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Effects of Temperature and Natural Disturbance on Growth, Reproduction, and Population Density in the Alpine Annual Hemiparasite *Euphrasia frigida*

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Abstract

The effects of temperature and "natural disturbance" on growth, seed production, and population density in the facultative hemiparasitic annual *Euphrasia frigida* (Scrophulariaceae) were examined in the middle alpine zone at Finse, southwest Norway. Experimentally elevated temperature increased growth and seed production significantly. Higher temperatures resulted in a small decrease in population densities during three seasons. The degree of "natural disturbance" did not influence growth and seed production, but population density was highest at intermediate disturbance levels. Thus, while temperature influenced the performance of *E. frigida,* disturbance affected the population dynamics. The effects of temperature on growth and reproduction may also be indirect on hemiparasites, through improved conditions for the host plants under elevated temperatures. It is hypothesized that the predicted global warming will result in increased seed output from *E. frigida* plants in the middle alpine zone. Population densities, however, are likely to decrease under elevated temperatures, due to lower disturbance levels by frost heave and increased vegetation cover.

Introduction

Low temperatures and the short, unpredictable growing season are limiting factors for plant growth and reproduction in arctic and alpine habitats (Bliss, 1962; Savile, 1972; Bell and Bliss, 1980). These factors strongly constrain seed production and seedling growth (Bell and Bliss, 1980; Spira and Pollak, 1986; Kudo, 1991), resulting in a vegetation dominated by long-lived perennials reproducing through vegetative growth (Savile, 1972; Archibold, 1984; Billings, 1987; Kudo, 1991; Callaghan et al., 1992; Weis and Hermanutz, 1993). In contrast, annuals are rare or absent (Savile, 1972; Billings, 1973, 1987; Spira and Pollak, 1986), as the persistence of such species may be particularly vulnerable to sudden declines in population density following unfavorable seasons.

One can predict that the projected increase in mean annual global surface temperature by 2 to 4°C during the next century (Houghton et al., 1996) may have positive impacts on growth and reproduction in alpine annuals, given the thermal and seasonal constraints on survival, growth, and reproductive output of plants in alpine environments. However, while many studies have found that increased temperature conditions increase the reproductive output of arctic and alpine perennials (e.g., Wookey et al., 1993, 1994, 1995; Parsons et al., 1994; Harte and Shaw, 1995), none have attempted to predict the fate of annuals under climate change. Molau (1993a) found that the number of flowers in *Euphrasia frigida* depends on environmental factors, such as temperature, plant density, and host plant availability. The long-term consequences of increased temperatures for alpine annuals are difficult to predict as population densities may increase due to higher seed production, or decrease due to denser perennial vegetation and lower availability of open sites for establishment under higher temperatures (Silvertown and Lovett Doust, 1993).

The International Tundra Experiment (ITEX) was established in 1990, as a response to predictions that global warming will have the highest impact on high latitudes (Henry and Molau, 1997). The ITEX program mainly monitor phenology, growth and reproduction in circumpolar plants in relation to temperature and length of the growing season (Henry and Molau, 1997).

In this study we examine the effects of experimentally increased growing season temperature and natural variation in disturbance on growth, reproductive output, and population density of the alpine hemiparasitic annual, *Euphrasia frigida* Pugsley (Scrophulariaceae).

Materials and Methods

STUDY SPECIES

Euphrasia frigida is a facultative root hemiparasite (Seel and Press, 1993). Such species often have a wide host range, and differences in host species may cause size-differences among hemiparasites within the same population (Seel and Press, 1993; and references therein). Although some hemiparasites are reported with only one host (like *Pedicularis dasyantha,* Gauslaa and Odasz, 1990), *E. frigida* are found connected to a variety of hosts (Seel and Press, 1993). *Euphrasia frigida* may also grow and reproduce unattached to a host (Seel and Press, 1993). The species is mainly self-pollinating, has low abortion rates and very low seed predation (Molau, 1993a; Nyléhn, unpublished data), and the primary seed dispersal distance is highly restricted (Molau, 1993a). Establishment from seeds requires small open patches in the vegetation, and *E. frigida* typically grows in sites with some disturbance, at least in alpine areas (Molau, 1993a; Seel and Press, 1993). In the study area, *E. frigida* germinates in late June or early July, flowers in the middle of August and has ripe seeds in the beginning of September.

