Are heat and cold resistance of arctic species affected by successive extreme temperature events?

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Summary

• Extreme temperature events are projected to increase in frequency in a future climate. As successive extremes could occur more frequently, patches of vulnerable tundra vegetation were exposed to two consecutive heat waves (HWs) of 10 d each, with a 5-d recovery period in between.
• Surface temperatures during the HWs were increased approximately 6°C using infrared irradiation sources.
• In three of the four target species (Pyrola grandiflora, Polygonum viviparum and Carex bigelowii), plant conditions improved upon the first exposure. Depending on species, leaf relative growth, leaf chlorophyll content or maximal photochemical efficiency was increased. In P. grandiflora the positive effects of the heat on the photosynthetic apparatus led to augmented net photosynthesis. By contrast, Salix arctica responded mainly negatively, indicating species-specific responses.
• During the second HW, leaf mortality suddenly increased, indicating that the heat stress induced by the extreme events lasted too long and negatively influenced the species resistance to high temperature. After the HWs, when plants were exposed to (low) ambient temperatures again, plant performance deteriorated further, indicating possible loss of cold resistance.

Key words: global change, extreme temperature event, arctic tundra, chlorophyll fluorescence, heat and cold resistance.


Introduction

Studies on the effects of global warming on plants raise increasing concerns on the future fate of plant communities and plant diversity. Warming affects plant functioning in a variety of ways because of the pervasive role of temperature in the regulation of biochemical reaction rates, morphogenetic processes, and matter and energy exchange with the environment (Taiz & Zeiger, 1991). To date, mainly consequences of increases in mean air temperatures have been considered, and major uncertainties exist about the future role that extreme temperatures may play in shaping community assemblage (Press et al., 1998). To date, mainly consequences of increases in mean air temperatures have been considered, and major uncertainties exist about the future role that extreme temperatures may play in shaping community assemblage (Press et al., 1998). Small changes in the mean climate can drastically alter the frequency of extreme temperature events (Wigley, 1985; Karl & Nicholls, 1997). The environmental impacts from such events can be significantly greater than those associated with mean increases (Karl & Nicholls, 1997).

Despite this, few studies have investigated the biological effects of temperature extremes on plant communities. Some records exist on the community impact of extreme heat, which can change community composition, for example, by favouring the expansion of C₄ over C₃ species (White et al., 2000, 2001). Conversely, much research has been done on effects of temperature extremes on individual plants in controlled environments. For example, many studies have focused on molecular mechanisms, such as the synthesis of specific proteins upon heat-shock exposure (Howarth, 1991). However, a hiatus exists concerning the effects of heat waves (or acute heat stress) on the intermediate level of leaf and whole-plant physiology on plants in the wild. Larcher (2003)
stated that stress is a state in which increasing demands made upon the plant lead to an initial destabilization of vital functions, followed by normalization and improved tolerance or resistance. However, if the limit of a plant’s ability to adjust is reached, hitherto latent damage develops into chronic disease, irreversible injury or death. For plants exposed to heat extremes, a resistance–resilience scheme therefore seems most appropriate to characterize the impact, with resistance being defined as the ability of a species’ biomass to withstand displacement from control levels and resilience as the speed of recovery from a stress state back to control levels (Westman, 1978).

As general circulation models predict greatest temperature changes at high latitudes, and as these regions are at the same time highly vulnerable to climate warming (Phoenix & Lee, 2004), we investigated effects of heat extremes on tundra vegetation. Arctic plants are generally well adapted to survive in a moisture-, heat- and nutrient-deficient environment (Press et al., 1998). For example, they synthesize cold acclimatization proteins, dissolved in the cytoplasm, which lower the freezing point of the cell (Salisbury & Ross, 1992). However, it is uncertain whether they can also withstand a surplus of heat. In previous experiments during both 2001 and 2003, we exposed tundra vegetation to a single heat wave (Marchand et al., 2005). In 2001, plant performance was improved during this extreme event (increased stomatal conductance \( g_s \) and photosystem II (PSII) maximum efficiency \( F_v/F_m \)), while it deteriorated afterwards. The latter was ascribed to the fact that the plants acclimatized to the warmer conditions and the threshold of heat stress susceptibility in arctic plants.

