle Ranch Preserve, 48 km west of St. George, Utah (37°9'N, 114°1'W, elevation 850 m), during March of 1989 and 1991. Lytle Ranch is in the northeastern Mojave Desert near the northern distributional limit of Y. brevifolia. Extensive Yucca woodlands occur on benches adjacent to Beaver Dam Wash. Other common species on the benches are Coleogyne ramosissima, Ambrosia dumosa, Larrea tridentata, Thamnosma montana, and Krameria grayi. Average annual temperature and precipitation at St. George are 16.5°C and 209 mm, respectively.

**METHODS**

Orientation of rosettes was assessed for 44 trees chosen systematically at 15-m intervals...
Along permanently marked transects on two benches. Each tree had fewer than 60 branches, and we measured azimuth and inclination of all branches on every tree. Azimuth was measured clockwise from true north to the nearest degree with a compass by sighting along the longitudinal axis of each rosette. Inclination of the rosette axis from horizontal was determined using an angle gauge with a built-in level.

Carbon isotope composition and total leaf nitrogen were measured in leaves collected in March 1989 from eight trees on the permanent transects. On each tree one fully expanded young leaf was taken from a rosette pointing due south, and a paired leaf sample was taken from a rosette pointing due north. Samples were dried and ground and then submitted to the Stable Isotope Research Facility for Environmental Research at the University of Utah for determination of carbon isotope ratios. Total leaf nitrogen was determined on subsamples of the paired leaf samples with a LECO C-H-N analyzer at the Holm Research Center, University of Idaho.

Carbon isotope discrimination (\( \Delta \)) was calculated from the carbon isotope ratios according to Farquhar and Richards (1984), assuming that the isotopic composition of the air was \(-7.8^{\circ}/oo\). Carbon isotope discrimination is related linearly to the intercellular concentration of CO\(_2\) \( (c_i) \):

\[
\Delta = a + (b - a)(c_i/c_a) 
\]

where \( a \) is the discrimination against \(^{13}\)CO\(_2\) relative to \(^{12}\)CO\(_2\) associated with diffusion in air \( (4.4^{\circ}/oo) \), \( b \) is discrimination against the heavy isotope by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) \( (27^{\circ}/oo) \), and \( c_a \) is the concentration of CO\(_2\) in the atmosphere \( (about \ 350 \mu L/L^{-1}) \). Because \( b, a, \) and \( c_a \) are usually constant, variation in \( \Delta \) reflects variation in \( c_i/c_a \), which results from variation in stomatal conductance and in demand for CO\(_2\) by the photosynthetic apparatus (Farquhar et al. 1982). Equation 1 was used to estimate \( c_i \) for leaves in north- and south-facing rosettes.

We measured leaf conductance to water vapor \( (g_{sw}) \) on 21 and 22 March 1991 with a LI-COR 1600 steady-state porometer. On both days a high cloud cover was present from dawn until dusk, which blocked direct sunlight and created uniform light conditions on all sides of the trees. Nine trees in the vicinity of the permanent transects, each having at least two north-facing and two south-facing rosettes, were chosen for sampling. A fully expanded leaf near the apex of the rosette was sampled in each of two rosettes on the north and south sides of each tree. Means of the two measurements were used for statistical analyses. A preliminary sample indicated that conductances of abaxial and adaxial leaf surfaces were similar, as reported by Smith et al. (1983); so, for convenience in holding the porometer in place, we sampled only adaxial surfaces. Paired measurements were made from north- and south-facing rosettes on the nine trees between 0900 and 1200 h (MDT). Photosynthetic photon flux density (PFD) was measured with a LI-COR 170 quantum sensor (LI-COR, Inc., Lincoln, Nebraska, USA). PFD varied from 200 to 800 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) during the measurement periods, but for the paired sample on each tree PFD was essentially constant and equal on both sides of the tree.

