WATER RELATIONS OF WHITE ALDER[1]

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Abstract: White alder (Alnus rhombifolia) *is a potentially valuable indicator of water stress along California's waterways. Measurements of stomatal conductance, water potential and tissue water relations in conjunction with growth and morphological studies give evidence for the sensitivity of this species to changes in water availability. Potted seedlings and naturally occurring seedlings and trees were monitored during the 1986 and 1987 growing seasons to determine responses to artificial and natural water regimes. Osmotic adjustment provides a mechanism for drought hardening, but the process is less effective in preventing stress in seedlings than trees. Measurements of leaf area and mean instantaneous conductance were sensitive indicators of alder water status. These two parameters should be included in any physiological monitoring programs of white alder.*

White alder (*Alnus rhombifolia Nutt.*) *is* a dominant riparian tree along the western slope of the Sierra Nevada and in portions of the south coast ranges. It occurs at sea level in the Sacramento-San Joaquin Delta and at scattered locations in the Mojave desert. Its northern distribution extends into Canada and eastward to Idaho. Within California, white alder is restricted primarily to perennial watercourses (Griffin and Critchfield 1972). This habitat specificity makes white alder a potentially valuable indicator of water stress within many riparian communities. The purpose of this study is to provide a physiological framework for this key riparian species that will aid in the understanding of ecological processes along California's streams.

The effects of water stress on plants have been well documented. Initially, a plant may respond with conservative stomatal behavior, but continued water deficits can lead to permanent changes such as reduction in leaf size, the number or size of stomata, or an increased density of leaf hairs (Daubenmire 1974; Ehleringer 1984; Hsiao 1973; Levitt 1980). Flower and fruit production of stressed plants may be reduced or abandoned (Hinckley and others 1979). Seedlings may be more sensitive to water stress than mature plants (Kramer 1983). Riparian plants have not been the subject of extensive physiological studies. In a compilation of flooding and drought tolerances of wetland plants (Walters and others 1980), white alder is indicated as very tolerant of flooding, but there is no indication of the plant's tolerance to drought.

Methods

Study Populations

In 1986, 120 alder seedlings were grown under controlled watering regimes to induce drought stress. The experimental treatments were based on a dry-down trial where the condition of five seedlings was monitored over a 10-day period without watering. Moderate stress (stomatal closure, loss of turgor) appeared after 5 days and severe stress (loss of leaves, die-back) occurred after 10 days of no water. A control group was watered every day and showed no signs of stress. During the experiment, water was applied automatically according to 1-, 5-, or 10-day schedules. Seedlings were grown outside in Sacramento County and exposed to full sun from dawn to 1900. The experiment was terminated after 80 days by rainfall in September.

During the summer of 1987, 31 white alder seedlings were tagged along a gravel bar approximately 500 m downstream from Camanche Dam on the Mokelumne River within Van Assen Park, San Joaquin County, California. Seedlings were selected to represent the range of environmental settings being colonized by white alder. The seedlings were exposed to full sun from dawn until at least 1600. Water relations of white alder trees were studied at two locations along the lower American River in Sacramento County, California. Twelve (12) trees were selected from stands on coarse alluvium at the upstream end of Sailor Bar, approximately 1 km downstream from Nimbus Dam. Three (3) additional individuals were located on a silty terrace across from the Gristmill Access Area about 18 km downstream. Trees were selected to represent the wide range of leaf and canopy morphologies present along the river. Canopies of the selected trees were exposed to full sun from dawn until 1600 or later during physiological sampling. All of the study sites occur between 10 and 70 meters in elevation.

Physiological Measurements

Diurnal patterns of stomatal conductance were measured using a transient porometer (Model LI-700, LI-COR, Lincoln, Nebraska). Conductance curves for 60

[1]Presented at the California Riparian Systems Conference; September 22-24, 1988; Davis, California

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experimental seedlings (20 plants in each of the three treatment groups) were recorded on initiation of the treatments (days 2-9), mid-way through the experiment (days 36-45), and at the end of the experiment (day 67 and days 69-72). Stomatal conductance curves for Mokelumne River seedlings were recorded on 29 and 30 August, and 30 September. For trees at Sailor bar, diurnal patterns of stomatal conductance were sampled five times over the months of June, July and August. Trees at Gristmill were sampled once in August.

