Final Report

DE-FG03-93ER61668

ENVIRONMENTAL, GENETIC, AND ECOPHYSIOLOGICAL VARIATION OF WESTERN AND UTAH JUNIPER AND THEIR HYBRIDS: A MODEL SYSTEM FOR VEGETATION RESPONSE TO CLIMATE CHANGE

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DISCLAIMER

SUMMARY OF ACCOMPLISHMENTS

Funding from this project has contributed to the following activities: FG03-93ER61668

EDUCATION

Postdoctoral students

Dr. Randall Terry was a postdoctoral research for the period of October 1994 to August 1997. Dr. Terry is currently Assistant Professor, Department of Biological Sciences, University of Montana.

Graduate students

A total of four graduate students participated in this project. Two M.S. graduate students, Mr. Xiaoliu Geng and Mr. Darrin Moore, and their research were supported by this project. Mr. Geng graduated in December 1997, and Mr. Moore will graduate in May 1998. Mr. Geng is currently applying for Ph.D. programs, and Mr. Moore is currently employed by the University of Georgia Marine Institute. Thesis titles are:

Geng, X. Relationship of hydrogen and oxygen stable isotopes in cellulose and xylem water to drought severity.

Moore, D.J. Gas exchange of *Juniperus osteosperma* and *Juniperus occidentalis* across local and regional environmental gradients in the Great Basin of western North America.

In addition, another M.S. graduate student, Ms. Katrina Leavitt, received salary support from this project, although her research was not supported by this project. Ms. Leavitt's responsibilities included data analyses, graphing, and statistical analyses. Finally, a Ph.D. student, Mr. James Lyons-Weiler helped analyze the vegetation data from this project as part of his dissertation research.

Undergraduate students

Fourteen undergraduate students received salary support from this project while at the same time gained valuable work and educational experience. These students were: Will Amy, Kevin Burke, Lori Campbell, Steve Garcia, Tony Giglini, Gill Jackson, Dave Johnson, Alan Kirk, Tammy Leger, Molly Malone, Rachael Maxey, Neelam Shukla, Sara Sweitzer and Luan Van.

Professional research staff

Mr. Craig Biggart, research technician, obtained approximately 75% of his salary support from this project over the duration of the project. In addition, Ms. Belinda Love, herbarium curator, received partial support over a 1-year period.

PUBLICATIONS AND PRESENTATIONS

Publications

To date, two of the chapters of this final report, Chapters 1 and 6, have been published. Citations for these publications are:

Terry, R.G., R.J. Tausch, R.S. Nowak, N.C. Shukla, E.S. LaHood, and P. Keim. Hybridization and genetic diversity in populations of Utah (*Juniperus osteosperma*) and western (*Juniperus occidentalis*) juniper: Evidence from nuclear ribosomal and chloroplast DNA. Great Basin Naturalist (accepted pending revisions).

Nowak, R.S., D.J. Moore, and R.J. Tausch. 1998. Ecophysiological patterns of pinyon and juniper. IN: S.B. Monsen, R. Stevens, R.J. Tausch, R. Miller, and S. Goodrich (eds.). Proceedings: Ecology and Management of Pinyon-Juniper Communities within the Interior West. Gen. Tech. Rep. RM-GTR-000. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Manuscripts in preparation

Chapters 2-5 and 7 of this final report represent drafts of manuscripts for publication. Chapter 2 is an initial draft of a manuscript targeted for *American Journal of Botany*. Chapter 3 is a manuscript in the final stages of revisions prior to submission to *Plant Cell and Environment*. Chapter 4 is the second draft of a manuscript targeted for *Great Basin Naturalist*. Chapter 5 is a manuscript in the final stages of revision prior to submission to *Tree Physiology*. Chapter 7 is the first draft of a manuscript targeted for *American Journal of Botany*.

Preprints

Removed for separate processing

Published abstracts -

Geng, X., and R.S. Nowak. 1996. Relationship of hydrogen and oxygen stable isotopes in cellulose and drought severity. Ecological Society of America, Annual Meeting, Providence RI.

Moore, D.J., and R.S. Nowak. 1996. Gas exchange of *Juniperus occidentalis* and *Juniperus osteosperma* across local and regional environmental gradients in the Great Basin. Ecological Society of America, Annual Meeting, Providence RI.

Presentations

Nowak, R.S. 1996. Response of Great Basin Vegetation to Global Change: Patterns and Processes. Invited seminar, Department of Biological Sciences, Idaho State University.

Nowak, R.S. 1996. Plant Responses to Global Changes. Invited seminar, Environmental Sciences and Health Graduate Program, University of Nevada, Reno.

Nowak, R.S. 1997. Ecophysiological patterns in pinyon-juniper woodlands. Ecology and Management of Pinyon-Juniper Communities within the Interior West, Conference, Provo UT.

Nowak, R.S. and R.J. Tausch. 1995. Environmental, Genetic, and Ecophysiological Variation of Western and Utah Juniper and their Hybrids: A Model System for Vegetation Response to Climate Change. US DOE Program for Ecosystem Research Principal Investigator's Meeting, Knoxville, TN.

CHAPTER 1: HYBRIDIZATION AND GENETIC DIVERSITY IN POPULATIONS OF UTAH (*JUNIPERUS OSTEOSPERMA*) AND WESTERN (*JUNIPERUS OCCIDENTALIS*) JUNIPER: EVIDENCE FROM NUCLEAR RIBOSOMAL AND CHLOROPLAST DNA

Randall G. Terry, Robin J. Tausch, Robert S. Nowak, Neelam C. Shukla, Eric S. Lahood, and Paul Keim

ABSTRACT

Genetic variation in populations of *J. osteosperma* and *J. occidentalis* was studied in order to test morphologically-based hypotheses of interspecific gene flow, examine relationships between hybridization and genetic diversity, and better understand the role of hybridization and other population genetic factors in determining genetic structure in these species. Nineteen restriction fragment length polymorphisms in nuclear ribosomal (nrDNA) and chloroplast DNA (cpDNA) were identified that are polymorphic within populations or species. Five of these polymorphisms, three nrDNA markers and two cpDNA haplotypes, had significantly different mean frequencies among species or subspecies and were used to make inferences regarding gene flow across species' boundaries. The geographic and taxonomic distributions of these markers as well as cluster analysis of nrDNA allele presence/absence data support limited gene flow between populations of each of the two subspecies of *J. occidentalis* and *J. osteosperma*. High levels of genetic variation exist within populations of both species, with mean gene diversities for the nuclear and cytoplasmic loci examined being 0.70 and 0.15 respectively. Differences in the extent of intrapopulation genetic variation are attributed in part to variation in population size, density, and mating system, and pronounced genetic differentiation among populations in nrDNA suggests that levels of gene flow have not been sufficient to appreciably influence population genetic structure at this locus. These results corroborate isozyme-based population genetic studies and paleoecological data which predict high levels of genetic diversity in relict conifer populations of the Great Basin, although we find little support for the contention that genetic diversity is a consequence of introgression.

INTRODUCTION

Utah (*Juniperus osteosperma* (Torr.) Little) and western (*Juniperus occidentalis* Hook) juniper are dominant members of woodland communities in the intermountain west (West et al. 1978). Along with single leaf pinyon (*Pinus monophylla* Torr. & Frem.), *J. osteosperma* forms the overstory of woodlands that cover about 71,500 km^2 in the Great Basin (West et al. 1978). In contrast, *J. occidentalis* is confined largely to the Sierra Nevada and Cascade ranges, although a few populations occur in the extreme northwestern portion of the Great Basin floristic province (Little 1971). Two subspecies of *J. occidentalis* have been recognized (Vasek 1966; Adams 1993): *J. occidentalis occidentalis*, which ranges from extreme northeastern California and adjacent areas of northwestern Nevada, northward into eastern Oregon, southwestern Idaho, and south-central Washington; and *J. occidentalis australis*, which has scattered populations that range from the mountains of southern California (San Gabriel Mtns., Los Angeles Co., San Bernadino Mtns., San Bernadino Co., CA) northward into the Mojave desert (Panamint Mts., Inyo Co., CA) and Sierra Nevada of northeastern California (Little 1971).

Polymorphism in taxonomically important morphological features has been documented in populations of *J. osteosperma* and *J. occidentalis* from the western Great Basin (Vasek 1966; R. Terry and R. Tausch, pers. obs.). A consequence has been considerable uncertainty regarding the biogeographic, taxonomic, and phylogenetic limits of species, as evidenced by the misidentification of hundreds of herbarium specimens of both species collected from western Nevada and adjacent California (Vasek 1966). Hybridization has been documented in several species of Juniperus (see Adams & Kistler 1991) and it has been proposed as causative mechanism in the generation of morphological intergradation in allopatric or locally sympatric populations of *J. osteosperma* and *J. occidentalis* from the western Great Basin. Moreover, studies of plant macrofossils have documented the nearly continuous existence of *J. osteosperma* in the northwest Great Basin over the last 30,000 years, and it has been proposed that genetic diversity generated by interspecific gene flow has been an important factor in adaptation of juniper populations to climatic change over this time interval (Nowak et al. 1994a, 1994b). Consequently, the issue of interspecific hybridization between *J. osteosperma* and *J. occidentalis* is one of both taxonomic and evolutionary importance.

In this study, we examine genetic variability in nuclear ribosomal (nrDNA) and chloroplast DNA (cpDNA) in populations of *J. osteosperma* and *J. occidentalis* from the western Great Basin and adjacent Sierra Nevada. Our principle objectives are; 1) to determine if patterns of genetic variation are consistent with the proposed hybridization of *J. osteosperma* and *J. occidentalis*, 2) if hybridization is supported, examine the relationship between interspecific gene flow and genetic diversity, and 3) to determine if differences in population genetic structure exist between *J.*

osteosperma and *J. occidentalis* and, if so, what factors (e. g., history, population size, and mating system) may be contributing to these differences. Nuclear ribosomal genes exist as tandem repeats that encode for ribonucleic acid components of the functional ribosome. Repeat copy number is variable and can range up to several thousand in land plants (Appels and Honeycutt 1986). Population genetic studies have documented variability in nrDNA within and between populations (Doyle and Beachy 1985, Flavell et al. 1986, Learn and Schaal 1987), and genetic variation in nrDNA has been used to study hybridization in several plant species (cites) . Chloroplast DNA exists as a covalently closed chromosome of 120-150 kilobases (kb) in most land plants (Palmer et al. 1988). Conservative rates of change in cpDNA have made it particularly useful in the study of historical relationships at higher taxonomic levels (i.e., genus and above). However, documentation of intraspecific variation in cpDNA has become increasingly common and has been attributed in many cases to "chloroplast capture" following genetic exchange across species boundaries (Wagner & al. 1987; Govindaraju & al. 1989; Milligan 1991; Soltis & al. 1991; Bobola & al. 1996; Mason-Gamer & al. 1995; see Soltis & al. 1992, Rieseberg & Wendel 1993, and Rieseberg 1995 for reviews; Bain & Jansen 1996). Because the chloroplast genome is non-recombining and uniparentally inherited, the ancestry of individual haplotypes can be easily followed and the effects of different modes of inheritance of nuclear and cytoplasmic loci on patterns of genetic variation studied. These features have prompted the use of cpDNA in plant hybridization studies (Rieseberg and Brunsfeld 1992).

MATERIALS AND METHODS

Plant Sampling

Leaf tissue was sampled from 119 individuals collected from 14 populations of *J. osteosperma* and *J. occidentalis*. A total of nine populations of *J. osteosperma* were sampled from locales ranging from southeastern Nevada (near Las Vegas) to central and extreme western Nevada (near Reno; see Fig. 1). Five populations of *J. occidentalis* were sampled from a north-south transect that extends from Juniper Ridge (northeast of Susanville, CA) to Lake Tahoe (Fig. 1). Populations from each of the two recognized subspecies of *J. occidentalis* were included in the study. Taxonomic determinations were based on the treatments of Adams (1993) and Vasek (1966). Voucher specimens for all individuals included in this study are stored at the USDA-Forest Service Intermountain Research Station, Reno, NV.

DNA Extraction and Analysis

Five grams of leaf tissue was homogenized in 30 mL of homogenization buffer (50mM Tris, pH 8.0, 5.0 mM EDTA, 1.0% polyethylene glycol, 0.5 mM spermidine, 0.1% 2-mercaptoethanol, 350 mM sucrose), filtered through four layers of cheese cloth, and centrifuged at 3700 x g in a Sorvall HS-4 swinging bucket rotor. The resulting pellet (containing nuclei, chloroplasts, and mitochondria) was resuspended in 15 mL of wash buffer (50 mM Tris, pH 8.0, 25 mM EDTA, 0.5 mM spermidine, 0.1% 2-mercaptoethanol, and 350 mM sucrose), 2.0 mL of CTAB solution (10% cetyltrimethylammoniumbromide, 0.7 M NaCl), 0.75 mL of 20% lauryl sulfate, and 3.0 mL of 5M NaCl, and incubated at 60 °C for 1 hr. Following extraction with an equal volume of chloroform, samples were centrifuged at 4500g for 30 mins. Nucleic acids were precipitated with an equal volume of 2-propanol, washed in 70% ethanol, and resuspended in volumes of 0.1X TE ranging from 0.75 to 1.0 mL. Samples were treated with RNase at 37 °C for 1 hr. and quantified fluorometrically.

Approximately 5 mg of genomic DNA was restricted with each of two restriction endonucleases (EcoRI and HindIII) according to the supplier's suggestions (Promega Corp.). Restriction fragments were electrophoresed in 0.7% agarose (SeaKem, FMC Bioproducts) at 80V for approximately 4 hrs. in 1X TAE, blotted onto positively charged nylon membranes in phosphate buffer (0.4 M NaH2PO4, 0.6 M Na2HPO4) following depurination and denaturation, and cross linked by baking at 80 °C for 1 hr. Blots were probed with a recombinant plasmid (RB115) containing the 18S, 5.8S, and 26S ribosomal RNA genes of soybean (Jackson and Lark 1982) and a fragment cloned from the chloroplast genome of Pinus contorta (pPCE227; Lidholm and Gustafsson 1991). Probes were labeled using random primer extension and a-32P dCTP, and hybridized to target sequences from 6 hrs. to overnight at 65 °C (Sambrook et al. 1989). Three post-hybridization washes were conducted, each at 65 °C for 30 min. using 0.2X SSC and SDS concentrations at 0.5%, 0.2%, 0.1%, respectively. Hybridized blots were exposed to X-ray film for periods ranging from 6 to 48 hrs.

