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Tolerance to Sand Burial, Trampling, and Drought of Two Subarctic Coastal Plant Species (*Leymus mollis* and *Trisetum spicatum*)

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ABSTRACT. In order to ensure the sustainable development of the North, increased anthropogenic pressure on subarctic environments must be accompanied by appropriate restoration techniques. Locally adapted restoration guidelines need to rely on sound ecological knowledge of the species used in restoration trials. We evaluate the tolerance (emergence and biomass production) of two coastal species (*Leymus mollis* and *Trisetum spicatum*) to sand burial, trampling, and drought, all major constraints to plant colonization in the village of Whapmagoostui-Kuujjuarapik in subarctic Quebec. In three 11-week greenhouse experiments, plants were submitted to three intensities of sand burial (0.0, 0.5, and 1.0 cm per week), trampling events (none, once per week, once per day) and drought (50 mL of water every other day, every week, and every other week). While *T. spicatum* performance decreased under both moderate and high sand burial intensities, *L. mollis* tolerated moderate burial intensity. Both species were able to sustain trampling, although the performance of *T. spicatum* was reduced under high trampling intensity. Finally, neither species could tolerate moderate and high drought intensities, suggesting that watering needs to be included in any restoration initiatives. Since *L. mollis* performed better than *T. spicatum* in the sand burial experiment, we recommend the use of this species in future small-scale restoration trials.

Key words: biomass production, coastal subarctic ecosystem, drought, greenhouse experiments, *Leymus mollis*, restoration, sand burial, seedling emergence, trampling, *Trisetum spicatum*

RÉSUMÉ. Dans le but d'assurer le développement durable du Nord, des méthodes de restauration appropriées doivent être développées en réponse aux perturbations de nature anthropique accrues. De telles techniques de restauration régionales doivent cependant reposer sur de solides connaissances de l'écologie des espèces utilisées. Dans cette étude, nous avons évalué la tolérance (émergence et production de la biomasse) de deux espèces côtières (*Leymus mollis* et *Trisetum spicatum*) à l'ensablement, au piétinement et à la sécheresse, trois contraintes majeures inhibant la recolonisation végétale dans le village subarctique de Whapmagoostui-Kuujjuarapik, au Québec. Pour ce faire, trois expériences en serre d'une durée de 11 semaines ont été menées dans lesquelles les individus des deux espèces ont été soumis respectivement à trois intensités d'ensablement (0,0, 0,5 et 1,0 cm par semaine), de piétinement (aucun, une fois par semaine, une fois par jour) et de sécheresse (50 mL d'eau à tous les 2, 7 et 14 jours). Alors que la performance de *T. spicatum* a diminué lorsque soumis aux régimes d'ensablement intermédiaire et élevé, *L. mollis* a toléré le régime d'ensablement intermédiaire. Dans l'expérience de piétinement, les deux espèces considérées ont relativement bien supporté le piétinement imposé, si ce n'est d'une légère diminution de la performance de *T. spicatum* lorsque soumis à un fort piétinement. Finalement, ni l'une ni l'autre des espèces ne pouvait tolérer les deux intensités de sécheresse (intermédiaire et élevé), ce qui laisse entendre que les plantes doivent être arrosées dans le cadre d'initiatives de restauration. Puisque *L. mollis* a donné de meilleurs résultats que *T. spicatum* en matière d'ensablement, nous privilégions l'utilisation de *L. mollis* pour les futures initiatives de restauration à petite échelle.

Mots clés : production de la biomasse, écosystème côtier subarctique, sécheresse, expérience en serre, *Leymus mollis*, restauration, ensablement, émergence des plantules, piétinement, *Trisetum spicatum*

INTRODUCTION

Anthropogenic pressure from the exploitation of mineral and hydrological resources, settlement of northern communities, and development of ecotourism ventures has constantly increased over the last 50 years in subarctic environments in North America. As a consequence, plant cover, which in many cases has taken several decades or centuries to become established, is often disturbed in the vicinity of these activities. To ensure the sustainable development of the North, low-cost and efficient restoration techniques adapted to the local environment must be developed rapidly. Such restoration techniques must necessarily rely on good knowledge of the ecology of the target species.

Restoration of areas disturbed by anthropogenic activities is often limited by constraints inherent to the disturbed sites. Substrate instability (Arnalds, 1987; Walker and Del Moral, 2003), compaction (Billings, 1987), desiccation

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(Kershaw, 1983; Arnalds, 1987; Cargill and Chapin, 1987; Chapin, 1993), absence of suitable microsites for seed germination (Wood and Morris, 1990), poor nutritional status of the substrate as a result of nutrient leaching (Arnalds, 1987), unbalanced N:P ratio (Blanke et al., 2005), and N deficit following topsoil removal (Arnalds, 1987; Bradshaw, 1987) are among the most important constraints that limit the rate of plant recovery. In subarctic environments, however, restoration trials must also deal with a harsh climate that reduces primary productivity in terrestrial and aquatic ecosystems. Sub-optimal temperatures combined with a short growing season slow down soil development (Kershaw, 1983; Harper and Kershaw, 1997), resulting in soil with low nutrient availability (Van Cleve and Viereck, 1981). Biological factors such as the absence of viable seeds (Ebersole, 1989; Forbes and Jefferies, 1999; Urbanska and Fattorini, 2000; Prach et al., 2001; Pywell et al., 2002) or of mycorrhizal inoculum (Reeves et al., 1979; Allen, 1991; Gange et al., 1993; Greipsson and El-Mayas, 1999; Blanke et al., 2005), and herbivory (including granivory: Arnalds, 1987; Bradshaw, 1987) may also contribute to the slow rate of plant recovery.

