

LETTER

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Range shifts and global warming: ecological responses of *Empetrum nigrum* L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin

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Abstract

Global change is expected to lead to range shifts of plant species. The ecological mechanisms underpinning these shifts are currently not well understood. Here, we compared ecological responses possibly underlying southern range contraction and northern range expansion of *Empetrum nigrum*, a key species in northern heathlands, which may be related to global change. We hypothesized a negative response to warming in the 'south' (i.e. the Netherlands) and a positive response at the northern range margin (the tundra on Svalbard). Open top chambers (OTCs) were used to simulate global warming. In the 'south', OTC warming caused enhanced shoot growth and growth rate, biomass increment, advanced phenology, larger and heavier berries of *Empetrum*, while its growing season was extended by 75 days. Under OTC warming co-occurring *Calluna vulgaris* also showed an increased growing season length (by 98 days) as well as increased shoot growth rate and biomass growth, plant cover and height. Still, we found no evidence for increased competitiveness relative to *Empetrum*. In the 'north', *Empetrum* responded with increased shoot and biomass growth, enhanced berry development and ripening to warming. These responses exceeded those of co-occurring *Cassiope tetragona* with the exception of its biomass response. The direct and indirect ecological responses found do not readily explain the observed northward retreat of *Empetrum* at the southern range margin. The direct ecological responses found at its northern range margin are, on the other hand, in line with the increased occurrences of this species on Svalbard.

Keywords: *Empetrum nigrum*, global change, geographical range margins, range shifts, OTCs, growing season, phenology, annual growth, leaf life span, competition

1. Introduction

Current contraction and expansion of the geographical distribution range of plant species has often been attributed to global change (e.g. Walther *et al* 2002, Root *et al* 2003) and our study focuses more specifically on artificial warming by open top chambers (referred to as OTCs). Range margins of 1598 Northern Hemisphere species moved on average 6.1 km northward per decade or 6.1 m upward per decade (Parmesan 2006) and rapid northern shifts in plant distribution are likely the result of climate warming (Aerts *et al* 2006). Especially plants that grow at their natural range margins are expected to be vulnerable or responsive to climate change (Aerts *et al* 2006, Crawford 2008, Fosaa *et al* 2004, Menzel *et al* 2006, Neilson *et al* 2005, Walther 2004, Walther *et al* 2002, Wilson and Nilsson 2009, Root *et al* 2003). Additional evidence for the susceptibility of plant species to global warming comes from modelling studies (Fosaa *et al* 2004, Harrison *et al* 2006, Trivedi *et al* 2008, Neilson *et al* 2005).

Both Sturm *et al* (2001) and Myers-Smith *et al* (2011) discuss observations of rapidly circumpolar increase of shrub abundance. Global warming is considered to be the primary driver of similar changes in Alpine vegetation where ongoing range contraction of subnival and nival species at the lower altitudinal limit and a concurrent expansion of Alpine pioneer species at the upper limit are observed (Pauli *et al* 2007). This increased (Arctic) shrub expansion may not solely be due to warming during the summer growing season, but also to warming during winter (Chapin *et al* 1995, Sturm *et al* 2005).

Empetrum nigrum (referred to as *Empetrum*) is a key species in northern heathlands and has been linked to (sub-) Arctic shrub encroachment (Wilson and Nilsson 2009). *Empetrum* mainly consists of diploid dioecious plants in boreal-Arctic Europe and of tetraploid monoecious plants at high altitudes and latitudes (Elven 2011). Both subspecies vary considerably with overlapping morphological characters and both are known to co-occur and hybridize (Li *et al* 2002, Suda 2002). Differences between diploids and tetraploids are not regarded relevant for the present study (cf Nilsson *et al* 2000). Overall these long-lived evergreen prostrate dwarf-shrubs are considered to be morphologically and physiologically adapted to ecological conditions in a similar way. Therefore we justify a comparison of responses of *Empetrum* to increased temperature at the southern and northern range margin is liable.

The European distribution of *Empetrum* is limited to (sub-) Alpine and (sub-) Arctic biomes and the species is essentially boreal-Arctic in its climatic preferences (Bell and Tallis 1973). In the Netherlands, *Empetrum* is at its southern European range margin (Rozema *et al* 1985, Van der Meijden 2005). During the past decades, *Empetrum* occurrences in Great Britain, Ireland (BSBI 2011, NBN 2011), Germany (Floraweb 2011) and the Netherlands (Van der Meijden *et al* 1989) decreased. Simultaneous declines in Arctic–Alpine and boreo-montane lichen species have been found (van Herk *et al* 2002), while the number of thermophilic plant species increased significantly recently (Tamis *et al* 2005). Both northward retreat and reduced occurrences at lowland sites

