

Geese and grazing lawns: responses of the grass *Festuca rubra* to defoliation in a subarctic coastal marsh

P. C. O, P. M. Kotanen, and K. F. Abraham

Abstract: In coastal marshes on James Bay and southern Hudson Bay, Canada, the grass *Festuca rubra* L. is heavily used for forage by both Snow (*Chen caerulescens caerulescens* (Linnaeus)) and Canada Geese (*Branta canadensis* (Linnaeus)). On Akimiski Island, James Bay, this grass occurs in a mosaic of short, heavily grazed patches and tall, lightly grazed patches. We investigated whether short plants are primarily a plastic morphological response to grazing by geese. Over two growing seasons, we measured growth of short patches protected from grazing and of tall patches subjected to mowing treatments, with unmanipulated short and tall controls. Protection resulted in rapid conversion from a short growth form to a tall form, similar in height and biomass to plants in tall control plots. Mowed tall plants also rapidly recovered to near tall control values for height and biomass. A single 3 week treatment episode often permitted nearly full recovery to tall form. In some cases, more sustained protection was required, but repeated mowing ultimately may have reduced growth rates. These results indicate that the morphology of individual plants of *Festuca rubra* plastically recovers from changes in defoliation pressure. Consequently, short patches likely represent grazing lawns maintained by intensive foraging by geese.

Key words: Akimiski Island, *Festuca rubra*, grazing, Lesser Snow Goose, Canada Goose, herbivory.

Résumé : Dans les marais côtiers de la baie James et du sud de la baie d'Hudson, au Canada, la graminée *Festuca rubra* L. est largement utilisée comme fourrage, par l'oie des neiges (*Chen caerulescens caerulescens* (Linnaeus)) et l'oie du Canada (*Branta canadensis* (Linnaeus)). À l'île Akimiski, sur la baie James, cette graminée vient sous forme de mosaïques constituées de surfaces fortement pâturées à herbe basse et légèrement pâturées à herbe haute. Les auteurs ont d'abord vérifié si les plantes courtes résultent principalement d'une réaction morphologique plastique au pâturage par les oies. Au cours de deux saisons de croissance, ils ont mesuré la croissance sur des surfaces à herbes courtes protégées contre le pâturage, et à herbes élevées soumises à des traitements de tonte, ainsi que sur des parcelles témoins à herbes courtes et élevées. La protection a induit une conversion rapide de la forme courte à la forme élevée, avec des hauteurs et des biomasses semblables à celle des parcelles témoins. Les grandes plantes soumises à la tonte ont également repoussé rapidement pour atteindre presque les valeurs des plantes témoins élevées. Un seul épisode de trois semaines de traitement a fréquemment permis un retour complet à la forme élevée. Dans certains cas, une protection plus soutenue a été nécessaire, mais une tonte répétée aurait peut-être réduit les taux de croissance. Ces résultats indiquent que la morphologie des plantes individuelles du *Festuca rubra* reprennent plastiquement, suite à des changements de pression de défoliation. Conséquemment, les parcelles à herbe courte représentent vraisemblablement des pelouses de paissance, maintenues suite au pâturage intense par les oies.

Mots clés : île Akimiski, *Festuca rubra*, pâturage, petite oie des neiges, oie du Canada, herbivorie.

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Introduction

Intense grazing by vertebrates can convert grassland vegetation to "grazing lawns" characterized by short stature, reduced flowering, increased tillering, and increased growth rate, nutrient content, and palatability (Jameson 1963; McNaughton 1984; Coughenour 1985). The result can be vegetation that is both better able to tolerate intense defoliation and better able to nutritionally support the herbivores that created it. Ungulates in East African savannas (McNaughton 1979a, 1979b, 1984), Black-tailed Prairie Dogs in North American grasslands (Painter et al. 1993), and Black Brant in Alaska (Person et al. 2003) are examples of wild herbivores that create grazing lawns in natural environments.

The conversion of tall vegetation to a grazing lawn can result both from phenotypic plasticity (Coughenour 1985) and from selection for smaller, more clonal genotypes (Jaramillo and Detling 1988; Painter et al. 1993). Although these two mechanisms may produce superficially similar results, they have different implications. Plastic change is likely to be much more rapid, requiring only growth responses by grazed individuals rather than generations of natural selection. As such, plastic changes represent a flexible response to variable damage. In contrast, grazing-adapted genotypes may represent a stable solution to long-term grazing pressure, but are unlikely to be as flexible in response to changing conditions.