Along the Hudson Bay coast in northwestern Quebec, the village of Whapmagoostui-Kuujjuarapik is a good example of a site heavily disturbed by anthropogenic activities. The construction of a military base in the 1950s and successive waves of urbanization partially destroyed the original plant cover composed of mosses, lichens, and grasses (Desormeaux, 2005). Nowadays, the plant cover is highly fragmented and sparse, covering only 54% of the area occupied by the village (based on 2001 aerial photo analysis: Desormeaux, 2005). Plant cover disturbance in the village is such that it is believed that the constraints to plant colonization are similar to the ones on the foredune: low nutrient and water availability and substrate instability (sand burial). Heavy trampling by both pedestrians and all-terrain vehicles (ATVs) must also be considered as major constraints as the prohibitive cost of building materials precludes fencing of large areas.

In a previous study, Deshaies et al. (in press) evaluated the impact of mineral and organic fertilization on the performance of indigenous species believed to be good candidates for restoration in subarctic environments. In the present study, our main objective was to evaluate the performance of two of these species (*Leymus mollis* and *Trisetum spicatum*) in response to sand burial, trampling, and drought. To do so, we conducted a series of greenhouse experiments in order to evaluate the impact of these constraints on seedling emergence, survival, and productivity.

MATERIAL AND METHODS

Study Species

Two herbaceous plant species were chosen on the basis of their observed success in natural regeneration on the adjacent sand dune system (Desormeaux, 2005), their availability as a seed source, and their aesthetics. *Leymus mollis* (Trin.) Pilg. is a tall perennial plant (approximately 100 cm in height). It forms an extensive system of horizontal and vertical rhizomes, which constitutes the "skeleton" of the foredune. Its fruits are small, linear caryopses about 4–5 mm in length. *Trisetum spicatum* (L.) Richter, a short perennial growing to 30 cm, is a late successional species found mainly on older dunes. Recently, a new cultivar of this species (ARC Sentinel Spike Trisetum) was released by the Alberta Research Council Inc. for reclamation and revegetation of disturbed sites at high elevations in the Rocky Mountains of Alberta (Woosaree et al., 2005).

Experiments

Greenhouse experiments were conducted at the Whapmagoostui-Kuujjuarapik Research Station of Centre d'études nordiques (55˚81′79″ N, 77˚84′59″ W; hereafter referred to as Whapmagoostui only) on the east coast of Hudson Bay in subarctic Quebec, Canada. Three experiments were carried out over 11 weeks to evaluate the performance of *L. mollis* and *T. spicatum* in response to different intensities of sand burial, trampling, and drought. During the experiments, which lasted from May to August 2007, the photoperiod was kept constant at 14 hours, and day temperature followed the temperature outside the greenhouse. On sunny days, however, temperature in the greenhouse was ca. 4˚C warmer than outside temperatures. Seeds used in the two experiments were either harvested in August 2006 on the adjacent sand dune system (*L. mollis*) or bought from a commercial seed provider (*T. spicatum*). In both cases, seed viability (based on germination trials and manufacturer information, respectively) exceeded 90%.

In the third week of May 2007, sand from bared surfaces was collected in the village and sieved (2 mm mesh). Plastic pots (1940 cm^3) were then filled, and the sand was moistened prior to sowing. Each pot received either 100 seeds of *L. mollis* or 1500 seeds of *T. spicatum* (0.29 g). We did not standardize the seeding rate because the two species differ significantly in size, and our objective was to determine the impact of the various treatments on the performance of individual species. All seeds were then covered with 200 mL of dry sand (about 1.1 cm of sand). The first watering was carried out with 100 mL of water at room temperature. This amount was adjusted to 50 mL for subsequent waterings, once every other day, except for the drought treatments (see below). For each experiment, all experimental units (pots) were randomly assigned one treatment and were placed in a block design (10 blocks of 6 pots). The emergence of the two species was monitored weekly. Individuals with green tissue were considered to be alive. At the end of the experiments, individuals from each pot were harvested and washed carefully to prevent the loss of fine roots; their biomass was then divided between leaves and roots/rhizomes. Biomass for each pot was dried at 80˚C for 48 hours before being weighed.