A pressure chamber (PMS Instruments, Corvallis, Oregon) was used to estimate plant water potential. Pre-dawn measurements of three randomly selected seedlings in each treatment group were made once mid-way through the pot study. The diurnal course of water potential in Mokelumne River seedlings was recorded once during July. Diurnal water potential curves were recorded from trees at Sailor Bar in June and August, and pre-dawn and mid-day readings were recorded from these trees in July. Diurnal curves were recorded from trees at Gristmill in August.

The tissue water relations of white alder were examined using a pressure chamber and the pressure-volume (P-V) curve technique (Tyree and Hammel 1972). The plants chosen for this analysis included 3 control group and 3 stressed seedlings from the pot experiment, 5 randomly selected seedlings from the Mokelumne River field site, 11 of the 12 trees at Sailor Bar, and 2 of the 3 trees at Gristmill. In all, 24 individuals were sampled during September of 1986 or 1987, and 106 P-V curves were generated and analyzed. One of the plants failed to produce usable data due to mishandling of the samples.

In this analysis of P-V curve parameters, the osmotic line was laid by hand. Most plots contained 12 observations with 5 to 8 points falling on the osmotic line. The turgor loss point was calculated using the ratio technique reported by Schulte and Hinckley (1985). The osmotic potential at full turgor and the apoplastic fraction were estimated by a least squares regression of points falling along the osmotic line (Robichaux and others 1984). The bulk moduli of elasticity were calculated as a function of the slope of the P-V curve at full hydration (Stemmerman 1983).

Morphology and Growth

The effects of drought stress on morphology and growth of white alder were examined through measurement of leaf area, leaf shape index, leaf curling index, stomatal and hair densities, and an index of canopy coverage. Changes in the reproductive output of trees and root-to-shoot ratios of seedlings also were examined for responses to water stress.

Results

Stomatal Conductance

Experimentally stressed seedlings showed reduced stomatal conductance by the fourth day of the pot study. Highly significant differences were detected in mean stomatal conductance at the close of the experiment (where df is 2, F is 1,920, and P=.0). Less frequently watered plants endured the greatest degree of stomatal closure (table 1). As the experiment progressed, there was a decrease in the recovery of stressed plants upon watering. Individual responses to the treatments were more varied in stressed plants than in the control group. Control group seedlings had decreased conductance at the end of the experiment when they had become root-bound in the 1-gallon pots. The Mokelumne River seedlings were most similar to the control group of experimental seedlings and had the highest mean instantaneous conductances of all the white alders studied. Maximum conductance values for white alder of 0.400 mol/m2/sec were recorded from control group seedlings.

Table 1 - Stomatal conductance and water potential of white alder seedlings and trees.

	Conductance[1]	Water Potential[1,2]	
		Pre-dawn	Mid-day
Seedlings:			
severe stress	.095± .008	-0.90	-
moderate stress	.181±.006	-0.40	-
control	.244±.003	-0.20	-
Mokelumne R.	.261±.003	-0.05	-0.75
Trees:			
(severe stress)			
GM-1	0.41±.005	-1.25	-1.50
GM-2	.050±.005	-0.45	-1.23
GM-3	.070±.012	-1.25	-1.40
SB-12	.134±.007	-0.20	-1.18
SB-6	.142±.009	-0.20	-1.53
SB-2	.143±.003	-0.20	-1.54
(moderate stress)			
SB-1	.173±.009	-0.20	-1.66
SB-4	.184±.011	-0.15	-1.80
SR-11	.204±.008	-0.20	-1.63
SB-3	.209±.011	-0.15	-1.75
(unstressed)			
SB-8	.214±.010	-0.20	-1.75
SB-5	.222±.011	-0.15	-1.80
SB-10	.230±.012	-0.25	-1.61
SB-7	.244±.011	-0.15	-1.43
SB-9	.251±.010	-0.10	-1.61

[1]Mean instantaneous conductance (mol/m2/sec) of sunlit eaves and standard errors.
[2]Mean maximum and minimum water potentials (MPa)

Field investigations of the stomatal conductance of trees revealed a similar range of response. Arbitrary condition classes were assigned to individual trees based on their mean instantaneous conductance. The designations of severe, moderate, or unstressed condition correspond to treatment classes of the seedling experiment. Trees with mean instantaneous conductances less than 0.150 mol/m2/sec suffered severe water stress.