Because of the complexity of the architecture of \( Y. \) brevifolia (Fig. 1B), it was beyond the scope of this study to model light interception of whole trees, taking into consideration shading by other branches and self-shading within rosettes. Instead, we predicted the incident PFD for leaves in rosettes on the south and north sides of trees for 22 December, 21 March, and 21 June. Solar azimuths and inclinations for those dates at the latitude of Lytle Ranch were calculated according to Ehleringer (1989b). We calculated the cosine of the angle of incidence (\( \cos i \)), the fraction of the direct beam of solar radiation that is intercepted by a leaf, for leaves in hypothetical rosettes facing either due south or due north and having an inclination of 60°. Excluding trees with only one branch, this was the mean inclination of the population. \( \cos i \) was calculated for four leaves per hypothetical rosette: leaves on the top and bottom, with their axes perpendicular to the ground, and leaves on both sides, with their axes parallel to the ground. Because of the symmetry of whorls of leaves in rosettes (Fig. 1A), estimates of incident radiation for those four leaves should be proportional to that for an entire rosette. We assumed that leaves were planar and that each leaf was inserted at an angle of 55° from the rosette axis, the mean value for the youngest fully
expanded leaves on several trees. Cos i was calculated for both surfaces of each leaf (i.e., when cos i was negative, indicating that light would strike the abaxial side of a leaf, the absolute value was used). Thus, estimates of incident PFD include both abaxial and adaxial surfaces of the four leaves. Direct solar beam PFD values were predicted from a polynomial regression equation based on actual PFD measurements made throughout a clear day in mid-March at Lytle Ranch. Direct-beam PFD estimates were multiplied by cos i of each hypothetical leaf for a given date/time to estimate incident PFD. Those values were averaged for the four leaves as an index of incident PFD for the hypothetical rosettes.

Statistics were calculated according to Zar (1984). Mean azimuths and inclinations were calculated trigonometrically for individual trees, and those means were used to calculate a grand mean for all trees. Uniformity of leaf whorl azimuths within each tree was tested with the Watson U2 statistic. A chi-square goodness-of-fit statistic was used to test for random distribution of whorl azimuths pooled for all trees sampled using twelve 30° classes. Association between azimuth and inclination was tested using a two-way contingency table, with inclinations and azimuths grouped in 30° classes. Paired t tests were used to determine whether $\Delta$, total leaf nitrogen, or $g_w$ differed between the south and north sides of the trees.

RESULTS

Rosette azimuths within trees having more than four branches (the minimum required for the Watson U2 test) were not distributed randomly ($P < .001$ in all 23 cases). Azimuths for individual branches (pooled for all trees) fell predominantly between 90° and 270° (Fig. 2A); this distribution was also nonrandom ($X^2 = 78.13$, d.f. = 11, $P < .001$). All mean rosette azimuths for trees with two or more branches fell between 90° and 280°, with one exception that had a mean azimuth of 10° (Fig. 2B). Mean azimuths of individual trees were tightly clustered around the grand mean of the population, 163° (angular deviation $s = 42$, $n = 44$; Fig. 2B).

The mean inclination of rosettes on trees having two or more branches fell between 42° and 82° from the horizontal. Trees with two to five branches had more steeply inclined rosettes than did trees with six or more branches. Inclination was associated with azimuth ($X^2 = 39.45$, d.f. = 22, $P < .025$); rosettes having northerly azimuths (170°–90°) were more steeply inclined than those with southerly azimuths (Fig. 3).

Simulation of light interception shows that leaves in rosettes facing south would intercept substantially more direct sunlight than those in rosettes facing north at all times of year, but the difference is much larger in winter and spring than in summer (Fig. 4). When sun
angles are low, little direct sunlight is intercepted by abaxial surfaces of leaves in rosettes facing southeast and adaxial surfaces of leaves in rosettes facing north; those surfaces contribute more to total interception with increasing sun angles. Morning and afternoon peaks for leaves in the north-facing rosette in March are a consequence of the insertion angle (55°) for the two horizontally opposed leaves.

