Influence of an environmental gradient on physiology of singleleaf pinyon

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Abstract

The acquisition of water and regulation of its loss are important to plant 'success' in arid environments. Species existing over a range of environmental conditions should respond physiologically to varying conditions to maximize water use efficiency and avoid low tissue water potentials. Seasonal and diurnal ecophysiological responses of singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) were investigated along an environmental gradient involving elevation, moisture and temperature in Nevada. The gradient was represented by study sites in black sagebrush (*Artemisia nova* A. Nels), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* Nutt.), and mountain mahogany (*Cercocarpus ledifolius* Nutt.) communities. Xylem pressure potential, conductance, and transpiration were measured over 2 growing seasons. Xylem pressure potential and leaf conductance ranged from -3.0 to -0.7 MPa and 0.01 to 0.43 cm s⁻¹, respectively, during the study. Carbon isotope discrimination (Δ) of needles was determined in August 1990. Differences in Δ values were not significant between sites at the lowest and highest elevations but were significant between the driest site (black sage) and the relatively wetter site (mountain mahogany). Leaf conductance was influenced by but not strongly correlated with predawn xylem pressure potentials, relative humidity, and temperature. Generally, there was little difference in water use characteristics of singleleaf pinyon along the environmental gradient in this study. Thus, it appears that singleleaf pinyon's ability to exist over a range of environmental conditions is not a function of variable ecophysiological responses but an opportunistic response to the availability of resources and conditions suitable for growth to occur.

Key Words: carbon isotope discrimination, elevation, leaf conductance, transpiration, *Pinus monophylla*, xylem pressure potential

Adaptations which enable plants to exploit limited soil water in

space and time, while simultaneously minimizing water loss and maximizing growth, are important in arid environments (DeLucia et al. 1989). Singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) is found throughout the semi-arid portion of the Central Great Basin and has greatly expanded its range within the last 100 years (West et al. 1975). Its range extends from the hot, xeric black sagebrush (*Artemisia nova* A. Nels) zone in the lower elevation foothills and slopes to the cooler, more mesic mountain mahogany (*Cercocarpus ledifolius* Nutt.) zone at higher elevations just below the coniferous forest (Cronquist et al. 1972, Eddleman and Jaendl 1994). We investigated singleleaf pinyon's ecophysiological response to environmental changes in conditions at different sites to help understanding its success and expansion over the wide array of environmental conditions in which it is found.

Differences in resource-use efficiency and drought tolerance exist between species of different growth forms in the western Great Basin (DeLucia et al. 1988, DeLucia and Heckathorn 1989, DeLucia and Schlesinger 1991). Among pines, differences in needle morphology have been suggested as adaptations to water stress (Haller 1965, Neilson 1987, Tausch and West 1987). Within a species, recent investigations suggest that water-use efficiency, as indicated by $\delta^{13}\text{C}$ values, varies with altitude (Korner et al. 1988, Vitousek et al. 1988). These findings raise the possibility that a single highly competitive species growing over a wide range of environmental conditions may respond to environmental variation through changes in both morphological and physiological characteristics.

Previous studies have investigated patterns of growth and water relations in singleleaf pinyon (Drivas and Everett 1987, Tausch and West 1987, DeLucia et al. 1988, DeLucia and Schlesinger 1991), but its response over a range of environmental conditions has not been reported. During 2 growing seasons, we assessed plant water relations and growth of singleleaf pinyon along an elevational and moisture gradient on a mountain range in east-central Nevada. We hypothesized that singleleaf pinyon would respond to changes in environmental conditions through variations in stomatal control, as measured by transpiration and conductance, and a decline in growth in relation to drier environmental conditions.

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Materials and Methods

Site Description

Data were gathered from June 1989 through September 1990 at Great Basin National Park on the east slope of the South Snake Range (39°00' N, 114°14' W) in Nevada, USA. Climate in this area is influenced by winter storms which originate in the Pacific and by "Arizona Monsoon" storms in the summer (James 1988). The eastern slopes lie in the rain shadow of the South Snake Range in winter, but are situated in a more favorable location to intercept precipitation from summer storms. Annual precipitation at a nearby permanent weather station situated in the big sagebrush (*Artemisia tridentata* Nutt.) zone (2,070 m elevation) averages 330 mm and is distributed evenly throughout the year.

