



2-8-2013

## Seed source affects establishment of *Elymus multisetus* in postfire revegetation in the Great Basin

Courtney L. J. Rowe

University of Nevada, Reno, NV, [cjrowe@fs.fed.us](mailto:cjrowe@fs.fed.us)

Elizabeth A. Leger

University of Nevada, Reno, NV, [eleger@cabnr.unr.edu](mailto:eleger@cabnr.unr.edu)

Follow this and additional works at: <https://scholarsarchive.byu.edu/wnan>



Part of the [Anatomy Commons](#), [Botany Commons](#), [Physiology Commons](#), and the [Zoology Commons](#)

### Recommended Citation

Rowe, Courtney L. J. and Leger, Elizabeth A. (2013) "Seed source affects establishment of *Elymus multisetus* in postfire revegetation in the Great Basin," *Western North American Naturalist*. Vol. 72 : No. 4 , Article 10.

Available at: <https://scholarsarchive.byu.edu/wnan/vol72/iss4/10>

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact [scholarsarchive@byu.edu](mailto:scholarsarchive@byu.edu), [ellen\\_amatangelo@byu.edu](mailto:ellen_amatangelo@byu.edu).

## SEED SOURCE AFFECTS ESTABLISHMENT OF *ELYMUS MULTISETUS* IN POSTFIRE REVEGETATION IN THE GREAT BASIN

Courtney L. J. Rowe<sup>1,2</sup> and Elizabeth A. Leger<sup>1,3</sup>

**ABSTRACT.**—Postfire revegetation with native perennial grasses is difficult to achieve in disturbed arid rangelands. If local populations are adapted to current conditions, then locally collected seed would be predicted to have higher survival than nonlocal seed, and using local seed should improve revegetation success. However, for revegetation projects in the Great Basin, sufficient quantity of local seed is often difficult to obtain commercially, so seeds often originate from source populations that are hundreds of kilometers from the project site. We investigated whether seed source affected first-year establishment of big squirreltail (*Elymus multisetus* M.E. Jones) seedlings in a common garden field trial 50 km north of Reno, Nevada. For the trial, we used wild, locally collected seed and commercially produced seed originating from Oregon, Idaho, and California. Several phenological and growth traits varied significantly between source populations. Eighty-six percent of local seeds emerged, compared to 71%, 61%, and 12% of seeds from Idaho, Oregon, and California, respectively. Local seeds emerged, on average, 9 days earlier than seeds from other sources. Fourteen percent of the local seedlings survived through the first year, exceeding survival by Oregon (12%), Idaho (8%), and California (2%) seedlings. Though survivorship was highest for local seed, local seedlings were smaller, producing 24% fewer leaves than the most productive seedlings from the Idaho seed source. Our data suggest that seed source is an important factor in seedling establishment. If local seed can survive significantly better than regionally collected, commercially produced seed, it may be both ecologically and economically beneficial to use local seed in revegetation.

**RESUMEN.**—Después de un incendio, es difícil lograr la revegetación con hierbas perennes nativas en tierras áridas de pastoreo afectadas. Si las poblaciones locales están adaptadas a las condiciones actuales, las semillas recolectadas localmente tendrían más posibilidades de sobrevivir que las semillas que no son del lugar, y el uso de las semillas del lugar debería mejorar el éxito de la revegetación. Sin embargo, para los proyectos de revegetación en la Gran Cuenca (Great Basin), generalmente es difícil conseguir comercialmente una cantidad suficiente de semillas del lugar, por lo que a menudo las semillas provienen de poblaciones de origen que se encuentran a cientos de kilómetros del sitio del proyecto. Investigamos si la procedencia de las semillas afecta el primer año de establecimiento de las plántulas de centeno silvestre o big squirreltail (*Elymus multisetus* M.E. Jones), en una prueba de campo de jardín común a 50 km al norte de Reno, Nevada, mediante el uso de semillas silvestres recolectadas en el lugar y semillas producidas comercialmente provenientes de Oregon, Idaho y California. Varias características fenológicas y de crecimiento variaron de manera significativa entre las poblaciones de origen. 86% de las semillas locales emergieron, comparadas con el 71%, 61% y 12% de las semillas de Idaho, Oregon y California, respectivamente. Las semillas del lugar emergieron, en promedio, nueve días antes que las otras fuentes de semillas. 14% de las plántulas locales sobrevivieron durante el primer año, lo que excedió en supervivencia a las plántulas de Oregon (12%), Idaho (8%) y California (2%). Aunque la supervivencia fue mayor para las semillas locales, las plántulas locales fueron más pequeñas y produjeron un 24% menos hojas que las plántulas más productivas provenientes de la fuente de semillas de Idaho. Nuestros datos sugieren que el origen de las semillas es un factor importante en el establecimiento de plántulas. Si las semillas del lugar pueden sobrevivir considerablemente mejor que las semillas recolectadas regionalmente y producidas comercialmente, el uso de semillas locales para la revegetación puede ser beneficioso ecológicamente y económicamente.

Reciprocal transplant and common garden studies have repeatedly shown that plant populations can be highly adapted to local environmental conditions (Clausen et al. 1940, Joshi et al. 2001, Leimu and Fischer 2008). This adaptivity leads to the expectation that, when native seed material is chosen for a revegetation project, seeds collected near the project site should yield higher survival rates than commercially produced seed collected from

distant sources (Knapp and Rice 1994)—a hypothesis supported in field tests (e.g., Cotts et al. 1991, Petersen et al. 2004, Gustafson et al. 2004, Rice and Knapp 2008). In addition to concerns about reduced performance during restoration, there is also concern that the use of nonlocal seed may reduce in situ genetic variation in natural populations by overwhelming local gene pools with an influx of commercial seeds (Montalvo and Ellstrand 2001,

<sup>1</sup>Department of Natural Resources and Environmental Science, MS 186, University of Nevada, 1664 North Virginia St., Reno, NV 89557.

<sup>2</sup>Present address: USDA Forest Service, Plumas National Forest, 39696 Highway 70, Quincy, CA 95961.

