

POLYMORPHIC INDIAN RICEGRASS POPULATIONS RESULT FROM OVERLAPPING WAVES OF MIGRATION

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ABSTRACT.—Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) is a rangeland species native to western North America with populations that may exhibit distinct seed-size morphs borne on separate plants. These morphs are often associated with very different levels of seed dormancy. We compared RAPD profiles of the relatively infrequent and highly dormant jumbo seed morph to its more germinable small or large (non-jumbo) companion seed morphs collected from 9 sites where they were sympatric. Jumbo seed accessions from 9 additional sites that did not exhibit seed polymorphism were included to better sample this seed morph across the species' range. Sympatric seed morphs were consistently distinguishable by their RAPD profiles, and sympatric seed morphs were no more likely to cluster together than nonsympatric seed morphs. The ability of sympatric seed morphs to maintain their genetic identity is compatible with the hypothesis of a predominately autogamous breeding system. Furthermore, these data support the hypothesis that local polymorphic populations result from overlapping waves of migration with distinct geographical origins. The jumbo seed morphs exhibited moderate correlation between genetic distance and geographic distance, but the non-jumbo seed morphs exhibited no such correlation. Jumbo seed morphs that were collected at or east of the Continental Divide in New Mexico and Colorado are more genetically homogeneous than those west of the Continental Divide, and non-jumbo seed morphs from the east are more genetically variable than jumbo seed morphs from the same locations. This suggests that gene flow eastward across the Rocky Mountains has been more frequent for the non-jumbo seed morphs than for the jumbo seed morphs.

Key words: seed polymorphism, migration, seed dormancy.

Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) is a native rangeland bunchgrass of the Stipeae tribe with a distribution extending from the Nebraska sandhills to the eastern slopes of the Cascade and Sierra Nevada ranges and from Mexico to Canada at elevations up to 3000 m (Booth et al. 1980). Early reports of seed-size polymorphism were made by Huntamer (1934) and Stoddart and Wilkinson (1938). These seed morphs are borne on different plants, and the trait is heritable (Huntamer 1934). Jones and Nielson (1996) conservatively estimated that 21% of 318 populations sampled exhibited multiple discrete seed-size morphs (e.g., small, large, or jumbo; Fig. 1). Of 384 seed morphs examined from the 318 populations, about 72% were small, 22% were large, and 6% were jumbo. Of 11 regions sampled, seed polymorphism was most frequent in the southeastern Great Basin (34% of 91 accessions). The jumbo

seed morph was most frequent in the southwestern Great Plains (33% of 6 morphs).

Seed dormancy is a major component of the germination ecology of Indian ricegrass (Jones 1990). This seed dormancy is partly mechanical, controlled by the thickness of the lemma and palea (collectively referred to as the "hull"), and partly physiological (Huntamer 1934). Toole (1940) and Fendall (1966) showed that the hull excludes O₂, which is necessary for triggering germination. Zemetra and Cuany (1984) reported variation for lemma thickness among accessions. Across a wide range of accessions grown in 2 common gardens, Zemetra (1979) found a negative correlation between lemma thickness and germination percentage. Jones and Nielson (1999) found that seed mass, seed dormancy, and lemma and palea thicknesses were positively correlated among sympatric small, large, and jumbo seed morphs of T-593 (Star Lake, NM) Indian ricegrass (Fig. 1). These results suggest that (1) seed

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Fig. 1. Jumbo (T-593j, left), large (T-593g, center), and small (T-593s, right) seed morphs of T-593 Indian ricegrass (Star Lake, NM).

dormancy is associated with hull thickness, in agreement with Huntamer's (1934) observation, and (2) the positive relationship between seed size and seed dormancy may be partly due to a positive relationship between hull thickness and seed dormancy.

Indian ricegrass seed morphs typically differ in seed dormancy (Jones and Nielson 1999) as well as vegetative morphological characters (T.A. Jones personal observation). Seed dormancy is generally greater for large seed morphs than for small seed morphs (Huntamer 1934, Stoddart and Wilkinson 1938, Toole 1940, Young and Evans 1984). Relative seed morph frequencies at a site could fluctuate over time based on how recent environmental conditions have differentially favored seed morphs with prolonged versus shortened dormancy.