of *Empetrum* in Britain have been attributed to increasing winter temperatures (Bell and Tallis 1973, Van der Meijden *et al* 1989). Simultaneously, *Empetrum* invaded Scandinavian mountains (Kullman 2010, Wilson and Nilsson 2009). On Svalbard, it was until recently observed in a few localities only (Elvebakk and Spjelkavik 1995, Rønning 1996), but the number of observations is increasing markedly (Alsos *et al* 2007, 2011). Also changes at its northern margin may be related to global warming, as temperatures at both margins have been rising in recent decades (table 1; DNMI 2011). If so, a further northward retreat at the southern range margin and increased occurrences in Svalbard are to be expected as a further increase of the annual global average air temperature by 1.4 °C to 4.0–5.8 °C is predicted for high latitudes in the northern hemisphere for this century (IPCC 2007)⁴.

Global warming may affect the geographical distribution of *Empetrum* through its impacts on the growing season length (referred to as GSL) and the number of growing degree days (a measure for the growing season intensity, referred to as GDD) which in turn is expected to result in phenological advances of leafing, flowering and fruiting (Parmesan and Yohe 2003, Parmesan 2006, Root *et al* 2003, Førland *et al* 2004, Linderholm 2006). The phenological based GSL_p increased with 10.8 days since 1993 (EPG 2011) and by 1.1–4.9 days on average per decade since 1951 (Menzel *et al* 2006). At its southern margin, meteorological GSL has increased with 29 days since 1901 (KNMI 2011) and with 21 days since 1990. This lengthening is particularly attributed to higher temperatures in early spring and late autumn (Visser 2002). At the northern margin, the onset of the growing season associated ecologically with the flowering of *Salix polaris* (unlike the end, associated with the yellowing of leaves of *Salix polaris*) showed large year-to-year variation. Despite this variation, during the period 2000–9, the area with a growing season exceeding 60 days clearly extended (Karlsen *et al* 2010).

Despite the ecological relevance of *Empetrum*, its documented range shifts and co-occurring warming, the ecological mechanisms through which its geographical distribution is affected, are currently not well understood. Here, we present evidence, based on experimental warming, on the extent to which warming influences phenology and growth parameters of *Empetrum*, both at its southern and northern range margin. We hypothesized experimental warming to differently affect growth and flowering phenology of *Empetrum* at its respective natural margins. At the southern range margin, we expect a reduction in plant growth parameters including shoot growth rate, biomass increment, berry weight and diameter, area covered and plant height. We expect advanced flowering phenology as *Empetrum* is a ‘cool’ boreal-Arctic species and, since vegetative growth of *Empetrum* starts only after flowering, also an earlier onset and end of the vegetative growth is expected. The growing season length is expected to reduce at the southern margin. At the northern margin, we expect shoot growth rate, biomass increment, berry weight and diameter, area

⁴ World Meteorological Organisation: www.wmo.int.

Table 1. (A) Climate characteristics at the southern range margin of *Empetrum nigrum* at 52°N, Bergen aan Zee, the Netherlands and at the northern range margin at 78°N, Endalen, Svalbard, Norway. * = significant at 0.05; ns = not significant. Ambient south: www.knmi.nl. Ambient north: www.dnmi.no. ΔT °C represents the temperature difference between OTC and control plots. For south average ΔT °C values for the period 2005–10 and for north average values for the period 2008–10 are given. (B) Growing degree days (GDD), representing accumulated heat (°C), with thresholds of 1 and 5 °C; growing season length (GSL), representing the number of days exceeding thresholds of 1 °C or 5 °C. Ambient south: www.knmi.nl. Ambient north: www.dnmi.no.

(A)								
	Ambient south			OTC	Ambient north			OTC
Temp (°C)	1961–90	1991–2010	Change	ΔT °C 2005–10	1961–90	1991–2010	Change	ΔT °C 2008–10
Annual	9.3	10.2	+0.9*	+1.2*	−6.0	−4.6	+1.4*	
Summer	14.3	15.1	+0.8*	+2.0*	4.9	5.2	+0.3*	+1.7*
Winter	3.2	3.9	+0.7*	0.0 ^{ns}	−14.2	−11.7	+2.5*	0.0 ^{ns}
(B)								
	1961–90	1991–2010	Change		1981–90	1991–2000	2001–10	Change
GDD ₁					362.7	401.9	503.7	+141.0*
GDD ₅	1716	1915	+199*		7.6	85.9	131.2	+56.6*
GSL ₁					91.3	97.6	110.8	+19.5*
GSL ₅	270	291	+21*		91.3	43.4	60.9	+21.7*