Sand Burial Experiment

Three sand burial treatments were randomly assigned to the pots of each species within a block. In the control treatment, no sand was added to the pot (0 mL week^{-1}). In the moderate sand burial treatment, 90 mL of sand was added weekly to raise the sand level by 0.5 cm, while in the high sand burial treatment, 180 mL of sand was added weekly to raise the sand level by 1.0 cm. Overall, 0, 5, and 10 cm of sand were added in the different treatments. The sides of the pots were raised once a week using coffee sticks and tape. This design allowed the pot area to remain constant throughout the experiment. Pots were sufficiently spaced on the table to prevent any shading. The high sand burial treatment is representative of the maximal rate of sand burial in the village. Cumulative sand burial from May to August, measured at six locations in the village during summer 2007, varied between 0 and 9.8 cm (S. Boudreau and J. Faure-Lacroix, unpubl. data).

Trampling Experiment

Three trampling intensity treatments were randomly assigned to the pots of each species within a block. In the control treatment, plants grew without undergoing any trampling. The intermediate-intensity trampling treatment consisted of one trampling event per week, while the high-intensity trampling treatment consisted of one event per day. The simulated trampling was inspired by the dropped weight method developed by Kellomaki and Saastamoinen (1975). Trampling was simulated with a flat circular device with a diameter slightly inferior to the diameter of the pots. A trampling event consisted of firmly hitting the sand surface five times with this device. All trampling treatments were applied by the same person for consistency. Such trampling treatment is believed to be representative of the impact of pedestrians. However, it does not simulate ATV traffic, which can tear up plant parts or uproot individuals. On the basis of personal observations, we believe that the heavily disturbed areas in the village undergo at least one trampling event per day during the snow-free season.

Drought Experiment

Three drought intensity treatments were randomly assigned to the pots of each species within a block. The treatments were 1) no water limitation (50 mL every 2 days), 2) intermediate water limitation (50 mL per week), and 3) high water limitation (50 mL every other week). These treatments were chosen in response to a request made by the local authorities (Cree Band Council) to use as little water as possible throughout the restoration process, as fresh water availability for residents in the village may be a major concern during drought spells. According to the available historical weather data (1978 – 2007), long drought spells are frequent during the growing season in this area (Table 1).

TABLE 1. Drought spell events at Whapmagoostui-Kuujjuarapik over the last 30 years (1978–2007). Drought spells are classified by duration and consist of the number of consecutive days with less than 1 mm of rain per day from the beginning of May to the end of September.

Drought Spell Duration	Occurrences	Frequency
20 days +	6	every 5.0 yr
15–19 days	18	every 1.7 yr
10–14 days	52	every 0.6 yr
5–9 days	173	every 0.2 yr

Statistical Analyses

All analyses were performed with the *Statistical Package for Social Sciences* (SPSS, v. 13.0 for Windows). Emergence of the individual species was analyzed with the General Linear Model Repeated Measures (GLMRM) procedure because of the temporal autocorrelation of the samples. A GLM multivariate procedure, which provides analysis of variance for multiple dependent variables in relation to one or more factor variables, was used for the analyses of belowground and aboveground biomass at the end of the different experiments. When the multivariate procedure indicated that one treatment was significant overall, we conducted GLM univariate analyses on individual species. Data were tested for normality.

RESULTS

Sand Burial Experiment

For both species, seedling emergence (and survival) varied through time as a function of burial intensity according to the GLMRM (Table 2, Fig. 1). For *L. mollis*, emergence was inversely proportional to sand burial intensity. The largest number of seedlings was recorded in the control treatment, peaking at ca. 77 seedlings per pot after nine weeks and dropping to ca. 66 seedlings per pot through week 11. Moderate burial intensity reduced the emergence of *L. mollis* by almost 50%: the number of seedlings peaked at week 6 (ca. 42 seedlings) before stabilizing around 34 individuals per pot for the last five weeks of the experiment. Under high sand burial intensity, less than one seedling per pot survived through to week 11. For *T. spicatum*, emergence was also greater in the control treatment (ca. 220 seedlings after week 10). However, emergence was substantially reduced under both moderate and high sand burial (ca. 7 and 0 seedlings per pot, respectively, at the end of the experiment).

Multivariate analysis indicates that the aboveground and belowground biomass per pot of both species varied between the different sand burial treatments (species • treatment, Wilks' Lambda: 0.707, $F_{4,88} = 4854$, $p < 0.001$). For both species, aboveground and belowground biomass per pot followed the same trends as emergence. For *L. mollis*, both final biomasses were inversely proportional to the

TABLE 2. Repeated measures ANOVAs on the number of individuals of *L. mollis* and *T. spicatum* in response to sand burial, trampling, and drought treatments during an 11-week fully factorial block design greenhouse experiment. The Huynh–Feldt adjusted *p*-values are presented; significant *p*-values are in bold.

