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Intrapopulation genetic variation for seed dormancy in Indian ricegrass

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Abstract

Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkw. = *Oryzopsis hymenoides* [Roem. & Schult.] Ricker = *Stipa hymenoides* Roem. & Schult.) may buffer its seed banks over time via morphological (lemma and palea) and physiological (seed coat) seed dormancy. However, Indian ricegrass seed dormancy has usually not been examined from a genetic perspective. Because a positive relationship between seed dormancy and seed size has long been noted within Indian ricegrass populations, we wanted to determine if genetic variation for seed dormancy was present among seed morphs. We also wanted to determine if genetic variation for seed dormancy was present in material without polymorphism. The T-593 population from McKinley Co., N.M., has 3 seed morphs produced on genetically distinct plants, 'elongate' (2.24 mg/seed), 'globose' (3.00 mg/seed), and 'jumbo' (8.70 mg/seed). Following a 3-week prechill, elongate seed showed higher germination (66%) than globose seed (20%) over 6 tests (pairs of seed lots), while jumbo seed did not germinate without scarification. Jumbo seed had thicker (181 μg) lemmas than globose (93 μg) or elongate (52 μg) seed. Individual plants of the nonpolymorphic cultivar, Rimrock, were selected for high or low germination following a 3-week prechill. The spring following seed harvest, germination with prechill was greater for progeny lines of the high-germination selections (45.5%) than low-germination selections (3.8%) with Rimrock intermediate (11.8%). This heritable difference in germination was accompanied by only small differences in lemma and palea thickness and no difference in seed mass. Genetic variation in seed dormancy may be found both between morphs (interpreted as variation for morphological dormancy) and within morphs (interpreted as variation for physiological dormancy). Genetic variation for seed dormancy can be as great within a population as between populations.

Key Words: *Achnatherum hymenoides, Oryzopsis hymenoides,* **seed polymorphism,** *Stipa hymenoides*

Huntamer (1934) first described the 2 generally recognized seed dormancy mechanisms of Indian ricegrass (*Achnatherum*

Resumen

A través del tiempo "Indian ricegrass" (*Achnatherum hymenoides* [Roem. & Schult.] Barkw.= *Oryzopsis hymenoides* [Roem. & Schult.] Rickler = *Stipa hymenoides* Roem. & Schult.) puede amortiguar sus bancos de semilla vía dormancia de semilla por causas morfológicas (lema y palea) y fisiológicas (cubierta de semilla). Sin embargo, la dormancia de la semilla de "Indian ricegrass" usualmente no se ha examinado desde una perspectiva genética. Debido a que dentro de poblaciones de "Indian ricegrass" se ha notado una relación positiva entre dormancia y tamaño de la semilla, quisimos determinar si la variación genética para dormancia de semilla estuvo presente entre formas morfológicas de semilla. También quisimos determinar si la variación genética para dormancia de semilla estuvo presente en material sin polimorfismo. La población T-593, proveniente de McKinley Co., N.M., tiene 3 formas morfológicas de semilla producidas en plantas genéticamente distintas, 'elongada' (2.24 mg/semilla), 'globosa' (3.00 mg/semilla) y 'jumbo' (8.7 mg/semilla). Los resultados de 6 pruebas (pares de lotes de semilla) indicaron que después de 3 semanas de acondicionamiento en frío, la semilla 'elongada' tuvó mayor germinación (66%) que la 'globosa' (20%) mientras que la semilla 'jumbo' no germinó sin escarificación. La semilla 'jumbo' tenia la lema más gruesa (181 μg) que la 'globosa' (93 μg) o la 'elongada' (52 μg). Se seleccionaron plantas individuales de un cultivar sin polimorfismo (Rimrock) y fueron seleccionadas por tener un alto o bajo porcentaje de germinación después de 3 semanas de acondicionamiento en frío. En la primavera posterior a la cosecha de la semilla, la germinación con acondicionamiento con frío fue mayor en la progenie de selecciones de alta germinación (45.5%) que las selecciones con baja germinación (3.8%) y la Rimrock fue intermedia (11.8%). Esta diferencia heredable en germinación estuvo acompañada solo por pequeñas diferencias en el grosor de la lema y la palea y sin diferencias en la masa de la semilla. La variación genética en la dormancia de la semilla puede ser encontrada entre formas morfológicas (interpretado como la variación para la dormancia morfológica) y dentro de formas morfológicas (interpretados como variación para la dormancia fisiológica). La variación genética respecto a dormancia de semilla puede ser tan grande dentro de una poblacion como entre poblaciones.