<sup>3</sup>Corresponding author. E-mail: eleger@cabnr.unr.edu

McKay et al. 2005). Commercially available seed is often derived from a single source population and occasionally from a single genotype (Young et al. 2003, Jones and Larson 2005, Shaw et al. 2005). Inadvertent selection can occur in the collection and propagation of seed, and it can alter genetic variation (Campbell and Sorensen 1984, Meyer and Kitchen 1994). There is now widespread support for the use of locally collected seed in restoration (Linhart 1995, Hufford and Mazer 2003, Broadhurst et al. 2008) and in the preservation of local genetic variation in restored plant populations (Buck et al. 1970, Guinon 1993, Meyer and Mosen 1993, Richards et al. 1998).

Why isn't locally collected native seed used in all restoration attempts? First, local seed from native species can be difficult to obtain in sufficient quantity for large-scale projects, and it is considerably more expensive than commercially available alternatives (Roundy et al. 1997, Shaw et al. 2005). Secondly, the preservation of local genetic variation may not guarantee that local seed material performs optimally at restoration sites; highly adapted populations may also be at greater risk of maladaptation under changing conditions (Crespi 2000). If conditions have changed from those under which a local population has evolved, which can be the case in disturbed ecosystems, then local populations may not possess sufficient genetic variation to produce a successful phenotype in the new environment (Rice and Emery 2003, Jones and Monaco 2009). Furthermore, the success of some invasive species demonstrates that nonlocal genotypes can effectively compete in novel environments without significant genetic differentiation or local adaptation (e.g., Williams et al. 1995).

Genetic variation and local adaptation of seed material receive considerable attention in restoration studies, but there have been few field-based examinations of their impacts on restoration of rangelands degraded by cheatgrass (*Bromus tectorum* L.) in the Great Basin (e.g., Humphrey and Schupp 2002). Big squirreltail (*Elymus multisetus* M.E. Jones) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) are native perennial bunchgrasses that are considered promising species for use in restoration of cheatgrass-invaded sites (Jones 1998, Richards et al. 1998) because they are able to persist alongside cheatgrass (Hironaka

and Tisdale 1963, Booth et al. 2003, Leger 2008, Rowe and Leger 2011). The 2 species are so closely related that they are considered conspecific by some taxonomists (Holmgren and Holmgren 1977, Arnow 1993) and are often treated as a species complex (Jones 1998), as they will be here. Squirreltail populations exhibit both high genetic and high phenotypic variation in the Great Basin (Jones et al. 2003, Larson et al. 2003). In populations sampled primarily in Oregon and Idaho, but also in California and Nevada, phenological and phenotypic traits were strongly correlated with collection elevation and location, which is evidence of local adaptation (Parsons et al. 2011). In Utah, Humphrey and Schupp (2002) compared local and commercial seed sources of squirreltail and found that local seeds showed first- and second-year survival advantages over commercial seed, but the advantage disappeared after 3 years. In the neighboring Sierra Nevada, reciprocal transplants of squirreltail demonstrated fitness differences that varied with aspect and elevation ( $\pm 300$  m), with local seed outperforming nonlocal seed (Rice et al. 2009).

Our goal was to evaluate whether seedling establishment in postfire revegetation is affected by seed source of big squirreltail by testing the relative performance of wild-collected, local seed and commercially available seed in a common garden experiment. We used a precision seeding method that allowed us to track the emergence and survival of individual seeds, and we addressed the following questions: Does performance vary among seed sources in squirreltail during revegetation? If so, what are the implications for managing revegetation seed sources and restored populations of squirreltail in the Great Basin?

## METHODS

We conducted a common garden field experiment at the Hallelujah Junction Wildlife Refuge, near Bordertown, Sierra County, California, approximately 30 miles north of Reno, Nevada. Elevation at the field site is  $\sim 1500$  m above sea level, and slope ranges from 2% to 15%. The soil type is Trosi very stony sandy loam, with parent material consisting mostly of alluvium derived from mixed bedrock (NRCS 2008). This soil type is considered non-saline, exhibits very low water-holding capacity

TABLE 1. Seed source information. Generation status is the number of generations removed from original collection at the seed source.

Source	Generation status	Collection site	Production Site
Local	G <sub>0</sub>	Sierra County, CA <sup>a</sup>	N/A
California	G <sub>1</sub>	Tehama County, CA	Yolo County, CA
Oregon	G <sub>2</sub>	Jefferson County, OR	Franklin County, WA
Idaho	G <sub>1</sub> –G <sub>3</sub> <sup>b</sup>	Gem County, ID	Utah County, UT

<sup>a</sup>Collected within 0.4 km of study location

<sup>b</sup>Generation status of each seed is not known but is limited to first 3 generations

(0.00–0.254 mm · hr<sup>-1</sup>), and has very low available water (~38.1 mm) (NRCS 2008). Average temperature is 0.4 °C in January and 21.3 °C in July, with annual precipitation averaging 265.2 mm (NCDC 2002). The site is managed by the California Department of Fish and Game and has been rotationally grazed for over 50 years. Since a moderate-intensity fire in 2007, the study area has not been grazed. The plant community is shrubsteppe dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young). The main graminoid components are Sandberg's bluegrass (*Poa secunda* J. Presl. ssp. *secunda*), big squirreltail, and cheatgrass. While cheatgrass exists at the site, there has not been complete conversion as has been seen on many other sites with an extended grazing history in the Great Basin.

On 20 November 2008, we sowed 250 big squirreltail seeds from each of 4 seed sources (Table 1). All seed sources key to *E. multisetus*, though Sand Hollow seeds were originally released as *E. elymoides* (Jones et al. 2004). Seeds from commercial sources were randomly selected from 1-kg bags. Locally sourced seeds were randomly selected from a 2008 collection bulked from ~100 individual plants. Prior to planting, awns were removed manually for local seed and mechanically for commercial seed. Our design combined the effects of seed source with seed collection method (seeds were either local and hand-collected or commercially grown and machine-harvested), but hand-collection of seed for restoration projects is not uncommon. Seed viability was assessed by tetrazolium testing (described in Miller 2005), with 4 replicate treatments of 10 seeds from each seed source (160 seeds total).