Seeds of 3 Indian ricegrass cultivars, Paloma (origin in Pueblo, CO), Nezpar (origin in Whitebird, ID), and Rimrock (origin in Billings, MT), are currently commercially available for rangeland rehabilitation and restoration efforts. Paloma has large seeds, and Nezpar and Rimrock have small seeds. Seeds are raised by individual growers or seed companies and typically must be certified for genetic purity as a condition of purchase by federal or state agencies. Seed certification (Jones 2005) is granted or denied by an official certifying agency according to standards for Indian ricegrass adopted by the Association of Official Seed Certifying Agencies (AOSCA 2005). Knowledge of a species' mating system (degree of outcrossing), determined by research, is important in development of meaningful standards to ensure that isolation distance between seed fields of the same or closely related species is adequate to preclude pollen contamination.

Little information regarding mating system is available within the Stipeae grass tribe (M.E. Barkworth personal communication), though the genetic data of Larson et al. (2001) strongly support autogamy for purple needlegrass (*Nassella pulchra* [Hitchc.] Barkworth). A sizable

literature on naturally occurring hybrids of Indian ricegrass with other species of the Stipeae tribe (Johnson and Rogler 1943, Johnson 1945, 1960, 1962, 1963, Nielson and Rogler 1952, Weber 1957) has given some the impression that Indian ricegrass is predominately allogamous. Nevertheless, Jones and Nielson (1989) found no self-incompatibility in this species.

Our objectives were to use RAPD markers to (1) characterize genetic similarity of sympatric seed morphs, and (2) compare genetic variation across locations of jumbo versus non-jumbo seed morphs.

METHODS

We analyzed seeds of the jumbo seed morph from 18 collection locations (accessions) in Arizona, Colorado, Nevada, New Mexico, and Utah (Table 1, Fig. 2). Seeds were collected in bulk from 25 or more individual plants at each site. Nine of the locations were monomorphic for the jumbo seed morph, and 9 were polymorphic. Of these 9 polymorphic sites, 7 were dimorphic with 1 non-jumbo seed morph (either large or small), and 2 were trimorphic with 2 non-jumbo seed morphs (large and small). Thus, we examined a total of 18 jumbo and 11 sympatric non-jumbo seed morphs.

Care was taken to avoid sites with evidence of seeding; therefore, we believe all of our materials to be naturally occurring on their respective sites. None of the 3 cultivars possesses jumbo seeds, so it is unlikely that the geographical distribution of jumbo seeds has been anthropogenically influenced. The 3 large-seeded accessions, the same morph as Paloma, did not cluster near one another in the dendrogram (Fig. 3), so there was no evidence that more than 1 of them might be Paloma. With 1 exception (T-804s from Patterson Wash, NV, and T-848s from Leamington, UT), the 8 small-seeded accessions, the same

TABLE 1. Locations of 18 sites in 6 western states where 18 jumbo and 11 non-jumbo seed morphs were collected.

Location	Jumbo	Large	Small
1 seed morph per site			
1. Cane Beds, AZ	T-752j	—	—
2. Mt. Trumbull, AZ	T-755j	—	—
3. Abbott, NM	T-866j	—	—
4. Cuba, NM	T-591j	—	—
5. Calf Creek, UT	T-717j	—	—
6. Dugway, UT	T-854j	—	—
7. Escalante, UT	T-715j	—	—
8. Iosepa, UT	T-852j	—	—
9. NE Kanab, UT	T-724j	—	—
2 seed morphs per site			
10. Cameron, AZ	T-740j	—	T-740s
11. Hawley, CO	T-877j	T-877g	—
12. Montello, NV	T-27j	—	T-26s
13. Patterson Wash, NV	T-804j	—	T-804s
14. NW Kanab, UT	T-758j	—	T-758s
15. Leamington, UT	T-849j	—	T-848s
16. Nephi, UT	T-851j	—	T-851s
3 seed morphs per site			
17. Buena Vista, CO	T-465j	T-464g	T-465s
18. Star Lake, NM	T-593j	T-593g	T-593s

morph as Nezpar and Rimrock, did not cluster near one another either (Fig. 3).

Seeds from each collection site were separated into seed morphs in the laboratory, and each seed morph was increased in a field block of up to 49 individuals.