covered and plant height to increase, flowering phenology to advance and an extended vegetative growing season. For leaf life span (referred to as LLS) we expect a reduced time needed to develop new leaves in a warming climate and thus LLS to reduce with OTC warming at the southern and north range margins. Also we expect LLS to be less in the warmer ‘south’ than in the colder ‘north’. These expected direct ecological responses may help to explain the observed range contraction ‘south’ and the increased occurrences ‘north’. Given that the northward retreat might additionally be related to decreased competitiveness of *Empetrum* relative to co-occurring Atlantic-continental *Calluna vulgaris* (L.) Hull (referred to as *Calluna*), while the increased occurrences of *Empetrum* might also be linked with increased competitiveness of boreal-Arctic *Empetrum* relative to the co-occurring species *Cassiope tetragona* (L.) D. Don (referred to as *Cassiope*), we also determined the concomitant changes in growth and phenology parameters for these species.

2. Materials and methods

2.1. Site description

At its southern range margin, *Empetrum* was studied in a coastal dune valley near Bergen aan Zee, the Netherlands (52°40′N, 4°38′E; 4–5 m above sea level), together with co-occurring *Calluna*. At its northern range margin *Empetrum* was studied at Endalen (78°11′N 15°44′E) with its co-occurring *Cassiope*.

2.2. Experimental warming (OTC)

In March 2005, OTCs (diameter 2.20 m; height 0.6 m) were installed in Bergen aan Zee (Henry and Molau 1997, Marion *et al* 1997); OTC ($n = 10$) and control plots ($n = 10$) were randomly chosen with *Empetrum* and *Calluna* present in each plot. From the end of May 2008, a paired setup, due to the

limited presence of *Empetrum*, was chosen for OTCs ($n = 10$) and control plots ($n = 10$) at Endalen. At both range margins, OTCs stayed in the field year-round.

2.3. Growing degree days

GDD value is a measure for the growing season intensity and is defined as the annually accumulated degree sum above a chosen threshold temperature (Førland *et al* 2004) and is calculated as

$$\text{GDD}_x = \sum_{i=1}^{365} (T_i - x) \quad T_i \geq x$$

where T_i is the daily mean temperature (°C) for day i and x the selected threshold temperature. We used the evidence based threshold temperature of 1 °C, as in Svalbard flowering of *Empetrum* starts immediately after snowmelt. We retrieved data from the Dutch (ECAD 2011) and Norwegian meteorological databases (DNMI 2011).

2.4. Growing season length

GSL is meteorologically expressed as the number of days with average temperatures above the threshold temperature of 5 °C (GSL₅). We calculated GSL₅ for ‘south’ (ECAD 2011) and GSL₁ (with a threshold temperature of 1 °C.) and GSL₅ for ‘north’ (DNMI 2011). In addition a phenological based growing season length (GSL_p) was assessed by determining the onset of vegetative growth, indicated by a bright green colour of the apex of shoots, senescence (brown colouring) of the leaves indicated the end of vegetative growth.

2.5. Temperature and plant parameter measurements

Temperature and plant parameter measurements, randomly labelling of shoots ($n = 5$ per species per plot) and positioning of temperature loggers were performed in a central section of 50 cm × 50 cm inside each OTC and control plot. Temperature

was measured synchronously in OTCs and control plots at hourly intervals with Gemini Tinytag loggers (TG-0050, Chichester, UK) that were installed 10 cm above soil level. The loggers were protected from direct sun radiation and precipitation by a plastic screen, $\phi = 10$ cm. Average temperatures over 24 h, 12 h (06.00–18.00) and 4 h intervals (10.00–14.00) were calculated to assess differences between OTCs and controls.

Shoot length increase (millimetre) was determined from the year boundaries on stems to the shoot apex. Measurement was abandoned when no growth was observed during two weeks at the end of August (at the northern margin) or September (at the southern margin).

Shoot growth rate (mm day^{-1}) was calculated as $1/2L_{\text{max}}/t_{75} - t_{25}$ where L_{max} is the maximum shoot length and $t_{75} - t_{25}$ the number of days between the date when 75% respectively 25% of the final shoot enhancement was attained (Bannister 1978). Plant cover (m^2) and height (cm; $n = 10$ per plot) of *Empetrum* and *Calluna* were measured in OTCs and control plots, to determine the possible effect of OTC warming on the competition between these species. *Empetrum* and *Calluna* plants were mapped per plot (scale 1:15 cm) and plant cover was determined in Adobe Photoshop CS4. In Bergen aan Zee, the accumulated annual biomass increment (2005–10) was determined after destructive final harvest in February 2011. At Endalen, we determined the mean annual biomass increment (2008–10) of harvested individual shoots of *Empetrum* and *Cassiope*. Immediately next to the OTC experiment, annual shoot growth ($n = 5$) in plots ($10 \text{ cm} \times 10 \text{ cm}$, $n = 5$) with equal cover (50%) of both species ('mixed') and in plots ($10 \text{ cm} \times 10 \text{ cm}$, $n = 5$) with either *Empetrum* or *Cassiope* ('monospecific') was determined. LLS was determined as the ratio between the number of green leaves and total number of leaves or leaf scar positions developed per year (Karlsson 1992).

