Responses of Big Sagebrush and Spiny Hopsage to Increasing Water Stress

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Abstract—Ecophysiological observations were taken on big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and spiny hopsage (*Grayia spinosa*) to assess their response to increasing seasonal water stress. Non-destructive whole plant leaf area measurements indicated that big sagebrush produced more leaf area than spiny hopsage. Stem diameter dynamics revealed similar patterns for both species with diameter increases in the spring and shrinkage in the summer. The final stem diameter increase was greater for big sagebrush than spiny hopsage. Xylem pressure potential values were much lower by summer for spiny hopsage than for big sagebrush. Net photosynthesis, stomatal conductance and transpiration were maximal in the spring and declined thereafter for both species.

Desert plants are usually grouped by the manner in which they cope with water stress. One coping mechanism has to do with the maintenance of foliage. Most desert shrubs are drought deciduous or evergreen. Many evergreens will drop portions of their canopy in response to drought, but because they retain some active foliage they are considered evergreen (Smith and Nobel 1986). Drought deciduous shrubs drop foliage as xylem pressure potential (Ψ) falls until all foliage is gone (Smith and others 1990). Drought deciduous species exhibit a wide range of Ψ at which they can maintain turgor, and Ψ values can be lower than those found in evergreen species (Smith and Nobel 1986). We compared the responses of spiny hopsage (*Grayia spinosa*), a drought deciduous shrub, to the evergreen shrub, big sagebrush (*Artemisia tridentata* ssp. *tridentata*), under increasing seasonal water stress.

Spiny hopsage is a chenopod endemic to the western United States. It is distributed east of the Cascades and Sierra Nevada from central Washington to southern California and eastward to southwestern Montana and western Colorado (Shaw and Haferkamp 1990). Rickard (1965) observed that spiny hopsage accumulated high levels of K and Mg in leaves, suggesting it has a high potential for osmotic adjustment. Branson and others (1976) found that spiny hopsage dropped its leaves earlier in the summer than five other deciduous shrubs, had a relatively shallow rooting depth of only 60 cm, and had a minimal Ψ of –8.0 MPa. This value was lower than that of big sagebrush (–6.5 MPa), but was only mid-range among the other species (–4.0 to –10.5 MPa). Smith and others (1990) found that spiny hopsage had a minimum predawn Ψ of –7.6 MPa and dropped foliage through the season as Ψ values dropped.

Big sagebrush is a member of the Compositae family and is distributed throughout the Great Basin, the Columbia Basin, and the Colorado Plateau regions of the Intermountain West (West 1979; Hironaka 1979). Big sagebrush can potentially gain carbon all year because it is evergreen, but highest photosynthetic rates occur in late spring, declining to minimal values in late summer with increasing water stress (DePuit and Caldwell 1973). Minimal values of Ψ have been recorded between –6.0 and –7.0 MPa with physiological activity (Branson and others 1976; DeLucia and Schlesinger 1990; Evans and others 1992). Caldwell (1979), in reviewing the physiology of big sagebrush, concluded that although it is geographically successful, it is not physiologically superior to other coexisting species. It has relatively low rates of photosynthesis, rates are reduced at moderate plant water stress and high temperature, and its roots are costly to maintain. Its success may be related to photosynthetic activity at low temperatures, maintenance of active foliage, sensitive stomatal control, and the ability to withdraw water from dry soils (Caldwell 1979).

The objective of this study was to compare changes in leaf area, stem diameter dynamics, water relations, and gas exchange responses of spiny hopsage and big sagebrush as seasonal water stress increased in a summer-dry climate.

Materials and Methods

The study site (46°35'N, 119°44'W, 244 m elevation) is on the United States Department of Energy's Hanford Site in southeastern Washington. The area is semiarid with warm, dry summers and cool, wet winters. Average yearly precipitation at the study area is about 160 mm,

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falling mostly in the fall and winter (Rickard 1988a). The area is dominated by spiny hopsage and big sagebrush.

Precipitation and other meteorological variables were collected at the site and are summarized in Link and others (1990).

Non-destructive measurements of leaf area dynamics were made with an automated point frame (Caldwell and others 1983). Observations were taken in March and May on the same three individuals of each species, yielding whole plant leaf area values. These values were then converted to a percentage increase.