In the summer of 2004, six plots (40 × 50 cm) of tundra shrub vegetation were selected in the vicinity of the Arctic Station of the University of Copenhagen, located in West Greenland on Disko Island (69°15′ N, 53°34’ W). Within these plots, four target species were selected for physiological and growth measurements, Salix arctica Pall., Polygonum viviparum L., Pyrola grandiflora Radius and Carex bigelowii Tor. ex Schwein. Other species in the community, not used for measurements owing to too small leaves or insufficient abundance, were Vaccinium uliginosum L., Empetrum nigrum L., Betula nana L. and mosses. In the region, the annual air temperature and precipitation are −3.9°C and 447 mm, respectively (averages between 1960 and 1991, Nielsen et al., 2001) and the permafrost is continuous.

At the onset of the experiment, cover and species composition were determined, using a 500-point frame. On each point of the frame, the species intercepting a vertical laser beam was recorded. The six plots were subsequently appointed to two temperature groups to have similar cover and species composition before heating began (MANOVA of cover per species with treatment as fixed factor, \( P > 0.05 \)). The three heated plots were exposed to two consecutive heat waves of 10 d each, with a 5-d recovery period (R1) in between, while the other three plots served as controls. Both the first heat wave (HW1) from 18 June (day of the year (DOY) 170) to 28 June (DOY 180) and the second heat wave (HW2) from 4 July (DOY 186) to 14 July (DOY 196) were generated with the free air temperature increase (FATI) system. The latter was designed to homogeneously heat limited areas of short vegetation (< 30 cm), by emitting a constant flux density of infrared irradiation (0.8–3 µm) – see Nijs et al. (2000) for technical details. Each heated plot had an individual FATI-unit placed on the north side, whereas the control plots had dummy units without lamps. The maximum capacity of the equipment, which was set in the current study, yielded approx. 8°C increase of the vegetation temperature \( T_{\text{vegetation}} \) in earlier experiments. While the FATI technique increases vegetation and soil temperature similar to global change scenarios, the surrounding air temperature is heated less than expected in an actual warmer climate, because it is warmed indirectly. Plant parts that are ‘shaded’ from the IR flux by other plant parts might therefore experience less warming than intended. However, the leaf area index in our tundra plots being low (30–50% was bare ground, see the Results section), we assume that shading was limited and warming uniform. A more important drawback of the FATI technique is that it cannot generate constant relative humidity relative to ambient conditions, as predicted by global change scenarios (Kimball, 2005) (although water vapour added to the air through enhanced evapotranspiration in response to warming may mitigate this; I. Nijs, pers. comm.). Kimball (2005) has suggested correcting for the excess water loss under FATI with a drip irrigation system, but this solution was not yet available at the time of our experiment. As a consequence, we have stimulated the not unlikely scenario of a heat wave that coincides with a lower than average humidity of the air (Chaves, 1991).

Materials and Methods

Set up

In the summer of 2004, six plots (40 × 50 cm) of tundra shrub vegetation were selected in the vicinity of the Arctic
Environmental measurements

Soil volumetric water content of the plots was measured 12 times during the experimental period with time domain reflectometry (Trime-FM; Eijkelkamp Agrisearch Equipment, Giesbeck, the Netherlands), and depth of the active layer 6 times with a fibreglass rod (both recorded at four locations per plot, one per quadrant). Each 30 min between 14:00 h local daylight time (LDT) on 18 June (DOY 170) and 13:00 h LDT on 26 July (DOY 208), data loggers (16 kb, 12-bit, eight-channel, DL2E; Delta T, Cambridge, UK) recorded the following seven climate parameters: photon flux density (PFD) of photosynthetically active radiation (PAR), measured with a gallium arsenide sensor (JYP-1000; SDEC, Reignac sur Indre, France) fixed in an open place near the FATI site; T_{vegetation}*, monitored with noncontact semiconductor sensors ('infracouple', type OS39-MVC-6; Omega Engineering, Stamford, CT, USA); air temperature (T_{air}) at 5 cm height and soil temperature (T_{soil}) at 2.5, 7.5, 15 and 30 cm depth, recorded with precision centigrade temperature sensors (LM35A; National Semiconductor, Arlington, TX, USA).