Flowering phenology was assessed, with intervals of 3–4 days, as the percentage of phenological stages P1–P6 (the gradual description for male flowering development from P1: bud visible, to P6: male parts diminish and dry out) and P1–P6 (the gradual description for female flowering from P1: petals and stigmas visible, to P6: black berries, $\phi = 5$ –10 mm; Molau 1996). At Bergen aan Zee, the measurement of flowering phenology started the first week of February and lasted until after full senescence of anthers was reached by March and berries had coloured completely black by May and June. At Endalen, measurements started immediately after snowmelt in early June and assessment was finished at the end of August, when some ripe (black) berries were present. Berries ($n = 30$ per plot) were randomly collected ('south': July, 'north': August) and their diameter and weight determined. Simultaneously with phenological observations, the onset of vegetative growth, indicated by a bright green colour of the apex of *Empetrum* shoots was determined as well as the end of the vegetative growth period indicated by senescing (brown colouring) of leaves; growth parameters of *Cassiope* (2008–10) were determined on 14 June 2011.

2.6. Statistics

Differences between average air temperature in control plots and OTCs were analysed using a paired samples *t*-tests for three different time intervals (24, 12 and 4 h). Differences between shoot growth, leaf life span and berry weight and diameter in OTCs and control plots were assessed by one-way ANOVAs. To test whether OTC warming affected growth parameters across all consecutive years, a one-way ANOVA with repeated measurements was used, with temperature as the between-subject factor and time as within-subject factor. The OTC-effect on timing of the different phenological stages was analysed through chi-square tests of homogeneity with warming treatment and phenological stage as factors. Chi-square tests were essential to explicitly account for the dependences among the proportions of plants attributed to a particular phenological stage. All assessment dates and male and female data were analysed separately. Upon rejection of the overall null hypothesis for a particular chi-square test for homogeneity, a subset chi-square analysis was run to determine which phenological stage contributed most to the observed significant effect of warming treatment. Subset analysis was based on the progressive deletion of the stage-treatment combination with the highest contribution to the calculated chi-square value. Statistical data analysis was performed in SPSS 16.0.

3. Results

3.1. Temperatures

OTC placement significantly increased the mean annual and mean summer temperature at Bergen aan Zee ($p < 0.001$) and the mean summer temperature at Endalen ($p < 0.004$; table 1). Between 1961 and 1990 ambient average summer temperature has increased with 0.8°C in the Netherlands. Here, placement of OTCs led to an increase in average summer temperature by 2.0°C . At Svalbard, ambient average summer temperature has increased with 0.3°C between 1961 and 1990. Here, temperatures were on average 1.7°C higher in OTCs than in control plots. Mean annual values of both GDD_5 ($p < 0.001$) and GSL_5 ($p < 0.001$), in the Netherlands, as well as GDD_1 ($p < 0.001$) GDD_5 ($p < 0.001$), GSL_1 ($p = 0.008$) and GSL_5 ($p < 0.001$) at Svalbard have significantly increased since 1981 (table 1). The warming effect of OTCs for both north and south is shown in figure 1.

3.2. Plant responses at the southern range margin

OTCs resulted in an increase of the vegetative growing season length (GSL_p) of *Empetrum* by 75 days, starting 21 March and ending 5 September. The vegetative growing season length (GSL_p) of *Calluna* increased by 98 days after OTC placement (table 2: 1, 2). Also the annual mean shoot growth of both *Empetrum* ($p = 0.001$) and *Calluna* ($p = 0.001$) enhanced significantly, while daily growth rate of *Empetrum* increased by 1.25 mm day^{-1} and of *Calluna* by 1.96 mm day^{-1} ($p < 0.001$). The flowering season length of *Empetrum* with

