Determining the Optimal Sowing Density for a Mixture of Native Plants Used to Revegetate Degraded Ecosystems

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Abstract

No standardized, objective methodology exists for optimizing seeding rates when establishing herbaceous plant cover for pastures, hay fields, ecological restoration, or other revegetation activities. Seeding densities, fertilizer use, season of seeding, and the interaction of these treatments were tested using native plants on degraded sites in northern British Columbia, Canada. A mixture of 20% *Achillea millefolium*, 20% *Carex aenea*, 20% *Elymus glaucus*, 20% *Festuca occidentalis*, 16% *Geum macrophyllum*, and 4% *Lupinus polyphyllus* seed was applied at 0, 375, 750, 1,500, 3,000, and 6,000 pure live seed (PLS) per m^2 in 2.5 × 2.5–m rototilled test plots, established in the fall and spring, with and without fertilizer. There was no significant difference in plant cover of sown species between fall seeding and spring seeding, and few treatment interactions were identified in the first 2 years after sowing. There was no significant difference in cover between seed densities of 3,000 and 6,000 PLS/m^2 in the first year, nor among 1,500, 3,000, and 6,000 PLS/m^2 treatments in the second year. Seed densities as low as 375 PLS/m^2 produced year 2 plant cover equivalent to that observed at 3,000 PLS/m^2 in year 1. Plots sown to seed densities less than or equal to 750 PLS/m^2 generally exhibited an increase (infilling) in plant density from year 1 to year 2, whereas plots sown to seed densities greater than or equal to 1,500 PLS/m^2 generally exhibited a decrease (density-dependent mortality) in plant density. These results imply a most efficient sowing density between 750 and 1,500 PLS/m^2 (corresponding to 190–301 established plants·m^{-2} after two growing seasons). It is suggested that net changes in plant populations observed over a range of sowing densities are a robust and objective means of determining optimal sowing densities for the establishment of herbaceous perennials.

Key words: cover production, degraded soils, ecological restoration, fertilization, seeding densities, soil rehabilitation.

Introduction

Rapid establishment of vegetation by seeding to control erosion, rebuild soil, and improve visual appearance of degraded sites is an important aspect of ecosystem restoration. Maintenance of biodiversity and ecosystem function, provision of wildlife habitat, and aesthetic appeal are also important considerations. The use of native species in revegetation is often desired when addressing these issues, but there is little information regarding their use. Furthermore, there is no standard methodology in agronomy, revegetation science, or restoration ecology to determine the optimal density of seeds to use on a project site. This paper seeks to alleviate some of these information gaps in restoration ecology.

Humankind has been purposely sowing plant seed for millennia, first for food production and more recently for pasture establishment, revegetation, and ecological restoration. The objective for most agricultural management of crop plants (and the applied science of agronomy) is to maximize yields per unit land area. The density of seed sown is a primary factor under manipulation for low densities will not fully occupy the growing space available and high densities may result in intense competition that inhibits the growth and yield of individual plants (Willey & Heath 1969; Harper 1977; Fairey & Lefkovitch 1995). Under extremely high densities, plants can even exhibit self-thinning or density-dependent mortality, indicating a waste of the original input of seed even if crop yields are not compromised (Harper 1977; Silvertown 1982).

The goal in managing forage crops, typically consisting of grass and legume mixtures, is usually the maximization of foliage production. Goals for ecological restoration and reclamation are generally similar, with foliage production providing the means for erosion control and improved aesthetics. But the amount of herbaceous foliage can only increase so far before within-plant shading and between-plant competition limit further production, though there is evidence that increased productivity can be achieved by

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combining species of different stature, growth form, phenology, or rooting structure (Trenbath 1974).

Few studies discuss how seeding densities recommended for revegetation purposes were derived, nor what criteria might have been used in deriving those recommendations. Surprisingly, there appears to be no standard protocol in the fields of agronomy, reclamation, or ecological restoration for selecting optimal seed or plant densities. We can envision several possible criteria for identifying optimal plant densities.

(1) The minimum density of seeds or plants required to meet an arbitrary yield or cover goal (e.g., 50% plant cover).
(2) The minimum density of seeds or plants required to achieve maximum yield, where more seeds result in no further increase (or even a decrease) in yield.
(3) The point of inflection or declining marginal gains on the yield versus density curve.
(4) An equilibrial plant demography, in which there is no further infilling or self-thinning in a stand.

We suspect that criterion 3 has often been used in the fields of revegetation and erosion control, for which a goal of greater than 70% cover is considered desirable on slopes (Carr 1980; Grigg 2001). As portrayed in the Universal Soil Loss Equation and its supporting calibration research, there is a negative exponential relationship between the amount of erosion and the cover of living plants or plant residue covering the soil surface. When bare soil surfaces have slopes greater than 9%, sharp decreases in soil loss can be achieved with additional amounts of plant cover up to 60% or 70%, after which increasingly greater amounts of plant or litter cover are required to achieve progressively smaller reductions in erosion (Brady & Weil 2002).

First attempts at revegetation in North America extended the practices of pasture establishment and rangeland seeding, depending widely on the use of domesticated grass and legume species of European origin. The widespread introduction of Eurasian species, both intentional and accidental, has resulted in concerns over ecosystem integrity and the conservation of indigenous biodiversity. It is estimated that from 5% to 25% of the vascular plant species in United States nature reserves are non-native; in Canada, non-native species are estimated to make up 24% of the flora (Vitousek et al. 1996). Berger (1993) estimated that approximately 3,000 different exotic plant species grow wild in North America and few areas remain free of their influence. In an attempt to stem this tide and improve options for the wider use of native species for revegetation, we worked with native plant species for the investigation reported here.

Methods

Study Area

Six sites degraded through industrial forestry operations (road construction, log loading, log sorting) or agricultural activities were selected for treatment. These sites are located in northwestern British Columbia (B.C.), Canada, between lat 54°00′N and 55°12′N, long 126°20′W and 129°07′W, and between 200 and 920 m in elevation. They share a similar continental climate, modified by mountainous terrain, having long cold winters with deep snow, and cool moist summers (Canada Committee on Ecological Land Classification 1989). Mean annual temperature averages 2.9°C, and mean annual precipitation ranges from 429 to 982 mm/yr (Burton 2003). The length of the growing season ranges from 69 to 176 frost-free days in the four biogeoclimatic subzones represented by these sites (Banner et al. 1993). Research sites were not instrumented for meteorological monitoring, but data from three nearby weather stations confirm that differences in temperature and precipitation among sites are similar to the year-to-year differences at any given site. For the two growing seasons under consideration, mean summer (June through August) temperatures in 2000 averaged 12.4 to 14.5°C among weather stations, whereas the summer of 2001 was slightly cooler (daily temperatures averaging 11.8 to 13.9°C). Spring and summer precipitation (April through August) ranged from 77 to 176 mm in 2000 and was 45 to 115% greater in 2001.