Plant measurements

The cover and species composition measurements conducted with the pin-frame method at the start of the experiment (see earlier), were repeated after HW1 and HW2 and after the second recovery period (R2, at the end of the experiment). Relative chlorophyll content was measured every 2 d with the Chlorophyll Content Meter (CCM-200; Opti-science, Tyngsboro, MA, USA), on five leaves per target species per plot (no data for _C. bigelowii_ owing to too-narrow leaves). Simultaneously, length and width of the youngest leaf were measured in five labelled plants per target species per plot. From this, we calculated the leaf area with the formula of an ellipse for _S. arctica_, _P. viviparum_ and _P. grandiflora_ and as length \times width (measured at half leaf length) for _C. bigelowii_. Relative growth rate (RGR) of the newly appearing leaf area (youngest leaf at the start + newly appeared leaves) on the plant (_P. viviparum_ and _P. grandiflora_), the twig (_S. arctica_) or the shoot (_C. bigelowii_ was then determined for each 2-d interval.

Chlorophyll a fluorescence was measured three times during the day every 2 or 3 d with a plant efficiency analyser (PEA; Hansatech Ltd, King’s Lynn, UK), on three leaves per target species per plot. After 30 min of dark adaptation, fluorescence transients were recorded for 1 s with a data acquisition rate of 10 µs for the first 2 ms and 1 ms for the rest of the time. Upon sudden illumination of a dark-adapted leaf, PSII fluorescence yield increases following polyphasic kinetics (Strasser et al., 1995). A selection of normalized fluorescence variables were calculated from the fluorescence transients according to the energy flux theory of Strasser & Strasser (1995) and Strasser et al. (2000), using the BIOLYZER software (R. M. Rodriguez, The Bioenergetics Laboratory, University of Geneva, Switzerland):

- $F_0$, the fluorescence intensity at 50 µs when all reaction centres (RC) of PSII are open;
- $F_{\infty}$, the maximum fluorescence intensity, assuming that excitation intensity is high enough to close all RCs;
- $F_v/F_m = (F_m - F_0)/F_m$, the maximum efficiency with which an absorbed photon is trapped by a reaction centre of PSII, in other words, the maximum yield of primary photochemistry.

With a portable photosynthesis system (CIRAS; PPSystems, Herts, UK), which consisted of the CIRAS-1 Differential CO$_2$/H$_2$O Infra-Red Gas Analyser, the Integral Cuvette Air Supply Unit and the PLC broad leaf chamber, we measured three parameters: net CO$_2$ assimilation rate (photosynthesis, $P_{\text{net}}$), stomatal conductance ($g$) and ratio of internal to atmospheric CO$_2$ concentration ($C/C_a$), on three leaves per target species per plot. $C/C_a$ represents a balance between the rates of inward CO$_2$ diffusion (controlled by stomatal conductance) and CO$_2$ assimilation (controlled by photosynthetic light/dark reactions) (Ehleringer & Cerling, 1995). Measurements were done four times during the day to encompass a range of PAR levels. If the measured leaf did not fill the chamber, a digital picture was taken. To calculate the leaf area, the percentage of the chamber area (2.5 cm) covered by the leaf was determined with an image analysis system.

Statistics

Variables measured at plot level (e.g. the environmental parameters, cover or mortality) or at species level if measured on the same plant (e.g. RGR) were analysed with repeated measures analysis of variance (RM-ANOVA) to detect effects of the heat waves (treatment as fixed factor). DOY was the repeated factor. These tests were done separately for each period (HW1, R1, HW2 and R2). In cases without repeated measures (e.g. $F_v/F_m$) ANOVA-tests were all done per period per species, as these factors interacted with treatment in the overall ANOVAs (not shown). Treatment effects on $g$, $C/C_a$ and $P_{\text{net}}$ were tested with analysis of covariance (ANCOVA), with PFD as covariate. The PFD data associated with the $P_{\text{net}}$ measurements were log-transformed to improve linearity. In all tests, plot was nested within treatment to avoid pseudoreplication. All variables were examined for normality and heterogeneity of variance and all statistical tests were considered significant at $P < 0.05$. Analyses were performed using SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

Results

Environmental measurements

The average background air temperatures during June and July 2004 (5.6°C and 6.4°C, respectively; recorded by the Arctic Station’s meteorological station, R. Erjnaes, pers.
calculated that, in a future climate, successive extremes could occur more frequently. We therefore exposed the plots to a scenario of two such events, one succeeding the other with a short recovery period in between.

In both heat waves, $T_{\text{vegetation}}$ was increased approx. 6.5°C (see Table 1) above a relatively constant (between periods and FATI-units) mean $T_{\text{vegetation}}$ in the unheated plots. This increment was slightly below the maximum capacity of the FATI-system, probably because our plots were quite wet (at least in the beginning of the experiment), causing much of the added energy to be dissipated as latent heat in evapotranspiration. In the upper soil layer, temperatures were increased only about 3°C during HW1 (Fig. 1a) but 5°C during HW2 (Fig. 1b).

