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Experimental warming had little effect on carbon-based secondary compounds, carbon and nitrogen in selected alpine plants and lichens

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Running title: Effects of warming on alpine plants and lichens

Abstract

Global warming is expected to change plant defence through its influence on plant primary resources. Increased temperature (T) will increase photosynthesis, and thus carbon (C) availability, but may also increase soil mineralization and availability of nitrogen (N). More access to C and N is expected to mainly increase plant growth, and, according to hypotheses on resource based defence, this could lower plant concentrations of carbon-based secondary compounds (CBSCs).

We used two already established warming experiment with open top chambers (OTCs) and control plots in alpine south-western Norway, one on a ridge (8 years' treatment) and a one in a leeside (3 years' treatment), to study the effects of warming on plant and lichen defensive compound concentrations. The study included five vascular plant and six lichen species.

One vascular plant species had lower concentration of CBSCs under elevated T, while the others did not respond to the treatment. In lichens there were no effects of warming on CBSCs, but a tendency to reduced total C concentrations. However, there were effects of warming on nitrogen, as the concentration decreased inside OTCs for three species, while it increased for one lichen species. Lichens generally had higher CBSC and total C concentrations on the ridge than in the leeside, but no such pattern were seen for vascular plants.

No elevated temperature effect on CBCSs is most probably a result of high constitutive defence under the limiting alpine conditions, suggesting that chemical defence is little subject to change under climate warming, at least on a short-term basis. We suggest that the driving forces of plant defence in the arctic-alpine should be tested individually under controlled conditions, and suggest that competition from other plants may be a greater threat under climate warming than increased herbivory or disease attacks.

K**ey Words:** Vascular plants, lichens, secondary compounds, CBSC, lichen compound, temperature, carbon, nitrogen.

1. Introduction

Carbon-based secondary compounds (CBSCs), generally phenolics and terpenoids, defend plants against damaging radiation, herbivores, and competition from other plants. The variation in CBSC concentration and composition within and between species is only partly understood, and ecologists have put forward several hypotheses where the CBSC level has been positively linked to available photosynthates (carbon, C), and negatively linked to growth and nutrient status (nitrogen, N) in the plants (e.g. the Carbon Nutrient Balance (CNB) Hypothesis, Bryant et al., 1983, see Stamp, 2003 for an overview). The predictions are, in short, that plants growing in environments with high resource (nutrient) availability will prioritize growth (simply because they can), and spend less on defence, while plants in (nutrient) limiting environments will invest more in C-based defence because growth is restricted and C may be in excess (Herms and Mattson, 1992 and references therein). In line with this, it is also expected that slow-growing species and perennials will invest more in defence than pioneer plants and annuals (Tuomi et al., 1991; Stamp, 2003).

Light intensity will also affect the defence level of plants, as it affects photosynthesis and thus assimilation of C. Shade plants may thus have lowered defence levels (Bryant et al., 1983; Mole et al., 1988; Nichols-Orians, 1991). Experimental studies have both supported (e.g. Bryant et al., 1983; Coley et al., 2002; Leser and Treutter, 2005) and opposed (e.g. Baldwin et al., 1993; Iason and Hester, 1993; Lamontagne et al., 2000) these hypotheses. However, recent biochemical and molecular studies strongly support the idea that secondary metabolites are regulated in response to C and nitrogen N status in the plant (Fritz et al., 2006; Matt et al., 2002), meaning that the availability of resources is central for the level of defence. At the same time, both hypotheses (Bryant et al., 1983; Tuomi et al., 1988; 1991; Stamp, 2003) and experimental evidence suggest (Muzika et al., 1989; Holopainen et al., 1995; Koricheva et al., 1998) that defence levels are not exclusively dependent on resource levels. However, the CNB hypothesis also predicts that some C-based defence is produced independently of the resource situation, in conjunction with growth, so that plants, to different extents, have a fixed level of defence, often called constitutive defence (genetically decided). For example, woody plants adapted to low resource situations are expected to have a low growth rate and therefore low capacity for compensatory growth after herbivory, which in turn would favour selection for maintenance of high defence levels and carbon surplus into storage rather than defence (little or no plasticity in defence). For genotypes with high plasticity in defence, any effects of resource conditions (shading, nutrient availability, increased photosynthesis) on the carbon:nutrient ratio can cause changes in the total defence levels (Bryant et al., 1983; Tuomi et al., 1988; Stamp, 2003).

Plant growth in high altitude and latitude environments is limited by low temperatures (T) (Bliss, 1962; Körner 1999) and lack of nutrients (Chapin et al., 1980; Callaghan and Jonasson, 1995, Klanderud and Totland, 2005). Growing under nutrient limited conditions, arctic-alpine plants would be expected to invest strongly in defence (according to resource-based hypotheses, reviewed by Herms and Mattson; 1992 and Stamp, 2003), but T-limited photosynthesis (C acquisition) and metabolism probably also imply restrictions on the production of defence compounds. Alpine and arctic habitats are expected to experience significant future climate warming (ACIA, 2005; IPCC, 2007), and, more specifically, the mean T increase per decade over Norway is expected to be between 0.2 and 0.5 ˚C (Hanssen-Bauer and Førland, 2001). The effect of warming on arctic-alpine plant defence has been little studied, and with inconsistent results (Dormann, 2003; Hansen et al., 2006; Nybakken et al., 2008). Previous studies have focused more widely in growth responses to T showing early stimulation followed by a gradual cessation of effects in the longer term (Arft et al., 1999). In long term experiments, warming increased height and cover of deciduous shrubs and graminoids, and decreased cover of mosses and lichens (Walker et al., 2006). In a synthesis of 16 warming studies including lichens, Cornelissen et al. (2001) defended the hypothesis that lichen-decline in sub- and mid-arctic ecosystems is a function of increases in vascular plant biomass, but did not find a relationship for the coldest high-arctic and alpine sites. Dormann and Woodin (2002) reviewed 36 warming experiments of different types in the Arctic, and also found greatest growth responses for grasses and shrubs, while Richardson et al. (2002) found no significant effect of warming on plant growth in a synthesis of warming experiments from sub-Arctic Abisko after 9 years. The varying effects of warming on growth of different life forms imply that effects on defence compounds should also vary. Furthermore, as the herbs and cryptogams that grow slowly, faster growing shrubs and graminoids might shade them (Klanderud and Totland, 2005), resulting in a reduction in C resources for defence. Lichens also contain CBSCs that function as herbivore and/ or solar defences (Emmerich et al., 1993; Gauslaa, 2005; Lawrey, 1983; Pöykkö et al., 2005, Solhaug and Gauslaa, 1996; Solhaug et al., 2010), and the concentrations of some lichen CBSCs have been shown to be a direct function of available light (Gauslaa and Ustvedt, 2003; Gauslaa and McEvoy, 2005;