Treatment of Data and Statistical Analysis

Each unique restriction fragment profile was coded as an allele or haplotype respectively for the nrDNA and cpDNA loci examined in this study (see Brubaker and Wendel 1994 and references therein). Matches between individual fragments of alleles were determined by comparison of relative electrophoretic migration distances to those

of molecular weight markers (l-Hind III controls). At least three lanes of control markers were run for each gel of 36 lanes. Fragments appearing to have subtly different lengths that were difficult to score unambiguously were placed in a single size class having limits defined as ±5% of the molecular weight of the most common fragment for that class.

Population genetic diversities were calculated using the frequencies of nrDNA alleles and cpDNA haplotypes (Nei and Tajima, 1981; Nei, 1987). Permutation tests were used to identify those diversities that were significantly high or low compared to random data. These tests were conducted by randomizing individuals among populations and calculating population diversities for each of 1000 iterations. Comparisons to the distribution generated by the permutations allowed identification of those diversity values that were statistically significant ($p \leq 0.05$). Additional measures of genetic diversity within populations included calculating the mean distance between all pairwise combinations of individuals as measured by Sorensen's index and the mean number of unique alleles per individual for each population (Table 1).

Genetic differentiation among populations was examined using methods described in Nei (1987) and Gregorius and Roberds (1986). Two substructuring indices (Gst and d) were calculated for each of five groups: 1) *J. occidentalis* (subspecies combined); 2) *J. occidentalis occidentalis*; 3) *J. occidentalis australis*; 4) *J. osteosperma*; and 5) all populations combined. Gst partitions total variability into within population and between population components (see table 3; Nei 1987), and δ measures the mean of the distances between each population and its complement for all populations in an arbitrarily defined group (Gregorius and Roberds 1986).

Statistical differences in group means (Table 2) for nrDNA allele and cpDNA haplotype frequencies were examined using one-way analysis of variance (ANOVA), two-sample t tests, and least-significant difference comparison of means (Statistix, version 4.0 ; Analytical Software, Tallahassee, Florida). Frequency data were transformation prior to statistical analysis according to Sokal & Rohlf (1982) were $\alpha = \arcsin p^{1/2}$ and p is the population frequency . Simple linear regressions and group-average cluster analysis (UPGMA) of Sorensen's distances were performed using PC-ORD, version 2.01 (McCune and Mefford 1995).

RESULTS

A total of 17 multi-fragment alleles was detected by HindIII restriction of the nuclear ribosomal DNA repeat (Table 1). Of these, five (alleles 13-17) were unique to populations of *J. osteosperma*, five (alleles 1,3,7,8 and 12) were unique to populations of *J. occidentalis* , and seven were present in at least one population of both species. Eight alleles had mean frequencies that were statistically different between species or subspecies (alleles 1,2,3,5,6,7,8, and 10 of Table 1). Of these, three (alleles 2,5, and 10) were polymorphic within species and thus potentially informative with respective to hybridization. Mean frequencies for alleles 2 and 5 were significantly different between *J. osteosperma* and *J. occidentalis* and relatively high in *J. osteosperma*, with mean frequencies of 36.4 (p 0. 0 1) and 27.9 ($p \leq 0.03$) respectively. One-way ANOVA and comparison of means indicated the mean frequency of allele 10 was significantly different between *J. occidentalis australis* and the group containing *J. occidentalis occidentalis* and *J. osteosperma*, having a relatively high frequency of 39.7 ($p \leq 0.003$) in *J. occidentalis australis*. All populations were polymorphic for nrDNA alleles detected by HindIII digestion, but monomorphic for an EcoRI restriction fragment profile.

EcoRI digestion revealed two cpDNA haplotypes, each characterized by a single fragment of either 1.7 or 6.0 kb (Table 1). Two-sample T tests and one-way ANOVA indicated significant ($p = 0.002$) differences in mean haplotype frequencies between *J. occidentalis occidentalis* and *J. occidentalis australis* and *J. osteosperma*. Mean frequencies for the 6.0 haplotype were high in *J. occidentalis occidentalis* (0.84 ± 0.23) compared to those in *J. occidentalis australis* (0.17 ± 0.29) and *J. osteosperma* (0.11 ± 0.20). Populations of *J. osteosperma* that had some individuals with the 6.0 cpDNA haplotype included Kumiva Peak, Fort Sage, Mullen Canyon, and Pine Nut (Table 1). All populations were monomorphic for cpDNA variation detected by HindIII digestion.

Mean values for the number of unique alleles per individual, pairwise distance between individuals, and gene diversity for nrDNA were highest in *J. occidentalis occidentalis*, lowest in *J. occidentalis australis*, and intermediate in *J. osteosperma* (Table 2). In contrast, genetic diversity in cpDNA haplotype was highest in *J. occidentalis occidentalis*, lowest in *J. osteosperma*, and intermediate in *J. occidentalis australis*. Gene diversity values for nrDNA ranged from 0.46 (Griff Creek) to 0.83 (Virginia Mtns.) and averaged 0.70 (± 0.12 S.D.) over all populations, while diversity values for the six populations polymorphic for cpDNA haplotype ranged from 0.16 (Fort Sage) to 0.52 (Kumiva Peak) and averaged 0.35 (± 0.16 S. D.; see Table 2). Permutation tests indicated that the Doyle and Griff Creek populations of *J. occidentalis australis* as well as the Kumiva Peak, Fort Sage, and Lovell Summit populations of *J. osteosperma* had diversities that were lower than expected by chance ($p \leq 0.05$; Table 2).

Total gene diversity and genetic differentiation between populations were higher in *J. occidentalis* than *J. osteosperma*, although the average gene diversity within populations was 0.70 for both species (Table 3). δ values were

relatively high for *J. occidentalis occidentalis* and *J. occidentalis australis* (0.60 and 0.69 respectively), while values of Gst were high for *J. occidentalis australis* (0.25) but low for *J. occidentalis occidentalis* (0.06). The largest discrepancy between Gst and δ occurred in *J. occidentalis occidentalis*. Discordance between values of Gst and δ for *J. occidentalis occidentalis* appears attributable to a characteristic of Gst that is manifested when mean population diversities are high. Gst partitions total variability into within and between population components. When within population variability is high, a smaller portion of the total variability is attributed to variability between populations, even though populations may share few if any alleles. For example, a Gst value of 0.11 will be obtained for two populations (n=5 for both populations) where each individual is genetically unique. In contrast, if two populations are monomorphic for different alleles, the value of Gst is 1.00 (complete differentiation). However, in both examples, no genetic elements are shared between the populations. These findings are relevant because intrapopulation genetic variation in nrDNA is particularly high in the two sampled populations of *J. occidentalis occidentalis* and may result in a downwardly biased estimate of Gst.

Regression analysis indicated no significant correlation between the extent of hybridization, as measured using the relative frequencies of either nrDNA or chloroplast DNA markers, and intrapopulation genetic diversity in nrDNA. A statistically significant relationship was found at $p \leq 0.06$ between the number of unique alleles present in a population and the frequency of the 6.0 cpDNA haplotype for the Fort Sage, Mullen Canyon, and Pine Nut populations. However, this relationships was not strongly supported when Kumiva Peak was included in the analysis ($p \leq 0.29$).

Cluster analysis of allele presence/absence data identified two principal groups of populations. One group consisted of all populations *J. occidentalis australis* and the Fort Sage, Mullen Canyon, Pine Nut, and Virginia Mts. populations of *J. osteosperma* (Fig. 2). The other consisted of both populations of *J. occidentalis occidentalis* and the Kumiva Peak, E. Bob Scott, Lovell Summit, War Canyon, and Mt. Airy Summit populations of *J. osteosperma*.

DISCUSSION

Studies of hybridization in plants using molecular methods typically involve the identification of genetic markers that are diagnostic for parental lines, i. e., markers that are monomorphic within but different between taxa (Keim et al. 1989; Wang and Schmidt 1994; Bobola et al. 1996). Comparisons of patterns of variation in differentially inherited genetic markers (e. g., nuclear and cytoplasmic loci) or between genetic and morphological characters are then used to address hypotheses of gene flow between divergent lineages. Thus hybrid individuals possess combinations of characters that suggest alternative taxonomic or phylogenetic affinities. When the diagnostic utility of a feature is assessed within the context of parental limits defined by a second character, the original character will be perceived as being polymorphic within those limits. This is a consequence of conflict among characters in supporting the parental affinities of hybrids. However, if enough samples are taken outside the hybrid zone, the mean frequencies of characters that are phylogenetically diagnostic for different species but polymorphic within zones of hybridization are expected to be statistically different, with the highest frequency being indicative of phylogenetic (i. e., parental) limits. In this study, five genetic markers (nrDNA alleles 2, 5, and 10 and the 1.7 and 6.0 cpDNA haplotypes) were identified that have mean frequencies that are statistically different between species or subspecies of *J. osteosperma* and *J. occidentalis*. Ten individuals from six populations of both species possessed nrDNA alleles that have a mean frequency characteristic of the other species. In addition, seven individuals from four populations of *J. osteosperma* possessed a cpDNA haplotype (i. e., the 6.0 haplotype) that has a mean frequency that is characteristic for *J. occidentalis occidentalis*. These patterns of genetic variation are consistent with morphologically-based hypotheses of hybridization between populations of *J. osteosperma* and *J. occidentalis* in the northwestern Great Basin and adjacent Sierra Nevada. Vasek (1966) studied quantitative variation in morphological features and concluded that, while individual traits have broad ranges of overlap, allopatric populations of *J. osteosperma* and *J. occidentalis* could be reliably differentiated using suites of characters in combination with differences in ecological preference and geographic range. However, he noted populations of *J. occidentalis occidentalis* sympatric with populations of *J. osteosperma* in northwestern Nevada that were morphologically intermediate between *J. occidentalis occidentalis* and *J. osteosperma*, as well as populations of *J. osteosperma* from the Pine Nut Mts. (Douglas Co., NV) and from the "hills north of Reno" (Washoe CO., NV) that were morphologically similar to *J. occidentalis australis* (Vasek 1966). These patterns of variation were attributed to introgression between sympatric or closely parapatric populations of each subspecies of *J. occidentalis* and *J. osteosperma* (Vasek 1966).

Patterns of genetic variation encountered in this study suggest nuclear introgression has occurred preferentially in two directions: 1) from *J. osteosperma* to *J. occidentalis occidentalis*; and 2) from *J. occidentalis australis* to *J. osteosperma*. For example, of the two nrDNA alleles (alleles 2 and 5) that are characteristic of *J. osteosperma*, 3 of 4 possible instances (i. .e, two populations over two alleles) support nuclear introgression from *J. osteosperma* to *J. occidentalis occidentalis*. One and two individuals from the Ram's Horn had alleles 5 and 2 respectively, while 2

individuals from the Juniper Ridge population had allele 5. Thus five of 16 (31%) individuals from the two populations of *J. occidentalis occidentalis* included in this study had either nrDNA allele 2 or 5. In contrast, there is only one of six possible population/allele combinations in which nuclear introgression from *J. osteosperma* to *J. occidentalis australis* is supported, i.e., three individuals from the Doyle population, or 12% of the individuals from *J. occidentalis australis* included in this study, had allele 2. Similarly, variation in nrDNA allele supports nuclear introgression from *J. occidentalis australis* to *J. osteosperma*, while no support for nuclear introgression in the opposite direction is evident. One individual from each of three populations of *J. osteosperma* from extreme western Nevada (Fort Sage, Pine Nut, and Virginia Mts.) had nrDNA allele 10, an allele that is characteristic for the populations of *J. occidentalis australis* sampled in this study. These findings corroborate phytogeographic patterns of morphological variation that suggest hybridization between peripheral populations of *J. osteosperma* and *J. occidentalis occidentalis* and *J. occidentalis australis* and *J. osteosperma* respectively from the western Great Basin (Vasek 1966).

Despite conservative rates of change in the chloroplast genome, six of the fourteen populations sampled in this study are polymorphic for chloroplast haplotype. Intrapopulation variation in chloroplast haplotype could be attributable to relatively high mutation rates within species, or to cytoplasmic gene flow between species that are differentiated at the loci being examined. Hybridization seems to be most plausible hypothesis in explaining haplotypic diversity encountered in this study for several reasons. First, there appears to be little divergence between the chloroplast genomes of *J. occidentalis* and *J. osteosperma*, and we expect variation within species to be minimal. We have recently sequenced the noncoding region of cpDNA that separates the trnL and trnF genes from six species of serrate juniper, including individuals from 11 populations of *J. osteosperma* extending from western Colorado to western Nevada, as well as five populations from both subspecies of *J. occidentalis* extending from northern California into southern Oregon. Phylogenetic analysis of these data indicate *J. occidentalis* and *J. osteosperma* are sister groups, and interspecific distances between sequences obtained from populations well outside the expected hybridization zone average about 1.0 % (data not shown). Considering these low levels of divergence, it seems unlikely that intraspecific divergence would be detected using the single enzyme/probe combination used in this study. However, if the chloroplast genomes of *J. occidentalis* and *J. osteosperma* have diverged at some loci as a result of speciation, secondary contact would be expected to result in hybrid populations that are polymorphic for these loci. Secondly, analysis of trnL-trnF sequence variation supports cytoplasmic gene flow between *J. occidentalis* and *J. osteosperma* over a wide geographic area in extreme northeastern California and western Nevada that includes many of the sites sampled in this study. Thus, it is expected that many of the populations sampled in this study should contain some introgressants, and genetic variation within populations, particularly for chloroplast DNA haplotype, is consistent with that expectation. Thirdly, the geographic distribution of markers having characteristic frequencies in one species but being present in the other species is consistent with the hypothesis of hybridization between divergent lineages (see Fig. 1 and discussion below).

