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GENETIC DIVERSITY AND LOW REPRODUCTIVE SUCCESS
IN ISOLATED POPULATIONS OF UTAH JUNIPER
(*JUNIPERUS OSTEOSPERMA*, CUPRESSACEAE)

Loreen Allphin^{1,2}, Amy F. Hunt¹, and Val J. Anderson¹

ABSTRACT.—Utah juniper (*Juniperus osteosperma*) has greatly expanded its historical range in the western United States. Management plans for the species have focused on curtailing its encroachment into sagebrush and grassland communities. These plans often include burning or other methods of elimination. These methods may result in subdivision or fragmentation of existing juniper stands. We initiated a study at Dugway Proving Ground, a U.S. Army facility, to examine the effects of fragmentation on the reproductive success of Utah juniper in isolated populations. We used enzyme electrophoresis to quantify genetic variability in isolated populations. We also determined population reproductive success by examining juniper fruits for evidence of seed abortion and/or presence of insect parasites. We compared reproductive and genetic variability in isolated populations at Dugway to 2 nonisolated and encroaching Utah juniper populations. The Dugway populations exhibited reduced seed set due to high seed abortion and/or insect seed parasitism, and a loss of genetic variability in comparison to the nonisolated populations. Additionally, there was a significant correlation between reproductive success and genetic variability.

Key words: genetic variability, inbreeding, *Juniperus osteosperma*, reproductive isolation, seed abortion, seed set, Utah juniper.

Utah juniper (*Juniperus osteosperma*) is a long-lived, shrubby tree species that is a native endemic of the western United States (Loehle 1988). Utah juniper currently covers an estimated 71,500 km² in the west central Rocky Mountains and the Great Basin of the western United States (Terry et al. 2000b; Fig. 1). This hardy species can withstand severe drought, extreme temperatures, and rocky soil (Springfield 1976, Zarn 1977).

Utah juniper has expanded its historical geographic range in the western U.S. since European colonization (Betancourt 1987, Loehle 1988, Tausch 1999). Moreover, stands that were once open-canopied (i.e., savanna-like) have become dense, thick forests (Tausch 1999). Utah juniper has also encroached into other ecological communities (i.e., sagebrush and grassland communities; Aro 1971, Tausch 1999). Ecological expansion and encroachment by Utah juniper has occurred in response to overgrazing (including the reduction of fine fuels by livestock grazing), fire suppression, and change to warmer, drier climates (Clary et al. 1974, Betancourt 1987, Tausch 1999).

Thus, much research on Utah juniper is aimed at controlling its encroachment (Aro

1971, Springfield 1976, Everett and Clary 1985, Evans 1988, Stevens 1999). Methods such as herbicide application, chaining, and controlled burning have been used to eradicate encroaching Utah juniper populations (Blackburn and Tueller 1970, Aro 1971, Bunting et al. 1987, Despain 1987). These methods often result in subdivision or fragmentation of juniper stands. The effect of this fragmentation on the integrity of remaining juniper populations has been given little consideration. Although the species is thought to be invasive, one might expect long-term genetic and reproductive consequences to result from subdivision or fragmentation of juniper populations, which is accomplished through controlled burns (Wilcox 1980, Barrett and Kohn 1991, Sun 1996, Fahrig 1997, Gaines et al. 1997, Allphin and Windham 2002).

Populations of Utah juniper that were historically isolated by elevation and distance have also become further isolated as a result of recent wildfires, which burn through existing populations by using invasive *Bromus tectorum* (cheatgrass) as fuel (Aro 1971, Everett and Clary 1985). If wildfires or controlled burns create even further fragmentation and reproductive isolation of juniper populations,

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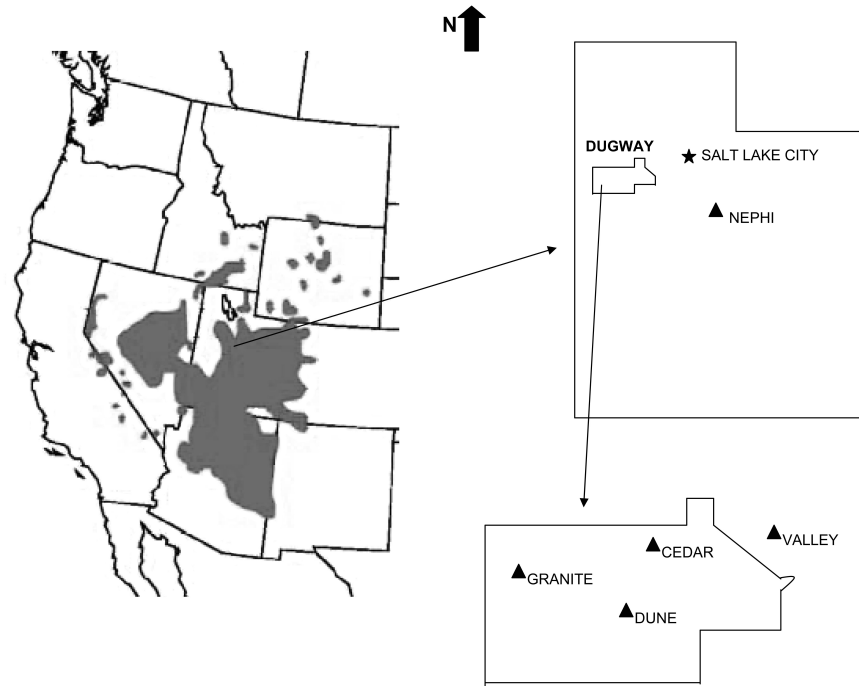


Fig. 1. Distribution of *Juniperus osteosperma* in Western North America, including a map of Utah indicating the 5 collection sites of *J. osteosperma* used in this study.

fewer nonrelated individuals may be available for mating (Levin 1984, Daehler 1999, Sorenson 1999) and inbreeding might become an increasing problem in these forest stands (Charlesworth and Charlesworth 1987, Waser 1993, Allphin et al. 2002). In isolated populations where inbreeding may ultimately result in loss of genetic diversity, reproductive success may decrease (Danzmann et al. 1986, Ledig 1986, Levin 1989, Nickrent and Wiens 1989, Daehler 1999, Sorenson 1999).