Nybakken et al., 2007; Solhaug et al., 2003; Solhaug et al., 2009), which suggests that lichen defence would decrease with warming because of increased shading.

Increases in air T subsequently increase soil T (e.g. Klanderud and Totland, 2005), and possibly improve soil mineralization and soil nutrient status (Bonan et al., 1992; Nadelhoffer et al., 1991; White, 1999), which could also increase growth and decrease defence. According to Wookey et al. (2009), the ability to take advantage of an increased N availability should also vary between life forms, as biomass and production per unit of N varies greatly among tissue types and the relative amount of each tissue type a plant has. Evergreen shrubs have for example been shown to produce more biomass per unit N than graminoids (Shaver and Shapin, 1991, Suding et al., 2004). Lichens would probably not get any advantage of increased soil N at all, as they withdraw most of their nutrients from atmospheric sources (Nash, 2008).

In the slopes of the mountain Sanddalsnuten (1300 -1550 m a.s.l.) at Finse, south-western Norway (60˚N, 7˚E) several warming experiments with Open Top Chambers (OTCs) have been run since the late 1990s, showing that both T and N limit plant growth in this area, and that warming and increased nutrient availability increase growth of graminoids and some forbs at the cost of low stature forbs, club mosses, lichens and mosses (Klanderud and Totland, 2005, Klanderud, 2008). In the present study, our aim was to measure effects of warming on total C, N and C-based defence in arctic-alpine lichens and vascular plants of different functional groups. We sampled plant leaves and lichen thalli from OTCs and control plots from two different experiments, one on a ridge close to the mountain peak, and one from the leeside. The treatments had been running for 8 (ridge) and 3 (leeside) years when the current analysis was conducted. In line with hypotheses on resource-based defence, we expected reduced defence in the OTCs, as warming could reduce growth limitations, by both increased T and N. We expected differences according to functional groups, as they have been shown to respond differently to both T and N. Some functional groups, like shrubs, may have a fixed level of defence, and thus be little subject to change on individual basis. Also, as some species may show less or no growth response, we expected that increased shading from the responsive plants would cause defence decreases also for the less responsive ones.

2. Material and methods

2.1. Study area

The study area is southwest-exposed and located at Sanddalsnuten (60˚ N, 7˚E) at Finse, southern Norway. The climate at Finse is alpine-oceanic. The mean summer temperature from June to August is 6.3˚C (Aune, 1993) and the mean monthly precipitation is 89 mm (Førland, 1993). The vegetation consists of a *Dryas octopetala* heath alternating with alpine meadows. We collected lichens and leaves from common vascular plants inside and outside open top chambers (OTCs) in two locations differing in altitude, exposure, moisture, and productivity; ridge (1550 m) and leeside (1450 m). The ridge, close to the summit of Sanddalsnuten, is windy, with a ca 3 weeks longer growing season compared to the leeside, where snow accumulates and melts later. In the leeside, snow accumulation, in addition to water drainage from above results in ca 50 % higher soil moisture, ca 20 % higher content of soil organic matter as well as 6 times higher total C and more than 4 times higher total N (Olsen, 2010). Mean air temperature (July - August) was 8.7 ºC at the leeside and 7.5 ºC at the ridge and mean soil temperature (-5 cm) was 7.5 ºC at the leeside and 7.2 ºC at the ridge (Tinytag 12 Plus G data loggers, Intab Interface-Teknik AB, Stenkullen Sweden). The OTCs had been permanently established for 3 (leeside) and 8 (ridge) years prior to the sampling, and increased mean air temperature by ca 1.5 ºC and soil temperature by ca 1.0 ºC in both the leeside (Sandvik and Eide, 2009) and the ridge (Klanderud and Totland, 2005). These moderate increases in temperature correspond well with the predicted increase in summer temperature for this area the next 50-100 years (Hanssen-Bauer and Førland, 2001; Christensen et al., 2007). Open top chambers are commonly used to increase growth season temperature with minimal unwanted side effects on other environmental factors, such as light, precipitation and gas exchange (Arft et al., 1999; Hollister et al., 2000). Moreover, soil analyses inside and outside OTCs after four treatment years at the ridge site at Finse showed no differences in soil moisture (unpublished data K. Klanderud). Open top chambers may act as a physical barrier for some groups of herbivores, and thus be a potential confounding effect with increased T. We did not register herbivory inside and outside the OTCs systematically, but observed that insect larvae, lemmings and bigger herbivores (hares) occasionally were feeding also on plants inside OTCs (K. Klanderud and S. M. Sandvik, personal observation). For more details on the experimental setups see Klanderud and Totland (2005) and Sandvik and Eide (2009).

2.2 Measurements of vegetation height

Vegetation height was measured from the ground to the tallest point of the tallest plant at eight points inside each of 10 OTCs and 10 control plots at each location (ridge and leeside) in the beginning of August.