STUDY SITE

All the data for this study was collected in August and September 1995, August 1996 and July 1997 on mountain San-

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TABLE 1

Mean and standard errors (SE) of plant performance variables of Euphrasia frigida *inside OTCs and in control plots at Finse in 1995. F and P values for treatment effect from two-factor randomized block design ANOVAs are shown below means.*

Treatment	No. leaves	Leaf area	Plant height (mm)	Plant weight (mg)	No. fruits	Seeds/fruit	No. seeds	Seed weight (mg)
Control	8.6 ± 0.4	7.72 ± 0.46	15.1 ± 0.6	61.22 ± 7.61	2.4 ± 0.2	4.9 ± 0.2	12.7 ± 1.6	2.03 ± 0.10
OTC	10.4 ± 0.4	12.87 ± 1.10	24.4 ± 1.0	146.72 ± 2.46	4.2 ± 0.4	5.2 ± 0.3	23.7 ± 3.1	2.54 ± 0.12
F	16.58	14.45	89.97	14.12	34.11	1.02	15.62	12.20
P	0.003	0.004	0.000006	0.005	0.0003	0.34	0.003	0.007

dalsnuten, at Finse, southwest Norway (60°37′N, 7°32′E). The Finse area has a suboceanic, alpine climate with high precipitation and strong winds. Temperatures are generally low, even during the growing season (mean June temperature = 5.0°C, July = 7.0°C, August = 6.8°C, September = 3.0°C), and the growing season is shortened by deep snow cover. The study site is situated on a south-facing slope at 1500 m elevation, in the middle alpine zone. Common associated species are *Salix herbacea, Ranunculus acris, Carex bigelowii, Thalictrum alpinum, Bistorta vivipara, Poa alpina, Veronica alpina, Bartsia alpina, Silene acaulis, Saussurea alpina,* and *Antennaria alpina* (nomenclature are following Lid and Lid, 1994). These species are also likely host species of *E. frigida* in the site. The site is sheltered from the main wind direction (west) by a ridge running southwest from the top of Sandalsnuten. The study site is disturbed mainly by running water from melting snow, cryogenic movements of soil, and small rodents.

GROWTH AND REPRODUCTION

Eleven open top chambers (OTCs, as developed within the ITEX Programme; Henry and Molau, 1997) were erected and 11 control plots of equal size were chosen on 16 July 1994. The OTCs and control plots were positioned in pairs. From 27 July to 3 August 1995 the OTCs raised air temperature 5 cm above ground by 2.3°C compared to control, soil temperature 5 cm below ground by 0.8°C, and soil surface temperature by 3.1°C above control (see Totland, 1997, for more details).

The OTCs have basal area of 60 × 60 cm^2 and a height of 40 cm, and 80° inwardly inclined walls. They are made of UV-resistant polycarbonate that transmit 88.3% of photosynthetic active radiation as measured with a LI-COR (LI-250 quantum sensor) in 1997. The OTCs did not protect the plants from herbivores like small rodents. Large grazing mammals, like sheep, were excluded from the study site by a fence.

To examine the effects of experimentally increased temperatures on plant size and seed production, 10 randomly selected plants within 10 OTCs and 10 control plots were harvested on 2 to 4 September 1995. For each harvested plant the following parameters were measured: Stem height from the soil surface to the uppermost capsule, number of leaves, length and width of the largest leaf, total weight of the above-ground plant including reproductive parts, number of flowers, number of capsules, number of seeds per capsule, total number of seeds per plant, total number of aborted seeds per plant, and weight of 10 randomly selected seeds in each plant. Weights were measured with a Mettler AE 160 after drying at room temperature for ca. 4 mo. We calculated means of all variables in all plots and used these in a randomized block ANOVA, where the effects of the OTC-treatment and block on the performance variables mentioned above were examined. In these analyses seed weight, total seed number, and leaf area were log-transformed, and plant height was squareroot-transformed to meet the assumptions of normality and homogeneity of variance. None of the other variables required transformation.

To examine if "natural disturbance" influenced growth and seed production, the percentage of bare soil was estimated in 5 × 5 cm plots around each of 80 randomly selected plants growing in natural conditions at the study site on 5 and 6 September 1995. These plants were collected, and the same performance variables as mentioned above were measured. The effects of disturbance, plant size (weight and height), and appropriate reproductive variables, on reproductive performance (fruit number, seed number per fruit, total seed number, and seed weight) were analysed by separate multiple regressions (one for each reproductive variable). We included both a linear and a quadratic component of disturbance level because scatterplot between disturbance and reproductive variables suggested that relationships might be unimodal. In these analyses seed weight, seed number, and plant weight, were log-transformed, and plant height was squareroot-transformed in order to meet the assumptions of regression analysis. Seeds per fruit and fruit number did not require transformation.