For the analysis shown in Figure 4, it is assumed that the four modeled leaves would be exposed to direct-beam solar radiation throughout the day. Clearly, that assumption would not hold for all leaves at all times of day. Because of the low density of Joshua tree stands and low stature of other plants in the community, shading by other individuals occurs rarely. However, self-shading occurs among leaves within rosettes and among branches within trees. Both would be minimized for branches having southerly aspects (Geller and Nobel 1986). Smith et al. (1983) asserted that the nonoverlapping arrangement of leaves of *Y. brevifolia* resulted in effective penetration of light into a rosette from the top. Leaves in rosettes having northerly azimuths would receive more shade from the rosette in which they occur, from other branches on the same tree, and from the main trunk of the tree, based on the patterns of shadows cast by
Fig. 5. Direction and length of shadows cast from early morning until late afternoon by an object 1 unit in height (1 unit = distance between concentric dashed circles) at the latitude of Lytle Ranch Preserve, Utah, for (1) 22 December, (2) 21 March, and (3) 21 June.

Carbon isotope discrimination was lower in leaves of rosettes that faced south than in leaves of rosettes that faced north (Table 1). Estimates of $c_i$ based on these $\Delta$ values were 141 $\mu$L L$^{-1}$ for leaves in rosettes on the south side of trees and 156 $\mu$L L$^{-1}$ for leaves in rosettes on the north side. The corresponding ratios of $c_i/c_a$, assuming $c_a$ was 350 $\mu$L L$^{-1}$, would be 0.40 and 0.45, respectively.

Total nitrogen content of leaves in rosettes facing south was higher than that in rosettes facing north (Table 1). For seven of the eight paired samples, the estimate of total leaf nitrogen was higher for the leaf from the south-facing rosette.

Leaves in rosettes on the south side of trees had higher conductances to water vapor than did leaves on the north side (Table 1). Mean $g_w$ was higher on the south side in each of the nine trees tested.

**DISCUSSION**

The distribution of rosette azimuths of *Yucca brevifolia* is clearly not random; rosettes point predominantly in southerly directions. Furthermore, branches on the north side of trees tend to be more steeply inclined than those on the south, which would tend to elevate the rosettes and reduce self-shading. Rosettes on the south side intercept substantially more direct solar radiation throughout the year, and the difference is especially pronounced in winter and early spring when sun angles are relatively low (Fig. 4). It is at this time that the bulk of annual carbon gain occurs (Smith et al. 1983). Shading of leaves in north-facing rosettes also would be greatest during the winter and early spring. Self-shading would magnify differences in incident direct-beam radiation between leaves in south- vs. north-facing rosettes shown in Figure 4. Thus, a second advantage of positioning rosettes on the south side of trees is to minimize self-shading.

The nonrandom branch orientation in Joshua trees appears to be closely coordinated with parameters related to photosynthetic capacity. Lower $\Delta$ in leaves on the south vs. north side of trees indicates that leaves on the south operate at a lower average $c_i$. As shown in equation 1, $\Delta$ is a time-integrated measure of $c_i$ reflecting the importance of both stomatal limitation to diffusion of CO$_2$ and capacity of the mesophyll to fix CO$_2$ (Farquhar et al. 1982). Numerous studies have shown that instantaneous gas exchange measurements are related to $\Delta$ as predicted by the theory (Hubick et al. 1986, Ehleringer et al. 1992).

We found that $g_w$ was higher in leaves of south-facing whorls, indicating that lower $c_i$ was associated with higher $g_w$. Because we measured $g_w$ under conditions when both sides of trees were equally illuminated, we assume that observed differences in $g_w$ reflect intrinsic differences related to photosynthetic capacity. These results imply that photosynthetic capacity was higher in leaves of south-facing rosettes.