Decreased reproductive success in inbred populations may manifest itself as low seed set. Because outcrossing populations (like monoecious, wind-pollinated Utah juniper) are able to maintain potentially lethal recessive alleles in the heterozygous state (genetic load), inbreeding in isolated and/or fragmented populations may increase the frequency of homozygous combinations of lethal recessives. Populations with high levels of deleterious recessive alleles may exhibit reduced reproductive success when lethal alleles are exposed during sexual recombination, resulting in the abortion of developing seeds (Hardon 1961, Sorenson 1969, Wiens 1984, Wiens et al. 1987, Allphin

et al. 2002). Moreover, genetic drift in small, isolated populations could also lead to a fixation of mildly deleterious alleles that might also limit reproductive success.

Utah juniper populations persist after fires because of the survival of a few tall (and usually very old) trees that reseed the area (Covington and DeBano 1990). Population persistence in Utah juniper after fire may also be due to recruitment from an existing seed bank in the soil. Therefore, if Utah juniper populations have diminished reproductive capacity, their persistence after future fires becomes even less probable.

Isolated populations of Utah juniper at Dugway Proving Ground (DPG), a U.S. Army testing and training facility in the West Desert of Utah (est. 1942), appear to suffer from low recruitment and low population reproductive success. Initial field surveys of Utah juniper populations at DPG in spring 2000 revealed that there were fewer juveniles in the DPG populations than in nearby nonisolated juniper populations. We counted only 2 juveniles in a 3-km² area of a Utah juniper population located on Granite Mountain at DPG. In contrast, a

Utah juniper population located 225 km (air distance) southeast of DPG had more than 20 juveniles in a similarly sized area. Initial examination of mature fruits of Utah juniper at DPG populations revealed high levels of seed abortion and insect parasitism of seeds.

Historically, Utah juniper populations at DPG have been geographically isolated from other populations. Fires, caused by spent ammunition during army training, have resulted in the significant loss of the already isolated Utah juniper populations at DPG. Recently, natural wildfires have also threatened, destroyed, and/or further isolated many of the juniper woodlands at DPG.

Therefore, we suggest that loss of genetic variability and reproductive isolation might be contributing to decreased reproductive success (low recruitment and low reproductive success) in isolated juniper populations at DPG. To examine the effects of fragmentation and isolation on reproductive success in Utah juniper at DPG, we assessed both reproductive success (seed set) and genetic diversity in isolated populations of Utah juniper at DPG. We examined the contribution of seed abortion and insect parasitism of seed to overall reproductive success in this taxon. We compared reproductive success and genetic diversity in these isolated populations at DPG with 2 nonisolated, expanding populations of the same species. We predicted that isolated populations of Utah juniper at DPG would exhibit lower genetic variability and lower reproductive success than nonisolated, expanding populations. We further predicted that small populations with reduced genetic diversity would also exhibit increased abortion of developing seeds because of familial breeding (inbreeding) and increased insect parasitism of seed because of decreased resistance.

METHODS

Study Area

We selected 5 study populations in Utah in which to examine the effects of fragmentation and isolation on reproductive success in Utah juniper at DPG (Fig. 1). Three of the study populations were located on DPG (Granite Mountain, Cedar Mountain, and Dune; Fig. 1). The Granite Mountain (Granite) population is thought to have been isolated from the other

Dugway populations for the last several hundred years by elevation and/or distance. The Cedar Mountain (Cedar) and Dune populations have been more recently isolated by wildfire.

For comparative purposes, we also sampled 2 populations not located on DPG (Fig. 1). These control populations were large, continuous, encroaching populations growing in similar soil and climatic conditions at roughly the same elevation as the DPG populations. One population (Valley) was located in a valley ~16 km east of DPG. The other control population (Nephi) was located at the north end of Juab County, ~225 km south of DPG, near the town of Nephi, Utah. Both control populations were considered isolated from DPG (because of geographic distance and/or the south-southwest prevailing wind patterns) and were not thought to interbreed with the populations at DPG, either historically or currently.

Field Sampling

We collected leaf tissue and berries for genetic and reproductive studies from Utah juniper trees at all 5 of the study populations (Fig. 1). At each population, we used the point-quarter method (Cottom and Curtis 1956) to randomly select ~40 individuals from which leaf tissue and mature fruits were collected (Table 1). All leaf tissue and fruit samples were collected during the fruiting season (March–April) of 2000 and 2001.

Because the sampled trees were located in rough mountain terrain, as well as within areas that were near restricted weapons-testing sites at DPG, we collected samples where access roads to populations were available. Five access roads were designated for each population. From these access roads, we established 2 sampling points at 50-m distances in opposite compass directions and perpendicular to the access road. These became the sampling points for the point-quarter method (Cottom and Curtis 1956).

