

1991

Photosynthetic Efficiency of Drought-Induced Leaves in *Neviusia alabamensis*

Jennifer Martsolf

University of Central Arkansas

Robert D. Wright

University of Central Arkansas

Follow this and additional works at: <http://scholarworks.uark.edu/jaas>

 Part of the [Plant Biology Commons](#)

Recommended Citation

Martsolf, Jennifer and Wright, Robert D. (1991) "Photosynthetic Efficiency of Drought-Induced Leaves in *Neviusia alabamensis*," *Journal of the Arkansas Academy of Science*: Vol. 45 , Article 18.

Available at: <http://scholarworks.uark.edu/jaas/vol45/iss1/18>

This article is available for use under the Creative Commons license: Attribution-NoDerivatives 4.0 International (CC BY-ND 4.0). Users are able to read, download, copy, print, distribute, search, link to the full texts of these articles, or use them for any other lawful purpose, without asking prior permission from the publisher or the author.

This Article is brought to you for free and open access by ScholarWorks@UARK. It has been accepted for inclusion in Journal of the Arkansas Academy of Science by an authorized editor of ScholarWorks@UARK. For more information, please contact scholar@uark.edu.

PHOTOSYNTHETIC EFFICIENCY OF DROUGHT-INDUCED LEAVES IN *NEVIUSIA ALABAMENSIS*

JENNIFER MARTSOLF and ROBERT WRIGHT
Department of Biology, University of Central Arkansas
Conway, AR 72032

ABSTRACT

Plants in one stand of *Neviusia alabamensis* Gray (Rosaceae), a rare shrub, became drought deciduous in July, 1990, and grew new leaves following rains in August. In September the photosynthetic efficiency of the new leaves was compared with that of old leaves in another stand of the same population. Although leaf area from regrowth was much less than old leaf area retained, photosynthetic efficiency in new leaves was about 3 times higher than in old leaves. This response is discussed in terms of compensation for drought-induced loss of leaves.

INTRODUCTION

"*Neviusia alabamensis* Gray (Rosaceae) is a perennial shrub with numerous slender primary stems and short lateral branches. The bright green leaves are simple and alternating. The flowers are odorless and lack petals; however, the stamens are numerous (usually over 100) and showy, flowering may occur between March and May" (Long, 1983).

N. alabamensis is listed as an endangered species in Arkansas, Alabama and Missouri, and has only recently been discovered in Tennessee and Mississippi. The genus seems to be found only above stream banks in generally dry soils. It appears to be capable of reproducing only by root sprouts (Long, 1983).

The two sites at which this study took place are the east and west ends of the Conway County, Arkansas population. This population extends along a southeast-facing ridge above Cadron Creek between Conway and Menifee, Arkansas. The population is separated into two colonies by 100 meters of forest (Long, 1989). The plants at these two sites are possibly all one genet (Freiley, pers. comm.). There are only three other known populations in Arkansas.

Since *N. alabamensis* is mostly found in dry conditions, the strategies to deal with water stress must be an important part of the plant's ability to survive. In September 1990, plants in sites only 100 meters apart were observed to be in strikingly different condition following summer drought. Plants at the east Conway County site, site 1, retained the original leaves produced in spring while the plants at the west Conway County site, site 2, had dropped most of these mature leaves and, following several weeks of rain, had grown new leaves.

Plants growing in different environments have leaves of characteristic sizes and shapes. According to Townsend and Solbrig (1980), for example, tree leaves in the temperate zone are normally of moderate size with toothed or serrated margins; evergreen plants from warm semidesert regions have smaller leaves, sub-canopy tropical trees have very large leaves with entire margins and pointed apices; and many trees in tropical and subtropical savannas have compound leaves. Even on the same tree, leaves exposed to the sun tend to be smaller than those in the shade.

Leaves are the main biochemical factories of the plant, intercepting light and transforming that energy to fix CO₂ and synthesize sugars. The leaf needs adequate light, ample raw materials, plenty of water, and appropriate temperatures to function effectively. Securing these conditions presents difficulties to the plant, considering, among other things, that for every molecule of CO₂ that is fixed, anywhere from 300 to 1000 molecules of H₂O vapor are lost. The adaptive problem the plant faces is how to maintain adequate water and nutrients while maximizing net photosynthesis (Townsend and Solbrig, 1980).

Plant species can maintain physiological activity during periods of drought through a variety of mechanisms. These mechanisms can be grouped as avoidance or tolerance of drought. One avoidance strategy, conversion to a dormant phase, becomes more important as environmental moisture stress becomes increasingly severe (Chabot and Bunce, 1979).

