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Resource Allocation Pattern under Simulated Environmental Change and Seedling Establishment of Alpine Dwarf Shrubs in A Mid-Latitude Mountain

By

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S u m m a r y

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We set up 11 open-top chambers (OTCs) on a fell-field (1680 m a.s.l.) in the Taisetsu Mountains, northern Japan to assess responses to warming of circumpolar plants growing around their southern distribution margins. The OTCs increased the daily mean air-temperature by 1.7°C throughout the growing season. For five alpine species - two deciduous shrubs: *Arctous alpinus* and *Vaccinium uliginosum* and three evergreen shrubs: *Ledum palustre* subsp. *decumbens*, *Vaccinium vitis-idaea*, and *Empetrum nigrum* var. *japonicum* - effects of artificial warming on reproductive components were investigated during five (for flower production) or four (for fruit production) years. In addition, seedling establishments were compared among the three vegetation types and bare ground. Flower production in the OTCs was enhanced significantly in both deciduous species over that of control plots. In contrast, comparison to the control plots showed a significant decrease in flower production in the OTCs in two of the evergreen species. Fruit production of *V. uliginosum* and *L. palustre* was enhanced in the OTCs relative to the control plots. Both deciduous species allocated their resources to reproduction rather than to vegetative growth. Seedling establishment was very rare and was restricted on bare ground in this study site. We concluded that the difficulty of seedling establishment gives advantage to some species, which show active vegetative growth under global warming, to develop their vegetation cover.

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Introduction

Global warming is expected to strongly affect terrestrial ecosystems in arctic tundra and high mountain regions (MAXWELL 1992). A current challenge is to predict the way in which climatic change will alter species distributions. Numerous field experiments of artificial warming have been conducted mainly in polar semi-desert (HENRY & al. 1986, WOOKEY & al. 1993, ROBINSON & al. 1998), arctic tundra (CHAPIN & SHAVER 1985, CHAPIN & al. 1995, HOBIE & CHAPIN 1998), and subarctic ecosystems (PARSONS & al. 1994, PRESS & al. 1998, GRAGLIA & al. 2001). However, few experiments were conducted in mid-latitude alpine ecosystems scattered around southern margins of the geographical distribution of many circumpolar species (WADA & al. 2002, KUDO & SUZUKI 2003). Plants from arctic and mid-latitude alpine populations may have different responses to warming. Responses of plants to environmental changes are classifiable into several levels and time scales: (1) changes in phenology and leaf traits at a month-seasonal time scale (WELKER & al. 1993, WOOKEY & al. 1993, PARSONS & al. 1994), (2) changes in activity of growth or reproduction, and vegetation structure at the annual-several-year time scale (ARFT & al. 1999, KUDO & SUZUKI 2003), and (3) changes in species composition on a decadal time scale (CHAPIN & al. 1995, PRESS & al. 1998, SHAVER & al. 1998).

Two ways exist for plants to maintain their population and to migrate to other places. Seedling establishment and vegetative growth determine species distributions. ARFT & al. 1999 used field experiments to show that warmer, low arctic and alpine sites produced the strongest vegetative growth responses, whereas high arctic sites produced a greater reproductive response to increased temperature. KUDO & SUZUKI 2003 investigated the change in vegetative growth and vegetation structure of alpine dwarf shrubs under artificial warming in the mid-latitude mountain. As reported by ARFT & al. 1999, vegetative growth was strongly enhanced, but this response appeared only in evergreen species (KUDO & SUZUKI 2003). However, that study did not fully consider reproduction and seedling establishment.

The present study specifically addresses the reproductive component and seedling establishment, which are important characteristics for species distribution. This study is intended to explore climate-induced changes in reproduction of alpine dwarf shrubs over five years under artificial warming. In addition, we discuss the way in which changes in the allocation pattern (i.e. vegetative growth or reproduction) and seedling establishment are associated with the vegetation change.

Material and Methods

This study was conducted at a fellfield on a plateau of 1680 m a.s.l. in a central area of the Taisetsu Mountains (43°33'N, 142°53'E), northern Japan. At the end of the growing season in 1994, we set up 11 open-top chambers (OTCs), which are pentagonal enclosures made of clear, 3-mm-thick acrylic boards. They are 30 cm high, with 0.15 m² open-top area and 0.43 m² ground area (SUZUKI & KUDO 1997). One control plot was established in the vicinity of each OTC: therefore, 11 control plots were set up.