At each sampling point, we measured the distance from the point to the nearest tree in each of 4 quarters and the distance from the sampled tree to its nearest neighbor within each quarter. We assigned each sampled tree and its nearest neighbor to 1 of 3 age classes: seedling, juvenile (prereproductive), or mature (Bunderson 1983). From these data we determined the proportion of measured individuals

TABLE 1. Characteristics of the 5 Utah juniper populations in this study, including population location, estimated population size, number of individuals sampled, proportions of individuals sampled and nearest neighbors in 3 age classes, and population density.

Population	Population location	Estimated population size	Total individuals sampled	Proportion seedlings	Proportion juveniles ^a	Proportion adults	Population density (individuals · km ⁻²)
Granite	DPG ^b	250–300	40	0.056	0.097	0.847	4.8
Cedar	DPG	300–350	40	0.058	0.115	0.827	9.9
Dune	DPG	100	40	0.035	0.089	0.893	6.4
Valley	20 km east of DPG	1000+	32 ^c	0.194	0.083	0.722	28.4
Nephi	250 km SE of DPG	1000+	40	0.194	0.082	0.726	9.5

^aJuveniles are prereproductive individuals, not the current year's seedlings.

^bDugway Proving Ground, U.S. Army testing facility in the West Desert of Utah.

^cOnly 32 individuals were sampled due to problems associated with access to private property.

falling into each age class for each population.

We used the point-to-organism and nearest-neighbor distances to compute an unbiased estimate of juniper density (Diggle 1975). Diggle's (1975) estimate of density is a compound estimate based on the geometric mean of juniper density computed from point-quarter data (point-to-organism distances) following Pollard (1971) and the density computed from nearest neighbor distances following Byth and Ripley (1980).

Reproductive Analyses

For reproductive analyses, we randomly collected approximately 40–60 juniper berries from all parts of each mature tree that we sampled, and then we stored the berries in a cool, dry place until analysis. For reproductive analysis, these sampled berries were split open and the seeds were identified as normal, aborted, or parasitized by larval insects.

From these reproductive data, we calculated mean seed-per-ovule (S/O) ratio (i.e., the proportion of ovules that mature into seeds), mean proportion seed aborted, and mean proportion seed parasitism by insect larvae for each population. (We note here that S/O ratios are likely to be overestimates because we do not take into consideration berries that might have fallen from the trees because of the abortions of premature seeds.) An arcsine transformation was performed to normalize proportion data for statistical analyses (Zar 1996). Significant differences in population and yearly effects of these parameters, as well as year-population interactions, were identified using a 2-way ANOVA. We ran post hoc Tukey comparisons to assess significant differences among the individual populations for these means. All sta-

tistical analyses were performed using SYSTAT 9 (SPSS 1999).

We looked for a potential relationship between stand density and reproductive success. In order to determine if these 2 parameters were correlated, we used SYSTAT 9 to perform 3 linear regressions (using mean population values across both years of study, $n = 5$): stand density against S/O ratio, stand density against insect seed parasitism, and stand density against seed abortion.

Allozyme Analyses

We determined genetic variability within and among the sampled populations using enzyme electrophoresis. Leaf tissue samples collected from field populations were placed in moistened plastic bags and stored on ice (or in a refrigerator) until they could be ground for electrophoresis (<48 hours). Tissue samples were ground in a PVP-phosphate grinding buffer (Soltis et al. 1983). The ground material was absorbed into Whatman 3MM filter paper wicks and stored at -70°C until electrophoresis. Each tissue sample was surveyed for genetic variability at 15 enzyme loci using a variety of gel and electrode conditions (Soltis et al. 1983, Odrzykoski and Gottlieb 1984). Twelve enzyme loci provided consistent, variable, and interpretable results (Table 2).

Diversity statistics were calculated for the 12 variable loci following Wright (1943), Weir (1996), and Hartl and Clark (1997). Genetic data analysis (GDA) software was used to analyze allelic data (Lewis and Zaykin 2001). The following descriptive statistics were computed to assess the genetic diversity within each population: mean observed heterozygosity (H_o ; direct estimate), Hardy-Weinberg (H-W)

TABLE 2. Enzymes and buffer systems used in allozyme population genetic analysis of *Juniperus osteosperma*.

Enzyme	Acronym	EC number ^a	Buffers ^b	Loci scored
Aldolase	Ald	4.1.2.13	11, M	1
Esterase	Est	3.1.1.1	6	1
Fructose-1,6-diphosphatase	f1,6dp	3.1.3.11	11, M	1
Isocitrate dehydrogenase	Idh	1.1.1.42	1, 11, M	1
Leucine-aminopeptidase	Lap	3.4.11.—	6, 8	2
Malate dehydrogenase	Mdh	1.1.1.37	11, M	2
Malic enzyme	Me	1.1.1.40	11	1
Phosphoglucomutase	Pgm	2.7.5.1	6	1
6-phosphogluco dehydrogenase	6-pgd	1.1.1.44	M	1
Shikimate dehydrogenase	Skdh	1.1.1.25	M	1
TOTAL LOCI				12

^aEnzyme commission number^bSystems 6,8,11 after Soltis et al. (1983); system M, a 7.5 pH version of the morpholine citrate system after Odrzykoski and Gottlieb (1984).

expected heterozygosity (H_e), polymorphic index (PI = mean proportion of polymorphic loci), mean number of alleles per locus (A), and fixation index (f). We performed a Fisher shuffling test (exact test) of H-W disequilibrium (Fisher 1935, Haldane 1954) for each locus and each study population using GDA (Lewis and Zaykin 2001).

The distribution of genetic variation among the *J. osteosperma* populations was also determined using GDA. The following F-statistics were calculated: F_{IS} , F_{IT} , and F_{ST} (Wright 1921, 1943, Weir 1996, Hartl and Clark 1997). For this study, F_{IS} and F_{IT} were computed using GDA. We calculated F_{ST} among the populations following Wright (1943).