Cluster analysis of nrDNA allele presence/absence data identifies two principal groups of populations (Fig. 2). One of these groups consists of all *J. occidentalis australis* populations and only the western-most populations of *J. osteosperma* (OSW) included in this study (Figs. 1 and 2). The *J. occidentalis australis* populations are exclusively from the east slope of the Sierra Nevada, while the OSW populations are either one (Pine Nut, Fort Sage) or two (Virginia Mtns., Mullen Canyon) ranges removed from the Sierra Nevada. No OSW population is greater than about 60 km away from a *J. occidentalis australis* population. In contrast, the two closest populations of *J. occidentalis australis* and those populations of *J. osteosperma* sampled from the Great Basin of central Nevada (OSC of Fig. 2, excluding Lovell Summit) are separated by about 130 km, and the average distance between populations of these two groups is about 260 km. These results suggest: 1) gene flow between populations of *J. occidentalis australis* and those populations of *J. osteosperma* from the extreme western Great Basin; and 2) genetic relatedness of populations is influenced by geographic proximity.

It remains unclear what factors may be contributing to genetic relationships between populations of *J. occidentalis occidentalis* and those of *J. osteosperma* from central Nevada (Fig. 3). Considering the geographic distances separating these populations, gene flow either via pollen or seed should be minimal. However, current patterns of genetic variation and the relationships they suggest are likely the consequence of complex interactions involving historical biogeography, population demography, and life-history characteristics. For example, paleoecological studies indicate that populations of *J. osteosperma* and *J. occidentalis* were likely sympatric or closely allopatric in northern Nevada about 12,000 years ago (Thompson et al. 1986, Nowak et al. 1994a). In addition, geographic ranges in both species have been dynamic in response to changing climate and topographic variability, and numerous zones of sympatry have probably existed ephemerally over geologic time (Betancourt et al. 1990). If the occurrence of introgression in ancestral populations was dictated largely by geographic proximity, then interspecific gene flow may have been frequent in such areas. Considering the number of generations (about 500 to 1000 for populations of about 100 individuals) required for isolated populations to reach genetic equilibrium (Slatkin and Barton

1989), as well the longevity of individuals of both Utah and *J. occidentalis* (at least several hundred years; Vasek 1966), current patterns of genetic variation may be strongly influenced by historical associations. Detailed studies of the concurrence-occurrences of morphological and molecular features that are diagnostic at the species level should allow hypotheses of introgression and their consequences for population genetic structure to be addressed more conclusively.

These data do not support a positive correlation between the extent of hybridization, as measured using the relative frequencies of either nrDNA or chloroplast DNA markers, and intrapopulation genetic diversity in nrDNA. This finding could be attributable in part to concerted evolution of nrDNA, which has the effect of genetically homogenizing repeat units and increasing the probability of convergence on the same repeat type in different populations (cites). In addition, most of the error associated with estimating genetic diversity in populations is attributable to sampling among loci (Nei 1987). Consequently, the relative levels of genetic variation in nrDNA among populations may not be representative of those at other loci, and more accurate estimates resulting from increased sampling of loci may allow finer resolution of populations with respect to differences in mean gene diversity. However, other tests provide results that are not inconsistent with the hypothesis of a causal relationship between hybridization and genetic diversity. For example, excluding the Kumiva Peak population, those populations of *J. osteosperma* that possess nuclear and chloroplast markers indicative of hybridization have a mean nrDNA gene diversity that is significantly different ($p \leq 0.03$) and higher than that of non-hybrid *J. osteosperma* populations (data not shown). In addition, there is a significant relationship at the 94% confidence interval between the frequency of the 6.0 cpDNA haplotype (characteristic of *J. occidentalis occidentalis*) and the number of unique nrDNA alleles present in populations of *J. osteosperma*, excluding Kumiva Peak (Kumiva Peak is among the smallest of the *J. osteosperma* populations sampled and low levels of genetic variation may be a consequence of genetic drift; see discussion below as it pertains to populations of *J. occidentalis australis*). Studies of plant macrofossils extracted from packrat (*Neotoma* spp.) middens in the northwest Great Basin document the nearly continuous existence of *J. osteosperma* over the last 30,000 years, and it has been suggested that genetic diversity generated by interspecific gene flow has been an important factor in adaptation of juniper populations to climate change over this time interval (Nowak et al. 1994a, 1994b). Several authors have stressed the importance of genetic variation to the adaptive potential of a population in a changing environment (Grant 1963; Lewontin and Birch 1966; Stebbins 1966). Because mutation rates generally are slow relative to the rates at which environments can change, Stebbins (1959) viewed genetic recombination as critical to the adaptive potential of populations, and he supported hybridization between populations having different adaptive norms as one mechanism by which such variation could be generated and maintained. Estimation of mean gene diversities from many loci will facilitate a more detailed study of the relationship between hybridization and genetic variation in populations of Juniperus.

Levels of intra- and interpopulation genetic diversity in nrDNA are high for the populations of Utah and *J. occidentalis* sampled in this study. Mean gene diversity values reported here are about 4 times those based on isozyme analysis of other Great Basin conifers (Hamrick et al. 1994). This finding is likely due in part to differences in mutation rates between nuclear ribosomal loci and those which encode the soluble enzymes used in isozyme studies. Nuclear ribosomal DNA repeats can exhibit [illegible]ive variation in noncoding spacer regions, resulting in pronounced variation within and between populations of some species (Flavell et al 1986, Learn and Schall 1987). In contrast, rates of substitution at loci encoding soluble cytosolic enzymes are relatively conserved, and variation in electrophoretic mobility of isozymes occurs only when amino acid substitutions take place that affect the charge characteristics of the isozyme (Soltis and Soltis 1989). Despite these differences, results presented here corroborate isozyme studies of Great Basin conifers in several ways (Hamrick et al. 1994). First, gene diversities are relatively high for conifer populations in the Great Basin compared to those from the Rocky Mountain mainland. Secondly, a large proportion of the total genetic variability resides within populations (0.82 vs. 0.91 respectively for this study and for isozyme-based studies of other Great Basin conifers; see Hamrick et al. 1994). Thirdly, genetic differentiation between populations is pronounced. This appears to be the consequence of limited gene flow between montane-island populations, and genetic drift associated with climatically induced fluctuations in effective population size (Hamrick et al. 1994).

Both populations of *J. occidentalis occidentalis* exhibited high levels of diversity at the nrDNA locus, with Ram's Horn Camp and Juniper Ridge having the highest and second highest values respectively for HsNuc (Table 2). This finding may be attributable in part to the large size and high plant density of these *J. occidentalis occidentalis* populations, both of which promote outcrossing in wind-pollinated species (Adams et al. 1992). In addition, populations of *J. occidentalis occidentalis* can contain individuals that are either monoecious or dioecious, with about 50% of individuals on average being unisexual (Vasek 1966, Adams 1993). Thus, population size and density as well as mating system appear to be important factors in determining genetic diversity in populations of *J. occidentalis occidentalis*. In contrast, individuals of *J. osteosperma* are mostly monoecious (Vasek 1966), and differences in mating system may account for decreased genetic variability in populations of *J. osteosperma* relative to *J. occidentalis*

occidentalis (see Table 2), despite comparable sizes and densities for the sampled populations of these taxa. This inference is based on the expectation that the incidence of inbreeding is higher in monoecious individuals relative to that occurring in mixed monoecious/dioecious populations, although other factors such as quantities of pollen produced, the relative timing of pollen release and female receptivity, and wind conditions at the time of pollen release will effect levels of selfing in monoecious individuals (Mitton 1992).

Values of both Gst and δ indicate greater population differentiation in *J. occidentalis* (values of 0.21 and 0.71 respectively) than in *J. osteosperma* (values of 0.16 and 0.40 respectively; see Fig. 2). This result appears largely attributable to extensive differentiation in *J. occidentalis australis* (Gst = 0.25, δ = 0.69), in which the sampled populations are small and disjunct. Estimates of the number of reproductive age trees at the Griff Creek, Bear Valley, and Doyle sites are 25, 15, and 35 respectively, and juniper comprises a secondary component in these forest ecosystems. In contrast, the sampled trees of *J. occidentalis occidentalis* and *J. osteosperma* are from extensive populations (hundreds to thousands of individuals) that are typical of populations that dominate landscapes over much of the Great Basin. Theory predicts that small effective population size in concert with genetic drift and inbreeding will increase differentiation among populations, increase genetic uniformity within populations, and decrease population diversity (Falconer 1989). Increased differentiation between and relatively low levels of genetic variation within the sampled populations of *J. occidentalis australis* (see Mean Allele, Sxy, HsNuc, and results from permutation tests in Table 2) are consistent with the hypothesis that drift has been important in determining population genetic structure in this subspecies. Griffin and Critchfield (1972) report over 160 populations of *J. occidentalis australis* from northern California in which stands are less than 2 miles across or are of unknown size. In contrast, only about 50 populations of *J. occidentalis occidentalis* having this size characteristic have been reported (Griffin and Critchfield 1972). Thus, if differences in size and density between the sampled populations of *J. occidentalis australis* and *J. occidentalis occidentalis* reflect the historical influence of drift on population genetic structure, then basic differences in the extent of genetic variation within and between populations are expected between subspecies. Genetic studies that include larger sample sizes as well as comparison of genetic structure in populations of *J. occidentalis australis* and *J. occidentalis occidentalis* having comparable sizes and densities will allow a more rigorous test of this hypothesis.

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Table 1. Frequencies by population for each of 17 nrDNA alleles (1-17) and for each of two chloroplast DNA haplotypes (cp). Numbers separated by commas in the allele column indicate either the presence (1) or absence (0) of DNA fragments that constitute the fragment profile of that allele or haplotype. Fragment sizes in kilobases and listed from left to right are 23.0, 17.0, 14.5, 11.5, 8.9, and 7.5 for the nuclear alleles, and are 6.0 and 1.7 for the chloroplast haplotypes.

#	Allele	Taxon[a] and Population[b]													
		Juococ		Juocau			Juos								
		rhc	jnr	brv	grc	doy	ebs	kva	fts	lvs	mas	mlc	pnu	vmt	wrc
1	0,0,0,1,0,1	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0,0,1,0,0,0	0.29	0	0	0	0.30	0.43	0.60	0.27	0.20	0.4	0.40	0.36	0.21	0.38
3	0,0,0,1,0,0	0.14	0.11	0	0	0	0	0	0	0	0	0	0	0	0
4	0,1,0,0,0,1	0.14	0	0.38	0.14	0	0	0	0.18	0	0	0.10	0	0.07	0
5	0,1,0,0,0,0	0.14	0.22	0	0	0	0.29	0.40	0.27	0.60	0.29	0.20	0	0.21	0.25
6	0,1,0,0,1,0	0.14	0.22	0	0	0	0.14	0	0	0	0	0	0.09	0	0.25
7	1,0,0,0,1,0	0	0.11	0.13	0	0	0	0	0	0	0	0	0	0	0
8	0,0,0,0,1,0	0	0.22	0	0	0	0	0	0	0	0	0	0	0	0
9	1,1,0,0,0,0	0	0.11	0	0	0	0	0	0	0.20	0.14	0	0	0	0.13
10	0,0,0,0,0,1	0	0	0.38	0.71	0.10	0	0	0.09	0	0	0	0.09	0.07	0
11	0,0,1,0,0,1	0	0	0.13	0.14	0.40	0.14	0	0	0	0	0.20	0.18	0.21	0
12	1,0,0,0,0,1	0	0	0	0	0.20	0	0	0	0	0	0	0	0	0
13	0,1,1,0,0,0	0	0	0	0	0	0	0	0.18	0	0	0.10	0	0.07	0
14	1,0,1,0,0,0	0	0	0	0	0	0	0	0	0	0.14	0	0	0	0
15	0,0,1,0,1,0	0	0	0	0	0	0	0	0	0	0	0	0.09	0	0
16	0,1,0,1,0,0	0	0	0	0	0	0	0	0	0	0	0	0.18	0	0
17	0,1,1,0,0,1	0	0	0	0	0	0	0	0	0	0	0	0	0.14	0
18	(cp) 0,1	0	0.33	1.00	1.00	0.50	1.00	0.40	0.91	1.00	1.00	0.90	0.82	1.00	1.00
19	(cp) 1,0	1.00	0.67	0	0	0.50	0	0.60	0.09	0	0	0.10	0.18	0	0

a - Taxon designations: Juococ - *Juniperus occidentalis* subsp. *occidentalis*; Juocau - *Juniperus occidentalis* subsp. *australis*; Juos - *Juniperus osteosperma*

b - Population designations: rhc - Ram's Horn Camp; jnr - Juniper Ridge; brv - Bear Valley; grc - Griff Creek; doy - Doyle; ebs - East Bob Scott; kva - Kumiva Peak; fts - Fort Sage; lvs - Lovell Summit; mas - Mt. Airy Summit; mlc - Mullen Canyon; pnu - Pine Nut; vmt - Virginia Mountains; wrc - War Canyon

Table 2. Population genetic data grouped according to species/subspecies. Group means and standard deviations are given in parentheses. * - denotes observed gene diversities that are significantly low based on permutation tests.