We examined two deciduous dwarf shrubs (*Arctous alpinus* and *Vaccinium uliginosum*) and three evergreen dwarf shrubs (*Ledum palustre* subsp. *decumbens*, *Vaccinium vitis-idaea*, and

Empetrum nigrum var. *japonicum*). They are circumpolar species with a wide distribution range from mid-latitude alpine to subarctic or arctic regions.

In late May 1995, we selected several (6-10) plants of each species from each OTC and control plot and marked them with numbered tags. For each marked plant, one stem that was produced in 1994 was selected and shoot growth and flower production were monitored over the next five years (1995-1999), but four years (1996-1999) for *V. vitis-idaea* and *E. nigrum*. To estimate reproductive success, we counted the number of matured fruits from 1995 to 1998 (1996-1998, for *V. vitis-idaea*), except for *E. nigrum*. Cumulative flower and fruit productions of individual species during the previous 4 or 5 years were compared between control and OTC treatments. We used a Poisson log-linear model (the general linear model for data having a Poisson distribution) to fit the number of flowers or fruits of individual plants (VENABLES & RIPLEY 2002), in which treatment and plot (i.e. individual pairs of control and OTC) were treated as independent factors.

To investigate seedling establishment, we set up 25 quadrats (0.5 m × 0.5 m) and counted seedlings within the quadrats for all three vegetation types - *A. alpinus*-, *V. uliginosum*-, and Lichen-dominated types - in mid-September 1998. We looked for 25 areas of bare ground, regarded them as ellipses, and calculated the approximate area (the mode is 0.05-0.10 m², n = 9) by measuring their major and minor axes. Seedlings were counted within the bare-ground plots. Kruskal-Wallis test and a subsequent post-hoc test (Steel-Dwass test) were used to examine differences in established seedling number among vegetation types and bare ground.

Results and Discussion

Daily mean, maximum, and minimum air temperature in the OTCs respectively increased 1.7, 7.0, and 0.3°C throughout the growing season. The warming effect of the OTCs appeared to be large during the daytime on sunny days (SUZUKI & KUDO 1997). The influence of the OTCs on soil-surface temperature during the summer was marginal in 1995 and 1996; it tended to be lower from 1.1 (1997) to 1.8°C (1998 and 1999) in the OTCs than control plots, probably because of the reduced the amount of solar radiation as a result of the increased plant cover (KUDO & SUZUKI 2003). Relative air humidity was reduced by approximately 15%, in addition, abaxial leaf temperature increased 1.1°C in similar OTCs (WOOKEY & al. 1993). These microclimate changes in the OTCs were probably due to protection from wind, but this study did not measure wind speed.

Table 1. Number of flowers (mean ± SE) produced during five seasons (four seasons for *Vaccinium vitis-idaea* and *Empetrum nigrum*) of five species in the OTCs and the control plots. n indicates the plot number.

| Species | OTC | n | Control | n | P-value |
|------------------------------|-----------|---|-----------|---|---------|
| <i>Arctous alpinus</i> | 4.3 ± 1.2 | 4 | 2.3 ± 0.3 | 4 | <0.0001 |
| <i>Vaccinium uliginosum</i> | 7.4 ± 1.1 | 6 | 3.1 ± 0.5 | 6 | <0.0001 |
| <i>Ledum palustre</i> | 5.0 ± 1.8 | 6 | 5.0 ± 1.9 | 6 | 0.92 |
| <i>Vaccinium vitis-idaea</i> | 0.3 ± 0.3 | 3 | 1.2 ± 0.6 | 3 | <0.001 |
| <i>Empetrum nigrum</i> | 6.6 ± 3.0 | 6 | 7.9 ± 2.2 | 6 | <0.05 |

Flower productions of both deciduous species, *A. alpinus* and *V. uliginosum*, were enhanced significantly in the OTCs in comparison to the control plots. In contrast, flower productions of the two evergreen species, *V. vitis-idaea* and *E. nigrum*, were decreased significantly in the OTCs in comparison to the

control plots. No significant difference was evident in the flower production of *L. palustre*, an evergreen species, between treatments (Table 1). Larger resource investment to vegetative growth in the OTCs than in the control plots, as reported in KUDO & SUZUKI 2003, may engender reduced reproductive efforts.