POPULATION DENSITIES

To examine if increased growing season temperature influenced population density, the number of individuals in each OTC and control plot were counted on 14 August in 1995, on 28 August in 1996 and on 23 July in 1997. The number of individuals was not counted in 1994. The effects of treatment, year, their interaction, and block on the number of plants were examined by a randomized block design ANOVA, using the squareroot of the total number of plants per plot as the dependent variable. Year was considered as a random factor in this analysis, so the error term of the treatment effect was the treatment by year interaction.

To examine if the degree of "natural disturbance" influenced plant density, the number of plants inside 100 randomly situated 20 × 20 cm plots was counted. Disturbance was estimated as the percentage of open soil, estimated to the nearest 5% in all plots. The relationship between degree of disturbance and number of plants in the plots was examined by a second order polynomial regression.

Results

OPEN TOP CHAMBER-TREATMENT

Plants of *E. frigida* responded strongly to experimental warming. Significant increases in all aspects of growth and reproduction measured, except for the number of seed per fruit, were found (Table 1). Although statistically significant, the increase in leaf number was small. Leaf area and plant height,

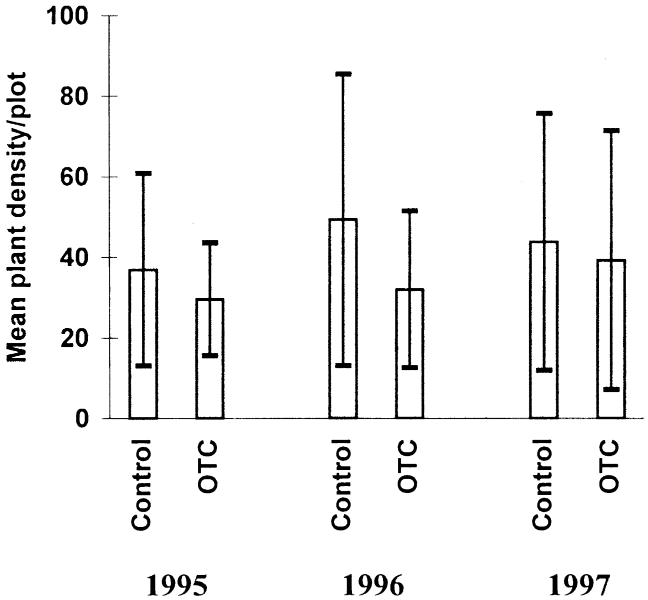

FIGURE 1. Relationship between percentage bare soil (natural disturbance level) and number of Euphrasia frigida *plants inside 20 × 20 cm squares (plant density) at Finse in 1995. Line shown is the 2. order polynomial.*

however, nearly doubled as a response to experimental warming. This resulted in more than a two-fold increase in vegetative plant weight. Fruit number increased by 43% in response warming, whereas the seed number per fruit did not differ between plants from the warmed and ambient temperature conditions. Nevertheless, total seed production per plant was 46% higher under warmer conditions compared to controls. There were no differences in any of the measured variables among blocks ($P > 0.06$ for all variables).

Although the warmer temperatures increased growth and reproduction of plants to a large extent, this did not translate into a higher plant density (Fig. 1). In fact, the OTC-treatment had a significant negative effect on plant density (Table 2), which was highest in the control plots in all years. There was no significant difference in plant density between years, and the effect of temperature did not differ between the years (Table 2). The effect of block, which correspond to the pairs of OTCs and controls and represent the spatial position of plants, was, however, significant in explaining the variation in plant density (Table 2).

NATURAL DISTURBANCE GRADIENT

Individual reproductive performance showed little relationship to disturbance levels in a series of multiple regressions, with the exception of seed number per fruit (Table 3). All reproductive variables, with the exception of seed weight, which does not appear to be influenced by any of the measured factors, was positively correlated to plant weight (Table 3). Fruit number was the only reproductive variable that was correlated (positive) to plant height. Seed number appeared to be positively correlated to fruit number (Table 3). Plant weight, which is highly important for reproductive output, did not show any relationship to disturbance level in a polynomial regression (1. order: $P = 0.81$, 2. order: $P = 0.88$, ANOVA: $P = 0.94$).

