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Growth and Reproductive Responses of *Cassiope tetragona*, a Circumpolar Evergreen Shrub, to Experimentally Delayed Snowmelt

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Abstract

While there has been a general trend of climate warming in the Arctic causing early snowmelt and prolonged growing season, climate change models for some areas in the High Arctic suggest increased snow accumulation, delayed spring melt, and consequently shorter growing season. We tested the vegetative and reproductive responses of *Cassiope tetragona*, an arctic shrub, to increased snow depth and delayed snowmelt using a snow fence experiment in Adventdalen, Norway (78°54′N, 18°01′E). We recorded seasonal shoot length, number of leaves, and capsules per shoot for three summers (2005–2007): two prior and one after the treatment began. Phenological events were recorded in 2007. The number of seeds per capsule was counted and seed germination was tested. Phenological development was significantly delayed behind fences, with lower shoot length, number of leaves, capsules, and seeds per shoot segment (16, 20, 54 and 11%, respectively) compared to controls, but there was no difference in these parameters between plots prior to fence establishment. Seed viability was unaffected by treatment. A delay in start of growing season due to delayed snowmelt decreased vegetative and reproductive performance of *C. tetragona*; earlier melt may therefore improve performance. This may lead to floral composition change in some high arctic locations.

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Introduction

Despite recent studies suggesting a general trend of climate warming in the Arctic causing increased rate of glacier retreat, drying of shallow arctic ponds, early snowmelt, and enhanced growing season length (Kaufman et al., 2009; Smol and Douglas, 2007; Axford et al., 2009; Barber et al., 2008), increased winter temperatures and hence winter precipitation in the High Arctic (Hartmann et al., 2000; Shindell et al., 1999; Thompson and Wallace, 2001; ACIA, 2005; Sharratt, 1992) may increase snowfall. Increased snow depth leads to shorter growing seasons (ACIA, 2005; Buus-Hinkler et al., 2006; Cooper et al., 2011) if not counteracted by an earlier snowmelt due to warmer spring weather. Buus-Hinkler et al. (2006) indicated that the timing of snowmelt in NE Greenland is affected by both precipitation and temperature, and suggested that climate change could lead to heavier snow packs and negative impacts on vegetation in this region. Projected changes for NE Greenland and the European High Arctic are opposite to the expected elongation of growing seasons in many subarctic areas, thus underlining the importance of taking into account regional variation in projections and responses.

In 2006 we established a snow depth manipulation experiment in Advendalen, Svalbard (similar to that of Rieley et al. (1995) in Ny Ålesund, Svalbard) to investigate how high arctic vegetation and soil processes will respond to increases in winter precipitation. We found that the duration of the active growing season behind the fences was shorter for the majority of the species present, causing a shift in timing of phenological events with reduced flowering for several key species such as *Cassiope tetragona*, *Dryas octopetala*, and *Stellaria crassipes* (Cooper et al., 2011). Indications suggest that these reductions in growing season alter important life history traits related to flowering and reduce seed viability. This has been further investigated in this study.

We selected the evergreen ericaceous dwarf shrub *C. tetragona* as a model study species based on its high abundance and circumpolar distribution across arctic Canada, Norway and the Svalbard Archipelago, and northern Siberia (ACIA, 2005; Callaghan et al., 2005). Beside its wide distribution in the arctic, it is also a long-lived plant with easily recognizable growth pattern exhibiting distinct seasonal growth segments (Havström et al., 1993, 1995; Welker et al., 2005; Rosema et al., 2009). *Cassiope tetragona* is a heath species which usually grows in natural snowbeds/hollows covered by relatively deep snow in winter, therefore often experiences naturally late melt-out. In some years it makes important use of snowmelt water to control leaf gas exchange (photosynthesis) (Welker et al., 2005).

Snow fences have been used to manipulate snow accumulation for several decades and were promoted early on by Tabler (1971), who aimed primarily at providing an effective means of keeping snow off highways. Snow fences have also been used by researchers to study vegetation responses to reduced snow depth in windward side and increased snow depth at the leeward side (see Wipf and Rixen, 2010, for a review). Several authors studied the effects of increased snow depth as a possible outcome of climate change in the High Arctic (Buus-Hinkler et al., 2006; Morgner et al., 2010; Cooper et al., 2011; Rogers et al., 2011) and in Alaska a long-term study has been underway since 1994 (Jones et al., 1998; Walker et al., 1999; Schimel et al., 2004; Sturm et al., 2005; Wahren et al., 2005; Welker 2005). Collectively these studies indicate that deeper snow will have cascading effects on soil

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thermal properties (warmer), higher N mineralization, higher leaf N, and stronger C feedbacks to climate. However, the extent to which deeper snow and its associated shortening of the growing season alter life history traits are uncertain.