Species	Factor	df	MS	F	*p*
Sand Burial					
L. mollis	Time	2.992	17,363.5	54.1	**< 0.001**
	Time•Block	26.924	445.1	1.4	0.152
	Time•Treatment	5.983	8,144.8	25.4	**< 0.001**
	Error	53.848	320.7		
T. spicatum	Time	3.552	48,859.4	116.7	**< 0.001**
	Time•Block	31.966	456.8	1.1	0.375
	Time•Treatment	7.104	52,522.5	125.5	**< 0.001**
	Error	63.933	418.6		
Trampling					
L. mollis	Time	7.181	20935.0	312.2	**< 0.001**
	Time•Block	64.629	53.7	0.8	0.839
	Time•Treatment	14.362	120.3	1.8	**0.045**
	Error	129.258	67.0		
T. spicatum	Time	2.793	196,923.7	97.7	**< 0.001**
	Time•Block	25.141	2,728.8	1.4	0.178
	Time•Treatment	5.587	9,296.2	4.6	**< 0.001**
	Error	50.282	2,014.9		
Drought					
L. mollis	Time	3.156	908.4	31.7	**< 0.001**
	Time•Block	28.404	27.7	1.0	0.528
	Time•Treatment	6.312	1403.3	49.0	**< 0.001**
	Error	56.808	28.6		
T. spicatum	Time	2.057	21930.5	8.6	**< 0.001**
	Time•Block	18.511	2378.7	0.9	0.555
	Time•Treatment	4.113	30498.3	11.9	**< 0.001**
	Error	37.021	2562.8		

intensity of sand burial (Table 3, Fig. 2a). Moderate sand burial intensity reduced aboveground and belowground biomass per pot by ca. 35% and 44%, respectively, compared to ca. 90% and 88% for high sand burial intensity. For *T. spicatum*, sand burial had an even stronger effect, reducing aboveground biomass per pot by ca. 64% and 98% (moderate and high intensity, respectively) and belowground biomass per pot by ca. 44% and 99%.

Trampling Experiment

The emergence of both species varied through time and with trampling intensity (Table 2, Fig. 3). The number of *L. mollis* individuals increased at an almost constant rate for the first 8 weeks of the experiment and subsequently stabilized. Although the GLMRM revealed that the emergence of *L. mollis* varied between the different trampling intensities through time (intermediate trampling intensity with lower number of individuals), LSD tests conducted on the final emergence revealed no significant differences between the treatments (58 to 68 individuals per pot). For *T. spicatum*, pots assigned to the high trampling intensity had significantly lower numbers of individuals at the end of the experiment than the two other treatments (ca. 90 vs. ca. 160).

Multivariate analysis indicated that the aboveground and belowground biomass per pot of both species varied between the different trampling treatments (treatment, Wilks' Lambda: 0.685, $F_{4,88}$ = 4580, $p = 0.002$). For *L. mollis*, trampling intensity had no effect on the aboveground biomass per pot (Table 4, Fig. 2b), but moderate and high trampling intensity significantly reduced the production of belowground biomass per pot. For *T. spicatum*, moderate trampling intensity had no impact on aboveground

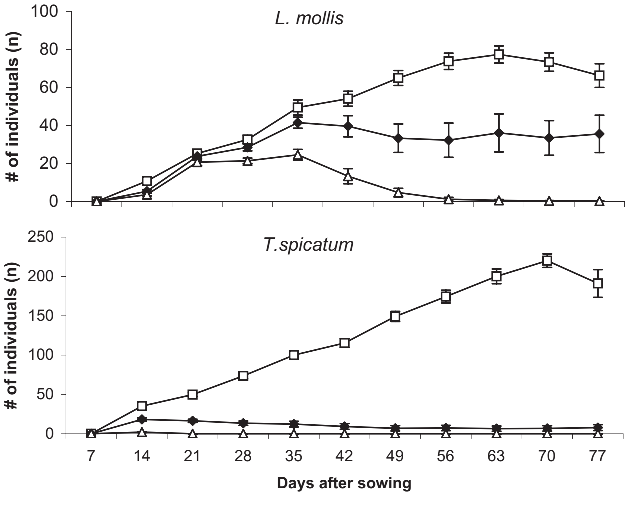


FIG. 1. Emergence of *Leymus mollis* and *Trisetum spicatum* in response to sand burial intensity. Seeding rate: *L. mollis* – 100 seeds, *T. spicatum* – ca. 1500 seeds. Open square: no sand burial (0.0 cm wk^{-1}); black diamond: moderate sand burial (0.5 cm wk^{-1}); open triangle: high sand burial (1.0 cm wk^{-1}). Mean ± 1 standard error.

TABLE 3. ANOVAs on the aboveground and belowground biomass of *L. mollis* and *T. spicatum* in response to sand burial treatment at the end of an 11-week fully factorial block design greenhouse experiment. Significant *p*-values are in bold.

Species	Factor	df	MS	F	*p*
L. mollis					
Aboveground biomass	Intercept	1	2.699	148.1	**< 0.001**
	Block	9	0.035	1.9	0.112
	Treatment	2	0.5501	30.2	**< 0.001**
	Error	18	0.018		
Belowground biomass	Intercept	1	14.331	139.6	**< 0.001**
	Block	9	0.169	1.6	0.177
	Treatment	2	2.860	27.9	**< 0.001**
	Error	18	0.103		
T. spicatum					
Aboveground biomass	Intercept	1	0.191	581.5	**< 0.001**
	Block	9	0.000	1.2	0.327
	Treatment	2	0.171	520.9	**< 0.001**
	Error	18	0.000		
Belowground biomass	Intercept	1	1.015	163.5	**< 0.001**
	Block	9	0.006	0.9	0.524
	Treatment	2	0.842	135.7	**< 0.001**
	Error	18	0.006		

and belowground biomass per pot, while high trampling intensity reduced both.