Vaccinium uliginosum exhibited significantly higher fruit production corresponding to larger flower production in the OTCs than in the control plots. *Ledum palustre* showed significantly enhanced fruit production in the OTCs irrespective of similar flower production between treatments. No significant differences were evident in fruit productions of *A. alpinus* and *V. vitis-idaea* (Table 2). Short-term artificial warming (a few years) enhanced flower and fruit production for dwarf shrubs, perennial herbs, and graminoids (WOOKEY & al. 1993, PARSONS & al. 1995, but see STENSTRÖM & al. 1997). The increased air temperature in the OTCs hardly affected pollinator frequency (personal observation) because the activity of pollinators was strongly affected by field climate (KUDO & SUZUKI 2002). These results demonstrate that low temperature physiologically constrained flower and seed productions of many tundra plants. In addition, the OTCs may have physically protected plants from winds (MARION & al. 1997), thereby decreasing fruit damage.

Table 2. Number of fruits (mean \pm SE) produced during four seasons (three seasons for *Vaccinium vitis-idaea*) of four species except for *Empetrum nigrum* in the OTCs and the control plots. n indicates plot number.

| Species | OTC | n | Control | n | P-value |
|------------------------------|---------------|---|---------------|---|---------|
| <i>Arctous alpinus</i> | 0.3 \pm 0.1 | 4 | 0.1 \pm 0.1 | 4 | 0.065 |
| <i>Vaccinium uliginosum</i> | 2.2 \pm 0.4 | 6 | 1.4 \pm 0.3 | 6 | <0.05 |
| <i>Ledum palustre</i> | 3.1 \pm 1.1 | 6 | 1.9 \pm 1.0 | 6 | <0.0001 |
| <i>Vaccinium vitis-idaea</i> | 0.3 \pm 0.3 | 3 | 0.6 \pm 0.4 | 3 | 0.092 |

Table 3. Established-seedling number at three vegetation types and bare ground. Identical superscript letters indicate a non-significant difference using a multiple-comparison test ($P < 0.05$, Steel-Dwass test). n indicates sample size. Mean \pm SE.

| Species | Seedling density (m ⁻²) | n |
|--|-------------------------------------|----|
| <i>Arctous alpinus</i> -dominated | 0.5 \pm 0.4 ^a | 25 |
| <i>Vaccinium uliginosum</i> -dominated | 1.0 \pm 0.6 ^a | 25 |
| Lichen-dominated | 0.2 \pm 0.2 ^a | 25 |
| Bare ground | 5.3 \pm 1.6 ^b | 25 |

Seedling densities were 0.5, 1.0, 0.2 and 5.3 per square meter at *A. alpinus*-, *V. uliginosum*-, and Lichen-dominated vegetations, and bare ground, respectively. Not all of these seedlings were identifiable: they had only cotyledons. Seedling establishment was significantly greater on bare ground than with any vegetation type (Table 3). Plant colonization is attainable by seedling establishment on bare ground in the High Arctic and through vegetative growth in the Sub-Arctic (ROBINSON & al. 1998). In this study, seedling establishment was very rare and restricted to bare ground although effects of artificial warming on seedling establishment were not investigated.

Environmental change by the OTCs extended leaf life-span of all species (SUZUKI & KUDO 2000). Global warming prolongs the growing season and increases resource acquisition by plants. The present study showed a striking difference in resource allocation patterns among species by setting OTCs: *A. alpinus* and *V. uliginosum* invested their photosynthetic products for reproductive efforts (Table 1), whereas *L. palustre* and *E. nigrum* invested their products for vegetative growth (KUDO & SUZUKI 2003). Vigorous vegetative growth under mild conditions would be particularly advantageous for *L. palustre* and *E. nigrum* because of the scarcity of seedling establishment in this site (Table 3). Thus, the proportion of these species is expected to increase gradually with global warming.

Vertical stratification of vegetation develops with the increasing plant cover of specific species. The plant heights of major component species differed significantly among species, and between the OTCs and control plots (KUDO & SUZUKI 2003). Consequently, interspecific competition for light acquisition will be serious, and dominant species may be determined according to the competition. Potential distribution ranges of plants are strongly determined by the physiological responses of respective species to environmental changes. Patterns of plant distribution largely reflect the ecological situations caused by interactions among species (MUELLER-DOMBOIS & ELLENBERG 1974). Species composition may be determined by changes in competitive abilities of individual species along environmental gradients. Species diversity may decrease because of acceleration of competitive situations among plants if global warming acts to mitigate environmental stress in alpine ecosystem.

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