"Plants grow by the progressive accumulation of repeated elements: leaves, buds, internodes, branches, and flowers" (Maillette, 1985), which together contribute to the particular shape of a plant. In most plants the number of elements is not fixed; it changes with time because of growth

and senescence processes. Changes in the number of parts can be caused by demographic events, births, and deaths; plants can be viewed as a population of parts. Because leaves photosynthesize, their demography is of special interest. (Maillette, 1985).

N. alabamensis at sites 1 and 2 responded to drought conditions in two different manners, which were retention, and drop followed by regrowth. Research has shown that the rate of photosynthesis per unit of leaf area typically increases after leaf emergence, reaches an optimum at about the time of full leaf expansion, and then declines (Yamaguchi and Friend, 1979; Catzky and Ticha, 1980; Constable and Rawson, 1980; Bongi *et al.*, 1987; and Nilsen, *et al.*, 1988). This investigation of the effect of leaf age on photosynthesis was designed to consider the strategies of retaining leaves or dropping leaves in *N. alabamensis*.

MATERIALS AND METHODS

Using a portable photosynthesis system, four of the variables used in this report were measured in intact leaves at each site, in September, 1990. At site 1, most plants retained original leaves produced in the spring which had survived the summer drought. For analysis, 130 mature leaves were randomly selected and placed in the chamber of a LI-COR portable photosynthesis system (LI-COR, Inc., Lincoln, NE). After the unit calculated the rates or amounts of net photosynthesis, light intensity, leaf temperature, and CO₂ flow, the leaf was harvested. Each leaf was then traced onto tracing paper and the resulting leaf copy cut out, weighed, and compared to the weight of a known area of tracing paper to determine leaf area in square centimeters. Leaf area data produced the fifth variable considered in this study and were entered into the instrument's computer to produce corrected values of the five (Table 1) variables for each leaf.

Table 1. Analysis of Variance for hypothesis of no overall site effect.

Variable	Site	Mean	Standard Deviation
photosynthesis	1	2.52	1.16**
	2	7.19	3.20**
light intensity	1	731.92	67.08**
	2	337.06	232.16**
leaf temperature	1	29.94	6.39 n.s.
	2	28.60	1.30 n.s.
CO ₂ flow	1	357.01	17.38
	2	381.97	20.83
Leaf area	1	12.50	13.77**
	2	4.70	1.27**

Site 1 = Conway East, 130 leaf observations, mature leaves

Site 2 = Conway West, 33 leaf observations, new leaves

** - highly significant, $P < .001$

n.s. - not significant

Photosynthetic Efficiency of Drought-Induced Leaves in *Neviusia alabamensis*

At site 2, the *N. alabamensis* plants held virtually no original leaves. Within three days of the site 1 analysis, 33 leaves at site 2 were analyzed in the same manner. These leaves were replacements of those abscised during summer drought.

RESULTS

Multivariate analysis of variance (MANOVA) for the hypothesis of no overall site effect revealed a significant difference, ($P < .0001$), between the two sites. Table 1 displays a univariate analysis for the hypothesis of no overall site effect for each variable. The probabilities exhibit significant difference, ($P < .01$), between the two sites for all variables except leaf temperature.

Table 2 displays a stepwise discriminant analysis summary which shows a highly significant difference for three of the five variables, ($P < .001$), and a significant difference for the other two variables, ($P < .05$). This stepwise analysis was performed in order to determine the rank of each variable in terms of predominance. Photosynthesis is shown to explain 54% of the variance between site 1 and 2. Leaf area and light intensity at the time of analysis each account for about 20% of variance between sites. Carbon dioxide and leaf temperature account for little of the variance.

Table 2. Stepwise Discriminant Analysis Summary.

Step	Variable	R ²
1	photosynthesis	.54**
2	leaf area	.205**
3	light intensity	.195**
4	CO ₂ flow	.04*
5	leaf temperature	.02*

** - $P < .01$

* - $P < .05$

DISCUSSION

Net photosynthetic rate for the young leaves at site 2 is significantly higher than the net rate at site 1 which is composed of plants with mature leaves. The light during the times of data collection was different, being more intense when measurements were taken at site 1, so the efficiency of photosynthesis in new leaves was accomplished even at significantly lower levels of irradiance. This higher efficiency is probably a factor of the leaf age. Catzky and Ticha (1980) and Constable and Rawson (1980) found net photosynthesis rates to be low in young, unfolding leaves, increasing rapidly as leaves expanded and gradually declining thereafter, reaching low values at senescence. Pasian and Lieth (1989) found no clear pattern in photosynthetic efficiency associated with leaf age, possibly because the study they conducted examined leaves of 10, 20, 30 and 40 days of age. Their study suggested that 10-day-old rose leaves have an almost completely developed photosynthetic mechanism, while senescence does not begin until rose leaves are older than 40 days. According to Bong (1987), the effect of leaf age on apparent photosynthesis was shown graphically to increase the first 6 months and remain at a level plateau for about 12 months, declining the last 6 months prior to senescence, in olive leaves.

