
ECOPHYSIOLOGY AND GROWTH OF ASHE AND REDBERRY JUNIPER

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Introduction

Ecophysiology is the study of the physiological processes that enable a plant or animal to adapt and survive in its' natural habitat. A plant that is better able to alter patterns of carbon gain, water use, allocation to growth, and/or secondary chemistry in response to environmental stimuli has a greater chance of survival and growth than other plants. Obviously, Ashe and redberry junipers are survivors since their distribution and density has increased greatly in Texas over the last several hundred years. Originally these species were limited to rocky hillsides and draws where there was insufficient soil for vigorous grass growth. Since around the time of European settlement in the New World these species have expanded their distribution to include bottomlands where grasses once flourished. Deeper soils and run-on of rainfall make these sites atypical of where Ashe and redberry juniper evolved. It is essential that we understand how these tree species have adapted to their new environments so we can devise realistic management strategies.

The genus *Juniperus*, represented by 17 species in the western United States, has become dominant in many semiarid communities. The ecology of *Juniperus* communities and invasion dynamics have been studied on areas as diverse as the pinyon/juniper types in the Great Basin (Tueller et al. 1979), Utah juniper (*J. osteosperma*) in Wyoming (Wight and Fisser 1968), and redberry juniper (*J. pinchotii*) in Texas (McPherson and Wright 1989). These and other studies agree that herbaceous production is generally reduced as the tree

community matures until there is little or no herbaceous production under closed canopy communities. This lack of herbaceous biomass reduces domestic livestock production, wildlife diversity, watershed protection, and community stability.

Previous chapters have documented changes in how these plant communities are organized and function. The question remains of how individual plants are capable of surviving and growing in an often harsh environment. We have been investigating how juniper and associated tree species alter their gain carbon and use water patterns in response to canopy structure and environmental stimuli. We have directed our efforts at 1.) understanding plant allometry (or structure), 2.) determining how leaf level processes including gas exchange and secondary chemistry change to the environment, 3.) developing a whole plant canopy model of carbon gain and water use, and 4.) combining the canopy model with plant community structure to determine transpirational water loss at the community level.

The results of the Ashe juniper and live oak research presented in this report are from projects conducted at the Sonora Research Station, the Annandale Ranch near Concan, and at the Wayne Cheney Ranch near D'Hanis. The Sonora Station represents a site with relatively flat terrain and shallow soils. It is on the Edwards Aquifer drainage area. The Annandale Ranch site is steep, rocky site that is directly on the Edwards Aquifer Recharge area. The Wayne Cheney Ranch is a flat, moderately

deep-soil site that is on the Edwards Aquifer Recharge Area.

Research on redberry juniper allometry and photosynthesis was conducted on an upland clay loam site on the Y Ranch west of Crowell in north central Texas (elev. 1630 ft, annual rainfall 18 in). The site is dominated by an overstory of redberry juniper and honey mesquite (*Prosopis glandulosa*). Primary grass species are tobosagrass (*Hilaria mutica*), sideoats grama (*Bouteloua curtipendula*), Texas wintergrass (*Stipa leucotricha*) and buffalograss (*Buchloe dactyloides*).