Species/Subspecies/Population	N[a]	Mean Allele[b]	Sxy[c]	Hs Nuc[d]	Hs Cp[e]
J. occidentalis subsp. *occidentalis*					
1. Juniper Ridge	9	0.67	0.57	0.82 (0.05)	0.44 (0.08)
2. Ram's Horn	7	0.86	0.47	0.82 (0.06)	0.00
Mean ± SD		0.77 ± 0.13	0.52 ± 0.07	0.82 ± 0.00	0.22 ± 0.31
J. occidentalis subsp. *australis*					
3. Bear Valley	8	0.50	0.28	0.68 (0.07)	0.00
4. Doyle	10	0.40	0.47	0.69 (0.04)*	0.50 (0.04)
5. Griff Creek	7	0.43	0.11	0.46 (0.14)*	0.00
Mean ± SD		0.44 ± 0.18	0.29 ± 0.18	0.61 ± 0.13	0.17 ± 0.29
J. osteosperma					
6. E. Bob Scott	7	0.57	0.37	0.70 (0.09)	0.00
7. Kumiva Peak	5	0.40	0.60	0.48 (0.09)*	0.52 (0.09)
8. Fort Sage	11	0.45	0.40	0.78 (0.04)*	0.16 (0.10)
9. Lovell Summit	5	0.60	0.27	0.56 (0.14)*	0.00
10. Mt. Airy	7	0.57	0.35	0.70 (0.09)	0.00
11. Mullen Canyon	10	0.50	0.39	0.74 (0.06)	0.18 (0.11)
12. Pine Nut	11	0.55	0.51	0.78 (0.05)	0.30 (0.11)
13. Virginia Mountains	14	0.50	0.31	0.83 (0.03)	0.00
14. War Canyon	8	0.50	0.37	0.72 (0.06)	0.00
Mean ± SD		0.52 ± 0.06	0.40 ± 0.10	0.70 ± 0.11	0.13 ± 0.18

a - number of individuals sampled
b - mean number of unique alleles per individual; *e.g.*, Mean Allele = 0.6 if three unique alleles are present in a sample of five individuals
c - mean pairwise distance between individuals
d - estimated gene diversity for nrDNA with standard errors in parentheses
e - estimated gene diversity for cpDNA haplotype with standard errors in parentheses

Table 3. Genetic differentiation in nrDNA among populations of *Juniperus* grouped according to species and subspecies.

Species/Subspecies	Ht[a]	Hs[b]	Dst[d]	Gst[d]	δ[e]
J. occidentalis	0.89	0.70	0.19	0.21	0.71
J. occidentalis occidentalis	0.89	0.82	0.07	0.08	0.60
J. occidentalis australis	0.81	0.61	0.20	0.25	0.69
J. osteosperma	0.83	0.70	0.13	0.16	0.40
Combined	0.85	0.70	0.15	0.18	0.52

a - total gene diversity
b - mean gene diversity within populations
c - mean gene diversity between populations
d - coefficient of gene differentiation among populations, *i.e.* Gst = Dst/Ht
e - differentiation among populations calculated according to Gregorius and Roberds (1986)

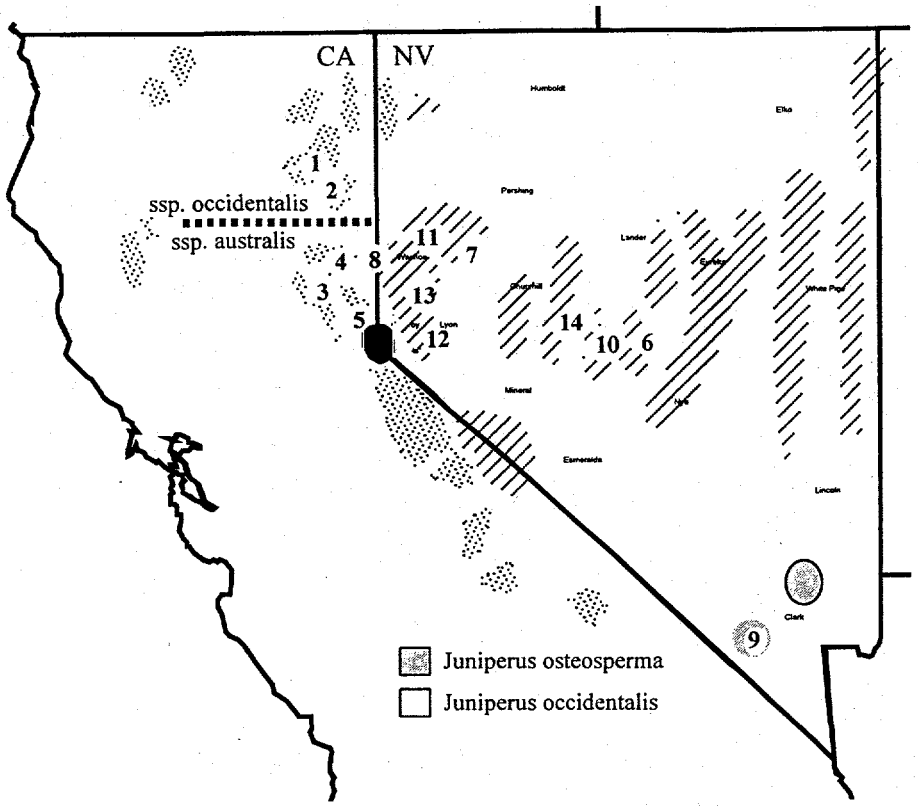

Fig. 1. Map of collection sites of Utah and western juniper included in this study. Population numbers are given in Table 2.

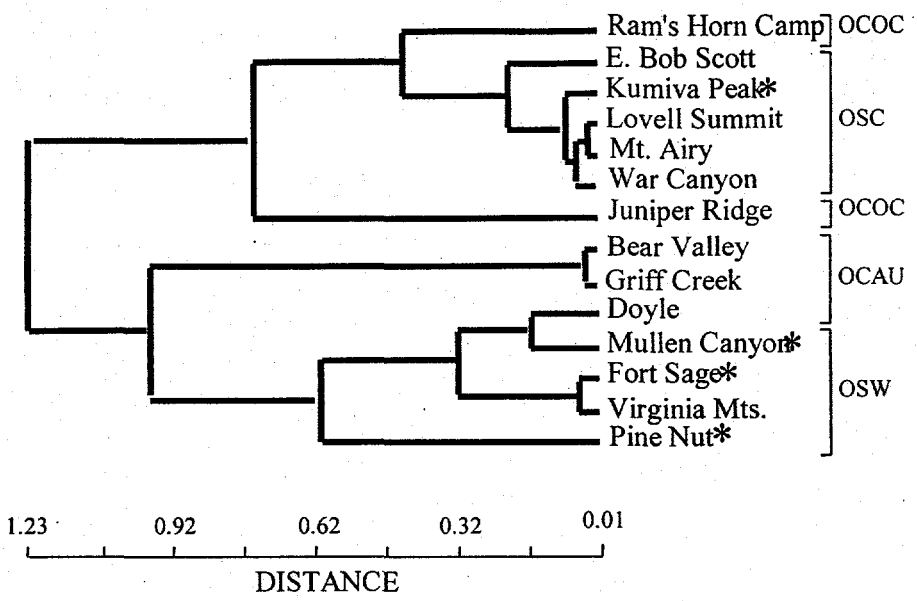

Fig. 2. UPGMA phenogram based on Sorensen's similarity index. The phenogram was generated from cluster analysis of distances derived from the presence/absence of alleles at the nrDNA locus. Brackets designate taxonomic limits and regional affinities as follows: OCOC - J. occidentalis subsp. occidentalis; OCAU - J. occidentalis subsp. australis; OSW - the western-most populations of J. osteosperma ; OSC - populations of Utah juniper collected from central and southern Nevada. * - denotes populations of Utah juniper that possess a chloroplast haplotype having a statistically diagnostic frequency for western juniper subsp. occidentalis (i.e., the 6.0 haplotype; table 2).

CHAPTER 6: ECOPHYSIOLOGICAL PATTERNS OF PINYON AND JUNIPER

Robert S. Nowak, Darrin J. Moore, and Robin J. Tausch

ABSTRACT

Although species that dominate over 30 million ha may be expected to have aggressive ecophysiological traits, pinyon and juniper generally are conservative in their acquisition and use of resources when measured on a per gram of foliage basis. For example, maximum assimilation and conductance of pinyon and juniper are considerably less than those of sagebrush, and their photosynthetic apparatus is less tolerant of severe water stress. Pinyon and juniper are also more dependent on the episodic availability of water and nitrogen in the top 0.2 m of soil than sagebrush. Assimilation rates of pinyon and especially of juniper are very uniform over different types and scales of environmental gradients. Although pinyon and juniper often intermix, some subtle ecophysiological differences exist between the two genera that appear to influence plant distribution. For example, juniper has greater drought tolerance and a better ability to acquire resources from shallow soils and intercanopy areas, which help it tolerate more xeric conditions. Pinyon is more responsive to increased water and nitrogen availability, which partially accounts for the greater abundance of pinyon in more benign environments. These conservative ecophysiological traits help pinyon and juniper dominate the landscape in two ways: first, they allow the conifers to support a much greater amount of foliage biomass than co-occurring shrubs, given the same amount of resources; and second, when coupled with distinct ecophysiological differences between juvenile and adult plants, they help pinyon and juniper establish under, then tolerate, and ultimately outsize and outlive their shrub-steppe nurse plants.

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INTRODUCTION

Pinyon-juniper woodland are a major vegetation assemblage in southwestern North America. Pinyon and juniper occur on approximately 30 million ha (West, this volume), which is a 50% increase from estimates near 20 million ha in 1986 (Buckman and Wolters 1987). Three of the more common juniper species are one-seed juniper (Juniperus monosperma), western juniper (J. occidentalis), and Utah juniper (J. osteosperma), and two of the more common pinyon species are pinyon pine (Pinus edulis) and singleleaf pinyon (P. monophylla). Although many parts of this woodland type have one species of juniper co-dominant with one of pinyon, a single juniper or pinyon species can dominate particular sites, to the exclusion of other tree species.

Invasive species are often thought to have aggressive, opportunistic ecophysiological traits such as high photosynthetic rates, high growth rates, and rapid responses to changes in resource availability (Bazzaz 1986). For example, two of the most successful invasive exotics in western North America are cheatgrass (Bromus tectorum) and saltcedar (Tamarix ramosissima). Both species share a number of traits that may account for their aggressive invasiveness, such as flexibility in life history attributes, ability to germinate over a wide range of environmental conditions, rapid growth, and high allocation to root growth during plant establishment (Smith and others 1997).

The primary purpose of this paper is to provide a summary review of the physiological ecology of pinyons and junipers with the ultimate goal to understand how their ecophysiological traits may explain plant distribution, population dynamics, and the ability of these species to invade and ultimately dominate shrub communities. First, we summarize ecophysiological information about carbon gain and water relations of pinyons and junipers. In many cases, data on only one or a limited number of species are available. Next, ecophysiological traits of pinyon and juniper will be contrasted with each other, then contrasted with another major dominant of semiarid lands in the West, sagebrush (Artemisia tridentata) to investigate possible sources of tree dominance.

ECOPHYSIOLOGICAL TRAITS

Carbon Gain

Assimilation Rates – Diurnal changes in assimilation rates for western juniper (Miller and others 1992) follow a pattern similar to those of other Great Basin plants (Smith and Nowak 1990). During spring and early summer when soil moisture is plentiful, assimilation rates typically track irradiance (Miller and others 1992). Assimilation rate increases during the morning as the sun rises higher into the sky, stays near maximum rates for about six hours during the middle part of the day, then declines rapidly at the end of the day as irradiance decreases. As soil moisture decreases, assimilation rates peak earlier in the day, and a large midday depression in assimilation occurs. By the end of summer, assimilation often peaks within 2-3 h of sunrise and declines to near zero by early afternoon.

The maximum rate of assimilation that occurs during the day does not vary greatly from spring through fall (fig. 1A). During winter, maximum assimilation rates are very close to zero, which is similar to other Great Basin species such as crested and bluebunch wheatgrass (Nowak and Caldwell 1984). By April, maximum assimilation rates are relatively high and decline only slightly until fall, when maximum rates decline more rapidly. Presumably, cold air and leaf temperatures during fall and winter are the primary reason for low maximum rates of assimilation during these time periods.

The total amount of carbon gained during the day follows a seasonal pattern similar to that for maximum assimilation rates except for an earlier decline in fall (fig. 1B). Daily carbon gain is low in winter, relatively high for much of the time period from April through August, then declines rapidly during fall. Both water stress and air temperature interact to produce this seasonal pattern of carbon gain, but the importance of temperature becomes apparent when comparisons are made at different elevations. Daily carbon gain of western and Utah junipers at low elevations tend to be highest earlier in the year and lower in the fall (Table 1). In contrast at high elevations, daily carbon gain gradually increases from spring to its largest value in fall. Relatively cooler temperatures at higher elevation appear to decrease daily carbon gain in spring relative to that at lower elevation, even though both elevations had adequate soil moisture. However, despite these differences in the temporal pattern of when maximum daily carbon gain occurred, the average rates over the entire growing season were remarkably similar: 151 $\mu mol\ g^{-1}\ d^{-1}$ for plants at low elevation sites and 147 $\mu mol\ g^{-1}\ d^{-1}$ at high elevation sites. The similarity in seasonal carbon gain extends to a regional scale of geography (fig. 2). Based on estimates of carbon gain over the entire time period from spring through fall, results from six mountain ranges sorted into 2 statistical groups despite large differences in climate: a north-northwest group of three ranges (Juniper Mountain, Virginia Mountains, and Monitor Range) and a south-southeast group of three ranges (Sonora Pass, Snake Range, and Spring Mountains). What is especially striking about both groups is that both contain one mountain range that has western juniper and two ranges that contain Utah juniper. Thus, even though climatic influences on carbon gain are relatively small, climatic influences appear to be more important than taxonomic influences.

Dependence of Assimilation on Environmental Factors – Patterns of assimilation response to irradiance and temperature for western juniper (Miller and others 1995) are similar to those for other Great Basin species (Smith and Nowak 1990). For adults trees, assimilation rates are saturated at an irradiance level approximately equivalent to one-half solar irradiance, i.e. approximately 1.1 $mmol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD). The light compensation point is relatively low for C_3 plants at approximately 0.05 $mmol\ m^{-2}\ s^{-1}$ PPFD. Western juniper appears to have a rather broad temperature optimum for assimilation; assimilation rates were within 80% of maximum values over a leaf temperature range of 15-35 C. Low temperature compensation point is near 0 C, and high temperature compensation point is near 45 C.