Seeds that were bulked within each field block were placed on moist blotter paper in plastic boxes with fitted lids. The boxes were prechilled at 5°C for 3 weeks before germination at 15°C in the dark. Germinated seedlings were transplanted into a steam-sterilized 75% sand / 25% peat moss v:v mixture and were grown in the greenhouse until DNA was harvested. Young leaves were collected and placed on ice for 0–3 hours prior to DNA isolation. For each accession, DNA from 2 individuals was analyzed separately.

DNA was isolated from fresh leaves by a modified CTAB extraction method (Lassner et al. 1989, Williams et al. 1993). We used the 20 primers in Operon RAPD 10mer Kit A (Qiagen, Alameda, CA). DNA was amplified in 25 μ L reactions containing 10 mM Tris-HCl (pH 8.3), 10 mM KCl, 0.2 mM each dNTP, 3 mM MgCl₂, 0.8–0.12 μ M primer (OPAA series, OperonTech., Alameda, CA), 0.08 U \cdot μ L⁻¹ Taq DNA polymerase (Stoeffel fragment, Perkin-Elmer, Branchberg, NJ), and 20 ng \cdot μ L⁻¹ template DNA. After being heated to 100°C for 2 minutes, the samples were subjected to

40 amplification cycles (1 minute at 93°C, 1 minute at 35°C, 2 minutes at 71°C) using a Perkin-Elmer 9600 GeneAmp PCR System. RAPD products were separated electrophoretically on 2% agarose gels run in 45 mM Tris-borate, 1 mM EDTA containing 0.4 μ m \cdot mL⁻¹ ethidium bromide. For each primer pair, we performed a simultaneous PCR amplification of DNA from 2 individual plants for each of the 29 accessions and then fractionated the 58 PCR products on the same agarose gel (run 1). The presence or absence of bands was scored from photographs of the stained gels. To test overall repeatability of RAPD analyses, 12 DNA samples (6 accessions) were replicated on a 2nd day for 2 primer pairs (run 2) to assess variation from experimental error.

The proportion of shared bands (F) for all pairs of 29 accessions was calculated as $2a/(2a + b + c)$, where a = the number of shared bands, b = the number of bands present in the 1st accession but not the 2nd, and c = the number of bands present in the 2nd accession but not the 1st (Nei and Li 1979). Genetic analysis was performed based on corresponding estimates of genetic distance (1 – F) using PAUP* version 4.0b10 (Sinauer Associates, Inc., Sunderland, MA). Bootstrap values were calculated from 1000 replicates. TREEVIEW (Page 1996) was used to graph the dendrogram. A geographical distance matrix for the

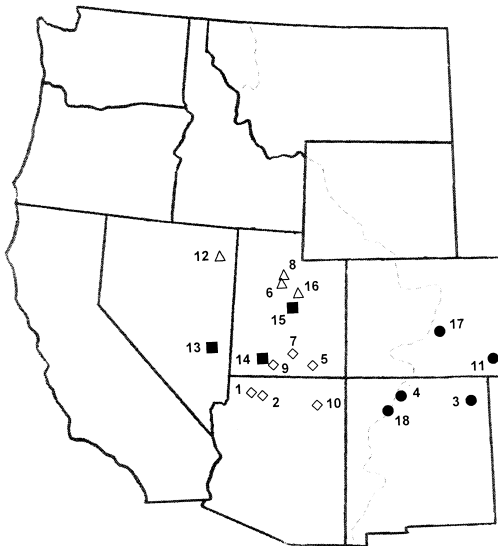


Fig. 2. Locations of 18 jumbo accessions (1–18; \triangle = northeastern Great Basin, \diamond = southern Colorado Plateau, \blacksquare = intermediate, and \bullet = eastern jumbo clusters) and 11 non-jumbo accessions from 9 sites (10–18)

29 Indian ricegrass accessions was assembled to assess the relationship between geographical distance and genetic distance for all accessions and for several subsets of accessions. Mantel's (1967) test was used to judge the statistical significance of these correlations using NTSYS (Exeter Software, Setauket, NY).

RESULTS AND DISCUSSION

We scored a total of 118 RAPD fragments, 102 of which were polymorphic across the 29 Indian ricegrass accessions. The number of fragments per accession averaged 59.1 (range 51–70), and the proportion of shared fragments (F) between 2 accessions (Nei and Li 1979) averaged 0.70 (range 0.57–0.96; Table 2). The modest range in fragments per accession indicates that the level of genomic complexity within the study is relatively homogeneous. In other words, there does not appear to be major variation due to such factors as multiple ploidy levels, heterozygosity, or spurious RAPD amplification.