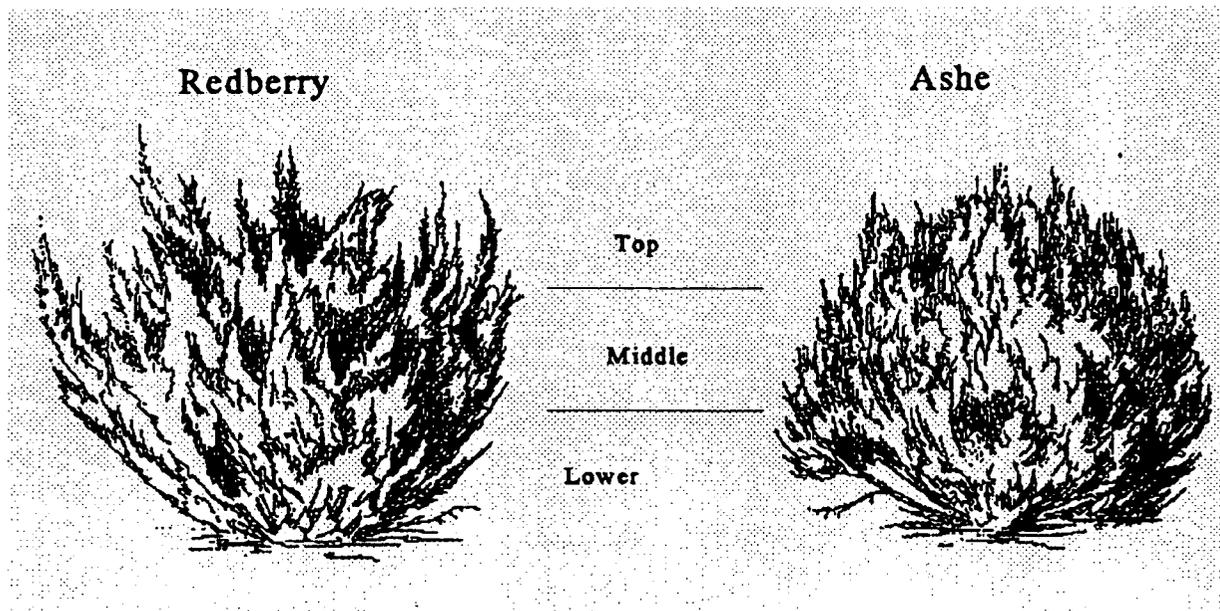
Plant Allometry

Tree canopies are not a uniform assemblage of leaves that all act in a similar manner. Light, humidity, and temperature vary according to where the leaf occurs in the canopy. Shading by other leaves, by supporting structures such as branches and trunks, and by other, taller trees can limit the ability of the leaf to function and to limit the

contribution of the leaf to the overall growth of the plant. A considerable amount of research has been done on canopy structure and function of trees (Caldwell et al. 1986, Comstock et al. 1988, Ellsworth and Reich 1993), and we need to consider the effects of the canopy growth and structure on juniper tree physiology.

Potential of juniper stands to influence understory growth and water yield are directly related to plant and community leaf area and leaf area index (LAI). Due to the difficulties of measuring whole plant leaf area in juniper species, various indirect methods of estimating leaf area have been developed (Miller et al. 1987). Allometric methods yield better estimates of conifer leaf area and LAI than light interception or plant canopy analyzer techniques (Smith et al. 1991, Gower and Norman 1991, and DeBlonde et al. 1994). Few studies have estimated leaf area and standing biomass for individual ashe or redberry juniper trees.

Figure 1.



Accurate estimate of shrub leaf area by allometric methods depends on measurement of such factors as tree or canopy growth and structure, trunk diameter or sapwood area, and specific leaf area (SLA) (White 1983, Jurik et al. 1985, Gower et al. 1987, Miller et al. 1987, Coyea and Margolis 1992). Trunk diameter and sapwood area are not easily obtained for junipers because they have numerous main stems that emerge from a short, furrowed trunk, and it often forms a broad globular or open, irregular crown (Correll and Johnson 1970). SLA is influenced by site-specific environmental factors such as precipitation and soil type (Sprugel 1989, Cregg 1992, Callaway et al. 1994).

Ashe juniper and redberry juniper have different growth forms that may influence leaf level processes. Ashe juniper has a globular, or rounded, shape with typically a single main trunk. Redberry juniper, due to its sprouting nature, often has several large trunks which results in a more uneven canopy shape (Fig. 1). Mature trees of both species are usually less than 15 ft tall with a canopy diameter of about 12 ft (Owens 1996, Dye et al. 1995).

Specific Leaf Area

Specific leaf area (SLA) is an estimate of leaf area per unit of dry weight (e.g. square centimeters per gram or square inches per ounce). In this report, SLA will be based on the area of one side of the leaf. Specific leaf area is a useful measure in ecophysiological studies because it provides a uniform basis for comparing between species and between the same species on different sites. Spatially-uniform SLA across trees is unusual (Woodward 1983, Hager and Sterba 1984, Borghetti et al. 1986, Rawson et al. 1987, Allard et al. 1991, Chapman and Gower 1991, Vertessy et al. 1995). Leaves produced along environmental and seasonal water gradients show decreased SLA as available water decreases (Kramer and Kozlowski 1979,

Ansley et al. 1992). Sunlit leaves often have lower SLA than shaded leaves in grasses, broadleaved trees and conifers (Rawson et al. 1987, Chapman and Gower 1991, Hager and Sterba 1984, Borghetti et al. 1986, Cregg 1992, McCrady and Jokela 1996).

Ashe juniper SLA ranges from 36.2 cm² per gram in the Seco Creek watershed, to 38.8 cm² per gram at the Annandale Ranch and 32.7 cm² per gram at the Sonora Station. These differences may reflect the growth conditions at each of these sites. Average annual precipitation declines from the Seco Creek site to the Sonora Station. Hicks and Dugas (1997) reported that there were no differences in SLA in different portions of Ashe juniper canopies. For comparison purposes, SLA of live oak at these three sites were 59.8, 56.7, and 51.3 cm² per gram at Seco Creek, Annandale and Sonora, respectively. Specific leaf area of redberry juniper in north Texas was 28.0, 32.7, 32.3 and 30.8 when sampled in March, June, July and August 1993.