Assimilation rates decline with increased plant water stress for both pinyon and juniper species (fig. 3). The declines for pinyon pine and singleleaf pinyon are very steep, with assimilation rates near zero at leaf water potentials between -1.5 and -2.5 MPa. Assimilation rates of Utah and one-seed juniper foliage do not reach zero until leaf water potentials of approximately -3.3 and -4.5 MPa, respectively.

Assimilation and Leaf Nitrogen – Because nitrogen is essential for constructing enzymes, leaf nitrogen content is often related to assimilation rate. Leaf nitrogen content of both pinyon and juniper increase with nitrogen fertilization (Lajtha and Barnes 1991; Marshall and others 1994; Miller and others 1991). However, seasonal variations in leaf nitrogen content are small for both Utah and western junipers (fig. 1C).

As with many C_3 plants (Field and Mooney 1986), assimilation rate of pinyon pine increases linearly with increased leaf nitrogen (fig. 4A). Thus, fertilization of pinyon plants leads to increased leaf nitrogen and consequently increased assimilation rates; in other words, increased availability of nitrogen in soil benefits pinyon pine through increased assimilation rates. The linear relationship between assimilation and leaf nitrogen content

holds during both dry and wet portions of the year, although the slope of the relationship is much less during the dry portion of the year. Interestingly, results for fertilized and non-fertilized plants are along the same regression line for a particular part of the year (dry or wet). Thus, soil water availability, but not soil nitrogen availability, fundamentally changes the functional relationship between assimilation and leaf nitrogen.

Evidence for a linear relationship between leaf nitrogen content and assimilation is mixed for juniper. Lajtha and Barnes (1991) did not find a significant linear relationship between assimilation rate and leaf nitrogen content for one-seeded juniper (fig. 4B). Although Marshall and others (1994) report a significant linear relationship for Utah juniper, the slope of the relationship for Utah juniper is much smaller than that reported by Field and Mooney (1986) for a number of plant species as well as for pinyon pine (fig. 4B). Thus, increased soil nitrogen availability, at best, only marginally increases the assimilation rate of junipers.

Water relations

Plant Water Potential – Diurnal changes in leaf water potential (Ψ) occur for most plants, including pinyon and juniper. For Utah juniper in spring, Ψ decreased from approximately -0.7 MPa to -1.7 MPa over the 4 hour time period from 6 AM to 10 AM, then remained near -1.7 MPa to about 1 PM (Ehleringer and others 1986). Between 1 and 5 PM, leaf water status improved slightly to -1.5 MPa, but after 5 PM the rate of recovery increased greatly. By the end of summer, however, diurnal changes in Ψ were very small for Utah juniper: Ψ was between -1.5 and -1.7 MPa for almost the entire time period from 8 AM to 6 PM. Diurnal measurements of Ψ for singleleaf pinyon over 2 years at three different sites indicate a very rapid decrease in Ψ from predawn measurements (Jaindl and others 1995). Typically, Ψ of singleleaf pinyon dropped to near its minimum value by 7 or 8 AM, then was relatively constant until 3 PM. Unfortunately, measurements were not made after 3 PM, and thus we do not know how rapidly leaf water status recovered during late afternoon and evening. Malusa (1992) also observed a very rapid drop in Ψ during early morning for pinyon pine and California pinyon (Pinus californiarum).

Seasonal variation in Ψ are relatively small for pinyon and juniper. Average values for predawn or midday measurements of Ψ vary by approximately 1 MPa for Utah juniper over the summer (fig. 5A). For example, predawn Ψ measurements averaged -1.8 MPa during midsummer in southern Utah, but averaged -0.6 MPa after a rainstorm at the end of summer. However, tree-to-tree variation under drought conditions was much larger than the seasonal variation: minimum and maximum predawn measurements in midsummer were -4.2 and -0.7 MPa, respectively, whereas those after the rainstorm were -1.0 and -0.5 MPa, respectively (Marshall and Ehleringer 1990). Seasonal variation in Ψ for western juniper is larger than that of Utah juniper: the difference between minimum and maximum predawn and midday Ψ measurements during the year were approximately 2.0 MPa (Miller and other 1992). Seasonal variations in Ψ for pinyon pine and California pinyon are generally less than 1.0 MPa for predawn measurements and quite small for midday measurements (figs. 5C, 5D).

A key characteristics that is used to distinguish groups of pinyon pines is the number of needles per fascicle, and this feature has been hypothesized to have physiological, and hence evolutionary, significance. Neilsor (1987) speculated that number of needles per fascicle in pinyons follows a gradient in summer precipitation, with four-needle Parry pine (Pinus quadrifolia) and five-needle Sierra Juarez pinyon (P. juarezensis) occurring at the conjunction of two summer moisture gradients whereas singleleaf pinyon is confined primarily to the Great Basin, which receives predominately winter precipitation. The rational for this speculation is that lack of summer precipitation induces greater water stress on plants with a greater number of needles per fascicle, and hence selects for plants with fewer needles. However, Malusa (1992) did not find any significant differences in midday Ψ between the single-needle California pinyon and the double-needle pinyon pine over 2 years. Although significant differences in predawn Ψ occurred, the trend was contrary to expectations: results from double-needle trees indicated less water stress than single-needle trees.

Leaf Conductance and Transpiration – Water loss through transpiration ultimately is controlled by stomata, but few researchers have measured changes in stomatal conductance with changes in environmental factors for pinyon and juniper. Angell and Miller (1994) successfully simulated leaf conductance of western juniper by relaying primarily on three environmental factors: soil temperature, soil water content, and vapor density deficit. In spring when soils are relatively moist, conductance increases as a hyperbolic function of soil temperature. Conductance is near its maximum value when soil temperature at 10-cm depth is above approximately 10 C, but conductance drops rapidly with decreased soil temperature to nearly complete stomatal closure when soil temperature is near 0 C. The relationship between conductance and soil water content is more complex: conductance is at its maximum value when soils are near field capacity, but conductance drops as a logistic function of soil water. Similarly, Miller and others (1995) found a curvilinear relationship between conductance and plant water potential for western juniper:

conductance is near its maximum value when plant Ψ is above approximately -1 MPa, but drops to less than 20% of its maximum value at plant Ψ less than - 4 MPa. Finally, conductance linearly decreases with vapor density deficit: as relative humidity decreases and air becomes progressively dryer, stomata close. These patterns of stomatal response to environmental factors are not unlike those noted in other Great Basin species (Smith and Nowak 1990).

As with assimilation, diurnal variation in conductance occurs for Utah juniper, western juniper, and singleleaf pinyon (Ehleringer and others 1986; Miller and others 1992; Jaindl and others 1995). Maximum conductance almost always occurs in morning, and often conductance peaks within 2-3 hours after sunrise. As soil water availability decreases during the year, the amplitude of the diurnal change in conductance decreases markedly. In addition, singleleaf pinyon has a general pattern of decreased diurnal amplitude of conductance with decreased soil water availability where variation in soil water availability occurred along an environmental gradient (Jaindl and others 1995).

Variation in conductance over the year is somewhat larger than that of assimilation (figs. 6A, 6B). Conductance is highest in spring and early summer, then drops rapidly to a minimum value in late summer or early fall. Interestingly, both western juniper and singleleaf pinyon exhibit increased conductance in late fall, with or without significant fall precipitation in the case of juniper (Angell and Miller 1994) or without significant fall precipitation in the case of pinyon (Jaindl and others 1995).

The total amount of water transpired by a leaf over the entire day does not follow the same seasonal pattern as conductance. Leaf water use reaches a maximum in mid- or late summer for western and Utah junipers (fig. 6C), whereas conductance tends to peak earlier (fig. 6A). This lag between conductance and transpiration occurs largely because vapor gradients have different effects on conductance and transpiration: everything else being constant, increased vapor gradients induce stomatal closure, but lead to increased transpiration rates. Although similar analyses have not been conducted for pinyons, whole tree water use over the day for singleleaf pinyon increased as amount of foliage increased (fig. 6D). As tree size increases, greater self-shading and stratification of the light environment within the canopy occur, and the exchange of water vapor from within the canopy to bulk air decreases, which in turn lead to the nonlinear relationship between tree size and water use (DeRocher and Tausch 1994). Thus, the amount of water used per unit of needle biomass was over six times greater for the smallest seedling than for the larger trees. In addition, number of resin canals greatly improved regressions between foliage biomass and whole tree water use; however, the functional significance of the increased number of resin canals to plant water use is not clear.

Water Use Efficiency – The effects of drought conditions on water use efficiency are not consistent for either pinyon or for juniper. Daily water use efficiency, as calculated from daily carbon gain divided by daily water loss, is highest in spring and fall and lowest in midsummer and winter for junipers (fig. 7A). During the year, lower water use efficiency tends to occur when plants experience greater water stress, unlike other Great Basin species that tend to increase water use efficiency with increased water stress (Toft and others 1989). However, results from sites across regional or elevational environmental gradients are not consistent with this inverse relationship between water use efficiency and drought stress. Daily water use efficiency was not significantly different among 6 mountain ranges that included either Utah or western juniper (fig. 2) nor was it significantly different between high and low elevations within each mountain range (unpublished results of authors). In further contrast, results from carbon isotope composition, which represents a long-term measure of water use efficiency, suggests the opposite trend for singleleaf pinyon, pinyon pine, and one-seed juniper: water use efficiency tends to be greater at low elevation sites (fig. 7B), which are assumed to represent sites with increased water stress. Jaindl and others (1993) corroborated this trend with irrigation treatments: more water decreased carbon isotope content, which indicates lower water use efficiency. Unfortunately, instantaneous measurements of water use efficiency do not help resolve the relationship between drought and water use efficiency. Instantaneous water use efficiency showed little variation as plant Ψ decreased in pinyon pine, but for one-seed juniper, it increased gradually from -0.5 to -3.5 MPa, then declined rapidly as Ψ decreased further (Lajtha and Barnes 1991).

COMPARATIVE ECOPHYSIOLOGY

Pinyon vs. Juniper

Assimilation – Pinyon appears to have a greater potential for carbon gain than juniper. Maximum assimilation rates of pinyon pine are greater than those of one-seed juniper as measured under both controlled environment and natural, field-grown plants (Lajtha and Barnes 1991). Maximum rates for pinyon pine were 26-38 nmol g^{-1} s^{-1} in the controlled environment and slightly less under natural conditions. Maximum values for one-seed juniper were 13-28 nmol g^{-1} s^{-1} in the controlled environment, but did not exceed 20 nmol g^{-1} s^{-1} in the field. As

noted above (fig. 4), N fertilization greatly increases assimilation of pinyon pine, but the response of assimilation to fertilization in one-seed juniper is very small.

Although pinyon has a greater potential for carbon gain, the photosynthetic apparatus of juniper is more tolerant of water stress than that of pinyon. Assimilation for pinyon pine and singleleaf pinyon drop much more rapidly with leaf Ψ than for one-seed and Utah junipers (fig. 3). Whereas pines have essentially lost their ability for positive carbon assimilation at a leaf Ψ of -2 MPa, assimilation is still at 35-50% of capacity for junipers.

Instantaneous water use efficiency of one-seed juniper were greater than those of pinyon pine under drought conditions, although they were similar under low water stress conditions (Lajtha and Barnes 1991). However, contrary to expectations, long-term water use efficiency as indicated by carbon isotope composition were slightly greater for pinyon pine than for one-seed juniper (fig. 7B) as well as greater for singleleaf pinyon than for Utah juniper (DeLucia and Schlesinger 1991); note that species comparisons of carbon isotope composition can be confounded by other factors, and direct interpolation to water use efficiency should be done cautiously. Interestingly, conflicting results have also been observed in studies of the effect of nitrogen on water use efficiency. Nitrogen fertilization increased instantaneous water use efficiency for pinyon pine whereas it did not affect that of one-seed juniper, but N fertilization did not affect long-term water use efficiency as indicated by carbon isotope composition in pinyon pine whereas it significantly increased that for one-seed juniper (Lajtha and Barnes 1991).

Water Relations – In addition to a greater tolerance of its photosynthetic apparatus to water stress, additional data also suggest that juniper has more favorable water relations than pinyon. In measurements of plant Ψ over an elevational gradient, Barnes and Cunningham (1987) noted that Ψ of one-seed juniper was less negative than that of pinyon pine when soils were wet, but more negative when soils were relatively dry. Hence, when water is plentiful, juniper has lower levels of water stress than pinyon; but as soils dry, juniper has a greater capability to tolerate water stress. Furthermore, this shift in relative ranking of Ψ for these two species is due to the small seasonal variation in Ψ for pinyon pine relative to that of one-seed juniper. Little variation in predawn Ψ for pinyon pine also occurs across a seral gradient, whereas Ψ of one-seed juniper becomes more negative as seral development nears climax (Schott and Piper 1987). Finally, water potential components such as Ψ at the turgor loss point are good indicators of drought tolerance, and Ψ at the turgor loss point was more negative for Utah juniper (mean over two sampling dates was -4.1 MPa) than for pinyon pine (mean was -3.7 MPa) (Wilkins and Klopatek 1987).

Recent evidence also suggests that one-seed juniper is better able to extract soil moisture from areas between canopies than pinyon pine (Breshears and others 1997). In a well-developed stand of pinyon-juniper woodland, Breshears and others (1997) documented a small, but significantly greater, difference in soil moisture in the area between tree canopies than that under tree canopies. By carefully measuring soil moisture content and both plant and soil Ψ under natural and irrigated conditions, they determined that one-seed juniper made better use of shallow soil moisture between canopies than pinyon pine.

Responses of Juveniles vs. Adults – Both pinyon and juniper have dimorphic foliage that is associated with plant growth stage, but the physiological importance of juvenile versus adult foliage has only been investigated for western juniper. The physiological performance of juvenile foliage differs from adult foliage when soil moisture is relatively plentiful (Miller and others 1995). The maximum assimilation rate during the day of juvenile foliage is significantly greater than that of adult foliage from April to July (fig. 8A). This difference is maximum assimilation is partially due to increased stomatal conductance (fig. 8B). The greater assimilation rates of juvenile foliage results in a 28% increase in carbon gain over the period from April to October, which likely aids in the rapid establishment of juvenile plants (Miller and others 1995).

