

Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community

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Abstract

Positive and negative species interactions are important factors in structuring vegetation communities. Studies in many ecosystems have focussed on competition; however, facilitation has often been found to outweigh competition under harsh environmental conditions. The balance between positive and negative species interactions is known to shift along spatial, temporal and environmental gradients and thus is likely to be affected by climate change.

Winter temperature and precipitation patterns in Interior Alaska are rapidly changing and could lead to warmer winters with a shallow, early melting snow cover in the near future. We conducted snow manipulation and neighbour removal experiments to test whether the relative importance of positive and negative species interactions differs between three winter climate scenarios in a subarctic tundra community. In plots with ambient, manually advanced or delayed snowmelt, we assessed the relative importance of neighbours for survival, phenology, growth and reproduction of two dwarf shrub species. Under ambient conditions and after delayed snowmelt, positive and negative neighbour effects were generally balanced, but when snowmelt was advanced we found overall facilitative neighbour effects on survival, phenology, growth and reproduction of *Empetrum nigrum*, the earlier developing of the two target species. As earlier snowmelt was correlated with colder spring temperatures and a higher number of frosts, we conclude that plants experienced harsher environmental conditions after early snowmelt and that neighbours could have played an important role in ameliorating the physical environment at the beginning of the growing season.

Keywords: dwarf shrub heath, *Empetrum nigrum*, facilitation, growth, neighbour removal experiment, phenology, reproduction, *Vaccinium vitis-idaea*, winter climate change

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Introduction

Negative species interactions like competition are a main force in structuring species assemblages and communities (Grime, 1974, 1977). However, depending on environmental conditions, the disadvantage of having neighbours competing for the same resources may be outweighed by the advantages, such as amelioration of the physical environment (Bertness, 1991; Greenlee & Callaway, 1996; Tielbörger & Kadmon, 2000). Thus, either competitive or facilitative effects may dominate

species interactions in a given community. Models predict that the net positive effect of neighbour interactions should be greater under harsh growing conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997; Brooker & Callaghan, 1998). Indeed, facilitation has been found to outweigh competition in ecosystems of various harsh environments, such as deserts (Muller, 1953; Wilby & Shachak, 2004), sand dunes (Franks & Peterson, 2003), salt marshes (Bertness, 1991; Mulder & Ruess, 1998), alpine (Choler *et al.*, 2001; Callaway *et al.*, 2002) and arctic communities (Carlsson & Callaghan, 1991; Dormann & Brooker, 2002; Olofsson, 2004).

The balance between positive and negative species interactions is not stable but can shift along spatial and environmental gradients (Choler *et al.*, 2001; Callaway

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et al., 2002), or as a reaction to temporal fluctuations in climate (Tielbörger & Kadmon, 2000). Therefore, the balance between competition and facilitation can be expected to shift under climate change, which could eventually result in the dominance of some species and the competitive exclusion of others. Thus, understanding the balance between positive and negative species interactions could help to assess the potential of climate change effects on vegetation dynamics.

In tundra plant communities, neighbour removal experiments have induced positive (Sammul *et al.*, 2000; Gerdol *et al.*, 2002), negative (Shevtsova *et al.*, 1997; Aksenova *et al.*, 1998) and neutral responses (i.e. no interactions, or positive and negative interactions equally strong) (Bret-Harte *et al.*, 2004; Totland *et al.*, 2004). Thus, competition and facilitation are both of importance in tundra communities and whether one or the other factor dominated can vary in space, time or between species studied. Such balanced systems are probably sensitive to even minor environmental changes and may therefore be especially suitable to test for vegetation responses under climate change.

Climate change is predominantly affecting high latitudes (Serreze *et al.*, 2000). Especially Alaska is experiencing a great warming; since the 1960s the annual mean temperature has risen by 3 °C and the winter mean temperature by 4.5 °C (Alaska Regional Assessment Group, 1999). The growing season in Interior Alaska has lengthened by 2.6 days per decade, while leaf onset has advanced by 1.1 days per decade (Keyser *et al.*, 2000). Future rises in air temperatures, too, are projected to be greater in winter rather than summer: by 2050, December–February temperatures are predicted to increase by up to 6 °C, June–August temperatures by up to 3 °C (projections by the Canadian Centre for Climate Modelling and Analysis, Boer *et al.*, 2000).

A likely impact of rising temperatures and changing precipitation patterns is an earlier snowmelt, which recently has been detected in high latitudes of the Northern hemisphere (Serreze *et al.*, 2000; Dye, 2002). For the vegetation, an earlier snowmelt potentially results in a longer growing season and higher growing-degree days. However, an increase in frost damages due to a higher number of frost events (i.e. subzero temperatures), or due to earlier dehardening and thus higher frost sensitivity of plants are a possible consequence of earlier snowmelt (Kimmins & Lavender, 1992; Cumming & Burton, 1996; Inouye, 2000; Gorsuch & Oberbauer, 2002).