The perennial grass *Festuca rubra* L. (hereafter: *Festuca*) is an important source of forage for Lesser Snow Geese and Canada Geese in supratidal areas throughout much of the southern Hudson – James Bay system. Research at other locations has shown that moderate levels of grazing by Snow Geese can maintain highly productive grazing lawns of intertidal species, primarily the grass *Puccinellia phryganodes* (Trin.) Scribn. & Merr. (Cargill and Jefferies 1984; Bazely and Jefferies 1989b; Hik and Jefferies 1990). Whether geese that heavily use *Festuca* maintain similar lawns has not been demonstrated experimentally, though at our study site, Akimiski Island, large expanses of short (1–4 cm), heavily grazed *Festuca* do exist. These are typically interspersed with patches of much taller (8–10 cm), lightly grazed *Festuca*, forming a vegetational mosaic (Fig. 1). The goals of our research were to determine (i) whether the short form of *Festuca* is maintained by grazing and (ii) whether this short form represents a plastic response. To accomplish this, we used exclosures to remove grazing pressure from short patches, to see whether we could convert them to tall-form plants; we also experimentally mowed tall patches, to see whether we could convert them to short-form plants. Our results indicate that geese play a key role in producing the distinctive mosaic vegetation of this coastal system.

Materials and methods

Study site

Akimiski Island, Nunavut Territory, Canada (53°N, 81°W, 3800 km²), is the largest island in James Bay. As many as 2000 pairs of Lesser Snow Geese (*Chen caerulescens caerulescens* (Linnaeus)) nested along a 35 km stretch of the north shore of this island in the 1990s (Abraham et al. 1999), while about 10 000 pairs of Interior Canada Geese (*Branta canadensis* (Linnaeus) interior Todd) nest throughout it (Leafloor et al. 1996), including the areas used by Snow Geese. During spring and fall, these breeding birds briefly are supplemented by thousands of migrating Lesser Snow, Giant Canada (*Branta canadensis* (Linnaeus) maxima Delacour), Cackling (*Branta hutchinsii* Richardson), and Brant (*Branta bernicla* (Linnaeus) hrota Müller) geese. Snow Geese are responsible for the majority of summer grazing close to their colony, with a significant contribution by nesting and brood-rearing Canada Geese.

Intertidal vegetation on Akimiski is dominated by the highly palatable forage grass, *Puccinellia phryganodes* (Trin.) Scribn. & Merr. However, intense grazing pressure in the area of the Snow Goose colony has depleted this re-

source, largely replacing it with unvegetated mudflats (O et al. 2005; Jefferies et al. 2006). In contrast, *Festuca* still forms extensive, nearly pure pastures in areas used by nesting and brood-rearing Snow Geese, where the tall and short forms of this grass co-occur with exposed mudflats (Fig. 1). The short form does not simply constitute tall plants truncated by grazing, but is a dwarf form strikingly distinct in a suite of vegetative and reproductive characteristics including smaller leaf size, increased prostrateness, reduced leaf toughness, etc. Patches of short *Festuca* are intensely grazed, but leaves of taller plants are clipped infrequently, probably because of a combination of greater toughness, handling difficulties, and (or) lower nutritional quality.