Unfortunately, the strategy of juvenile foliage to increase assimilation by increasing conductance has the cost of increased water use. The increased water use does decrease instantaneous water use efficiency of juvenile foliage with respect to adult foliage in late-summer (fig. 8C). However, water use efficiency of the two types of foliage does not differ during late spring and early summer, and water use efficiency of juvenile foliage is actually greater than that of adult foliage in early spring. None-the-less, increased water use does impact plant water status: midday Ψ of juvenile foliage was lower than that of adult foliage over the entire measurement period of April through October, and predawn Ψ of juvenile foliage was lower than that of adult foliage from July through October (fig. 8D). Thus, although increased water use of juvenile foliage only decreased water use efficiency in late summer, juvenile foliage experienced greater water stress over much of spring, summer, and fall. The more negative predawn Ψ are especially intriguing: they suggest that juvenile western juniper depletes soil moisture faster than adults and/or have a smaller rooting volume.

Juvenile and adult plants also differ in how they allocate their resources: juvenile plants allocate a larger proportion of their biomass to belowground tissues. Both the root:shoot ratio and the ratio of fine root:foliage are larger for juvenile western junipers than for sub-adults (fig. 8E). Although this greater allocation to roots likely helps juvenile junipers acquire soil moisture, greater allocation does not completely mitigate greater water use of juvenile foliage, as evidenced by more negative Ψ of juvenile foliage. The greater allocation to roots may also increase the ability of juvenile plants to compete with co-occurring species.

Contrasts with Sagebrush

Carbon Gain and Water Relations – The potential for carbon gain on a per gram of foliage basis are much lower for both juniper and pinyon than for co-occurring shrub-steppe species such as sagebrush. For example, maximum assimilation for sagebrush is approximately an order of magnitude greater than that for Utah juniper and about six times greater than that for singleleaf pinyon (fig. 9A). When expressed on a per unit nitrogen basis, differences between sagebrush and the conifers decrease, but sagebrush is still six and four times greater than Utah juniper and singleleaf pinyon, respectively. In addition, stomatal conductance, leaf nitrogen content, and leaf phosphorous content of sagebrush are also significantly greater than those for the conifers (DeLucia and Schlesinger 1991).

Assimilation of sagebrush is also more drought tolerant than that of the conifers. The drop in assimilation with increased drought stress is more gradual for sagebrush than for one-seed and Utah junipers, and much more gradual than for singleleaf pinyon and pinyon pine (fig. 9B). To extend comparisons made above: when predawn Ψ is near -2 MPa, assimilation rates of the 2 pinyon species are near zero, that of Utah juniper is approximately 1/3 of maximum, that of one-seed juniper is near 1/2 of maximum, while that of sagebrush is near 2/3 of maximum. Interestingly, water use efficiency of sagebrush is less than that of the conifers. However, high water use efficiency under competitive, water-limited conditions may not confer a large ecological advantage (DeLucia and Schlesinger 1991): during the first part of the growing season when water-limited conditions have yet to occur, water that is not used by the more efficient conifers will likely be used by co-occurring species.

Water and Nitrogen Sources – Pinyon pine and Utah juniper are more dependent on the episodic availability of water near the soil surface than sagebrush. Using the stable isotope deuterium in water, Flanagan and others (1992) demonstrated that pinyon pine and Utah juniper have a greater reliance on summer precipitation than sagebrush. They measured the deuterium content (δD) of precipitation at their study site (closed diamonds and solid line in fig. 10A). If δD of water in xylem of plants is near or above this precipitation line, then the plant is predominantly utilizing current precipitation as its water source. In April, all three species had similar δD values, which means that all three species were utilizing similar sources of water (current precipitation as well as water stored in the soil profile). However, from late spring to midsummer, the two conifer species had δD values near or above the precipitation line whereas δD of sagebrush was substantially below the line. Hence, the two conifers had greater reliance on current precipitation during late-spring to midsummer time period. Even by late summer, when δD of sagebrush suggests use of current precipitation, the relative ranking of the three species suggest that a greater proportion of water for the conifers came from shallow soils. These results plus measurements of plant water potential suggest that the conifers have a greater proportion of their active roots in shallow soils than sagebrush (Flanagan and others 1992). This greater proportion of roots in shallow soils for the conifers does not necessarily imply that they are more able to exploit summer precipitation than sagebrush: in a year with a dry spring and early summer, roots of sagebrush were more responsive to small precipitation events during summer than Utah juniper (Flanagan and others 1992).

Utah juniper appears to receive a large proportion of its nitrogen from shallow soils. Evans and Ehleringer (1994) used measurements of the nitrogen stable isotope content ($\delta^{15}N$) of plant tissues to determine the source of nitrogen for Utah juniper, pinyon pine, and sagebrush. $\delta^{15}N$ of nitrogen fixed by nitrogen fixation, including that fixed by cryptobiotic crust at their study site, is zero (fig. 10B). If $\delta^{15}N$ of plant tissues is near zero, than the plant acquires most of its nitrogen from nitrogen fixation; as $\delta^{15}N$ increases, the proportion of nitrogen from nitrogen fixation decreases. $\delta^{15}N$ of Utah juniper was very close to zero, whereas those for pinyon pine and sagebrush were greater than zero, although similar to each other (fig. 10B). Thus, Utah juniper appears to acquire most of its nitrogen from nitrogen fixation by the cryptobiotic crust, and the portion of the root system that is most active in nitrogen uptake must be in close proximity to the cryptobiotic crust.

Community-level Foliage Biomass – For sites with the same potential resources, foliage biomass of singleleaf pinyon communities greatly exceeds that of shrub communities. Total foliage biomass per unit ground

area of both singleleaf pinyon and sagebrush dominated communities have significant positive relationships with site potential (Tausch and Tueller 1990). In addition, total foliage biomass of shrub-dominated communities has a significant positive relationship with that of adjacent singleleaf pinyon-dominated communities with the same site potential (fig. 11A). However, this relationship is heavily weighted in favor of the trees. Furthermore, the relationship is not uniform over the range of site potential: foliage biomass of pinyon exceeds that of the sagebrush-dominated community by a factor of 25 on low potential, drier sites but only by a factor of 12 on the sites with the highest potential (fig. 11B). Thus, given the same water and nutrient resources on a site, pinyon is able to sustain considerably more foliage biomass than sagebrush. The lower nutrient content of pinyon foliage likely contributes to the ability of pinyon to support much more foliage per unit ground area on any particular site.

Although the physiological performance of sagebrush exceeds that of pinyon when measured on a per unit foliage basis, the greater foliage biomass per unit ground area for the conifers appears to compensate for their conservative ecophysiology. The average increase in foliage biomass over the range of sites in figure 11B was about 16. Thus, even though the assimilation rate per unit foliage of sagebrush is four to six times greater than that of pinyon, the pinyon-dominated community has the potential to assimilate at least two to three times more carbon than sagebrush-dominated communities when measured on a ground area basis. The differences in foliage biomass in figure 11B were determined at peak biomass in early to mid summer. During late-fall, winter, and early-spring, sagebrush and associated perennial grasses lose a large proportion of their foliage, whereas pinyon loses almost none. Thus, during these time periods, and especially in early spring when growth starts, the potential for carbon gain by pinyon is even greater than the 2-3 times indicated above. Water use would follow an analogous pattern: greater foliage biomass per unit ground area of pinyon overcompensates for more conservative water use per unit foliage, with the difference between pinyon and the shrub-steppe community enhanced during earlier spring when water availability is near its peak. However, the extent that these differences in phenology and size confer a competitive advantage for pinyon needs a thorough investigation. None-the-less, these opposite differences in ecophysiology and foliage biomass between sagebrush and pinyon appear to be important for community changes. Tausch and West (1995) found that the period of rapid increase in tree dominance and in understory suppression began when pinyon foliage biomass was over twice that of the sagebrush community on a unit ground area basis, which corresponds with the time that potential carbon gain as well as potential water use of pinyon on a per unit ground area is roughly equivalent to that of the shrub-steppe community. Interestingly, the shift in species dominance also occurs after the pinyons have largely lost their juvenile foliage.

SUMMARY

The ecophysiological traits of juniper are often qualitatively similar to those of pinyon. For example, seasonal variation in ecophysiological characteristics tend to be small for both genera. However, some small quantitative differences between the two genera may partially account for some of their differences in geographic distribution. Greater drought tolerance of juniper allows it to occupy more xeric sites, whereas greater potential for carbon gain in pinyon may increase its potential to exploit more benign environments, especially those with high nitrogen availability.

Compared to other species, and especially with sagebrush, pinyon and juniper have conservative ecophysiological traits when measured on a per unit foliage basis. Sagebrush has greater potential for carbon gain per unit foliage, and its photosynthetic apparatus is more tolerant of water stress than that of the conifers. The small variation in seasonal assimilation for both genera and in assimilation-leaf nitrogen relationships for juniper suggests that the foliage of the conifers has limited capabilities for rapid exploitation of abundant resources. The conifers are also more dependent on the episodic availability of water in shallow soils than sagebrush. Finally, juniper acquires a large proportion of its nitrogen almost directly from nitrogen fixation by the cryptobiotic crust, whereas pinyon and sagebrush acquire their nitrogen from a larger proportion of the soil profile.

The generally conservative ecophysiological traits of pinyon and juniper appear to be at odds with its ability to almost triple its dominance of the landscape over the last 20 years. If sagebrush has superior ecophysiological traits, then why have the conifers been so successful at invading shrub-steppe? Clearly, ecophysiological traits do not provide, by themselves, the mechanism for success. However, these conservative traits may benefit the conifers in at least 2 major ways. First, accumulating evidence that nurse plants are important for establishment of juniper and almost essential for pinyon (Chambers and others, this volume) suggests one important role. Although nurse plants likely moderate microclimate for pinyon and juniper seedlings, the conifers still must be able to tolerate reduced resource availability as well as compete effectively for resources. Interestingly, the ecophysiological performance of singleleaf pinyon seedlings is generally better when growing under sagebrush plants than when they grow in the open or in a location where sagebrush has been removed (Callaway and others

1996). A generally conservative ecophysiology as well as the attributes of juvenile foliage likely enhance the establishment and growth of pinyon and juniper under nurse plants. Second, their conservative ecophysiology, especially the low nutrient content per unit foliage, allow the conifers to produce much more foliage biomass per unit ground area than sagebrush. Thus, the conservative ecophysiological traits of these conifers coupled with their greater longevity allow pinyons and junipers to establish, maintain growth under competitive conditions, and ultimately outsize and outlive their nurse plants and other shrub-steppe competitors.

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Table 1 – Mean total carbon assimilation ($\mu mol\ g^{-1}\ d^{-1}$) over the 10-hour daylight period from 8 AM to 6 PM for Utah and western juniper. Measurements were made at 2-hour intervals with a LiCor 6200 (Lincoln, NE) under ambient conditions for each of 12 trees at a low elevation site and at a high elevation site on each of six mountain ranges. Low elevation sites were near the lower elevational limit of juniper on the particular range and high elevation sites were near the upper elevational limit. Measurements were made on two mountain ranges that had western juniper (Juniper Mountain and Sonora Pass) and on four ranges that had Utah juniper (Virginia Mountains, Monitor Range, Snake Range, and Spring Mountains).

Elevation	Late-May	Mid-July	Mid-September
Western juniper			
Low elevation	185	200	103
High elevation	126	152	154
Utah juniper			
Low elevation	155	129	152
High elevation	139	108	199

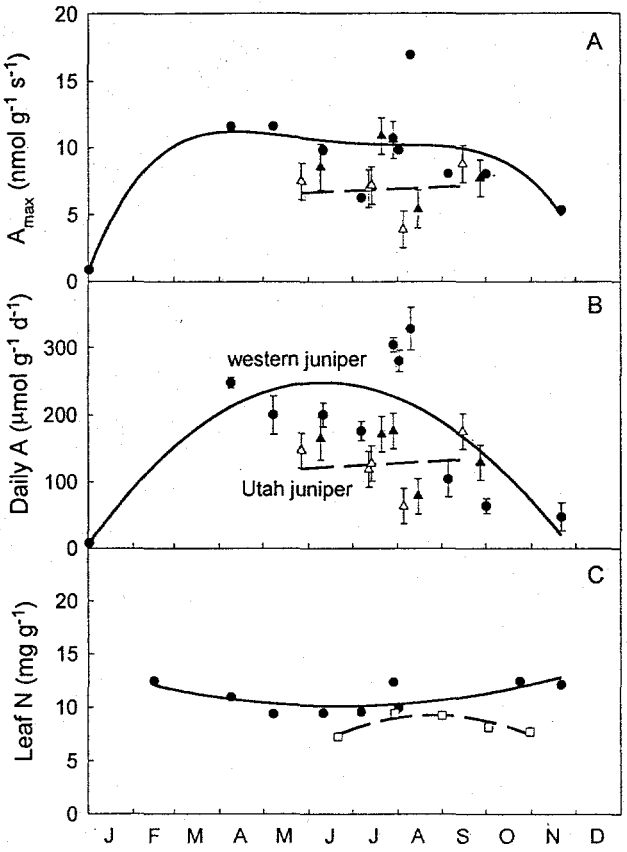

Figure 1. (A) Maximum assimilation rate during the day; (B) total daily carbon gain; and (C) nitrogen content of foliage on different dates during the year for western juniper (closed symbols, solid lines) and Utah juniper (open symbols, dashed lines). Error bars are standard errors. Different symbol shapes indicate sources of data: circles are data from Miller and others (1992: fig. 3, Table 2), triangles are unpublished data of the authors, and squares are data from Ehleringer and others (1986: fig. 5). Although lines are from polynomial curve fitting, they are meant primarily as a guide to general trends of data.