We used a precision seeding method designed to track and identify individual seedlings from particular seeds in the field. To do this, each seed was individually weighed and

then glued to a toothpick using water-soluble glue. Seeds on toothpicks were sown directly into undisturbed soil to a depth of ~2 mm in a completely randomized design with 25 rows of 40 seeds each. Each row was spaced 1-m apart and seeds were spaced 0.5-m apart within rows. Some toothpicks were physically touching an extant plant, so competition status (i.e., touching or not touching extant plant) was noted for each seed to allow for analysis of possible competition effects.

Seedling establishment is commonly used as a measurement of success for restoration projects (Zedler and Callaway 2000, Ruiz-Jaen and Aide 2005). Seedling emergence—a measurement that combines germination and successful elongation of cotyledons—was tracked weekly from 20 November 2008 through 20 April 2009. Since big squirreltail is a cool-season perennial grass, it experiences summer dormancy, which can potentially complicate measurement of survivorship because dormant plants are difficult to distinguish from dead plants; for this reason, the number of plants exhibiting active growth (i.e., green tissue) was used as a proxy for survivorship. Active growth was assessed in April, May, June, July, and September 2009 and again in January and April 2010. Numbers of viable seed were approximated by multiplying mean viability percentage (determined by tetrazolium test) and quantity sown. We report adjusted emergence (% viable seed × number emerged) and survivorship (% viable seed × number exhibiting active growth) percentages. A sharp decline in active growth of experimental plants in July was used to demark the end of the first growing season; other on-site perennial grasses senesced from late June to late July.

Measurements of leaf length and quantity were taken monthly from May to September 2009. Leaf length is strongly correlated with total biomass in perennial grasses (e.g., Scheiner 1989, Svejcar 1990, Arredondo et al. 1998,

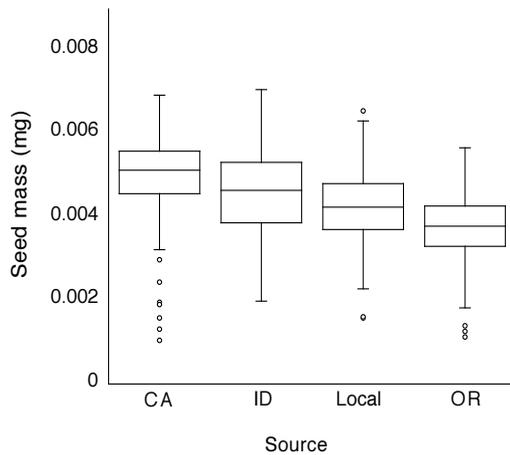


Fig. 1. Distribution of seed mass by seed source (CA = California, ID = Idaho, OR = Oregon). Center line of box plots represents median seed mass for each seed source, box outline represents  $\pm 25\%$  from the median, and bars represent 10% and 90% percentiles. Letters indicate significant ( $\alpha = 0.05$ ) differences between means, determined with a Tukey–Kramer HSD test.

Leger 2008). We used leaf length as a proxy for biomass so that we did not have to destructively harvest plants. No plants produced seed during the experiment. In May and June, a subsampling of leaf-length measurements was taken from 20 randomly selected individual plants from each source ( $N = 69$ ; only 9 actively growing plants from California source). By July, the number of actively growing plants was severely reduced, and censuses were conducted in July ( $N = 133$ ) and September ( $N = 24$ ). Total leaf length was calculated by summing the lengths of all leaves exhibiting active growth in July.

All analyses were performed in JMP 7.0.2 (SAS Institute 2007). Emergence and active growth were analyzed using logistic regression. ANOVA was used to analyze the effects of seed source, seed mass (continuous covariate), and competition status on emergence timing and July leaf length. The effects of seed source on seed viability and seed mass, as well as the effects of emergence timing (continuous covariate) on active growth and leaf length, were analyzed using ANOVA. Significant results ( $\alpha = 0.05$ ) were analyzed *a posteriori* using the Tukey–Kramer HSD method. For seed mass and emergence timing, transformations were not required to meet assumptions of normality and homogeneity of variance for

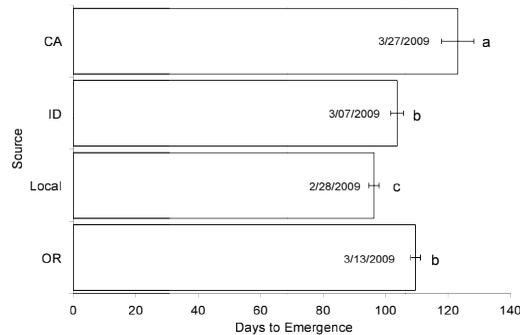


Fig. 2. Days to emergence by seed source (mean  $\pm$  SE; CA = California, ID = Idaho, OR = Oregon). Mean emergence dates are indicated. Significant differences ( $\alpha = 0.05$ ) among seed sources were determined using a Tukey–Kramer HSD test and are indicated with lowercase letters.

ANOVA, but leaf lengths were log-transformed to achieve a normal distribution. For leaf-length analysis, the California source was excluded because only one plant was actively growing. Means and standard errors of untransformed data are presented in all figures.

## RESULTS

Seed mass varied significantly among seed sources ( $F_{3,996} = 96.0$ ,  $r^2 = 0.22$ ,  $P < 0.0001$ ), with each source exhibiting a significantly different mean value in a *posteriori* comparison (Fig. 1). The range of seed mass was narrow (1–7 mg), and there was substantial overlap in seed mass variation among seed sources. Tetrazolium testing of seed viability revealed significant differences between seed sources ( $F_{3,12} = 14.3$ ,  $r^2 = 0.72$ ,  $P = 0.0003$ ). Viability percentages were 100% for Oregon and local sources, 93% for Idaho, and 70% for California, with the California source being significantly different than the remaining 3 in a *posteriori* comparison.