This $\Delta T_{\text{soil}}$ declined towards the deeper layers, making the temperature profile steeper, and remained greater during HW2 at all depths. Soil moisture was higher in the heated plots during the first heat wave (Fig. 1c), which probably reflects the situation before heating began. As expected, the soil desiccated more in these plots, which made them drier than the control plots during HW2. By contrast, the active layer depth (mean ± SD around 43.7 ± 9.6 cm) was not significantly altered by the heat waves (not shown; $P = 0.14$).

### Plant measurements

Although the heating seemed to increase the cover of the four target species (Fig. 2a), no significant treatment effect occurred. Also, at community level, there was no significant difference between the two treatments (Fig. 2b). However, the cover of dead plant parts increased substantially in the heated plots during HW2 (Fig. 2c).

By contrast, during the heat waves we recorded various improved plant conditions in three of the four target species: *P. grandiflora*, *P. viviparum* and *C. bigelowii*. For example,

#### Table 1

<table>
<thead>
<tr>
<th>Heat wave period 1 (18–28 June 2004)</th>
<th>$T_{\text{vegetation}}$ (°C)</th>
<th>$\Delta T_{\text{vegetation}}$ (°C)</th>
<th>$T_{\text{air}}$ (°C)</th>
<th>$\Delta T_{\text{air}}$ (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FATI 1</td>
<td>10.9</td>
<td>−0.7 ± 1.0</td>
<td>9.6</td>
<td>−0.7 ± 0.9</td>
</tr>
<tr>
<td>FATI 2</td>
<td>9.3</td>
<td>0.0 ± 0.9</td>
<td>8.7</td>
<td>0.7 ± 0.9</td>
</tr>
<tr>
<td>FATI 3</td>
<td>11.2</td>
<td>−0.3 ± 1.1</td>
<td>8.8</td>
<td>−0.4 ± 0.8</td>
</tr>
<tr>
<td>Recovery period 1 (29 June–3 July 2004)</td>
<td>10.9</td>
<td>−0.7 ± 1.0</td>
<td>9.6</td>
<td>−0.7 ± 0.9</td>
</tr>
<tr>
<td>FATI 1</td>
<td>9.3</td>
<td>0.0 ± 0.9</td>
<td>8.7</td>
<td>0.7 ± 0.9</td>
</tr>
<tr>
<td>FATI 2</td>
<td>11.2</td>
<td>−0.3 ± 1.1</td>
<td>8.8</td>
<td>−0.4 ± 0.8</td>
</tr>
</tbody>
</table>

*A separate FATI-unit was used for each heated plot (FATI 1, 2 and 3), associated with an unheated reference plot.*
RGR was stimulated during HW1 in *C. bigelowii* and *P. viviparum* (Fig. 3). Leaf relative chlorophyll content was enhanced during both heat waves in *P. grandiflora* and *P. viviparum* (Fig. 4). We also found evidence for a positive effect of the heat on the photosynthetic apparatus. In *P. grandiflora* and *P. viviparum*, the PSII maximal efficiency ($F_{v}/F_{m}$) was enhanced in the heated plots compared with their unheated counterparts during both heat waves (Fig. 5a,c). Conversely, in *C. bigelowii* the positive effect of the heat on $F_{v}/F_{m}$ was only apparent during HW2 (Fig. 5e).

In the three species that responded predominantly positively during the heat waves (*P. grandiflora*, *P. viviparum* and *C. bigelowii*), the aforementioned changes in chlorophyll
fluorescence resulted in increased net photosynthesis ($P_{\text{net}}$) only in *P. grandiflora* during HW1 (Fig. 5b). In the other two species, $P_{\text{net}}$ was never stimulated during the exposure (Fig. 5d,f). Stomatal conductance was not affected during the heat waves in *P. grandiflora*, *P. viviparum* and *C. bigelowii* (Fig. 6a,c,e). The only consistently negative effect in these three species was an increased $C_i/C_a$ ratio during HW2 (Fig. 6b,d,f), while $g_s$ was not altered at that time (see earlier). This indicates that the demand of CO$_2$ was reduced relative to the supply, despite the fact that maximal photochemical capacity was raised (see earlier). This deterioration of plant functioning coincided with the aforementioned augmented leaf mortality (cf. Figure 2b).