Whole Plant Biomass and Leaf Area

Mean canopy size for Ashe juniper trees on the Annandale site was 298.2 ft² (SE = 91.5) and for oak (*Quercus virginiana*) on the same site was 336.9 ft² (SE = 57.0) (Owens 1996). Mature Ashe juniper trees averaged 1,528 ft² of leaf area, with almost 538 ft² in the upper canopy. Oak trees had a much lower leaf area with only 623.2 ft² of total leaf area. Leaf area index, which is a measure of square feet of leaf area per square foot of ground area, was about 3 times higher for Ashe juniper than for live oak. Leaf area index was greatest in the middle canopy for both Ashe juniper and live oak. Almost 55% of the leaves on the entire tree were in the middle canopy while the remaining 45% was evenly split between the lower and upper canopy zones. About 57% of the leaves in both tree species were located on the south and east sides of the tree while the remaining 43% was evenly distributed on the north and west sides of the tree. Similar leaf distributions

were reported by Hicks and Dugas (1997) in a mature Ashe juniper community in the Seco Creek watershed near Hondo. This presentation of the leaf canopy in this manner will maximize light interception in these plant communities and will have a serious effect on whole canopy gas exchange and water use, which we will demonstrate in a later section.

Seventy-five redberry juniper trees ranging in height from 2.5 to 15 ft. (0.8 to 4.6 m) were harvested west of Crowell, TX during March 1993. Tree height and width were measured on each tree prior to harvest. Tree canopy area was determined from 2 perpendicular width measurements using the formula: πab where a and b are the radii at 2 points in the canopy. Plant tissue was separated into wood and leaves and oven dried. Leaf subsamples were collected from several trees prior to oven drying and two-dimensional leaf areas were measured with an area meter and multiplied by $\pi/2$ to correct for curvature of the juniper leaf (Miller et al. 1987, Cregg 1992) and account for the non-random distribution and orientation of conifer leaves (Sprugel 1989, Gower and Norman 1991). Leaf area for each tree (whole plant leaf area, WPLA) was determined by

multiplying tree oven dry leaf biomass by the average SLA. Leaf area index (plant leaf area/plant canopy area) was calculated using the single surface leaf area.

In general, about 25 to 35% of the total above ground dry weight of redberry juniper was leaf tissue. Relationships between plant height, canopy area, total plant weight, whole plant leaf area and leaf area index (LAI) are shown in Figures 2 and 3. Total above ground biomass (leaf+wood) per tree ranged from 2 to 485 lbs (<1 to 220 kg) (Figure 2, top). The increase in biomass was exponential with increasing plant height. Biomass did not begin to rise sharply until plants exceeded about 7 ft (2 m) height.

Whole plant leaf area (WPLA) of redberry juniper ranged from 5 to 2045 ft² (0.5 to 190 m²) (Figure 2, bottom). This increase was also exponential as tree height increased, and suggests that redberry juniper does not severely impact water use on a site by leaf transpiration until plant height exceeds 7-8 ft. The relationship between WPLA and plant canopy area was linear over a canopy area range of 5 to 97 ft² (0.5 to 9 m²) (Figure 3, top).

Figure 2.