Drought Experiment

The emergence of both species varied through time and with drought intensity (Table 2, Fig. 4). For *L. mollis*, moderate and severe drought treatment resulted in both lower germination rates and higher seedling mortality (from the fourth week). Under the stress imposed by both treatments, no seedling survived beyond the sixth week of the experiment. Similar results were obtained for *T. spicatum*. Seedling mortality began as soon as the third week, and no seedling survived more than five weeks.

Production of aboveground and belowground biomass per pot followed the same trend as emergence (Table 5, Fig. 2). For both species, moderate and severe drought treatments greatly reduced both aboveground and belowground biomass.

DISCUSSION

In such remote places as the subarctic environment, large-scale restoration trials are often too costly to undertake. However, small-scale restoration projects managed by the community can be cost-efficient alternatives, as long as they are based on ecologically sound restoration guidelines. As part of a research program that aims to identify the modalities (species, treatments) of such community-based restoration projects, our study aimed to evaluate the response to sand burial, trampling, and drought of two indigenous species believed to be potential candidates for restoration.

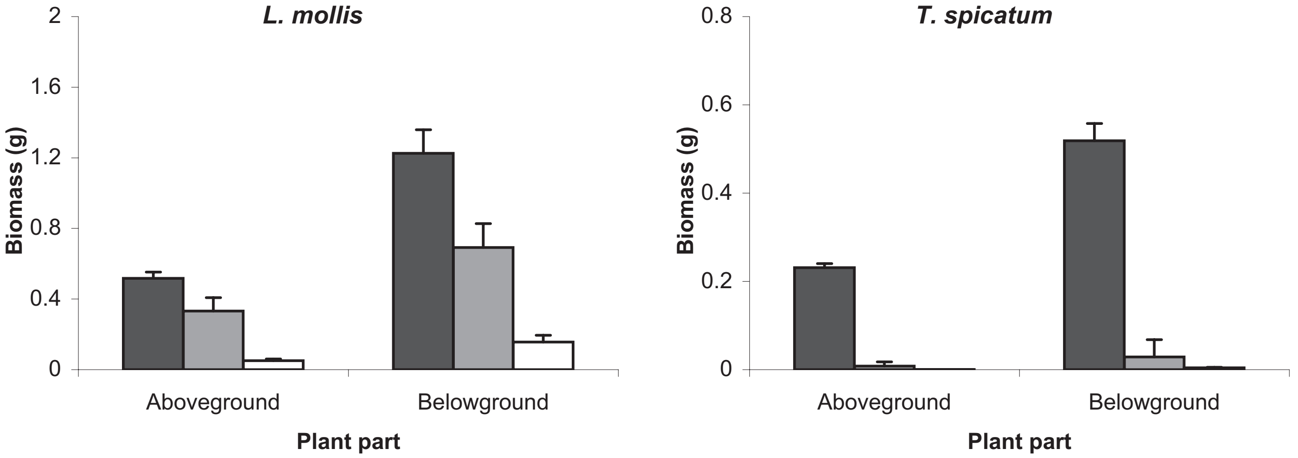
We believe that the results presented here are of interest for most northern communities throughout subarctic North America. First, the constraints used in this study are among the most important ones that limit the recovery of the plant cover following disturbances. Second, these constraints are common to most northern villages. In subarctic Quebec, for example, they apply to every single village. Finally, the species used in our study are characterized by a circumpolar distribution and therefore could be used in restoration trials throughout the subarctic biome.

Sand Burial

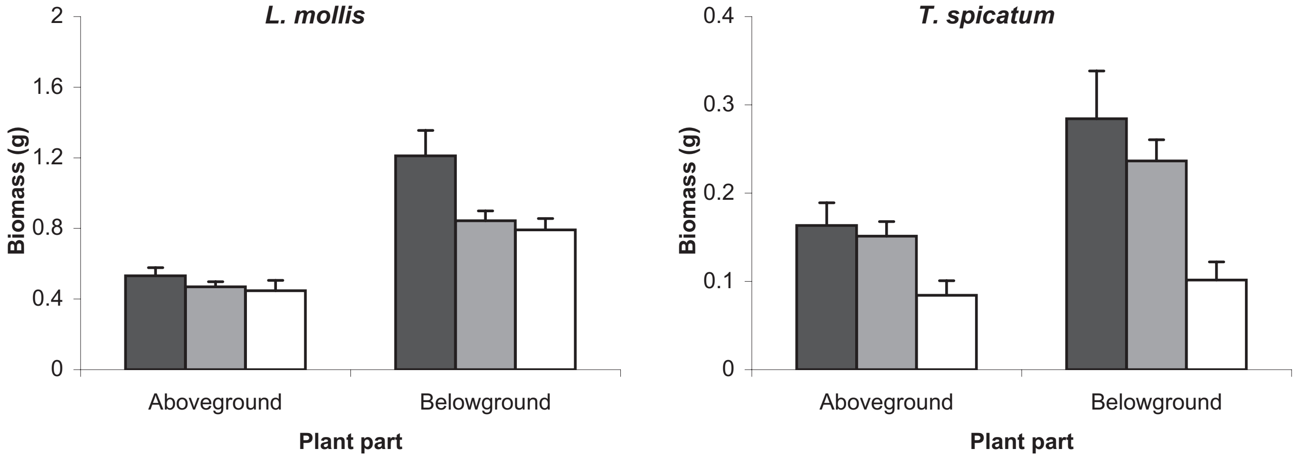
Sand burial can have both positive and negative effects on seed germination. Shallow burial increases contact with mineral soil and humidity around the seeds (Baldwin and Maun, 1983; Maun, 1998), both of which tend to favour seed germination (Maun, 1998). Zhang and Maun (1994) showed that, for several sand dune species, seeds buried at depths varying between 5 and 10 cm had a higher germination rate (> 75%) than seeds buried deeper. In fact, burial at greater depths might strengthen seed dormancy or cause the seed to rot due to fungal infection (Maun, 1998). Once seeds have germinated, emergence above the soil surface depends on the energy available to the seedling (Zhang and Maun, 1993). Burial at a depth greater than 6 cm significantly decreased seedling emergence in other studies (Maun, 1981; Maun and Lapierre, 1986), although some species—for example, *Panicum virgatum* (Zhang and Maun, 1990a) and *Strophostyles helvula* (Yanful and Maun, 1996)—can withstand burial greater than 15 cm.