Emergence timing (i.e., days to emergence) varied significantly by seed source (Fig. 2) and competition status but was not significantly affected by seed weight (Table 2A). The average emergence timing of local seed was between 7 and 27 days earlier than the average germination timing of other seed sources (Fig. 2). The difference in emergence between seeds experiencing competition (111 days) and those not experiencing competition (102 days) was also 9 days (Table 2A). Seeds

TABLE 2. Results of (A) ANOVA for days to emergence and July leaf length and (B)  $\chi^2$  tests for percent emergence and percent active growth, with all models including the effects of seed source, seed mass, and competition status. Bolded results are significant ( $\alpha = 0.05$ ). For April 2010, data are presented with and without exclusion of questionably identified seedlings, with exclusions in parentheses. Sample size is indicated by  $n$ . Model fit is indicated with  $r^2$ . Numerator degrees of freedom (df),  $F$  or  $\chi^2$  test statistics, and  $P$  values are shown.

A.	$n$	$r^2$	Source			Seed mass			Competition at sowing		
			df	$F$	$P$	df	$F$	$P$	df	$F$	$P$
Days to emergence	557	0.09	3	16.2	<0.0001	1	3.3	0.0689	1	10	<b>0.0015</b>
July mean leaf length	131	0.07	2	4.68	<b>0.011</b>	1	0	0.976	1	0.41	0.5241
B.	$n$	$r^2$	df	$\chi^2$	$P$	df	$\chi^2$	$P$	df	$\chi^2$	$P$
Emergence percentage	1000	0.29	3	374.38	<0.0001	1	11.74	<b>0.0006</b>	1	3.41	0.0646
Active growth											
April 2009	1000	0.28	3	365.39	<0.0001	1	13.46	<b>0.0002</b>	1	0.57	0.4491
May 2009	1000	0.26	3	338.45	<0.0001	1	11.68	<b>0.0006</b>	1	0.12	0.7266
June 2009	1000	0.13	3	123.98	<0.0001	1	5.99	<b>0.0144</b>	1	2.79	0.0951
July 2009	1000	0.11	3	85.76	<0.0001	1	8.76	<b>0.0031</b>	1	0.74	0.3882
September 2009	1000	0.08	3	16.88	<b>0.0007</b>	1	2.17	0.1411	1	0.97	0.3253
January 2010	1000	0.07	3	23.25	<0.0001	1	2.4	0.121	1	0.11	0.7323
April 2010	1000	0.07	3	36.36	<0.0001	1	0.67	0.4127	1	0.67	0.6092
April 2010 exclusions	(952)	(0.06)	3	(19.32)	(0.0002)	1	(2.16)	(0.1414)	1	(0.63)	(0.4257)

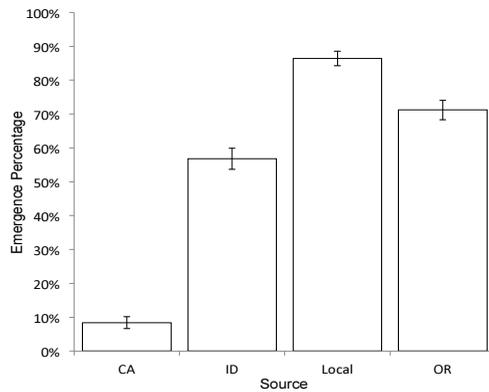


Fig. 3. Comparison of emergence percentages among seed sources (CA = California, ID = Idaho, OR = Oregon).

with higher seed mass generally required less time to emerge, but the relationship was not significant (Table 2A).

Emergence percentage varied significantly by seed source and seed mass (Table 2B). Local seeds exhibited the highest emergence percentage (86.4%), followed by the commercial sources (Oregon, 71.2%; Idaho, 56.8%; California, 8.4%; Fig. 3). Accounting for seed viability, adjusted emergence increased to 12.0% for California and 61% for Idaho; local (86.4%) and Oregon (71.2%) sources were unchanged. Emergence percentage increased with increasing seed mass (Table 2B). Emergence percentage was not affected by competition status at time of sowing (Table 2B), but there was a nonsignificant trend for competition to suppress emergence (57.5% emergence without competition; 46.7% with competition).

The number of plants exhibiting active growth was significantly different among seed sources at all 7 assessments (Table 2B, Fig. 4). In April, May, and June 2009, the greatest quantity of actively growing plants was from the local source (Fig. 4). By July, plants from local and Oregon sources were nearly equal in abundance ( $N_{\text{local}} = 48$ ;  $N_{\text{OR}} = 51$ ), while both were more abundant than the other 2 sources ( $N_{\text{CA}} = 1$ ;  $N_{\text{ID}} = 8$ ). The Oregon seed source exhibited the highest viability-adjusted percentage of actively growing plants in July (20.4%), followed by local (19.2%), Idaho (14.3%), and California (0.6%) (Table 2B). There was a sharp decline in active growth in all plants through June and July (Fig. 4). In September 2009 and January 2010, total active growth

was very low (2.7% and 4.9%, respectively), but increased slightly (9.5%) by April 2010.

At the end of data collection (April 2010), the local seed exhibited the highest adjusted percentage of actively growing plants (13.6%), followed by Oregon (12.4%), Idaho (7.8%), and California (1.7%), with significant differences among sources (Table 2B). In total, there were 86 actively growing plants from 557 emergents sown from 1000 seeds; of these, 40% ( $n = 34$ ) were from local seed. During the last assessment, because many seeds were no longer glued to toothpicks, there were 38 instances in which we had difficulty determining if the seedling found nearest the toothpick was sown as part of the experiment. Even when these seedlings were excluded from analysis, significant differences remained among sources (Table 2B). Local seedlings still exhibited the highest percentage of active growth—6.0%, compared to 4.8%, 4.32%, and 0.6% for Oregon, Idaho, and California, respectively. At all assessments, active growth was not significantly affected by competition status (Table 2B). From April to July 2009, active growth increased significantly with seed mass but exhibited no significant relationship to seed mass in the following 3 assessments. Active growth was significantly affected by emergence timing in May, June, July, and September 2009 and January and April 2010 (data not shown; all  $P < 0.02$ ), though not in April 2009 ( $P = 0.053$ ); during the last 6 assessments, plants with earlier emergence dates were more likely to exhibit active growth.