In this paper we report the response of *C. tetragona* to experimental snow accumulation and delayed snowmelt in the High Arctic. Our main objective was to study the immediate effect of deep-snow-induced delay to the start of growing season on phenological development, vegetative growth, and reproductive success of *C. tetragona.* We hypothesized that (1) the seasonal vegetative growth of *C. tetragona* would be lower in the deeper snow areas due to the delayed start of growing season; and (2) since the leaf and flower primordia of *C. tetragona* form in the previous autumn, delayed snowmelt in the first year of study will not affect the number of leaves and capsules per shoot segment, but the lower shoot growth would reduce seed production and seed viability.

Materials and Methods

We conducted this study in Adventdalen, a glacial valley on Spitsbergen, in the archipelago of Svalbard, Norway (78°10′N, 16°04′E). This inner fjørd area is one of the warmest in Svalbard and is classified by the Circum-Arctic Vegetation Map as the *Cassiope tetragona* zone of the mid-arctic. Mean annual precipitation is approximately 190 mm, most of which is snow (http://www.eklima.no; Forland and Hanssen-Bauer, 2003). The annual mean temperature is −6.7 °C (1969–1990 mean at Svalbard airport; http://www.eklima.no), with February as the coldest month at −16.2 °C and July the warmest at 5.9 °C. The study area was a flat terrain with well developed terraces stretching along both sides of a river. Soil was thin with many rock fragments and shale. The thin soil layer was limited by permafrost, which was about 50 cm below the surface. The area covered by the experiment was approximately 2.5 × 1.5 km. The dominant vascular plants were *Cassiope tetragona*, *Dryas octopetala*, *Salix polaris*, *Alopecurus borealis*, *Luzula arcuata* subsp. *confusa*, and *Bistorta vivipara*. Vegetation height, as elsewhere in the High Arctic, is under 20 cm due to strong wind, short growth season, and low temperature. The vegetation was exposed to occasional disturbance from reindeer (*Rangifer tarandus platyrhynchus*), but *C. tetragona* is not grazed by reindeer or other herbivores, making it an ideal field study species.

Snow fences were erected in the autumn of 2006; they were 6.2 m long and 1.5 m high, and established perpendicular to the prevailing southeasterly winter wind direction. Nearby plots without snow fence served as controls. Of the 12 paired fences and control areas established (Morgner et al., 2010), one was without *C. tetragona*, so only 11 were used in this study. Prevailing winter winds allowed the fences to accumulate snow behind them to an average depth of 130 cm in late May, compared to about 27 cm in the control areas (Morgner et al., 2010). Although the experimental increase of snow depth by 1 m was large, resulting in fence plots with much deeper snow than the controls, it was within the range of snow depths naturally found for *Cassiope tetragona* on Svalbard. Deeper snow insulated the ground from the cold air and resulted in warmer soils in winter and cooler and moister in summer than in controls (Morgner et al., 2010; Cooper et al., 2011). The fenced and control plots were checked daily at the start of June 2007 to determine the date they became snow-free. Observations of 3 plots per fence and control (total 66 plots) gave the date of green-up and senescence of *C. tetragona.* Green-up was defined when the *Cassiope* leaves changed color from brown to green, and senescence when the green color was lost from the leaves. From these dates we determined the duration of the growing season (details in Cooper et al., 2011). The dates of flower opening and ripe seed dispersal were also recorded.