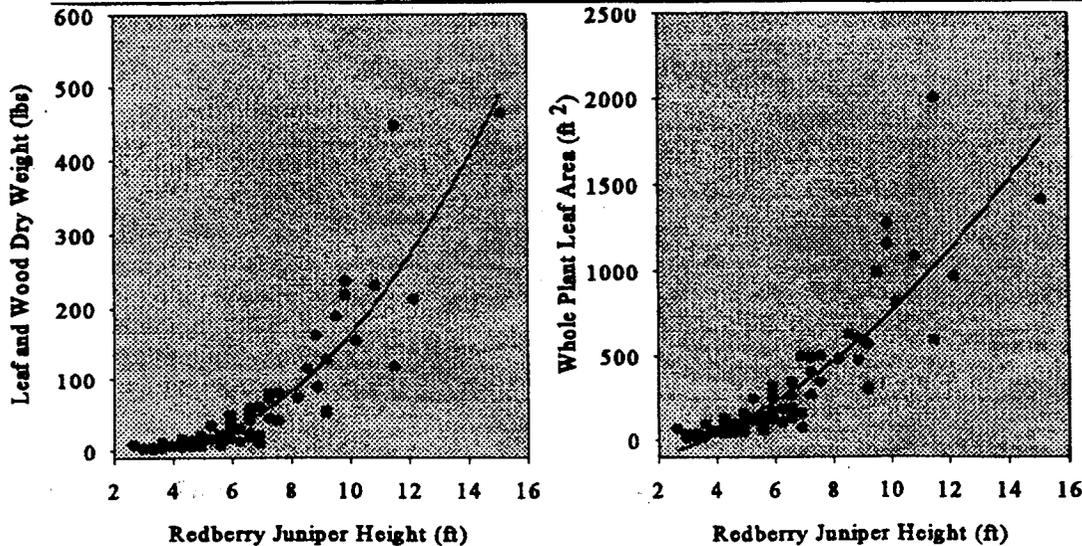
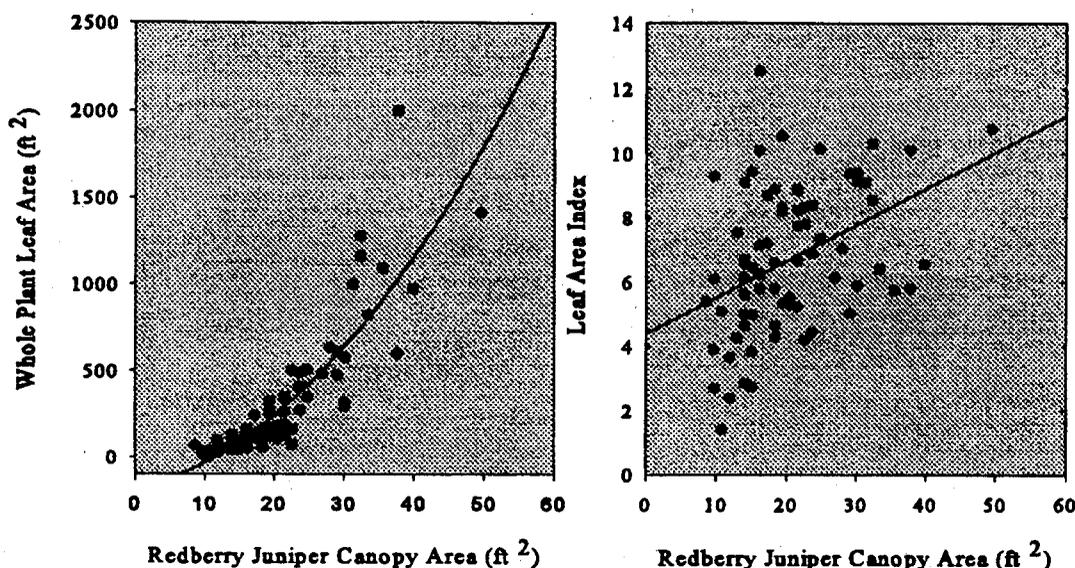


Figure 3.



Leaf area index (LAI) of redberry juniper ranged from 1.5 to 12.5 (Figure 3, bottom). Interestingly, we found no strong relationship between plant height and leaf area index (data not shown), or canopy area and LAI. The smallest diameter plants had the greatest range of LAI's. This large range in LAI's is probably because there was a large range of plant heights of trees with small canopy areas. As plants became larger, the range of LAI's narrowed to 10-20, but LAI did not increase or decrease with increasing canopy area. This probably is due to the centers of large redberry junipers thinning as plant size increases.

LEAF LEVEL PROCESSES

Photosynthesis and Transpiration

To understand how a plant survives and dominates in a plant community, it is necessary to understand how it gains and uses its' resources. The process of gaining carbon for base metabolism, growth and reproduction is a complex physiological problem that can have major ramifications on ecological processes. Nutrient availability, light, water and competition all play an important role in resource acquisition, but ultimately the amount

of carbon that enters through the stomata, or pores, on the leaf surface affects plant growth and survival. This is important because if the stomata are open to allow the entry of carbon dioxide, then water vapor can also exit from the leaf. In a semiarid environment, balancing carbon gain, water loss and nutrient acquisition can often dictate which plants survive and which plants die (DeLucia and Schlesinger 1991). This section will focus on how Ashe and redberry juniper gain carbon and use water in their native habitats.

There are several different scales of gas exchange that are important for understanding the ecophysiology of these species. First, we will look at gas exchange at the individual leaf level within a plant canopy, then at the daily (diurnal) patterns at different canopy positions and finally at seasonal patterns of gas exchange for the entire canopy. Later we will integrate all this information into a model of canopy and community gas exchange and transpirational water loss.

