Controlling invasive *Arrhenatherum elatius* and promoting native prairie grasses through mowing

Wilson, Mark V.* & Clark, Deborah L.

Department of Botany and Plant Pathology, Oregon State University, Cordley 2082, Corvallis, OR 97331-2902, USA ;
*Corresponding author; Fax +15417373573; E-mail wilsonm@bcc.orst.edu

Abstract. Control of invasive plants is a key element of conservation and restoration efforts. We report results from a five-year field experiment in western Oregon, USA that evaluates the effects of different mowing regimes on the non-native and invasive perennial grass *Arrhenatherum elatius*, the native perennial prairie grasses *Danthonia californica* and *Festuca roemeri*, and groups of other native and non-native grasses and forbs. Eight treatments were designed to test hypotheses about the role of mowing height and time of application on the plant community.

Differences among treatments emerged only after two or three years of treatment. This delay in response reinforces the need for long-term studies. Annual mowing was most effective at reducing *Arrhenatherum* cover and flowering when applied in late spring or early summer, the time of *Arrhenatherum* flowering and expected maximum above-ground allocation. Double mowing and mowing at 15 cm were more effective in reducing *Arrhenatherum* cover than were single mowing and mowing at 50 cm. All treatments increased the cover and flowering of *Danthonia*. Statistical model analysis showed that increases in cover and flowering of the native grass *Danthonia* were caused by its release from suppression by *Arrhenatherum*. Four years of the most effective treatment, mowing at 15 cm in late spring, converted an *Arrhenatherum*-dominated site to a prairie dominated by native grasses. This is one of the few documented cases of pest plant control causing an increase in native plant abundance. These results show that mowing, properly applied, can be an effective tool for restoring degraded, *Arrhenatherum*-dominated prairies.

Keywords: *Danthonia californica*; *Festuca roemeri*; Non-native plants; Pest plant control; Prairie restoration; Release from suppression; Vegetation management.

Nomenclature: Hitchcock & Cronquist (1973).

Abbreviations: AIC$_c$ = Corrected Akaike Information Coefficient; EI = Effectiveness Index.

Introduction

Invasive non-native pest plants can change ecosystem processes, contribute to the loss of native plants and animals, and reduce the economic and aesthetic value of native ecosystems (e.g. Vitousek 1990; Anon. 1993; Mack & D'Antonio 1998). As a result, restoration and conservation management efforts often focus on pest-plant control (Anderson 1995; Randall 1996; Shea et al. 1998). Despite the importance being placed on the control of invasive plants, few studies have evaluated the expected restoration and conservation benefits (D'Antonio & Vitousek 1992; Parker & Reichard 1998).

Mowing is an important tool for the management and restoration of prairie vegetation. Although mowing is largely non-selective, varying the time of mowing can be used to target specific species (Hover & Bragg 1981; Mitchell et al. 1996). When species differ in height, mowing at the proper height can be used to target taller species (Hulme et al. 1999) with little harm to shorter species. In many short-grass prairies, invading non-native plants tend to be taller than the natives.

Our twin objectives in this study were to determine if mowing can be used to reduce *Arrhenatherum elatius*, an important non-native invasive plant in western Oregon upland prairies, and to determine if control of *Arrhenatherum* promotes native plant species. We address six hypotheses about the role of mowing in managing these upland prairies.

1. A common pattern in weed control is that mowing is most effective at the time of flowering, when carbohydrate concentrations in above-ground tissue are highest (Zimdahl 1993; Becker & Fawcett 1998; Ross & Lembi 1999). Because above-ground allocations in *Arrhenatherum* peak around May in our study area (Tanphiphat & Appleby 1990) and flowering peaks in early June, we predicted that mowing at these times would be most effective in *Arrhenatherum* control.

2. Pest plant control actions often must be repeated during a given year to be effective, because of the ability of most prairie plants to regrow or establish after the removal of above-ground biomass (Hewett 1985; Pakeman

& Marrs 1994; Bobbink & Willems 1993). Therefore, we predicted that two mowings per year would be more effective at *Arrhenatherum* control than annual treatments.

3. Because the perennial *Arrhenatherum* can increase through vegetative spread as well as through sexual reproduction and seedling establishment (Pfitzenmeyer 1962; Schmidt & Brübach 1993) and was well established in the study system, we predicted that mowing treatments that targeted vegetative tissue would be more effective at reducing *Arrhenatherum* abundance than treatments that targeted only reproductive tissues.

4. Pest-plant control sometimes stimulates seedling establishment, either through a decrease in competitive pressure (Silvertown & Tremlett 1989; Aguilera & Laurenroth 1993; Reader 1993), a resulting reduction in litter thickness (Oomes et al. 1996; Foster & Gross 1997), or diminishing shelter for seedling herbivores. Therefore, we predicted that the number of seedlings of native species would increase with the effectiveness of *Arrhenatherum* control and be negatively related to the resulting thickness of the litter layer.

5. The important native grasses in the study area (*Danthonia californica* and *Festuca roemeri*) have more or less the same phenology as *Arrhenatherum* but the bulk of their foliage is shorter than typical mowing height. Therefore, we predicted that mowing would have little direct impact on these native grasses.