At the end of the first growing season (July 2009), mean leaf length varied significantly by seed source but not by competition status or seed mass (Table 2A). Seedlings from the Idaho commercial source exhibited the greatest mean leaf length ( $22.9 \pm 3.0$  cm), mostly due to 3 very large outliers. Mean leaf lengths for California, Oregon, and local sources were 17.0 cm ( $n = 1$ ),  $18.1 \pm 2.4$  cm, and  $11.9 \pm 2.5$  cm, respectively. In *a posteriori* comparisons, there were not significant differences in leaf length between the Idaho and local sources or between the Idaho and Oregon sources, but there were significant differences between local and Oregon sources. Mean leaf length was also correlated with emergence timing, with earlier emerging seedlings exhibiting greater leaf lengths ( $r^2 = 0.03$ ,  $F_{1,131} = 4.30$ ,  $P = 0.0401$ ). The Oregon source produced the

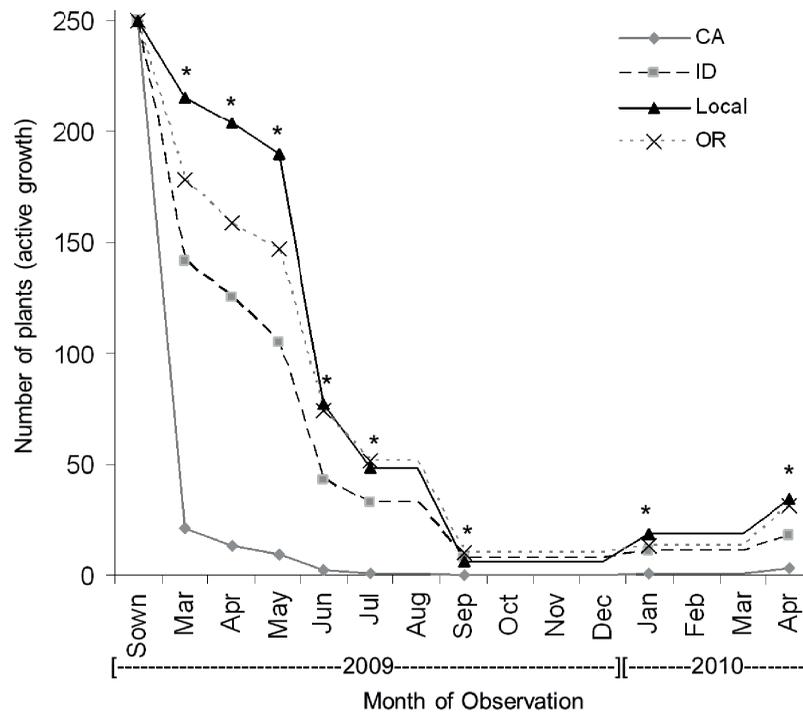


Fig. 4. Plants exhibiting active growth (a proxy for survivorship) by seed source (CA = California, ID = Idaho, OR = Oregon) by month. Measurements were taken in March, April, June, July, and November 2009 and January and April 2010. Asterisks indicate significant differences ( $\alpha = 0.05$ ) between seed sources.

greatest total leaf length (922 cm), followed by the Idaho (755 cm), local (573 cm), and California sources (17 cm).

#### DISCUSSION

Seed source appears to be an important component of seedling establishment in big squirreltail, as there were significant differences among seed sources for all performance measurements. Local seed significantly outperformed other seed sources in emergence and survivorship, though not in size. In addition to seed source, emergence timing was an important driver of seedling establishment, but seed mass was not.

#### Performance was Related to Early Emergence

Plants that emerged earlier were more likely to survive and, at the end of the first growing season, produced higher mean leaf lengths. Early germination has been shown to increase both short-term survivorship and long-term (9-year) fitness in perennials (Verdu and Traveset 2005, De Luis et al. 2008).

Perennials that initiate early growth may be able to preempt the colonization of annual species—a potentially important advantage in cheatgrass-dominated areas (James et al. 2006). The strong relationship between early emergence and first-season survivorship may warrant investigation into the use of germination or emergence timing as screening tools for big squirreltail seed intended for use as restoration material (e.g., Jones et al. 2004).

Germination timing is often closely correlated with seed-source environmental conditions (e.g., Meyer and Monsen 1991, Erickson et al. 2004). Traits exhibiting this type of correlation are likely to have evolved under selective pressure (Endler 1986). Germination timing has been found to vary among seed sources in other squirreltail populations (Parsons et al. 2011). In our experiment, emergence timing and seed source were strongly related, with local seeds emerging much earlier than seeds from other sources. This relationship suggests that emergence timing may be heritable and that local seed may have a competitive advantage.

Validation of local adaptation would, however, require reciprocal transplant studies.

#### Local Seeds were More Likely to Emerge and Survive

For perennial species, quantification of lifetime fitness requires measurement of survivorship and fecundity over several years and is rarely attained in anything but long-term ecological monitoring. Nonetheless, seedling establishment—which can be quantified in short time frames—is critically important to survivorship. In this measure, local seed was superior. Compared to all commercial sources, local seed produced the most emerged seedlings and, from April to June of the first growing season, the most seedlings exhibiting active growth (Fig. 4). At the start of the second growing season, after dormancy, local seedlings reemerged in greater quantity than those of any other seed source (Fig. 4). This increase suggests that local seedlings are likely to continue as superior survivorship performers, though follow-up monitoring of out-year performance, as well as seed production, could provide further insight into the relationship between seed source and fitness.