In this short-term experiment, we study how neighbour removal and advanced and postponed melt-out affect the survival, phenology, growth and reproduction of two common subarctic dwarf shrub species, *Empetrum nigrum* and *Vaccinium vitis-idaea*. We test whether

and how the balance between positive and negative species interactions is affected by modifications of snowmelt, which is a likely consequence of a changed spring climate in subarctic tundra ecosystems. We expect the positive effect of neighbours to increase as the harshness of growth conditions increases. Our results will thus help to clarify whether advanced or postponed snowmelt will improve or impair growth conditions for tundra species in the short term.

Methods

Study site and species

We conducted our study above treeline at Murphy Dome, near Fairbanks, AK, USA (64°57'N, 148°22'W, 850 m a.s.l.) from August 2002 to August 2003. Mean air temperatures \pm SD and minimum temperatures (in parentheses) for the summer months (measured to the nearest 0.1 °C every 15 min by a shaded HOBO temperature logger (Onset Computer Corporation, Pocasset, MA, USA)), were 5.1 ± 7.1 °C (–11.1) in May, 11.7 ± 6.7 °C (–2.9) in June, 11.9 ± 5.7 °C (–1.5) in July and 9.8 ± 5.0 °C (–2.4) from 1 to 18 August 2003 (end of experiment). The vegetation community is a subarctic, species-poor tundra and corresponds to the low-shrub subshrub tundra of the low-arctic zone (Bliss, 1981). Evergreen and deciduous dwarf shrubs, many of the Ericaceae family, dominate this tundra type. Frequent species in this community include *Vaccinium uliginosum*, *E. nigrum*, *V. vitis-idaea*, *Ledum decumbens*, *Carex bigelowii*, *Betula nana* and various *Salix* species (Viereck & Little, 1986, order according to abundance in our plots). In our study, we focused on *E. nigrum* ssp. *hermaphroditum* (Hagerup) Böcher (crowberry, Empetraceae) and *V. vitis-idaea* ssp. *minor* (Lodd.) Hultén (lowbush cranberry, Ericaceae) (see Ritchie, 1955; resp. Bell & Tallis, 1973 for descriptions). The phenological development of *E. nigrum*, one of the earliest-flowering tundra species, is probably synchronized with snowmelt (S. Wipf, unpublished data); thus its performance is likely to be more sensitive to changes in snowmelt timing than that of *V. vitis-idaea*, which flowers later in summer.

Experimental design and treatments

To quantify the relative importance of competition vs. facilitation, we compared the performance of shoots with and without plant neighbours. Because of the clonal growth of both species, we used shoots as the basic unit of this study. We chose shoots for our experimental treatments that were not directly surrounded by other shoots of the same species to minimize impacts of clonally integrated neighbours outside of the treatment

area. In each of a total of 12 plots of approximately 1 m² at two sites (six per site) we wired and flagged six shoots of each species that were randomly chosen within these criteria. The distance was approximately 400 m between sites, 3–15 m between plots at each site and 0.4–1 m between shoots within plots. A neighbour removal treatment was randomly assigned to three marked shoots per species in each plot in the end of August 2002. Within a circle with a radius of 0.1 m around a shoot, we carefully clipped and removed all biomass to approximately 2 cm below the surface of the bryophyte cover. A 3-day cold spell 10 days after the treatment (from 9 September 2002 onwards) probably ended the 2002 growing season and thus prevented clipped plants from resprouting. Freeze-up was uniform in the three sites equipped with miniature temperature loggers during the whole experiment: soil surface temperatures reached freezing on 1 October and constantly remained below 0 °C until snowmelt.

To test whether the relative importance of competition vs. facilitation may be altered by winter climate change, we randomly assigned one of three different snowmelt treatments to each plot on 18 April 2003: (1) advanced snowmelt, by manually reducing the snow cover by half to approximately 10 cm and then letting it melt naturally; (2) delayed snowmelt, by adding approximately 50 cm snow on an otherwise continuous snow cover; and (3) unmanipulated control plots.

Miniature temperature loggers in each plot measured the subnivean temperatures at soil surface to the nearest 0.5 °C in 3 h intervals between January and snowmelt. These measurements, along with regular inspections (twice per week), allowed us to estimate the day of melt-out as the first day when temperatures at soil surface reached either +5 °C at day or +1 °C at night and when the daily temperature amplitude exceeded 5 °C (i.e. temperature characteristics that could not have developed under snow). Snow depth within plots and at the location of the logger was measured twice per month between January and March 2003 to check for natural variability of the snow cover.

To compare the number of potential frost events and growing-degree days that shoots experience after different snowmelt treatments, we used data from the nearest weather station (Keystone Ridge, approximately 5 km from our study site on 500 m a.s.l.). Potential frost days were recorded as the number of days with a minimum temperatures of below 0 °C between snowmelt and the end of the experiment. Growing-degree days were calculated as the sum of all daily mean temperatures above 5 °C between snowmelt and the end of the experiment (mid-August 2003).