Singleleaf pinyon was studied at 3 sites along an environmental gradient. Sites were recognized by plant community types and were located at different elevations spanning the driest to most mesic locations occupied by singleleaf pinyon in this area. The driest site was on an exposed ridge at 2,130 m in a black sagebrush community (hereafter black sagebrush site). Soils are shallow with a calcium carbonate layer at 30 cm. Vegetative cover was approximately 15% black sagebrush and <5% singleleaf pinyon on the south slope and >5% singleleaf pinyon on the north slope. The second site was located at the lower, drier edge of the mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* Nutt.) zone (hereafter big sagebrush site). It was selected because it represents the approximate center of the zone of domination by singleleaf pinyon. The big sagebrush site was on a gently sloping alluvial fan at 2,070 m. The soil is rocky, sandy alluvium, and deeper than at the black sagebrush site. This site formerly supported a mountain big sagebrush/bluebunch wheatgrass [*Agropyron spicatum* (Pursh.) Scribn.] mutton grass [*Poa fendleriana* (Steud.) Vasey] plant community (Eddleman and Jaindl 1994) but is now dominated by singleleaf pinyon. Foliar cover was approximately 32% singleleaf pinyon, 13% Utah juniper [*Juniperus osteosperma* (Torr.) Little], and 1% mountain mahogany (*Cercocarpus ledifolius* Nutt. ex Torr. and Gray). Other shrubs present on the site included mountain big sagebrush, mormon tea (*Ephedra viridis* Cov.), and bitterbrush [*Purshia tridentata* (Pursh.) DC]. These contributed less than 1% cover. Foliar cover of grasses and forbs was 3 and 1%, respectively, with the dominant grass being mutton grass. The third site was the most mesic and was a transition zone between mountain big sagebrush and mountain mahogany (hereafter mountain mahogany site). It was a ridge crest at 2,745 m and was the upper limit of singleleaf pinyon in this area. Soil at the high elevation site is a gravelly clay loam of quartzite parent material with fractured bedrock at approximately 75 cm. Vegetation belongs to the mountain mahogany-singleleaf pinyon/snowberry (*Symphoricarpos oreophilus* Gray) plant community (Eddleman and Jaindl 1994). Cover averaged 59, 6, 16, and 6% for mountain mahogany, singleleaf pinyon, snowberry, and mountain big sagebrush, respectively. Bluebunch wheatgrass and mutton grass were the dominant grasses.

Climatological and Soil Parameters

Micrometeorological stations located at each of the study sites augmented data collected at a permanent weather station. The permanent weather station, which had been in operation for 51 years, was at 2,070 m and was 0.5, 1.5, and 6.0 km from the big sagebrush, black sagebrush, and mountain mahogany sites,

respectively. Elevation, aspect, and vegetation at the permanent weather station were similar to those at the big sagebrush site. Parameters measured at each site included air temperature 0.25 m above-ground in the open areas between trees and relative humidity. Rainfall was measured at the big sagebrush and mountain mahogany sites during the growing seasons. Air temperature, relative humidity, and rainfall were measured using thermistors, relative humidity sensors and tipping bucket rain gauges, respectively, connected to a continuously recording measurement and control module (model CR10, Campbell Scientific, Inc., Logan, Ut.) programmed to measure every 60 sec and average hourly. The tipping bucket rain gauges did not allow measurement of precipitation as snow; however, precipitation as snowfall was measured at the permanent weather station. Rainfall at the black sagebrush site was taken as equal to that at the permanent weather station though the site was effectively drier because of exposure and shallow depth of soils. Vapor pressure deficit was calculated from air temperature and relative humidity.

Percent soil water was measured gravimetrically at 0–0.05, 0.15–0.25, and 0.35–0.50 m depths in the open area between trees at each of the 3 sites. Two to 5 samples from each depth at each site were collected at the beginning of each month from May to November 1989, and May to September 1990.

Plant Materials

Five mature singleleaf pinyon trees at each site were selected randomly for study. Tree ages were estimated from core samples and averaged 53, 58, and 45 years for the black sagebrush, big sagebrush, and mountain mahogany sites, respectively. Trees averaged 3.4, 3.1, and 2.2 m in height, and 17, 13, and 13 cm in bole diameter at the black sagebrush, big sagebrush, and mountain mahogany sites, respectively. Trees within a site were located within 100 m of each other. Growth and plant-water relations were measured on the lower 1–2 m of crown on the south side of each tree. Measurements were recorded monthly during the growing season from June to November 1989, and May to September 1990.