Photosynthetic capacity and Rubisco activity often are positively correlated with leaf nitrogen content (Wong et al. 1985, Field and
Mooney 1986, Evans 1989). Field (1983) predicted that net photosynthesis would be maximized if nitrogen were allocated preferentially to leaves that receive more light. This is precisely what we observed; leaves in south-facing rosettes had higher nitrogen concentrations than those from rosettes on the north side of trees. Relatively low leaf nitrogen contents of Y. brevifolia were in a range where any increase in nitrogen would be expected to increase photosynthetic capacity.

One might expect lower $\Delta$ and lower $c_i$ in leaves of south-facing rosettes to be a consequence of lower stomatal conductance. However, observation of the pattern found here is not without precedence. Korner et al. (1988) reported that $\Delta$ decreased in plants with increasing altitude while carboxylation efficiency and stomatal conductance increased. Leaf nitrogen content also increased with altitude, which contributed to an increased photosynthetic capacity (Korner et al. 1988). Lower $\Delta$ is associated with higher photosynthetic capacity in peanut cultivars (Hubick et al. 1986, Wright et al. 1993) and sunflower (G. Farquhar personal communication).

Other factors could contribute to the observed difference in $\Delta$ between leaves on the north vs. south side of trees. Maximum stomatal conductance may occur at light levels somewhat below light saturation for photosynthesis, as observed in other species (e.g., Anderson 1982). Thus, leaves on the north side might receive sufficient diffuse radiation to open stomata but not saturate the photosynthetic apparatus, which could result in higher average $c_i$ than would occur if photosynthetic tissues were light saturated. Also, shading typically results in near instantaneous reductions in photosynthesis, whereas conductance changes more slowly (Anderson 1982, Knapp and Smith 1987). Therefore, $c_i$ of leaves on the north side might be higher in comparison to those on the south because those on the north experience shading more frequently, particularly during the winter-spring growing season when sun angles are relatively low.

Although differential light levels and intermittent shading may contribute directly to observed differences in $c_i$, the coincidence of lower $c_p$, higher $g_w$, and higher nitrogen content in leaves of south-facing rosettes provides strong evidence that the lower $c_i$ is primarily a consequence of higher photosynthetic capacity.

We conclude that differential allocation of nitrogen to leaves on the south side of Joshua trees results in substantially higher photosynthetic capacities in those leaves. This, coupled with orientation of rosettes to increase interception of sunlight during the period most favorable for photosynthesis, would enhance productivity of whole trees for a given level of nitrogen availability.

The $\Delta$ values for Y. brevifolia are among the lowest reported for C_3 plants (cf. Ehleringer 1989a, Korner et al. 1991, Ehleringer et al. 1992). Ehleringer (1989a) reported carbon isotope ratios for desert C_3 plants corresponding to $\Delta$ values ranging from 13‰ to 23‰, but values for Y. brevifolia are generally much lower than those reported by Ehleringer et al. (1992) and Schuster et al. (1992) for desert shrubs such as Ambrosia dumosa, Larrea tridentata, and Coleogyne ramosissima that often occur with Joshua trees. $\Delta$ is negatively correlated with water-use efficiency (Farquhar et al. 1989). Low $\Delta$ values and corresponding estimates of $c_i$ indicate that Y. brevifolia leaves have very low stomatal conductances relative to their photosynthetic capacities. This would translate to high water-use efficiency compared to co-occurring C_3 plants, assuming they were subjected to comparable leaf-air vapor pressure deficits.

ACKNOWLEDGMENTS

This research was supported by the Pat Kolbet Undergraduate Research Fund and the Department of Biological Sciences at Idaho State University. We thank the personnel at Lytle Ranch Preserve and the Monte L. Bean Life Sciences Museum at Brigham Young University for their cooperation. We also thank Marjorie Daly, Kelly Green, Mike Haslett, and Jeff Henry for help with data collection and Drs. Graham Farquhar and Christopher Field for helpful comments on an earlier version of the manuscript.

LITERATURE CITED


Received 23 May 1994
Accepted 5 July 1994