Plant response

After snowmelt, we visited the plots every 3–5 days to record the number of living shoots, the phenological state and the presence and number of flower buds, flowers, fruits and preformed generative buds for 2004 for each shoot. We recorded the phenology as the date when a shoot entered a new vegetative or reproductive stage. We defined the following vegetative stages: (1) first leaf entirely green (reduction of anthocyanins, see Oberbauer & Starr, 2002), (2) all leaves entirely green and (3) apical growth of shoot. Reproductive stages were defined as (1) flower buds swelling, (2) first flower open, (3) first flower senescent, (4) first fruit developing and (5) first fruit ripe. In mid-August 2003, we harvested the shoots and dried them to constant weight at room temperature. We then measured shoot length, growth increments, length of the longest new leaf and number and mass of berries of all surviving shoots. The relative neighbour effect (RNE) was calculated according to Markham & Chanway (1996) as

$$\text{RNE} = (P_{-N} - P_{+N})/x,$$

where P is the performance of a plant without ($_{-N}$) and with ($_{+N}$) neighbours and x is either P_{-N} or P_{+N} , whichever is greater. As for example Callaway *et al.* (2002), we present our results in reverse, with positive values indicating facilitation (i.e. positive greater than negative species interactions) and vice versa.

Statistical analysis

We used R 2.1.0 (R Development Core Team, 2004) for Generalized Linear Models (GLMs) and SPSS 11.0.0 (SPSS Inc., 2001) for all other analyses. Because of their clonal nature and, thus, possible genetic similarity between close neighbours, we used the means of the three shoots per species, plot and removal treatment in all analyses and checked for differences between the two sites, which were nonsignificant. Binomial variables (survival, occurrence of vegetative growth, reproduction in 2003 and formation of flower buds for 2004) were analysed using GLMs with a logistic regression model for proportions with a logit link and a binomial error function (for reproduction 2003 and buds 2004 we employed a quasibinomial error function because deviances were overdispersed). Deviances were tested for significance with a χ^2 test. We analysed whether the odds that a shoot in a plot was alive, growing vegetatively, producing berries in 2003 or preforming generative buds for 2004 responded to neighbour removal and melt-out treatments and whether the effects of

neighbour removal depended on the melt-out treatment (interaction between neighbour removal and snowmelt treatment). Continuous variables were analysed with ANOVA with type I sequential sums of squares and the same explanatory variables. Standardized residual deviances and sums of squares, respectively, were visually checked for normality and homogeneity and log-transformation was applied to shoot growth increments to meet the assumptions of ANOVA. Whether the RNE per species and treatment differed from 0 was tested with one-sample *t*-tests.

Results

Effects of snowmelt treatments on snow depth and temperature

Snow depths and winter soil surface temperatures did not differ between the three snowmelt treatments before snow manipulation ($F_{2,9} = 0.57$ and 0.50 , respectively). Timing of and temperatures during natural melt-out (on 28 April in control plots) were close to the long-term mean, although winter mean temperatures had been approximately 5°C above and snow cover depth 50% below long-term mean (as measured in Fairbanks, AK, USA, NOAA, 2002–2003). Snow manipulations caused melt-out to occur on 20 April in advanced plots and 7 May in postponed plots, changing the length of the growing season (snow-free to first frost below -5°C) by $+6\%$ and -7% , respectively. Correspondingly, the temperature sum accumulated (i.e. growing-degree days above 5°C) was increased by 6% and decreased by 5% in the advanced and postponed melt-out treatments, respectively ($F_{2,9} = 22.5$, $P < 0.001$, Fig. 1). The number of potential frosts (air temperatures below 0°C) during the growing season, however, was the higher the earlier snow had melted ($N = 12$, $R^2 = 0.94$, $P < 0.001$, Fig. 1) and was increased by 21% and decreased by 45% by the advanced and postponed melt-out, respectively ($F_{2,9} = 19.6$, $P < 0.001$). The mean summer temperature was decreased by 0.3°C in early melting and increased by 0.6°C in late melting plots ($F_{2,9} = 12.4$, $P = 0.003$, Fig. 1).

Survival

Overall, 86% of a total of 72 *E. nigrum* shoots had survived at the end of our experiment. There was a significant interaction between effects of snow treatment and neighbour removal on the survival of *E. nigrum* shoots ($\chi^2_2 = 7.8$, $P = 0.02$, Fig. 2). More than 80% of the shoots growing with neighbours, or growing in controls and late melting plots survived, but only 50% of shoots with advanced melt-out survived when