2.3 Sampling of leaves and lichens

We collected leaves from the five vascular plant species of four functional groups that were growing in all plots in either leeside and/or ridge: *Saussurea alpina* L. (perennial forb, ridge), *Tofieldia pusilla* (Michx.) Pers. (perennial forb, both sites), *Carex vaginata* (Tausch.) (sedge, ridge), *Vaccinium uliginosum* L. (dwarf-shrub, ridge), and *Selaginella selaginoides* L. (club moss, both sites). Furthermore, we collected thalli of six lichen species; *Flavocetraria nivalis* (L.) Kärnefelt & Thell, *Cetraria islandica* (L.) Ach, *Cladonia arbuscula* (Wallr.) Flot., *Peltigera aphthosa* (L.) Willd., and *Stereocaulon* spp. (all in both sites), and *Thamnolia vermicularis* (Sw.) Schaer. (ridge). *Peltigera aphthosa* is a tripartite lichen with cyanobacteria in the cephalodia, while the other species have green algal photobionts only. We collected samples as a mix of three individuals in 10 OTCs and 10 control plots (some exceptions when species were absent, see Table 1) in each location on August 5th 2007. Plants and lichens were always sampled from the central part of the OTCs, as plants near the walls may have a different chemistry due to the UV-resistant Plexiglas (3 mm Lexan®Exell). Leaf and lichen samples were put in small paper bags, and left to dry in room temperature for two weeks or two days, respectively. This is the preferred method for drying plant material for later analysis of phenolic compounds (Julkunen-Tiitto and Sorsa, 2001). The samples were then stored in a freezer (-18°C) until extraction. Before extraction, the samples were kept at room temperature over night. We measured the dry weight (DW) and then removed the main veins and stems from leaves with a scalpel. From *S. selaginoides* we used all material from the upper 1 cm of one stem. The sample was then transferred to pre-weighed Eppendorf vials containing one conic stainless steel bead of 5 mm diameter. We crushed the sample to powder for 2 min in a Retsch mixer mill (Model MM301) at frequency 30.0 before it was weighed into to batches, one for analyses for C and N and one for extraction of CBSCs.

2.4 Chemical Analyses

Carbon and nitrogen concentrations were quantified at the Department of Animal and Aquacultural Sciences (Norwegian University of Life Sciences, Ås, Norway) using the CHN-N method with an EA 1108 Elementar Analyser (Fison) (Säntis Analytical Scandinavia AB, Läby Österby, 75592 Uppsala). Before the analysis of CBSCs (according to Julkunen-Tiitto et al., 1996), leaf samples were extracted by adding 600 µl methanol (MeOH) and mixed with an Ultra-Turrax homogenizer for 30 sec. The sample was then placed in an ice bath for 15 min, homogenized for 15 sec, centrifuged 15 000 rpm for 3 min and then the supernatant was poured into a clean glass tube. The residue was added 600 µl MeOH, homogenized for 15sec and again centrifuged. The last procedure was repeated twice, and the residue was then totally colourless. Lichen samples were extracted according to Nybakken and Julkunen-Tiitto (2007) by adding 500 µl acetone and vortexing the sample for 30 s before it was left to stand for 10 minutes before the supernatant was poured off. This procedure was repeated three times. For both sample types the supernatants were combined and the MeOH or acetone evaporated with gaseous nitrogen. The dried extracts were stored at –18ºC until analysis.

The leaf extracts were dissolved in 300µl MeOH, added 300µl Milli-Q water and analysed on HPLC as described in Julkunen-Tiitto et al. (1996). We identified the compounds according to retention times and UV-spectra, quantified them at 220, 320 or 360 nm, and calculated the concentrations using the following commercial standards (supplier in parenthesis): caffeic acid (Aldrich, Steinheim, Germany), chlorogenic acid (Aldrich), 4-hydroxycinnamic acid (Aldrich), salidroside (Thieme, Germany), (+) catechin (Aldrich), myricetin-3-rhamnoside (Apin Chemicals, Abingdon, UK), quercetin-3- glucoside (Extrasynthese), apigenin-7-glucoside (Roth), luteolin-7-glucoside (Extrasynthese). As compounds within the same chemical group generally responded similarly to the treatments in the studied species (Table 1), we chose to present concentrations (mg g^{-1} DW) and statistics for compound groups, and not for individual compounds when appropriate (Table 1).

The lichen extracts were dissolved in 500 µl acetone and analysed on HPLC according to (Nybakken and Julkunen-Tiitto, 2007). The detection wavelength was 245 nm, and the identification of compounds was based on retention times, online UV-spectra, co-chromatography of commercial standards (atranorin, fumarprotocetraric acid (Apin Chemicals), usnic acid (Sigma)) and standards of baeomycetic acid, squamatic acid, tenuiorin, gyrophoric acid and lobaric acid was provided by Dr. H.J. Sipman (Botanischer Garten und Botanischer Museum Berlin-Dahlem, Berling, Germany). The compounds were quantified against response curves of the above-mentioned standards. Concentrations of methylgyrophoric acid were calculated from the response curve of gyrophoric acid.

2.5 Statistical analyses

Two-way ANOVAs were run with the statistical package, SPSS 15.0.1 for Windows, with Treatment (control/OTC), Location (leeside/ridge) and the interaction Treatment × Location as fixed factors, and with concentration of C, N or CBSCs as response variables. One-way ANOVAs were used when species occurred only in one of the locations. Number of samples analyzed of the different species from the different treatments and locations can be found in Table 1.

3. Results

3.1. Vegetation height

The vegetation canopy was taller inside OTCs than in controls (leeside, ca 2.4 cm outside and 4.1 cm inside the OTCs; ridge ca 2.1 cm outside and 2.8 cm inside the OTCs) ($p = 0.003$).