Leaf position within the canopy of Ashe juniper and live oak influenced photosynthesis,

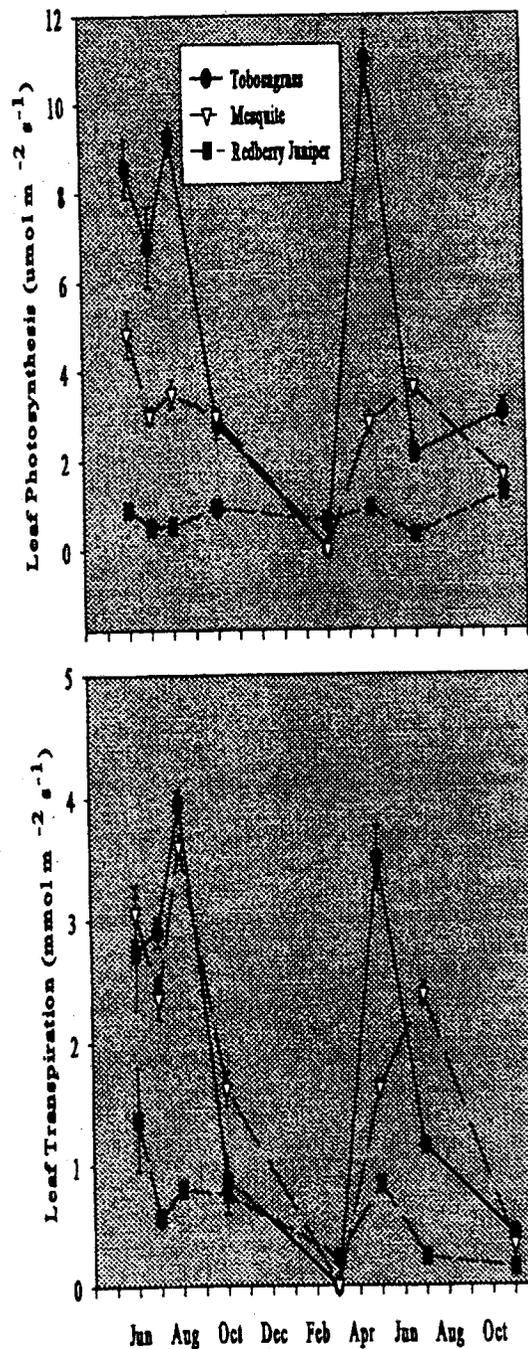
transpiration and leaf conductance in a study on the Annandale Ranch. Leaves in the top portion of the canopy had the greatest gas exchange rates during most, but not all, months (Owens 1996). Photosynthetic rates in the lower canopy of oak trees were 30 to 40% lower than rates in the upper canopy during months with greater than 1 inch of precipitation. The difference was slightly less (20-25%) for Ashe juniper trees. There were no differences in gas exchange rates between the canopy levels when rainfall was less than 1 inch per month. This makes intuitive sense in that when water is limiting, there is no effect of leaf position within the canopy but when water is plentiful then differences are apparent. The cardinal direction, canopy level and time of day interacted to affect leaf level gas exchange. Photosynthetic rates were highest in the mornings on the east, south and north sides of the tree and highest in the afternoons on the west side. Transpiration rates were greater in the afternoon than in the morning for both live oak and Ashe juniper, regardless of the leaf position.

Neither live oak or Ashe juniper demonstrated consistent seasonal patterns of carbon gain and water use. Both species were capable of active gas exchange during any month of the year, but the level of activity was largely determined by the amount of precipitation during the month preceding the sample. When precipitation was extremely low, as during July 1989, gas exchange rates for both Ashe juniper and live oak were essentially zero. Following a 4 inch rain during August 1989, both species quickly regained growth rates with live oak gas exchange rates being about 3 times greater than the Ashe juniper rates.

Leaf photosynthesis and transpiration of redberry juniper was measured simultaneously with 2 co-existing species, honey mesquite and tobosagrass on a north Texas site in 1993 and 1994. Sunlit aspects of five plants of each

species were measured 3 times each day (morning, midday and afternoon). All sample days were clear or had very few clouds. Diurnal values were averaged into daily means.

Figure 4.



During the peak part of the growing season (May-September), tobosagrass usually had greater leaf photosynthesis than the 2 shrub species (Figure 4, top). Honey mesquite photosynthesis was about 5 to 7 times greater than redberry juniper photosynthesis during both 1993 and 1994, except during the March sample period when mesquite had no leaves. Seasonal and daily leaf transpiration patterns of these 3 species were similar to photosynthesis patterns, except that mesquite transpiration was more similar to tobosagrass (Figure 4, bottom). Redberry juniper had very stable seasonal patterns (range 0.24 to 1.38 mmol m⁻² s⁻¹), although transpiration was slightly higher in the spring or early summer (May-June) than the rest of the year. Redberry juniper leaf transpiration was also slightly greater during the wetter year (1993). During July 1994, when the drought was extreme, daily leaf transpiration was 10 times greater in mesquite

than redberry juniper (2.39 vs. 0.24 mmol m⁻² s⁻¹).