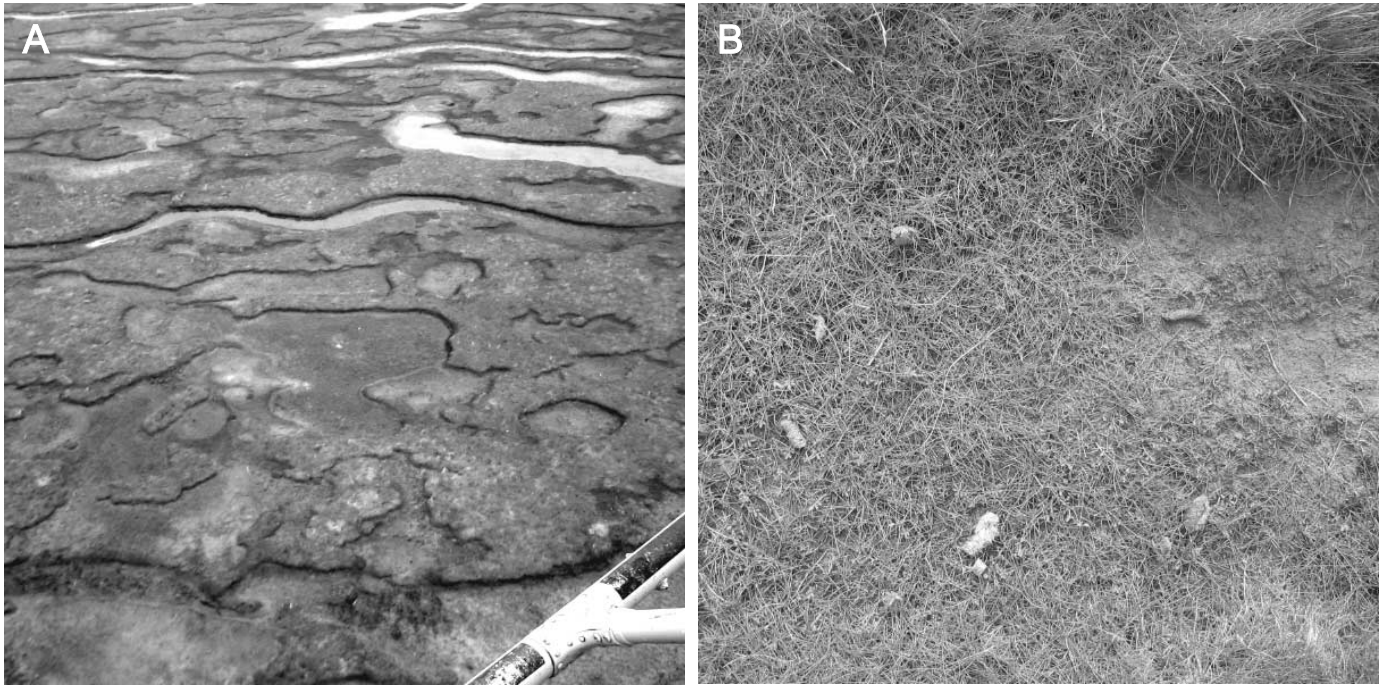
Experimental design

This study was conducted in nearly monospecific supratidal *Festuca* marshes on the east and west sides of a small river (locally called the Thompson River: 53°11'38"N, 81°26'38"W), within the relatively high-density nesting area of the Snow Goose colony. Two linked experiments were established in May 2001 and maintained until June–July 2002. The first experiment was designed to examine the effects of sustained (“press”) changes in the intensity of defoliation. Twenty 1 m × 2 m plots were established in patches of short *Festuca*, 10 of which were protected from further goose grazing with chickenwire exclosures. Similarly, twenty 1 m × 2 m plots were established in tall patches. Ten of these tall plots were mowed on each sampling date, using a weed whacker, to simulate grazing by geese; these plots were then exclosed to prevent further defoliation by geese. The remaining 10 plots were not mowed; these were not exclosed, since geese naturally avoid tall vegetation. The second experiment was similar, except that new 1 m × 1 m plots (10 per treatment) were established and treated as required at each sampling. This was done so that short-term responses of plants to transient (“pulse”) changes in grazing pressure could be monitored throughout the summer. This helped to determine whether progressive changes in the press experiment represent gradual responses to repeated experimental treatment or seasonal variation in growth. Altogether, both experiments comprised four treatments: two natural “controls” (grazed short and ungrazed tall) and two “manipulations” (exclosed short and mowed tall); all treatments could be interspersed because of the mosaic nature of this habitat.

For both experiments, plots were sampled on five dates. For the press experiment, the same plots were sampled repeatedly; for the pulse experiment, each plot was sampled twice (“initial” and “final” samplings) and abandoned once it had been sampled for the second time. Most samplings were separated by approximately 3 weeks; however, in each experiment one sampling episode stretched over the winter. At each sampling, heights (mm) of five randomly chosen nonflowering green shoots were measured in each plot. A randomly chosen 10 cm × 10 cm turf was then cut from each plot and transferred to the lab, where all aboveground vegetation was clipped, washed, and sorted. Green *Festuca* was separated from any other species, dried at 50–70 °C, and weighed (mg).

Plant height, standing crop, and net aboveground primary production (NAPP) were analyzed with one-way ANOVAs;

Fig. 1. (a) Coastal grazing flats. Islands of *Festuca rubra* L. are separated by ponds and mudflats. Image near centre is roughly 15 m across; most vegetated islands are on the order of 1–5 m wide. (b) Close-up of a *Festuca* grazing lawn. Taller ungrazed plants are visible in the background. Image is approximately 50 cm across.



significant tests were followed by post hoc Tukey–Kramer analyses. The five plant heights measured for each plot were averaged before analysis. NAPP was calculated as $(\text{standing crop at } t_2 - \text{standing crop at } t_1) / (t_2 - t_1)$.

NAPP could not be measured in plots exposed to grazing by geese, since the continual removal of tissue by these birds would lead to serious underestimates of biomass production.

Results

Plant height

In 2001, the initial sampling of the press experiment indicated that there was a statistically significant difference in height between grass in short patches and that in tall patches (Fig. 2); this simply confirms that the observed differences between these vegetation types are real. At the next sampling of these plots, plants in enclosed short patches had grown significantly taller than the grazed plants in unprotected short patches, and by late July their height equalled plants of unmowed tall plants (Fig. 2). Mowing reduced tall plants to heights almost identical to naturally short plants, but despite repeated clipping, mowed plants rapidly recovered to equal the height of unmowed plants (Fig. 2). In June 2002, the original pattern of tall and short patches no longer existed, although unenclosed short plants still ranked shortest. By July, plants in all other treatments were taller than plants in unenclosed short swards.