3.2. Carbon and nitrogen

The C concentration in the vascular plants varied between 435 (*S. alpina*) and 512 (*Vaccinium uligonosum*) mg g^{-1} DW, while the corresponding values for lichens were between 386 (*Cetraria islandica*, leeside) and 454 mg g^{-1} (*Peltigera aphthosa*, ridge) (Table 1). The difference in N concentration was much more pronounced; between 15.7 (*Tofieldia pusilla*, ridge and leeside) and 25.2 mg g^{-1} DW (*V. uliginosum*, ridge) for vascular plants and as low as between 5 and 10 mg g^{-1} DWfor green algal lichens. The tripartite lichen *P. aphthosa* with cyanobacteria in cephalodia had an N concentration comparable with vascular plants, varying between 23 and 25 mg g^{-1} DW (Table 1).

The experimental warming decreased the N concentration in *Carex vaginata*, *Saussurea alpina* and *Selaginella selaginoides*, while it increased in the lichen *Thamnolia vermicularis*. In all plants, the carbon concentration was unaffected. The carbon concentration in *P. aphthosa* was lower inside the OTCs, and the same tendency was seen for most of the other lichens, although not statistically significant. Two plants (*S. selaginoides* and *T. pusilla*) and five lichens (*C. islandica*, *Flavocetraria nivalis*, *Cladonia arbuscula*, *P. aphthosa* and *Stereocaulon* spp.) were analyzed from both ridge and leeside. For the plants, there were no location effects on their total C and N concentrations. In contrast, the C concentration in lichen thalli from the ridge was significantly higher than in those from the leeside for all species except *F. nivalis* (Table 1). The N concentration was significantly higher at the leeside for *C. arbuscula*, but was not influenced by location in any of the other lichen species. The interaction Treatment × Location was not statistically significant for any of the studied taxa (results not shown).

3.3. Carbon based secondary compounds

The identified CBSCs of the vascular plants were grouped according to their aglycon or as phenolic acids in Table 1. In *C. vaginata* and *T. pusilla* the CBSCs constituted around 5 % of the DW. *Selaginella selaginoides* contained only between 2 and 4 %, while *S. alpina* and *V. uliginosum* had as much as from 12 up to 40 % CBSCs (Table 1, Figure 1).

Lichens generally contained fewer CBSCs, with the individual compounds identified listed in Table 1. The studied *C. arbuscula* and *F. nivalis* specimens contained only usnic acid in measurable amounts. In *C. islandica* we identified fumarprotocetraric acid and one compound following shortly after it in the chromatogram and with similar UV-spectrum. This compound was tentatively named "fumarprotocetraric acid derivative". *Peltigera aphthosa* contained tenuiorin and methylgyrophoric acid, while the *Stereocaulon* species contained lobaric acid and atranorin, and is thus probably *Stereocaulon alpinum* (Krog et al., 1994). The *T. vermicularis* population growing in our experimental field contained squamatic acid and baeomycesic acid, and thus belonged to the chemotype II according to Krog et al. (1994). The total concentration of CBSCs of the lichens varied between 1.2 % (*P. aphthosa*, leeside) and 6.0 % (*T. vermicularis*) of the DW (Table 1, Figure 2).

The warming significantly affected the CBSCs in only one vascular plant species (*T. pusilla*) and in one lichen species (*C. arbuscula*) (Table 1, Figures 1, 2). Nearly all compounds in *T. pusilla* (except the apigenin-glycosides) decreased inside the OTCs. In *S. selaginoides*, all individual CBSCs had the highest concentration at the ridge (not statistically significant for the phenolic acids). For *T. pusilla* the opposite was found; all compounds were highest at the leeside (not significant for the apigenin-glycosides). In the lichen species, four species had higher total concentration of secondary compounds at the ridge, while *C. arbuscula* had a higher concentration at the leeside (Figure 2). If the species contained more than one secondary compound, the pattern was the same for all compounds that had different concentration at the two sites. The interaction Treatment × Location was not statistically significant for any studied species (results not shown).

4. Discussion

Experimental warming in arctic-alpine environments often leads to increased growth of some plant species, while others are less responsive and often out-competed over the long run (Arft et al., 1999; Walker et al., 2006). According to resource-based hypotheses on plant defence (summarized by Herms and Mattson, 1992), we expected that warming would reduce C-based defence in arctic-alpine plants because of increased growth, and also that less growth-responsive plants and lichens would have less C resources for defence because of increased shading from more growth-responsive plants.

The CBSC concentrations decreased with warming in one plant (*Tofielda pusilla*) and one lichen (*Cladonia arbuscula*). All other plant and lichen species, however, showed no response in CBSC concentrations, although the vegetation height increased significantly inside OTCs. There are few earlier published studies of effects of warming on plant defence in the arctic-alpine, but our results are in line with those that exist, as there were either no effect (*Salix polaris* (Dormann, 2003), *Bistorta vivipara*, *Dryas octopetala* and *Salix reticulata* (Nybakken et al., 2008) or small decreases (*Cassiope tetragona* and *Salix herbacea × polaris* (Hansen et al., 2006) in CBSCs. So, in contrast to our expectations, many species did not reduce their defence levels when T increases. One explanation could be that growth did not increase much in most plants and lichens inside the OTCs. However, three of the plant species (*Saussurea alpina*, *C. vaginata* and *S. selaginoides*) had lower leaf N concentrations in the OTCs compared to the controls at the ridge, with the same tendency for *T. pusilla*, *Vaccinium uliginosum* and *S. selaginoides* in the leeside. Comparable experiments with plants in arctic-alpine environments have either shown no effect of warming on leaf N content (*S. polaris*, (Dormann, 2003); *Oxyria digyna* and *Carex stans*, (Tolvanen and Henry, 2001) or a decrease (*C. tetragona*, *S. herbacea × polaris* and *Vaccinium vitis-ideae*, (Hansen et al., 2006); *C. tetragona*, *Dryas integrifolia* and *Salix arctica*, (Tolvanen and Henry, 2001); *Cerastium cerastoides, Epilobium anagallidifolium,* and *Carex lachenalii* (Sandvik and Eide, 2010). This suggests that there was no or only minor increase in soil N mineralization, and that decreased leaf N concentrations were results of dilution when growth increased. Generally, N mineralization rates are less responsive to warming in tundra than in forested ecosystems (Rustad et al., 2001), and the duration of our experiments have possibly been too short to see tissue-effects. Mineralization rates increased after 9 years of experimental warming in tussock tundra in arctic Alaska (Chapin et al., 1995). One lichen species, *T. vermicularis*, showed increased N concentrations in the OTCs, which may be a result of improved N uptake (from rainwater or dew) at higher T. Obviously, lichens are not able to take up N from the soil (Nash, 2008).

