Light Dynamics in Nevada Saltbush *(Atriplex torreyi)* Canopies

DAVID P. GROENEVELD
Plant Ecologist
County of Inyo Water Department
301 East Line Street, Suite C
Bishop, California 93514

Abstract

A. torreyi canopies assume the shape of a hemispheric leafed shell when growing in open locations. The influence of light upon the growth and development of *A. torreyi* canopy shape was investigated by measuring the intensity of photosynthetically active radiation at points in the canopy within one hour of solar noon. A light compensation point that determines the critical light level for abscission was found as a divergence from an exponential Beer's Law relationship calculated from the percent remaining of the incident light at the top of the canopy versus the cumulative leaf area above the point of measurement. The light compensation point corresponded to the position of the inner margin of the leafed layer and was equal to the light transmittted through single leaves, which suggests that the compensation point is structured to avoid leaf abscission due to temporary occlusion by overlying leaves.

Introduction

Atriplex torreyi (Wats.) Wats. (Chenopodiaceae) is an evergreen dioecious phreatophytic shrub of the flowering plant family Chenopodiaceae of the northern Mojave Desert and the western Great Basin [Munz and Keck, 1959]. The shrub is an intense halophyte [Hall and Clements, 1923] occupying saline areas that are the invariable consequence of shallow groundwater in an arid environment [Kovda *et al.*, 1979] such as the Owens Valley.

A. torreyi canopies are commonly shaped like inverted half spheres with leaves filling an outer shell. Within the Owens Valley such canopies are prevalent on the more productive sites but may not develop on sites with marginal soils or high interspecific competition. The inner portions of *A. torreyi* canopies are generally devoid of leaves. Consequently, light levels from solar radiation can be expected to be appreciably different between the interior and exterior of the canopy. Light attenuation is therefore an obvious factor that may play a role for leaf retention in the canopy's interior.

Beer's Law describes the attenuation of light as it passes through a transparent medium with optical properties (**k**) that absorb, scatter, or reflect the light along some distance (**x**) into the medium. In this case, the optical medium is simply the leafy portion of the *A. torreyi* canopy. The formula for Beer's Law describes a decay curve with the remaining light

(I) in terms of the incident light (Io):

$$\mathbf{I = A * Io * e^{-kx}}$$

(where A is an empirical factor)

The many leaves forming a plant canopy have average optical properties that permit the application of Beer's Law to plant canopies if the distance, **x**, is converted to cumulative leaf-area index [Brown and Blaser, 1968]. Leaf-area index (LAI) is a term that describes the average number of leaf layers that overlie any chosen sample area.

By rearranging the factors in the Beer's Law formula, the attenuation factor, **k**, can be calculated as the slope of the line describing the relationship between the fraction of incident light remaining and the cumulative LAI through which the light passed:

$$\mathbf{\ln \frac{I}{I_o} = -k * \text{cumulative leaf area index.}}$$

Methods

Fifteen mature specimens of *A. torreyi*, both male and female, were selected for the study of canopy shape versus solar radiation. These were located on a highly productive shallow groundwater site near Independence in the Owens Valley, California. Each of the specimens studied had thick canopy growth, with the inner leafless portions of the canopy well differentiated from the overlying leafed shell.

Solar radiation was detected with a Li-190S-1 manufactured by Li-Cor Instruments of Lincoln, Nebraska. This sensor measures photosynthetically active radiation (PAR) between wavelengths of 0.4 and 0.7 microns with sensitivity of 0.05 at the radiation strength of the measurement.

The depth of the leafed shell "D" within the canopy was measured, and light readings were obtained with the PAR sensor lowered by 10 cm increments "d" (Fig. 1). This suite of measurements was obtained within the canopies of 15 *A. torreyi* during early July, 1984. Branches on the shaded side of each canopy were removed in a notch to facilitate the measurements. The sampling was accomplished with the sun within one hour of zenith on consecutive days during calm and dry weather. The plants were in a stage of bud initiation preparatory to flowering.

A point-frequency frame [Goodall, 1952] was used to vertically lower a pin to determine the LAI through the center of each shrub canopy. The pin was lowered five times through each shrub, and the total number of contacts of the lowered pin point was recorded. The

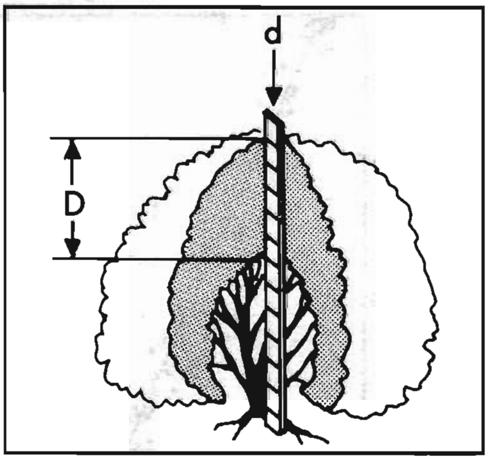

Figure 1. An idealized canopy with a wedge removed to access measurements. The drawing shows the leafed shell of thickness, "D," with a meter stick emplaced for measuring the distance below the canopy surface, "d."

total of leaf/pin contacts divided by the number of repetitions for lowering the pin randomly through the canopy center gave an estimate of LAI, assuming horizontal leaf alignment. The LAI calculated in this manner represented the mean of the pin/leaf contact of the five vertical pins per canopy. These data were again averaged among the 15 shrubs to yield an overall average LAI of 1.67.