The soils of all sites were heavily compacted loamy sand or sandy loam, consisting of mixed Brunisolic topsoil and subsoil, or subsoil only. Sites were deficient in nitrogen but had no obvious limitations related to salinity or texture (Burton 2003). Most sites were very level (<1% slope), although one roadside site had undulating relief with slopes ranging from 0 to 5% in individual plots.

Seed Mixture

A standard seed mixture with a fixed proportion of pure live seeds (PLS) for each of six species was used in all treatments. This mixture consisted of 20% Common yarrow (*Achillea millefolium* L.), 20% Bronze sedge (*Carex aenea* Fern.), 20% Blue wildrye (*Elymus glaucus* Bukl.), 20% Western fescue (*Festuca occidentalis* Hook), 16% Large-leaved avens (*Geum macrophyllum* Willd.), and 4% Large-leaved lupine (*Lupinus polyphyllus* Lindl.). These species were chosen to represent a balance of life histories, statures, rooting behavior, and physiological traits as constrained by the results of germination tests and the availability of sufficient seed supplies (Table 1). Although many populations found in eastern North America are derived from European stock, *A. millefolium* in western Canada is considered native (Frankton & Mulligan 1970; Cody 1996). We identified several populations to the subspecies or varietal level as *A. millefolium* ssp. *lanulosa* (Nutt.) Piper, indigenous to western North America (Cody 1996; Douglas et al. 1998), and encountered no populations of the European *A. millefolium* ssp. *millefolium* L., but we did not key out all seed sources used in establishing seed increase plots, so we nominally refer to this plant only at the species level. All seed used

Table 1. Characteristics[a] of the native plant species sown in this experiment.

		Stature					
Species	*Family*	*Vegetative (cm tall)*	*Flowering (cm tall)*	*Rooting*	*Preferred Habitat*	*Mean Seed Size (seeds/g)*	*Germination Capacity[b] (%)*
Achillea millefolium	Asteraceae	10–15	≤60	short rhizomes	dry, open slopes	8,105	86
Carex aenea	Cyperaceae	25–50	≤100	fibrous	disturbed openings	1,399	73
Elymus glaucus	Poaceae	20–50	110–180	short rhizomes	meadows, open forest	219	85
Festuca occidentalis	Poaceae	5–12	40–60	shallow, fibrous	open, shallow soils	3,058	85
Geum macrophyllum	Rosaceae	10–20	30–100	fibrous	rich soils or seeps	2,895	76
Lupinus polyphyllus	Fabaceae	40–80	≤150	tap, N-fixing	open, fine-textured soils	96	62

[a] Summarized from Burton and Burton (2003).
[b] Specific to the seed lots used in this experiment.

was derived from native populations originally found in open habitats and invading recently disturbed (but not urban or agricultural) areas in northern interior of B.C. Seed sown in this experiment was produced from multilineal polycross populations grown in cultivation from collections of wild seed, using the protocol described in Burton and Burton (2002).

Experimental Design

Six replicate sites were established and are treated as statistical blocks. The main treatments consisted of all combinations of six seeding densities, with and without fertilizer, assigned randomly to twelve 2.5 × 2.5–m contiguous plots sown in the early fall of 1999 and then again to another 12 nearby plots sown in the late spring of 2000. The season of seeding treatment was applied as a "split block" factor (Little & Hills 1978) as it was necessary to divide the sites into fall subblocks and spring subblocks in order for plots to be cultivated immediately before seeding, and it was impractical to rototill small plots individually.

To provide a uniform and favorable seedbed, each 75-m^2 subblock was first cleared of large rocks and any preexisting (generally sparse) vegetation, rototilled to a depth of approximate 12 cm, and raked by hand immediately prior to sowing. Each subblock was then divided into twelve 2.5 × 2.5–m plots. Seeding density × fertilization treatments were randomly allocated to each of the 12 plots in each subblock at each site. The seed densities sown (0, 375, 750, 1,500, 3,000, or 6,000 PLS/m^2) broadly bracket the minimal densities required to obtain more than 50% cover within a year or two, as determined by preliminary trials and the recommendations of other researchers (Hardy BBT Limited 1989; Schwab 1991; Hammermeister 1998). The seed mixture was assembled by weight, based on a laboratory analysis of the purity and viability of each seed lot, where each species' contribution to the total package to be weighed out for a 6.25-m^2 plot was calculated as:

$$\frac{\%\text{ of mixture} \times \text{density treatment}\,(\text{PLS/m}^2) \times 6.25(\text{m}^2)}{\text{seeds/g} \times \%\text{ germination} \times \text{purity}} \tag{1}$$

Preweighed seed packages were thoroughly mixed before being evenly spread by hand on the newly prepared soil. Each plot was randomly assigned a fertilizer treatment consisting of "fertilized" or "not fertilized." Fertilizer was applied immediately after the seed was sown, at a level of 295 kg/ha of 18-18-18 NPK granular fertilizer (184.5 g per plot). All plots were lightly raked after the seed and fertilizer were applied.

Data Collection and Analysis

Plots were monitored for plant density (count) and cover at each location in mid-September in 2000 and late August in 2001, using a 0.25-m^2 (0.5 × 0.5–m square) quadrat randomly located at three nonoverlapping locations within each plot. Emergent seedlings of sown species were first counted, and then the shoot cover of each species was estimated. Exotic species and volunteer (nonsown) native species growing within the quadrat were also identified to species, counted, and assigned a cover estimate as well. In evaluating optimal sowing densities, primarily the results for the sown species are emphasized here; plant community dynamics will be covered in a separate paper.