We observed only minor differences in banding patterns between runs 1 and 2. On average, approximately 96% of the bands were shared (repeated) between replicated DNA samples. These minor differences appeared to

be related to the efficiency of PCR and DNA staining in the gel; that is, clear but faint bands that were observed in 1 run were not always visible in the other run. Our inability to consistently detect the faint bands may have been related to our using photographs of the gels for scoring rather than electronic images. Importantly, DNA isolated from the 2 different plants of each accession always produced identical banding patterns within a run. Thus, the data themselves directly demonstrate a high degree of reliability within the experimental provisions of the study.

Genetic Similarity of Sympatric Seed Morphs

Intercalation of jumbo and non-jumbo seed morphs is common in the dendrogram (Fig. 3), suggesting that seed morph has no legitimate taxonomic status. Of the 118 markers, none was consistently present for 1 morph and consistently absent for another. Perhaps seed morph is controlled by 1 or a few major genes. This hypothesis may be tested by analyzing segregation ratios of seed morphs in F_2 progeny of biparental crosses between seed morphs.

Our results indicate that sympatric seed morphs are mostly genetically dissimilar. Sympatric seed morphs never clustered together in 13 comparisons (7 from 7 dimorphic sites and 6 from 2 trimorphic sites), even at an extremely liberal bootstrap value of 50%. In fact, for 10 of 13 sympatric comparisons, the 2 seed morphs clustered apart with a bootstrap value $\geq 78\%$ (Fig. 3). The 3 less clearly disassociated pairs were from Montello, Nevada (T-26s, T-27j), Nephi, Utah (T-851s, T-851j), and Star Lake, New Mexico (T-593s, T-593g). We also tested whether genetic similarity among sympatric seed morphs (13 comparisons) is greater than among nonsympatric seed morphs (177 comparisons). The mean proportion of shared bands (F) was 0.70 ± 0.03 (means are accompanied by a 95% confidence interval) for pairs of sympatric seed morphs and 0.68 ± 0.01 for pairs of nonsympatric seed morphs. Thus, sympatric morphs were no more similar than nonsympatric morphs.

If outcrossing rates between morphs were high, one would expect that sympatric accessions would be much more similar to each other than to accessions from distant locations. In general, this was not the case. Assuming