For the fenced plots we randomly collected 30 shoots of *C. tetragona* from a 4 × 8 m area between 3 and 12 m away from the fence at the leeward side (the area with the deepest and longest lasting snow; see Morgner et al., 2010). From the paired unfenced plots we randomly collected another 30 shoots from a 4 × 8 m area. The shoots were placed in paper bags and brought to the laboratory. We determined seasonal shoot growth for two seasons prior to treatment (2005 and 2006) and after one season of treatment (2007). Segments of shoots were measured between two successive smaller autumn leaves following Havström et al. (1995). We recorded the number of leaves per annual growth segment of *C. tetragona* for all shoots for all three growing seasons (2005–2007). From each of the current and previous years' growth segments we determined the number of capsules per shoot segment. This was possible because the stalk of the capsules were still attached to the shoot segments. However, since some previous years' capsules were dropped from the stalk, we measured seed production by counting the number of seeds per capsules for only current year (2007) capsules for all shoots collected. Seeds produced in 2007 extracted from 30 capsules per fence/control plots were kept at −5 °C for 5 weeks followed by 0.5 °C for 3 d and then acclimatized at 4 °C for 4 d before germination, following Cooper et al. (2004). Twenty-five seeds per fence/control plots were spread on distilled water-soaked filter paper in Petri-dishes, and kept at 18 °C in a 24 hr photoperiod (150 μmol m^{-2} s^{-1}) for 12 weeks, simulating the maximum growing season on Svalbard at constant light and at a temperature known to produce high germination for many Svalbard plant species (Cooper et al., 2004). The filter paper was moistened once every 2 days and checked for germination each week. Total seed germination was tallied as a value out of 25 possible germinations. In total we tested 550 seeds (25 per Petri-dish × 11 replications × 2 fence and control) for germination.

Differences in timing of the phenological phases of green-up, senescence, flowering, and seed dispersal between treatment and control areas were tested by linear mixed effects models (function lme in the R-package *nlme*; Pinheiro et al., 2008) with random effects of fence treatment estimated for each of the four different experimental blocks. The delay in reaching a defined phenophase was determined by subtracting mean date of occurrence at controls from the date of occurrence behind fences. The difference in the active growing season duration was determined by subtracting mean durations behind fences from those of controls, with positive values indicating a shortening of the growing season length. Data analyses for seasonal shoot length and number of leaves and capsules per seasonal shoot segment were restricted to comparing mean values within the plots before and after fence installation (−2, −1, and +1 year of treatment—2005, 2006, and 2007, respectively) by one-way ANOVA. Mean values of each parameter were calculated for each study plot, and plot means were used in all statistical analyses. We used *t*-tests for treatment significance in the number of seeds per capsule and seed germination. SPSS ver. 13 was used for the ANOVA and *t*-tests.

Results

Significantly more snow accumulated in the fenced plots compared to the control plots with snow depths in late May of 130 ± 25 cm (mean ± standard error) and 27 ± 13 cm, respectively.

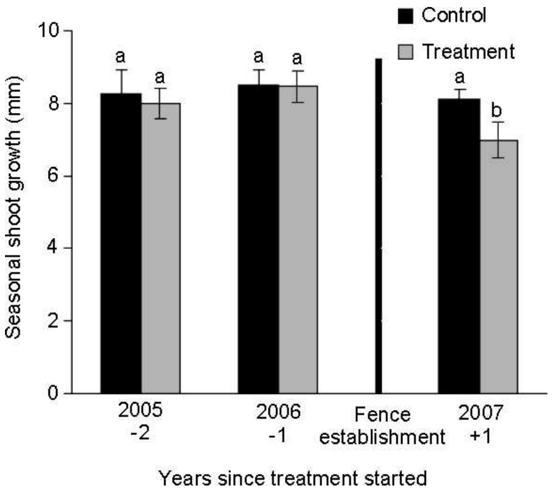

FIGURE 1. Seasonal shoot length (mean ± SE) of *C. tetragona* in unfenced (control) and fenced (treatment) plots. The vertical line indicates snow fence installation in the autumn of 2006. Differing letters above the histograms indicate significant difference ($p \leq 0.05$).