Plant counts[1] allowed us to estimate the proportion of sown seeds that had germinated successfully (as expressed in terms of percent emergence) and to explore demographic trends. Plant emergence was calculated at the end of year 1

[1] We use the term plant "count" throughout, rather than plant "density," in order to better distinguish observed plant numbers per quadrat from the seeding density treatments per m^2; plant count values are expressed as the number of individuals per 0.25-m^2 quadrat.

from the number of plants counted per 0.25-m^2 quadrat, divided by the estimated density of viable seed sown in the same treatment plot (or year 2 if plants had not gone to seed in year 1 but more had appeared in year 2). Percent values were arc-sine square-root transformed prior to analysis of variance (ANOVA) to test for treatment effects.

The experiment is a balanced three-way factorial design replicated in six blocks. Data from the three sample quadrats within plots were averaged before statistical analysis, with replication provided by the six locations. Collected data were analyzed using SAS procedure ANOVA (SAS Institute Inc. 1988) with error terms specified to accommodate the split-block design (Appendix 1). When ANOVA results revealed a significant density effect, a Tukey multiple comparison test was conducted to identify which density treatments differed significantly (at $p = 0.05$) from each other. Linear regression (SAS procedure REG) was used to interpolate and extrapolate the effects of seeding density.

Results

Plant Count

Monitoring confirmed that mean total sown plant count successfully increased with sown density under all treatments in 2000 (year 1) and 2001 (year 2). The highest mean plant count occurred in the fall-seeded, fertilized 6,000 PLS/m^2 plots in both years (Table 2). By the second year, the number of sown plants generally increased at the low seeding densities and decreased at high densities (Table 2). Notably, the mean density of surviving plants across all treatments receiving greater than or equal to 1,500 PLS/m^2 decreased from year 1 to year 2, whereas the mean density of surviving plants across all treatments less than or equal to 750 PLS/m^2 increased from year 1 to year 2 (Fig. 1). Such year-to-year differences did not prove significant ($F_{[1,47]} = 5.66$, $p > 0.0633$) at any of the sowing densities tested. Nevertheless, 9 of the 12 treatment combinations with sown density less than or equal to 750 PLS/m^2 showed average increases in plant count, and the remaining three treatment combinations showed average decreases in count by fewer than 1.4 plants per quadrat. In contrast, 11 of the 12 treatment combinations sown to greater than or equal to 1,500 PLS/m^2 supported fewer plants in the second year.

Sowing density was the only treatment to exhibit a significant effect on plant count in year 1 ($F_{[5,55]} = 42.60$, $p = 0.0001$). Surprisingly, treatment effects were more pronounced in year 2, when density ($F_{[5,55]} = 47.04$, $p = 0.0001$), fertilization ($F_{[1,55]} = 22.20$, $p = 0.0001$), season of seeding ($F_{[1,5]} = 15.95$, $p = 0.0104$), and the interaction of fertilizer × season of seeding ($F_{[1,55]} = 20.65$, $p = 0.0001$) all resulted in statistically significant effects on observed plant count. Fall seeding, fertilization, and their interaction promoted greater densities of the sown plant species in the second year.

Table 2. Summary of plant counts (number of individuals per 0.25-m^2 quadrat) of sown species at the end of each of the two growing seasons under all treatment combinations.

			Year 1		*Year 2*	
Season Sown	*Fertilization*	*Sown Density*	$\bar{X}$	*SD*	$\bar{X}$	*SD*
Fall	fertilized	0	6.2	8.2	19.8	15.4
		375	31.8	16.8	31.7	20.8
		750	52.1	39.1	86.4	62.3
		1,500	75.7	38.0	88.4	44.8
		3,000	99.1	40.9	96.0	29.0
		6,000	176.6	114.8	148.7	67.0
	nonfertilized	0	2.4	3.0	6.2	5.5
		375	24.2	13.1	26.0	8.5
		750	24.1	8.1	23.4	11.0
		1,500	65.9	32.3	39.3	15.5
		3,000	84.7	57.5	53.3	23.3
		6,000	147.7	85.9	78.7	41.4
Spring	fertilized	0	0.2	0.3	0.6	0.8
		375	15.3	7.0	17.4	7.4
		750	30.5	15.9	29.2	12.2
		1,500	50.3	30.3	46.8	13.6
		3,000	86.4	52.4	77.7	34.0
		6,000	112.8	60.8	105.2	47.0
	nonfertilized	0	0.9	1.6	1.2	2.0
		375	16.5	13.3	18.1	10.8
		750	24.0	15.1	25.2	11.2
		1,500	44.6	23.9	39.6	21.5
		3,000	83.4	49.7	72.1	22.5
		6,000	127.2	80.3	112.6	38.4

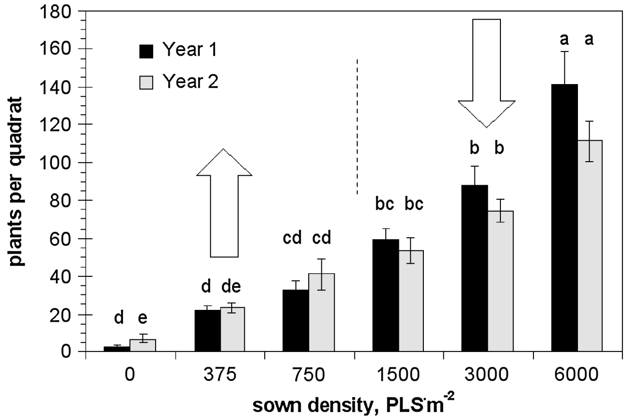

Figure 1. Mean (±SEM) density (number of individual plants per 0.25-m^2 quadrat) of sown species in response to seeding density treatments, summarized for all six locations, both fertilization treatments and both seasons of sowing, $n = 24$. Means within the same year that are annotated with the same letter are not significantly different at the $p = 0.05$ significance level. No sowing density supported significant differences from year 1 to year 2, but seeding treatments less than 1,500 PLS/m^2 showed a general increase in plant densities in the second year, and treatments greater than or equal to 1,500 PLS/m^2 generally suffered mortalities (note open arrows).

Plant Emergence

Emergence percentages were generally low at all seeding densities, resulting in comparatively low plant counts relative to the density of seed sown (Table 3). *Elymus glaucus* (exhibiting 33% emergence) and *Lupinus polyphyllus* (31%) were the most successful germinators, followed by *Festuca occidentalis* (25%). Three species (*Achillea millefolium*, *Geum macrophyllum*, and *Carex aenea*) had emergence rates less than 9%, with *Carex* less than 1%.