Natural plant density peaked at intermediate levels of disturbance (Fig. 2). In a polynomial regression, percentage of bare soil explained 37% of the variation in plant density. Both the

TABLE 2

Randomized block design ANOVA on the effects of OTC-treatment and year (both fixed) on plant density of Euphrasia frigida *at Finse in 1995 and 1996. Degrees of freedom (df), mean squares* (MS)*, F-ratio* (F)*, and significance value* (P) *are shown. This model explains 63% of the variation in plant density.* N = 66.

Source of variation	df	*MS*	*F*	*P*
Treatment	1	11.002	19.71	0.047
Year	2	1.212	0.41	0.66
Treatment × Year	2	0.558	0.19	0.83
Block	10	23.789	8.12	<0.00001
Error	50	2.931		

first and second order polynomial coefficients, and the overall model were highly significant ($P < 0.0001$ in all cases).

Discussion

The growth and seed production of *E. frigida* plants were largely temperature dependent. Except for seed weight and number of seeds per capsule, all measures of size and reproductive output were increased by the elevated temperatures inside OTCs. This agrees with previous studies of temperature effects on arctic and alpine perennials (Wookey et al., 1993, 1994, 1995; Parsons et al., 1994; Harte and Shaw, 1995; Henry and Molau, 1997). However, it appears that the impacts of temperature on growth and reproduction in *E. frigida* are stronger than in perennials. This might reflect more plasticity in the annual *E. frigida* than that of perennial vegetation. This is a likely consequence of the annual life history, where available resources are used to maximize reproduction before winter onset.

The size and physiological conditions of the host plant could have influenced the growth and seed production of *E. frigida.* Thus, the increased growth and seed production of *E. frigida* inside OTCs may also have been caused indirectly by increased vigor of host plants due to elevated temperatures. One of the perennials, *Bistorta vivipara,* had significantly higher plant weigth within the OTCs used in this experiment (Totland and Nyléhn, 1998). Host species quality is reported to affect growth and reproduction in *E. frigida,* but the main difference reported was between nitrogen fixing hosts and nonfixing hosts (Seel and Press, 1993). In the present study no nitrogen fixating species occurred in the study site (Nyléhn and Totland, pers. observ.). The species composition were almost the same in the OTCs compared with controls, the only exceptions were that *Salix herbacea* had ca. 15% lower density in the OTCs, and the density of moss and lichens were reduced by ca. 50 and 80% in the OTCs, respectively (Totland and Eide, unpublished data).

In 1995–1997 the population densities were lower under warmer temperatures than in control. Thus, although increased temperatures result in higher seed set, other factors appear to restrict germination and establishment in such a way that population density does not increase under elevated temperatures. In particular, cover of herbs and graminoids were ca. 19 and 15% higher under experimental warming compared to control plots in 1997 (measured by point-fraiming, Totland and Eide, unpublished). This may result in reduced opportunities for the germination and establishment of *E. frigida,* and could counteract the effect of higher seed availability on population density.

Population densities were highest at intermediate levels of open soil. This probably reflects a balance between the availability of open soil for germination, higher light levels for seed-

TABLE 3

Multiple regression on the effects of disturbance (quadratic), plant weight (log-transformed), plant height (squareroot-transformed), fruit number, and seed number (log-transformed) on reproductive variables (dependent) in Euphrasia frigida *at Finse in 1995. Regression coefficients and their standard error (SE), partial correlation (r_{part}), t-values (t) and significance value (P) are shown. F_{ANOVA} and P_{ANOVA} are from ANOVA on the full model. R^2 is the coefficient of multiple determination of significant model.*