Plant Growth

Five branches on each sample tree were tagged with colored wire in April 1989. New branches were tagged in April 1990. Stem length and total number of needles and needles per fascicle on the terminal 20–30 mm of each tagged branch above the colored wire were measured monthly starting in April.

Plant-water Relations

Predawn and diurnal xylem pressure potential of needles and diurnal conductance of branchlets were measured at the 3 sites on 3 consecutive days at the beginning of each month from June to November 1989, and May to September 1990. Predawn xylem pressure potential was measured between 12:00 a.m. and 2:00 a.m. (Pacific Standard Time) using a pressure chamber (model 1000, PMS Instrument Company, Corvallis, Ore.) (Ritchie and Hinckley 1975). Xylem pressure potential and conductance were measured hourly between 7:00 a.m. and 3:00 a.m. Leaf conductance (g) was measured on a 2–5 cm branchlet from each sample tree on each site using a null balance porometer (model 4000, PMS Instrument Company, Corvallis, Ore.). Branchlets were removed at the end of the day and dried for subsequent leaf area determinations with a photo-electric leaf area meter (LI-3100, Li-

Cor Inc., Lincoln, Nebr.). Little change in needle size was observed as a result of drying. Readings from the leaf area meter were multiplied by π to estimate total exposed leaf surface area (the shape of the needle was assumed to be cylindrical) (Miller and Shultz 1987). Transpiration (J) was calculated from simultaneous measurements of conductance and vapor pressure deficit (VPD) using the equation $J=(g)(VPD)$. Missing data on the afternoon of May 1990 were due to a major change in weather conditions (snow storm) which prohibited use of the porometer and in September 1990 at the black sagebrush and mountain mahogany sites due to malfunction of the porometer.

Values of $\delta^{13}C$ were determined on samples collected in August 1990 from each sample tree at each site. Needles were removed from shoot tips which contained growth from that year. Dried samples were ground by mortar and pestle and carbon isotope ratios ($\delta^{13}C$) determined with an isotope ratio mass spectrometer at the Department of Biology, Stable Isotope Lab, Boston University. Carbon isotope ratios ($\delta^{13}C$) were converted to carbon isotope discrimination ($\Delta, \text{‰}$) values, utilizing an atmospheric carbon dioxide value of -8‰ (Farquhar et al. 1989) and the formula

$$\Delta = (\delta_a - \delta_p) / (1 + \delta_p)$$

where δ_a = carbon isotope of air and δ_p = carbon isotope of the plant. The $\delta^{13}C$ values are related to the ratio of intercellular CO_2 concentration (c_i) to ambient CO_2 concentration of air (c_a) and reflect potential water use efficiency (Ehleringer and Osmond 1989).

Predawn and midday xylem pressure potential, midday conductance and transpiration, and growth measurements were analyzed with an analysis of variance in a 2-factor (site, time) repeated measures design with trees within sites as replications (Winer et al. 1991). Data were analyzed separately for each year. Means were separated using Tukey's mean separation procedure (Steel and Torrie 1980). Only differences significant at $P = 0.05$ or less are reported. Differences in Δ values between sites were also determined by analysis of variance. Multiple regression analysis was used to evaluate relationships among plant-water parameters and between plant-water parameters and environmental parameters. These included average monthly temperature and relative humidity for the previous month; temperature, relative humidity, and vapor pressure deficit at sampling time; and predawn xylem pressure potentials, which we assumed were a reflection of soil water availability.

Results

Climate and Soil Water

Precipitation at the permanent weather station during the 1988–89 and 1989–90 growth years (October–September) was 96% and 94% of the 51-year annual average. Winter precipitation (October to May) was 74% and 76% of the long-term average in 1988–89 and 1989–90 growth years, respectively (Fig. 1). Temperatures at the big sagebrush site were below the 51-year average measured at the permanent weather station during the winter of 1990 and above average during the summer of 1990. Average temperatures at the black sagebrush site were similar to those at the big sagebrush site during the summer but were approximately $4^\circ C$ warmer during the winter. The mountain

Fig. 1. Mean monthly air temperature and relative humidity from June 1989 to August 1990 at 3 sites along an environmental gradient on the South Snake Range (black sagebrush site —, big sagebrush site - - -, mountain mahogany site ···) and monthly precipitation during the growing season at the big sagebrush site (diagonal line) and the mountain mahogany site (cross hatch) and throughout the year at the permanent weather station in the lower big sagebrush zone (open bar).

mahogany site averaged approximately $4^\circ C$ colder than the big sagebrush site except during the winter when temperatures were similar at the 2 locations.