Stem diameter changes were measured with sensitive (± 0.1 μm) strain gauges attached to stems (Beedlow and others 1986). Data from the strain gauges were collected hourly with a Campbell Scientific CR7-X data acquisition system from March through July on three individuals of each species. Initial values were set to zero for all sensors so that all subsequent values represented a change from initial conditions.

Plant water status was determined with a pressure chamber (Soil Water Equipment Co.) and with a psychrometer (Decagon Devices). Water potential data were collected at midday in March, April, May and July in conjunction with gas exchange observations on six individuals of each species. Xylem pressure potential data were obtained by placing cut stems (about 10 cm in length) in the pressure chamber and slowly pressurizing with nitrogen gas until the tip of the stem first showed evidence of a color change due to expressed water. A wet paper towel was placed in the chamber to maintain a humid atmosphere around the stem and leaf material during pressurization. Leaves were then stripped from the stems, placed in Tygon tubing, capped and placed on dry ice for determination of osmotic potential (Ψ_π) with the psychrometer (Evans and others 1990).

Net photosynthesis (P_n) and stomatal conductance (g) data were gathered with a null-balance gas exchange system (Data Design Group Co.) in March, April, May and July on three individuals of each species. The same individuals were observed in each month. Standard conditions of light (full sun), leaf temperature (30°C), and vapor pressure gradient (3.2 kPa) were maintained in the exposure chamber for all observations. Rates were expressed on a single-sided leaf area basis with leaf area values obtained with a Licor-3100 leaf area meter (Licor, Inc.).

Data are presented as means with one standard-error bar. Comparisons were made with Student's t-test. Species effects for water relations and gas exchange variables were tested using second order polynomial regression relationships in time. Regression relationships were compared using a general linear test (Neter and Wasserman 1974). Hypotheses were tested using an F test. Hypotheses were tested at the $\alpha = 0.05$ level.

Results

Non-destructive leaf area estimates indicated an increase from March to June of 319 ± 72% for big sagebrush and 197 ± 54% for spiny hopsage.

Stem diameter dynamics were observed for both species between days 67 and 203 (Fig. 1). After an initial stem

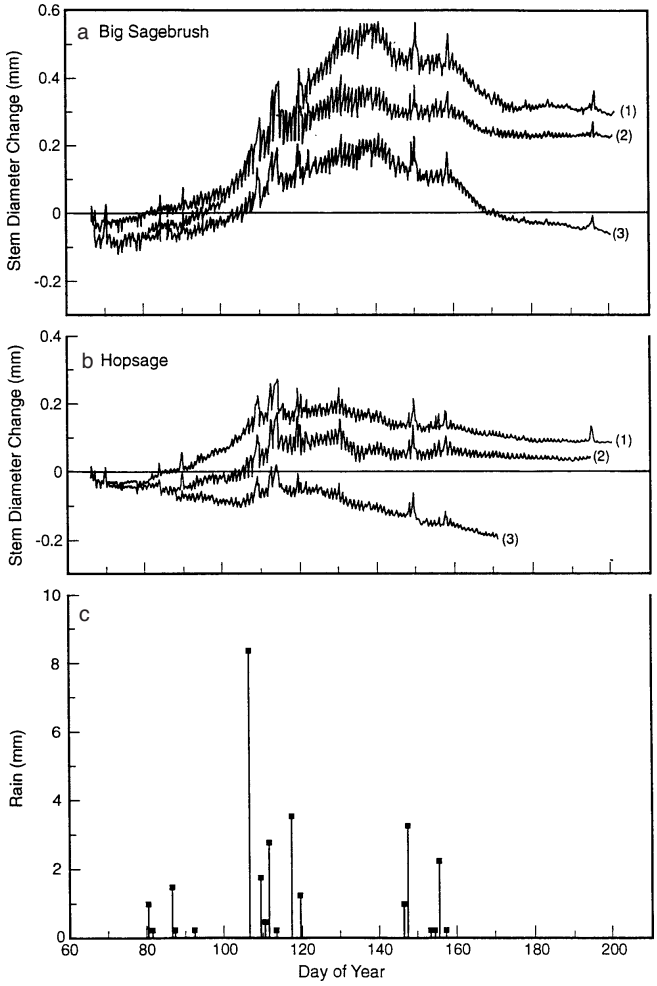

Figure 1—Change in stem diameter of (a) big sagebrush and (b) spiny hopsage and (c) total daily precipitation at McGee Ranch for days 70 to 194.