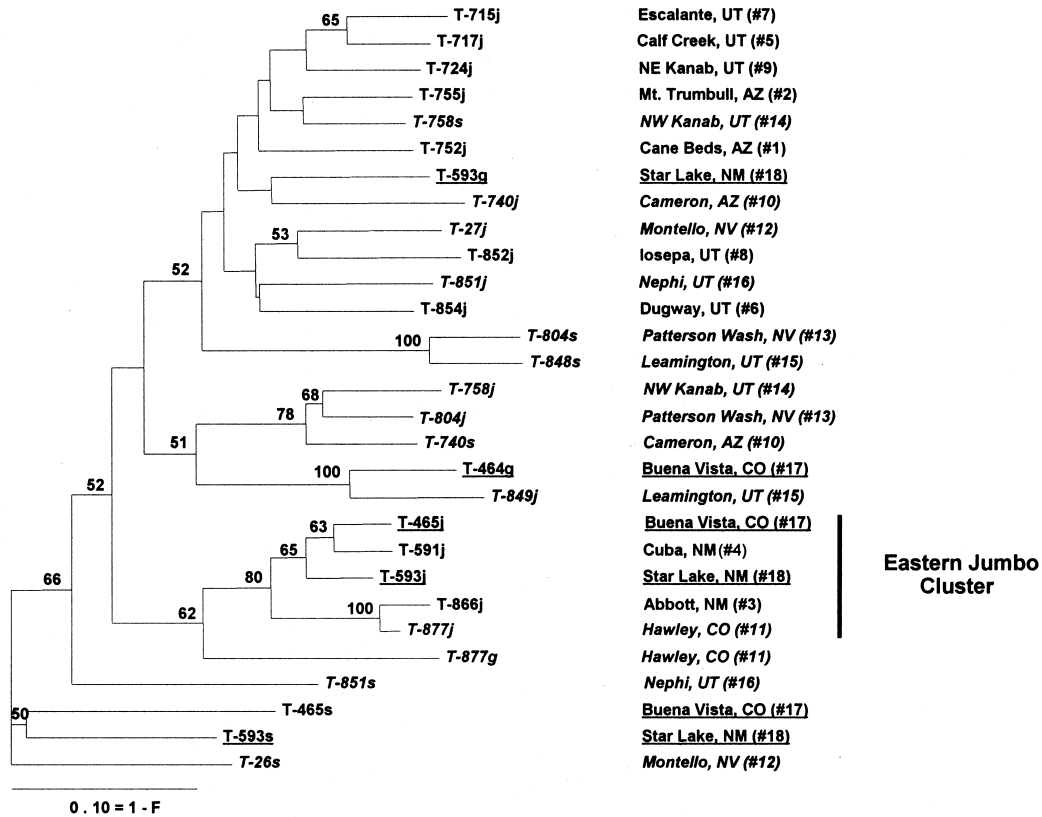


Fig. 3. Neighbor-joining dendrogram based on Nei's genetic distance for 18 jumbo (j = jumbo) accessions from 18 locations and 11 non-jumbo (g = large, s = small) accessions from 9 locations (numbered at right; see Table 1, Fig. 2). Dimorphic locations are italicized, and trimorphic locations are underlined. Bootstrap values ≥ 50 are shown.

that no genetic barriers preclude hybridization between morphs (i.e., morphs have no legitimate taxonomic status, these findings support the hypothesis of an autogamous mating system). The lack of similarity between sympatric morphs suggests not only that hybridization between seed morphs is at most minimal, but also that sympatric morphs likely have independent points of origin.

Each branch of the dendrogram (Fig. 3) represents the 2 plants of each accession, which were grown in the greenhouse from a seed lot harvested in bulk from a corresponding field block in a common garden. As stated above, no differences in RAPD profiles were seen between the 2 plants for any accession. While accessions were increased in separate field blocks, these blocks were adjacent, so an opportunity for cross-pollination was present if outcrossing were to occur. Therefore, the observation that each pair of plants possessed

identical RAPD profiles is compatible with the hypothesis of a predominately autogamous mating system. Previous data have shown that self-incompatibility is absent in Indian ricegrass, as open-pollinated and bagged panicles did not differ in seed set (Jones and Nielson 1989).

The conclusion that Indian ricegrass possesses an autogamous mating system is important because of a past presumption that Indian ricegrass is self-incompatible and cross-pollinated. This has been the ostensible justification for overly strict genetic purity standards in seed certification regulations. Specifically, a minimum isolation distance between seed fields of different Indian ricegrass cultivars has been required in order to minimize pollen admixture among them, based on the presumption of the predominance of cross-pollination.

This erroneous stance has been based on data of Smith (1944), cited by Fryxell (1957),

purporting a 94% reduction in seed set of bagged plants relative to open-pollinated plants. This appears to be a result of an arithmetic error (Smith 1944: table 3). Reduction of seed set in bagged plants recalculated from the data presented by Smith (1944) is only 33%. This reduction may have possibly resulted from unfavorable environmental conditions for seed set under a bag. Our data presented here and previous data (Jones and Nielson 1989) have been used to justify a relaxation of isolation standards to reflect Indian ricegrass' predominantly autogamous mating system (Association of Official Seed Certifying Agencies 2002).

Despite this evidence for autogamy, several reports cited above indicate naturally occurring interspecific hybridization. Interspecific hybrids between Indian ricegrass and green needlegrass (*Nassella viridula* [Trin.] Barkworth) have sporadically appeared in green needlegrass breeding lines (Johnson and Rogler 1943). Conversely, we have made several observations of interspecific hybrids in Indian ricegrass breeding lines. Thus, it appears that Indian ricegrass may occasionally outcross as either a male or female parent.

Genetic Variation of Seed Morphs

Our data indicate that the correlation coefficient between geographical distance and genetic distance is much stronger for jumbo seed morphs than for non-jumbo seed morphs. Over all accessions, $r = 0.39$ ($P < 0.01$). However, for the 18 jumbo seed morphs, $r = 0.48$ ($P < 0.01$) compared to $r = 0.21$ ($P < 0.10$) and $r = 0.20$ ($P > 0.10$) for the 11 non-jumbo seed morphs and the 8 small seed morphs, respectively. These results suggest that historical dispersion of the jumbo seed morph may have been simpler than that of the non-jumbo seed morphs. Perhaps the jumbo seed morphs have a common genetic origin, whereas the non-jumbo seed morphs have 2 or more origins.