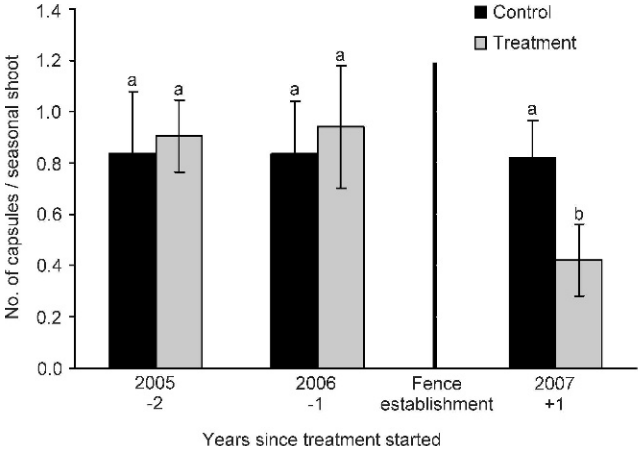

FIGURE 3. Number of capsules (mean ± SE) per seasonal segment of *C. tetragona* from unfenced (control) and fenced (treatment) plots. The vertical line indicates snow fence installation in the autumn of 2006. Differing letters above the histograms indicate significant difference ($p \leq 0.001$).

Snow melted significantly later behind fences than in control areas. Snowmelt was delayed in 2007 by 7 days (average snow-free date for control plots: 11 June; fence plots: 18 June). There were significant delays in the timing of plant development. Following snowmelt, green-up occurred after 20 days behind fences and after 19 days in control, with green-up happening 9 ± 2 (mean ± standard deviation) days ($p < 0.001$) later in fence plots than controls. Senescence was delayed by 4 ± 2 days ($p = 0.048$) behind fences. The active growing season length was thus shortened by 5 ± 2 days to 28 ± 5 days ($p = 0.014$) in the fence plots. Flowering behind fences occurred 13 ± 2 days after controls ($p < 0.001$), whereas ripe seed dispersal was delayed by 3 ± 2 days ($p = 0.080$).

Seasonal shoot growth and number of leaves per seasonal shoot segment of *C. tetragona* in 2005 and 2006 (2 and 1 year prior to treatment) and that of the unfenced plots in 2007 did not differ significantly (Appendix). However in 2007, shoot length behind fences was significantly lower than in the same plants in pre-fenced years and 16% lower than those of control plants in 2007 (df = 65, $p = 0.030$; Fig. 1). Similarly, the number of leaves per seasonal growth segment in 2007 was significantly lower in fence treatment compared to the pre-fenced seasons (2005, 2006) and 19% lower than the 2007 control (df = 65, $p = 0.01$; Fig. 2). No significant year-to-year differences were found for shoot growth and number of leaves per seasonal shoot in the controls.

Plants from the deep snow area had 49% fewer capsules than controls (df = 65, $p = 0.001$; Fig. 3), reflecting a decrease in reproductive effort. This was further compounded by significantly fewer seeds per capsule (df = 20, $p = 0.002$) in the deep snow areas compared to controls (Fig. 4). Seed germination was low in plants from the deep snow area (ranging 35 to 41%) but not significantly different from controls (df = 20, $p = 0.460$; Fig. 4).

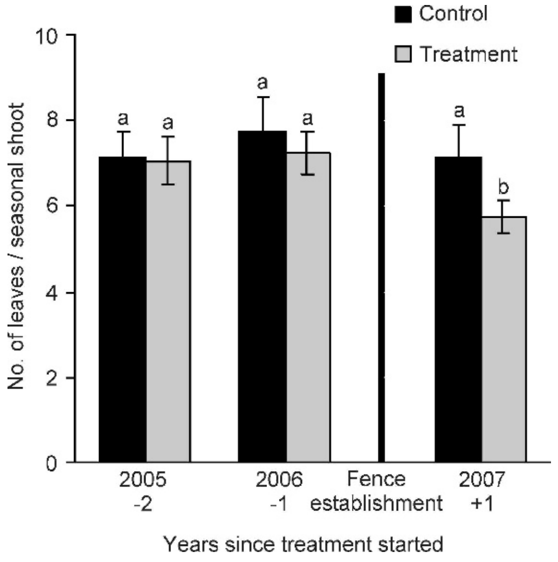

FIGURE 2. Number of leaves (mean ± SE) per segment of seasonal shoots of *C. tetragona* in unfenced (control) and fenced (treatment) plots. The vertical line indicates snow fence installation in the autumn of 2006. Differing letters above the histograms indicate significant difference ($p \leq 0.01$).