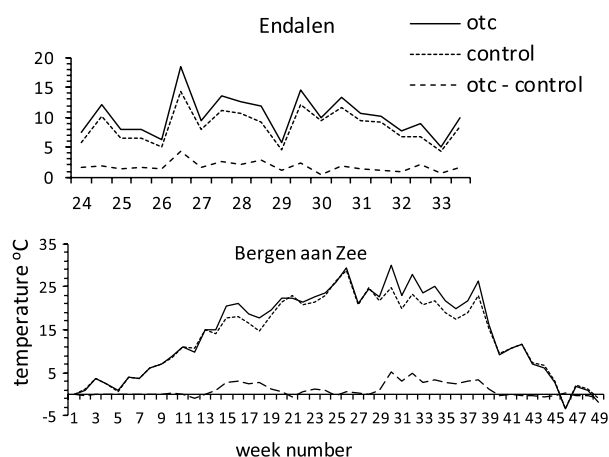


Figure 1. Average air temperature inside open top chambers (OTCs) and control plots south (Bergen aan Zee) and north (Endalen) for the year 2009. Average temperature values of 12 h (daytime: 06.00–18.00 h) intervals. The temperature difference between OTCs and control sites is at the bottom of the graph. Average temperature data of 2005–10 (south) and of 2008–10 (north) have been summarized in table 1.

ambient temperatures (137 days) decreased by 15 days, while phenology was affected in OTCs as follows (table 2: 8–12): initial bud burst (P1) was advanced (5–8 days; $p = 0.004$), and full development of anthers (P5) advanced (14–20 days; $p = 0.005$). Full development of ripe black berries (P5, P6) advanced (15–20 days; $p = 0.004$) too. In addition, berries achieved higher weight ($p < 0.001$) and larger diameter ($p < 0.001$; table 2: 13, 14). In OTCs, biomass had significantly increased both for *Calluna* ($p = 0.009$) and *Empetrum* ($p < 0.001$) and plant cover of *Calluna* significantly increased ($p < 0.001$), but not for *Empetrum* ($p = 0.139$; table 2: 15–18). Mean plant height of both species increased significantly in OTCs ($p < 0.001$ table 2: 19, 20). After five seasons in OTCs (2009), LLS of *Empetrum* had decreased approximately by two months ($p < 0.001$) and in the sixth season (2010) LLS had decreased up to 4 months ($p < 0.001$; table 2).

3.3. Plant responses at the northern range margin

GSL_p of *Empetrum* lasted from 1 June until 25 August and was similar for both OTCs and control plots (table 2: 1). Usually snow does not melt before the end of May or the beginning of June, and low temperatures occur at the end of August and/or the beginning of September (1.4 °C average September temperature; 1991–2010; DNMI 2011). Tundra soil in Endalen is frozen and snow covered from September until the end of May (DNMI 2011). Ecologically, this implies that extension of GSL through warming by OTCs is limited to some days only due to the prolonged presence of snow (table 1). In OTCs, annual mean shoot growth of *Empetrum* ($p < 0.005$) and of co-occurring *Cassiope* significantly increased ($p < 0.001$). No change in LLS ($p = 0.898$) was observed after three seasons of experimental warming (2008–10; table 2: 21). In OTCs, the phenological stages (P1–P6) showed no advance (table 2: 8–12). However,

in June 2011, immediately after snowmelt, we found many more berries (formed in 2010) in OTCs than in control plots. Also, by the end of August 2011, berries inside OTCs were all in stage P6 and were coloured black. These berries had also achieved higher weights ($p < 0.001$) and larger diameters ($p < 0.001$; table 2: 13, 14) than berries from control plots. Mean annual shoot length growth under ambient temperatures of *Empetrum* in monospecific stands (23.2 mm) showed no significant difference ($p = 0.840$) compared to mixed stands (24.8 mm) with *Cassiope*, while mean annual shoot length growth of *Cassiope* was significantly lower ($p = 0.03$) in mixed stands (13 mm) compared to monospecific stands (18.1 mm).

In table 2, column ‘R’ summarizes if the results are according to or opposite to the expected response direction. At the southern margin, responses 1, 3, 5, 13–15 and 19 of *Empetrum* are opposite to the expected response direction, while the responses 2, 4, 6–12, 16–18 and 20–21 are according to the expected response direction. Almost all responses were significant. In contrast, at the northern margin, most responses were insignificant. Those responses that were significant (i.e. responses 3–6 and 13–16) were all according to expectations.