#### Seed Mass Varied by Seed Source but did not Affect Performance Measurements

Higher seed mass has long been tied to enhanced seedling performance (Green and Hansen 1969, Buckley 1982). However, in our experiment, seed mass was a relatively poor indicator of seedling performance. Despite having the highest seed mass, the California seed had the lowest seed viability, for unknown reasons. Higher seed mass was positively correlated with emergence percentage and initial survival, but the relationship faded by September (Table 1). Emergence timing and biomass were not at all affected by seed mass. There were small but significant differences in seed mass between seed sources, but we could not determine whether this variation was due to genetic or maternal environment differences among sources. Nongenetic maternal provisioning is widely documented and can strongly influence seed mass (Eagles and Hardacre 1979, Antonovics and Schmitt 1986). Among our seed sources, growing conditions were very different, with local seeds collected from wild plants and commercial varieties grown under agronomic conditions at 3 different

sites. One might predict that commercially grown plants would have access to more resources and produce more and larger seeds that would outperform wild-collected seeds. However, we observed that wild-collected local seeds did not exhibit the lowest seed weights (Fig. 1). More importantly, they outperformed larger-seeded populations (i.e., California, Idaho) in relative emergence and survival (Figs. 3, 4). Future comparison of plants produced from seed grown and collected in a common garden could illuminate the relative importance of maternal versus genetic influence on seed mass or other traits.

#### Local Seeds Produced the Smallest Plants

At the end of the first growing season (July 2009), there were large differences among seed sources in both mean and total leaf length. Leaf length of big squirreltail is highly correlated with plant biomass (Leger 2008), and plant biomass is often correlated with fecundity and competitive ability (Aarssen and Taylor 1992, Scheiner 1993, Keddy et al. 2002). Since an equal number of seeds was sown for each source, higher total leaf length amounts to a greater biomass return for equal seed investment—an important performance measure for restorationists with a goal of maximizing native cover. Local seedlings exhibited the lowest mean leaf length and the second lowest total leaf length, though the higher survivorship of local seed compensated for small individual plant size: when total length is summed across sources, local material accounted for 25% of all leaf lengths—the proportion expected from sowing rates. Despite the greater emergence and first-year survivorship of local seedlings, if biomass is taken as a reliable indicator of fitness, then the relatively small size of local plants may hinder their long-term fitness.

The relationship between biomass and fitness, though widely documented, may not be ubiquitous. Biomass exhibits very high environmental plasticity (Bradshaw 1965, Schlichting 1986), and, in resource-limited conditions, it may be decoupled from fitness (Chambers and Aarssen 2009, Sheridan and Bickford 2011). There are circumstances in which being a small plant could be adaptive (Aarssen et al. 2006); for example, small plants may contribute disproportionately to population-level seed production in highly competitive conditions

(Neytcheva and Aarssen 2008). Small biomass may be also advantageous under drought conditions, as smaller seedlings have been observed to be more drought tolerant than larger seedlings (Hendrix et al 1991). Furthermore, for big squirreltail from the same source as the local seeds in our experiment, smaller seedlings were more tolerant of cheatgrass competition than larger seedlings, and plants from cheatgrass-invaded areas produced smaller seedlings than nearby plants from uninvaded and presumably more resource-rich areas (Rowe and Leger 2011). Plant size may not be a reliable indicator of fitness in the Great Basin's disturbed arid rangelands, where small size may increase survival under resource-limited conditions.

#### Seed Source Should be Considered in Revegetation

Local seed could be distinguished from commercial seed in every trait we measured—seed mass, emergence timing and percentage, survivorship, and biomass. As suggested in our study and in others, there may be important differences among squirreltail populations in the Great Basin (Larson et al. 2003, Parsons et al. 2011). In some populations, local seed may possess adaptive traits that improve revegetation performance; but, among all populations, there may exist a genetic uniqueness that deserves consideration and may warrant protection in its own right. The decision to introduce regional, agronomically produced squirreltail seed should involve a field-based performance evaluation of potential seed material. Although short-term performance measures do not capture lifetime fitness, they can be fast and efficient methods to experimentally differentiate between seed sources under consideration for revegetation. In the absence of clear evidence that commercially available seed exhibits superior performance, managers should favor revegetation with locally collected seed and the protection of potential genetic variation. While large-scale reciprocal transplant experiments are needed to provide guidelines about the scale and parameters of local adaptation (e.g., Johnson et al. 2010), small-scale field evaluations, such as ours, can provide individual managers with information relevant to their current revegetation sites, which should translate into better restoration outcomes.

#### ACKNOWLEDGMENTS

Matt Forister and Mary Peacock provided helpful suggestions for the manuscript. Jan Dawson, Chris Ross, and the California Department of Fish and Game provided historical information and access to the research property. To Sandra Li and Kestrel Schmidt, who graciously weighed and glued a thousand seeds to toothpicks, we offer as many thanks.

#### LITERATURE CITED

- AARSEN, L.W., B.S. SCHAMR, AND J. PITHER. 2006. Why are there so many small plants? Implications for species coexistence. *Journal of Ecology* 94:569–580.
- AARSEN, L.W., AND D.R. TAYLOR. 1992. Fecundity allocation in herbaceous plants. *Oikos* 65:225–232.
- ANTONOVICS, J., AND J. SCHMITT. 1986. Paternal and maternal effects on propagule size in *Anthoxanthum odoratum*. *Oecologia* 69:277–282.
- ARNOW, L.A. 1993. Gramineae. Pages 775–833 in S.L. Welsh, N.D. Atwood, S. Goodrich, and L.C. Higgins, editors, *A Utah flora*. Brigham Young University Press, Provo, UT.
- ARREDONDO, J.T., T.A. JONES, AND D.A. JOHNSON. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Journal of Range Management* 51:584–589.
- BOOTH, M.S., M.M. CALDWELL, AND J.M. STARK. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36–48.
- BRADSHAW, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13:115–155.
- BROADHURST, L.M., A. LOWE, D.J. COATES, S.A. CUNNINGHAM, M. McDONALD, P.A. VESK, AND C. YATES. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* 1:587–597.
- BUCK, J.M., R.S. ADAMS, J. CONE, M.T. CONKLE, W.J. LIBBY, C.J. EDEN, AND M.J. KNIGHT. 1970. California tree seed zones. USDA Forest Service, San Francisco, CA.
- BUCKLEY, R.C. 1982. Seed size and seedling establishment in tropical and dunecrest plants. *Biotropica* 14: 314–315.
- CAMPBELL, R.K., AND F.C. SORENSEN. 1984. Genetic implications of nursery practices. Pages 183–191 in M.L. Duryea and T.D. Landis, editors, *Forest nursery manual: production of bareroot seedlings*. USDA Forest Service, State and Private Forestry, Portland, OR.
- CHAMBERS, J., AND L.W. AARSEN. 2009. Offspring for the next generation: most are produced by small plants within herbaceous populations. *Evolutionary Ecology* 23:737–751.
- CLAUSEN, J., D. KECK, AND W. HEISEY. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institution of Washington Publications, Washington, DC.