To further assess the genetic interaction among populations, gene flow (Nm = effective number of migrants per generation) was calculated using methods of Wright (1943; $Nm = [1 - F_{ST}] / 4 \cdot F_{ST}$). We computed Nei's (1978) genetic distance for each population and generated a cluster phenogram of the genetic distance matrix among populations using the unweighted pair group method of averaging (UPGMA) and GDA software. We also performed a Mantel matrix randomization test (Mantel 1967) to determine if there was a significant relationship between geographic distance and genetic distance (Rohlf 1992).

We ran linear regressions (using population means for reproductive data averaged across the 2 years of sampling) to determine if any correlations existed between genetic variation (observed heterozygosity) and reproductive success (S/O, proportion seed abortion, proportion seed parasitism). Regressions were performed using SYSTAT 9.

RESULTS

Population Density and Age Structure

Density (individuals \cdot km⁻²) varied among study populations. The Valley population was significantly more dense (≥ 3 times more dense) than all other populations (28.4 individuals \cdot km⁻²; Table 1). The 2 smallest populations at DPG were the least dense (Granite: 4.8 individuals \cdot km⁻²; Dune: 6.4 individuals \cdot km⁻²; Table 1). The 3 DPG populations had fewer seedlings and a greater proportion of adults compared to the nonisolated populations (Table 1).

Reproductive Success

SEED-PER-OVULE RATIO.—Populations differed for S/O ratios ($P = 0.000$; Table 3). Specifically, the Valley and Nephi (nonisolated) populations had higher S/O ratios (almost 2-fold higher) than the isolated DPG populations (Table 3) in both 2000 and 2001. The S/O ratios decreased (by $\sim 7\%$ – 56%) over the 2 collection years in all study populations ($P = 0.007$; Table 3). Furthermore, the interaction between population and year was also significant ($P = 0.000$). We found no correlation between stand density and S/O ($r^2 = 0.351$, $P = 0.394$).

SEED PARASITISM.—Populations varied for seed parasitism by larval insects ($P \leq 0.0005$, range 1%–50%; Table 3). The Granite and Cedar populations at DPG exhibited the highest percentage of seeds parasitized. However, seed parasitism at the Dune population was not significantly different from the nonisolated

TABLE 3. Reproductive results indicating significant differences in S/O ratios, proportion insect parasitism of seeds, and proportion seed abortion in Utah juniper populations. Means in a column that share the same letter within a year do not differ significantly at $P \leq 0.05$. Each year is considered separately in this table and is thus represented by a different suite of letters.

Population	Year	S/O ratio	Parasitized seed	Aborted seed
Granite	2000	0.276 a	0.526 a	0.228 a
Cedar	2000	0.447 b	0.307 b	0.261 a
Dune	2000	0.355 b	0.098 c	0.562 b
Valley	2000	0.743 c	0.104 c,d	0.130 a
Nephi	2000	0.654 c	0.150 d	0.232 a
Mean	2000	0.495	0.237	0.283
Granite	2001	0.178 f	0.321 f	0.498 f
Cedar	2001	0.417 g	0.515 g	0.061 g
Dune	2001	0.196 f	0.293 f	0.510 f
Valley	2001	0.416 g,h	0.194 h	0.379 h
Nephi	2001	0.488 h	0.266 f	0.247 i
MEAN	2001	0.339	0.318	0.328

TABLE 4. Descriptive statistics of genetic variability within Utah juniper populations.

Population	Mean observed heterozygosity (H_o)	Mean expected heterozygosity (H_e)	Polymorphic index (P)	Mean number of alleles/locus (A)	Fixation index (f)
Granite ^a	0.140	0.441	1.00	2.92	0.686
Cedar ^a	0.171	0.359	1.00	2.83	0.527
Dune ^a	0.094	0.393	1.00	2.83	0.764
Valley	0.307	0.504	1.00	2.83	0.394
Nephi	0.256	0.477	1.00	2.92	0.466
ALL POPULATIONS	0.194	0.435	1.00	2.87	0.558

^aDugway populations exhibiting reduced fecundity

populations. Seed parasitism also varied between years ($P \leq 0.0005$). For example, seeds from the Granite population were heavily parasitized in 2000 (53%) but less parasitized in 2001 (32%). The Cedar population (DPG population) was also highly parasitized but exhibited the opposite pattern (31% in 2000 and 52% in 2001). Thus, the interaction between population and year was significant for percent seed parasitized ($P \leq 0.0005$). In addition, we found no relationship between stand density and seed parasitism ($r^2 = 0.232$, $P = 0.412$).

SEED ABORTION.—We observed differences among populations for percent seed aborted ($P \leq 0.0005$; Table 3). The Dune population at DPG exhibited the highest seed abortion rates (56% in 2000 and 50% in 2001; Table 3). The nonisolated populations, Valley and Nephi, had significantly lower seed abortion over the 2 collection years (Table 3). We observed differences among years for percent seed aborted ($P \leq 0.0005$) and an interaction between population and year ($P \leq 0.0005$). Percent seed abortion significantly increased (about 2-fold) in

the Granite population from 2000 to 2001, while it decreased in the Cedar population between years. In addition, we found no significant correlation between stand density and percent seed aborted ($r^2 = 0.008$, $P = 0.888$).