4. Discussion

4.1. Temperature enhancement

At both range margins, the open top chambers (OTCs), significantly increased temperatures (table 1), but they may have had additional effects on soil moisture, relative humidity, photosynthetic active radiation and may have had other microclimatological impacts, possibly influencing biological and ecological responses. Bokhorst *et al* (2011b) discusses intended as well as unintended climatological changes in OTCs relative to control plots. With reduced windspeed, temperature beneath the OTCs panels may strongly increase while soil temperature and relative humidity may decrease. In our setup, we assume these impacts to be limited since we used wide (2.20 m diameter) OTCs and monitored and sampled only the central parts of 50 cm × 50 cm in the OTCs. In the Antarctic OTCs delay soil thaw by 3–13 days and experience extreme temperatures, potentially exceeding the physiological threshold of tolerance of species in summer (Bokhorst *et al* 2011b). Also, warming outside the main growing season can have strong negative impacts on *Empetrum* in the sub-Arctic (Bokhorst *et al* 2011a). In our experiments at the southern margin, OTCs did not experience temperatures exceeding 25 °C longer than for 4 h during summer and never exceeding an increase of 4 °C or higher compared to ambient temperature. Frozen soil only occurred once during 2005–10 for two weeks, winter 2011. Likewise, at the northern margin, summer temperature rarely exceeded 20 °C. In the ‘south’ and ‘north’, neither warming outside the main growing season nor any damage to the vegetation in OTC and controls has been observed. Of course we cannot rule out that the ecological responses we obtained with the OTC treatment are not due to warming impacts only, but

Table 2. Phenological and growth responses (mean values) of *Empetrum nigrum*, including shoot growth, biomass, area covered and plant height of co-occurring *Calluna vulgaris* and *Cassiope tetragona* to experimental warming with OTCs at its southern (Atlantic) and northern (High Arctic) geographic range margin. * = significant at 0.05; ns = not significant. R = expected response direction: + response according to expectation; – response opposite to expectation; 0 no significant response.

Parameter	52°: southern margin				78°: northern margin			
	Control	OTC	Change	% R	Parameter	Control	OTC	Change % R
1. Length of vegetative growing season (GSL _p) of <i>Empetrum</i> (date; days)	11/4–15/7; 91	21/3–5/9; 161	+75*	82 –	1. Vegetative growing season length (GSL _p) <i>Empetrum</i> (date; days)	1/6–25/8; 70	1/6–25/8; 70	0 ns 0 0
2. Length of vegetative growing season (GSL _p) of <i>Calluna</i> (date; days)	25/4–11/7; 78	4/4–29/9; 176	+98*	126 +	2. Growing season length (GSL _p) <i>Cassiope</i> (days)	70	70	0 ns 0 0
3. Annual shoot length growth (mm) <i>Empetrum</i>	30	84	+54*	180 –	3. Annual shoot length growth (mm) <i>Empetrum</i>	16.1	23.3	+7.2* 45 +
4. Annual shoot length growth (mm) <i>Calluna</i>	56	96	+40*	71 +	4. Annual shoot length growth (mm) <i>Cassiope</i>	7.4	10.1	+2.7* 36 +
5. Shoot growth rate (mm day ⁻¹) <i>Empetrum</i>	0.4	1.25	+0.85*	212 –	5. Shoot growth rate (mm day ⁻¹) <i>Empetrum</i>	0.28	0.42	+0.14* 50 +
6. Shoot growth rate (mm day ⁻¹) <i>Calluna</i>	0.9	1.96	+1.06*	118 +	6. Shoot growth rate (mm day ⁻¹) <i>Cassiope</i>	0.13	0.18	0.05* 38 +
7. Flowering season length <i>Empetrum</i> (date/days +/–)	16/2–30/6; 137	11/2–10/6; 122	–15*	–11 +	7. Flowering season length <i>Empetrum</i> date/days advance	31/5–12/7; 43	31/5–12/7; 43	0 ns 0 0
8. Phenology: bud burst date/days advance (P1–P2)	16–21/2	11–14/2	–5–8*	–14–20*	8. Phenology: bud burst date/days advance (P1–P2)	31/5–2/6	31/5–2/6	0 ns 0 0
9. Phenology: fully developed anthers; date/days advance (P5)	27–29/3	8–15/3	–14–20*	–14–20*	9. Phenology: fully developed anthers; date/days advance (P5)	21–30/6	18–27/6	3 ns 0 0
10. Phenology: berries; date/days advance (P2) ø1–2 mm	22–29/3	15–22/3	–7*	–7*	10. Phenology: berries; date/days advance (P2) ø1–2 mm	6–16/6	6–16/6	0 ns 0 0
11. Phenology: berries colouring black; date/days advance (P5) ø4–6 mm	24–4/2–5	4–12/4	–20*	–20*	11. Phenology: berries colouring black; date/days advance (P5) ø4–6 mm	21–30/6	18–27/6	3 ns 0 0
12. Phenology: berries black; date/days advance (P6) ø5–10 mm	3–30/6	15/5–15/6	–20*	–20*	12. Phenology: berries black; date/days advance (P6) ø5–10 mm	27/6–12/7	27/6–12/7	0 ns 0 0
13. Berry size (ø mm)	6.8	8.2	+1.4*	21 –	13. Berry size (ø mm)	6.0	7.3	+1.3* 22 +
14. Berry weight (mg)	164	287	+123*	75 –	14. Berry weight (mg)	108	181	+73* 68 +
15. Total biomass 2005–2010 (mg) <i>Empetrum</i>	904	1909	+1005*	111 –	15. Biomass of branches 2008–2010 (mg) <i>Empetrum</i>	48.2	64.2	+16.0* 33 +
16. Total biomass 2005–2010 (mg) <i>Calluna</i>	2067	2321	+254*	12 +	16. Biomass of branches 2008–2010 (mg) <i>Cassiope</i>	28.4	43	+14.6* 51 +
17. Area covered (m ²) <i>Empetrum</i>	2.13	1.75	–0.38 ns	–18 +	17. Area covered (m ²) <i>Empetrum</i>	1.5	1.5	0 0 0
18. Area covered (m ²) <i>Calluna</i>	0.72	1.60	+0.88*	122 +	18. Area covered (m ²) <i>Cassiope</i>	0.5	0.5	0 0 0
19. Plant height (cm) <i>Empetrum</i>	22	38	+16*	73 –	19. Plant height (cm) <i>Empetrum</i>	5	5	0 0 0
20. Plant height (cm) <i>Calluna</i>	34	56	+22*	65 +	20. Plant height (cm) <i>Cassiope</i>	5	5	0 0 0
21. Leaf Life Span (year) <i>Empetrum</i>	1.6	1.3	+0.3*	–19 +	21. Leaf Life Span (year) <i>Empetrum</i>	2.5	2.5	0 ns 0 0