6. *Arrhenatherum*, like many invasive non-native plants, is widely considered to suppress shorter and slower growing native species (Grubb 1982; Blossey & Nötzold 1995). We predicted that treatments that cause significant decline in *Arrhenatherum* should release native grasses, allowing them to increase in abundance. Few studies have documented the competitive interactions between native plants and non-native invaders expected to be responsible for release of native species (Parker & Reichard 1998).

Methods

Study area

We conducted this study within the Baskett Slough National Wildlife Refuge (Polk County, Oregon, USA), which is administered by the US Fish and Wildlife Service. The climate of the refuge is characterized by mild, wet winters and moderate, dry summers. Mean temperatures at the Dallas weather station, 7 km from the study area, are 4.1°C in January and 18.7 °C in July; annual precipitation is 125 cm, with 81% occurring from October through March (Oregon Climate Service, 1961-1990).

The Refuge contains several types of vegetation, including unmanaged native prairie dominated by the native grasses *Danthonia californica* and *Festuca roemeri*.

US Fish and Wildlife management goals for the study area include maintaining its prairie physiognomy, controlling invasive plants like *Arrhenatherum*, and promoting native plants and animals, especially rare species protected by state or federal law (Wilson et al. 1997).

The experimental study area, dominated by *Arrhenatherum*, was a flat, upland, relatively homogeneous section of the Refuge (44° 58' N, 123° 15' W, elevation 110 m), mapped as Chehulpum silt loam (Knezevich 1982), a loamy, mixed, superactive, mesic, shallow Ultic Haploxeroll. *Arrhenatherum* is native to Eurasia but widely introduced throughout western North America, New Zealand and Australia (Pfitzenmeyer 1962). *Arrhenatherum* can be a pest in pastures and prairies, even within its native range (Grubb 1982; Schmid & Brübach 1993). *Arrhenatherum* is a tall (up to 180 cm), generally erect, tussock-forming perennial grass with very short rhizomes (Pfitzenmeyer 1962). The variety within the study area, *A. elatius* var. *elatius*, allocates more biomass to flowering and flowers earlier than the cormforming var. *bulbosum* (Khan & Morton 1994; Petit et al. 1996).

Germination of *Arrhenatherum* in the study area occurs soon after the onset of fall rains (Maret 1996); sprouts also emerge from the rhizomes of mature plants at this time (Tanphiphat & Appleby 1990). Little growth of seedlings or sprouts occurs during the winter, but rapid growth occurs in the spring, with dormancy occurring as soils dry during summer drought, usually by July (Tanphiphat & Appleby 1990).

Experimental design

We used a replicated before-after-control-intervention approach with a randomized complete block design. Each of the four blocks was 8 m × 12 m, and contained eight mowing treatments 3 m × 4 m in area. We initiated treatments in May of 1994 and continued for four years.

Treatments 1 - 4 were mowing at 10 - 15 cm with cut material left in the plots.
Treatment 1: plots mown each year in early spring (April 18 - April 21);
Treatment 2: mown in late spring (May 27 - June 9);
Treatment 3: mown in early summer (June 19 - June 26);
Treatment 4: mown in early fall (September 15 - October 6);
Treatment 5: mown at 10 - 15 cm in early summer, with removal of cut material;
Treatment 6: mown at 50 cm in early summer, when *Arrhenatherum* is > 50 cm tall and in bloom, but the foliage of *Danthonia* and *Festuca* is generally < 50 cm;
Treatment 7: double mowing at 10 - 15 cm, once in late spring and another in the following early spring. Cut material in Treatments 6 and 7 was left in the plots.
Treatment 8: unmanipulated control.
We applied mowing treatments with a hand-held rotary cutter, regulating mowing height with stakes set with their tops at the proper cutting height.

Table 1. Species encountered in the study, and composition of species groups. Dominant species within each category are in bold. Nomenclature follows Hitchcock & Cronquist (1973), except where noted.

Native grasses		Mosses	
Danthonia californica	**(perennial)**	***Brachythecium albicans* (Hedw.) B.S.G.**	
***Festuca roemeri* (Pavlick) E.B. Alexeev**	**(perennial)**	***Racomitrium canescens* (Hedw.) Bred. var.** *ericoides* Hampe.	
Native forbs		Non-native and cosmopolitan forbs	
Agoseris sp.	(perennial)	*Achillea millefolium*	(perennial)
Brodiaea coronaria	**(perennial)**	*Cerastium viscosum*	(annual)
***Clarkia* sp.**	**(annual)**	*Cirsium* sp.	(biennial)
Eriophyllum lanatum	(perennial)	***Daucus carota***	**(biennial)**
Fragaria virginiana	(perennial)	***Galium aparine***	**(annual)**
Lotus micranthus	(annual)	*Geranium carolinianum*	(annual)
Ranunculus occidentalis	(perennial)	*Geranium dissectum*	(annual)
Sanicula bipinnatifida	(perennial)	*Hieracium* sp.	(perennial)
		Hypericum perforatum	**(perennial)**
Non-native grasses		*Lathyrus sphaericus*	(annual)
Arrhenatherum elatius	**(perennial)**	***Myosotis discolor***	**(annual)**
Bromus mollis	**(annual)**	*Plantago lanceolata*	(perennial)
Bromus rigidus	**(annual)**	***Sherardia arvensis***	**(annual)**
Elymus caput-medusae	**(annual)**	*Sonchus* sp.	
Dactylis glomerata	(perennial)	*Torilis arvensis*	
Festuca megalura or ***myuros***	**(annual)**	***Vicia hirsuta***	**(annual)**
Festuca arundinacea	(perennial)	***Vicia sativa***	**(perennial)**
Festuca rubra	(perennial)	*Vicia cracca*	(perennial)

Measurements

In 1994, before treatments began, and each year until 1998, we collected data on plant abundance in late May, at the peak of the growing season for all major species in the study area. We always sampled before we applied late spring treatments. Measurements were done within two 1 m × 0.5 m permanently marked quadrats. A 1-m buffer surrounded each measurement area.