Discussion

Fences increased snow depth and subsequent later snowmelt delayed phenological development of *C. tetragona* at our study

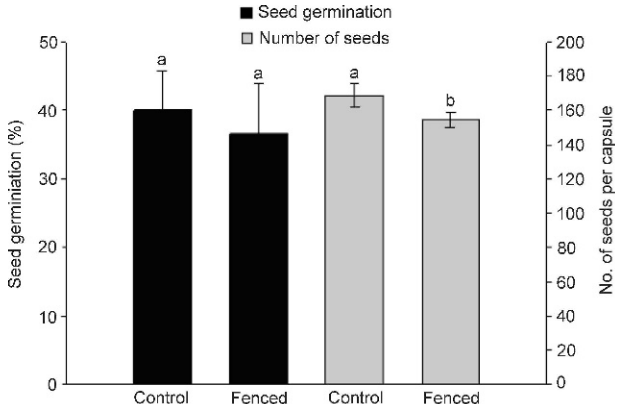

FIGURE 4. Number of seeds per capsule (mean ± SE) and seed germination (mean ± SE) of *C. tetragona* collected in autumn 2007 from control and fenced plots. Differing letters above the gray histograms indicate significant differences in numbers of seeds ($p \leq 0.01$); no significant difference in seed germination was found ($p = 0.46$).

site. The timing of plant development was delayed more at the start of season than extended at the end, resulting in a shortened growing season. This, together with cooler and moister soils behind the fences, led to a substantial decrease in vegetative growth (shoot length) of *C. tetragona*, whereas no significant year-to-year difference in shoot growth and number of leaves in pre-fenced years and in control plots were found, supporting our first hypothesis. The number of leaves and capsules per seasonal shoot segment were reduced in the deep snow areas, but seed viability remained unaffected, only partly supporting hypothesis 2 which postulated unchanged number of leaves and capsules per season and reduced seed production and viability. Although leaf and flower premordia were likely formed in the previous season, resources necessary to fully develop all the pre-formed leaf and flower buds were probably insufficient in the deep snow area due to shorter growing season.

In the Arctic, snow depth and rate of snowmelt dictate the duration of time available for resource assimilation by plants (Billings and Bliss, 1959; Galen and Stanton, 1993; Wookey et al., 1994, 1995; Walker et al., 1999), and a short growing season severely constrains vegetative growth (Thórhallsdóttir, 1998), in turn influencing reproductive performance of plants. Galen and Stanton (1993) showed a direct link between growing season length and plant performance in alpine buttercups (*Ranunculus adoneus*) similar to our data for *C. tetragona*. From a study conducted within the same experiment in Adventdalen, Cooper et al. (2011) demonstrated delayed phenological development for several species behind fences as a consequence of delayed snowmelt and compressed growing season. Snowmelt was delayed in 2008 by 6–12 days, which furthermore delayed the date of peak flowering by 1–2 weeks; reduced the number of flowers and seeds, and also reduced seed viability. If a species experiences a stronger reduction in vegetative growth and reproductive performance than its competitors, it will lose competitive advantage within the plant community, potentially having broader communitywide effects: altering vegetation patterns, community composition, and species richness (Walker et al., 1993, 1999; Callaghan et al., 1999). However, we recognize that to substantiate our assumption further multi-year studies involving many other species are required to also quantify interspecies variation in response (Cooper et al., 2011).

Havström et al. (1993) argued that since plants such as *C. tetragona* are typically long-lived, they would experience much environmental change per generation. Short dispersal distances of their seeds and sporadic establishment of seedlings limit their ability to relocate in more favorable areas or adapt to the altered environment (Callaghan et al., 1989, 1999, 2005; Carlsson and Callaghan, 1991; Havström et al., 1993). In the Arctic the production of viable seeds is limited by short and cool summers (Bell and Bliss, 1980) and enhanced by warmer summers and greater nutrient availability (Wookey et al., 1995). In Adventdalen, Cooper et al. (2011) showed that delayed start of growing led to a reduction in flower number for several species and reduced seed viability of *Dryas octopetala* and bulbils of *Bistorta vivipara*. Totland (1994) also reported a reduction in the number of seeds of *Ranunculus acris* in populations located in areas with greater snow accumulation. It is reasonable to assume that arctic plants that are unable to produce sufficient viable seeds due to shorter growing seasons would have difficulty in colonizing new habitats. In our study we observed almost 50% reduction in the number of capsules/shoot as well as a significant reduction (10%) in the number of seeds per capsule of *C. tetragona* in the fenced plots compared to control, but no change in seed viability. Presumably this loss of fecundity is also associated with a loss of energy in producing capsules with aborted seeds. If reduced capsule and seed production continued for successive years it would most likely have a population-level impact in the long run. In other parts of the Arctic that are experiencing warmer conditions this circumpolar plant might also face regeneration problems. Experimental studies of warming effects on *C. tetragona* showed increased reproductive success, but at a community level this species appeared to have low competitive ability under warmer conditions (Molau, 1997).