WHOLE PLANT PROCESSES

Plant Carbon Gain and Water Use

Leaf level observations indicate how individual parts of the plant are responding to environmental stimuli, but we must also understand how the physiological processes of individual leaves relate with leaf distribution to form a canopy. In order to do this, we built a simple gas exchange model which incorporates leaf level gas exchange rates and the plant allometric variables presented above. This simple model integrates carbon gain and water loss over two daily periods. A further refinement of this model to account for more of the diurnal variation in gas exchange is being conducted.

Table 1. Mean carbon gain, transpirational water loss, and water use efficiency of live oak and Ashe juniper in a semiarid savanna. From Owens 1996.

Species	Canopy location	Carbon gain (lb/d)	Water loss (gal/d)	WUE (%)
Live Oak	Lower	0.25	3.9	7.6
	Middle	0.62	5.0	8.9
	Upper	0.49	6.9	8.4
	Total	1.35	19.1	8.4
Ashe Juniper	Lower	0.28	5.4	6.3
	Middle	0.99	17.4	6.8
	Upper	0.56	10.4	6.4
	Total	1.83	33.1	6.6

Daily carbon gain from the model was significantly greater for Ashe juniper than for live oak (Table 1). Although the instantaneous carbon uptake was greater for live oak in the upper canopy, total carbon gain was greatest in the middle canopy layers due to the greater leaf area found in that portion of the canopy.

The middle layer contributed 46% of the total canopy gain while the lower layer contributed only 18% and the upper layer contributed 36%. Juniper trees followed a similar pattern, but the middle layer contributed significantly more (54%) than either the lower (15%) or upper (30%) layers of the canopy. Leaves on the

south and east sides of the tree accounted for about 60% of the total carbon gain for the tree.

Water loss was significantly greater for Ashe juniper than for live oak in all canopy layers (Table 1). A mature Ashe juniper tree transpired about 33 gallons of water per day while a mature oak tree of similar dimensions transpired about 19 gallons per day. These values are averaged over all environmental conditions throughout the 1988 and 1989 growing seasons. The water loss model is currently being refined to estimate water loss on a daily time step which can be summed to determine monthly or annual water use. At this point, it is interesting to note that Ashe juniper trees use almost twice as much water as live oak trees.

Leaf photosynthesis and transpiration data from redberry juniper, mesquite and tobosagrass have not been incorporated into the whole plant model at this time. However, a few projections can be made, based on the allometry data presented in this paper and mesquite leaf area determinations obtained from other nearby studies. Average height of the redberry juniper and mesquite that were measured on the Y Ranch site in north central Texas was 8.2 ft (2.5 m). Based on these heights, whole plant leaf area of redberry juniper was about 540 ft² (50 m²). Data from Ansley et al. (1991, 1992), and recent unpublished data from a site near the Y Ranch, indicate that whole plant leaf area of 8 ft tall honey mesquite is about 107 ft² (one sided leaf surface). If we focus on the June 1993 sample period in Figure 4 (top) and incorporate the above WPLA's, a rough estimate of carbon gain per tree is 182 and 194 $\mu\text{mol tree}^{-1} \text{s}^{-1}$ for redberry juniper and honey mesquite, respectively.

The estimate of per tree transpiration is 276 and 123 $\text{mmol tree}^{-1} \text{s}^{-1}$ (0.0013 and 0.0006 gallons $\text{tree}^{-1} \text{s}^{-1}$) for redberry juniper and honey mesquite, respectively. If projected on a daily basis (i.e., 10 hours of activity), water use by

each of these species is 46.8 and 20.9 gallons $\text{tree}^{-1} \text{day}^{-1}$ for redberry juniper and honey mesquite, respectively. These projections are very likely over-estimates because factors such as shading within the canopy, cloud cover, etc., have not been considered. However, the estimates provide a rough basis for comparing physiological strategies of each species. Mesquite leaf transpiration is 5 to 10 times greater than that of redberry juniper, yet whole plant responses of similar-sized trees are similar between these species because whole plant leaf area is so much greater in juniper.

Landscape relevance

We are currently developing a community water use model based on the canopy level model described above and plant demographic data. This model combines the age and size structure of the juniper population with the canopy gas exchange model to determine the amount of transpirational water loss. The demographic data required is the density of different size classes of juniper trees. Currently, demographic data is available only from the Sonora Station (Table 2, derived from Smeins et al 1994).

When these density estimates are combined with the canopy model, transpirational water loss can be estimated for each of the grazing management scenarios in Table 2. The juniper population in the ungrazed pasture would transpire an average of 1.4 acre-feet per year, the lightly browsed pasture would transpire 0.97 acre feet per year and the heavily browsed pastures would use 0.34 acre-feet per year. The model is being refined to include different aged juniper trees, trees in different competitive situations, as well as including additional species such as oak, mountain laurel, sideoats grama, and other grasses. At this point, the model does not include interception losses which may be significant (T. Thurow, pers. com.).