shrinkage, big sagebrush stems increased in size until day 137 with shrinkage thereafter (Fig. 1a). Final stem diameter increases ranged from 0.04 to 0.37 mm. Observations on spiny hopsage also indicated initial stem shrinkage with a maximal value on day 129 and shrinkage thereafter (Fig. 1b). Final stem diameter increases were 0.08 and 0.13 mm for two individuals, while the stem of the third apparently died. Maximal stem diameter increases occurred later for big sagebrush than for spiny hopsage, and the average final stem diameter increase was greater for big sagebrush (0.23 mm) than for spiny hopsage (0.11 mm). The periodic spikes on the stem diameter graphs occur with precipitation events (Fig. 1c). Precipitation occurred during three periods: days 80 to 93, 108 to 120 and 146 to 158. The greatest amount of precipitation (8.5 mm) fell on day 108. Other daily totals were less than 4 mm.

Water relations varied with time and species. Xylem pressure potential (Fig. 2a) decreased from values near –2.0 MPa for both species in March to –6.2 MPa for spiny hopsage and –3.3 MPa for big sagebrush in July. Regression relationships were significantly different for the two species ($F^* = 55.75 > 2.76$) with values for spiny hopsage

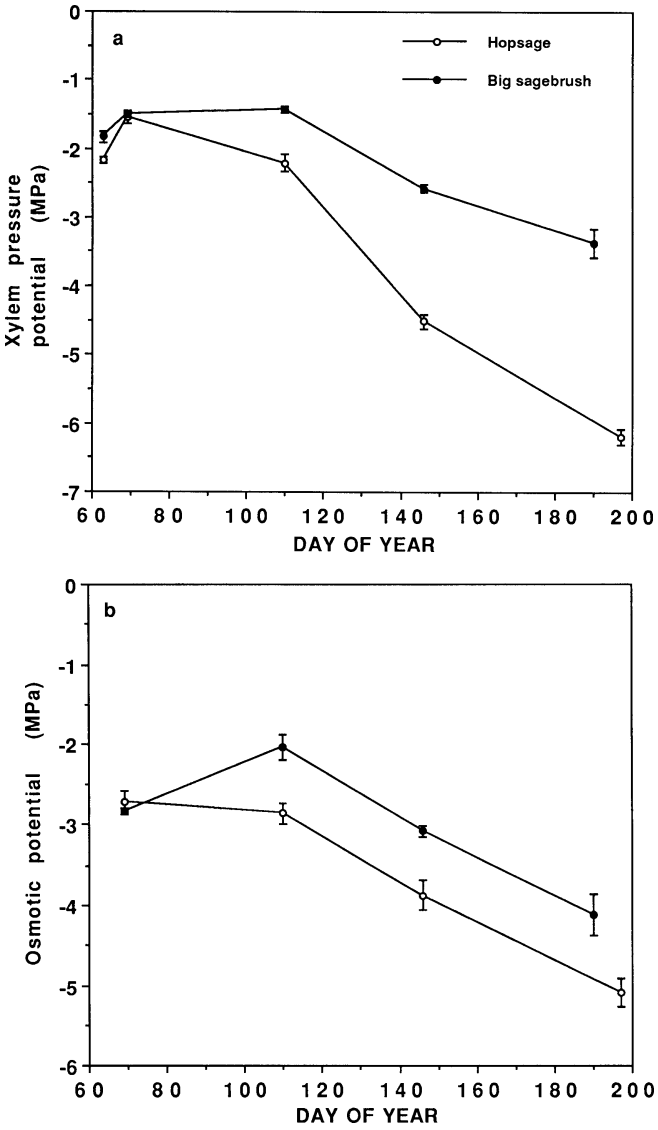

Figure 2—Average xylem pressure potential (a) and osmotic potential (b), for big sagebrush and spiny hopsage at midday from March to July. Error bars are one standard error of the mean ($n = 6$).

lower than those of big sagebrush. Osmotic potential was near –2.7 MPa for both species in March, did not change for spiny hopsage and increased to –2.1 MPa for big sagebrush in April (Fig. 2b). Values decreased for both species after April, to –5.1 MPa for spiny hopsage and –4.2 MPa for big sagebrush. Regression relationships were significantly different ($F^* = 8.48 > 2.87$) for the two species with values for spiny hopsage lower than those of big sagebrush.