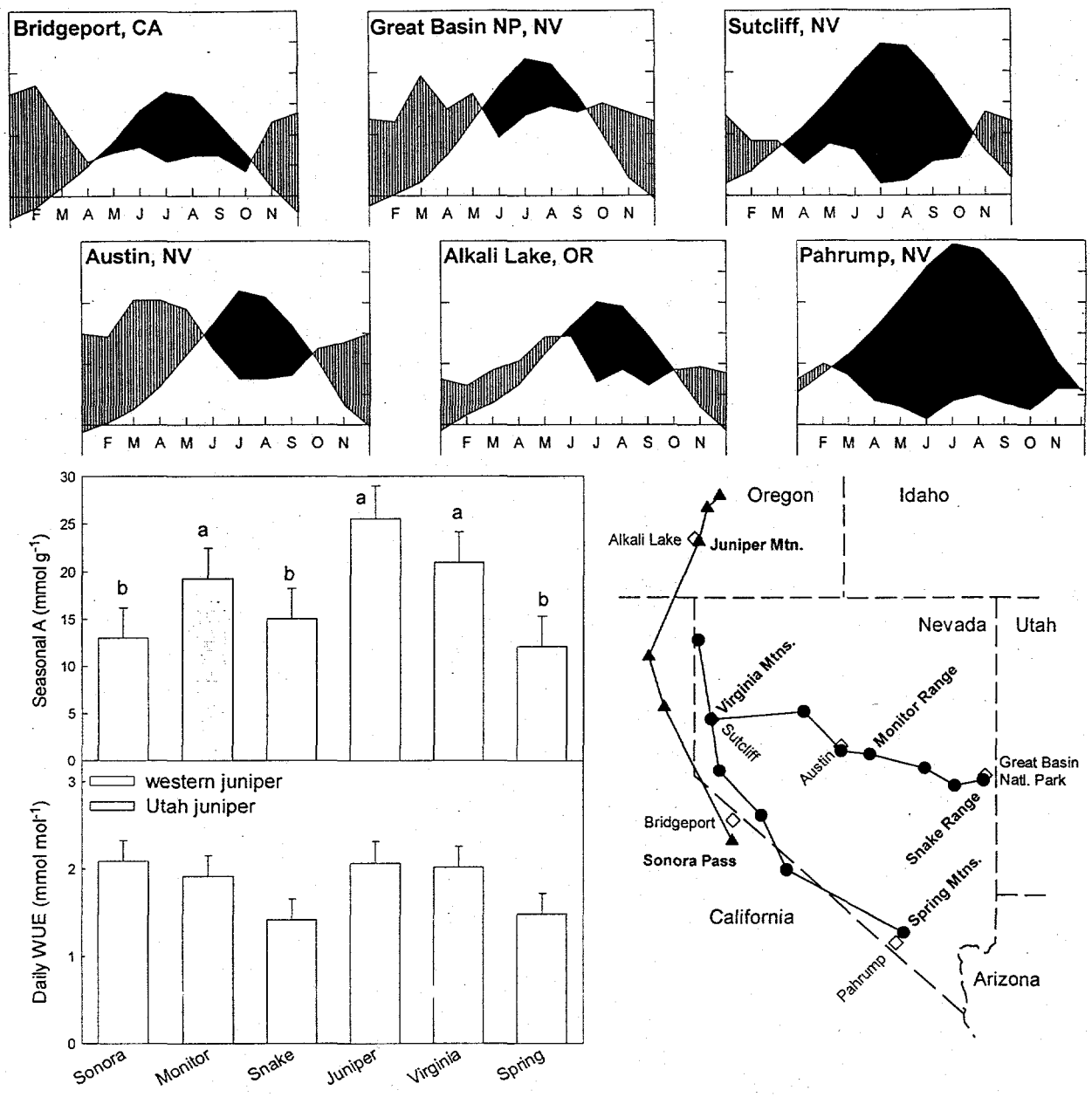

Figure 2.Climatic and leaf gas exchange data for six mountain ranges along three cross-basin transects. At the top are climate diagrams (sensu Walter and others 1975) for the climate station closest to each mountain range. Climate stations are ordered left to right based on increased annual drought severity; drought severity is estimated as the difference between the two types of shaded areas in the climate diagram. For each climate diagram, one line and left y-axis are mean monthly temperature, the other line and right y-axis are precipitation, area shaded with vertical lines represent periods during the year when precipitation is sufficient for plants, and solid area represents periods when water deficits occur. The two lower-left panels are carbon gain over and daily water use efficiency during the time period from mid-May through September. Ranges that include western juniper are indicated by open bars and those with Utah juniper are shaded. Ranges are ordered to correspond with their respective climate diagram. Data are unpublished data of the authors. Locations of each mountain range (bold text, solid symbols) and climate stations (open diamonds) are shown on the map, which also shows all study plot locations for western (triangles) and Utah (circles) juniper cross-basin transects of the authors.

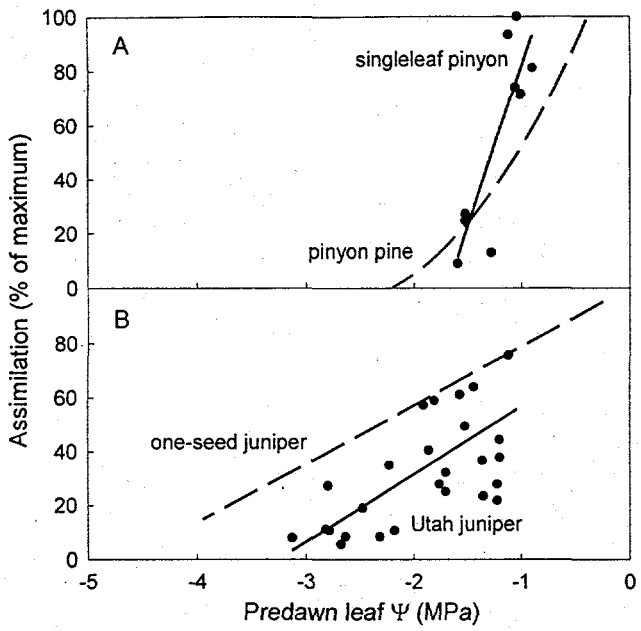

Figure 3. Relationship between assimilation rate (expressed as a percentage of maximum) and predawn leaf water potential for: (A) singleleaf pinyon (closed circles, solid line) and pinyon pine (dashed line); and (B) Utah juniper (closed circles, solid line) and one seed juniper (dashed line). Data for singleleaf pinyon and Utah juniper are from DeLucia and Schlesinger (1991: fig. 1), with solid lines as regressions of their data; dashed lines are second order and first order regression equations for pinyon pine and one-seed juniper, respectively, as reported by Lajtha and Barnes (1991: Table 1).

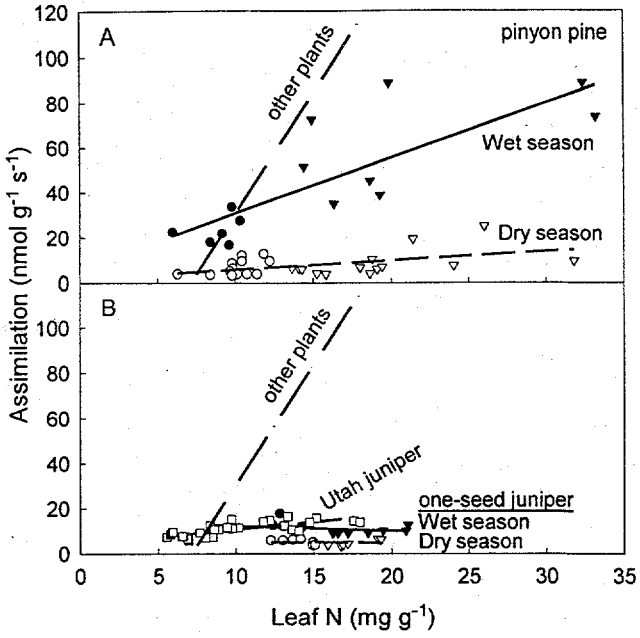

Figure 4. Relationship between assimilation and leaf nitrogen content for: (A) pinyon pine; and (B) Utah and one-seed junipers. For reference, the regression line for a number of other vascular plants from Field and Mooney (1986: fig. 1.2) (dot-dash line) is also shown in both panels. Data for pinyon pine and one-seed juniper are from Lajtha and Barnes (1991: fig. 3); closed symbols and solid line are data from the wetter portion of the year, open symbols and dashed lines are from the dryer portion, circles are from trees under natural soil nitrogen conditions, and triangles are from trees that were fertilized with nitrogen. Data for Utah juniper (open squares) are from Marshall and others (1994: fig. 2). All lines are first order regressions.

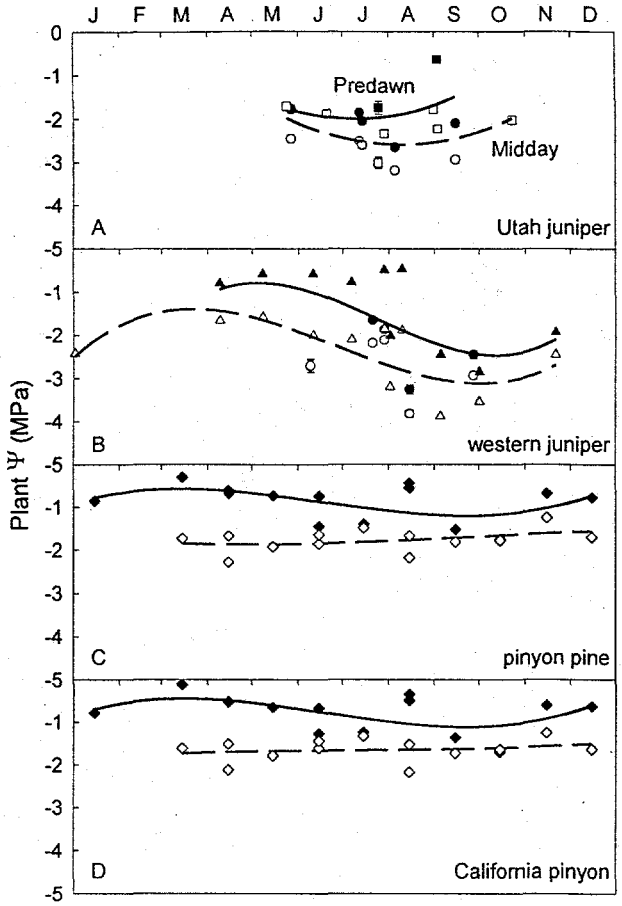

Figure 5. Changes in predawn (closed symbols, solid lines) and midday (open symbols, dashed lines) plant water potential during the year for: (A) Utah juniper; (B) western juniper; (C) pinyon pine; and (D) California pinyon. Different symbol shapes indicate sources of data: for Utah juniper, circles are unpublished data of the authors and squares are from Ehleringer and others (1986: fig. 3) and Marshall and Ehleringer (1990: Table 1); for western juniper, circles are unpublished data of the authors and triangles are from Miller and others (1992: fig. 6); for both pinyon species, data are from Malusa (1992: fig. 2). Error bars are standard errors. Although lines are from polynomial curve fitting, they are meant primarily as a guide to general trends of data.

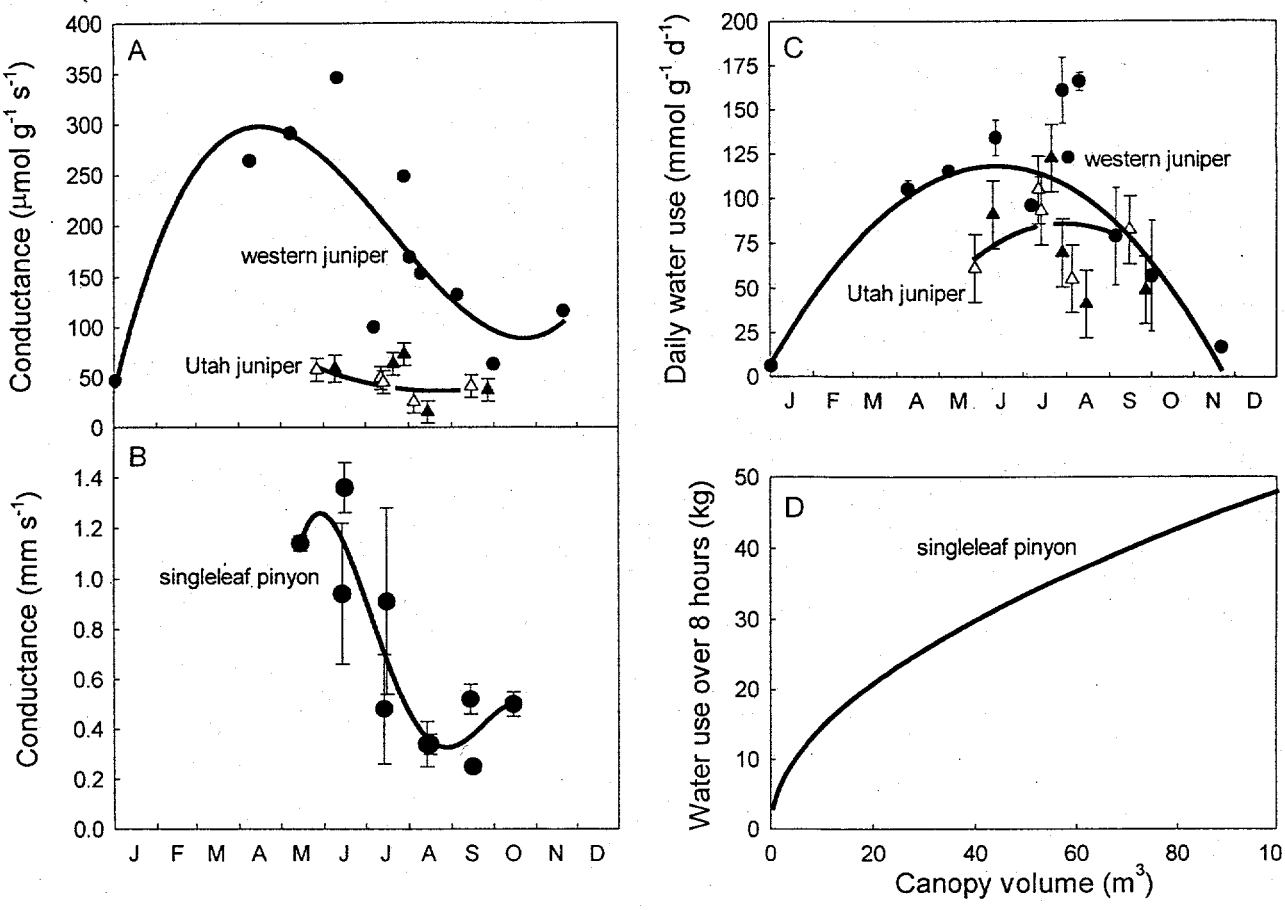

Figure 6. (A) Maximum conductance during the day for western (closed symbols, solid line) and Utah (open symbols, dashed line) junipers; (B) maximum conductance for singleleaf pinyon; (C) total daily water use for junipers; and (D) relationship between canopy volume of singleleaf pinyon and water use over the eight-hour period from 8 AM to 4 PM. Error bars are standard errors. Different symbol shapes in (A) and (C) indicate sources of data: circles are from Miller and others (1992: fig. 5); triangles are unpublished data of the authors. Data in (B) are from Jaindl and others (1995: figs. 4, 5). Regression line in (D) is from DeRocher and Tausch (1993: Table 1). Except for (D), lines are meant primarily as a guide to general trends of data, even though they are from polynomial curve fitting.