Although C-based plant defence is expected to be resource based, it is also thought that some level of defence is constitutive (fixed) and would be synthesized in conjunction with growth (Tuomi et al., 1988, Holopainen et al., 1995; Stamp, 2003). High proportions of constitutive defence is expected to be more common in slow growing perennials and under limiting conditions (typically many arctic-alpine plants) than in annuals, pioneer plants and under less limiting conditions (Tahvanainen et al., 1985; Coley, 1987; Folgarait et al., 1994; 1995). Only one of our species responded to the warming in defence levels, the perennial forb *T. pusilla*. The sedge, *C. vaginata*, and the other forb, *S. alpina*,could be expected to show the same response, but under the limiting conditions at this mid-alpine site one may probably expect high proportions of constitutive defence not only in woody species, but also in forbs and sedges. If growth increased, the increased C requirements to maintain high defence levels were probably met by T-increased photosynthesis, as none of the plants showed reductions in total C (Table 1). The C/N varied little between the vascular plant species, but the total CBSC concentrations did. This could be seen as a further support for a high level of constitutive defence in at least two of the species, as they differed so much from the others: *Vaccinium uligonosum* had almost 3 times the concentration of *S. alpina*, and more than six times the concentration of the rest of the species. The high level of (constitutive) defence in the woody *V. uligonosum* is according to the predictions of the CNB hypothesis (Bryant et al., 1983), but we have no explanations why *S. alpina* should be better defended/have another strategy than the rest of the species studied. Further complicating our interpretation is the fact that many arctic-alpine plants are clonal (in this study: *C. vaginata* and *V. uligonosum*), which means that resources may be transferred through rhizomes beyond the borders of OTCs, and thus for example reducing the effect of increased growth on resources available for defence. In summary, it would be difficult to prove that a defence level is fixed, as we cannot know what would happen if we for example increased the T with 1 ˚C or improved the nutrient availability by fertilization. However, in an earlier study from Sanddalsnuten, where T increase was combined with fertilization, the CBSC levels were reduced in the dwarf shrub *Salix reticulata*, while they stayed unchanged in the forb *Bistorta vivipara* and in the dwarf shrub *Dryas octopetala* (Nybakken et al., 2008). These results suggest that some species may have a fixed defence, while others are more subject to change, also under limiting conditions.

Most lichen species had a tendency to reduced total C inside OTCs, although statistically significant only for *P. aphthosa*, which is probably a result of the increased height of the plant canopy, leaving the low stature lichens in shade. This may be the first step towards carbon "starvation" of the lichens, as an earlier warming study from the same mountain slope showed that lichens decreased in abundance already after four years' warming (Klanderud and Totland, 2005), confirming a general trend shown in the arctic-alpine (Cornelissen et al., 2001; Walker et al., 2006). The effect of shading for the C economy of lichens is clearly seen if we compare the two experiments from two different habitats; all six species sampled from both habitats had higher C concentrations on the ridge than in the leeside, and the same was true for CBSCs for five of them (Table 1, Figure 2). As described in Material and Methods, the ridge is a more exposed habitat than the leeside, and the vegetation height in both control plots and OTCs is on average highest in the leeside and adds to the original light gradient. Cortical lichen CBSCs have been shown to increase along light gradients, both in transplanted lichens (usnic acid, Nybakken et al., 2007) and in lichens collected from their original habitat (atranorin, Solhaug et al., 2009). These compounds are situated above the algal layer in the lichen thallus, where they function as solar screens (e.g. Gauslaa et al., 2001; McEvoy et al., 2007). Our study shows that also CBSCs situated in the interior of lichens, in the medulla, have higher concentrations at the more exposed ridge (fumarprotocetraric acid in *Cetraria islandica*, tenuiorin in *P. aphthosa* and lobaric acid in *Stereocaulon*) compared to the leeside. This may suggest that also medullary compounds have functions in solar protection, e.g. as antioxidants or even as screening compounds for lower layers of the lichen. No such pattern was seen for vascular plants, which further suggests that shading of plants has not been a factor in this study (but mark that only two plant species were studied from both habitats and that habitat is not repeated!).

In conclusion, the lack of warming effects on CBSC levels in the studied plants and lichens, suggests that the defence levels are rather robust against raised temperatures, at least on a short-term basis. The robustness of plant defence in the arctic-alpine should be tested further, and a first step could be to grow a set of species from different functional groups under controlled light and nutrient conditions, searching for an optimum. At the moment, the threat for lichens, and possibly also for some of the plants, seem to be competition from other plants, rather than reduced defence in the first place. However, as warming could also improve conditions for e.g. herbivores and fungal diseases otherwise (milder winters, increased humidity (Hanssen-Bauer and Førland, 2001; Christensen et al., 2007), attacks may anyway increase in the future, and might require further development of the defence, both qualitatively and quantitatively.