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hymenoides [Roem. & Schult.] Barkw. = *Oryzopsis* hymenoides [Roem. & Schult.] Ricker = *Stipa hymenoides* Roem. & Schult.), mechanical and physiological. Mechanical dormancy results from an indurate lemma and palea, which may prevent the penetration of O_2, though not water, required for germination (Toole 1940, Fendall 1966). Zemetra and Cuany (1984) reported that seed mass and lemma thickness varied among 12 genetic strains, but did not differ across locations (eastern vs. western Colorado). No strain X location interaction was present. These results suggest that seed mass and lemma thickness are not greatly influenced by environmental conditions. No correlation was found between lemma thickness and seed mass of the strains. A weak relationship (r=–0.48) was found between lemma thickness and nonprechilled germination, which ranged from 0 to 8% (Zemetra 1979). He concluded that lemma thickness explains a small part of the variation for seed dormancy, but other factors, e.g., physiological dormancy, are responsible for much of the variation in newly harvested nonprechilled seed.

Huntamer (1934) was also the first to describe seed polymorphism in Indian ricegrass. Large and small dark seeds were produced by different plants. The progeny bred true to type, as would be expected for a self-pollinated species (Jones and Nielson 1989). The small seed morph exhibited higher germination than the large seed morph (Huntamer 1934). Young and Evans (1984) described large and small black seeds in a 'Nezpar' seed lot. Germination of small seeds was greater than large seeds when untreated at 20°C and following an enhanced treatment that included lemma and palea removal, pricking the seed coat, application of 100 ppm GA_3, and prechilling.

We evaluated seed dormancy in the polymorphic T-593 population collected near Star Lake, N.M. and Rimrock, a recently released nonpolymorphic cultivar from Billings, Mont. (Jones et al. 1998) (Fig. 1). Seed mass and lemma and palea thickness data were collected to determine whether any relationship could be found between these traits and seed dormancy. Our objective was to study the genetic basis for intrapopulation variation for morphological and physiological seed dormancy in Indian ricegrass.

Materials and Methods

T-593 Population

The T-593 Indian ricegrass population was originally collected by the authors in 1988 near Star Lake, McKinley Co., N.M. On close examination we discovered seed polymorphism in the seed lot (Fig. 1). Globose and elongate seed morphs were germinated in winter 1991, raised as seedlings in a greenhouse, and transplanted in spring 1991 to Greenville Farm (North Logan, Utah) on a Millville silt loam soil (coarse-silty, carbonatic, mesic Typic Rendolls; 2-4% slope) in a completely randomized design. Seedlings grown from jumbo seed were transplanted the same time to an adjacent plot.

Seed was harvested in 1992 by covering each plant with a paper bag before shattering began, and in 1993 and 1994 by covering about half of each plant with a paper bag and surrounding the remainder with a wire-screen funnel to trap seed as it shattered. Bags and wire screens were harvested separately and bulked across plants within morphs. Seed was cleaned by hand to prevent mechanical abrasion of the lemma and stored at room temperature until testing.