- COTTS, N.R., E.F. REDENTE, AND R. SCHILLER. 1991. Restoration methods for abandoned roads at lower elevations in Grand Teton National Park, Wyoming. *Arid Soil Research and Rehabilitation* 5:235–249.
- CRESPI, B.J. 2000. The evolution of maladaptation. *Heredity* 84:623–629.
- DE LUIS, M., M. VERDU, AND J. RAVENTOS. 2008. Early to rise makes a plant healthy, wealthy, and wise. *Ecology* 89:3061–3071.
- EAGLES, H.A., AND A.K. HARDACRE. 1979. Genetic-variation in maize (*Zea mays*) for germination and emergence at 10 °C. *Euphytica* 28:287–295.
- ENDLER, J.A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, NJ.
- ERICKSON, V.J., N.L. MANDEL, AND F.C. SORENSEN. 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). *Canadian Journal of Botany* 82: 1776–1789.
- GREEN, N.E., AND R.M. HANSEN. 1969. Relationship of seed weight to germination of 6 grasses. *Journal of Range Management* 22:133–134.
- GUINON, M. 1993. Promoting gene conservation through seed and plant procurement. Pages 82–100 in T.A. Landis, editor, *Proceedings of Western Forest Nursery Association*, 1992 September 14–18, Fallen Leaf Lake, CA. General Technical Report RM-GTR-221, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- GUSTAFSON, D.J., D.J. GIBSON, AND D.L. NICKRENT. 2004. Competitive relationships of *Andropogon gerardii* (big bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology* 18:451–457.
- HENDRIX, S.D., E. NIELSEN, T. NIELSEN, AND M. SCHUTT. 1991. Are seedlings from small seeds always inferior to seedlings from large seeds? Effects of seed biomass on seedling growth in *Pastinaca sativa* L. *New Phytologist* 119:299–305.
- HIRONAKA, M., AND E.W. TISDALE. 1963. Secondary succession in annual vegetation in southern Idaho. *Ecology* 44:810–812.
- HOLMGREN, A.H., AND N.H. HOLMGREN. 1977. Poaceae. Pages 174–464 in A. Cronquist, A.H. Holmgren, N.H. Holmgren, J.L. Reveal, and P.K. Holmgren, editors, *Intermountain flora*. Volume 6. Columbia University Press, New York, NY.
- HUFFORD, K.M., AND S.J. MAZER. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18: 147–155.
- HUMPHREY, L.D., AND E.W. SCHUPP. 2002. Seedling survival from locally and commercially obtained seeds on two semiarid sites. *Restoration Ecology* 10:88–95.
- JAMES, J.J., M.A. CAIRD, R.E. DRENOVSKY, AND R.L. SHELEY. 2006. Influence of resource pulses and perennial neighbors on the establishment of an invasive annual grass in the Mojave Desert. *Journal of Arid Environments* 67:528–534.
- JOHNSON, R.C., V.J. ERICKSON, N.L. MANDEL, J.B. ST. CLAIR, AND K.W. VANCE-BORLAND. 2010. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. *Botany-Botanique* 88:725–736.
- JONES, T.A. 1998. Viewpoint: the present status and future prospects of squirreltail research. *Journal of Range Management* 51:326–331.
- JONES, T.A., AND S.R. LARSON. 2005. Status and use of important native grasses adapted to sagebrush communities. Pages 49–55 in N.L. Shaw, M. Pellant, and S.B. Monsen, editors, *Proceedings of Sage Grouse Habitat Restoration Symposium*, 2001 June 4–7, Boise, ID. Proceedings RMRS-P-38, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- JONES, T.A., AND T.A. MONACO. 2009. A role for assisted evolution in designing native plant materials for domesticated landscapes. *Frontiers in Ecology and the Environment* 7:541–547.
- JONES, T.A., D.C. NIELSON, J.T. ARREDONDO, AND M.G. REDINBAUGH. 2003. Characterization of diversity among 3 squirreltail taxa. *Journal of Range Management* 56:474–482.
- JONES, T.A., D.C. NIELSON, S.R. LARSON, D.A. JOHNSON, T.A. MONACO, S.L. CAICCO, D.G. OGLE, AND S.A. YOUNG. 2004. Registration of Fish Creek bottlebrush squirreltail germplasm. *Crop Science* 44:1879–1880.
- JOSHI, J., B. SCHMIDT, M.C. CALDEIRA, P.G. DIMITRAKOPOULOS, J. GOOD, R. HARRIS, A. HECTOR, K. HUSS-DANELL, A. JUMPPONEN, A. MINNS, ET AL. 2001. Local adaptation enhances performance of common plant species. *Ecology Letters* 4:536–544.
- KEDDY, P., K. NIELSEN, E. WEIHER, AND R. LAWSON. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13:5–16.
- KNAPP, E.E., AND K.J. RICE. 1994. Starting from seed: genetic issues in using native grasses for restoration. *Restoration and Management Notes* 12:40–45.
- LARSON, S.R., T.A. JONES, C.L. MCCracken, AND K.B. JENSEN. 2003. Amplified fragment length polymorphism in *Elymus elymoides*, *Elymus multisetus*, and other *Elymus* taxa. *Canadian Journal of Botany* 81: 789–804.
- LEGER, E.A. 2008. The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. *Ecological Applications* 18:1226–1235.
- LEIMU, R., AND M. FISCHER. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3:1–8.
- LINHART, Y.B. 1995. Restoration, revegetation, and the importance of genetic and evolutionary perspectives. Pages 271–288 in B.A. Roundy, E.D. McArthur, J.S. Haley, and D.K. Mann, editors, *Proceedings of Wildland Shrub and Arid Land Restoration Symposium*, Oct. 19–21, 1993, Las Vegas NV. General Technical Report INT-GTR-315, USDA Forest Service, Intermountain Research Station, Ogden, UT.
- MCKAY, J.K., C.E. CHRISTIAN, S. HARRISON, AND K.J. RICE. 2005. How local is local? – a review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432–440.
- MEYER, S.E., AND S.G. KITCHEN. 1994. Life-history variation in blue flax (*Linum perenne*, Linaceae)—seed-germination phenology. *American Journal of Botany* 81:528–535.
- MEYER, S.E., AND S.B. MONSEN. 1991. Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seed-germination patterns. *Ecology* 72:739–742.
- \_\_\_\_\_. 1993. Genetic considerations in propagating native shrubs, forbs, and grasses from seed. Pages 125–132 in T.A. Landis, editors, *Proceedings of Western Forest Nursery Association*, 1992 September 14–18, Fallen Leaf Lake, CA. General Technical