In this area, soil water was expected to be highest in the spring, essentially depleted by mid-summer, and recharged in the fall and winter. During 1989, percent soil water did not appear to be recharged during the winter as there was little change over the measurement period, particularly at the black and big sagebrush sites (Fig. 2). In contrast, during 1990, a pattern of declining soil water from May to June or July was evident at all 3 sites.

Growth

Foliage grew primarily in June and July. Maximum stem elongation and needle production occurred in June each year on all sites except for the mountain mahogany site in 1989 when single-leaf pinyon produced most of its needles in July (data not shown).

Fig. 2. Gravimetric percent soil water in the open area between trees at 0.05, 0.15–0.25, and 0.35–0.50 m soil depths at the beginning of each month from May to November 1989 and May to September 1990 at 3 sites along an environmental gradient on the South Snake Range. Key to symbols: black sagebrush o; big sagebrush •; mountain mahogany ▽

Annual stem elongation and new needle production generally were significantly greater at the mountain mahogany site (Table 1). Double-needled fascicles were observed only at the mountain mahogany site. Double-needled fascicles made up 5–10% of the

Table 1. Mean stem elongation and number of needles produced per individual branch of singleleaf pinyon in 1989 and 1990 at 3 sites along an environmental gradient on the South Snake Range.

Site	Stem growth		Number of new needles	
	1989	1990	1989	1990
	(mm)			
Black sagebrush	21a ¹	6a	22a	18ab
Big sagebrush	11a	2a	12a	14a
Mountain mahogany	36b	33b	42b	32b
S.E.	2.8	3.1	4.7	4.1

¹Means within a column not sharing a common letter differ ($p < 0.05$).

Fig. 3. Singleleaf pinyon predawn and midday (11:00 a.m.) xylem pressure potentials (Ψ), and mid-day conductance and transpiration at the beginning of each month from June to November 1989 and May to September 1990 at 3 sites along an environmental gradient on the South Snake Range. Key to symbols: black sagebrush o; big sagebrush •; mountain mahogany ▽. * indicates missing data as a result of equipment malfunction.

total needles produced the year before this study but only 1% of the needles produced in 1989 and 1990.

Seasonal Water Relations

Singleleaf pinyon predawn xylem pressure potential during the growing season (May–September) declined from highs in May and June to lows in August and September (Fig. 3). Midday xylem pressure potential patterns varied between years. In 1989, midday values were less negative at the mountain mahogany site in June and November compared to the other sites. At other times, values averaged approximately -2.0 MPa at all sites. In 1990, midday xylem pressure potential of singleleaf pinyon did

not differ significantly between sites, and tended to be most negative in June (Fig. 3).

Transpiration and conductance varied significantly ($p \leq 0.05$) with site during both 1989 and 1990. In 1989, singleleaf pinyon at the mountain mahogany site (the highest elevation) had higher rates of transpiration and conductance through most of the growing season. In 1990, there was no significant difference in conductance or transpiration between sites until July. This may be a result of a combination of precipitation and temperatures that reduced physiological activity in May and June at the higher elevation site and promoted it at the lower elevations. Conductance neared minimum levels in August and September, increased in October, and dropped again in November when average daily temperatures were below 5°C . Seasonal patterns in transpiration were similar to those for conductance except at the big sagebrush site in June 1990, when conductance declined but transpiration increased. This reflected the higher vapor pressure deficit at that site during June compared to the other sites (Fig. 5).

Diurnal Water Relations

Diurnal patterns of most parameters varied with site and month, with the mountain mahogany site differing the most compared to the 2 lower-elevation sites. Xylem pressure potentials commonly declined to minimum diurnal levels (less than -2.0 MPa) by 8:00 a.m. and this level was generally maintained for the remainder of the day (Fig. 4 and 5). Several exceptions to this pattern occurred. In June 1989 xylem pressure potentials at the mountain mahogany site were similar to the predawn levels throughout the

day except at 7:00 a.m. (Fig. 4). In October 1989 xylem pressure potentials did not reach minimal levels until 12:00 p.m. (Fig. 4) and in May 1990 xylem pressure potentials at the black sagebrush and big sagebrush sites continued to decline throughout the morning and into early afternoon (Fig. 5).

Higher and more erratic conductance and transpiration diurnal responses in 1990, particularly for the 2 lower sites (Fig. 5), were probably due to variations in precipitation patterns between years and the occurrence of precipitation prior to the sampling dates. For instance, during the week prior to sampling in June 1990 (28 May–1 June), 36 and 37 mm of precipitation were recorded at the big sagebrush and mountain mahogany sites, respectively.