In *Flaveria trinervia*, a C₄ dicot, photosynthesis was found to vary considerably during leaf expansion. In partially expanded leaves (20% of full size), 10-12% of atmospheric CO₂ is assimilated directly by the C₃ pathway while with further leaf expansion, this bypass of the C₄ cycle decreases until the C₄ cycle is fully operational at leaf maturity (Moore and Edwards, 1988).

Bunce (1989) attempted to explain the response of growth rate per unit of ground area, by creating a leaf area index. He found crop growth to show

two patterns as leaf area index increases with growth. Growth rate either increased up to a plateau as more light was intercepted or decreased above an optimum leaf area index.

Nilsen *et al.* (1988) studied the changes that occur in leaf structure, such as aging of chloroplasts, which eventually causes a decrease in photosynthetic efficiency at some point after leaf maturity. He studied *Rhododendron maximum* L. which is a short flush species producing one cohort of leaves each year so that demographic patterns would be readily identifiable and differences between same age leaves would not be due to growth at different times in the season. They found that photosynthesis rates decreased with increasing leaf age, and decreased more rapidly in light saturated than in low light environments.

Photosynthetic rates of early and late leaves of honey mesquite were measured, exhibiting daily maximum photosynthetic rates of early leaves to be significantly greater than those of late leaves. The higher rates of early leaves were associated with higher nitrogen content per unit leaf area and a thicker leaf blade. (Wan and Sosebee, 1990).

Suzuki *et al.* (1987) suggested the influence of leaf age on photosynthesis rate was due to associated changes with the capacity of the photosynthesis cycle through control of a number of enzyme levels. He did, however, find similar leaf age patterns, reporting, "The rate of photosynthesis per unit area in the third leaf of wheat plants reached a maximum on the seventh day after leaf emergence and then declined to 1/3 of the maximum after 22 days."

For all leaf ages of *Rosa Hybrida* L. ev. *Samantha*, Bozarth *et al.* (1982) found maximum photosynthetic rates were reached at irradiance levels of 450-500 microeinsteins⁻² sec⁻¹. These rates were highest in the youngest leaves studied and lowest in the oldest. Photorespiration was shown not to be a major factor in this trend.

Tschaplinski *et al.* (1989) studied the physiological basis of reinvigoration after shoot decapitation. "Reinvigoration refers to the renewed vigor of growth and net photosynthesis following decapitation. Defoliation and shoot decapitation are known to increase net photosynthetic rates in the remaining leaves of tree and crop species." Waring *et al.* (1968) and Meidner (1969) also found that an increase in net photosynthesis usually occurs three to four days following shoot decapitation. Partial defoliation which results in an enhancement of photosynthetic rates in the remaining leaves may also occur in rose (Mor and Halevy, 1979). These studies suggest that not only is *N. alabamensis* displaying typical leaf age photosynthetic efficiencies, but it may also be displaying post defoliation reinvigoration.

Most of the studies charting a rise, plateau, and decline in photosynthetic efficiency of leaves as they age are dealing with senescence due to leaf age. Water deficit is also a cause of decline. Vu and Yelenosky (1988) found that water deficit reduced the photosynthetic CO₂ assimilation rate as well as the carboxylation reaction, and the soluble protein content in leaves of citrus trees. Aikin and Hanan (1975) found the net photosynthesis rate in "Forever Yours" rose to increase for the first 8-36 days, and decrease until the leaf is 40-68 days, when the leaf drops. However, internal plant water potential influenced the CO₂ uptake by reducing it at each increase of radiation energy, resulting in lower net photosynthesis with lower water potential.

Therefore it seems that at a certain minimum water potential, *N. alabamensis* plants at site 2 dropped their leaves. When rain brought more water in early fall, the plants were able to sprout new leaves, which exhibited the high photosynthetic efficiency characteristic of their young age as well as reinvigoration following defoliation.

If the population of *N. alabamensis* is a single genet, the differences exhibited in leaf holding may be due to differing soil water holding capacities between sites. Also, it would be interesting to observe over time if the same two strategies of holding versus dropping leaves are predictable after a dry summer and how this affects rate of growth as evidenced by plant biomass between the two sites.

Further study is necessary to make any conclusions as to the long term success of reinvigoration of leaves as a strategy to cope with water stress, in terms of net cost/benefits to the plant. However, regrowth of photosynthetically efficient leaves does extend the growing season for *Neviusia alabamensis*.

ACKNOWLEDGMENT

The authors would like to thank Mr. and Mrs. Alan Stallings for providing safe harbor for the Conway County population of *Neviusia alabamensis*.