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TABLE 1. Concentrations (mg g^{-1} DW) of C, N and CBSCs ±S.E in vascular plants and lichens under ambient (control) and warmed (OTC) conditions (treatment) in two different locations in alpine southern Norway[1]. Asterisks (*) behind the F-values denotes significance levels (*P<0.05; **P<0.01; ***P<0.001)

	Ridge		**Leeside**		**Treatment**	**Habitat**
	Control	OTC	Control	OTC	F	F
Vascular plants						
Carex vaginata	N = 10	N = 10				
C	455.1±0.9	453.8±1.3			0.78	
N	21.9±0.7	18.1±0.6			17.2***	
C:N	20.9±0.6	25.3±0.9			16.5***	
Luteolin-glyc.	35.9±4.1	45.6±5.6			1.74	
Apigenin-glyc.	2.2±0.2	3.1±0.5			2.11	
Sum, CBSCs	50.3±4.8	65.0±7.0			2.44	
Saussurea alpina	N = 10	N = 10				
C	434.9±1.7	432.7±1.9			0.71	
N	20.7±1.0	17.5±0.5			8.18**	
C:N	21.4±0.9	24.9±0.7			9.50**	
Phenolic acids	89.9±4.9	91.7±4.9			0.06	
Quercetin-glyc.	31.6±2.1	27.8±1.6			1.81	

Sum, CBSCs	121.5±4.6	119.5±5.4			0.07	
Selaginella selaginoides	N = 10	N = 10	N = 10	N = 10		
C	471.8±2.8	480.6±3.0	483.8±2.8	473.5±4.1	0.05	0.47
N	19.5±0.7	17.6±0.5	19.2±0.7	18.7±0.6	3.87	0.41
C:N	24.5±0.9	27.4±0.8	25.4±0.9	25.6±0.8	3.61	0.34
Phenolic acids	5.3±2.4	2.6±0.3	2.1±0.3	1.6±0.1	0.43	9.46
Apigenin der	0.3±0.1	0.4±0.1	0.1±0.02	0.2±0.03	1.53	2.71**
Kaempferol der	33.9±4.3	29.2±1.9	23.4±2.0	17.7±0.9	3.65	16.65**
Coumaryl-Kaempferols	2.8±0.3	3.3±0.3	2.1±0.2	1.7±0.1	0.08	20.63***
Sum, CBSCs	42.3±6.4	35.4±2.3	27.6±2.3	21.2±1.0	0.01	14.23***
Tofieldia pusilla	N = 4	N = 4	N = 10	N = 10		
C	448.3±2.9	445.6±3.6	450±1.2	446.9±1.9	1.83	0.48
N	14.9±0.5	15.7±1.0	14.9±0.5	15.4±0.9	0.19	0.02
C:N	30.2±1.2	28.9±2.1	30.5±1.0	29.6±1.5	0.22	0.01
Apigenin-glyc.	2.7±1.3	1.4±0.5	2.7±0.7	2.4±0.7	0.94	0.48
Quercetin-glyc.	14.0±2.5	7.6±1.5	16.3±0.9	12.8±2.0	8.84**	5.28*
Quercetin-diglyc.	14.9±2.7	9.6±1.3	17.4±0.6	14.9±2.0	5.31*	5.86*
Luteolin-glyc.	18.8±3.4	11.6±2.0	21.6±1.7	19.3±2.4	4.54	5.24*
Sum, CBSCs	50.3±8.8	30.1±4.6	58.1±2.9	49.3±5.8	7.01*	6.04*

Vaccinium uligonosum	N = 10	N = 10				
C	506.9±1.1	511.9±14.0			0.13	
N	25.2±0.4	23.7±0.7			3.35	
C:N	20.2±0.3	21.7±0.4			8.93**	
Catechin der.	88.9±34.7	198.1±152			0.53	
Phenolic acids	56.7±27.9	53.6±21.2			0.13	
Myricetrin	19.9±7.8	11.5±7.7			0.02	
Isoquercetin	143.1±68.3	110.5±52.3			2.57	
Kaempferol der	26.6±11.1	24.4±11.9			1.44	
Isorhamnetin	3.9±2.1	3.6±1.6			0.01	
Sum, CBSCs	339.1±150.8	401.7±239.4			0.04	
Lichens						
Cetraria islandica	N = 10	N = 10	N = 10	N = 10		
C	410.2±2.6	406.0±3.3	389.0±2.9	386.8±4.6	0.89	34.94***
N	5.7±0.2	5.5±0.1	5.6±0.2	6.0±0.4	0.24	0.58
C:N	72.8±2.3	73.9±2.0	70.1±1.6	67.2±4.7	0.09	2.57
Fumarprotocetraric acid	16.7±1.6	17.2±3.9	9.2±1.6	3.9±1.0	2.00	16.70***
Fumarprotocetraric acid der	8.7±0.9	8.3±1.9	6.2±1.3	10.4±1.6	1.39	0.01
Sum, CBSCs	25.4±2.5	25.5±5.7	15.2±1.8	14.3±1.0	0.65	16.47***