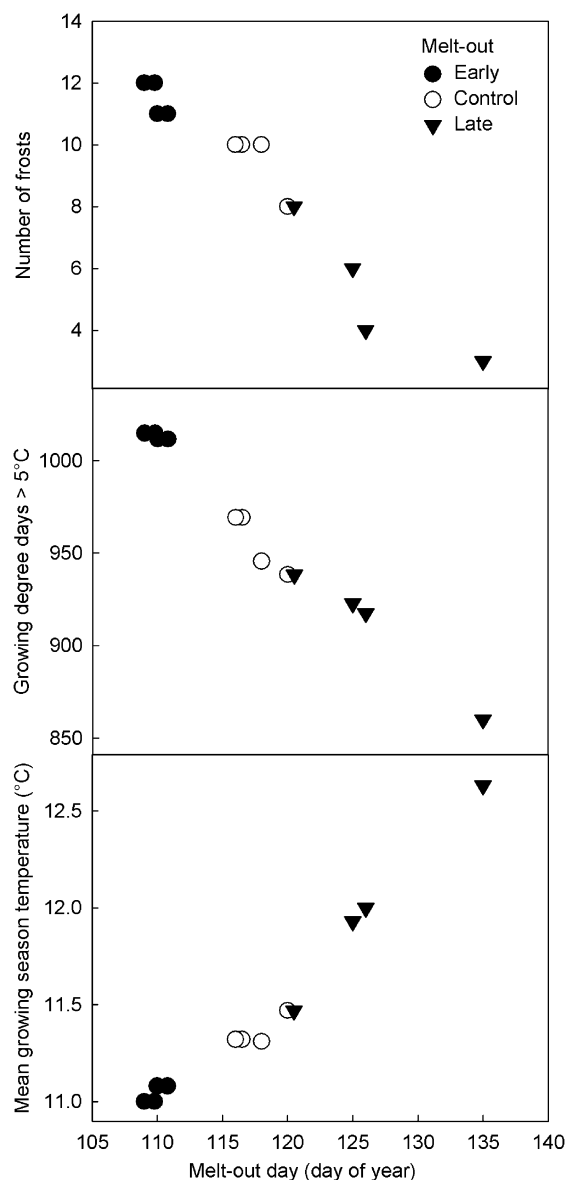


Fig. 1 The number of frost events (days with subzero temperatures), growing-degree days (sum of daily mean temperatures $> 5^{\circ}\text{C}$) and mean growing season temperatures in relation to the corresponding day of melt-out and melt-out treatment.

neighbours had been removed. The RNE on survival of *E. nigrum* shoots indicated a facilitative effect of neighbours in early melting sites (one-sample *t*-test, $N = 4$, $t = 3.0$, $P = 0.058$, Fig. 4). Forty per cent of *V. vitis-idaea* shoots died during our experiment. The survival was lower in plots with advanced melt-out and controls than in plots with delayed melt-out ($\chi^2_2 = 12.9$, $P = 0.002$, Fig. 2), but was not affected by neighbour removal ($P > 0.1$). Therefore, no RNE on survival of *V. vitis-idaea* was detected.

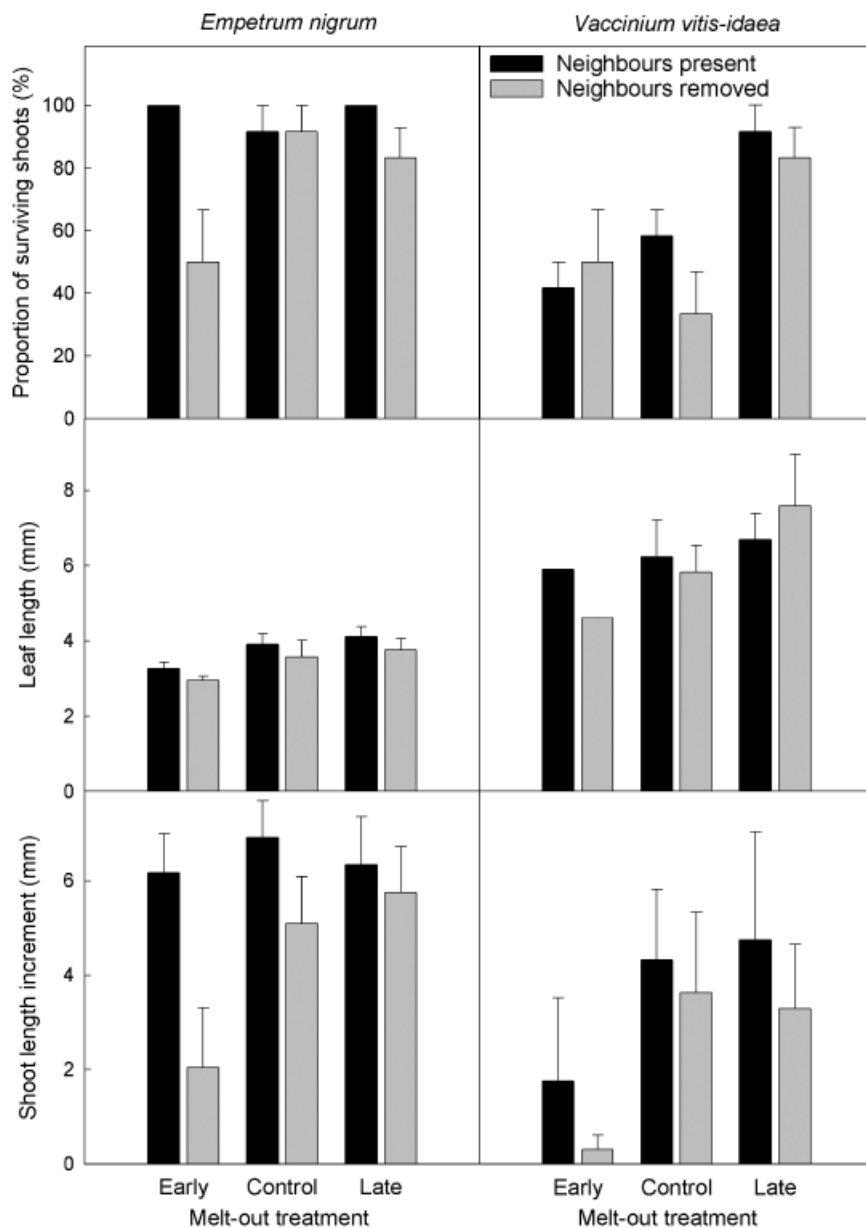


Fig. 2 Effects of melt-out and neighbour removal treatments on survival rate, leaf length and shoot length increment of *Empetrum nigrum* and *Vaccinium vitis-idaea* shoots (mean and standard error).