Within each quadrat we measured visually, aided by calibrated templates, the total cover of plant groups: all vascular plants, *Arrhenatherum*, *Danthonia*, *Festuca*[1], non-native grasses other than *Arrhenatherum* (most of which were annuals), non-native and cosmopolitan forbs, native forbs, and mosses (Table 1).

In late May or early June, before applying the early summer treatments, we recorded sexual reproduction and regeneration as the number of inflorescences of *Arrhenatherum*, *Danthonia*, and *Festuca* within quadrats (1997 and 1998) and as the number of seedlings within 300-cm^2 subplots (1995, 1997 and 1998). We recorded litter depth at four positions within each subplot. Phenological stages (preanthesis, anthesis, postanthesis, dispersing, and vegetative) and the predominant maximum heights of leaves and flowering structures of *Arrhenatherum*, *Danthonia*, and *Festuca* in the no-manipulation plots were recorded at the times of treatment.

Analysis

We used analysis of covariance to analyze the results. The main statistical model was

$$C_a = \beta_0 + \beta_1 \cdot C_b + \beta_2 \cdot B + \beta_3 \cdot T + \beta_4 \cdot B \cdot T + \varepsilon, \text{(1)}$$

where C_a is the cover or number of inflorescences of a species or group after treatment, C_b is cover before treatment (the covariate), B is the blocking effect, T is the treatment effect, $B \cdot T$ is the block × treatment interaction, and ε is error. Analysis followed the recommendations of Newman et al. (1997) and Underwood (1997) for blocked designs with subsampling. Square-root transformation of response variables and covariates were sometimes necessary to meet the assumptions of statistical analysis.

When main effects were significant, we examined differences between each treatment and the control with Dunnett's test, at the 0.05 level (Steel & Torrie 1980; Day & Quinn 1989). In cases where the block × treatment interaction was significant, we examined interaction plots to confirm the interpretation of the treatment effect.

We analysed treatment effects on number of seedlings with Friedman's non-parametric analysis, which has higher power than parametric analysis of variance with such strongly non-normal data (Conover 1980). We used Spearman's rank correlation to test for relationships of seedling number with total vascular plant cover, litter depth, and moss cover.

We used statistical models to test for direct effects of mowing on native grass cover vs. the indirect effect of release of native grasses from suppression by *Arrhenatherum*. These models included block effects (spatial

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[1]Recent research (Wilson 1999) has identified a second fescue taxon, *Festuca rubra*, at the site in small numbers.

variability), pre-treatment cover (initial conditions), treatment, and the post-treatment cover of *Arrhenatherum*. We used AIC_c, the corrected Akaike Information Coefficient (Burnham & Anderson 1998) to test the relative fit of different models. AIC_c measures the information-theoretic discrepancy between the modeled values and the true values, rewarding model accuracy and penalizing model complexity. Models with a lower AIC_c fit the data better. This type of discrepancy measure is needed when comparing non-hierarchical models, in this case the models with treatment vs. models with *Arrhenatherum* cover.

We also developed an Effectiveness Index (EI) to integrate individual patterns into an overall measure of the effectiveness of treatments in meeting management objectives. The index is the sum of the proportional *decline* in *Arrhenatherum* (Ar), the proportional *decline* in other non-native vascular plants (NN), and the proportional *increase* in native vascular plants (Nat). For example, for the first year of response,

$$EI = \frac{Ar_{94} - Ar_{95}}{Ar_{94}} + \frac{NN_{94} - NN_{95}}{NN_{94}} + \frac{Nat_{95} - Nat_{94}}{Nat_{94}} \quad (2)$$

Statistical analysis was performed with S-Plus 2000 (MathSoft, Inc.).

Results

Pre-manipulation community composition and phenology

Arrhenatherum had 14 - 33 % cover in 1994, ca. 30 - 50 % of the overall cover of vascular plants (41 - 60 %). Cover of the two native grasses was lower, with *Festuca* at 5 - 20 % and *Danthonia* at 8 - 20 %. The other non-native grasses were also abundant (11 -26 %). Most of these grasses were annuals, including *Bromus rigidus* and *Elymus caput-medusae*. Both native and non-native forbs had low cover in 1994 (0 - 6 %).

The dominant grasses followed similar patterns of development (Table 2). *Arrhenatherum*, *Danthonia* and *Festuca* usually flowered by early June and dispersed mature seeds in July. At all measurement times, *Arrhenatherum* leaves and inflorescences were considerably taller than the native grasses (Table 2).