Secondary Chemistry

Junipers contain a variety of secondary chemicals commonly known as mono-terpenoids, or volatile oils. The type and amount of oils varies according to each species and the particular profile of oils has often been used to determine if one species is truly different than another species. Chemo-systematics, or the identification of a species based on its' volatile oil profile, has been used extensively in the genus *Juniperus* (Adams 1977, Adams 1994). We have also been investigating the effects of the environment on the seasonal amount and composition of oils in Ashe juniper. The changing amounts and types of oils may have a great impact on plant flammability (for prescribed burning considerations) and plant palatability or acceptance.

The composition and amount of volatile oils in two populations of Ashe juniper were studied over a 16 month period at the Sonora Research Station and the Annandale Ranch. Twenty trees were permanently marked at each site for sampling on a 6-week interval from January 1993 until May 1994. Ten trees at each site were male and 10 were female. At each

sampling time, the following measurements were made: 1.) xylem water potential using a pressure bomb, 2.) gravimetric plant moisture, 3.) monoterpene concentration and composition, and 4.) caloric content estimated using a bomb calorimeter. The data were analyzed for significant seasonal patterns in individual monoterpenoids and in the total concentration using a split-plot ANOVA.

A total of 18 volatile oils were identified and quantified in Ashe juniper. Mean concentrations were greater in the Sonora population than in the Annandale population (\bar{x} = 12.13 vs. 8.69 mg · gm⁻¹ fresh weight), although the amount varied by season at each site (Fig. 5). Camphor, limonene, and bornyl acetate accounted for more than 75% of the total concentration of oils. The Sonora population had significantly greater amounts of limonene, cymene, g-terpinene, and myrcene than the plants at the Annandale site. The concentration of volatile oils did not exhibit a distinct seasonal pattern although concentrations were highest during the spring growing season

Table 2.

Canopy Diameter (m)	Stem Densities (acre)		
	No Graze	Light Browse	Heavy Browse
0.0-0.25	68	59	58
0.25-1.0	65	71	28
1.0-2.0	103	83	14
2.0-3.0	43	47	3
3.0-4.0	10	6	2
>4.0	19	10	7

Differences in the concentration of secondary chemicals observed between the 2 populations may be a reflection of environmental stress. Plants at the Sonora site were generally under greater water stress,

exhibited by a lower xylem water potential, but this stress was not reflected to gravimetric plant moisture or caloric content based on wet weight (Fig 6).

Figure 5.