Our results are in accordance with those of the previous studies. Both species had their greatest germination and emergence success in the control treatment (initially buried at a 1 cm depth). However, while the germination and emergence success of *L. mollis* was a function of the intensity of sand burial (reduced by ca. 50% and > 90% under moderate and high intensities, respectively), the performance of *T. spicatum* was greatly reduced under both moderate and high burial treatment (> 90%). This progressive response has been previously observed in *L. mollis*, as well as in other

a) Sand burial



b) trampling



c) drought

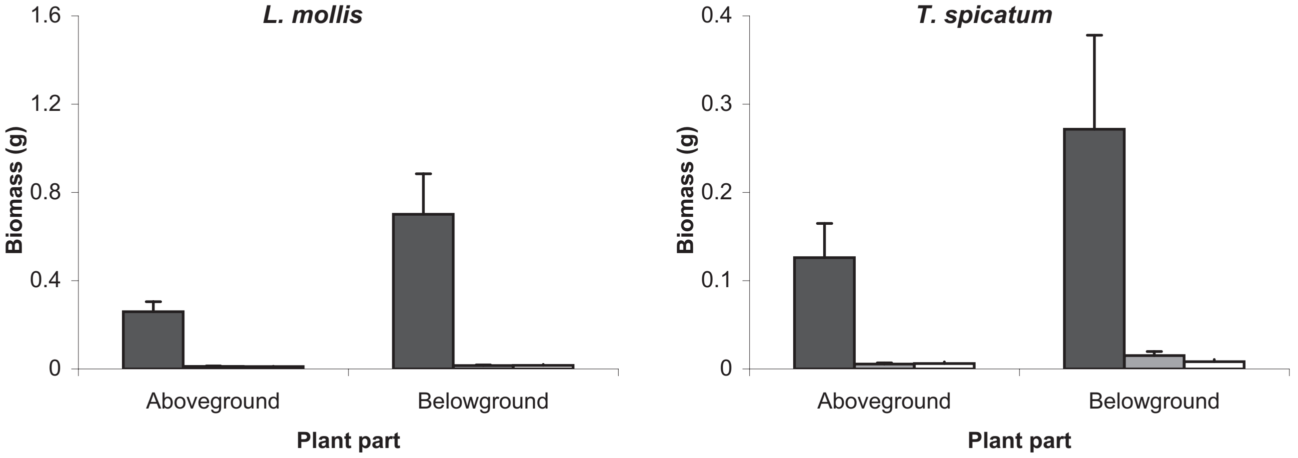


FIG. 2. Aboveground and belowground biomass of *Leymus mollis* and *Trisetum spicatum* in response to a) sand burial, b) trampling, and c) drought intensity at the end of the experiments. Black bars represent control groups; greybars, moderate-intensity treatments; and white bars, high-intensity treatments. Mean ± 1 standard error.

TABLE 4. ANOVAs on the aboveground and belowground biomass of *L. mollis* and *T. spicatum* in response to trampling treatment at the end of an 11-week fully factorial block design greenhouse experiment. Significant *p*-values are in bold.