Dependent	Predictors	Coefficient	SE	r_{part}	t	P	F_{ANOVA}	P_{ANOVA}	R^2
Fruit number	Constant	−4.52	0.79	0	−5.76	<0.0001	40.15	<0.00001	0.70
	Disturbance	−0.00185	0.015	−0.03	−0.12	0.90			
	(Disturbance)^2	−0.000008	0.00016	−0.01	−0.05	0.96			
	Plant weight	1.34	0.19	0.67	7.13	<0.0001			
	Plant height	0.59	0.27	0.22	2.21	0.03			
Seeds/fruit	Constant	−3.51	1.31	0	−2.67	0.009	14.38	<0.00001	0.46
	Disturbance	0.06	0.02	0.75	2.23	0.03			
	(Disturbance)^2	−0.0005	0.0003	−0.66	−2.05	0.04			
	Plant weight	1.23	0.31	0.49	3.92	0.0002			
	Plant height	0.75	0.45	0.23	1.68	0.10			
Seed number	Constant	−1.41	0.44	0	−3.19	0.002	49.04	<0.00001	0.78
	Disturbance	0.009	0.007	0.27	1.30	0.20			
	(Disturbance)^2	−0.00009	0.00007	−0.27	−1.31	0.19			
	Plant weight	0.67	0.11	0.61	5.83	<0.0001			
	Plant height	0.19	0.13	0.14	1.52	0.13			
	No. fruits	0.11	0.05	0.21	2.00	0.05			
Seed weight	Constant	0.09	0.64	0	0.14	0.88	1.54	0.21	
	Disturbance	0.006	0.007	0.54	0.94	0.36			
	(Disturbance)^2	−0.00009	0.00007	−0.75	−1.33	0.19			
	Plant weight	0.32	0.21	0.49	1.54	0.14			
	Plant height	−0.13	0.12	−0.25	−1.09	0.28			
	No. seeds	−0.15	0.23	−0.23	−0.66	0.51			

ling establishment and growth in disturbed soil, and the availability of host roots for further growth. Overall, it appears that the availability of "safe sites" (Silvertown and Lovett Doust, 1993), have a stronger influence on population density of *E. frigida* than increased seed production, under warmer temperatures.

Almost all (98%) sampled *E. frigida* plants managed to reproduce, all plants flowered, and flower abortion rates were extremely low (1%). Even *E. frigida* plants probably unattached to a host (growing in dense moss carpets) reproduced. Molau (1993a) also reports low abortion rates in *E. frigida,* and Seel and Press (1993) found that of three annual hemiparasites (*E. frigida, Rhinanthus minor,* and *Melampyrum sylvaticum*) in

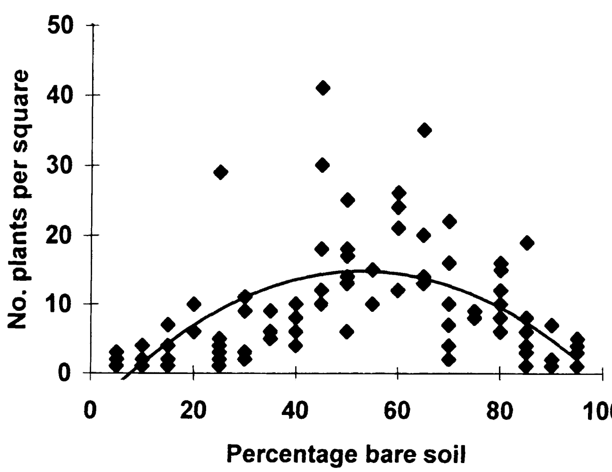

FIGURE 2. Bar-graph showing the mean number of Euphrasia frigida *plants in open top chambers (OTC) and control plots at Finse in 1995–1997. Vertical lines are standard deviations of the means.*

northern Sweden, only *E. frigida* managed to partition a considerable amount dry matter (ca. 44%) into reproductive structures when unattached to a host. Clearly, *E. frigida* is highly adapted for allocating resources into seed production under severe environmental conditions and host unpredictability.

The results of the present study suggest that the seed production of *E. frigida* will increase as a response to the forecasted 2 to 4°C increase in the annual mean global surface temperature (Houghton et al., 1996), supporting Molau (1993b), who predicted that late-flowering species, such as *E. frigida,* generally will be favored by increased temperature, mostly due to a prolonged seed maturation period. Thus, the seed production of alpine annuals might in general be increased by higher temperatures. In addition, since *E. frigida* has a wide host range (Seel and Press, 1993), changes in species composition due to global warming will probably not influence the availability of hosts.

However, population densities of *E. frigida* seem to be regulated more by the availability of safe sites for germination than by seed production, since *E. frigida* mainly grows in small openings generated by cryogenic soil movements and grazing by small rodents (mostly lemmings) in the study site. As the temperatures increases, disturbance by frost heave is likely to decrease, simultaneously as vegetation density increase. Therefore, the long-term effects of global warming on population density of *E. frigida* may be negative, despite increased reproductive output under warmer conditions.

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