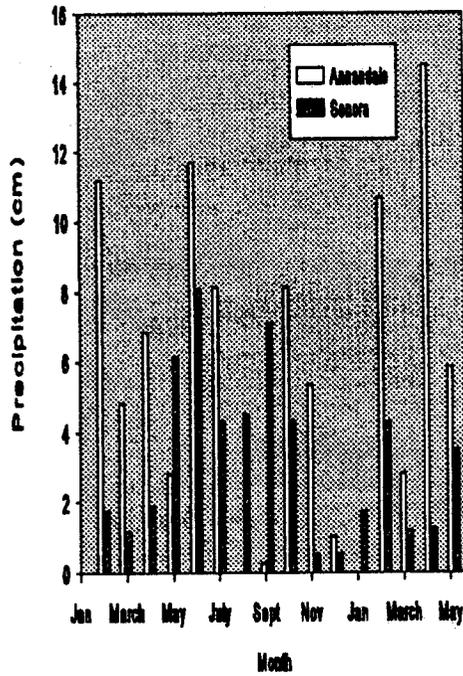
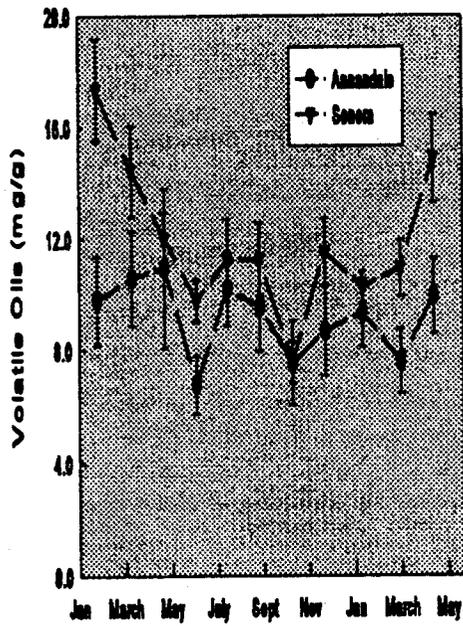
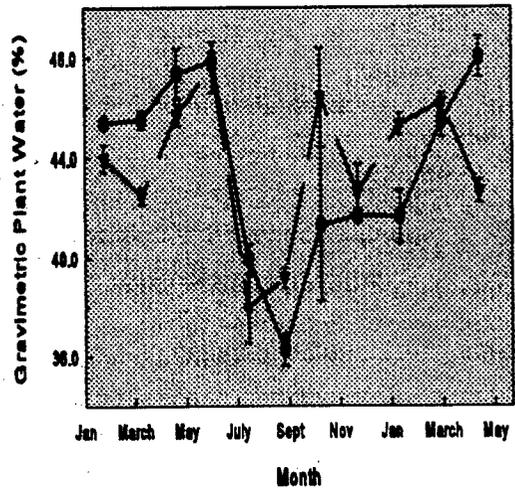
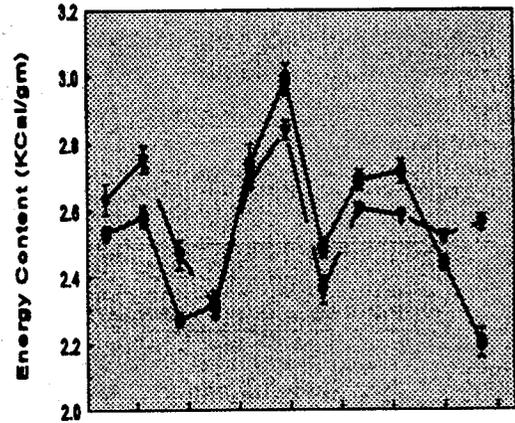
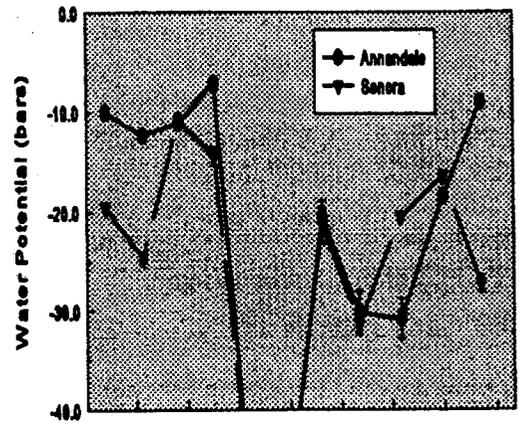


Figure 6.



The importance of secondary chemicals as anti-herbivore mechanisms and as a factor in determining the likelihood of a plant being consumed by fire will be addressed in later chapters.

Future Research Directions

Although much has been done in juniper ecophysiological research, a lot remains to be done. We currently have studies underway which investigate the gas exchange patterns and water use of 1) juvenile versus mature plants, 2) juveniles which are released from competing overstories versus juveniles under the canopy of mature trees, and 3) sprouting versus intact plants. Data are being collected at a variety of sites ranging from flat sites with relatively deep soil to very steep sites with shallow soil. This information will be useful in modeling plant water use on rangeland watersheds.

Additional ecophysiological data which is needed includes 1) juniper responses to drought and drought recovery, 2) nitrogen allocation and cycling, 3) physiological triggers for reproduction, and 4) effects of intraspecific competition on gas exchange and reproduction.

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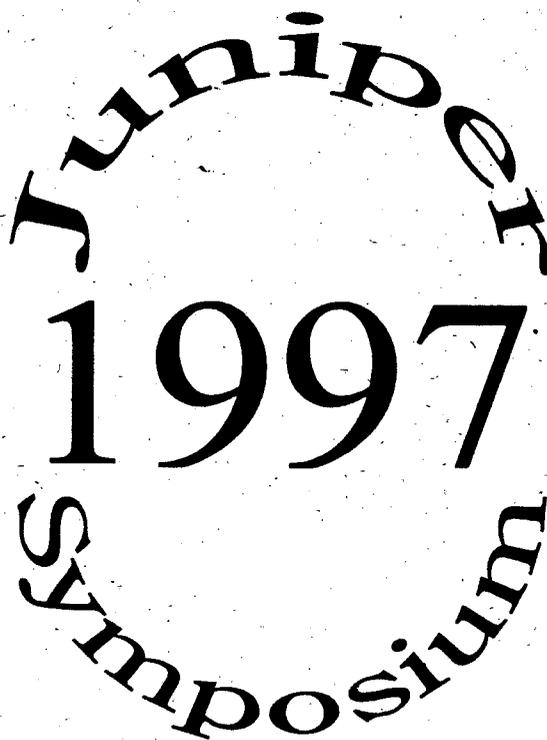
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Notes

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