LITERATURE CITED

- AIKIN, WARREN J. and JOE J. HANAN. 1975. Photosynthesis in the rose; effect of light intensity, water potential and leaf age. *J. Amer. Soc. Hort. Sci.* 100(5):551-553.
- BONGI, G., M. MENCUCCINI, and G. FONTANAZZA. 1987. Photosynthesis of olive leaves; effect of light flux density, leaf age, temperature, petioles, and H₂O vapor pressure deficit on gas exchange. *J. Amer. Soc. Hort. Sci.* 112(1):143-148.
- BOZARTH, CONNIE S., ROBERT A. KENNEDY, and KURT A. SCHEKEL. 1982. The effects of leaf age on photosynthesis in rose. *J. American Soc. Hort. Sci.* 107(5):707-712.
- BUNCE, JAMES A. 1989. Growth rate, photosynthesis and respiration in relation to leaf area index. *Annals of Botany*. 63:459-463.
- CATZKY, J. and I. TICHA. 1980. Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. *Photosynthetica*. 14:392-400.
- CHABOT, BRIAN F. and JAMES A. BUNCE. 1979. Drought-Stress Effects on Leaf Carbon Balance. *Topics in Plant Biology* (O. Solbrig, S. Jain, G. Johnson, and P. Raven, eds.). Columbia, University Press. N.Y. pp. 338-342.
- CONSTABLE, G.A. and H.M. RAWSON. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. *Austral. J. Plant Physiol.* 7:89-100.
- LONG, ALICE. A. 1983. *Neviusia alabamensis*: A phytogeographic analysis. *Arkansas Academy of Science Proceedings*. 37:94-96.
- LONG, ALICE. A. 1989. Disjunct populations of the rare shrub *Neviusia alabamensis* Gray. (Rosaceae). *Castanea*. 54(1):29-39.
- MAILLETTE, LUCIE. 1985. Modular demography and growth patterns of two annual weeds (*Chenopodium album* L. and *Spergula arvensis* L.). In *Relation to flowering. Studies on Plant Demography*. (James White, ed.) Academic Press. London. pp. 239-252.
- MEIDNER, H. 1969. Rate limiting resistances and photosynthesis. *Nature* 222:876-877.
- MOORE, BRANDON D. and GERALD E. EDWARDS. 1988. *Plant Physiology*. 88:125-130.
- MOR, Y. and A.H. HALEVY. 1979. Translocation of c-assimilates in roses. The effect of age of the shoot and location of the source leaf. *Physiol. Plant.* 45:177-182.
- NILSEN, E.T., D.A. STETLER and C.A. GUSSMAN. 1988. Influence of age and microclimate on the photo-chemistry of *Rhododendron maximum* leaves on chloroplast structure and photosynthetic light response. *Amer. J. Bot.* 75(10):1526-1534.
- PASIAN, C.C. and J.H. LIETH. 1989. Analysis of the response of net photosynthesis of rose leaves of varying ages to photosynthetically active radiation and temperature. *J. American Soc. Hort. Sci.* 114(4):581-586.
- SUZUKI, SHIGETOSHI, HITOSHI KU NAKAMOTO, S.B. MAURICE, and GERALD E. EDWARDS. 1987. Influence of leaf age on photosynthesis, enzyme activity, and metabolite levels in wheat. *Plant Physiology*. 84:1244-1248.
- TOWNSEND, COLIN R. and OTTO T. SOLBRIG. 1980. Energy, information and plant evolution. *Physiological Ecology, An Evolutionary Approach to Resource use*. Sinauer Associates, Sunderland, Massachusetts.
- TSCHAPLINSKI, TIMOTHY J. and TERENCE J. BLAKE. 1989. Photosynthetic reinvigoration of leaves following shoot decapitation and accelerated growth of coppice shoots. *Physiologia Plantarum*. 75:157-165.
- VU, JOSEPH C.V. and GEORGE YELENOSKY. 1988. Water deficit and associated changes in some photosynthetic parameters in leaves of "Valencia" orange. *Plant Physiology*. 88:375-378.
- WAN, CHANGGUI and RONALD E. SOSEBEE. 1990. Characteristics of photosynthesis and conductance in early and late leaves of honey mesquite. *Botanical Gazette*. 151(1):14-20.
- WAREING, P.F., M.M. KHALIFA, and K.J. TREHARNE. 1968. Rate limiting processes in photosynthesis at saturating light intensities. *Nature*. 220:453-457.
- YAMAGUCHI, T. and D.J.C. FRIEND. 1979. Effect of leaf age and irradiance on photosynthesis of *Coffea arabica*. *Photosynthetica*. 13(3):271-278.