We collected seed with wire-screen funnels to avoid potentially artificially high germination results that can result from paper bagging. This was found previously in Rimrock (PI 478833) (Jones and Nielson 1994) and globose and elongate morphs of T-593 (T.A. Jones, unpub. data). Using the funnels ensured that seed would not be lost to shattering. Indian ricegrass flowers indeterminately and seed produced at different times throughout the season may have different germination characteristics (unpub. data, J.A. Young, R.L. Cuany).

Except for the original collection, germination tests were conducted the spring following seed harvest after storage at room temperature. One hundred seeds were planted with a vacuum seed head on 250 g sand collected at an Indian ricegrass site (Box Elder Co., Utah) in a 110 X 110 X 35 mm plastic germination box. Four boxes were planted for each morph. The seeds were covered with a nontoxic steel blue germination blotter (Anchor Paper, St. Paul, Minn.), over which was poured 60 ml of tap water. The boxes were closed with fitted lids. Soil matric potential at planting was approximately –0.17 MPa (pers. comm., R.W. Brown), which is in the desirable range for germination in field-collected soil (Blank and Young 1992). Boxes were prechilled in the dark at 5°C for 3 weeks and germination counts were made after 2 weeks of dark incubation at 15°C. An arcsine transformation was applied to all germination data before analysis. Morphs were tested for differences in germination percentage by a t test with 4 replications (boxes).

Rimrock Cultivar

Seed of Rimrock, a nonpolymorphic cultivar (Fig. 1), was collected in 1994 and 1995 in wire-screen funnels from individual plants of an established 8 X 20 spaced-plant nursery (0.5-m centers). The nursery was located at Greenville Farm. While 160 plants were originally planted in the nursery, only 153 plants produced sufficient seed for testing in 1994 and 128 in 1995. Seed was collected with wire-screen funnels as described above and cleaned by hand to prevent mechanical abrasion of the lemma. Seed was stored at room temperature until germination testing as described above. Because of the large number of boxes, replications were not run simultaneous-

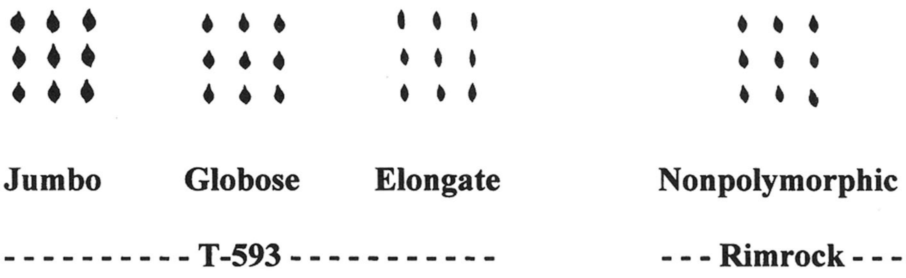

Fig. 1. Seed of jumbo, globose, and elongate morphs of T-593 and nonpolymorphic Rimrock Indian ricegrass.

Table 1. Germination of globose and elongate T-593 seed morphs after a 3-week prechill (5°C) and 2-week incubation (15°C) the spring of the test year.

Production Site	Production Year	Test Year	Germination Globose	Germination Elongate	CV
			(%)		
Star Lake, N.M.	1988	1991	52	83**	5.4
Greenville Farm	1992[1]	1993	29	75**	8.1
Greenville Farm	1993[1]	1994	16	67**	10.1
Greenville Farm	1993[2]	1994	2	55**	14.4
Greenville Farm	1994[1]	1995	17	61**	5.4
Greenville Farm	1994[2]	1995	5	57**	17.6
Mean			20	66	

[1] Seed production in paper bags.
[2] Seed production in wire-screen funnels.
**Morphs significantly different at $P < 0.01$.

ly. Final counts were made in January and February 1995 (1994 seed) and March and April 1996 (1995 seed).