Cladonia arbuscula	N = 10	N = 10	N = 10	N = 10		
C	429±1.6	426.4±2.0	422.4±2.3	423.0±1.5	0.26	7.32**
N	5.6±0.3	5.5±0.3	5.8±0.4	6.5±0.2	1.09	4.39*
C:N	78.9±4.5	80.0±4.7	76.0±6.3	65.7±1.9	1.07	3.76
Usnic acid	36.4±1.3	32.0±1.4	46.6±4.9	39.8±12.6	4.13*	10.91*
Flavocetraria nivalis	N = 10	N = 10	N = 6	N = 6		
C	409.0±1.9	407.7±2.3	402.9±3.1	396.4±2.9	2.26	11.46**
N	5.1±0.3	4.7±0.3	5.4±0.4	5.3±0.2	0.54	1.63
C:N	82.5±5.3	91.6±7.2	76.0±5.3	75.3±3.7	0.41	3.04
Usnic acid	53.7±2.2	51.2±2.4	49.6±2.0	43.1±5.4	2.19	4.03
Peltigera aphthosa	N = 5	N = 5	N = 9	N = 9		
C	454.4±1.1	438.6±1.5	430.0±2.1	427.4±2.5	16.80***	61.98***
N	24.2±0.8	23.7±1.5	24.9±1.0	22.8±1.1	1.17	0.001
C:N	18.9±0.6	18.9±1.1	17.5±0.7	19.1±0.9	0.75	0.48
Methylgyrophoric acid	1.7±0.1	1.7±0.5	1.3±0.3	1.4±0.2	0.02	1.97
Tenuiorin	18.5±1.7	17.0±2.1	11.7±0.9	10.5±0.9	1.00	25.35***
Sum, CBSCs	20.2±3.4	18.7±1.6	12.4±0.9	12.1±1.2	1.14	34.05***

Stereocaulon spp.	N = 10	N = 10	N = 10	N = 10		
C	423.4±3.3	422.7±2.2	412.9±1.5	414.7±1.6	0.05	17.02***
N	9.4±0.9	9.3±0.6	10.3±0.4	9.1±0.3	1.22	0.36
C:N	47.7±3.2	47.3±3.6	40.6±1.7	45.9±1.4	0.84	2.54
Lobaric acid	4.6±0.4	5.7±1.5	4.4±0.4	2.8±0.3	0.10	3.77
Atranorin	21.0±1.4	20.5±2.2	14.4±0.8	13.4±1.2	0.25	18.06***
Sum, CBSCs	25.6±2.1	26.2±3.4	18.8±1.1	16.1±1.3	0.004	14.80***
Thamnolia vermicularis	N = 10	N = 10				
C	409.9±5.1	421.3±7.5			1.59	
N	5.7±0.4	7.0±0.2			8.92**	
C:N	76.3±6.3	60.7±2.9			5.08*	
Squamatic acid	23.0±0.6	22.1±1.3			0.16	
Baeomycesic acid	37.2±1.9	32.1±2.2			2.50	
Sum, CBSC	60.2±2.2	54.2±3.3			1.59	

Figure legends

Figure 1. Total concentration (mg g^{-1} ± S.E.) of phenolic compounds in plant leaves (mg g^{-1} ± S.E.) from OTCs (black bars) and controls (grey bars) at the ridge and the leeside. Significant difference between controls and OTCs according to a one-way ANOVA is marked by * = $p<0.100$, ** = $p<0.050$ and *** = $p<0.001$.

Figure 2. Total concentration (mg g^{-1} ± S.E.) of phenolic compounds in lichen thalli from OTCs (black bars) and controls (grey bars) at the ridge and the leeside. Significant difference between controls and OTCs according to a one-way ANOVA is marked by * = $p<0.100$, ** = $p<0.050$ and *** = $p<0.001$.

Research Highlights

- Defensive compounds in arctic-alpine vascular plants and lichens are little subject to change under increased temperature
- Plant competition and shading effects caused by elevated temperatures are likely to be more ecologically important than impacts on plant defence
- Defensive compounds in arctic-alpine lichens are strongly responsive to solar exposure, and this holds also for compounds situated in the medulla (probably no function as solar screen).

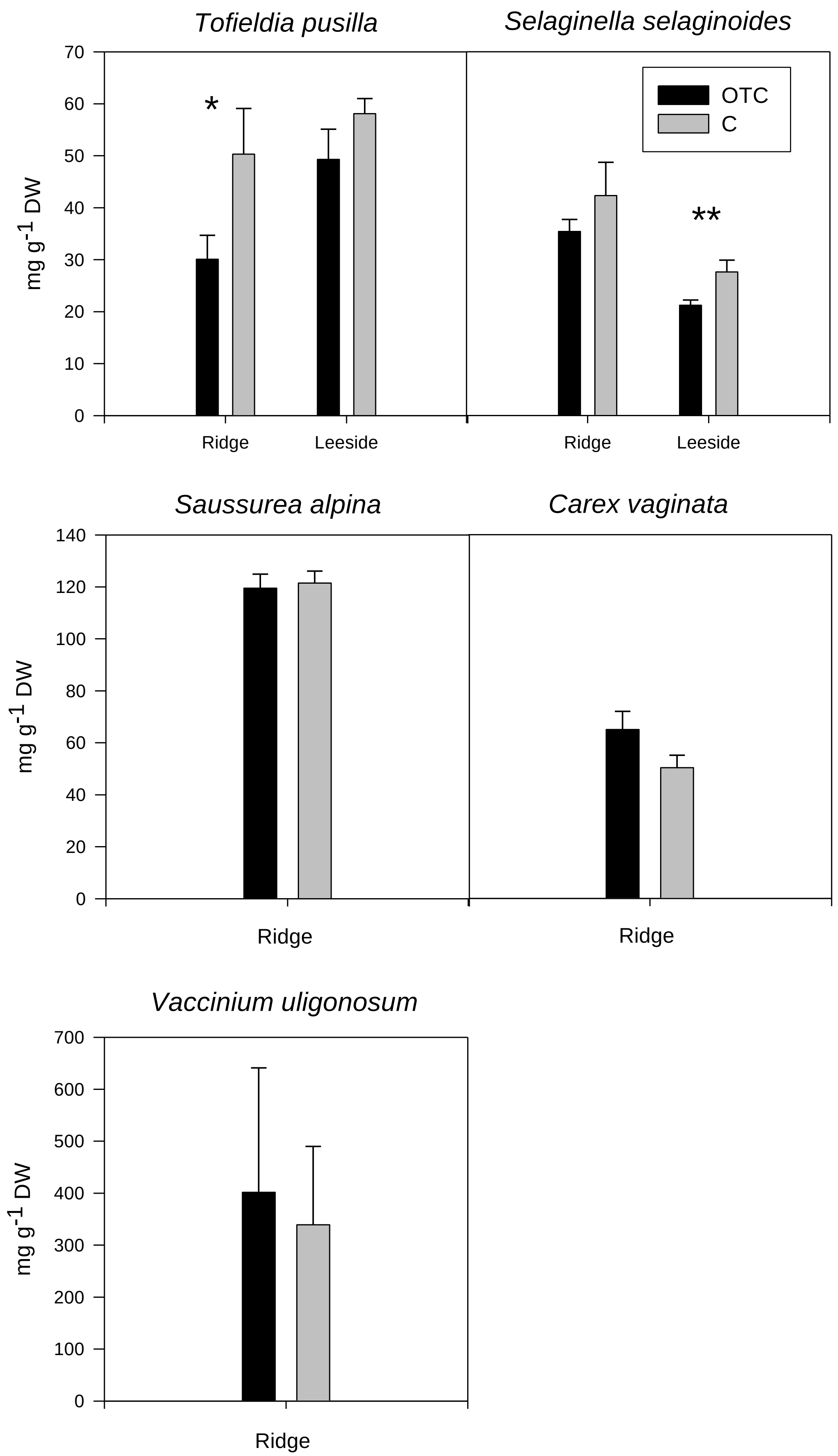
Tofieldia pusilla
Selaginella selaginoides
OTC
C
mg g-1 DW
*
**
Ridge
Leeside
Ridge
Leeside
Saussurea alpina
Carex vaginata
mg g-1 DW
Ridge
Ridge
Vaccinium uligonosum
mg g-1 DW
Ridge