Genetic variation of the relatively uncommon jumbo seed morph was comparable to that of the more typical non-jumbo seed morphs when they were compared across the same set of geographical sites. For the 9 sites in which both jumbo and non-jumbo seed morphs were present, the 95% confidence interval of average genetic distance among the 9 jumbo seed morphs (0.29 ± 0.03) overlapped the 95% con-

fidence interval of the average genetic distance among the 11 non-jumbo seed morphs (0.33 ± 0.02). On the other hand, the data suggest high genetic similarity among 5 jumbo seed morphs (T-465j, T-591j, T-593j, T-866j, T-877j) from the eastern portion of the sampled region (Fig. 3). These 5 jumbo accessions, the "eastern jumbo cluster," are all located at or east of the Continental Divide (Fig. 2). In contrast, the 13 jumbo seed morphs originating west of the divide in the Intermountain Region are much less genetically similar to one another. These results are best explained by a western origin of the jumbo morph and its eastward migration across the Continental Divide from a small founder population. The 5 similar eastern jumbo morphs may also have inflated the correlation between geographical and genetic distances for the jumbo morph.

Two other facts also lend credence to a western origin and eastern migration of the jumbo seed morph. First, Indian ricegrass is much more common west of the Continental Divide than east of it, particularly in the Great Basin and the Colorado Plateau. Second, the degree of seed polymorphism is greater in the southeastern Great Basin than in any of 10 other regions (Jones and Nielson 1996).

In contrast to the jumbo seed morphs of the Rocky Mountain region, the 3 large seed morphs (T-593g, T-464g, T-877g) and the 2 small seed morphs (T-465s, T-593s) from this region (Fig. 2) are not genetically similar to one another based on bootstrap values (Fig. 3). This suggests that gene flow eastward across the divide has been greater for the non-jumbo seed morphs than for the jumbo seed morph.

Besides the eastern jumbo cluster, 3 other groups of jumbo morphs have some degree of geographical similarity (Fig. 2), though none have strong statistical support (Fig. 3). Jumbo morphs T-715j (#7 Escalante, UT), T-717j (#5 Calf Creek, UT), T-724j (#9 NE Kanab, UT), T-755j (#2 Mt. Trumbull, AZ), T-752j (#1 Cane Beds, AZ), and T-740j (#10 Cameron, AZ) constitute a southern Colorado Plateau group. Jumbo morphs T-27j (#12 Montello, NV), T-852j (#8 Iosepa, UT), T-851j (#16 Nephi, UT), and T-854j (#6 Dugway, UT) constitute a north-eastern Great Basin group. Jumbo morphs T-758j (#14 NW Kanab, UT), T-804j (#13 Patterson Wash, NV), and T-849j (#15 Leamington, UT) constitute a group located between

TABLE 2. Number of RAPD fragments detected per plant in 29 Indian ricegrass accession genotypes (i.e., a + b or a Nei and Li 1979); and number of fragments in 1 or both accession genotypes (i.e., a + b + c; below diagonal). Thus, the and below-diagonal elements.