The 5 highest- and 5 lowest-germinating seed parents across the 2 years were identified (divergent selection). Seed from the 10 parent plants (10 progeny lines) was mechanically scarified with sandpaper to enhance germination, and seedlings were raised in a greenhouse before transplanting to Greenville Farm in April 1996. The 10 progeny lines and Rimrock were represented by 7 X 7 spaced-plant blocks (0.5-m centers), which were randomized in the field. In 1997 seed was harvested from these plots using wire-screen funnels, cleaned, and stored as described above. Germination tests were completed in May and June 1998. In addition to prechilled germination, 1997 seed lots were subjected to nonprechilled germination at 15°C. Germinated seedlings were counted at 3 and 5 weeks. T tests determined if differences were present between the 5 high and 5 low-germination progeny lines.

Seed Morphology Measurements

Seed mass determinations of the three, T-593 morphs (1993 and 1994 seed produced in paper bags) and the 10 Rimrock progeny lines (1996 and 1997 seed produced in wire-screen funnels) were based on 1,000 seeds. Standard errors of T-593 morphs were based on ten, 100-seed subsamples. Lemma and palea thicknesses were measured on 20 seeds of the 3 T-593 morphs (1993 and 1994 seed) and the 10 Rimrock progeny lines (1994 and 1995 seed). Seeds were held between 2 pieces of hard rubber and sliced through the midsection with a razor blade. Thickness was determined under a dissecting microscope with an ocular micrometer.

Results

T-593 Germination

T-593 includes jumbo, globose, and elongate seed morphs (Fig. 1). Untreated jumbo seed does not germinate the year following harvest, but scarification permits a small number to germinate (T.A. Jones, data not shown). We have found the jumbo morph at 22 other locations in 6 states, usually in the presence of other morphs (Jones and Nielson 1996, T.A. Jones, unpub. data). Elongate seed germination was higher than globose seed germination in all 6 pairs of seed lots ($P<0.01$) (Table 1). Germination was highest in the original 1988 Star Lake seed lot, probably because the seed was germinated 3 years after harvest instead of 1 year as with the other seed lots (Rogler 1960). Jumbo seed was not included in the comparisons because of its failure to germinate under the described conditions.

T-593 Seed Morphology

The three T-593 morphs differed in seed mass and lemma and palea thickness (Table 2). Mass of globose seed was 33% greater and mass of jumbo seed was 289% greater than mass of elongate seed across years. Zemetra and Cuany's (1984) 12 strains and cultivars ranged from 2.73 to 4.45 mg/seed, none being as light as T-593 elongate seed (2.33 mg/seed) and none as heavy as T-593 jumbo seed (8.62 mg/seed). Zemetra and Cuany (1984) did not characterize their material for seed morphology. Lemma (and palea) thicknesses of T-593 globose seed were 79 (71)% greater and those of jumbo seed were 248 (205)% greater than those of elongate seed across years. Zemetra and Cuany (1984) found a range of 42 to 76 mm in lemma thickness of 12 strains and cultivars. Thus, their thinnest lemmas were thinner than those of T-593 elongate seed and their thickest lemmas were thinner than those of T-593 jumbo or globose seed. While these workers found no relationship between seed mass and lemma thickness, we found these traits to be positively related among the three T-593 morphs. However, the 3 morphs spanned from 54 to 182 mm in thickness, a range nearly 4 times greater than Zemetra and Cuany's (1984) materials.

Rimrock Germination

Mean (and median) germination of seed harvested in 1994 and 1995 from the Rimrock spaced-plant nursery was 17.3 (12.0) and 22.0 (17.5)%, respectively. Median values were lower than means because distributions were skewed toward low germination. Correlation between the 2 years was high ($r^2 = 0.81$, $P<0.01$). Germination of high- and low-germination progeny lines averaged 61.8 and 0.3%, respectively, for 1994 seed, and 58.7 and 0.9%, respectively, for 1995 seed (Table 3). Randomized plots of high- and low-germination progeny lines averaged 45.5 and 3.8% for prechilled 1997 seed. As expected, Rimrock germination was intermediate at 11.5%. The difference between Rimrock progeny lines selected for high and low germination based on 1994 and 1995 seed lots was largely maintained after these lines were seed

Table 2. Seed mass and lemma and palea thickness of jumbo, globose, and elongate seed morphs of T-593 Indian ricegrass produced in paper bags at Greenville Farm.