Fig. 2

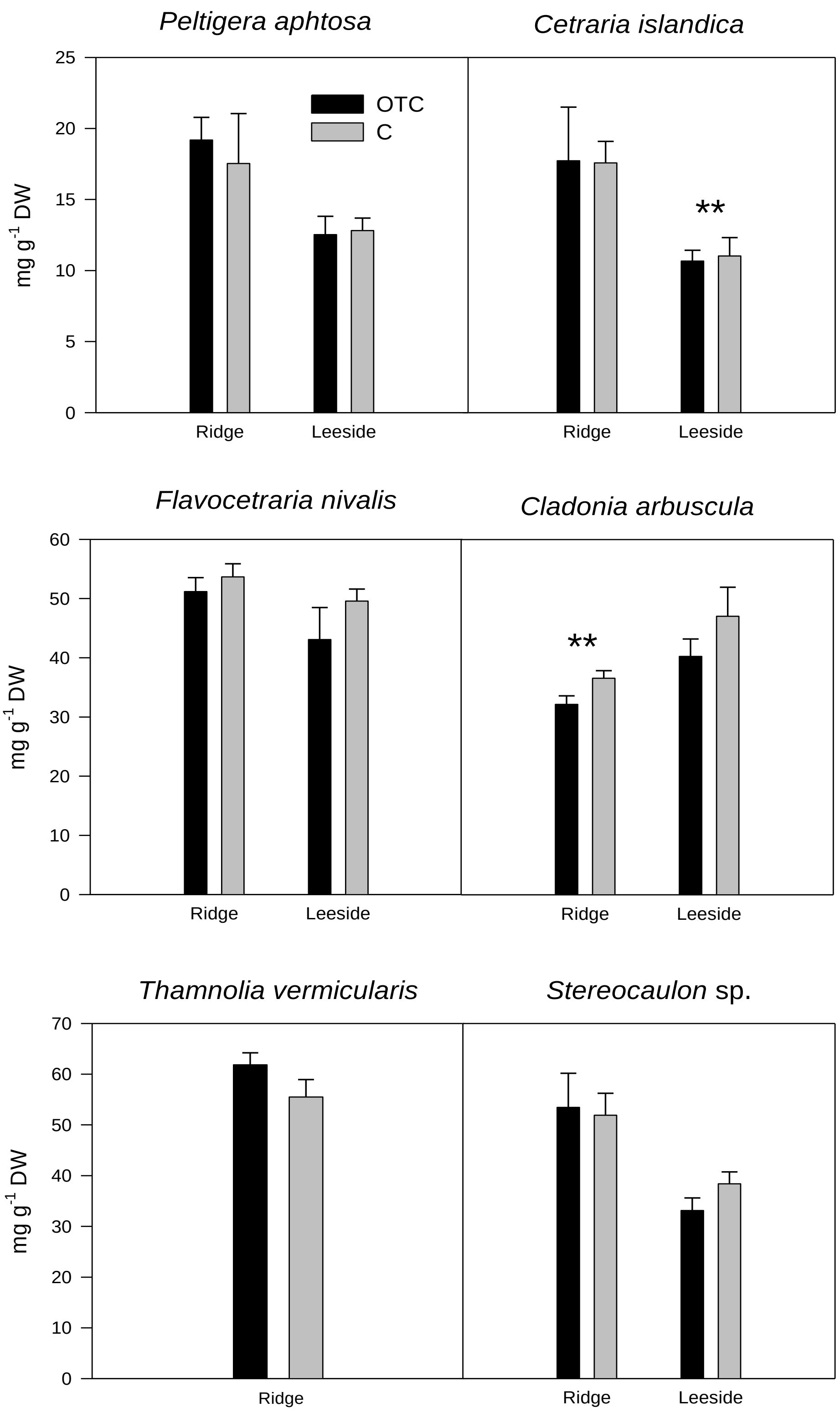
Peltigera aphtosa
Cetraria islandica
Flavocetraria nivalis
Cladonia arbuscula
Thamnolia vermicularis
Stereocaulon sp.
OTC
C
mg g-1 DW
**
Ridge
Leeside
0
5
10
15
20
25
30
40
50
60
70

Fig. 3