Water Potential

Pre-dawn water potentials of stressed and unstressed plants differed by as much as 1.2 megapascals (MPa; 1 MPa = 10 bars). Mokelumne River seedlings had pre-dawn potentials of -0.05 MPa while severely stressed trees at Gristmill had predawn potentials of -1.25 MPa. Most trees were at or near full hydration. Observations of stressed trees indicate that water deficits may occur at pre-dawn potentials as high as -0.3 MPa. In general, pre-dawn potentials were poor indicators of plant water status.

Mid-day minimum potentials were lowest for moderately stressed and unstressed trees (-2.0 MPa). Severely stressed trees had mid-day potentials that were as much as 0.5 MPa greater (-1.5 MPa). Field seedlings had the highest mid-day potentials (0.75 MPa). A rise in mid-day water potentials of 0.2 MPa from June to August was recorded from 6 trees at Sailor Bar.

Tissue Water Relations

Osmotic potential at full turgor and water potential at the turgor loss point were the two parameters of alder tissue water relations most indicative of plant water status (table 2). Mokelumne River seedlings had the highest osmotic potential and turgor loss points of all plants studied. Seedlings in general had higher osmotic potentials and turgor loss points than reproductively mature trees (fig. 1). The osmotic potential of a non-reproductive sapling (SB-9) was intermediate between seedlings and trees. The range of osmotic adjustment due to water stress was similar for seedlings and trees (0.19 MPa and 0.18 MPa, respectively).

With lower osmotic potentials, turgor loss occurs at lower water potentials. Comparison of estimated turgor loss points and field measurements of water potential indicate that water stressed alders maintain high turgor pressure, while unstressed plants reach water potentials close to or even exceeding their turgor loss points during the day. The stomata of unstressed plants are responsive to changes in plant water potential and may close and open during the day in response to slight turgor changes; this responsiveness is diminished in stressed plants (Hsiao 1973).

Other components of tissue water relations showed little or no pattern in response to drought stress. Relative water content at turgor loss was high for all plants sampled. The apoplastic fraction was variable and did not correspond to other drought-induced responses. The range of tissue elasticity was less than 10 MPa. Differences greater than this have been considered as a genetically determined drought adaptation (Stemmerman 1983).

Morphology and Growth

The experimental treatments resulted in substantial differences in mean leaf area (table 1). At the end of the experiment, 17 of the 40 severely stressed seedlings were dead. Only 1 of the 40 moderately stressed seedlings died. All plants in the control group survived. Severely stressed seedlings lost their water-expensive leaves and replaced them with small sparse canopies (fig. 2). Moderately stressed seedlings were able to maintain their existing canopies but showed little growth. Seedlings in the control group experienced rapid growth and increased their canopy areas by as much as 2.4 percent per day.

End-of-the-season leaf morphology of Mokelumne River seedlings was intermediate between the moderately stressed and control groups of the pot study. The growth rates of these naturally occurring plants were less than would be expected from their consistently high stomatal conductance. Herbivory, competition, low nutrient availability, and shorter effective day length may account for their reduced performance.

Other morphological responses to water stress included a 15 percent reduction in the density of stomata on the abaxial surface (bottom) of stressed leaves and an increased root-to-shoot ratio in seedlings. No difference was detected in the density of leaf pubescence in relation to water status.

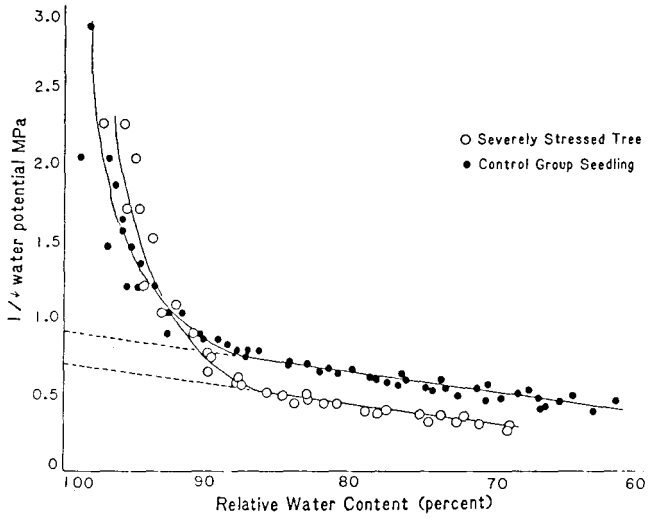

Figure 1– Pressure-volume curves for a control group seedling (closed circle) and severely stressed tree (open circle). The osmotic potential at full turgor is indicated by an extension of the curve's linear portion toward the Y axis (dashed lines). The tree has a more negative osmotic potential and is more resistant to water stress.