A. torreyi has an average leaf alignment of about 60 degrees from the horizontal, which would require a cosine correction using this angle to calculate the actual LAI. However, for this investigation, the LAI is calculated assuming horizontal leaf alignment, because the measurements were obtained with the sun vertically overhead, and the comparison of LAI to light is made in relation to the vertically impinging radiation. The actual LAI is a factor of the average angle of the leaves from the horizontal and can be calculated by an empirical factor derived either with the point frame aligned at varying angles [Warren-Wilson, 1963] or as a calculation based upon point frame contacts to harvested leaf area determined by planimetric technique (D. P. Groeneveld, unpublished data). Further reference to LAI here will be to this factor calculated using the assumption of horizontal leaf alignment.

A shortcut routine was used to calculate cumulative LAI as an average by assuming that the rate of light attenuation remained constant through the canopy:

$$\textbf{cumulative LAI} = \textbf{LAI} * \frac{\mathbf{d}}{\mathbf{D}}$$

The ratio of the distance into the canopy at each PAR measurement point by the thickness of the leafed shell was used to describe an estimate of the leaves above that point and "calibrate" for the canopy density of each specimen. This shortcut routine saved many hours of laborious measurement of the actual cumulative LAI and greatly shortened the number of days required for field work since the measurement were restricted to the period around solar zenith.

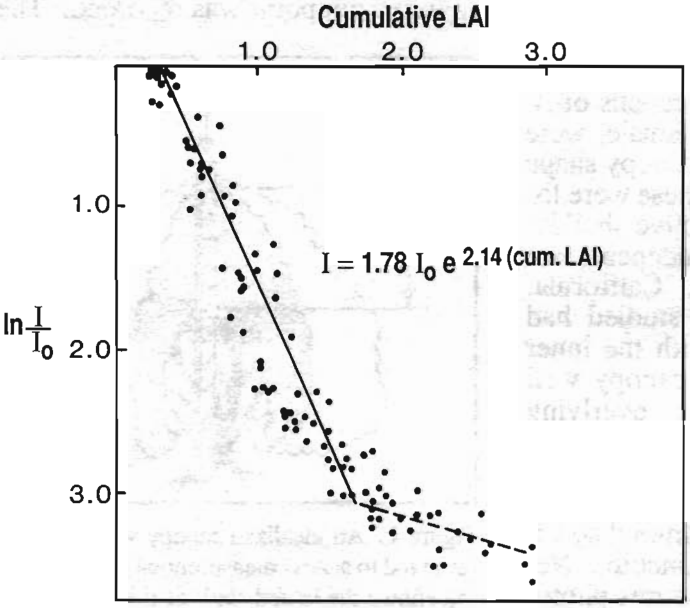

Figure 2. Light attenuation according to Beer's Law. The point of inflection occurred at the base of the leafed shell.

Results and Discussion

A linear relationship of slope, **k**, is visible between the natural log of the remaining **I/Io** ratio and cumulative LAI (Fig. 2). A break in the expected linear relationship is evident at the natural-log value of the **I/Io** ratio of approximately -3.0. The break decribes a markedly reduced magnitude of the slope of the attenuation and corresponds to a cumulative LAI of 1.67, which, due to the technique used for estimating cumulative LAI, also describes the light at the base of **D**, the thickness of the leafed shell. The natural log value of -3.0 converts to a ratio of approximately 0.05. The bottom of the leafed shell therefore occurs where the remaining light reaches about 5 percent of the incident light. Leaves apparently absice at light levels below this point.

Both shading alone and shading influences on carbohydrate production are implicated in leaf abscission [Addicott, 1982]. Leaves are shed when they become net carbohydrate sinks rather than sources. Therefore, the strong break in the curve on Figure 1 at the 5 percent of midday irradiance (which measured about 125 µE/m^2/s in July) suggests a light compensation point for net carbohydrate production and retention of leaves. The reduction of leaves according to a PAR compensation point may be an explanation for the markedly reduced *A. torreyi* leaf cover observed during the winter period which has far lower insolation due to shorter days and lower solar angles [Groeneveld *et al.*, 1986].