Gas exchange characteristics changed with time and were similar for the two species. Net photosynthesis decreased from near 18 μmol $m^{-2}s^{-1}$ and 16 μmol $m^{-2}s^{-1}$ in March to –2 μmol $m^{-2}s^{-1}$ and 0.5 μmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively (Fig. 3a). Regression relationships were not significantly different ($F^* = 0.70 < 3.51$) for the two species. Stomatal conductance was maximal in April and decreased thereafter for both species (Fig. 3b). Maximal values were near 200 mmol $m^{-2}s^{-1}$ and 150 mmol $m^{-2}s^{-1}$, falling to 15 mmol $m^{-2}s^{-1}$ and 25 mmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively. Regression relationships were not significantly different ($F^* = 1.17 < 3.23$) for the two species. Transpiration showed the same patterns as *g* because observations were obtained with constant values of the vapor pressure gradient. Maximal values were near 6 mmol $m^{-2}s^{-1}$ and 5 mmol $m^{-2}s^{-1}$, falling to 0.5 mmol $m^{-2}s^{-1}$ and 1 mmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively.

Discussion

Our data on the responses of big sagebrush and spiny hopsage to increasing seasonal water stress indicate that big sagebrush grew more than spiny hopsage, spiny hopsage had lower values of Ψ than big sagebrush as the season progressed, and there were no differences in gas exchange rates between the two species.

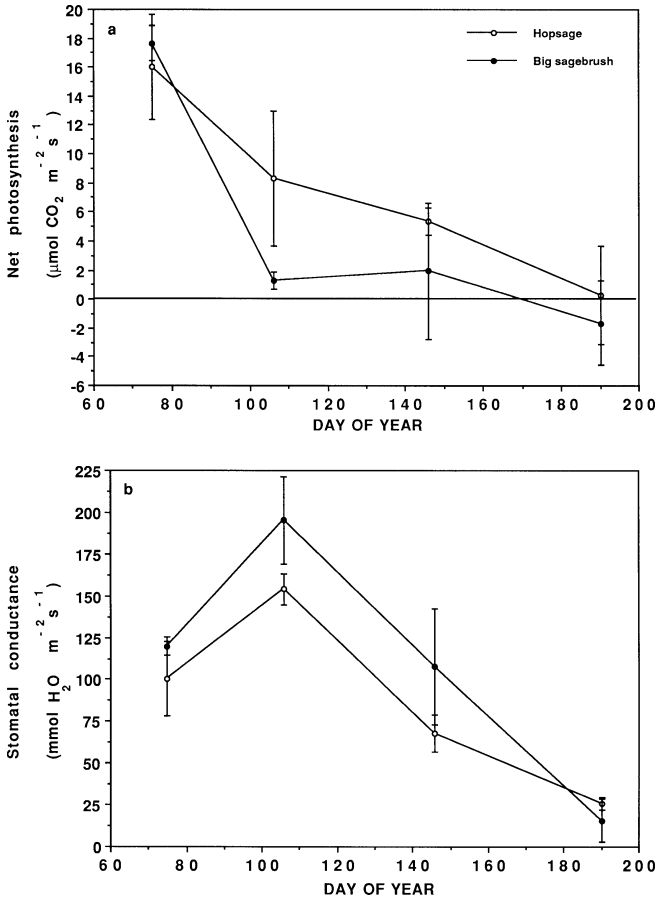

Figure 3—Average net photosynthesis (a) and stomatal conductance (b), for big sagebrush and spiny hopsage at midday from March to July. Error bars are one standard error of the mean ($n = 3$).

Growth

Big sagebrush grew more than spiny hopsage as assessed by percentage increase in leaf area. Spiny hopsage is deciduous and displays only one type of leaf during the growth period. Big sagebrush, in contrast, has a more complex phenology, having deciduous and evergreen leaves (Caldwell 1979). Initial leaf area measurements were made in March. At this time spiny hopsage leaves were new and very small in comparison to evergreen leaves of big sagebrush. Big sagebrush had considerably more leaf area than was present on spiny hopsage in March. The deciduous leaves of big sagebrush arise in the early spring, but fall in the early summer when water stress increases. The increase in big sagebrush leaf area was greater than that for spiny hopsage; in addition the initial leaf area of big sagebrush was greater; thus, the final leaf area of big sagebrush was proportionately much higher than that of spiny hopsage.