Table 2 - Tissue water relations of white alder seedlings and trees.

	Os^{1}_{FT}	WP^{2}_{TLP}	RWC^{3}_{TLP}	AF^{4}_{FT}	E^{5}
Seedlings:					
severe stress-1	-1.14 ±.04	-1.41 ±.06	.83±.02	.21±.02	1.84±.63
severe stress-2	-1.31 ±.01	-1.66 ±.03	.84±.01	.29±.03	4.78±.79
moderate stress	-1 .27±.05	-1 .61±.03	.78±.02	.13±.03	6.65±.76
control-1	-1.20 ±.02	-1.56 ±.03	.86±.01	.37±.04	4.75±.65
control-2	-1 .16±.02	-1 .44± .01	.85±.01	.43±.11	4.94±.79
control-3	-1.12 ±.02	-1.40 ±.04	.87±.01	.37±.03	5.48±.73
Mokelumne R.[6]	-0.26 ±.17	-0.81 ±.23	.88±.04	.19±.05	5.66±.45
Trees:					
(severe stress)					
GM-1	-1.42±.08	-1.88±.06	.80±.02	.13±.06	4.18±1.64
GM-2	-	-	-	-	-
GM-3	-1.30[7]	-1.70	.86	.51	3.19
SB-12	-	-	-	-	-
SB-6	-1.56±.04	-2.13±.86	.86±.001	.47±.02	4.50±.58
SB-2	-1.70±.11	-2.32±1.5	.82±.02	.41±.03	5.61±1.13
(moderate stress)					
SB-1	-1.55±.07	-2.08±.08	.83±.02	.28±.05	7.45±.09
SB-4	-1.45±.05	-1.92±.05	.89±.02	.38±.05	4.58±.45
SB-11	-1.35±.04	-1.80±.04	.86±.01	.41±.03	5.29±.74
SB-3	-1.57±.07	-1.96±.08	.84±.03	.29±.03	6.49±.47
(unstressed)					
SB-8	-1.59±.03	-1.95±.04	.90±.01	.39±.04	6.81±.73
SB-5	-1.54±.05	-1.98±.06	.86±.04	.50±.06	4.00±.86
SB-10	-	-	-	-	-
SB-7	-1.52±.12	-1.15±.04	.81±.02	.29±.04	3.95±.99
SB-9	-1.17±.02	-1.52±.04	.86±.01	.38±.04	4.07±.44

[1] Osmotic potential at full turgor (MPa)
[2] Water potential at turgor loss (MPa)
[3] Relative water content at turgor loss
[4] Apoplastic fraction at full turgor
[5] Bulk modulus of elasticity (MPa)
[6] Data are pooled from 6 individual seedlings
[7] 1 reading

Differences in the 3 arbitrary condition classes of trees could be detected by the mean leaf area of 60 randomly selected leaves with southern exposures (df=2, F=339, P=0; Shefe' post-hoc P=.05). Change in leaf shape, curling index, and canopy coverage could be detected in the severely stressed trees. Similarly, flower and seed production was altered by severe water stress. With exception of the severely stressed trees at Gristmill, stressed alders produced more flowers and fruit in relation to their respective leaf canopies than unstressd alders. The trees at Gristmill produced only a few small cones each. The relative germinability of seeds from stressed or unstressed trees was not tested.

Osmotic adjustment, or the accumulation of solutes in tissue, is most responsible for drought hardening in white alder (fig. 3). Lower osmotic potentials allow a plant to maintain favorable water status under drier conditions. The range of osmotic potentials was similar for seedlings and trees (table 2). However, the lower limit of osmotic adjustment is less for seedlings than for trees. When a plant's capacity for osmotic adjustment is reached, water stress occurs and results in reduced responsiveness of stomata, loss of leaves, cessation of flower and seed production, and an eventual increase in osmotic potentials.

Discussion

The lowered conductances and reduced leaf areas observed under moderate water stress did not threaten the lives of mature alders. Neither maintenance of a full canopy nor flower and fruit production were harmed by moderate water stress. In seedlings, moderate stress may endanger a plant's chance for establishment. Since leaves are photosynthetic organs, reduced leaf area reduces growth potential. As a colonizing species, alder depends on rapid growth to secure space, resources, and the firm anchorage necessary for successful establishment in the riparian zone.