Carbon Isotope Discrimination

Position of singleleaf pinyon along the environmental gradient influenced Δ values. Mean Δ of singleleaf pinyon at the black sagebrush, big sagebrush, and mountain mahogany sites were 14.1, 14.7, 15.2 ‰, respectively. The Δ of singleleaf pinyon at the black sagebrush site was significantly lower than the mountain mahogany site ($P < 0.05$). Carbon isotope values for singleleaf pinyon at the big sagebrush site did not differ from those of trees at the other sites ($\text{SE} = 0.39$).

Plant-water and Environmental Relationships

Regression analyses indicated that no single factor was highly correlated with conductance and transpiration (Table 2). Conductance was most highly correlated to predawn xylem pres-

Fig. 4. Singleleaf pinyon xylem pressure potential (Ψ), conductance, transpiration, and vapor pressure deficit (VPD) from 7:00 a.m. to 3:00 p.m. (P indicates predawn xylem pressure potential) at the beginning of each month from June to October 1989 at 3 sites along an environmental gradient on the South Snake Range. Key to symbols: black sagebrush o; big sagebrush •; mountain mahogany ∇ . * indicates missing data as a result of equipment malfunction.

Fig. 5. Singleleaf pinyon xylem pressure potential (Ψ), conductance, transpiration, and vapor pressure deficit (VPD) from 7:00 a.m. to 3:00 p.m. (P indicates predawn xylem pressure potential) at the beginning of each month from May to September 1990 at 3 sites along an environmental gradient on the South Snake Range. Key to symbols: black sagebrush $\circ$; big sagebrush $\bullet$; mountain mahogany ∇ . * indicates missing data as a result of equipment malfunction.

sure potential, relative humidity at sampling time, and average temperature for the previous month. Transpiration was most highly related to predawn and midday xylem pressure potential.

Discussion

Predawn xylem pressure potentials reported for singleleaf pinyon in the western Great Basin (DeLucia et al. 1988, Drivas and Everett 1988, DeLucia and Schlesinger 1991) are similar to those we measured at all sites along an elevational gradient in the central Great Basin. Despite differences in elevation and plant communities, xylem pressure potentials of singleleaf pinyon generally did not exceed -2.0 MPa in the summer. In the spring, after summer rains, and in the fall minimum xylem pressure potentials for stomatal closure did exceed -2.0 MPa. In a similar species, pinyon pine (*Pinus edulis* Engelm.), Lajtha and Barnes (1991) found that stomates closed when xylem pressure potential reached -2.0 MPa. In other conifers, stomates closed at leaf xylem pressure potentials between -1.4 and -2.5 MPa (Lopushinsky 1969, Jarvis 1980, Hinckley et al. 1978, Miller and Shultz 1987).

Differences in conductance and transpiration patterns between elevations were related to the temperature and water regimes of the study sites. Singleleaf pinyon at the lower-elevation black sagebrush and big sagebrush sites had higher conductance and transpiration rates in the spring (May 1990), but lower rates in the

early summer (July) than trees at the mountain mahogany site. Results of the relationship among and between plant-water relations and environmental parameters corresponded well with these observations. In the early spring, water was adequate but low temperatures limited conductance and transpiration at the highest elevation. Progressing into the summer, relatively high temperatures (Fig. 1) coupled with soil water becoming limiting earlier at the lower elevations (Fig. 2) resulted in lower rates of transpiration and conductance there compared to the high elevation. Soil water availability was reflected in the xylem pressure potentials. Since daily variation in relative humidity during the summer is mostly a function of incoming storms and is not controlled by soil water conditions or the previous month's average temperature, it also was important in explaining patterns in plant water relations (Table 2).

Differences in plant growth can be related to site- and elevational-mediated water availability, and to conductance and transpiration. Stem elongation was significantly greatest in both years and needle production was significantly greatest in one of two years (and tended to be greater in the other year) at an elevation about 700 m higher than the other sites. Soil water content was frequently greater at the higher site (Fig. 2), as were most monthly means of conductance in both years and transpiration in 1989 (Fig. 3). The cooler and relatively wetter conditions at the upper site allowed for greater physiological activity throughout the summer which was reflected in greater stem elongation and

Table 2. Relationships between leaf conductance or transpiration of singleleaf pinyon and plant and environmental variables. Relationships were developed from means (n=5) obtained on 30 different occasions in the period from June to November 1989 and May to September 1990 along an environmental gradient on the South Snake Range. Abbreviations are g=conductance; J=transpiration; XP_p =predawn xylem pressure potential (measured at midnight to 2:00 a.m.); RH_{st} =relative humidity at sampling time; $Temp_{ave}$ =average daily temperature for the previous month; $Temp_{st}$ =temperature at sampling time; XP_m =midday (11:00 a.m.) xylem pressure potential.