Effects of manipulations on vegetation cover

Treatment effects varied over the course of the study. For example, few strong patterns emerged in 1995, after only one year of manipulation (Fig. 1), but by 1996 cover of *Arrhenatherum* had declined significantly in some treatments. Other treatments, especially Treatment 5 (early summer mowing with removal of cut material) *increased* cover of the other non-native grasses by year 2. In general, meaningful patterns tended to emerge after two or more years of treatment. For example, *Danthonia* (Fig. 1) and *Festuca* did not increase in cover until after three or four years of treatment. These changes over time suggest that conclusions based on one or two years can be misleading, Patterns became apparent by 1998, however, suggesting that they reflect longer-term trends. Therefore, we focus on the 1998 results and do not present the statistical analysis of these early results.

After four years of manipulation, treatments significantly affected cover of *Arrhenatherum* ($F_{7,21} = 5.54$, $P < 0.01$), *Danthonia* ($F_{7,21} = 2.61$, $P=0.04$), and *Festuca* ($F_{7,21} = 3.01$, $P = 0.02$). All treatments resulted in less *Arrhenatherum* cover than in unmanipulated plots, with Treatments 2 (late spring mowing), 3 (early summer mowing) and 7 (double mowing in late spring and the following early spring) causing significant reductions, in comparison with no manipulation (Fig. 2).

In contrast, cover of the native grass *Danthonia* was 3 - 5 × higher under all mowing treatments (Fig. 2), significantly so in Treatments 2 (late spring mowing), 3 (early summer mowing), and 7 (double mowing in late spring

Table 2. Phenological stage and maximum heights of dominant grasses in unmanipulated control plots at the times when mowing treatments were applied to treatment plots. Stages recorded were preanthesis (Pre), anthesis, postanthesis but predispersal (Pos), dispersing, and vegetative (Veg). Leaf = height of the tallest leaves; Infl = height of inflorescences; – = no inflorescence present.

| Date	Corresponding Treatments	Phenological stages and maximum heights (cm, ± sd) at time of manipulation								
		Arrhenatherum elatius			*Danthonia californica*			*Festuca roemeri*		
		Stage	Leaf	Infl	Stage	Leaf	Infl	Stage	Leaf	Infl
Early spring (April 18 - April 21)	1, 7	Veg	26.3 ±5.3	–	Veg	11.3 ±1.5	–	Veg	21.2 ±5.4	–
Late spring (May 27 - June 9)	2, 7	Pre	60.9 ±11.0	82.1 ±15.4	Pre	25.0 ±5.0	40.0 ± 5.0	Veg-Pre	16.5 ± 4.0	56.8 ±11.4
Early summer (June 19 - June 26)	3, 5, 6	Pos	66.7 ±12.5	101.6 ± 21.3	Dis	18.3 ±2.9	68.3 ± 2.9	Pre-Pos	16.7 ± 4.5	49.6 ±28.3
Early fall (September 15 - October 6)	4	Veg	63.1 ±16.1	–	Veg	11.0 ±1.7	–	Veg	15.0 ±3.5	–
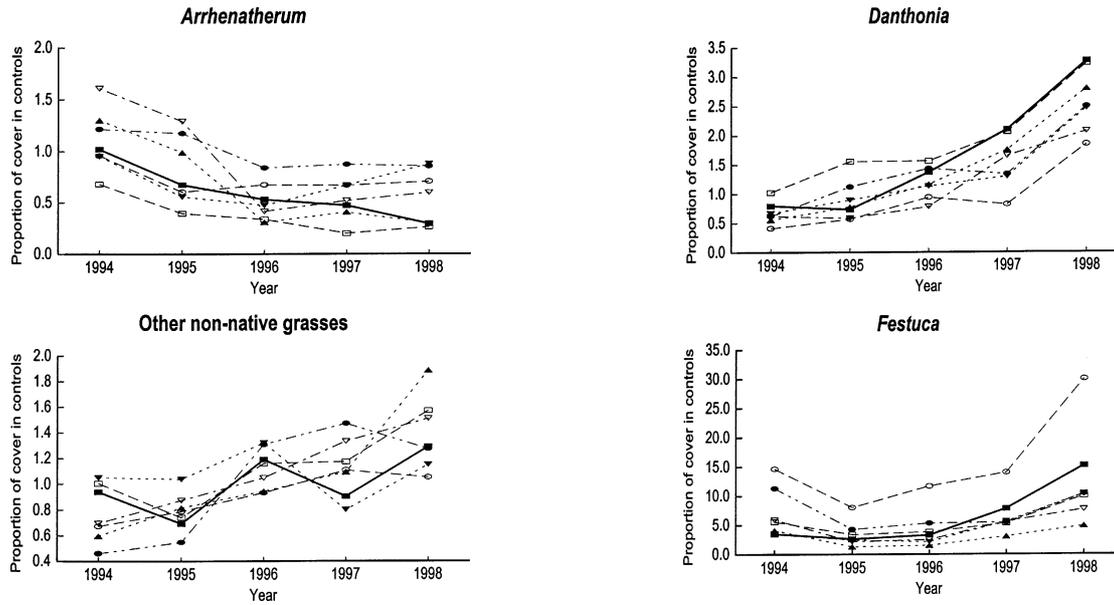
Fig. 1. Abundance of key taxa from before manipulation (1994) through four years of manipulation (1995-1998). Values shown are cover (%) as a proportion of cover in unmanipulated control plots to remove year-year variation. Key to mowing treatments: 1 (early spring), $--\triangledown--$; 2 (late spring), $—\blacksquare—$; 3 (early summer), $--\square--$; 4 (early fall), $--\blacktriangledown--$; 5 (early summer, with removal of cut material), $---\bullet---$; 6 (early summer, cut at 50 cm), $--\bigcirc--$; 7 (double mowing), $--\blacktriangle--$.