	Seed Mass[1] 1993	Seed Mass[1] 1994	Lemma Thickness[2] 1993	Lemma Thickness[2] 1994	Palea Thickness[2] 1993	Palea Thickness[2] 1994
	(mg/seed)		(mm)		(mm	
Jumbo	8.99 (0.04)	8.24 (0.04)	182 (3.4)	179 (2.5)	150 (2.8)	146 (3.4)
Globose	3.46 (0.07)	3.27 (0.06)	95 (3.0)	91 (1.2)	84 (2.4)	82 (1.4)
Elongate	2.37 (0.03)	2.29 (0.04)	54 (1.0)	50 (0.8)	49 (0.9)	48 (0.6)

[1] Mass based on 1,000-seed sample. Standard error of the mean based on 100-seed subsamples in parentheses.
[2] Mean based on 20 seeds. Standard error of the mean in parentheses.

Table 3. Germination, seed mass, and lemma and palea thickness of 5 high and 5 low-germination 'Rimrock' progeny lines.

Line no.	Germination[1]			Seed Mass		Lemma Thickness		Palea Thickness	
	1994	1995	1997	1996	1997	1994	1995	1994	1995
	(%)			(mg)		(μm)		(μm)	
				High-Germination Lines					
2-7	65.0	52.0	28.5	3.38	4.37	60.0	62.5	50.7	52.3
3-10	59.5	53.3	59.5	3.64	3.84	47.3	48.6	41.6	42.5
4-13	56.0	75.3	33.0	3.52	4.09	57.5	57.5	50.9	49.5
5-2	63.5	57.8	55.0	4.08	4.37	58.9	60.0	50.2	51.6
6-6	64.8	55.3	51.5	3.20	4.00	55.9	60.0	50.2	49.5
Mean[2]	61.8	58.7	45.5	3.56	4.13	55.9	57.7	48.7	49.1
				Low-Germination Lines					
2-11	0.0	1.0	5.0	3.75	3.94	61.4	59.8	52.3	51.1
2-13	0.3	0.3	4.5	3.59	3.94	60.0	63.2	53.0	53.9
3-15	0.8	0.0	1.3	4.27	4.45	65.2	65.2	55.9	56.4
7-20	0.3	2.3	3.8	2.51	3.85	61.1	54.8	53.0	47.5
8-19	0.0	1.0	4.5	3.22	3.81	63.4	62.5	55.2	51.8
Mean[2]	0.3	0.9	3.8	3.47	4.00	62.2	61.1	53.9	52.1
High vs. Low	N/A	N/A	*[2]	NS	NS	*	NS	*	NS
CV			22.6	14.8	6.1	6.6	8.0	5.9	7.1

[1] Seed tested the spring following the production year with a 3-week prechill (5° C) and 2-week (15° C) incubation. Data arcsine-transformed before analysis. 1994 and 1995 data are parent plants and 1997 data are progeny lines.

[2] Significant at $P<0.05$.

propagated in randomized plots in 1997. This demonstrates that we successfully selected for heritable genetic variation for seed dormancy in Rimrock.

Nonprechilled germination of 1997 seed was considerably lower than prechilled germination. The 5 low-germination progeny lines averaged 1.6% germination after 3 weeks at 15°C, with no additional germination between 3 and 5 weeks. Rimrock seed germinated 1.0% after 3 weeks at 15°C with no additional germination between 3 and 5 weeks. The 5 high-germination progeny lines averaged 4.0% germination after 3 weeks at 15°C and 0.2% additional germination after 5 weeks. Nonprechilled germination of progeny lines selected for high germination under prechill was similar to prechilled germination of progeny lines selected for low germination under prechill.

