

PLANT COMMUNITY RESPONSES TO SIMULATED ENVIRONMENTAL CHANGE AT A HIGH ARCTIC POLAR SEMI-DESERT

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Abstract. Impacts of climate change were simulated over five summer seasons in a high arctic polar semi-desert at Ny Ålesund, Svalbard, by using polythene tents to increase temperature, and by increasing precipitation and soil nutrient (NPK) availability. The effects of these treatments on vegetation cover were assessed at the start of the 1991, 1993, and 1995 field seasons, and at peak biomass in the same years. Over the first season of the experiment (1991), changes in percentage total living vegetation cover were significantly greater, and changes in dead vegetation cover significantly lower, in the tented treatments. In subsequent seasons, changes in total living cover were also greater under treatments simulating climate change, although the significant factors and interactions were year-specific. Between years, at both the early and mid-season sampling periods, the fertilizer application had the strongest effect on changes in plant cover, significantly decreasing cover of living *Dryas octopetala*, *Saxifraga oppositifolia*, and bare ground between 1991 and 1995, while increasing cover of bryophytes, *Salix polaris*, *Polygonum viviparum*, and total dead vegetation. Although cover of *D. octopetala* was greater during the first three years of fertilizer addition, marked winter injury occurred in this species on fertilized plots during winter 1993–1994. This resulted in reductions in total live cover and *D. octopetala* cover and an increase in total dead cover (by up to 22%) in watered and fertilized plots between 1991 and 1995. Seedlings of nitrophilous “immigrant” species were established naturally on bare ground in fertilized plots in the third year of the study and subsequently increased in number, so that after five seasons the community tended more toward bird-cliff vegetation rather than polar semi-desert vegetation. The tent treatment and the simulated increase in summer precipitation had little effect between seasons on the plant community, in comparison with the fertilizer treatment.

Key words: bare ground; colonization; extreme events; nitrogen; phosphorus; polar semi-desert; potassium; precipitation; temperature; tundra soils.

INTRODUCTION

General Circulation Models (GCMs) of the Earth's climate system predict profound changes in the abiotic environment of high-latitude ecosystems (Cattle and Crossley 1995). These include a mean temperature increase by 2°–4°C in summer and 1°–5°C in winter, and enhanced precipitation at high latitudes; for example, an average increase of 20–25% in precipitation is predicted over northern North America in all seasons (Mitchell et al. 1990, Maxwell 1992). In polar semi-deserts with large areas of bare ground, predicting plant community-scale responses to changes in the environment presents a particular challenge, since the potential exists for major adjustments in vegetation cover and biomass and for the encroachment of “immigrant” species onto uncolonized areas. By contrast, environmental change in the closed (complete vegetation cover)

tundra communities further south may shift the competitive balance between existing species, or change their year-on-year relative contribution to community productivity (Chapin and Shaver 1985), perhaps without exerting a major impact on total cover or productivity, at least in the short term (Shaver and Kummerow 1992). Opportunities for seedling establishment may also be much reduced due to the closed vegetation canopy in subarctic tundra, although disturbed microsites such as frost boils can be important sites of seedling recruitment (Gartner et al. 1986).

The contrast between the closed vegetation of the subarctic and the much more open communities of the high arctic polar deserts and semi-deserts is of interest not only from a fundamental ecological perspective, but also because changes in the areal extent and biogeochemistry of these systems, in response to climate change, have the potential to feed back to further global change. Such feedbacks could be caused by (1) changes in net trace gas fluxes between ecosystems and the atmosphere, and (2) by alterations in the surface energy and water balances associated with changes in vege-

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tation surface roughness, transpiration rates, and albedo (Foley et al. 1994). Since polar desert and semi-desert ecosystems cover in excess of 2.3×10^6 km², or 40% of the tundra biome (Oechel and Billings 1992), their potential significance at a regional or landscape scale cannot be overlooked. Thus, current predictions that large areas of closed tussock and wet coastal tundra could become net sources of CO₂ under a climate-change scenario (Shaver et al. 1992, Oechel et al. 1993), have not been balanced against the corresponding hypothesis that a migration of closed tundra into the high arctic could result, in the longer term, in increased removal of CO₂ from the atmosphere at those higher latitudes.