and the following early spring). Although treatments as a group significantly affected *Festuca* cover, no single mowing treatment differed significantly from the unmown control, which had intermediate levels of *Festuca* cover (Fig. 2). The cover of the Other non-native grass, Native forb, and Non-native forb groups were not significantly affected by treatments ($P > 0.10$). Nor did treatments significantly affect total cover or litter depth ($P > 0.25$).

As measured by AIC_c, models that included terms for 1998 cover of *Arrhenatherum* but not the treatment provided a better fit to the 1998 cover of *Danthonia* in the different treatment plots (AIC_c = 202.5 and 207.3) than did models with the treatment variable itself (Table 3). Plots with the greatest reduction in *Arrhenatherum* cover tended to have the largest increase in *Danthonia* cover ($r = -0.47$, Fig. 3), regardless of treatment. In contrast, the model of *Festuca* cover that included the treatment variable (without interaction) provided a slightly better fit (AIC_c = 153.7) than did models with a variable for the 1998 cover of *Arrhenatherum* (Table 3).

Effects of experimental manipulations on reproduction

We recorded two aspects of reproduction: flowering (measured as the production of inflorescences) and seedling density. The number of *Arrhenatherum* inflorescences in 1998 varied widely (Fig. 4) and significantly ($F_{7,21} = 7.62$, $P < 0.01$) among treatments. Treatments 2

Table 3. Relative discrepancies of models for native grass cover and flowering in 1998. Post-treatment cover of *Arrhenatherum* more closely explains the cover of the native grass *Danthonia* than does the Treatment variable, and post-treatment cover of *Danthonia* explains *Danthonia* flowering better than the Treatment variable. AIC_c is the corrected Akaike Information Coefficient. AIC_c rewards model accuracy while penalizing model complexity; models with lower AIC_c fit the data better. For each response variable, the best-fitting model is show in bold. B = block; C = cover of *Danthonia* (C_D) or *Festuca* (C_F) before treatments; T = treatments; A = cover of *Arrhenatherum* in 1998; P_D = post-treatment cover of *Danthonia*. Response variables were square-root transformed.

| Model structure	Model df	AIC_c
	Response variable:	
	Danthonia californica cover	
B, C_D	4	235.1
B, C_D, T	11	227.0
B, C_D, T, B×T	32	281.4
B, C_D, A	**5**	**202.5**
B, C_D, A, B×A	8	207.3
	Response variable:	
	Festuca roemeri cover	
B, C_F	4	161.6
B, C_F, T	**11**	**153.7**
B, C_F, T, B×T	32	225.8
B, C_F, A	5	162.6
B, C_F, A, B×A	8	169.5
	Response variable:	
	Danthonia californica inflorescences	
B, C_D	4	321.3
B, C_D, T	11	291.7
B, C_D, T, B×T	32	365.4
B, C_D, P_D	5	283.6
B, C_D, P_D, B×P_D	**8**	**270.7**
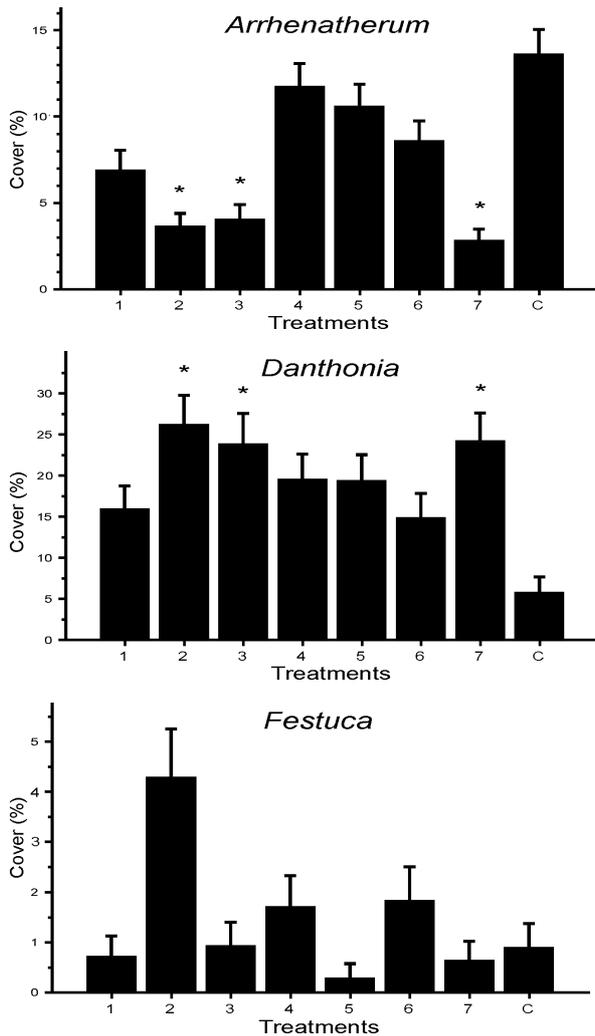
Fig. 2. Cover (± SE) of taxa significantly affected by four years of mowing treatments. Values are backtransformed adjusted means from analysis of variance. * = treatment mean differed significantly from the unmanipulated control (C) (Dunnett's test, α = 0.05). See text for explanation of treatments 1 - 7.