Some treatments and treatment combinations were statistically significant in their effects on seedling emergence. Sowing density had a significant effect on all species ($F_{[4,49]} > 3.07$, $p < 0.0251$) except *A. millefolium* ($F_{[4,45]} = 1.30$, $p = 0.2846$), with seedling emergence generally higher at low sowing densities. Fertilization had a significantly positive effect on the emergence of *Achillea* ($F_{[1,44]} = 15.09$, $p = 0.0003$), *E. glaucus* ($F_{[1,45]} = 4.50$, $p = 0.0394$), and *F. occidentalis* ($F_{[1,45]} = 28.12$, $p < 0.0001$) seedlings; a negative effect on the emergence of *L. polyphyllus* ($F_{[1,45]} = 8.13$, $p = 0.0065$); and no significant effect on *C. aenea* or *G. macrophyllum*. The season of seeding had no effect on the emergence of any species. The interaction of the density and season of seeding had a significant effect on *Elymus* ($F_{[4,45]} = 2.92$, $p = 0.0313$) and *Festuca* ($F_{[4,45]} = 3.12$, $p = 0.0237$), with fall seeding at low to intermediate densities promoting the greatest emergence. The interaction of fertilization and the season of seeding was also significant for *Festuca* ($F_{[4,45]} = 5.81$, $p = 0.0200$), with fall seeding and fertilization promoting superior emergence.

Plant Cover

Overall Trends. The effects on plant cover of sown species under the three treatment factors (spring vs. fall

Table 3. Total emergence[a] of sown plant species after one[b] growing season under all treatment combinations.

			Mean Plant Emergence, %						All Species	
Season Sown	Fertilization	Sown Density	*Achillea millefolium*	*Elymus glaucus*	*Festuca occidentalis*	*Carex aenea*	*Geum macrophyllum*	*Lupinus polyphyllus*	%	Plants/m^2
Fall	fertilized	375	14.8	43.6	65.3	3.0	20.7	37.0	30.1	113
		750	12.9	39.1	53.5	1.6	14.1	40.4	25.3	190
		1,500	11.9	39.6	39.2	0.4	5.9	23.0	20.1	301
		3,000	8.7	27.2	25.9	0.1	3.0	19.8	13.7	410
		6,000	8.4	25.5	24.2	0.0	2.8	14.5	12.7	759
	nonfertilized	375	9.5	66.2	30.5	1.8	13.3	46.3	25.6	96
		750	4.6	37.0	11.0	0.2	5.2	37.0	12.9	96
		1,500	5.9	48.7	20.4	0.8	5.9	37.0	17.6	264
		3,000	8.6	25.6	11.6	0.5	4.4	33.5	11.3	339
		6,000	6.2	23.9	11.2	0.2	3.9	23.6	9.8	591
Spring	fertilized	375	13.6	32.0	24.0	1.8	8.5	50.4	17.7	66
		750	9.9	31.4	32.9	0.3	6.7	29.6	17.2	129
		1,500	8.3	27.5	25.2	0.4	3.2	22.2	13.7	205
		3,000	6.9	23.5	22.2	0.2	3.5	21.7	12.0	359
		6,000	4.7	15.2	14.9	0.2	1.8	12.0	7.8	466
	nonfertilized	375	10.7	37.8	29.3	0.6	7.8	45.9	18.8	70
		750	5.9	33.6	15.3	0.9	9.3	38.5	14.2	106
		1,500	4.7	32.3	15.1	0.2	3.9	33.7	12.4	186
		3,000	4.7	28.9	14.8	0.4	2.4	34.1	11.5	346
		6,000	9.7	14.8	13.8	0.2	4.7	18.7	9.2	552
	overall average		8.5	32.7	25.0	0.7	6.5	31.0	15.7	282.2

[a] Emergence = (observed plant density/estimated density of seeds sown) × 100.
[b] Values in the shaded cells based on year 2 count due to delayed germination of some species under some treatments.

seeding, fertilizer vs. no fertilizer, and the six seeding densities), applied in all possible combinations, are the primary focus for the statistical results presented here (Table 4). When averaged across sowing density treatments, sown plant cover ranged from 15 to 38% in year 1 and 24 to 47% in year 2. In all but one of the 20 sown treatments, plant cover increased from year 1 to year 2 (Table 4). After two growing seasons, exotic species contributed average levels of 6 to 17% cover in the various sown plots; native volunteer species averaged 0.3 to 6.6% cover (Appendix 2). In contrast, unsown plots (0 PLS/m^2) averaged 12% exotic cover and 9% native volunteer cover by the end of year 2. Even when considering the contribution of volunteer species, the greatest native cover averaged 55% in year 1 and 64% in year 2 in the spring-sown fertilized plots sown at 6,000 PLS/m^2, with total plant cover (including exotic and native volunteer species) averaging 66% after 2 years in both spring- and fall-sown fertilized plots sown at 6,000 PLS/m^2 (Appendix 2).

Of all treatment combinations tested, the spring-sown fertilized plots produced the greatest plant cover in both year 1 (mean sown cover of 52.7%) and year 2 (mean sown cover of 62.3%). Some cover of sown plant species was also found in the control (0 PLS/m^2 sown density) plots, reflecting natural invasion from the surrounding vegetation or seed spillage from adjacent treatment plots. Mean "sown" cover on control plots ranged from 0.2 to 9.7% in year 1 and from 0.4 to 6.0% in year 2. In general, the treatments were effective in generating a wide range of total cover, but none of the treatments tested were able to reliably generate mean levels of sown cover or total cover at the nominal level of 70% desired for sloped sites, though several individual quadrats (44 of 360 by year 2) did so. Only the plots sown to the highest density averaged greater than 50% cover in both years; fertilized plots spring sown at 3,000 PLS/m^2 had a total cover of 62.8% (of which 12.3% was exotic) in year 1, but fell to less than 50% in year 2 (Appendix 2). By the end of the second growing season, 90 of 360 individual quadrats sampled in sown plots had attained greater than 50% cover by sown species.

Table 4. Total plant cover (%) for all sown plant species at the end of each of the first two growing seasons under all treatment combinations ($n = 6$).