These findings suggest that *C. tetragona* responds to both increased summer temperature and later growing season start by reduced competitive ability. If, in response to climatic change, the co-occurring and migrating species become more successful with enhanced growth and reproduction than *C. tetragona*, then a community-level change might occur (Wahren et al., 2005; Sturm et al., 2005). However, the results of our short-term experimental study must be interpreted with caution for several reasons: (i) plants in the Arctic normally experience large year-to-year variation in snow depths; for example, the weather station at Eureka, Nunavut (74°43′) recorded a 76 cm increase in snow depth from 1966 to 1967 (Environment Canada, 2009). Similar year-to-year variability in snow depths was also recorded at the Resolute (74°43′) weather station (Environment Canada, 2009). (ii) Considerable spatial variability in snow depth exists allowing early snowmelt and hence longer growing seasons in some locations than others, thus compensating for areas with deeper snow (Molau, 1997; Stone et al., 2002). (iii) The increase in snow depth in our experimental plots was much greater than the normal variability of snow depth in the study area, although it was within the natural range of depth usually found over *Cassiope* plants in nearby locations. In this experiment, plants usually covered by about 27 cm of snow experienced the buildup of about 1 m extra snow and a 7 day delay in snowmelt leading to a reduction of the active growing season by almost a week, producing a strong effect on plants behind fences. Many *Cassiope* plants experience this snow depth in their natural habitats, so it can be assumed that they do not perform as well as in habitats with shallower snow and/or an earlier start of season. Most of the climate change-related studies use abrupt rise in temperature and/or CO_2 to mimic the predicted climate (100 years later) and record biological responses for a short period (Bazzaz, 1990; Körner and Bazzaz, 1996; Wookey et al., 1993; Welker et al., 1997; Luo et al., 1999; Klironomos et al., 2005). Ours is no exception. Undoubtedly our results of immediate response of an important arctic plant species to increased snow depth and shortened growing season is very valuable from the population biology perspectives, but since changes in snow depth and date of snowmelt naturally vary dramatically from year to year, we need longer-term studies to further substantiate these conclusions. The study would also be improved by the inclusion of sampling from different distances behind the fences (different snow depths and melt-out dates), as well as from natural gradients. Likewise, we may expect a longer growing season resulting from a reduced snowpack (less snowfall, or more precipitation falling as rain rather than as snow) or from warmer spring-induced earlier snowmelt. This has yet to be addressed experimentally, and is currently being investigated in the ongoing study in Adventdalen.

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APPENDIX

Summary of statistical tests (one-way ANOVA and *t*-test) comparing seasonal shoot length, number of leaves and capsules per seasonal shoot, number of seeds per capsule, and seed germination of *C. tetragona* in control and fenced area. Fence established in autumn 2006. Mean ± standard error.

Year	Treatment	Seasonal shoot length (mm)	Number of leaves per seasonal shoot	Number of capsules per shoot	Number of seeds per capsule	Seed germination (%)
2005	Control	8.25 ± 0.7a	7.1 ± 0.6a	0.83 ± 0.2a		
	Fenced	8.00 ± 0.4a	7.0 ± 0.6a	0.91 ± 0.1a		
2006	Control	8.50 ± 0.4a	7.8 ± 0.8a	0.83 ± 0.2a		
	Fenced	8.48 ± 0.4a	7.3 ± 0.5a	0.94 ± 0.2a		
2007	Control	8.13 ± 0.6a	7.1 ± 0.8a	0.82 ± 0.2a	168.5 ± 7.1a	41 ± 5a
	Fenced	7.00 ± 0.3b	5.8 ± 0.4b	0.42 ± 0.1b	154.3 ± 4.3b	35 ± 7a
ANOVA	F or T	4.15	4. 72	12.5	12.5	0.58
or *t*-test	df	65	65	65	20	20
	P	0.03	0.01	0.001	0.002	0.46