Allozyme Data

GENETIC VARIATION WITHIN POPULATIONS.—Genetic diversity statistics for each of the studied populations are summarized in Table 4. The 2 nonisolated populations had the highest observed heterozygosity (H_o) of the 5 juniper populations we studied (Table 4). The 3 Dugway populations had significantly lower genetic variability. Of the 3 Dugway populations, Cedar, the largest and least fragmented population, was the most variable ($H_o = 0.171$). The Dune population, the smallest population, was the least genetically variable ($H_o = 0.094$; Table 4).

For each of the 5 juniper populations, the proportion of polymorphic loci (P) was 1.0. Thus, all 12 loci had allelic variability in each of the sampled populations. The mean number

TABLE 5. *P*-values for a Fisher's shuffling test of Hardy-Weinberg disequilibrium (Fisher 1935, Haldane 1954) for each Utah juniper population and locus generated using GDA. Significance was determined at $P \leq 0.05$.

Locus	Population				
	Granite ^a	Cedar ^a	Dune ^a	Valley	Nephi
Me-1	0.000	0.000	0.000	0.000	0.000
Lap-1	0.000	0.000	0.000	0.000	0.000
Lap-2	0.000	0.000	0.000	0.014	0.000
Idh-1	0.000	0.001	0.000	0.000	0.000
6pgd-1	0.000	1.000	0.041	0.181	1.000
Skdh-1	0.001	0.000	0.241	0.556	0.032
Pgm-1	0.000	0.106	0.000	0.001	0.043
Mdh-1	0.005	0.014	0.000	0.013	0.010
Mdh-2	0.000	0.000	0.000	0.001	0.000
Ald-1	0.000	0.001	0.000	0.712	0.009
f16dp-1	0.000	1.000	0.000	0.002	0.002
Est-1	0.038	0.002	0.000	0.001	1.000

^aLocated at Dugway Proving Ground, Utah

of alleles per locus (A) was 2.83 for the DPG populations, and it was slightly higher for the nonisolated populations ($A = 2.92$; Table 4).

DEVIATION FROM HARDY-WEINBERG EXPECTATIONS.—Expected heterozygosity (H_e) was lower than observed heterozygosity for each juniper population (Table 4). The smallest populations at DPG, Granite and Dune, exhibited the largest deviations from H-W expectations. The Granite population exhibited significant H-W disequilibrium at all surveyed loci (Table 5). The Dune population showed significant H-W disequilibrium at 11 of the 12 loci surveyed, and Cedar at 9 loci. However, the nonisolated populations also deviated significantly from H-W expectations for most loci (Valley at 9 loci and Nephi at 10 loci; Table 5).

The estimate of the fixation index (f) was lower for the control populations than for the DPG populations (Table 4). The fixation index was lowest for the Valley control population ($f = 0.394$). The 2 smallest populations, which were at DPG, had the highest fixation indices (Dune $f = 0.763$ and Granite $f = 0.686$; Table 4). However, all populations exhibited fixation indices >0 . The mean value of F_{IS} across all 12 loci was 0.566. This positive value indicates that there were fewer heterozygotes than expected within each of the populations (Table 6).

GENETIC VARIATION AMONG POPULATIONS.—The mean F_{IT} was 0.597 for these populations, indicating that there are fewer heterozygotes than expected among the study populations (Table 6). The mean F_{ST} was 0.071, indicating that the degree of genetic differentiation among

TABLE 6. *F* statistics for individual loci of Utah juniper.

Locus	F_{IS}	F_{IT}
Me-1	0.705	0.740
Lap-1	0.682	0.701
Idh-1	0.709	0.712
6pgd-1	0.201	0.348
Skdh-1	0.216	0.237
Pgm-1	0.473	0.471
Mdh-1	0.533	0.596
Mdh-2	0.770	0.805
Ald-1	0.514	0.564
f1,6dp-1	0.702	0.749
Lap-2	0.519	0.525
Est-1	0.298	0.311
OVERALL	0.566	0.597

the populations was moderate (Wright 1951). The estimated rate of gene flow (Nm), computed using F_{ST} , among the sampled populations was high for *J. osteosperma* ($Nm = 2.52$ migrants per generation).

Nei's (1978) genetic distances (D) ranged from 0.007 to 0.152, and geographic distances ranged from 10,393 m to 584,942 m (Table 7). The Mantel matrix randomization test showed no relationship between geographic and genetic distance among populations ($r^2 = 0.004$, $P = 0.863$).

While no relationship existed between geographic and genetic distance, the DPG populations appeared more closely related to one another than to the 2 nonisolated comparative populations (Fig. 2). In the UPGMA cluster phenogram, which was generated from genetic

TABLE 7. Geographic distances and genetic distances between sampled populations of Utah juniper. Geographic distances (m) are given above the diagonal, and Nei's (1972) genetic distances (D) are given below the diagonal.

Populations	Granite	Cedar	Dune	Valley	Nephi
Granite	—	33134.2	37683.3	59661.4	284921.4
Cedar	0.059	—	22279.8	31785.9	257045.9
Dune	0.008	0.063	—	24234.5	249494.5
Valley	0.062	0.152	0.092	—	225260.0
Nephi	0.060	0.127	0.078	0.048	—

distances, the 3 DPG populations clustered together (Fig. 2).

RELATIONSHIP BETWEEN GENETIC AND REPRODUCTIVE DATA.—We found a significant relationship between genetic variation and reproductive success. Mean observed heterozygosity was positively correlated with S/O ratios for both years of the study (2000: $r^2 = 0.892$, $P \leq 0.05$; 2001: $r^2 = 0.632$, $P \leq 0.05$). Each data point in the analysis represents a mean S/O ratio for the sampled individuals in each study population. We found a negative correlation between observed heterozygosity and percent seed abortion in 2000 ($r^2 = 0.624$, $P < 0.01$), but no relationship in 2001 ($r^2 = 0.098$, $P = 0.607$). However, we found no relationship between observed heterozygosity and percent insect parasitism of seeds ($r^2 = 0.218$, $P = 0.427$).