for logistic reasons, it was not feasible to study the potential impacts of these artefacts in the current study. However, based on the above, we assume these artefacts to be limited.

4.2. Ecological responses to OTC warming at the southern margin

OTCs significantly decreased LLS (table 2: 21), according to the expected response direction. This supports the hypothesis that leaf longevity tends to decrease with warmer climates with reduced time needed to develop new leaves (Aerts 1995, Chabot and Hicks 1982, Karlsson 1992, Suzuki and Kudo 2000). OTCs also significantly advanced the onset and completion of the phenological stages P1–P6 of *Empetrum* by 5–20 days (table 2: 8–12) and thereby facilitated an earlier onset of vegetative growth, since the latter starts only after the end of flowering. The observed advanced onset and termination of flowering (table 2: 7) confirms our hypothesis, reflecting the cool boreal-Arctic distribution range of *Empetrum* and is also consistent with other plant responses to climate warming in the Northern Hemisphere (Ahas *et al* 2002, Arft *et al* 1999, Fitter and Fitter 2002, Menzel *et al* 2006, Schwartz *et al* 2006). This is consistent with advanced flowering season of *Empetrum* from April to May towards February to March (Van der Meijden 2005) under influence of ambient temperature increase in the Netherlands during the last few decades (EPG 2011; table 1).

In addition to the earlier onset, we also expected earlier termination of the vegetative growing season, but we found the opposite, i.e. a delayed end of the growing season (table 2: 1). Most of the direct ecological responses (annual shoot growth, shoot growth rate, berry weight and berry diameter, biomass; table 2: 3, 5, 13–15) showed a consistent and significant increase, opposite to our expectations of response direction. These results do neither support the susceptibility (expecting reduced growth and reproduction) of *Empetrum* to global warming (Fosaa *et al* 2004, Harrison *et al* 2006, Trivedi *et al* 2008, Neilson *et al* 2005) nor the northward retreat of *Empetrum* in Britain that has been attributed to increasing winter temperatures (Bell and Tallis 1973). It is thus not possible to explain northward retreats of *Empetrum* by these direct ecological mechanisms.

In addition to direct effects of warming, we also hypothesized that an indirect competitive effect of co-occurring *Calluna* could possibly be related to the northward shift of *Empetrum* at its southern range margin. The direct ecological responses of *Calluna* (table 2: 4, 6, 16, 18, 20) with an Atlantic-continental distribution range are indeed according to our expectations. Also the reduced ground area covered by *Empetrum* (table 2: 17) is according to our expected response direction. However, annual shoot growth, growth rate and biomass of *Empetrum* (table 2: 3, 5, 15) in response to increased temperatures in OTCs (table 1) exceed that of *Calluna*. Therefore there is no evidence of increased competitiveness of *Calluna* relative to *Empetrum* with OTC increased temperature. In summary, neither direct nor indirect ecological responses of *Empetrum* (and neighbouring *Calluna*) provide conclusive evidence explaining the northward retreat of *Empetrum* at its southern range margin in the Netherlands.