Fig. 3. Change in *Danthonia* cover from 1994 to 1998 vs. change in *Arrhenatherum* cover from 1994 to 1998. Cover data were square-root transformed before calculating changes. Data from all treatment plots were combined for display. The line is a principal components regression fit.

1995, for example, 41 % of seedlings were in the Other non-native grass group and 57% were in the Non-native forb group. Seedling density and treatment were unrelated, except for *Arrhenatherum* in 1997, when unmanipulated plots had significantly more *Arrhenatherum* seedlings ($\bar{X}$ = 4.25 seedlings/300 cm^2, T_2 = 2.74, P = 0.04, Friedman test). Seedlings of *Festuca roemeri* and native forbs were very rare, with only 0.03 and 0.24 seedlings/300 cm^2 per year over the course of the study. Seedling density tended to be unrelated or negatively related to total vascular plant cover, moss cover, and litter depth (Table 4).

EI, the index of overall effectiveness of treatments in

(late spring mowing), 3 (early summer mowing), and 7 (double mowing) significantly reduced the number of *Arrhenatherum* inflorescences, compared with unmown controls (Fig. 4).

All treatments except Treatments 1 (mowing at 10 - 15 cm in early spring) and 6 (mowing at 50 cm in early summer) caused a significant and up to a 10 times increase in number of inflorescences of *Danthonia* in 1998 compared with unmanipulated plots (Fig. 4).

Few *Festuca* flowered in year 4 or in any other year of the study, with flowering intensity closely tied to pre-treatment *Festuca* cover.

Nearly all recorded seedlings were non-native grasses and forbs, most of which were annuals or biennials. In
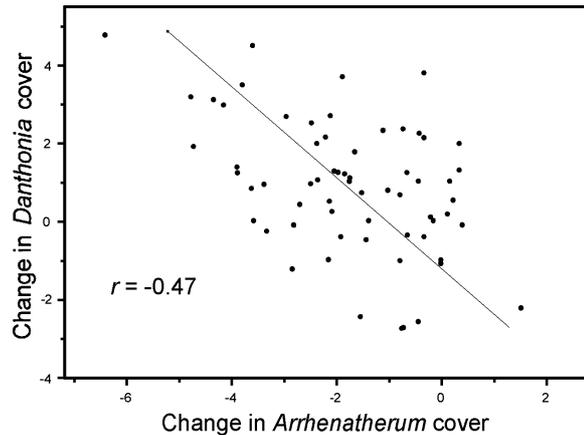
Table 4. Relationships between the number of seedlings recorded in various plant groups and total vascular plant cover, litter depth, and moss cover. Only those cases are shown that had adequate number of seedlings (≥ 0.5 per plot). Values are Spearman's rank correlation coefficients, r_s. * = $P < 0.05$, one-sided test of the negative effect of cover or litter on seedling numbers.

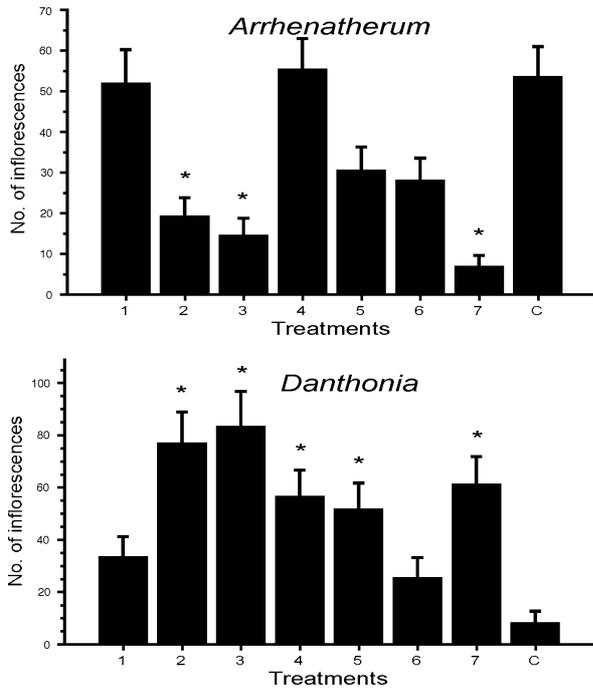|	Total cover	Moss cover	Litter depth
Arrhenatherum elatius seedlings			
1997	– 0.10	–0.05	0.06
1998	–0.46*	0.35	0.02
Other non-native grass seedlings (1995)	0.08	-0.25	0.17
Danthonia californica seedlings			
1997	0.08	0.02	–0.37*
1998	–0.05	0.11	0.12
Non-native forb seedlings			
1997	–0.02	–0.13	0.04
1998	0.27	–0.06	–0.33*

Fig. 4. Number of inflorescences per 0.5 m² plot (± SE) in 1998 for taxa significantly affected by mowing treatments. Values are backtransformed adjusted means from analysis of variance. * = treatment mean differed significantly from the unmanipulated control (C) (Dunnett's test, $\alpha = 0.05$). See text for explanation of treatments (1-7).