DISCUSSION

Reproductive success varied significantly among study populations. Specifically, S/O ratios were significantly lower in the isolated populations than in the nonisolated populations (with the exception of the largest DPG population, Cedar, in 2001). Moreover, the DPG populations exhibited S/O ratios at or significantly below the average for woody perennial plant species (0.327; Wiens 1984). The nonisolated encroaching Utah juniper populations exhibited S/O ratios much higher than average for woody perennials (Wiens 1984, Wiens et al. 1987). Unusually high S/O ratios in these large, nonisolated populations might contribute to their success and ability to encroach.

Low S/O ratios in the DPG populations were primarily due to high degrees of insect parasitism of seeds and/or high levels of abortion in developing seeds. Both environmental and genetic factors may contribute to high seed abortion and/or seed parasitism in natural populations of conifers and other woody

perennials (Carter 1939, DeBarr 1957, Hard 1963, Crane 1964, Krugman 1966, Dickmann and Kozlowski 1969, Bollard 1970, Goyer and Nachod 1976, Mattson 1978, Stephenson 1980, 1981, Bunderson 1983, Levin 1984, Wiens et al. 1987, Nakamura 1988, Charlesworth 1989, Oritz et al. 1998, Daehler 1999, Sorenson 1999, Garcia et al. 2000). Although this study focused primarily on genetic factors rather than environmental factors, we did show significant differences in reproductive data between the 2 years of our study. Specifically, all study populations but the Cedar population exhibited reduced reproductive success in 2001. In some populations, this reduction was due to an increase in seed abortion, while in others it was due to increased insect parasitism of seeds.

Precipitation might explain the decrease in reproductive success that we observed between years. Annual precipitation was higher at DPG in the year 2000 (21.9 cm) than in 2001 (5.45 cm; U.S. Army unpublished data, weather station at DPG). This difference in annual precipitation was partly due to high precipitation during the month of February 2000. Late winter and/or early spring precipitation might be particularly important for seed production in Utah juniper because this is the time when seeds are maturing on the trees.

Other environmental factors (i.e., light, water, soil nutrients, temperature, etc.) might affect the amount of insect parasitism of seeds in a population (Bunderson 1983, Cates and Redak 1986, Cochran 1998, Garcia 1998, Garcia et al. 2000). In a study of 17 *J. osteosperma* sites, Bunderson (1983) found a positive correlation between insect parasitism and higher levels of phosphorous and magnesium in the soil. However, Bunderson demonstrated that increased parasitism of Utah juniper seeds could not be explained by environmental factors alone (Bunderson 1983).

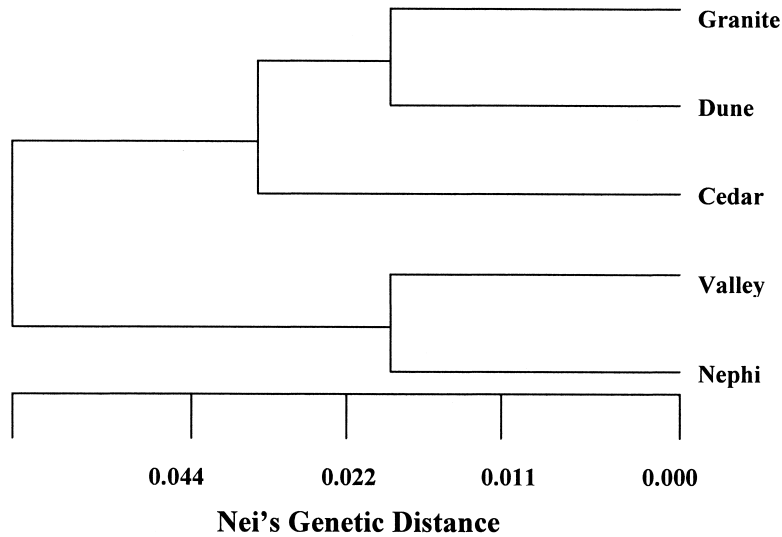


Fig. 2. UPGMA cluster phenogram showing genetic relationships of sampled populations based upon Nei's (1978) genetic distances among populations calculated by GDA, using allele frequencies computed from ~40 randomly sampled individuals in each study population.

The influence of environmental factors on seed set in the Utah juniper was not the focus of our study and merits further examination. Yet it is difficult to explain high levels of abortion with environmental factors alone, since the Dune population suffers greatly from abortion but has a very similar environment to other DPG populations. These data are consistent with other studies that have demonstrated a lack of correlation between resource availability and embryo abortion (Wiens et al. 1987, Lalonde and Roitberg 1989, 1994, Herrera 1991, Allphin et al. 2002, Wiens et al. 2002).

Studies of other conifers have suggested a relationship between susceptibility to insect parasitism and stand density (Ferrell et al. 1933, White 1974, Sturgeon 1979, Gambliel and Croteau 1984, Horner et al. 1987, Cochran 1998). Some have suggested that insect parasites are better able to track their hosts in less dense populations (Fauss and Pierce 1969, Sturgeon 1979) while others argue that tree age is a factor of resistance (Kennedy and Booth 1951, Dickman 1978, Wagner et al. 1989). However, in this study, we found no correlation between juniper stand density and predispersal insect parasitism of seeds. Though this find is interesting, we recognize the lack of robustness for this regression due to the small sample size.