In the pulse experiment, each plot generated two values: an initial value and a final value. As expected, each initial set of measurements confirmed statistically that short patches were shorter in stature than unmowed tall patches (Fig. 3). As well, the experiment confirmed that both ex-

closed and unenclosed short plants were initially the same height; mowed tall plots were similar to short plots or intermediate in height, indicating that mowing reduced plant height, though not always to the stature of unprotected short plants (Fig. 3). At each final sampling, however, this pattern had changed. For the 2001 sampling dates, plants in mowed tall plots had recovered to the same height as plants in unmowed tall plots; plants in enclosed short plots were taller than plants in unprotected short plots, except at the final sampling date (Fig. 3). At the single 2002 sampling, plants did not differ in height among treatments (Fig. 3), probably because measurable growth had not yet occurred by this early date.

Standing crop

Results for standing crop resemble results for height, though the trends are weaker. In 2001, treatments of the press experiment did not differ at the initial sampling (Fig. 4). Thereafter, as biomass accumulated, differences developed among treatments. By early July, unprotected short plots had less biomass than any other treatment (Fig. 4), reflecting ongoing grazing pressure by geese. By the next sampling, biomass in the enclosed short plots had begun to pull ahead of the other treatments, while mowing had reduced biomass in treated tall plots to values comparable to or lower than the other treatments. In 2002, enclosed short plots initially contained more biomass than mowed tall treatments, but differences among treatments were small; by July, enclosed short plots contained more biomass than any other treatment.

For the pulse experiment, initial values for biomass did not differ between enclosed and unprotected short patches in 2001, but usually were significantly greater in unmowed

Fig. 2. Plant height (mm) from the press experiment. Data presented are means \pm SEM; $n = 10$ per treatment. Lines connect successive within-season samplings; points for the overwinter (2001–2002) sampling episode are shown but not connected. * indicates that treatments at that sampling differed significantly (ANOVA: ***, $p < 0.001$; **, $p < 0.01$). For significant ANOVAs, letters indicate results of a posteriori analysis: means sharing the same letter do not differ significantly ($p > 0.05$; Tukey–Kramer’s tests). “Clipped” refers to height of “mowed tall” plants immediately following clipping; these values are not included in the ANOVAs.

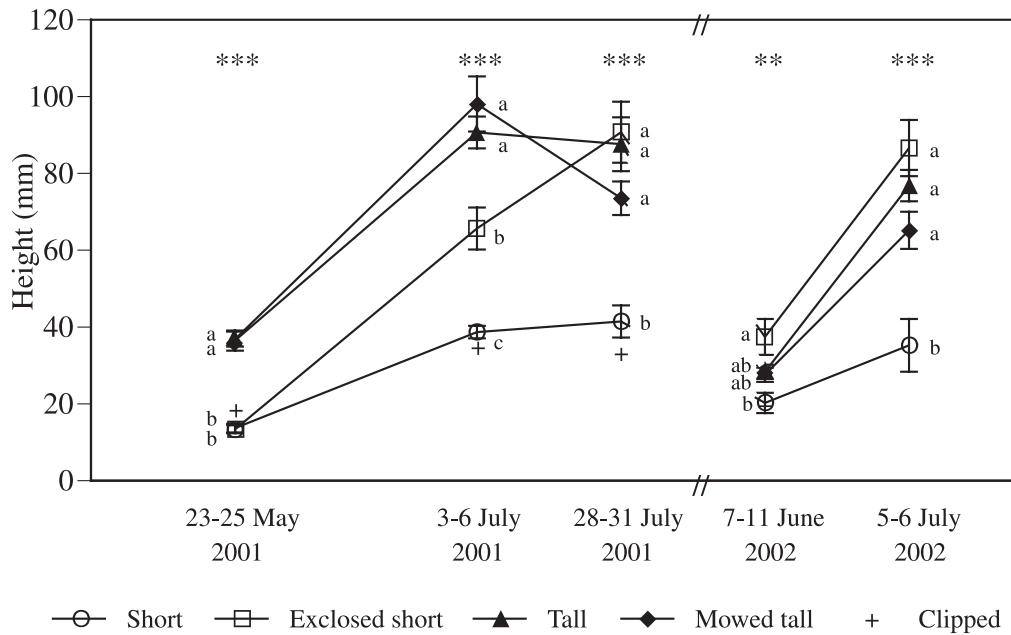
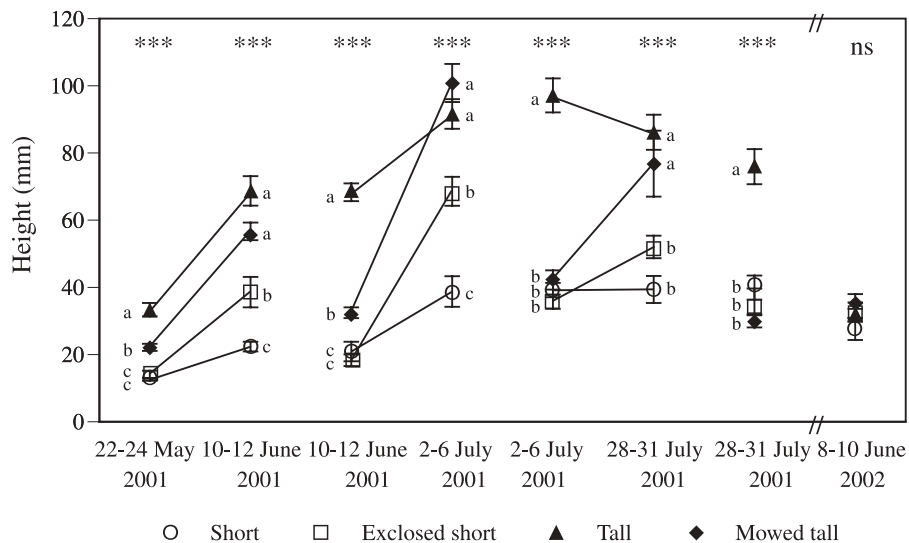