The PAR sensor was employed to determine the amount of light transmitted through *A. torreyi* leaves. Five leaves were removed from a shrub during early afternoon and placed across the PAR sensor positioned to point directly at the sun. The incident sunlight and the light transmitted through the leaves was recorded twice for each leaf through adaxial and abaxial surfaces. A ratio of the transmitted to the incident light yielded a value of 0.0544 (coefficient of variance was 10 percent), which was equivalent to the limiting light predicted for the inside edge of the leafed shell using Beer's Law. This strongly suggests that the light compensation point may be structured genetically to approximate the light transmitted through leaf tissue to avoid premature loss of leaf tissue due to temporary appression by overlying leaves during growth and development.

Recall that the average LAI at the 5 percent point of light attenuation was 1.67. This is two-thirds again the leaf-area index that would yield a 5 percent light compensation point by direct transmission vertically downward through the canopy. The additional leaf layering indicates that reflected light from all sides of the canopy may provide the extra illumination to fund the additional leaf layering. This factor was illustrated by moving the sensor around within the canopy but not pointed at the sun; significant light is introduced within the canopy by reflection even though the canopy was sufficiently thick to reduce or eliminate gaps between leaves. Such increased irradiance within the canopy interior is obviously aided by the reflective properties of the leaves themselves, since *Atriplex torreyi* leaves are oriented randomly, have complex curving shapes, and have a silvery covering of epidermal vesicles.

The leaves of the genus *Atriplex* are remarkable for their covering of vesiculated hairs that aid osmoregulation [Mozafar and Goodin, 1970], increase boundary-layer resistance to loss of water vapor [Black, 1954], and reduce midday radiation loads in environments with high insolation environments [Black, 1954; Mooney *et al..*, 1974]. The reflection of light to the canopy interior by the silvery vesicle surfaces may be an added benefit to *A. torreyi,* since the maintenance of a thicker leafed shell would confer greater production per given shrub surface area.

Summary

In open areas, mature canopies of *A. torreyi* resemble hemispherically leafed shells. In order to determine whether canopy shape is controlled by light, solar radiation was measured with a photocell sensitive to the photosynthetically active region of the spectrum. The sensor was used to evaluate both the light within the canopy and also the light transmitted by living leaves. Beer's Law, which describes the attenuation of light as it passes through a transparent medium, was found to apply to solar radiation within Nevada saltbush canopies. A light compensation point for leaf retention was inferred from mathematical calculations that compared the leaf-area index above the point of measurement to the percentage remaining of the incident solar radiation. This mathematically defined point indicates that canopy shape of Nevada saltbush is controlled by light.

The light transmitted through single leaves, measured as a percentage of incident light, was found to equal the light compensation point for leaf retention determined within the canopies. This relationship was then used to infer the relative importance of reflection (due to the shiny coating and complex orientation of leaves) to maintain light levels above the compensation point within the leafed shell of the canopy.

References

Addicott, F. T., *Abscission*, University of California Press, Berkeley. 369 pp., 1982.

Black, R. F., The leaf anatomy of Australian member of the genus *Atriplex, Australian Jour. Botany, 2,* 269-286, 1954.

Brown, R. J. and R. E. Blaser, Leaf area index and pasture growth, *Herbage Abstracts, 1,* 1-9, 1968.

Goodall, D. W., Some considerations in the use of point quadrats for the analysis of vegetation, *Australian Jour. Scientific Research, B 5,* 1-41, 1952.

Groeneveld, D. P., D. C. Warren, P. J. Hubbard, and I. S. Yamashita, Transpiration processes of shallow groundwater shrubs and grasses in the Owens Valley, California. Phase 1: Steady state conditions. Report prepared for the State of California Water Resources Control Board on Contract 3-081-225-0 and available through that agency. 130 pp., 1986.

Hall, H. M. and F. E. Clements, The phylogenetic method in taxonomy: The North American species of *Artemisia, Chrysothamnus* and *Atriplex, Carnegie Institute of Washington Publication, 325,* 473 pp., 1923.

Kovda, V. A., E. M. Samilova, J. L. Charley, and J. J. Skujins, Soil process in arid lands, in *Arid Land Ecosystems: Structure, Functioning and Management,* edited by D. W. Goodall and R. A. Perry, Cambridge University Press, New York, 177-192, 1979.

Mooney, H. A., O. Bjorkman, and J. H. Troughton, Seasonal changes in leaf characteristics of the desert shrub *Atriplex hymenelytra, Carnegie Institute of Washington Yearbook, 73,* 846-852, 1974.

Mozafar, A. and J. R. Goodin, Vesiculated hairs: a mechanism for salt tolerance in *Atriplex halimus* L., *Jour. Plant Physiology, 45*, 62-65, 1970.

Munz, P. A. and D. D. Keck, *A California Flora and Supplement*, University of California Press, Berkeley. 1681 pp. (Supplement 224 pp.), 1959.

Warren-Wilson, J., Estimation of foliage denseness and foliage angle by inclined point quadrats. *Australian Jour. Botany, 11*, 95-105, 1963.