Stand density has also been shown to affect fruit set and pollination success in conifers (Arista and Talvera 1994, 1996, Ortiz et al. 1998). However, we found no significant relationship between stand density and S/O ratio or percent seed abortion. Therefore, stand density does not likely explain our observed patterns of reproductive success in isolated populations of Utah juniper at DPG. Once again, we recognize that the lack of relationship might be a consequence of the small number of stands measured.

Because we found a significant relationship between observed heterozygosity and both S/O ratio and percent seed abortion, low reproductive success in the isolated populations of Utah juniper at DPG might also be explained by genetics. Populations at Dugway have been historically isolated and are becoming increasingly more isolated from one another because of fire. We found that the 3 isolated Dugway populations have lower genetic variability than the nonisolated comparative populations. The DPG populations also exhibited higher fixation (f) indices than the nonisolated populations.

However, all the Utah juniper populations in this study exhibited significant deviations from Hardy-Weinberg equilibrium at most loci. Moreover, all the populations had lower

observed heterozygosity (H_o) than H-W expected heterozygosity (H_e). Because the observed heterozygosity in the populations is less than predicted, it may be assumed that the populations are increasing in homozygosity, a characteristic of inbred mating systems. Populations that become progressively fragmented until they are isolated from one another may ultimately lose genetic variability (Wright 1943, Loveless and Hamrick 1984, Barrett and Kohn 1991, Godt et al. 1995, Allphin et al. 1998, Allphin and Windham 2002). Therefore, inbreeding due to isolation could result in the lower heterozygosity that we observed for the DPG populations.

The DPG populations typically exhibit significantly higher seed abortion rates than the nonisolated populations. Low reproductive success due to high abortion in DPG populations might be explained by inbreeding/genetic load (Wiens 1984, Wiens et al. 1987). Because outcrossing species, like Utah juniper, are able to maintain more potentially-lethal alleles in the heterozygous state (genetic load), inbreeding in isolated/fragmented populations may cause the frequency of homozygote combinations of lethal alleles to increase (Hardon 1961, Sorenson 1969, Levin 1984, Wiens 1984, Wiens et al. 1987, Nickrent and Wiens 1989, Allphin et al. 2002).

Reduced seed set in the isolated populations at DPG may be a result of low genetic diversity and inbreeding (familial breeding) in these small populations (Ellstrand and Elam 1993, Godt et al. 1997). The positive correlation between reproductive success (seed per ovule) and genetic variability in both years of the study supports this idea. The Dune population has the lowest H_o , the highest f , and the highest percentage of aborted seed of the studied populations. Dune also exhibits the highest percentage of aborted seed and is currently the smallest and 1 of the least dense of all the sampled populations. Therefore, the effects of low genetic diversity are likely most pronounced in the Dune population because of its small size.

The Granite and Cedar populations also have low genetic diversity and low population reproductive success. In the Granite population, these results might also be a consequence of small population size and low population density. However, the Cedar population is still

large and relatively dense. Moreover, this population has the highest reproductive success of the 3. It is also important to note that it is difficult to establish the true number of aborted seeds in the Granite and Cedar populations because of their higher parasitism rates. It is likely that many of the aborted seeds in these populations were categorized as parasitized because it was impossible to differentiate if a parasitized seed was once viable or if it was a late abortion.

Loss of genetic variability also often results in a loss of resistance to a variety of insects and other pathogens (Eidt and MacGillivray 1972, McDonald 1985, Cates and Redak 1986, Barret and Kohn 1991). The lack of correlation between heterozygosity and insect parasitism of seeds in our study populations is primarily due to the high level of abortion in the Dune population. If this population is removed from the analysis, there is a significant correlation over both years of our study ($r^2 = 0.877$; $P < 0.01$). Therefore, high predispersal insect parasitism of seeds might also be explained by a loss of genetic variability in small, isolated populations of Utah juniper. However, the Cedar population has higher levels of parasitism than expected for a relatively large, dense population. We suggest that this population may be experiencing genetic drift due to its relative isolation, and it is thus beginning to lose resistance to insect parasitism as it loses genetic diversity.

The historical genetic diversity and the degree of historical isolation of these populations are unknown. We note that historical, long-term isolation of these populations might best explain the loss of reproductive success and genetic variability in these populations. Moreover, little is known regarding the distance of pollen dispersal and seed dispersal in this species. Dispersal factors might also play a role in the degree of isolation in these stands. Additional study will be necessary to examine how dispersal and long-term isolation contribute to low reproductive success and genetic diversity in Utah juniper at DPG.

Low genetic diversity for DPG populations might also be explained by a more recent founder event (invasion) of Utah juniper into a marginal, more ephemeral habitat at DPG. These populations appear to be at the westernmost extension of the species' range in Utah

TABLE 8. Levels of allozyme variation at the species level for species with different characteristics or categories. The data on broad categories were extracted from Hamrick and Godt (1990). The data for *Juniperus rigida* and *J. coreana* were extracted from Huh and Huh (2000). Means followed by the same letter in a column do not differ significantly at $P \leq 0.05$. Standard errors are in parentheses.