Fig. 3. Plant height (mm) from the pulse experiment. Data presented are means \pm SEM; $n = 10$ per treatment. Lines connect each initial sampling to its corresponding within-season final sampling; points for the overwinter (2001–2002) sampling episode are shown but not connected. * indicates that treatments at that sampling differed significantly (***, $p < 0.001$; ns, $p > 0.05$; ANOVA). For significant ANOVAs, letters indicate results of a posteriori analysis: means sharing the same letter do not differ significantly ($p > 0.05$; Tukey–Kramer’s tests).



tall patches than in short patches (Fig. 5). The exception was the first sampling date, when summer growth had barely begun, and treatments therefore did not differ (Fig. 5). Mowing reduced the biomass of tall patches to resemble that of short patches (Fig. 5). Results differed among the final samplings. At the early June final sampling, ungrazed (exclosed short or unmowed tall) patches contained more biomass than grazed or mowed patches. At the early July final sampling, exclosed and mowed plots had grown faster than the unma-

nipulated treatments, so that no significant differences existed among treatments. At the late July final sampling, treatments had maintained their initial rankings, so that unmowed tall plots had more biomass than mowed tall plots, as in June 2001. In June 2002, treatments did not differ, reflecting low spring biomass.

Net aboveground primary production (NAPP)

It is not possible to measure NAPP in plots exposed to

Fig. 4. Standing crop ($\text{g}\cdot 100\text{ cm}^{-2}$) from the press experiment. Data presented are means \pm SEM; $n = 10$. Lines connect successive within-season samplings; points for the overwinter (2001–2002) sampling episode are shown but not connected. * indicates that treatments at that sampling differed significantly (*, $p < 0.05$; ***, $p < 0.001$; ns, $p > 0.05$: ANOVA). For significant ANOVAs, letters indicate results of a posteriori analysis: means sharing the same letter do not differ significantly ($p > 0.05$: Tukey–Kramer’s tests). “Clipped” refers to height of “mowed tall” plants immediately following clipping; these values were not included in the ANOVAs.