Season Sown	Fertilization	Sown Density	Year 1 $\bar{X}$	Year 1 SD	Year 2 $\bar{X}$	Year 2 SD
Fall	fertilized	0	6.0	6.2	9.7	10.5
		375	27.9	27.4	30.0	35.8
		750	27.3	11.3	36.8	17.1
		1,500	35.0	15.6	41.7	27.2
		3,000	29.8	13.7	41.9	17.5
		6,000	50.5	14.2	57.2	22.4
	nonfertilized	0	1.3	1.7	4.6	5.7
		375	9.7	8.1	25.7	24.7
		750	10.4	9.4	28.9	30.8
		1,500	13.7	8.2	27.0	26.4
		3,000	15.6	10.5	20.3	23.4
		6,000	26.3	14.9	32.6	32.9
Spring	fertilized	0	0.7	1.1	0.2	0.3
		375	19.7	17.5	23.2	15.7
		750	21.1	14.4	32.6	17.9
		1,500	28.2	17.7	37.6	30.7
		3,000	49.5	39.7	45.1	18.6
		6,000	52.7	45.4	62.3	25.0
	nonfertilized	0	0.4	0.6	0.2	0.2
		375	4.2	2.9	15.8	18.8
		750	9.9	12.0	13.7	14.0
		1,500	9.1	10.4	22.6	27.9
		3,000	13.4	10.2	24.4	21.6
		6,000	22.4	24.7	36.0	42.1

Seeding Density Effects. Mean sown cover varied significantly among density treatments for both years. The cover of sown species generated in noncontrol plots ranged from averages of 4.2 to 52.7% in year 1 ($F_{[5,55]} = 13.07$, $p = 0.0001$), and increased to 13.7 to 62.3% in year 2 ($F_{[5,55]} = 15.53$, $p = 0.0001$). The highest density of seeds yielded the highest mean cover (Fig. 2).

A Tukey multiple comparison test revealed that in year 1, the 6,000 PLS/m^2 treatment achieved significantly greater sown cover than all other densities except the 3,000 PLS/m^2 treatment. Treatments between 375 and 3,000 PLS/m^2 did not differ significantly from each other, and the cover produced by the 375 PLS/m^2 treatment was not significantly greater than in the control plots. By year 2, a Tukey test revealed that the 6,000 PLS/m^2 application again yielded the greatest sown cover but now was not significantly different from either the 3,000 or the 1,500 PLS/m^2 treatments. None of the 375 to 3,000 PLS/m^2 treatments differed significantly in year 2, but all produced greater cover than was found in the control plots. The

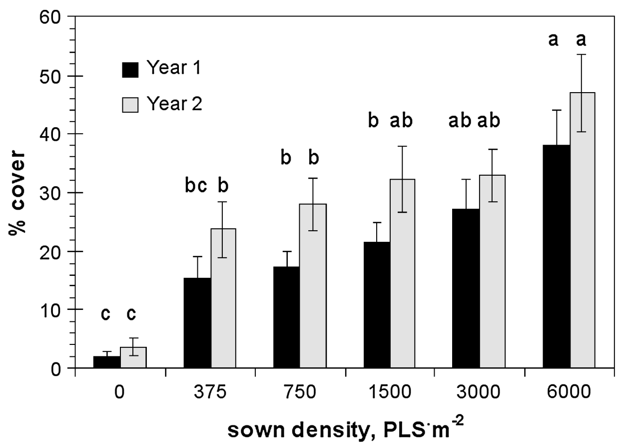

Figure 2. Mean (±SEM) cover of sown species in response to density treatments, summarized for all six locations, both fertilization treatments and both seasons of sowing, $n = 24$. Means within the same year that are annotated with the same letter are not significantly different at the $p = 0.05$ significance level.

individual growth responses of *A. millefolium*, *Elymus glaucus*, *F. occidentalis,* and *L. polyphyllus* contributed to the overall cover response, but *C. aenea* and *G. macrophyllum* were present in such low numbers that they showed no statistically significant response to the density of sowing (Table 5). Seeding density treatments did not have significant impact on native volunteer cover in year 1 ($F_{[5,55]} = 1.99$, $p = 0.0946$), but differences became significant in year 2 ($F_{[5,55]} = 3.65$, $p = 0.0063$), with treatment means ranging from 1 to 9% native volunteer cover. The highest density treatments (3,000 and 6,000 PLS/m^2) supported significantly less cover by nonsown native species than the 0 PLS/m^2 density treatments.

Other Effects. Fertilized plots achieved higher cover in each year than the corresponding nonfertilized plots. Achillea millefolium, Elymus glaucus, and Festuca occidentalis responded with significantly greater plant cover in both years (Table 6). Cover of sown species in fertilized plots averaged 29.0 ± 3.1% in year 1, significantly greater than the 11.4 ± 1.5% in the nonfertilized plots ($F_{[1,55]} = 42.15$, $p = 0.0001$). By year 2, fertilized plots achieved a mean sown cover of 34.9 ± 3.1%, significantly greater than the 21.0 ± 3.0% in the nonfertilized plots ($F_{[1,55]} = 22.13$, $p = 0.0001$). For every combination of seeding density × season of seeding, the fertilized plot produced more cover (often twice as much) than the corresponding unfertilized plot (Table 4). The response of *F. occidentalis* cover to sowing density and fertilization treatments combined (Fig. 3) is representative of that exhibited by the dominant species, with no interactions evident.

Exotic cover in year 1 averaged 12.8% in fertilized plots, significantly greater than 8.1% in the unfertilized plots ($F_{[1,55]} = 7.84$, $p = 0.0070$). The fertilization effect on exotic cover was no longer significant in year 2 ($F_{[1,55]} = 0.57$, $p = 0.4544$), with mean exotic cover reduced to 7.0 and 6.0% in fertilized and unfertilized plots, respectively.

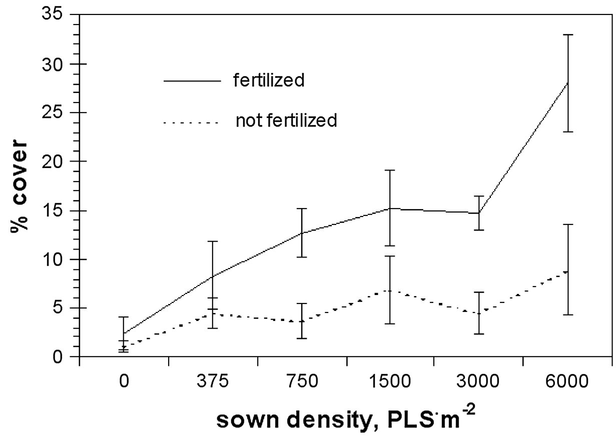

Figure 3. Year 2 mean cover (±SEM) of *Festuca occidentalis* in response to fertilization × density treatments, summarized for all six location and season of seeding treatments, $n = 36$.