Categories	N^*	Mean no. of populations	Mean no. of loci	P_s^\dagger	A_s^\ddagger	H_{es}^\S
Gymnosperms	55	8.5 (0.9)	16.1 (1.3)	70.9 (3.6) a	2.35 (0.12) a	0.173 (0.011) a
Long-lived woody						
perennials	110	9.3 (1.4)	17.0 (0.9)	64.7 (2.7) a	2.19 (0.09) a	0.177 (0.010) a
Regional species	193	10.4 (1.1)	16.7 (0.7)	52.9 (2.1) ab	1.94 (0.06) b	0.150 (0.008) b
Widespread species	105	25.5 (5.2)	14.6 (0.9)	58.9 (3.1) a	2.29 (0.13) a	0.202 (0.015) a
Outcrossing wind-						
pollinated species	105	10.7 (1.6)	16.7 (0.9)	66.1 (2.7) a	2.40 (0.13) a	0.162 (0.0009) ab
<i>Juniperus rigida</i>	—	12	22	72.7 (0.029)	2.63 (0.002) c	0.224 (0.00) c
<i>Juniperus coreana</i>	—	6	22	54.6 (0.006)	2.42 (0.005) ac	0.199 (0.00)a
<i>Juniperus osteosperma</i>	—	6	12	100	2.87 (0.002) c	0.435 (0.003) d

*Number of taxa represented

†Percentage polymorphic loci

‡Number of alleles per locus

§Expected H-W diversity or genetic diversity

(Fig. 1). However, further genetic studies need to be performed in a broader geographic context to explore this hypothesis.

While many genetic diversity studies have been conducted on conifers in the family *Pinaceae*, few have been conducted in the family *Cupressaceae* (Nowak et al. 1994, Zhang et al. 1997, Huh and Huh 2000, Terry et al. 2000a, Van der Merwe et al. 2000). However, we compared our genetic diversity data for Utah juniper with a synthesis paper by Hamrick and Godt (1990), which summarized levels of diversity across a wide sampling of gymnosperms and other plant species with similar life history traits. In addition, we compared our allozyme data with data observed for 2 other juniper species (Table 8; Huh and Huh 2000).

Our populations of Utah juniper exhibited a higher percentage of polymorphic loci than that observed for other gymnosperms, long-lived woody perennials, regional plant species, widespread plant species, outcrossing wind-pollinated species, or other junipers (Table 8). However, *J. rigida* and other gymnosperms were highly polymorphic. Our sampled populations of Utah juniper had a significantly higher mean number of alleles per locus than other gymnosperms and woody perennials, but they had values of the mean number of alleles per locus that were consistent with other junipers (Table 8; Hamrick and Godt 1990, Huh and Huh 2000). Finally, our Utah juniper populations had significantly higher

genetic diversity (H_{es}) than the other junipers, gymnosperms, and species with similar life histories (Table 8; Hamrick and Godt 1990, Huh and Huh 2000). We make general comparisons among allozyme data between similar species and note the inherent problems due to variation in loci analyzed for each species (see Hamrick and Godt 1990).

For Utah juniper in this study, the F_{ST} was 0.071, which indicated moderate genetic differentiation among populations (Wright 1943). Other wind-pollinated, long-lived, conifer populations exhibit F_{ST} values higher than our Utah juniper populations (Hamrick and Godt 1996). For example, F_{ST} values obtained for pine species in conservation studies range between 0.161 and 0.300 (Conckle 1981, Schiller et al. 1985, Hamrick et al. 1994).

Estimated gene flow among these Utah juniper populations was relatively high ($Nm = 2.52$). However, some conifer species have shown even higher rates of gene flow ($Nm = 4.48$; Parker et al. 1997). Although there was a moderately high estimate of gene flow between populations of the juniper based upon genetic distances, we could find no correlation between geographic and genetic distance in this species. This is not as expected under the isolation-by-distance model (Wright 1943, 1946). One might expect a lack of correlation between geographic and genetic distance if panmixia (or regular random mating) were occurring among populations (Wright 1946). This explanation seems unlikely for these populations of Utah juniper because of the historical isolation and

long distances separating many of these populations. Yet Lyford et al. (2003) has suggested that historically, populations of Utah juniper became established through long-distance dispersal events.

We suggest that N_m may not be reflective of actual gene flow events in the juniper, but possibly reflective of alleles shared through common ancestry or historic gene flow events. We used a variant of F_{ST} to estimate N_m . Though studies have shown F_{ST} to be an excellent measure of the extent of population structure, it is rare that F_{ST} can be translated into accurate N_m estimates (Whitlock and McCauley 1999). Therefore, low F_{ST} values among DPG populations may be responsible for the high N_m estimates, rather than actual migration between the DPG populations (Whitlock and McCauley 1999). Moreover, our lack of correlation between geographic and genetic distance might be a consequence of our limited data set with its limited range of distances among populations.

The findings of this study serve to compare only the 3 stagnant DPG populations with 2 continuous, encroaching Utah juniper populations. However, more information regarding the historical isolation of the DPG population is needed to aid data interpretation. Moreover, we included only 2 years of reproductive data in our analysis. Considering that this study occurred over abnormally dry years for DPG, additional years of reproductive data would provide more insight into the role of fecundity for long-term persistence of these juniper stands. Therefore, to provide a more definitive statement on the role of habitat fragmentation and isolation in the loss of reproductive success of Utah juniper populations, additional studies should be conducted on isolated populations and encroaching populations across the western U.S., over multiple years and across varying environmental regimes.

Conclusions

The populations at Dugway have been historically separated by elevation and distance, but they are becoming progressively fragmented as a result of fire. As populations become fragmented, there is an increased chance that gene flow will be reduced and that inbreeding may occur. The 3 Utah juniper populations located at Dugway appear to be suffering from

reduced seed set and a loss of genetic variability compared to the control populations.

These data have important implications for conservation officials and land managers. Management decisions regarding Utah juniper typically deal with the control of its encroachment. However, we have demonstrated some of the long-term effects of isolating populations of Utah juniper. Land managers should be careful to prevent isolation and maintain gene flow to preserve reproductive success and long-term persistence of *Juniperus osteosperma*, particularly at DPG.

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