Stem diameter increases were greater in big sagebrush than in spiny hopsage. A change in stem diameter is a result of growth processes and changes in hydration (Klepper and others 1973; Lassoie 1979). The extension of stem diameter increases for big sagebrush beyond that of spiny hopsage suggests that each of these species reaches a plant water status that critically influences the allocation of carbon to the measured stems. The ending measurements reflect the net amount of wood added to the stems over the growth period. Big sagebrush had greater stem diameter increases than spiny hopsage, indicative of greater growth. We conclude that big sagebrush grows more than spiny hopsage on the basis of leaf area and stem diameter changes over the time observed.

The relationship between stem diameter dynamics and plant water status was recognized in studies with *Gossypium hirsutum* (Klepper and others 1971), *Quercus alba* (Hinckley and Bruckerhoff 1975), *Pseudotsuga menziesii* (Lassoie 1979), and cacao trees (Alvim 1975). Three observations will help us interpret the relationship between plant water status and stem dynamics: the relationship between precipitation and stem dynamics, the size of diurnal fluctuations and long-term effects.

Precipitation events and spikes in stem diameters occurred at the same time (Fig. 1). This indicates that stems are rehydrated when it rains. Similar results were observed by Hinckley and Bruckerhoff (1975) and Alvim (1975). Hinckley and Bruckerhoff (1975) observed increases in stem circumference after a rain, and concluded that *Q. alba* takes up rain water from shallow depths in addition to water at deeper depths. We conclude that big sagebrush and spiny hopsage are able to take up water after light rains of 2 mm during a 24-hr period. These shrubs must have active roots near the surface, because such light rains do not infiltrate deeply. Big sagebrush also responds to infrequent summer rains (Romo and Haferkamp 1988; Evans and others 1992). Another explanation for the observed patterns is that during a rainy period the weather is usually cloudy and cool, reducing the transpiration. It is possible that the plants were still rehydrating from deeper soil water reservoirs faster than the losses because of transpiration; thus, stem diameters would increase.

The second observation that relates stem diameter to plant water status is the size of diurnal stem dynamics over the entire observation period. Diurnal dynamics were smaller in late winter (up to day 90) and in summer (after day 160), with larger values between days 90 and 160. Minimal values occurred after day 180. This pattern is similar to the pattern of *g*. Minimal *g* occurred around day 190, when stem diameter dynamics were also at a minimum, and so it is likely that diurnal stem diameter dynamics are positively correlated with diurnal transpiration rates. Lassoie (1979) found that diurnal stem shrinkage was closely related to daily water loss in *P. menziesii*. Hinckley and Bruckerhoff (1975) found a similar result for *Q. alba*, but concluded that a large component of daily transpiration was water stored in the trunk of the tree. Water is stored in the trunk during rehydration at night and makes up a substantial amount of transpiration before noon. They conclude that daily transpired water is made up of stem water and soil water, with that from the stem becoming appreciable when the soil reservoir becomes depleted. Water stored in stems is significant for large trees (Hinckley and Bruckerhoff 1975; Lassoie 1979), and may also be significant in these shrubs. The large increase in stem diameter after precipitation events suggests that stems can store relatively large amounts of water. This stored water may make up a significant amount of the transpiration stream, as in trees. However, there has been little work on the significance of stored water in stems for arid land shrubs.

The last observation that relates stem diameter to plant water status was long-term shrinkage of stems as the summer progressed. If carbon allocation to stems decreases as photosynthetic rates decline, then the decrease in stem size in big sagebrush must be caused by increasing dehydration. Stems must have a large potential to store water given the large increase in stem diameter after rains and the large decrease with increasing water stress and decreasing Ψ over time. Similar decreases with time with increasing water stress have been observed in *G. hirsutum* (Klepper and others 1973; Gensler and Diaz-Munoz 1983), *Q. alba* (Hinckley and Bruckerhoff 1975) and in *P. menziesii* (Lassoie 1979). These investigators concluded that the decrease was a result of continuing dehydration over time. Plants experiencing significant water stress can not rehydrate stems completely at night before transpiration and loss of water from living cells reduces stem diameters further (Lassoie 1979).