Species	Factor	df	MS	F	*p*
L. mollis					
Aboveground biomass	Intercept	1	6.982	456.4	**< 0.001**
	Block	9	0.034	2.2	0.073
	Treatment	2	0.019	1.2	0.312
	Error	18	0.015		
Belowground biomass	Intercept	1	27.003	283.3	**< 0.001**
	Block	9	0.090	0.9	0.512
	Treatment	2	0.521	5.5	**0.014**
	Error	18	0.095		
T. spicatum					
Aboveground biomass	Intercept	1	0.530	124.1	**< 0.001**
	Block	9	0.005	1.2	0.375
	Treatment	2	0.018	4.3	0.031
	Error	18	0.004		
Belowground biomass	Intercept	1	1.291	114.8	**< 0.001**
	Block	9	0.017	1.5	0.225
	Treatment	2	0.090	8.0	0.003
	Error	18	0.011		

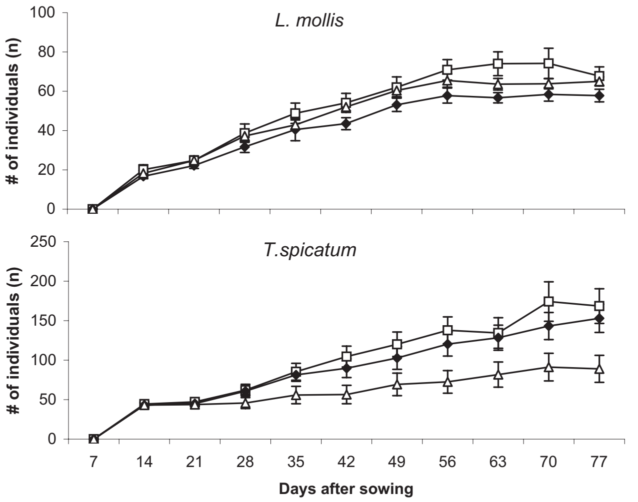


FIG. 3. Emergence of *Leymus mollis* and *Trisetum spicatum* in response to trampling intensity. Seeding rate: *L. mollis* – 100 seeds, *T. spicatum* – ca. 1500 seeds. Open square: no trampling; black diamond: moderate trampling (once per week); open triangle: high trampling (once per day). Mean ± 1 standard error.

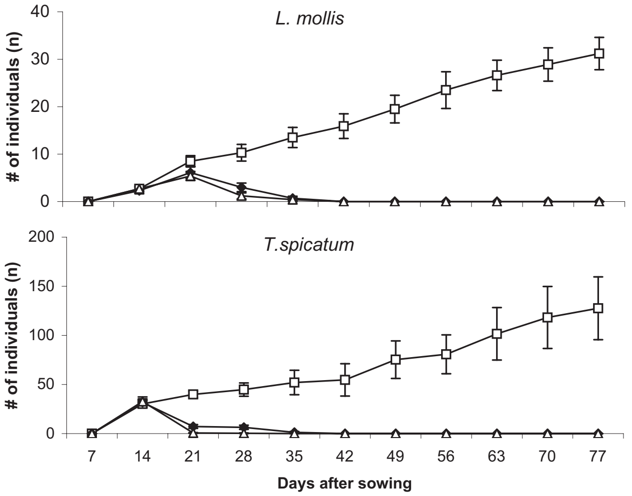


FIG. 4. Emergence of *Leymus mollis* and *Trisetum spicatum* in response to drought intensity. Seeding rate: *L. mollis* – 100 seeds, *T. spicatum* – ca. 1500 seeds. Open square: no drought (50 mL every other day); black diamond: moderate drought (50 mL every week); open triangle: high drought (50 mL every other week). Mean ± 1 standard error.

species (Chen and Kuo, 1999; Benvenuti et al., 2001; Gagné and Houle, 2002; Ren et al., 2002). These results are consistent with the successional stage in which we found these species on the sand dune system. While *L. mollis* tends to colonize the foredune, where the substrate is unstable and where sand burial is frequent, *T. spicatum* is found mainly on fixed dunes, where the substrate has already stabilized.

Biomass production per pot for both species followed trends similar to those of the germination and emergence results, with *L. mollis* showing a higher tolerance to intermediate levels of sand burial than *T. spicatum*. However, it is interesting to note that at the individual level, *L. mollis* individuals subjected to the intermediate intensity of sand burial appear to have produced more aboveground and belowground biomass (0.0099 and 0.021 g per individual) than the ones in the control treatment (0.0070 and 0.017 g per individual). Comparisons at the individual level were not performed for the other treatments as there were too few individuals. In fact, numerous studies have shown that, once emerged, seedlings that are partially buried can exhibit higher primary productivity than seedlings on a more stable substrate (Wagner, 1964; Zhang and Maun, 1990b; Yuan et al., 1993; Maun, 1994; Martinez and Moreno-Casasola, 1996; Yanful and Maun, 1996).

Trampling

The ecological impact of trampling varies from one ecological community to another (Bowles and Maun, 1982). Burden and Randerson (1972) showed that sand dunes are

TABLE 5. ANOVAs on the aboveground and belowground biomass of *L. mollis* and *T. spicatum* in response to drought treatment at the end of an 11-week fully factorial block design greenhouse experiment. Significant *p*-values are in bold.