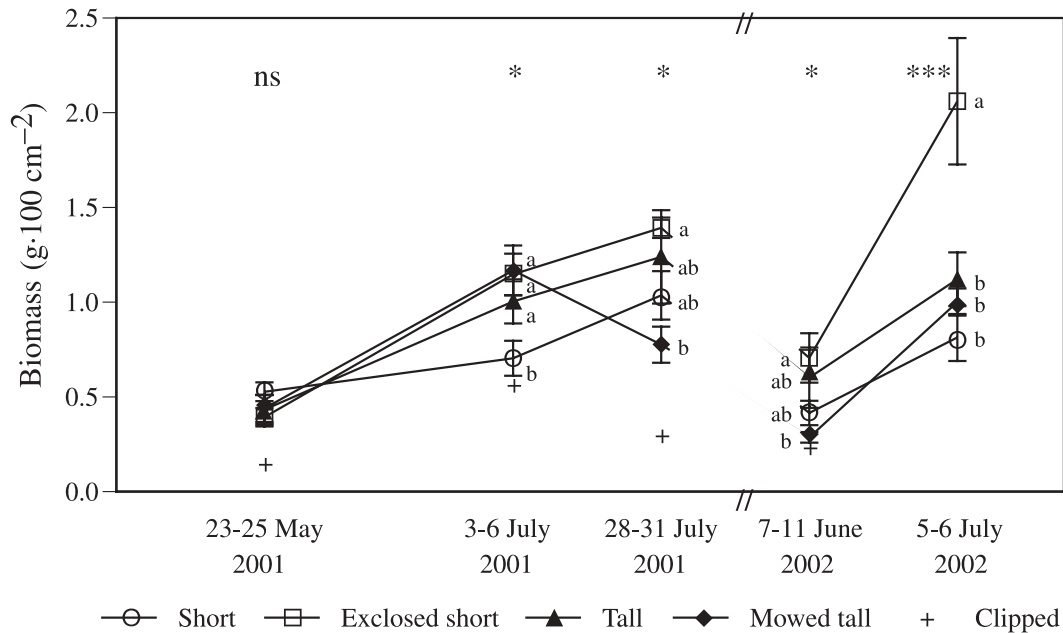
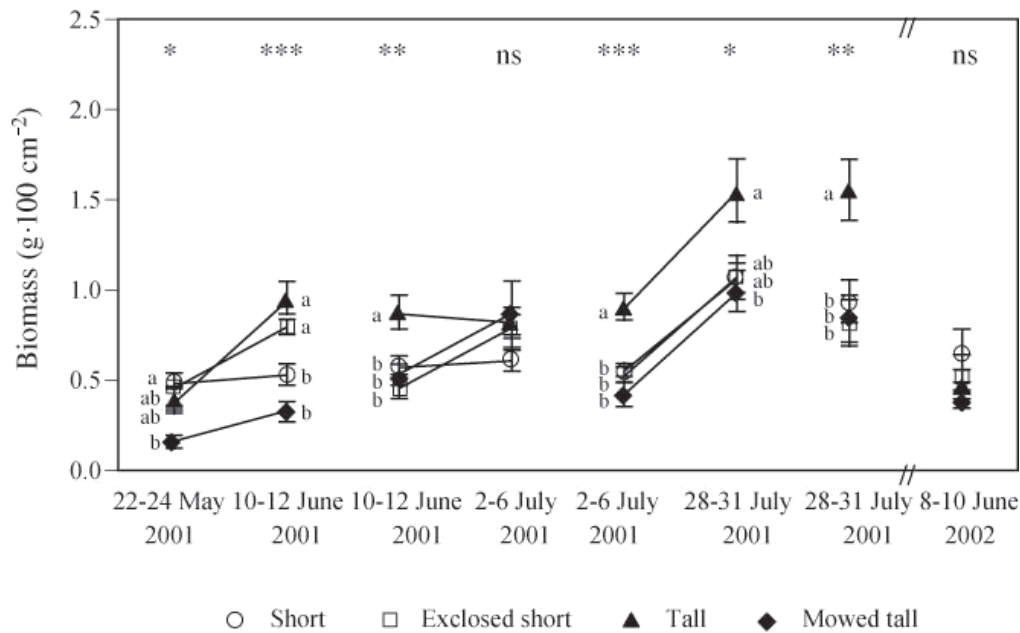


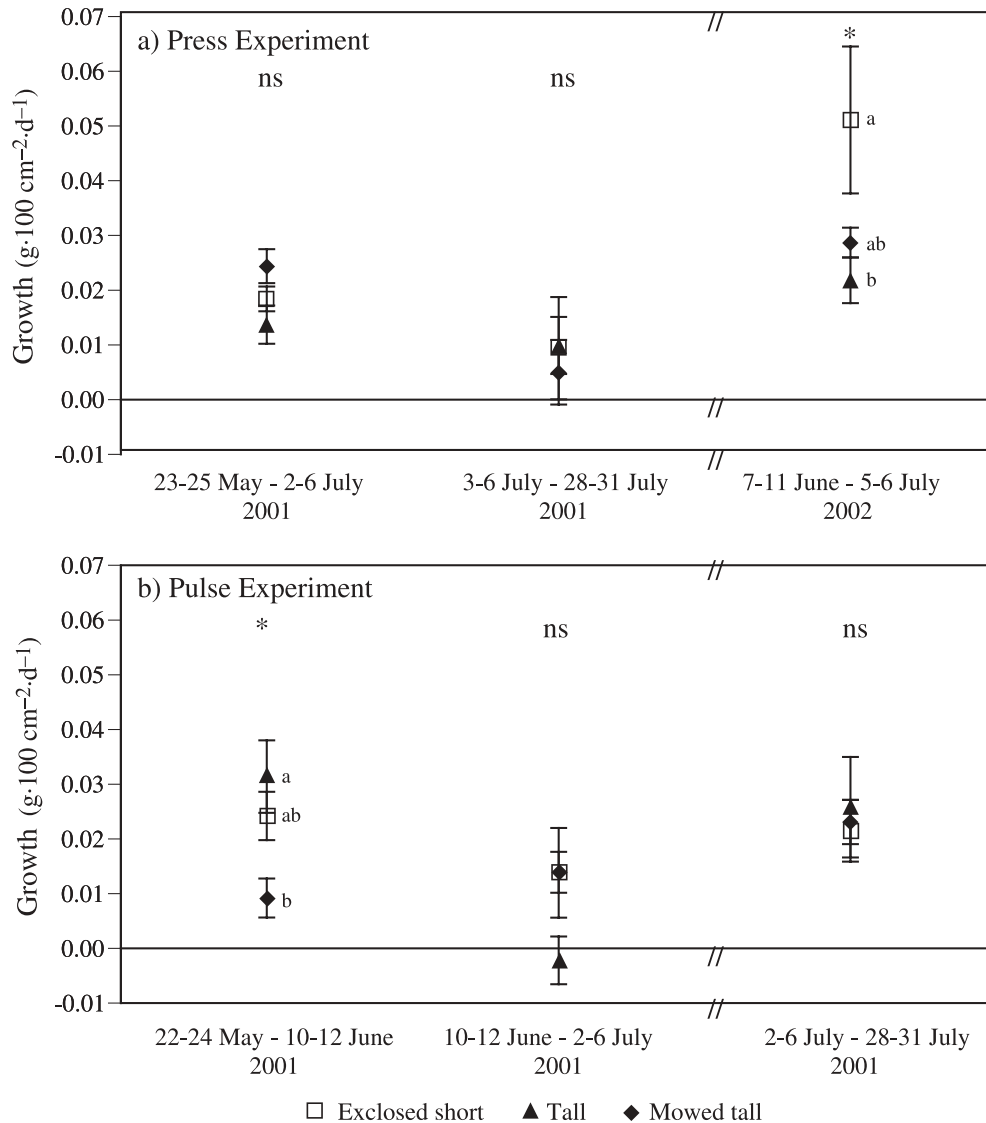
Fig. 5. Standing crop ($\text{g}\cdot 100\text{ cm}^{-2}$) from the pulse experiment. Data presented are means \pm SEM; $n = 10$. Lines connect each initial sampling to its corresponding within-season final sampling; points for the overwinter (2001–2002) sampling episode are shown but not connected. * indicates that treatments at that sampling differed significantly (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, $p > 0.05$: ANOVA). For significant ANOVAs, letters indicate results of a posteriori analysis: means sharing the same letter do not differ significantly ($p > 0.05$: Tukey–Kramer’s tests).