In contrast, fertilization had no significant effect on the cover of native volunteers ($p > 0.72$ in either year).

There was no significant effect of the season of seeding on sown cover or total cover production. In year 1, average sown cover was 21.1% in the fall plots and 19.3% in the spring plots ($F_{[1,5]} = 0.98$, $p = 0.3684$). In year 2, average sown cover was 29.7% in the fall plots and 26.1% in the spring plots ($F_{[1,5]} = 1.65$, $p = 0.2547$).

There were no significant interactions of density × fertilization, density × season of seeding, fertilizer × season of seeding, or density × fertilizer × season of seeding (Appendix 1) with respect to sown plant cover production in either year 1 (all $p > 0.12$) or year 2 (all $p > 0.16$).

Discussion

As expected, plant density of sown species increased as the seeding density was increased: whenever more seeds

Table 5. The effect of density treatments on mean cover (%) of individual species.

		Sown Density, PLS/m^2						ANOVA Results	
Year 1	*Overall*	*0*	*375*	*750*	*1,500*	*3,000*	*6,000*	$F_{[5,55]}$	*p*
Achillea millefolium	3.5	0.5 c	2.6 bc	3.1 abc	3.1 abc	5.2 ab	6.9 a	5.17	**0.0006**
Carex aenea	0.1	0.1 a	0.2 a	0.1 a	0.1 a	0.1 a	0.1 a	0.34	0.8850
Elymus glaucus	6.6	0.8 c	5.3 bc	5.8 b	7.6 ab	9.5 ab	10.9 a	9.10	**0.0001**
Festuca occidentalis	6.7	0.3 c	5.0 bc	5.5 bc	7.2 abc	8.0 ab	14.0 a	6.16	**0.0001**
Geum macrophyllum	0.6	0.3 a	0.7 a	0.4 a	0.6 a	0.8 a	1.0 a	1.10	0.3732
Lupinus polyphyllus	2.6	0.1 c	1.6 bc	2.4 bc	2.9 ab	3.5 ab	5.2 a	7.29	**0.0001**
Year 2									
A. millefolium	5.4	1.0 b	4.8 ab	5.2 ab	5.7 ab	8.1 a	7.7 a	4.15	**0.0029**
C. aenea	0.1	0.2 a	0.2 a	0.0 a	0.1 a	0.1 a	0.1 a	0.49	0.7859
E. glaucus	7.0	0.8 b	7.4 a	7.6 a	9.0 a	7.6 a	9.7 a	6.27	**0.0001**
F. occidentalis	9.2	1.7 c	6.4 bc	8.2 bc	11.0 b	9.6 b	18.5 a	12.5	**0.0001**
G. macrophyllum	1.8	0.1 b	1.7 ab	2.0 ab	1.7 ab	1.9 ab	3.2 a	1.92	0.1051
L. polyphyllus	4.4	0.0 c	3.2 bc	5.0 ab.	4.7 ab	5.7 ab	7.8 a	7.72	**0.0001**

Letters a,b,c, denote the results of Tukey multiple comparison tests; values on the same line sharing the same letter are not significantly different from each other ($p = 0.05$). Significant ANOVA results ($p < 0.05$) are highlighted in bold.

encountered available space, they were successfully able to establish more seedlings. The change in plant numbers from year 1 to year 2 suggests that there is a "natural" or "equilibrial" density between 750 and 1,500 PLS/m^2 for this mixture of species on these sites. As these perennials continued to grow in their second year, they began to interfere with each other at the higher sown densities, resulting in some mortality or "thinning" at sown densities greater than or equal to 1,500 PLS/m^2, presumably because there were resource limitations. On the other hand, there were resources available for new seedlings (from introduced seeds that remained dormant during the first growing season or, in some cases, from seeds and rhizomes produced by the plants that had established in that first year) to "fill in" the stands sown to densities less than 1,500 PLS/m^2.

Achieving Plant Cover Objectives

Seeding density and fertilization treatments had a significant effect on plant cover, but season of seeding did not. When judiciously prescribed and applied, fertilizer can reliably enhance plant growth on degraded sites (Hollowell & Tysdal 1948; McKell 1982; Green et al. 1992; McCaughey & Simons 1996; Bulmer 1998). Likewise, the "law of constant yield" (Harper 1977) suggests that increasing the density of plants will result in increased cover until all available space is effectively occupied. The density of plants in plots sown to large amounts of seed declined from year 1 to year 2, but the cover in all treatments still generally increased in the second year. Though plants were getting bigger they still came nowhere near to occupying all of the aboveground growing space: the highest mean cover was only 62%, and it cannot be said that asymptotic yields were achieved by the treatments employed. Perhaps the inability to achieve full cover may reflect the fact that *Carex aenea* and *Geum macrophyllum* had not yet achieved their full stature after only two growing seasons. Full native plant cover may not be achievable over short time frames on these degraded sites, or with this species mix, due to compacted soils, nutrient stress, or other belowground limitations and undocumented factors such as landscape context.

Although the season of seeding was not a significant factor in plant cover measured in this experiment, previous research suggests that the decision of when to sow will depend on site location and condition, and on the species selected (Brown & Chambers 1990; Schwab 1991; Kennedy 1992; Gerling et al. 1996; Pahl & Smreciu 1999; Smith & Smith 2000). Such flexibility in seeding time is an important factor for revegetation with native plants because it provides options for field operations, depending on what other activities (e.g., site preparation, weed control) have to be completed first, whether snow melt limits spring access, and on what species are in a seed mix.

High densities of seed may be needed on some sites in order for successful revegetation to be achieved. But how dense this seeding should be seems to depend on the definition of what level of plant cover constitutes "successful revegetation." Is 62% cover of the desired species "adequate," or is more cover needed? There are few specific recommendations in the literature for minimum acceptable cover on degraded level sites. General recommendations range from 20 to 80% cover, dependent on site factors such as slope, soil texture, and precipitation (Carr 1980; Dickey et al. 1986; Bugg et al. 1997; Grigg 2001).