Species	Factor	df	MS	F	*p*
L. mollis					
Aboveground biomass	Intercept	1	0.263	38.6	**< 0.001**
	Block	9	0.007	1.0	0.451
	Treatment	2	0.206	30.2	**< 0.001**
	Error	18	0.007		
Belowground biomass	Intercept	1	1.788	15.8	**< 0.001**
	Block	9	0.112	1.0	0.484
	Treatment	2	1.563	13.8	**< 0.001**
	Error	18	0.113		
T. spicatum					
Aboveground biomass	Intercept	1	0.063	12.8	**0.002**
	Block	9	0.005	1.1	0.422
	Treatment	2	0.048	9.8	**0.001**
	Error	18	0.005		
Belowground biomass	Intercept	1	0.290	7.7	**0.012**
	Block	9	0.038	1.0	0.464
	Treatment	2	0.225	6.0	**0.010**
	Error	18	0.038		

among the most fragile natural systems. Moderate to high trampling intensity on coastal sand dunes decreases plant diversity, cover, and productivity (Andersen, 1995; Kutiel et al., 2000; Grunewald, 2006) and contributes to dune erosion and instability (Van der Merwe, 1988). At the community level, tolerance to trampling depends mainly on the intensity and nature of trampling (Liddle, 1974; Bowles and Maun, 1982; Kutiel et al., 2000), species composition (Bayfield, 1979) and growth form (Andersen, 1995), substrate properties, and environmental conditions (Liddle and Greig-Smith, 1975). In their review, Davenport and Davenport (2006) showed that the use of ATVs on vegetated beaches is damaging not only to the plant communities, but also to the natural fauna (insects, birds, reptiles).

Replicating the effects of trampling is a frequent problem in experiments in controlled environments. Trampling in nature may be erratic, with alternation between periods of very high and low trampling intensity, depending on the season (Cole, 1993; Monz, 2002). While pedestrian trampling may slightly crush the plant species, trampling by ATVs may uproot some individuals or at least expose their root system. The trampling treatment applied in our experiment and in others (Kellomaki and Saastamoinen, 1975; Sun and Liddle, 1993) is believed to be representative of pedestrian trampling, but it hardly simulates the more severe impacts of ATV traffic. However, our personal observations strongly suggest that no plant species could tolerate the actual level of ATV traffic going on around Whapmagoostui and that the successful restoration of the plant cover will be linked to a behavioral change on the part of the residents to using their ATVs and other vehicles only on the road. In this regard, the pavement of the roads, started in 2007, might help to reduce off-road traffic in the village.

High pedestrian-like trampling intensity reduced *T. spicatum* germination and emergence by ca. 45%, while no significant differences were detected for *L. mollis*. However, while both aboveground and belowground biomass of *T. spicatum* were reduced only under high trampling intensity, *L. mollis* belowground biomass was also reduced under moderate trampling intensity. Overall, our results revealed that both species are able to survive and grow under high trampling intensity, although *L. mollis* performed somewhat better than *T. spicatum*.

Drought

Of the numerous abiotic factors that can restrict establishment, growth, and survival of plant species on coastal sand dunes, the availability of water is one of the most important (Maun, 1994). Sandy substrates have poor water-holding capacity, with rapid percolation of precipitated water (Salisbury, 1952). During the warmest months, the superficial layer (0–10 cm) of sandy substrate dries rapidly, imposing significant water stress on seedlings. For instance, Maun and Krajnyk (1989) showed that over 90% of *Ammophila breviligulata* seedlings survived an entire growth season with weekly watering, while none survived under natural conditions. In fact, desiccation accounts for up to 80% of seedling mortality in various coastal sand dune species (see review in Maun, 1994).

Our results showed that neither species tolerates drought spells longer than seven days at the seedling stage. The negative impacts of drought on the germination and emergence success of *L. mollis* and *T. spicatum* became evident during the third week of the experiment. From the fifth week on, no seedlings survived under either drought treatment. Biomass production followed the same pattern, with almost no biomass at the end of the experiment for individuals submitted to any level of water stress. Previous studies by Gagné and Houle (2002) showed that seedlings of *L. mollis* could survive at least five days of drought if moisture was plentiful between drought events. However, even in this case, drought spells longer than three days caused a significant decrease in biomass production.

CONCLUSION

Although both species tested here performed well on the adjacent sand dune system, their slightly different responses to some of these constraints may be enough to compromise the success of a restoration trial. In our study, the two species showed similar responses to simulated trampling and drought but differed in regard to sand burial. Our results suggest that both species are relatively tolerant to simulated pedestrian-like trampling. Further experimentation would be necessary, however, to evaluate their specific tolerance to ATV traffic. In addition, both species were so sensitive to drought spells of seven or more days that any restoration trial with these species should incorporate regular watering treatments to prevent seedling desiccation and mortality. Last but not least, the performance of the two species under various sand burial intensities differed slightly. Seedlings of *L. mollis* appeared to tolerate moderate sand burial, whereas *T. spicatum* showed an important decrease in both seedling emergence and productivity even under moderate sand burial. In light of these results, *L. mollis* appears to be better adapted to the constraints that limit plant colonization in the village, at least in areas where sand burial might be important.

This study emphasizes the need to evaluate the impacts of the major constraints that limit plant colonization on the performance of species that are candidates for restoration trials on disturbed sites. Such studies are an essential step toward providing ecologically sound restoration guidelines to Arctic and subarctic communities that wish to implement small-scale and low-cost restoration initiatives. However, multi-year in situ experimental studies (in the village) must be conducted to corroborate the results obtained in this study before one can provide restoration guidelines to local communities.

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