Phenology

For *E. nigrum*, the timing and duration of all vegetative and the first reproductive stages were affected by the experimental treatments. After advanced melt-out, the time span to the beginning of anthocyanin reduction (noted as greening of the first leaf) was increased ($F_{2,18} = 5.9$, $P = 0.011$, Fig. 3a). However, greening of the first leaf still occurred at a significantly earlier date in early melting and controls than in late melting plots ($F_{2,18} = 10.0$, $P = 0.001$) and was advanced by neighbour removal in all snow treatments ($F_{1,18} = 6.5$, $P = 0.020$).

At the time all leaves became green, the difference between treatments had mostly vanished, only shoots from plots with late melting plots were marginally delayed ($F_{2,18} = 3.0$, $P = 0.077$). Vegetative shoot growth in controls and plots with delayed melt-out, however, started 4.5 days earlier than in plots with advanced melt-out ($F_{2,18} = 13.5$, $P < 0.001$). Thus, shoots in controls and plots with delayed melt-out, respectively, required only 81% and 54% of the time to vegetative growth compared with plots with advanced melt-out ($F_{2,18} = 6.8$, $P = 0.007$). Neighbour removal generally postponed the start of vegetative growth ($F_{1,18} = 9.5$,

$P = 0.007$), this effect being largest in plots with advanced melt-out (interaction snowmelt \times neighbour

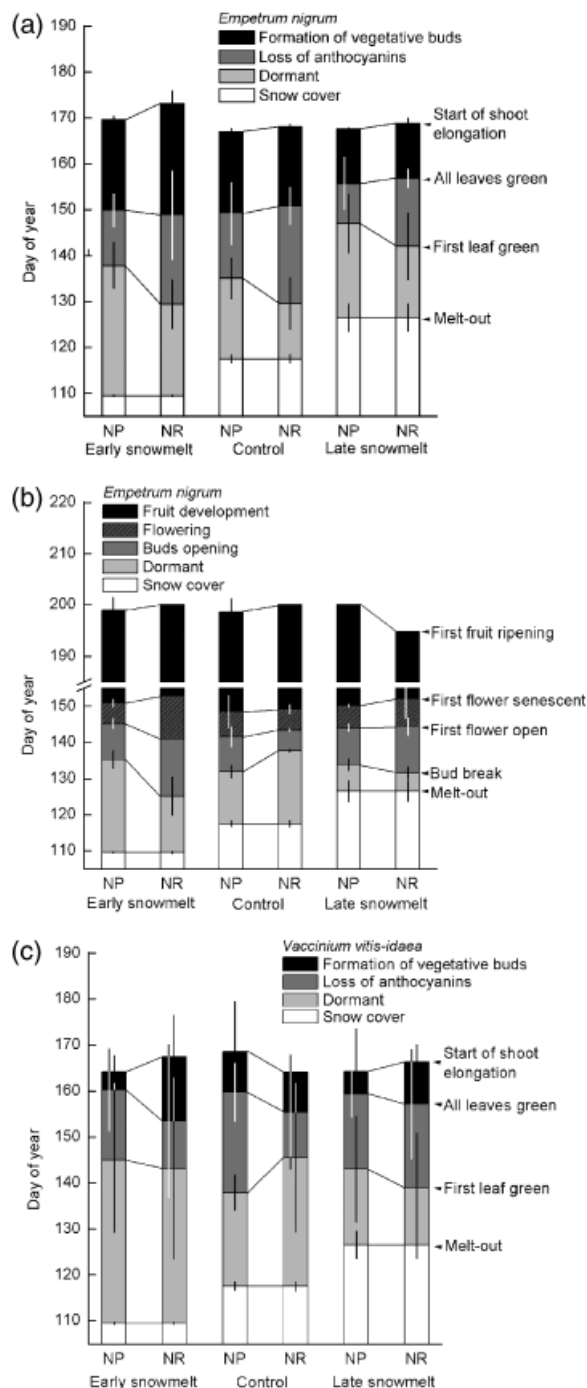


Fig. 3 Effects of melt-out and neighbour removal treatments on the phenological development of *Empetrum nigrum* and *Vaccinium vitis-idaea* shoots (means \pm standard error of dates and duration of phenological traits). (a) Vegetative and (b) reproductive stages of *E. nigrum*, (c) vegetative stages of *V. vitis-idaea*. Reproduction of *V. vitis-idaea* only occurred in three plots and was therefore omitted. NP, neighbours present; NR, neighbours removed.

removal treatment, $F_{2,18} = 4.9$, $P = 0.021$). The time between melt-out and swelling of flower buds was shortest in late melting plots ($F_{2,18} = 15.1$, $P < 0.001$, Fig. 3b), furthermore, neighbour removal tended to decrease this time span in plots with advanced melt-out and increase it in control plots (interaction snowmelt \times neighbour removal treatment, $F_{2,18} = 3.1$, $P = 0.084$). The timing of all other reproductive stages was unaffected by snowmelt and neighbour removal treatments (Fig. 3b).