Model	r ²
Conductance	
<u>1 factor</u>	
$g = -0.08 + 0.003RH_{st}$	0.43
$0.15 + 0.070XP_p$	0.44
<u>2 factor</u>	
$g = 0.085 + 0.057XP_p + 0.002RH_{st}$	0.71
$0.21 + 0.073XP_p - 0.002Temp_{st}$	0.64
$0.18 + 0.057XP_p - 0.003Temp_{ave}$	0.64
$0.18 + 0.007XP_p - 0.002VPD$	0.66
<u>3 factor</u>	
$g = 0.12 + 0.056XP_p + 0.002RH_{st} - 0.002Temp_{ave}$	0.75
Transpiration	
<u>1 factor</u>	
$J = 2.40 + 1.11XP_p$	0.46
<u>2 factor</u>	
$J = 1.68 - 0.41XP_m + 1.22XP_p$	0.53
<u>3 factor</u>	
$J = 2.00 - 0.31XP_m + 1.16XP_p - 0.013Temp_{ave}$	0.55
<u>4 factor</u>	
$J = 7.16 + 0.19XP_m + 1.24XP_p - 0.070RH_{ave} - 0.123Temp_{ave}$	0.66
<u>5 factor</u>	
$J = 7.23 + 0.42XP_m + 1.03XP_p + 0.037Temp_{st} - 0.073RH_{ave} - 0.18Temp_{ave}$	0.75

needle production compared to the 2 lower sites.

It has been hypothesized that needle number per fascicle is an adaptation to water stress (Haller 1965, Tausch and West 1987). While Malusa (1992) did not find this relationship in central Arizona, in our study, some production of double needle fascicles was observed at the higher elevation where air temperatures were cooler and precipitation higher. Less than normal precipitation during the years of this study was assumed to have affected production of double-needed fascicles, as previous years growth appeared to have more abundant double needles. For this reason, double needle production is expected to be greater in years with average or better precipitation. Thus, needle number per fascicle in singleleaf pinyon pine in this study appeared to be related to water stress and increases as water stress decreases.

Recent investigations of the effect of elevation on $\delta^{13}C$ values have generally shown higher $\delta^{13}C$ values with increasing altitude (Korner et al. 1988, Vitousek et al. 1988, Morecroft et al. 1992). However, these observations are not consistent. Vitousek et al. (1990) reported less negative values with increasing elevation under wet conditions, but no consistent patterns in $\delta^{13}C$ values under dry conditions for a tree which grows on lava flows in Hawaii. Leaf $\delta^{13}C$ values in both *Nardus stricta* L. and *Vaccinium myrtillus* L. exhibited no change with elevation in one year and more negative values the following year in a study in Scotland (Friend et al. 1989). Numerous factors have been suggested which influence altitudinal trends in carbon isotope ratio of plants (Morecroft et al. 1992, Lajtha and Getz 1993). Thus, a complete explanation of altitudinal trends in $\delta^{13}C$ remains elu-

sive. Significant differences in Δ between the driest and the wettest sites likely reflect effects of water availability, as influenced by humidity, temperature, and soil water. Lajtha and Getz (1993) drew the same conclusion from a study of pinyon pine along a 180-m elevational gradient in New Mexico. Thus, environmental conditions which affect water availability rather than altitude may be the important factor in influencing stomatal conductance and water use efficiency.

Singleleaf pinyon responds to humidity, temperature, and soil water as reflected in xylem pressure potential by varying growth, conductance, and transpiration rates. While it appears to consistently, tightly regulate water loss to maintain a minimum xylem water potential even along a gradient which varied in temperature, precipitation, soil water, and elevation, it did not vary its ecophysiological response to environmental changes. Thus, variation in ecophysiological response to environmental conditions does not appear to be the means by which singleleaf pinyon has succeeded in expanding over a wide range of environmental conditions in which it is found. Rather, it can be characterized as opportunistic and responds to the availability of resources and conditions that are suitable for growth.

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