Rimrock Seed Morphology

Seed mass of high- and low-germination Rimrock progeny lines did not differ ($P>0.10$) in 1996 or 1997 (Table 2). Lemma and palea thickness were both 11% greater ($P<0.05$) in low than in high-germination progeny lines in 1994, but differences were only about half as great and were nonsignificant ($P>0.10$) in 1995. When lemma and palea thickness data were combined over the 2 years, values were higher ($P<0.01$) for low- than for high-germination progeny lines. These differences in lemma and palea thickness are smaller and less consistent than those seen among T- 593 morphs. This is likely to be the case when comparing nonpolymorphic progeny lines differing in germination (as described here for Rimrock selections), to morphs within populations (as described for T-593), or to different populations (as described by Zemetra and Cuany 1984).

Discussion

Other than mention of selection for enhanced germination without prechilling (Zemetra and Cuany 1984), this is the first report of nonpolymorphic genetic variation for seed dormancy within an Indian ricegrass population. The degree of variation in Rimrock was larger than we anticipated. We have no data suggesting that large amounts of genetic variation for seed dormancy are a common feature in nonpolymorphic Indian ricegrass populations. However, in extensive evaluations we have found great genetic variation among Indian ricegrass populations for seed dormancy. Therefore, a search for nonpolymorphic within-population variation is merited. Furthermore, seed polymorphism similar to that associated with seed dormancy in T-593 was found in 21% of 318 populations examined (Jones and Nielson 1996). It was most frequent in the southern and eastern portions of the Great Basin, a region where Indian ricegrass is very common and the environment may be harsh and highly variable from year to year. However, in the great majority of these polymorphic populations, only 2 morphs were present. Three morphs were found in only 3 other populations, T-464 (Chaffee Co., Colo.), T-591 (McKinley Co., N.M.), and T-728 (Kane Co., Utah).

Zemetra and Cuany (1984) advocated breeding to eliminate the need for scarification for Indian ricegrass stand establishment. Conversely, Orodho et al. (1998) argued that an Indian ricegrass cultivar free of dormancy would have reduced probability of long-term survival. It is important to note that considerable dormancy is present in the 5 high-germination progeny lines, particularly when prechilling is not applied. The broad range for seed dormancy in Rimrock suggests that this population simultaneously employs contrasting survival strategies in nature. Natural selection may have preserved readily germinable genotypes as well as highly dormant genotypes.

Our data suggest that genetic variation in seed dormancy can be as great within a population as between populations. Genetic effects combined with environmental effects (Jones and Nielson 1994) and probable genotype X environment interactions determine the seed dormancy phenotype of an individual seed. Because the Indian ricegrass seed production environment affects seed dormancy (Jones and Nielson 1994), and because flowering in this grass is indeterminate, even seeds maturing at different times on the same plant in the same year likely display contrasting germination patterns (R.L. Cuany, pers. comm.). These interactions may be documented by collecting ripe seed on individual plants at discrete points in time as soil and atmospheric environments are varied. A broad phenotypic array would theoretically allow a population to appropriately respond to a wide range of environmental conditions, thereby maximizing fitness.

Our research demonstrates 2 genetically controlled sources of variance for seed dormancy—between seed morphs and related to seed mass and lemma and palea thicknesses, as seen here with T-593, and within seed morphs and unrelated to morphological features of the seed, as seen here with Rimrock. Researchers investigating Indian ricegrass seed dormancy have agreed that the paradigm of mechanical and physiological seed dormancy is appropriate for this species (Jones 1990). If so, variation in lemma and palea thickness among morphs, and its correlation with germination may explain variation for mechanical dormancy. Nonpolymorphic variation for germination may correspond to variation for physiological dormancy. Future research should be directed towards explaining the relative influence of environmental variables on these 2 sources of variance for seed dormancy.

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