Plant Water Relations

Plant water relations, narrowly defined, refer to Ψ and Ψ_π and how the plant responds to them. Arid land shrubs are able to tolerate low soil water potentials by actively or passively adjusting cellular osmotic concentrations so that water can be withdrawn from the soil while maintaining cellular turgor (Turner and Jones 1980). We found that the Ψ of spiny hopsage fell to much lower values than for big sagebrush by July; yet, both species maintained turgor and physiological activity. We hypothesized that Ψ_π values would be similarly different for the two species to maintain turgor. Although the Ψ_π of spiny hopsage was

lower than that of big sagebrush after March, values did not exhibit the same pattern as for Ψ. We feel that when leaves were ground for Ψ_π measurement, apoplastic water diluted the symplastic osmotica yielding artificially high values. This may be the case for spiny hopsage and not for big sagebrush. Spiny hopsage, a halophyte, has higher levels of K, Cl and Na than big sagebrush, which supports the hypothesis that spiny hopsage can actively adjust Ψ_π to maintain turgor (Rickard 1988b). If turgor pressure is the difference between Ψ and Ψ_π, and if the true turgor pressure of spiny hopsage is 0.5 to 1.0 MPa, we can hypothesize that its true Ψ_π was closer to –6.7 to –7.2 MPa at the end of the season. Big sagebrush, in contrast, passively adjusts Ψ_π by decreasing leaf water volumes to maintain turgor (Evans and other 1992). Dilution bias in Ψ_π is probably small in big sagebrush.

The lower values of Ψ for spiny hopsage (–6.2 MPa) compared to big sagebrush (–3.3 MPa) in July may be related to differences in soil moisture profiles. Spiny hopsage must have extracted more water from the profile than big sagebrush. We have observed differences in soil water profiles for these shrubs at the same study site (Link and others 1994). Soil water down to 125 cm was extracted more rapidly by spiny hopsage than by big sagebrush from February to May. After May, little water was extracted by spiny hopsage, while big sagebrush continued to extract significant amounts of water until July. This pattern of soil water extraction is correlated with the differences observed in Ψ even though these observations were taken in different years. Volumetric soil water content at the 45 cm depth on August 3 was 3% beneath spiny hopsage and 6% beneath big sagebrush. There were no significant differences at deeper depths beneath these two species (both were 7%). Roots were observed down to 200 cm under both species. Root biomass was an order of magnitude greater under spiny hopsage than under big sagebrush down to 75 cm, which could account for the dryer profile under spiny hopsage at shallow depths. The consequence of this is that spiny hopsage can remove water from the soil at lower soil water potentials than can big sagebrush.

Gas Exchange

Net photosynthesis and *g* were similar for both species with P_n decreasing over time. Because temperature, relative humidity, CO_2 and light were constant during these measurements, other factors must account for the observed pattern in P_n. A strong determinant of P_n is *g*. Stomatal conductance decreased from April to July, accounting for some of the decrease in P_n over that period. The decrease in *g* from April to July is associated with decreases in Ψ. Reductions in *g* with increasing water stress are a common response for plants (Larcher 1980) and have been observed in big sagebrush (DePuit and Caldwell 1973; Evans and Black 1993). Reductions in *g* cannot account for all the variation in P_n, however, because P_n decreased from March to April while *g* increased. This observation may be due to high respiration rates associated with young tissue (Larcher 1980). Big sagebrush leaves grow rapidly in April at this site and have high respiration rates (Evans and Black 1993). Leaves of spiny hopsage have expanded by April and most likely have lower respiration rates that could account for the higher rates of P_n at this time, compared with big sagebrush. The low rates of P_n observed in big sagebrush can also be due to the temperature at which data were collected (30°C). DePuit and Caldwell (1973) observed that big sagebrush has an optimum temperature of 20°C with high respiration and low P_n rates at 30°C.

Conclusions

Ecophysiological observations taken on big sagebrush and spiny hopsage to assess their response to increasing seasonal water stress indicated that big sagebrush grew more than spiny hopsage, and spiny hopsage experienced more water stress than did big sagebrush. One possible reason for lower growth rates in spiny hopsage than big sagebrush is that spiny hopsage expends energy to maintaining turgor, while big sagebrush does not. This possibility is a topic of current research.

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