Fig. 5. Effectiveness Index (EI) for each year of experimental manipulation. To simplify comparisons, values for 1994 are set to 0.0. Positive values indicate success in attaining management objectives; negative values indicate decreases in vegetation quality. Key to mowing treatments: 1 (early spring), – – ▽ – – ; 2 (late spring), —■— ; 3 (early summer), – – □ – – ; 4 (early fall) , - - ▼ - - ; 5 (early summer, with removal of cut material), - - - ● - - - ; 6 (early summer, cut at 50 cm), – – ○ – – ; 7 (double mowing), - - ▲ - -; unmanipulated control — △ — . *: treatment means differ significantly from unmanipulated control (C) by the end of the study (Dunnett's test, $\alpha = 0.05$, rank transformation).

meeting management objectives, varied from year to year (Fig. 5). Treatment 5 (mowing in early summer with removal of cut material) was the least effective, especially in 1996 and 1997, largely because of high cover of the other non-native grasses. By the end of the study (1998), treatments had a significant effect on EI ($F_{7,21} = 2.51$, $P = 0.05$), with values of EI significantly higher in Treatments 2, 3, and 4 compared with unmanipulated controls (Fig. 5; Dunnet's test, $\alpha = 0.05$).

Discussion

Response of Arrhenatherum elatius to the timing, frequency, and height of mowing treatments

As predicted (hypothesis 1), annual mowing was most effective at reducing *Arrhenatherum* vigor (cover and flowering) when applied near the time of *Arrhenatherum* flowering, in late spring to early summer. The success of Treatment 2 (mowing in late spring) is particularly striking because responses were measured almost a full year after this treatment was applied. The
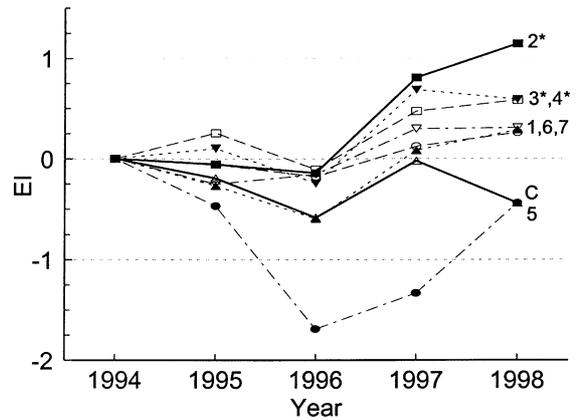
consistent reduction in *Arrhenatherum* cover by Treatment 2 and the other mowing treatments was probably caused by direct depletion of resources through removal of above-ground tissues (Hewett 1985). Our phenological data (Table 2) and observations of the closely related *Arrhenatherum elatius* var. *bulbosum* (Tanphiphat & Appleby 1990) suggest that shoot and corm development peaks in late May in the Willamette Valley. After this period of rapid growth and flowering, translocation of resources to roots becomes more rapid. These patterns suggest that late spring mowing was effective because mowing at this time removed a higher proportion of *Arrhenatherum* resources. Berendse (1992) suggest that nitrogen is the key resource lost by *Arrhenatherum* with clipping or mowing.

Treatment 7 (double mowing in late spring followed by early spring the next year) caused slightly greater reductions in *Arrhenatherum* than did Treatment 2 (a single mowing in late spring). Treatment 1 plots (mowing in early spring) were almost uniformly intermediate in abundance of *Arrhenatherum* between double mowing plots and the unmanipulated plots. These patterns suggest that, as expected (hypothesis 2), two mowings per year was more effective at *Arrhenatherum* control than annual mowing, but that most of the effect of double mowing on cover derives from the single, late

spring mowing. Double-mowing was very effective in reducing *Arrhenatherum* flowering. These patterns match the greater effectiveness of multiple mowings per year reported for the control of other pest plants (Hewitt 1985; Bobbink & Willems 1993; Pakeman & Marrs 1994; O'Keefe 1995).

The effect of mowing height (hypothesis 3) can be examined by comparing Treatment 3 (mowing in early summer at 10-15 cm) with Treatment 6 (mowing in early summer at 50 cm). At the time of mowing, the tallest leaves of *Arrhenatherum* were about 70 cm and the tallest inflorescences about 100 cm (Table 2). Mowing at 50 cm removed nearly all *Arrhenatherum* inflorescences but a relatively small amount of vegetative biomass compared with the shorter mowing. The much deeper reduction in *Arrhenatherum* cover with Treatment 3 compared with Treatment 6 supports our hypothesis that targeting vegetative tissues is more important than mowing only reproductive structures. Unexpectedly, mowing at a lower height (10-15 cm) resulted in about half of the number of *Arrhenatherum* inflorescences in plots mowed at 50 cm at the same date. This pattern suggests that mowing treatments reduced *Arrhenatherum* flowering both directly, through the removal of flowering tillers, and indirectly, through a reduction in vegetative vigor.