The RNE indicated facilitation in the first phenological stages and in early melting plots only. In plots with early melt-out, the presence of neighbours advanced the date of first greening (RNE = 0.1; one-sample t -test $N = 4$, $t = 4.2$, $P = 0.025$) and shortened the time between melting and the beginning of greening (RNE = 0.52; $t = 8.3$, $P = 0.014$) and between melting and swelling of flower buds (RNE = 0.53; $t = 4.3$, $P = 0.024$).

In the phenology of *V. vitis-idaea*, there was no difference between snowmelt treatments except for the time lag between snowmelt and start of greening, which was inversely related to the timing of melt-out, i.e. longest in early and shortest in late melting plots ($F_{2,18} = 4.0$, $P = 0.038$, Fig. 3c). Neighbour removal did not affect the timing of the phenological development and thus, RNE did not differ from 0 in any treatment at any stage.

Growth

Vegetative growth in *E. nigrum* was generally negatively affected by neighbour removal and advanced melt-out. The proportion of surviving *E. nigrum* shoots that showed vegetative growth in 2003 was reduced after neighbour removal ($\chi^2_1 = 8.7$, $P = 0.003$), but unaffected by snow treatments ($\chi^2_2 = 1.5$; Fig. 2). The growth increments of shoots were reduced by advanced melt-out ($F_{2,18} = 3.8$, $P = 0.043$) and neighbour removal ($F_{1,18} = 7.4$, $P = 0.014$), however, the negative effect of neighbour removal tended to diminish from advanced to postponed melt-out (interaction snowmelt \times neighbour removal treatment, $F_{2,18} = 3.0$, $P = 0.073$, Fig. 2). The length of the longest leaf produced in 2003 differed between snowmelt treatments ($F_{2,16} = 3.6$, $P = 0.05$), being smallest in early and greatest in late melting plots (Fig. 2). Within shoots without neighbours, growth increments were negatively correlated to the amount of standing biomass that had been removed by the neighbour removal treatment in 2002 ($N = 12$, $R^2 = 0.52$, $P = 0.008$). Furthermore, the RNE on growth was positively correlated with standing biomass removed ($N = 12$, $R^2 = 0.49$, $P = 0.011$). This suggests that the facilitative effect of the neighbouring vegetation on growth was related to the amount of its standing biomass. The RNE was moreover positively correlated

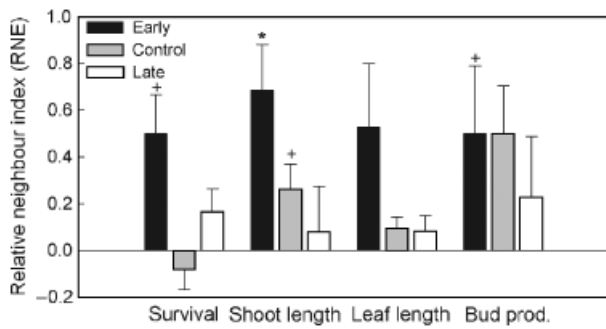


Fig. 4 The relative neighbour effect (RNE) on survival rate, shoot length, leaf length and the proportion of shoots with preformed generative buds for 2004 of *Empetrum nigrum* in each melt-out treatment (mean and standard error). Significant and marginally significant differences from 0 (one-sample *t*-test) are indicated by * $P < 0.05$ and + $P < 0.1$.

with snowmelt date ($N = 12$, $R^2 = 0.56$, $P = 0.005$) and facilitation was strong and significant in plots with advanced melt-out (one-sample *t*-test, $N = 4$, $t = 3.51$, $P = 0.039$) and weak and only marginally significant in control plots ($t = 2.48$, $P = 0.089$, Fig. 4). The proportion of live *V. vitis-idaea* shoots that showed vegetative growth did not respond to snowmelt manipulation or neighbour removal. However, shoot growth increments tended to be reduced after advanced melt-out compared with controls and plots with delayed melt-out ($F_{1,17} = 3.5$, $P = 0.053$, Fig. 2). Other growth parameters and RNE were not significantly affected by the experimental treatments.