- Report RM-GTR-221, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- MILLER, A.M. 2005. Tetrazolium testing for flower seeds. Pages 171–190 in M.B. McDonald and F.Y. Kwong, editors. Flower seeds: biology and technology. CABI Publishing, Oxfordshire, United Kingdom.
- MONTALVO, A.M., AND N.C. ELLSTRAND. 2001. Nonlocal transplantation and outbreeding depression in the shrub *Lotus scoparius* (Fabaceae). *American Journal of Botany* 88:258–269.
- [NCDC] NATIONAL CLIMATIC DATA CENTER. 2002. Climatology of the United States No. 81: monthly station normals of temperature, precipitation, and heating and cooling degree days 1971–2000. National Oceanic and Atmospheric Administration; National Environmental Satellite, Data, and Information Service; National Climatic Data Center; Asheville, NC.
- [NRCS] NATURAL RESOURCE CONSERVATION SERVICE. 2008. Natural Soil Survey Geographic (SSURGO) Database [online]. [Cited 30 October 2008]. Available from: <http://soildatamart.nrcs.usda.gov>
- NEYTCHEVA, M.S., AND L.W. AARSEN. 2008. More plant biomass results in more offspring production in annuals, or does it? *Oikos* 117:1298–1307.
- PARSONS, M.C., T.A. JONES, AND T.A. MONACO. 2011. Genetic variation for adaptive traits in bottlebrush squirreltail in the northern Intermountain West, United States. *Restoration Ecology* 19:460–469.
- PETERSEN, S.L., B.A. ROUNDY, AND R.M. BRYANT. 2004. Revegetation methods for high-elevation roadsides at Bryce Canyon National Park, Utah. *Restoration Ecology* 12:248–257.
- RICE, K.J., AND N.C. EMERY. 2003. Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* 1:469–478.
- RICE, K.J., J. KITZMILLER, AND L. HANSON. 2009. Scale of adaptation and determining seed zones for native grass restoration in the Sierra Nevada. 2–9 August. Paper presented at the 94th Ecological Society of America Annual Meeting, Albuquerque, NM.
- RICE, K.J., AND E.E. KNAPP. 2008. Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. *Restoration Ecology* 16:12–23.
- RICHARDS, R.T., J.C. CHAMBERS, AND C. ROSS. 1998. Use of native plants on federal lands: policy and practice. *Journal of Range Management* 51:625–632.
- ROUNDY, B.A., N.L. SHAW, AND D.T. BOOTH. 1997. Using native seeds on rangelands. Pages 1–8 in N.L. Shaw and B.A. Roundy, editors, Proceedings—Using Seeds of Native Species on Rangelands, 16–21 February 1997; Rapid City, SD. General Technical Report INT-GTR-372, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.
- ROWE, C.L.J., AND E.A. LEGER. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* 4:485–498.
- RUIZ-JAEN, M.C., AND T.M. AIDE. 2005. Restoration success: how is it being measured? *Restoration Ecology* 13:569–577.
- SAS INSTITUTE. 2007. JMP, Version 7. SAS Institute Inc., Cary, NC.
- SCHEINER, S.M. 1989. Variable selection along a successional gradient. *Evolution* 43:548–562.
- \_\_\_\_\_. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24: 35–68.
- SCHLICHTING, C.D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17:667–693.
- SHAW, N.L., S.M. LAMBER, A.M. DEBOLT, AND M. PELLANT. 2005. Increasing native forb seed supplies for the Great Basin. Pages 94–102 in R.K. Dumroese, L.E. Riley and T.D. Landis, editors, Proceedings of Forest and Conservation Nursery Associations, 2004 July 12–15, Charleston, NC. Proceedings RMRS-P-35, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- SHERIDAN, J.A., AND D. BICKFORD. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change*. Available from: <http://dx.doi.org/10.1038/NCLIMATE1259>
- SVEJCAR, T. 1990. Root length, leaf-area, and biomass of crested wheatgrass and cheatgrass seedlings. *Journal of Range Management* 43:446–448.
- VERDU, M., AND A. TRAVESET. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology* 86:1385–1394.
- WILLIAMS, D.G., R.N. MACK, AND R.A. BLACK. 1995. Eco-physiology of introduced *Pennisetum setaceum* on Hawaii – the role of phenotypic plasticity. *Ecology* 76:1569–1580.
- YOUNG, S.A., B. SCHRUMPF, AND E. AMBERSON. 2003. Native Plant Connection Program. Association of Official Seed Certifying Agencies. [Cited 1 March 2010]. Available from: <http://www.aosca.org/aoscana tiveplantbrochure.pdf>
- ZEDLER, J.B., AND J.C. CALLAWAY. 2000. Evaluating the progress of engineered tidal wetlands. *Ecological Engineering* 15:211–225.

Received 29 December 2011

Accepted 14 September 2012