4.3. Ecological responses to OTC warming at the northern margin

OTCs significantly enhanced temperatures during the Arctic summer (table 1). However, neither GSL_p nor any of the flowering phenological stages (table 2: 1, 8–12) altered. Yet, in OTCs, massive ripening of berries with significantly increased diameter and weight compared to control plots was found (table 2: 13, 14). Small temperature differences, not captured by GSL , may influence biological processes (Körner and Basler 2010, EPG 2011, Suzuki and Kudo 1997) and may cause differences in phenology and extension of the growing season (Parmesan 2006, Suzuki and Kudo 1997). Instead, meteorologically obtained GDD-increases (using a 5 °C threshold) with global warming have been related to advanced timing and increased length of the growing season (Førland *et al* 2004, Linderholm 2006). A GDD, with a 1 °C threshold may even be more relevant for tundra plant species than a meteorological defined GDD, since many early spring flowering Alpine and Arctic species have a low temperature threshold (Körner 1999). Indeed, at the northern margin, the ambient mean annual GDD_1 significantly increased ($p < 0.001$) since 1981 (table 1). Therefore, the significant increase of direct ecological responses (table 2: 3, 5, 13–15) of *Empetrum* to the OTC treatment may be attributed to the increased GDD value, representing accumulated heat, despite the irresponsiveness of the growing season length.

In addition to the phenological responses, also the direct ecological responses, i.e. annual shoot growth, shoot growth rate and biomass (table 2: 3, 5, 15), were according to our expected response direction, based on the boreal-Arctic geographical range of *Empetrum*. Our findings do support increased shoot length reported from the Finnish sub-Arctic (Shevtsova *et al* 1997) and Alpine vegetation in Japan (Kudo and Suzuki 2003, Suzuki and Kudo 1997, 2000, Wada *et al* 2002) and increased berry diameter and weight (Suzuki and Kudo 1997). LLS of *Empetrum* did not change upon warming. However, consistent with expectations, LLS at the northern margin (2.5 years; table 2: 21) was much higher than in the temperate south (1.6 years), representing the increased time needed to develop new leaves at the northern margin. Since experimental warming at the northern margin only lasted for three years until now, LLS may not have changed yet, but may do with prolonged duration of the OTC treatment. If so, then we expect LLS to reduce with OTC warming, as we found at the southern margin. Altogether, at the northern margin, growth and reproduction increased while phenology of *Empetrum* remained unaltered, thereby supporting increased occurrences of *Empetrum* on Svalbard.

We had also hypothesized that, in addition to direct ecological responses to OTC warming, an indirect competitive advantage relative to co-occurring *Cassiope* may facilitate the expansion of *Empetrum* at its northern range margin. Indeed, OTC warming caused increased shoot length and growth rate of *Empetrum*, exceeding that of *Cassiope* (table 2: 4, 6). Also, outside the OTCs, annual shoot growth of *Empetrum* did not differ in monospecific and mixed stands while the annual shoot growth of *Cassiope* was significantly

reduced in mixed stands with *Empetrum*. This may indicate increased competitiveness of *Empetrum* relative to *Cassiope* at the northern margin, as was found previously for increased competitiveness of *E. nigrum* spp. *japonicum* relative to the Arctic and sub-Arctic *Loiseleuria procumbens* (Wada et al 2002). However, despite the enhanced growth rates inside the OTCs, it is *Cassiope* which showed a larger increase in biomass compared to *Empetrum* (table 2: 15, 16), opposite to the expected response direction. There is thus no conclusive evidence for increased competitiveness of *Empetrum* relative to co-occurring *Cassiope* with OTC warming. More and continued research on seed dispersal, germination and establishment in response to global warming is thus needed to unravel range expansion of *Empetrum* in the high Arctic (Graae et al 2008). A longer research period could provide a more robust picture as shown by Chapin et al (1995) studying Arctic tundra vegetation during nine years.

4.4. Conclusions

In conclusion, this study sought to understand the ecological mechanisms involved with the northward retreat of *Empetrum* at its southern range margin and increased occurrences at high Arctic Svalbard, as attributed to current global warming. By analysing various growth and phenological responses to OTC warming at its range margins, we obtained partial evidence for an ecological explanation of range shifts of *Empetrum*. Contrary to our expected response direction, *Empetrum* growth and biomass parameters increased with OTC warming at the southern margin, leaving its observed northward retreat unexplained. Neither have we found an indication of increased competitiveness of neighbouring *Calluna vulgaris* relative to *Empetrum* in response to OTC warming. This leaves the question if warming is causing the contraction of the southern range margin of boreal-(sub) Arctic *Empetrum* unanswered.

Increased occurrences on Svalbard may be explained by direct ecological responses of shoot and biomass growth, as well as berry production and size, while no conclusive evidence was found of increased competitiveness of *Empetrum* relative to co-occurring *Cassiope* upon warming.

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