Reproduction

All parameters of reproduction of *E. nigrum* in the 2003 season were unaffected by snowmelt treatments and neighbour removal: the proportion of shoots bearing berries, the proportion of generative buds (performed in the previous year) that had developed into ripe berries and the number and dry mass of berries did not respond to our treatments (Fig. 5). However, advanced melt-out and neighbour removal tended to reduce the proportion of shoots with generative buds preformed for the following year ($\chi^2_2 = 5.3$, $P = 0.069$ and $\chi^2_1 = 2.7$, $P = 0.099$, Fig. 5), indicating that a negative effect of advanced melt-out and neighbour removal on reproduction might have been found in the following year. The RNE on future reproduction (i.e. the proportion of shoots bearing preformed generative buds) tended to be positively related to snowmelt date ($N = 12$, $R^2 = 0.28$, $P = 0.078$) and facilitation was marginally significant in early melting plots (one-sample *t*-test, $N = 4$, $t = 3.0$, $P = 0.058$, Fig. 4). *V. vitis-idaea*

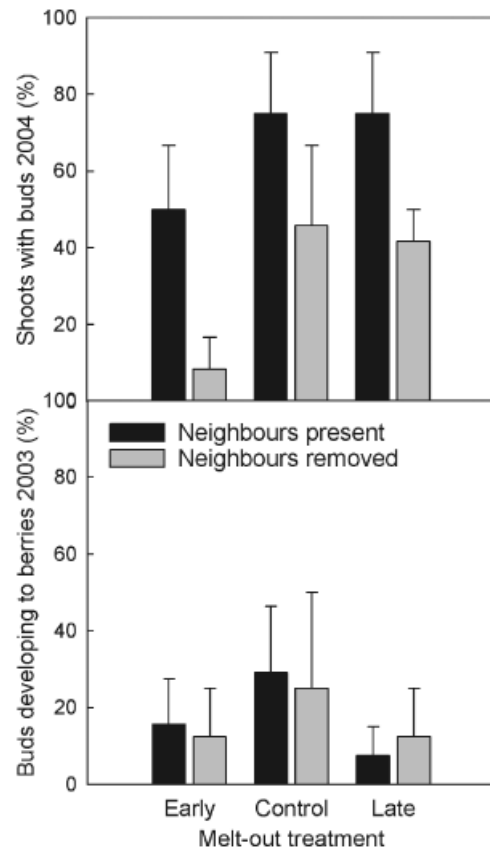


Fig. 5 Effects of melt-out and neighbour removal treatments on the proportion of shoots with preformed generative buds for 2004 and on the proportion of buds that developed into ripe berries in 2003 of *Empetrum nigrum* (mean and standard error).

reproduced in three of 12 plots only, thus, we omitted all analyses of reproductive parameters.

Discussion

Snowmelt date and plant performance

Our results demonstrate that changes in winter climate and snow cover characteristics can affect the performance of dominant subarctic plants in the short term. This is in line with other studies from arctic and alpine communities, which found that snow cover characteristics and the timing of snowmelt affect plant phenology (Rixen *et al.*, 2001; Dunne *et al.*, 2003), shoot growth (Walker *et al.*, 1995; Kudo *et al.*, 1999; Dorrepaal *et al.*, 2003), reproduction (Galen & Stanton, 1991; Inouye *et al.*, 2002; Saavedra *et al.*, 2003) and species abundance (Bell & Bliss, 1979; Galen & Stanton, 1993) in the short term and species composition (Scott & Rouse, 1995; Wahren *et al.*, 2005; Wipf *et al.*, 2005) in the long term. Thus, there is a growing body of evidence indicating

that changes in snow quantity and winter temperatures and resulting changes in snowmelt timing are key factors that have to be considered in climate change ecology in addition to changes in summer temperatures, nutrients and solar radiation. The melt-out treatments changed the pace of phenological development such that shoots from plots with advanced melt-out went through their first phenological stages more slowly than those from later melting plots. As a consequence, differences in phenology vanished throughout the summer in both target species. However, the initial differences between snowmelt treatments were greater and lasted longer in the early-flowering *E. nigrum* than in the later-flowering *V. vitis-idaea*. Both findings correspond to those of other snowmelt experiments with arctic and alpine species (Van der Wal *et al.*, 2000; Rixen *et al.*, 2001; Dunne *et al.*, 2003; Aerts *et al.*, 2004). The generally great synchrony between the phenology of early-developing species and the date of snowmelt (Galen & Stanton, 1995; Inouye *et al.*, 2000; Dunne *et al.*, 2003) might explain the fact that only *E. nigrum*, but not *V. vitis-idaea* strongly reacted to snowmelt treatments.

The phenological development is thought to be driven to a large extent by temperature (e.g. Sørensen, 1941; Thorhallsdottir, 1998 for tundra plants). The accumulated temperature (expressed as growing-degree days summed up from snowmelt to the date of a phenological trait) is often inversely related to the date of a phenological trait (Lindsey & Newman, 1956; Dunne *et al.*, 2003). However, as the phenological stages after differing melt-out timings aligned to each other, growing-degree days are unsuitable predictors of phenological development in snow manipulation experiments, but also in warming experiments in arctic tundra (Starr *et al.*, 2000; Hollister *et al.*, 2005). Thus, other factors related to snowmelt date (Galen & Stanton, 1995; Price & Waser, 1998) or to the occurrence, timing or intensity of frost (Schlüssel *et al.*, 2000) seem to dominate or mediate the effects of temperature on phenology (Hollister *et al.*, 2005).