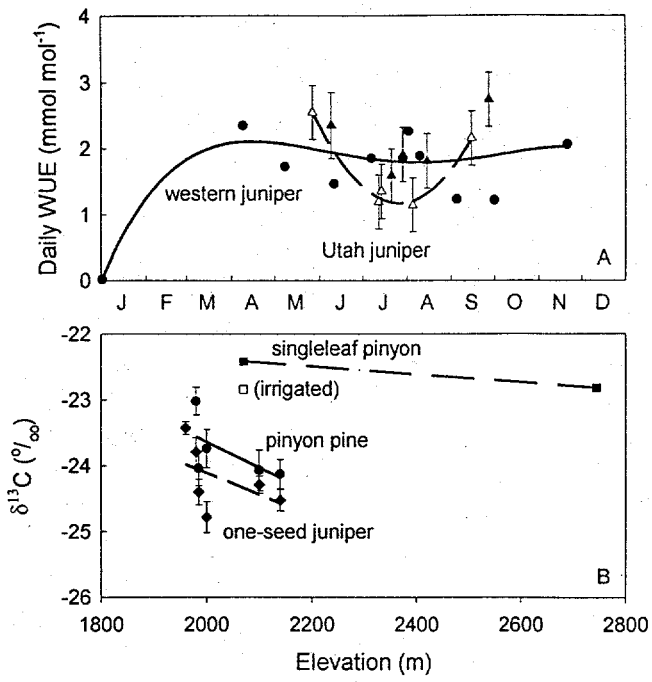

Figure 7. (A) Daily water use efficiency for western (closed symbols, solid line) and Utah (open symbols, dashed line) junipers during the year. Different symbol shapes indicate sources of data: circles are data from Miller and others (1992: fig. 12) and triangles are unpublished data of the authors. (B) Carbon isotope composition of singleleaf pinyon (squares, dot-dash line), pinyon pine (circles, solid line), and one-seed juniper (diamonds, dashed line) for plants on study sites located at different elevations. For singleleaf pinyon, results are also shown for an irrigated plot at the lower elevation (open square). Data for singleleaf pinyon are from Jaindl and others (1993: Table 2), and data for pinyon pine and one-seed juniper are from Lajtha and Getz (1993: Table 2). For both panels: error bars are standard errors, and lines are meant primarily as a guide to general trends of data, even though they are from polynomial curve fitting.

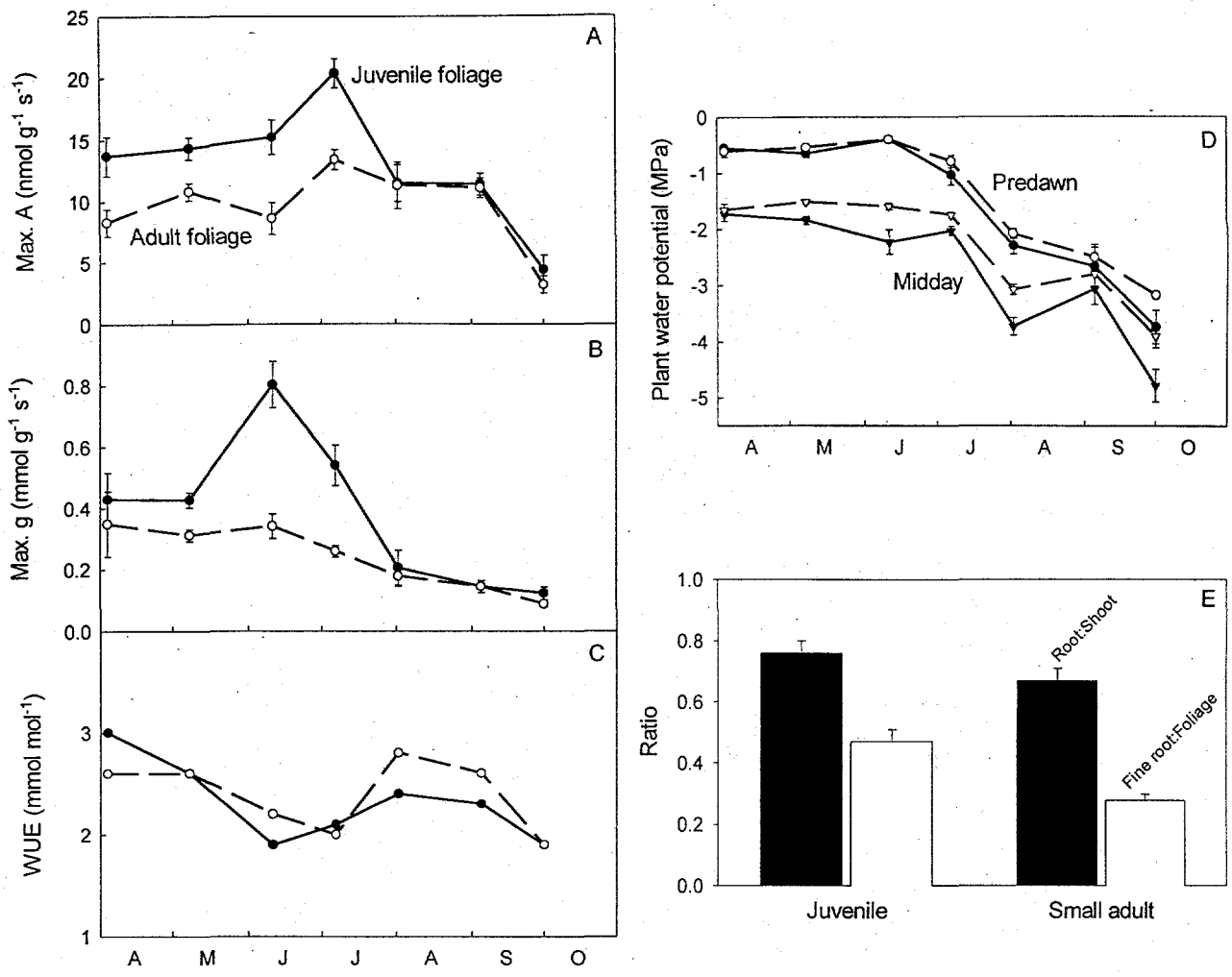

Figure 8.(A) Maximum assimilation rate during the day; (B) maximum stomatal conductance during the day; (C) instantaneous water use efficiency; (D) predawn (circles) and midday (inverted triangles) plant water potentials; and (E) root:shoot (solid bars) and fine root:foliage (open bars) ratios for juvenile and adult western juniper. Closed symbols in panels (A)-(D) are for juveniles, and open are for adults. Error bars are standard errors. Data are from Miller and others (1995: Tables 1, 3) except for data in (E), which is from Miller and others (1990: Table 5).

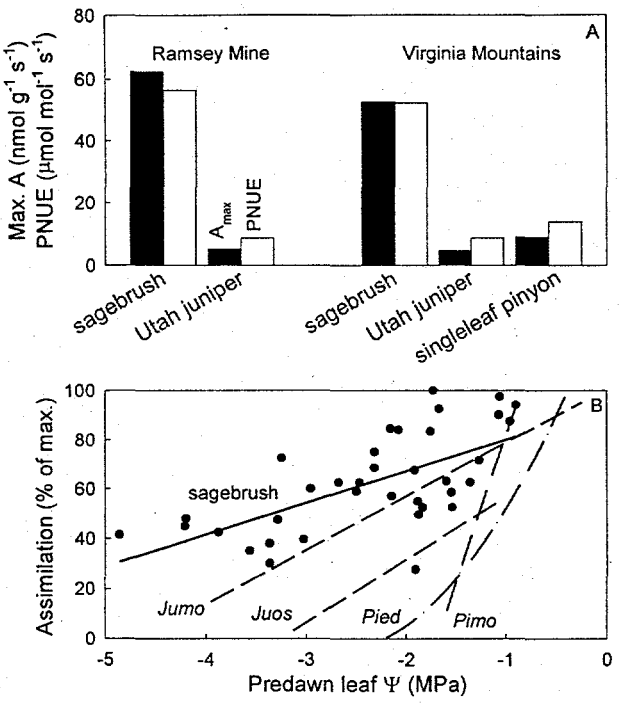

Figure 9. (A) Maximum assimilation (solid bars) and photosynthetic nitrogen use efficiency (shaded bars) for sagebrush and Utah juniper at two study sites and for singleleaf pinyon at the second study site. (B) Relationship between assimilation rate (expressed as a percentage of maximum) and predawn plant water potential for sagebrush (circles and solid line), contrasted with those for junipers (dashed lines; Jumo = one-seed juniper and Juos = Utah juniper) and pinyons (dot-dash lines; Pied = pinyon pine and Pimo = singleleaf pinyon). Lines are first order regressions, and lines for junipers and pinyons are the same as shown in figure 3. Data in (A) and for sagebrush in (B) are from DeLucia and Schlesinger (1991: Table 1, fig. 1)..

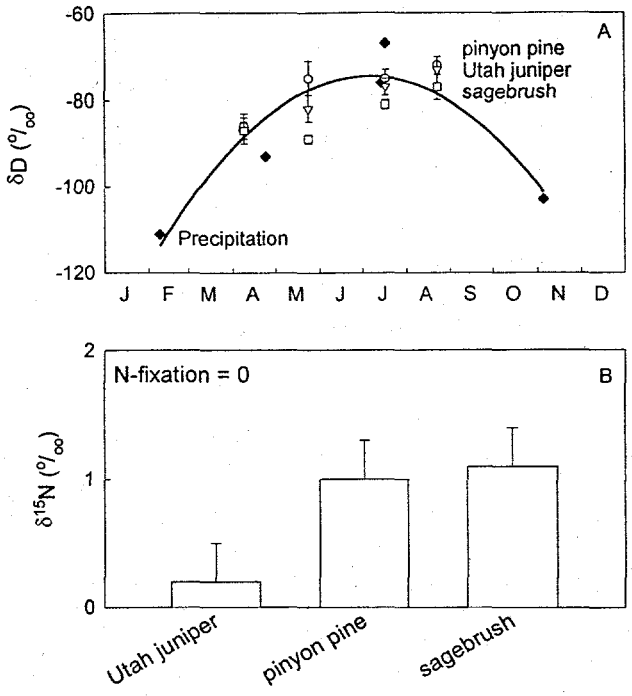

Figure 10. (A) Deuterium stable isotope content (δD) of precipitation (solid diamonds, solid line) and of xylem water from pinyon pine (open circles), Utah juniper (open inverted triangles), and sagebrush (open squares) during the year. Line is a second order regression of the precipitation data, and error bars are standard errors. Data are from Flanagan and others (1992: fig. 1, Table 1). (B) Nitrogen stable isotope content ($\delta^{15}N$) of foliage from Utah juniper, pinyon pine, and sagebrush. Data are from Evans and Ehleringer (1994: Table 1).

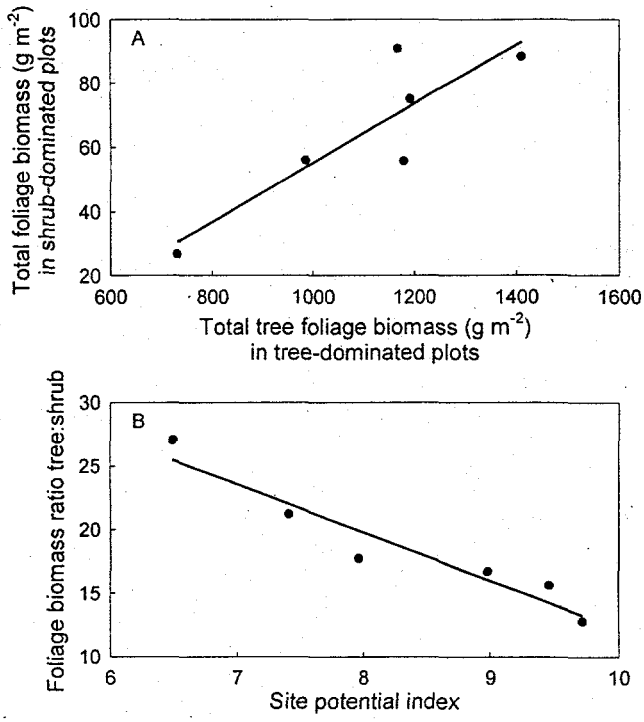

Figure 11. A) Relationship between total foliage biomass of singleleaf pinyon in plots dominated by pinyon and total foliage biomass of all species in plots dominated by shrubs for paired plots on sites with different site potential. B) Relationship between site potential, as indicated by a site index based upon tree height at age 200 years, and the ratio of foliage biomass of pinyon in plots dominated by pinyon to foliage biomass of all species in plots dominated by shrubs. For both (A) and (B), lines are linear regressions. Redrawn from Tausch and Tueller (1990; figs 4 and 5).