grazing by geese, since the continual removal of tissue by these birds would lead to serious underestimates in biomass production. In the press experiment, growth rates could be calculated for the remaining plots for two intervals in 2001 and one in 2002 (Fig. 6). Growth rates differed among treatments only at the final interval (June–July 2002), when

unmowed tall plants had a lower growth rate than exclosed short plants. In the pulse experiment, growth could be calculated for three dates in 2001. Mowed tall plants grew more slowly than unmowed tall plants during the late May – mid-June interval; differences at other intervals were not significant.

Fig. 6. Plant growth ($\text{g}\cdot 100\text{ cm}^{-2}\cdot\text{d}^{-1}$) in the (a) press and (b) pulse experiments. Data presented are means \pm SEM; $n = 10$. Note the different sampling dates for the two experiments. * indicates that treatments at that sampling differed significantly (*, $p < 0.05$; ns, $p > 0.05$: ANOVA). For significant ANOVAs, letters indicate results of a posteriori analysis: means sharing the same letter do not differ significantly ($p > 0.05$: Tukey–Kramer’s tests).



Discussion

In both of our experiments, initial differences in height between short and tall patches were strong and statistically significant; results for biomass were similar except very early in the year, before substantial annual growth had occurred. These results demonstrate that the two patch types are real and distinguishable by the methods used. Studies of *Festuca*-dominated marshes in Europe (e.g., Bakker et al. 1983; Berg et al. 1997; Van der Wal et al. 1998) also have found that sheep, hare, and goose grazing can create mosaics of short grazed patches interspersed with tall ungrazed patches, similar to those found on Akimiski Island.

We found that protecting short patches allowed rapid recovery in height. Protecting plants for a few weeks (as in the pulse experiment) was sufficient to allow protected plants to grow taller than unprotected short plants, but not as tall as naturally tall plants. However, an entire season of

enclosure (as in the press experiment) did allow growth to the same height as tall plants. Responses by biomass were also strong, with excluded short swards generally achieving values comparable to unmanipulated tall plots within a sampling interval. Growth rates were variable, possibly in response to weather, but growth was not restricted to the spring: some growth occurred throughout the summer.

Tall plants also recovered rapidly from mowing. Even though mowing reduced height and biomass to values close to naturally grazed plots, mowed plants always recovered to the same height as unmanipulated tall plants within a sampling interval. Biomass recovered more slowly. In the pulse experiment, complete recovery occurred only at the second sampling interval. In the press experiment, recovery to control values did occur by early July in both years, but in 2001, biomass in the mowed plots subsequently fell behind the controls, possibly indicating a cost to repeated defoliation. Estimated growth rates usually were similar between

mowed and unmowed tall plots, indicating no compensatory response to mowing, and were significantly lower at one sampling interval in the pulse experiment. Zellmer et al. (1993) also reported that an episode of grazing by snow geese had little effect on subsequent growth by *Festuca*.