Although the timing of later phenological traits after advanced snowmelt did not differ from controls, vegetative growth and the preformation of next year's flower buds responded negatively to advanced snowmelt in *E. nigrum*. The growth response of *V. vitis-idaea*, however, was nonsignificant. Negative and neutral responses to advanced melt-out are in accordance with numerous studies conducted in communities with relatively early natural snowmelt (Bell & Bliss, 1979; Starr *et al.*, 2000; Van der Wal *et al.*, 2000; Stinson, 2004). Our findings differ, however, from several snow manipulation studies where plant growth or fitness responded positively to advanced melt-out, a result that was often

found in communities with late natural melt-out (Galen & Stanton, 1993, 1995; Saavedra *et al.*, 2003) or with additional warming treatments (Price & Waser, 1998; Walker *et al.*, 1999; Starr *et al.*, 2000; de Valpine & Harte, 2001; but see Saavedra *et al.*, 2003). Delayed snowmelt, on the other hand, had no effect on growth and reproduction of both target species in our study, which corresponds to previous examples where a moderate delay in melt-out, although shortening the growing season, did not affect plant growth (Bell & Bliss, 1979; Scott & Rouse, 1995; Smith *et al.*, 1995; Walsh *et al.*, 1997; Walker *et al.*, 1999).

The varying responses to snow manipulations suggest that the effects of melt-out manipulations strongly depend on the conditions into which plants are released, but that the response is species specific. In our study, negative effects associated with early snowmelt (such as low temperatures at the start of the growing season, reduced mean summer temperatures, enhanced number of postmelt frosts or increased frost susceptibility of plants with early development), seemed to have outweighed the positive effects, such as increased growing season length and greater overall temperature accumulation (growing-degree days). However, longer term studies are needed to confirm our short-term results and to analyse the interactions between snow cover, timing of snowmelt, spring temperatures and frosts. Future studies might find positive effects of a prolonged growing season on plant fitness in years or sites with a mild spring climate, in communities with naturally late snowmelt or in experiments with additional warming treatments. Nevertheless, even a short-term experiment like ours points to the important role of changes in snow cover for the performance of subarctic plants.

Snowmelt date and neighbour effects

Positive species interactions were more pronounced after advanced melt-out in our study. Furthermore, reactions to neighbour removal were more pronounced in *E. nigrum*, which was also more responsive to snowmelt manipulation than *V. vitis-idaea*. As advanced melt-out generally resulted in unfavourable growing conditions, as shown by the mostly negative plant response to advanced snowmelt, our results confirm that positive species interactions are stronger under harsher conditions. This is consistent with numerous models (Grime, 1974, 1977; Brooker & Callaghan, 1998; Brooker *et al.*, 2005) and field studies (Choler *et al.*, 2001; Callaway *et al.*, 2002; Olofsson, 2004). A widely accepted explanation for this is that neighbours ameliorate the growing conditions within a plant community by forming a closed canopy and thereby lessening e.g. wind

exposure, water loss and radiative and wind cooling (see Koerner, 1999 for a summary). Thus, plywood shelters could have similar positive effects on arctic plants as neighbours (Carlsson & Callaghan, 1991). Our finding that the net positive effect of neighbours was higher in plots with more standing biomass indicates that physical protection among neighbours might in fact have been a key factor in this study.

During the period between fall frosts and the formation of a persistent snow cover, protection by neighbouring plants could be just as crucial as during spring and growing season. For practical reasons, we conducted the neighbour removal treatments before freeze-up; therefore, we cannot assess whether the physical protection by neighbours was more important during freeze-up or during melt-up and the growing season. However, as freeze-up occurred at the same time in all sites and treatments were randomly assigned, we do not expect the timing of the neighbour clipping treatment to have any influence on snowmelt by neighbour interactions.

Our results suggest that positive and negative species interactions are close to being in balance in this subarctic tundra community, but that this balance can be tipped through relatively moderate modifications in climate: the RNE on most variables and both species was neutral in controls, but shifted to facilitation after advanced melt-out. Similarly, shifts between net competition and net facilitation in the same community resulting from small changes in conditions have been found for different microsites (Choler *et al.*, 2001; Olofsson, 2004), different years (Shevtsova *et al.*, 1995) or different species (Choler *et al.*, 2001). Therefore, it is likely that the balance between positive and negative species interactions will be affected by climate change.

Conclusions

Advanced snowmelt, although lengthening the growing season, resulted in harsher growing conditions for subarctic dwarf shrubs, mainly affecting the early flowering *E. nigrum*. Thus, its shoots performed poorly after early snowmelt (as measured by survival, growth, leaf length and future reproduction), while shoots from late melting plots were able to compensate for the shortened growing season by accelerating their phenological development. Positive and negative species interactions were in balance in control plots, but facilitation was found in plots with advanced melt-out, which supports the concept that positive species interactions became more important under a harsher climate. We conclude that the balance between positive and negative species interaction in this tundra community is fragile and that a shift in this balance was induced through a moderate

and realistic change in climate (i.e. advancing snowmelt by 1 week). However, our results display short-term reactions of single species and species interactions only. We recommend that future research be conducted to determine whether and over which time periods such changes in the balance of neighbour interactions will lead to changes in the composition of subarctic tundra vegetation.

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