The optimum seeding density will vary according to the urgency with which cover must be established and how much cover is deemed desirable, both of which will be defined by the nature of the site and management objectives. For example, if cover is required quickly on a slope prone to erosion, the two highest densities (3,000 and 6,000 PLS/m^2) will provide significantly higher cover in the first year. But if immediate green-up is not imperative, the lowest seed density tested (375 PLS/m^2) will provide equivalent levels of cover by the end of two growing seasons. Because native seed is generally expensive and difficult to obtain, determining how quickly a site needs to be revegetated is an important consideration in deciding on the most appropriate seeding density.

If practitioners must reach particular cover goals over a specified period of time, the relationships observed in this experiment can help estimate the amount of seed needed. Expected sown plant cover at the end of the first growing season, after spring seeding and fertilization, can be described by the following regression equation:

$$\text{Cover} = 13.60635 + 0.00776 \times \text{PLS/m}^2 \quad (p = 0.0011, R^2 = 0.27, n = 36) \tag{2}$$

Similarly, sown plant cover expected at the end of the second growing season follows this relationship:

$$\text{Cover} = 17.56940 + 0.00821 \times \text{PLS/m}^2 \quad (p < 0.0001, R^2 = 0.40, n = 36) \tag{3}$$

Using the same species mixture on the same sorts of sites as tested here, this means that achieving 70% cover in the first growing season can be achieved by sowing 7,267 PLS/m^2 with spring seeding and fertilization with 18-18-18 at 295 kg/ha. Attaining 80% cover within two growing seasons would require 7,604 PLS/m^2. As these estimates are not much beyond the highest density tested in this experiment, such extrapolations are reasonable, though might be further enhanced by testing a range of different fertilization rates. Note that the sowing densities recommended to achieve such cover targets are much greater than those required to achieve 50% cover on such level sites and much greater than the 750 to 1,500 PLS/m^2 at which plant populations would appear to equilibrate.

Improving the Seed Mix

Emergence results suggest that *Elymus glaucus*, *Festuca occidentalis*, and *Lupinus polyphyllus* are the most promising candidates for future restoration work with native species in our area because they exhibited emergence rates greater than or equal to 25%. Although *Achillea millefolium* had low emergence (8.5%), it too established good cover and consistently went to seed by the end of the second growing season.

There was no significant effect of the season of seeding on the cover production of individual sown species (Table 6), total sown cover, or total cover. Although differences in *Lupinus* cover between fertilized and unfertilized treatments were not significant, they were nearly so by year 2 ($p = 0.07$ in year 2, compared to $p = 0.47$ in year 1). The neutral response to fertilizer does not mean that this species should be excluded from a mix if fertilizer is used. *Lupinus* did establish and went to seed in the fertilized plots as well as in the unfertilized plots, but as a nitrogen-fixing legume, it presumably does not have the same need for nitrogen as the other plants tested. In the long run, it may be important to include *Lupinus* (or another native legume) in a seed mix to provide nitrogen and growth enhancement to all vegetation once the benefits of a single application of commercial fertilizer have dissipated.

As expected, fertilization had a beneficial effect on plant cover at all densities tested on these degraded soils. A single application of fertilizer, applied at standard agronomic rates at the time of sowing, can be beneficial for at least 2 years without leading to dominance by weeds. This confirms earlier indications that fertilizer can serve to stretch limited supplies of native seed (Burton & Burton 2001), generating the most effective cover production for a given investment of seed. This result is contrary to recommendations for grassland restoration for which fertilizer use is discouraged, primarily because fast-growing exotic species are better at taking up nutrients than slower growing native perennials, so weed competition in such situations can be exacerbated by the addition of fertilizer (Huenneke et al. 1990; Wilson & Tilman 1991; Townley-Smith & Wright 1994; Stevenson & Wright 1996).

The poorly germinating *C. aena* and *G. macrophyllum* provided so little cover that they, in effect, acted as filler in the seed mix. Ignoring the contribution of these two species to sown cover results in only a loss of less than 4% cover in any treatment. If these two species were excluded from the mixture used in this experiment, the geometric progression of seed density nominally ranging from 375 to 6,000 PLS/m^2 would instead range from 240 PLS/m^2 to 3,840 PLS/m^2. There may yet be advantages (e.g., plant community diversity and resilience, wildlife use) to including an additional medium-statured, long-lived graminoid, and another small- or medium-statured forb in revegetation mixtures for these sorts of sites in northern B.C.

Future work could refine these estimates and match more precise recommendations to specific sites.

Conclusions

This experiment shows that degraded sites in northern B.C. can be successfully revegetated with native species. Cover production did not meet our arbitrary expectations of 70% mean cover (suitable for erosions control on steep sites) at even the highest seed density tested, although results indicate that 50% sown cover (a suitable goal for level sites) can be generated in 1 year by this seed mix if sown at 4,690 PLS/m^2, or in 2 years if sown at 3,950 PLS/m^2. The range of sown density treatments tested here showed no leveling off of plant cover, suggesting that even higher seed densities could produce yet more plant cover.

The highest sown cover (mean of 62%) was produced by fertilizing a spring-sown application of 6,000 PLS/m^2. Seed densities of 3,000 and 6,000 PLS/m^2 (or 1,920 and 3,840 PLS/m^2 if using a revised four-species mixture)

Table 6. Effect of fertilizer treatment and season of sowing on mean cover (%) of individual species.

	Main Fertilizer Effects				*Main Season Effects*			
	Treatment		*ANOVA Results*		*Treatment*		*ANOVA Results*	
Species	*Fertilized*	*Nonfertilized*	$F_{[1,55]}$	*p*	*Fall*	*Spring*	$F_{[1,55]}$	*p*
Year 1								
Achillea millefolium	4.7	2.4	8.64	**0.0048**	3.7	3.3	0.24	0.6417
Carex aenea	0.1	0.1	1.18	0.2827	0.2	0.1	3.33	0.1276
Elymus glaucus	9.8	3.5	40.34	**0.0001**	6.3	7.0	0.09	0.7808
Festuca occidentalis	11.2	2.2	37.54	**0.0001**	6.9	6.4	0.14	0.7231
Geum macrophyllum	0.8	1.8	1.23	0.2721	1.1	0.2	2.55	0.1710
Lupinus polyphyllus	2.5	2.8	0.52	0.4733	2.9	2.3	0.46	0.5498
Year 2								
A. millefolium	6.4	4.4	4.12	**0.0473**	5.5	5.3	0.08	0.7841
C. aenea	0.2	0.1	3.00	0.0888	0.1	0.1	0.15	0.7175
E. glaucus	9.1	5.0	15.34	**0.0003**	6.6	7.4	0.27	0.6250
F. occidentalis	13.6	4.9	45.52	**0.0001**	9.4	9.1	0.06	0.8231
G. macrophyllum	1.8	1.7	0.00	0.9885	2.8	0.7	1.48	0.2782
L. polyphyllus	3.9	5.0	1.95	0.1686	5.3	3.5	0.68	0.4466