	T26s	T27j	T464g	T465s	T465j	T591j	T593s	T593g	T593j	T715j	T717j	T724j	T740j	T740s	T752j
T26s	51	0.70	0.65	0.74	0.68	0.68	0.77	0.67	0.68	0.63	0.64	0.66	0.59	0.62	0.62
T27j	73	61	0.69	0.59	0.66	0.69	0.63	0.74	0.71	0.77	0.79	0.74	0.76	0.72	0.74
T464g	73	77	57	0.63	0.68	0.67	0.69	0.70	0.64	0.66	0.72	0.68	0.64	0.77	0.70
T465s	66	81	76	54	0.70	0.67	0.76	0.67	0.68	0.59	0.60	0.59	0.59	0.64	0.62
T465j	75	83	79	76	63	0.94	0.69	0.68	0.91	0.65	0.63	0.66	0.63	0.68	0.71
T591j	75	81	80	78	67	63	0.69	0.68	0.93	0.69	0.66	0.71	0.63	0.66	0.73
T593s	66	80	74	68	78	78	56	0.79	0.72	0.62	0.65	0.74	0.63	0.63	0.68
T593g	76	78	78	78	83	83	72	63	0.71	0.74	0.78	0.79	0.81	0.73	0.78
T593j	72	77	78	74	66	65	73	78	58	0.69	0.67	0.72	0.66	0.67	0.74
T715j	77	75	79	81	84	81	81	78	78	61	0.9	0.86	0.77	0.69	0.81
T717j	82	79	81	87	91	89	85	81	85	72	70	0.88	0.78	0.70	0.82
T724j	73	75	76	79	81	78	72	73	74	68	72	58	0.76	0.71	0.83
T740j	77	74	78	79	83	83	78	72	78	73	78	72	58	0.76	0.81
T740s	75	76	71	76	80	81	78	77	77	78	83	75	72	58	0.71
T752j	73	73	73	75	76	75	73	72	71	69	74	66	67	73	55
T755j	74	73	79	78	81	81	76	74	75	69	77	69	67	75	66
T758j	71	77	70	71	74	76	74	76	72	76	82	72	75	63	70
T758s	75	78	78	78	84	82	79	77	78	71	78	69	73	76	69
T804j	75	80	75	77	80	82	79	81	78	81	86	77	80	67	77
T804s	76	77	78	75	81	83	77	75	76	76	80	74	73	76	71
T848s	73	76	79	76	83	83	77	78	79	77	82	74	74	78	72
T849j	74	80	65	78	81	82	75	80	80	80	83	78	80	74	75
T851j	75	75	80	79	82	82	80	79	77	75	80	75	72	77	73
T851s	68	80	78	75	81	81	75	81	79	80	85	77	78	78	75
T852j	74	70	78	80	84	85	80	77	79	75	78	72	73	78	71
T854j	79	75	78	84	84	83	82	78	80	72	76	72	74	79	71
T866j	77	81	84	80	73	74	81	86	71	83	90	81	84	85	80
T877j	75	79	82	79	70	71	79	84	68	83	90	80	83	83	77
T877g	68	77	75	73	69	71	74	81	69	78	85	74	78	72	72

the southern Colorado Plateau and northeastern Great Basin groups.

CONCLUSIONS

A polymorphic Indian ricegrass seed collection made at a single site may be thought of as a mixture of coexisting subpopulations. If the degree of gene flow among seed morphs is low, which would occur with a high level of autogamy, these subpopulations would maintain a high degree of genetic uniqueness. This conclusion is supported by the finding that similarity among sympatric morphs is no greater than it is among nonsympatric morphs. If the subpopulations have migrated independently, a polymorphic population may have resulted from overlapping waves of migration of seed morphs with distinct points of origin.

Genetic variation of the jumbo seed morph east of the Continental Divide is lower than to the west, as evidenced by the homogeneous eastern jumbo cluster. Indian ricegrass gene flow over the Continental Divide could be lim-

ited by reduced fitness at higher elevations. Although Indian ricegrass is found at high elevations (Booth et al. 1980), it is much less common in montane areas than in lower-elevation valley floors. Furthermore, if the ecological advantage of the high-dormancy jumbo seed morph, in particular, is less pronounced at the high elevations, where precipitation is more dependable and evapotranspiration is less severe, then this could also limit dispersal across the Continental Divide. Alternatively, migration across the divide may be related to the inability to compete with a better-adapted genotype already present. At any rate, this apparent migration bottleneck for the jumbo seed morph did not appear to so stringently restrict eastward migration of the non-jumbo seed morphs.

Seed-size polymorphism in Indian ricegrass is an important mechanism providing genetic variation within local sites as well as across geographic space. While many restorationists have emphasized the importance of plant materials of local origin, these data suggest

+ c; diagonal); proportion of shared fragments (i.e., $F = 2a/[2a + b + c]$) between accession genotypes (above diagonal); overall RAPD profiles and the proportion of shared amplicons (above-diagonal elements) can be inferred from the diagonal