These results indicate that the *Festuca* grazing lawns at Akimiski Island largely are a rapidly reversible morphological response of individual plants to grazing by geese. If grazing is removed, short swards rapidly convert to tall; if (normally lightly grazed) tall plants are clipped and then protected from grazing, the effect of clipping is transient. These changes likely represent a combination of simple regrowth of clipped tissue, and changes in morphology and allocation patterns. It is very unlikely that significant genetic changes could have occurred in the short duration of these experiments, implying that the observed changes were almost entirely plastic in origin. Nonetheless, the strong plastic response that we observed does not preclude a genetic component to the difference between tall and short patches of *Festuca*, or argue against selection for shorter genotypes in grazed areas.

Studies of arctic goose-grazing systems have found that other species of grasses and sedges rapidly revert to a tall form when protected from grazing, evidently in a plastic response (e.g., *Puccinellia phryganodes*: Cargill and Jefferies 1984; Bazely and Jefferies 1989b). Some studies also have demonstrated the conversion of tall intertidal swards to lawns by goose grazing. For example, Person et al. (2003) provided evidence that grazing of coastal Alaskan marshes by Black Brant can plastically convert tall swards of *Carex ramenskii* Komarov to a dwarf growth form almost indistinguishable from *Carex subspathacea* Wormsk. ex Hornem. All of these studies considered long-lived clonal plants at goose colonies that are only a few decades in age and (or) have undergone recent increases in size (Cooke et al. 1995; Abraham et al. 1999; Person et al. 2003; Jefferies et al. 2006). In such examples, selection may have had insufficient time for response, while plasticity can be much more rapid.

Even if time for selection is sufficient, plasticity still may be the best strategy when faced with variable grazing pressure. Northern goose populations often experience unpredictable weather-driven variation in migration and nesting behaviour. For instance, bad weather farther north sometimes delays thousands of migrating Canada, Cackling, and Snow Geese, some of which may remain in their staging areas to nest (Abraham et al. 1999). This periodically occurs on Akimiski Island; as an extreme example, 295 000 staging Snow Geese were observed in May 1972 (S.G. Curtis, in Abraham et al. 1999). Such events can lead to large temporary increases in foraging pressure, and may have contributed to the loss of intertidal vegetation, that has occurred at both La Pérouse Bay, Manitoba, and Akimiski Island itself (Jefferies et al. 2006). Plastic growth by *Festuca* may help to buffer it against such short-term variation, potentially improving its ability to persist. Plasticity may even allow plants to escape variable grazing pressure: Person et al. (2003) argued that plasticity may lead to loss of forage, if temporary reductions in grazing pressure allow plants to recover to a tall, unpalatable form.

The development of grazing lawns has important conse-

quences for herbivores as well as plants. Benefits of grazing lawns to herbivores include high nitrogen content, high plant biomass concentration, reduced toughness, high productivity, and low litter accumulation (e.g., Bakker et al. 1983; McNaughton 1984; Bazely and Jefferies 1989a; Berg et al. 1997; Van der Graaf et al. 2005). Consequently, plants in grazing lawns may be more palatable, and hence more intensely grazed; this likely explains the heavier use of short than tall *Festuca* at Akimiski. In return, herbivores can help to maintain the desirable characteristics of grazing lawns, both by frequent defoliation and by the addition of resources such as faecal nitrogen (e.g., Snow Geese and *Puccinellia phryganodes*: Cargill and Jefferies 1984; Bazely and Jefferies 1985; Hik et al. 1991). On the other hand, high palatability can ultimately lead to over-use by herbivores and consequent habitat damage. Excessive grubbing of below-ground tissues by increasing populations of Lesser Snow Geese plus heavy grazing on remnant stands has led to the collapse of intertidal grazing lawns throughout much of the Hudson – James Bay system (Jano et al. 1998; Handa et al. 2002; Jefferies and Rockwell 2002; Jefferies et al. 2003, 2006). Supratidal pastures containing *Festuca* have also been lost as a consequence of foraging by Snow Geese at La Pérouse Bay (Handa et al. 2002). Close to the Snow Goose colony on the north shore of Akimiski, *Festuca* lawns are likewise grubbed and severely grazed, and many have been replaced by mudflats (O et al. 2005; Jefferies et al. 2006). The growth responses of this grass may, to some extent, buffer against these impacts (Kotani and Rosenthal 2000), as may the refuge from grazing provided by tall, unpalatable patches. Nonetheless, these advantages clearly have a limit: excessive foraging pressure still risks converting *Festuca* pastures to bare sediment.

In summary, this research answers our original questions by demonstrating (i) that the short form of *Festuca* is maintained by grazing and (ii) that this short form primarily represents a plastic response. It also suggests that taller patches of *Festuca* persist only because they are usually avoided by grazing geese. Thus, the mosaic vegetation that characterizes this area likely is self-reinforcing: because of a preference for more palatable shorter plants, geese ensure that tall patches stay tall, and short patches stay short.

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