If the *p* value given under ANOVA Results is less than 0.05 (as highlighted in bold), then the two preceding treatment means are significantly different.

produce the highest cover at the end of the first year, whereas even the 1,500 PLS/m^2 (or 960 PLS/m^2 of the revised mixture) produces an equivalent amount of cover by year 2. Similarly, seeding densities as low as 375 PLS/m^2 (or 240 PLS/m^2 of a revised four-species mixture) produces cover statistically equivalent to densities up to 3,000 PLS/m^2 (or 1,920 PLS/m^2 of the revised mixture) after two growing seasons. The two highest densities tested were the only ones to significantly inhibit the establishment of volunteer native species. Therefore, if the need to establish vegetation is not urgent, then lower densities can be just as effective, are more efficient in their use of expensive seed, and can facilitate the establishment and growth of naturally invading native species.

Fall seeding seemed to promote seedling emergence as expected, but this did not translate into a significant increase in cover production. On remote sites or those with a heavy snowpack, fall seeding may be still be preferable because such locations are difficult to access until late in the spring. Fertilization was clearly beneficial at all sites and for all density and sowing season treatments. Further research would be needed to determine the most cost-effective combination of seed densities and fertilizer application rates to achieve desired levels of plant cover on any particular site.

Clearly there is a need for more research on the species used in this experiment, as well as on other native species and native seed mixes, if we hope to use them widely for revegetation purposes. It must be remembered that when doing ecological revegetation or restoration work, all sites are unique in some respect and seeding prescriptions must take the local flora and site factors into account. The methods described in this paper, based on monitoring a geometric series of sowing densities over 2 or more years, could be used in other geographical areas to determine optimal sowing densities for plant establishment on disturbed areas.

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Appendix 1. ANOVA model employed for most hypothesis testing. This example uses year 2 total sown cover as the response (dependent) variable.

Source of Variation	*df*	*Error Term for F Test*	*ANOVA SS*	*Mean Square*	*F Value*	*p Value*
Main plot effects						
Location, $n = 6$	$(n - 1) = 5$	replicates; not tested				
Density, $d = 6$	$(d - 1) = 5$	location × density × fertilizer	24,286.75	4,857.35	15.53	0.0001
Fertilizer, $f = 2$	$(f - 1) = 1$	location × density × fertilizer	6,922.98	6,922.98	22.13	0.0001
Season*, $s = 2$	$(s - 1) = 1$	location × season	453.74	453.74	1.65	0.2551
Interaction terms						
Density × fertilizer	$(d - 1)(f - 1) = 5$	location × density × fertilizer	2,285.26	457.05	1.46	0.2174
Density × season	$(d - 1)(s - 1) = 5$	location × density × fertilizer × season	1,114.63	222.93	1.64	0.1647
Fertilizer × season	$(f - 1)(s - 1) = 1$	location × density × fertilizer × season	24.88	24.88	0.18	0.6704
Density × fertilizer × season	$(d - 1)(f - 1)(s - 1) = 5$	location × density × fertilizer × season	218.40	43.68	0.32	0.8980
Error terms						
Location × season	$(n - 1)(s - 1) = 5$					
Location × density × fertilizer	$(n - 1)(df - 1) = 55$					
Location × density × fertilizer × season	$(n - 1)(df - 1)(s - 1) = 55$					

SS, sum of squares.
* Denotes season of sowing.

Appendix 2. Breakdown of total plant cover by origin, after two growing seasons, under all treatment combinations.

			Plant Cover, %							
			Sown Species		Exotic Species		Native Volunteers		All Species	
Season Sown	Fertilization	Sown Density (PLS/m^2)	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Fall	fertilized	0	9.7	10.5	14.5	28.7	6.2	6.3	30.4	25.0
		375	30.0	35.8	15.6	20.6	9.2	14.2	54.8	44.7
		750	36.8	17.1	7.2	15.9	3.3	3.0	47.3	26.9
		1,500	41.7	27.2	4.3	9.9	2.3	2.7	48.3	28.5
		3,000	41.9	17.5	2.8	4.5	1.1	1.5	45.9	20.0
		6,000	57.2	22.4	7.8	19.0	1.3	1.3	66.3	32.9
	nonfertilized	0	4.6	5.7	9.8	20.9	13.2	24.0	27.6	32.1
		375	25.7	24.7	7.2	15.3	9.6	19.3	42.4	45.4
		750	28.9	30.8	7.8	18.9	2.7	4.3	39.4	43.6
		1,500	27.0	26.4	5.6	12.0	3.7	4.3	36.4	31.3
		3,000	20.3	23.4	4.6	11.1	0.8	0.5	25.6	33.7
		6,000	32.6	32.9	2.0	3.9	2.0	3.2	36.6	36.5
Spring	fertilized	0	0.2	0.3	13.2	16.8	7.6	7.8	21.0	14.4
		375	23.2	15.7	6.4	9.3	1.7	2.1	31.3	16.0
		750	32.6	17.9	3.4	5.6	2.4	2.3	38.5	18.6
		1,500	37.6	30.7	5.6	11.9	1.9	1.5	45.1	30.9
		3,000	45.1	18.6	1.1	2.2	1.2	2.1	47.1	19.8
		6,000	62.3	25.0	2.5	5.8	1.2	2.3	66.0	24.8
	nonfertilized	0	0.2	0.2	10.7	14.8	6.9	8.7	17.7	14.2
		375	15.8	18.8	6.1	14.4	1.5	2.1	23.4	24.3
		750	13.7	14.0	6.7	15.7	1.6	2.4	22.0	24.2
		1,500	22.6	27.9	7.6	17.7	1.3	1.6	31.6	36.3
		3,000	24.4	21.6	2.4	5.7	0.7	0.5	27.6	25.8
		6,000	36.0	42.1	1.7	3.4	0.7	1.0	38.3	43.2