T755j	T758j	T758s	T804j	T804s	T848s	T849j	T851j	T851s	T852j	T854j	T866j	T877j	T877g	
0.65	0.63	0.68	0.67	0.57	0.64	0.64	0.66	0.76	0.65	0.61	0.66	0.68	0.69	T26s
0.78	0.65	0.74	0.70	0.67	0.70	0.66	0.77	0.67	0.83	0.79	0.70	0.73	0.65	T27j
0.64	0.73	0.70	0.74	0.61	0.60	0.87	0.64	0.66	0.66	0.70	0.61	0.63	0.64	T464g
0.62	0.67	0.67	0.67	0.62	0.62	0.61	0.63	0.67	0.58	0.56	0.64	0.65	0.64	T465s
0.67	0.72	0.67	0.72	0.63	0.61	0.66	0.68	0.67	0.62	0.67	0.85	0.89	0.81	T465j
0.67	0.69	0.70	0.69	0.59	0.61	0.64	0.68	0.67	0.61	0.68	0.83	0.87	0.78	T591j
0.68	0.64	0.67	0.66	0.61	0.63	0.68	0.63	0.70	0.61	0.62	0.65	0.67	0.64	T593s
0.79	0.69	0.78	0.70	0.73	0.69	0.68	0.73	0.67	0.74	0.76	0.65	0.67	0.60	T593g
0.72	0.70	0.71	0.70	0.65	0.61	0.62	0.71	0.65	0.65	0.68	0.84	0.88	0.76	T593j
0.85	0.67	0.85	0.68	0.69	0.68	0.66	0.77	0.67	0.75	0.84	0.67	0.66	0.63	T715j
0.81	0.67	0.83	0.70	0.72	0.70	0.70	0.78	0.68	0.79	0.86	0.66	0.65	0.62	T717j
0.82	0.70	0.86	0.72	0.69	0.70	0.66	0.74	0.68	0.77	0.81	0.67	0.68	0.67	T724j
0.85	0.65	0.79	0.67	0.71	0.70	0.62	0.79	0.67	0.75	0.78	0.62	0.63	0.59	T740j
0.72	0.86	0.74	0.88	0.65	0.63	0.72	0.71	0.67	0.67	0.69	0.61	0.63	0.70	T740s
0.84	0.70	0.83	0.68	0.71	0.70	0.67	0.74	0.68	0.75	0.8	0.66	0.69	0.67	T752j
59	0.68	0.89	0.69	0.75	0.75	0.67	0.78	0.71	0.76	0.8	0.65	0.67	0.63	T755j
74	53	0.71	0.89	0.65	0.61	0.70	0.67	0.61	0.63	0.67	0.63	0.66	0.77	T758j
68	75	63	0.72	0.69	0.69	0.69	0.77	0.70	0.79	0.84	0.65	0.67	0.62	T758s
79	64	80	62	0.67	0.61	0.72	0.68	0.66	0.66	0.7	0.65	0.66	0.77	T804j
71	73	77	78	55	0.90	0.62	0.69	0.63	0.72	0.68	0.62	0.63	0.57	T804s
72	76	78	82	61	56	0.60	0.68	0.71	0.73	0.69	0.63	0.66	0.57	T848s
78	72	79	77	78	80	58	0.66	0.63	0.65	0.71	0.59	0.61	0.59	T859j
73	76	76	81	76	77	80	61	0.70	0.82	0.82	0.74	0.71	0.70	T851j
76	78	79	81	78	74	80	78	59	0.73	0.69	0.65	0.69	0.63	T851s
73	77	74	81	73	73	79	71	75	59	0.84	0.67	0.67	0.61	T852j
73	77	73	81	78	78	78	73	80	71	63	0.71	0.70	0.64	T854j
83	80	86	85	82	82	86	79	83	82	82	64	0.96	0.74	T866j
81	78	84	84	81	80	84	80	80	81	82	66	63	0.76	T877j
77	65	80	71	77	78	78	74	77	78	79	74	72	53	T877g

that nature has accommodated and maintained Indian ricegrass material that has emigrated from distant locales, resulting in coexistence with previous immigrants. Thus, for reintroduction of this species to a restoration site, a polymorphic seeding of a more germinable seed morph and a less germinable seed morph may be as or more genetically appropriate, and ecologically appropriate, than a monomorphic seeding.

Outbreeding depression, defined as a “reduction in mean population fitness resulting from hybridization between genetically distinct individuals or populations of the same species” is sometimes invoked as a reason for not introducing nonlocal material to a restoration site (Hufford and Mazer 2003). These authors term such genetically incompatible populations as “epitypes.” However, because of Indian ricegrass’ low outcrossing rate and the common occurrence of polymorphism in natural populations, concerns over possible maladaptation resulting from outbreeding depression in this species are probably unjustified.

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