Some water stressed alders in this study grew in close association with running water. White alder is shallow rooted and disruption of the roots can occur during floods. Field study along the lower American River took place the year after severe flooding in spring of 1986. Trees with an unbalanced canopy-to-root ratio could be subject to water stress. Large or rapid variations in streamflow during the growing season, particularly out-of-season flooding, may also lead to stress in white alder. A change of river stage of 12 inches in July of 1987 drowned hundreds of alder seedlings along the lower American River. While flooding, channel migration, downcutting and lowered water tables are natural consequences of life in the floodway, these same processes may lead to water stress in riparian plants.

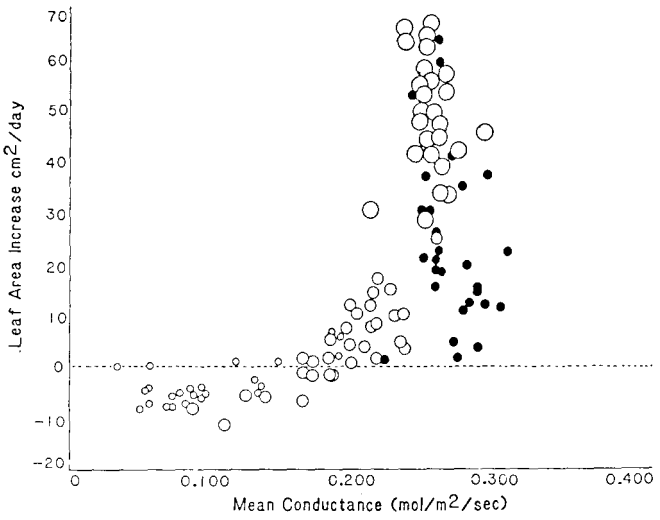

Figure 2— Growth in leaf area of white alder seedlings in relation to mean instantaneous conductance. Small, medium and large circles represent severely stressed, moderately stressed, and control group seedlings, respectively. Mokelumne River seedlings (black dots) had high conductances and a wide range of growth responses.

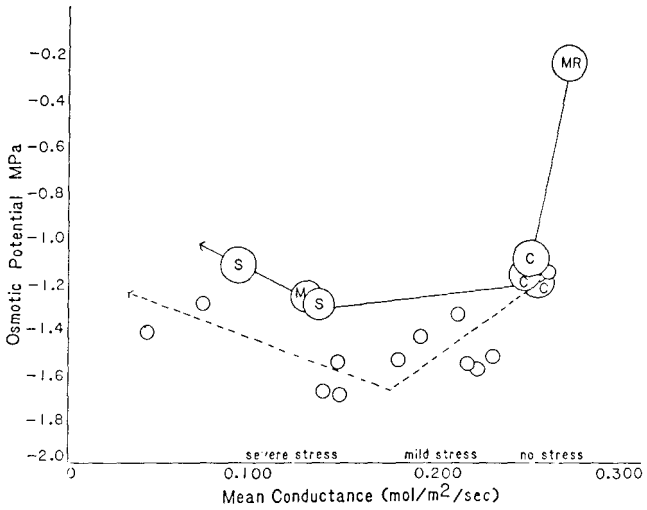

Figure 3— Drought hardening and water stress in alder seedlings and trees. The extent of osmotic adjustment for alder seedlings(large lettered circles: MR=Mokelumne River, C=control group, M=moderate stress, S=severe stress) is less than for trees (small circles).

The water relations of alder and other streamside plants need consideration as active agents in shaping riparian communities. Documentation of species differences in water relations parameters and rooting strategies will prove useful in understanding and managing riparian resources. In addition, effective monitoring of physiological condition requires knowledge of a species' limits and potentials under a variety of environmental settings. While the critical values detailed in this study may differ in other populations, reliable indications of white alder water status were obtained through measurements of mean instantaneous conductance and mean leaf area. Physiological monitoring programs involving white alder should include these two parameters.

Acknowledgements

I thank Dean Taylor for the generous loan of a transient porometer, Maryann Griggs and Shannon Fairres for their help with field sampling and Marda West and Bob Holland for their advice and comments on the manuscript. This study was supported in part by funding for graduate student research at California State University, Sacramento.

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