One species, *S. arctica*, was predominantly influenced negatively by the heat treatment. Its $F_i/F_m$ decreased during HW1 (Fig. 5g). Moreover, its $g_s$ declined during both heat waves (Fig. 6g), and its $C_i/C_a$ ratio was raised during HW2 (Fig. 6h). Relative growth rate and $P_{\text{net}}$ (Fig. 5h) were not influenced. The only positive effect of the heat in this species was a higher leaf relative chlorophyll content during HW2 (Fig. 4c).

We conclude that the responses to the successive extreme events were species-specific, with an improved performance during HW1 in three of the four target species, and less unequivocal effects during HW2. By contrast, plant performance in the heated plots deteriorated clearly after the heat waves in most species, in particular after HW2. For example, during R2, leaf relative chlorophyll content in *P. viviparum* and *S. arctica* became equal to or lower than the values measured in the unheated plots (Fig. 4b,c, ANOVA, treatment × DOY interaction, $P < 0.05$). The same phenomenon occurred in $F_i/F_m$ (all target species) and in $g_s$ (*P. grandiflora* and *C. bigelowii*) (Figs 5 and 6, respectively). A decline in $g_s$ was also observed in the other two target species during R2, but was not significant. The reductions were associated with a significant decline of $P_{\text{net}}$ in *P. viviparum* (Fig. 5d). No significant changes in $P_{\text{net}}$ were observed in the other species during the recovery periods despite their decreased photochemical efficiencies (see earlier).

**Discussion**

The first heat wave penetrated only into the upper soil layers, as the soil had a high moisture content and, consequently, a high heat capacity (Woo & Xia, 1996). However, by the time of the second heat wave the soil was more desiccated, which allowed soil temperatures to rise above 10°C also in the deeper layers. Nadelhoffer et al. (1991) observed that both microbial respiration and nitrogen (N) mineralization in arctic soils are almost insensitive to temperatures between 3°C and 9°C, but can increase by a factor of 2 or more between 9°C and 15°C. The heat waves may therefore have temporarily increased the rates of carbon (C) and N mineralization in our experiment. Although the associated soil drought may have counteracted this in HW2, the observed increase in leaf relative chlorophyll content in the heated plots seems to confirm the hypothesis of enhanced nutrient availability. According to Bowen (1991), exceeding the 10°C threshold similarly alleviates growth limitations in tundra species, which was demonstrated by the accelerated growth in *C. bigelowii* and *P. viviparum* during the first heat wave. Possibly, this was reinforced by more available nutrients (Jonasson, 1992; Parsons et al., 1995). Stënstrom & Jonsdottir (1997) observed that leaf growth in *C. bigelowii* is sensitive to warming, and responded to a 2°C temperature increment in open-top chambers.

By contrast, the improved growth conditions were apparently not exploited by our plants during the second heat wave, as all species had largely completed their growth cycle. Impact assessments of heat waves should therefore take into account...
the period in the season during which the extremes occur. As a consequence of the cessation of growth by early July, it was not possible to establish how long the stimulation of growth induced by the simulated extremes could persist. Given the limited amount of nutrients that can be made available in this harsh environment (Arft et al., 1999), lasting effects are unlikely. It cannot be excluded, however, that such changes nevertheless modify community composition in the long term as growth was not stimulated in all species.

Given the stimulation of photosynthetic pigment synthesis, we expected higher photosynthetic rates in the heated plots, in addition to the direct enhancement expected from higher enzyme activities, provided that the temperature optimum would not be exceeded (Berry & Björkman, 1980). Optimum temperatures differ between arctic species, but vary generally between 10°C and 20°C (Tieszen et al., 1981). In our experiment, the plants were exposed most of the time to ambient temperatures below this range, which the heating increased towards 15°C. Nevertheless, photosynthesis was stimulated only in P. grandiflora during the first heat wave, which originated from improved maximal photochemical efficiency (Fv/Fm). However, under exposure to the second heat wave net CO2 uptake of the P. grandiflora leaves was no longer stimulated. In fact, the observed increase in C/Co at