Density of seedlings

There were significant treatment effects on flowering of the non-native *Arrhenatherum* and the native *Danthonia*, and hence on their seed production. Yet treatments had little effect on the number of their seedlings nor on the number of native seedlings. We had hypothesized that decreased competition and reduced amounts of litter would lead to more seedling establishment, especially by natives (hypothesis 4). But treatments caused little variation in total vegetative cover and litter depth, because sharp declines in *Arrhenatherum* cover with mowing were offset by sharp increases in *Danthonia* cover. Moreover, in only three of the 14 pairwise comparisons where measured seedlings were abundant enough to test was there a significantly negative relationship between seedlings numbers and total cover or litter depth (Table 4).

The cover values of the other non-native grasses provide indirect evidence of patterns of seedling establishment, because > 95% of the cover of this group was contributed by annuals. By 1996, after two years of treatment, most treatments had increased cover of other non-native grasses. By 1998, the cover of other non-native grasses had almost tripled in the double-mowing treatment (Treatment 7), compared with the controls. These results suggest that mowing to control *Arrhena-*

therum can cause an increase in seedlings, but for reasons other than reduced competition or less litter (hypothesis 4). In this case, however, the seedlings promoted were undesirable, non-native annual grasses, a pattern reported in similar prairie systems (Maret & Wilson 2000).

Response of native grass cover and flowering

Danthonia cover and number of inflorescences were higher in all mowing treatments compared with unmanipulated controls. The direct effects of mowing should either be adverse (because of the removal of tissues) or nil (because most or all of the tissues of these native plants were below mowing height). Thus, any beneficial effects of mowing on *Danthonia* cover are likely to be indirect, through reduced competition pressure from the dominant *Arrhenatherum* (Mahmoud & Grime 1976; Grubb 1982; Marshall 1990) or through other alterations of growing conditions. In fact, variation in *Arrhenatherum* cover – in large part caused by mowing treatments – provided a better fit to the final cover of *Danthonia* than did the treatment variable itself (Table 3). These results support our prediction (hypotheses 5 and 6) that the benefits of mowing on *Danthonia* largely arose from the release of this native grass from suppression by *Arrhenatherum*.

The patterns were more complicated with *Festuca*. Treatments had significant effects on *Festuca* cover, but some treatments increased cover whereas other treatments decreased cover compared to controls. The treatment variable produced only a slightly better fit to *Festuca* cover than did *Arrhenatherum* cover (Table 3), suggesting that changes in *Festuca* cover arose from both the suppression of *Arrhenatherum* and from other, unknown treatment effects.

Unlike effects on cover, treatment effects on flowering could only be indirect because treatment timing allowed a full season of inflorescence development. Inflorescences of the dominant perennial grasses develop in early spring, but reach a height affected by our mowing treatments only after the early spring treatment (Treatment 1) (Table 2). The next treatment (2, mowing in late spring) occurred after we recorded inflorescences. Thus, any treatment effects on inflorescences must be mediated through changes in plant vigor or site conditions, such as nutrient availability, herbivores (Reader 1991; Hulme 1994; Maron 1997), soil microbial activity (Knapp & Seastedt 1986; Garcia & Rice 1994; Zink & Allen 1998), and a reduction in *Arrhenatherum* cover. Increased plant vigor explains much of the increase in *Danthonia* flowering, better than the direct treatment effect (Table 3). Since the increase in *Danthonia* cover seems to arise from its release from suppression, it is likely that *Danthonia* flowering also benefits from the control of *Arrhenatherum*.

These results for *Danthonia* provide one of the few documented cases of pest plant control causing an increase in native plant abundance and flowering (see also Rice et al. 1997).

Implications for management

Because management goals for most natural areas or restoration projects are multifaceted, the overall evaluation of treatments requires an integrative measure, like our Effectiveness Index (EI). Treatments differed considerably in their overall ability to meet management objectives of *Arrhenatherum* reduction, reduction of other non-native species, and increase of native species. Strong treatment effects on EI became clear only after three years of treatment (Fig. 5). An earlier effect was the poor performance of early summer mowing with removal of cut material. The poor performance of this treatment was due primarily to the relatively high inhibition of *Festuca* and dramatic increases in mostly annual non-native plant cover.

From 1994 (before treatments) to 1998, the vegetation in the unmanipulated control plots dropped markedly in quality (EI = − 0.44; Fig. 5). In contrast, late spring mowing produced marked increases in vegetation quality (EI = 1.14). Four years of this treatment converted a strongly degraded *Arrhenatherum*-dominated site to a prairie dominated by the native grass *Danthonia*. Early summer mowing and early fall mowing were also effective at meeting management objectives.

Taking into consideration overall mowing effects on the cover, flowering, and seedling densities of the community, we recommend late spring mowing with removal of cut material for restoring degraded, *Arrhenatherum elatius*-dominated prairies. Treatments must be continued for more than two or three years, a requirement typical in systems dominated by herbaceous perennials (Grubb 1982; Lowday & Marrs 1992; Meyer & Schmid 1999). Many ecosystems requiring restoration are depauperate in key native components. In our study system, native forbs were nearly absent (usually < 1% cover), even after effective control of *Arrhenatherum*. In such cases, successful restoration and management should combine effective pest plant control with sowing of underrepresented native plants (Stampfli & Zeiter 1999).

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