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**Fig. 5** Time course of maximal photosystem II (PSII) photochemical efficiency (Fv/Fm) (left panels) and leaf net photosynthesis (Pnet) (right panels) in the four target species. Averages ± 1 SE of 27 measurements (nine per plot) for Fv/Fm or of 12 measurements (four per plot) for Pnet in heated (closed circles, solid line) and unheated (open circles, broken line) plots, on different days of the year (DOY). Significance levels per period (ANOVA or ANCOVA with photon flux density as covariate in case of Pnet): ***, P < 0.001; **, P < 0.01; *, P < 0.05; otherwise not significant.
that time indicates deterioration of photosynthesis (although not significant), as stomatal conductance was not altered. This suggests that *P. grandiflora* was stressed during the second heat wave, despite the increased photochemical efficiency (given the aggravated drought, we exclude that the increased \( \text{C}_i/\text{C}_a \) originated from stomatal opening). A possible explanation for the change in response between HW1 and HW2 is the duration of the heat, as chronic stress can destabilize structural (e.g. proteins, biomembranes and cytoskeleton) as well as functional (e.g. biochemical processes and energy metabolism) characteristics, ‘exhausting’ the plant (Larcher, 2003). In *P. viviparum* and *C. bigelowii* we observed no changes in net photosynthesis during either heat wave, despite the fact that \( F_v/F_m \) was also enhanced in these species.

Temperatures may have exceeded the optimum in these two species during the first heat wave, causing photorespiration to increase (Tieszen *et al.*, 1981) and/or Calvin cycle enzyme activity to decrease (Xiong *et al.*, 1999). Similar to *P. grandiflora*, \( \text{C}_i/\text{C}_a \) was also higher in *P. viviparum* and *C. bigelowii* during the second heat wave, confirming that stress lasted too long and affected plant resistance in these species. The steep increase in leaf mortality during HW2 is in agreement with this hypothesis.

Contrary to the other three species, *S. arctica* mainly responded negatively to the heat waves. According to Arft *et al.* (1999), this genus has tight developmental control over meristem activity, which may limit the ability to react rapidly. Herbaceous species (*P. grandiflora*, *P. viviparum* and *C.*

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**Fig. 6** Time course of stomatal conductance \( (g_s) \) (left panels) and ratio of internal to atmospheric CO\(_2\) concentration \( (\text{C}_i/\text{C}_a) \) (right panels) in the four target species. Averages ± 1 SE of 12 measurements (four per plot) in heated (closed circles, solid line) and unheated (open circles, broken line) plots, on different days of the year (DOY). Significance levels per period (ANCOVA with photon flux density as covariate): ***, \( P < 0.001 \); **, \( P < 0.01 \); *, \( P < 0.05 \); otherwise not significant.
bigelowii in this research) have a more flexible morphology, a greater ability to scavenge for nutrients and hold greater reserves of such resources in the roots (Shaver et al., 1997). In accordance with this, chlorophyll content increased at the start of the first heat wave in heated P. grandiflora and P. viviparum plants, as opposed to only during the second heat wave in S. arctica. However, many other responses of S. arctica were negative, hence more frequent heat waves in a future climate might impair this species’ competitive ability.

Compared with the findings during the heat waves, we observed a clear deterioration of plant performance after the exposure in all species. The parameters \( g_c \) and \( \frac{F_v}{F_m} \) tended to decrease in the four target species after HW2 (though not all significantly). Polygonum viviparum and S. arctica also exhibited reduced chlorophyll content at that time, which resulted in reduced net photosynthesis only in P. viviparum (perhaps because only green leaves were used for measurements).

Possibly, the plants lost their cold acclimatization during the exposure, resulting in damage upon return to lower temperatures afterwards (Marchand et al., 2005). Cold acclimatization proteins, synthesized by arctic species (Salisbury & Ross, 1992), might have been broken down or immobilized by the heat. However, other cellular features involved in acclimatization to temperature (e.g. protective solutes, lipid composition, antioxidants) might have been altered during the heat waves (Ciamporova & Triginova, 1999; Somero, 2004) and could have caused loss of cold acclimatization.

We conclude that, during the first heat wave, the plants were functioning better. During the second heat wave we found, in addition to positive effects, indications that the induced heat lasted too long and negatively affected the resistance of the species to high temperatures. In addition, the resistance to low temperatures was probably lost since plant performance deteriorated substantially in the aftermath of the heat waves, excluding the resilience-issue in this study. The apparent impact of successive heat waves on the heat and cold resistance of arctic species should preferably be confirmed by biochemical research. Whether changes caused by heat stress diminish the competitive ability of arctic species against species from more southern latitudes that migrate into the Arctic in a future climate, remains to be explored. However, wider implications of the temporal variability of climate on biodiversity might be expected. For example, diverse communities experience an enhanced risk of local extinction under extreme stress (Van Peer et al., 2004).

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