Over the past two decades there have been a number of environmental manipulation studies on arctic vegetation. Such projects, until recently, have not only been restricted geographically, for example to the Canadian arctic (Haag 1974, Henry et al. 1986, Gold and Bliss 1995), but have also been limited to closed vegetation communities, for example to tussock and wet coastal tundra in subarctic Alaska (Shaver and Chapin 1980, Oechel et al. 1993, 1994, Chapin et al. 1995). The study reported here is part of a larger project examining the effects of temperature, precipitation, and nutrient perturbations on two contrasting European arctic ecosystems—a high arctic polar semi-desert community in Svalbard, Norway, and an understory subarctic dwarf shrub heath beneath *Betula pubescens* Ehrh. ssp. *tortuosa* in Swedish Lapland. These two ecosystems are expected to respond differently to climate change because one comprises open vegetation with extensive areas of bare ground, where plant proliferation is by seedling recruitment, whereas the other has closed vegetation of clonally proliferating species (Callaghan and Emanuelsson 1985). The vegetation responses in the parallel experiment carried out in the closed vegetation of the dwarf shrub heath have been documented by Press et al. (1998). Nutrients were added to simulate increases in decomposition and nutrient mineralization that may occur as a result of increases in temperature and moisture (Heal and French 1974, Oechel et al. 1994).

The current paper reports on the effects of temperature, precipitation, and nutrient perturbations on vegetation cover and seedling establishment in a European high arctic polar semi-desert ecosystem over a 5-yr period. Although polar desert and semi-desert tundra are characteristic of 93% of the high arctic land area (Bliss and Matveyeva 1992), this is the only study to date to simulate the effects of climate change on a polar semi-desert community in the Eurasian high arctic. The specific hypotheses tested were that the plant community in high arctic ecosystems with a large proportion of bare ground would respond to simulated climate change (1) by major adjustments of plant cover, and (2) by colonization by “immigrant” species.

Our experiment is allied to the International Tundra

TABLE 1. Mean cover of vegetation categories on 26 June 1991 at the polar semi-desert site at Ny Ålesund based on four 10-m line transects ($n = 4$), with recording every 100 mm (after Wookey et al. 1993).

Cover type	Percentage cover
Vascular plants	
<i>Dryas octopetala</i> L. ssp. <i>octopetala</i>	
Living	7.8
Dead	5.5
<i>Saxifraga oppositifolia</i> L.	
Living	3.5
Dead	0.8
<i>Salix polaris</i> Wahlenb.	
Living	1.5
Dead	0.0
<i>Polygonum viviparum</i> L.	
Living	1.5
Dead	0.0
<i>Silene acaulis</i> (L.) Jacq.	
Living	0.0
Dead	0.3
Lichens	8.8
Bryophytes	5.2
Litter/organic detritus	20.3
Bare ground	46.5

Experiment (ITEX), which has 26 sites in 11 circum-polar countries; its objective is to assess the potential impact of global warming on tundra plant species (Marion et al. 1997). There are, however, several differences in methodology between the experiment reported here and the ITEX studies (see *Methods*).

METHODS

Research sites and experimental design

The polar semi-desert outer fjord site is situated within the *Dryas octopetala* zone of Svalbard (Brattbakk 1986), 3 km to the west of Ny Ålesund (78°56' N, 11°50' E) at an elevation of 22 m a.s.l. Approximately 70% of the ground surface is unvegetated; the soil is a lithosol, pH 6.9–8.0, developed over limestone, and organic matter is present mostly under *Dryas* mats. The area is a well-drained interfluvium with little sign of frost-heave or sorting. At the start of the 1991 field season, the vegetation and areas of bare ground at the site were characterized using four 10-m line transects, with recordings taken at 100-mm intervals, the results of which are given in Table 1. At Ny Ålesund, mean air temperatures for the period June–August were 3.9°, 3.7°, 4.4°, 3.1°, and 4.0°C in the years 1991 to 1995, respectively, and precipitation sums over the same months in the same years were 92, 96, 140, 143, and 32 mm.

Fifty-four plots, measuring 1.5×1.5 m, were divided into six replicates of eight treatments, in a factorial combination of three perturbations: temperature (T), water (W), and nutrients (fertilizers) (F). In the temperature (+T) treatment, integrated mean summer

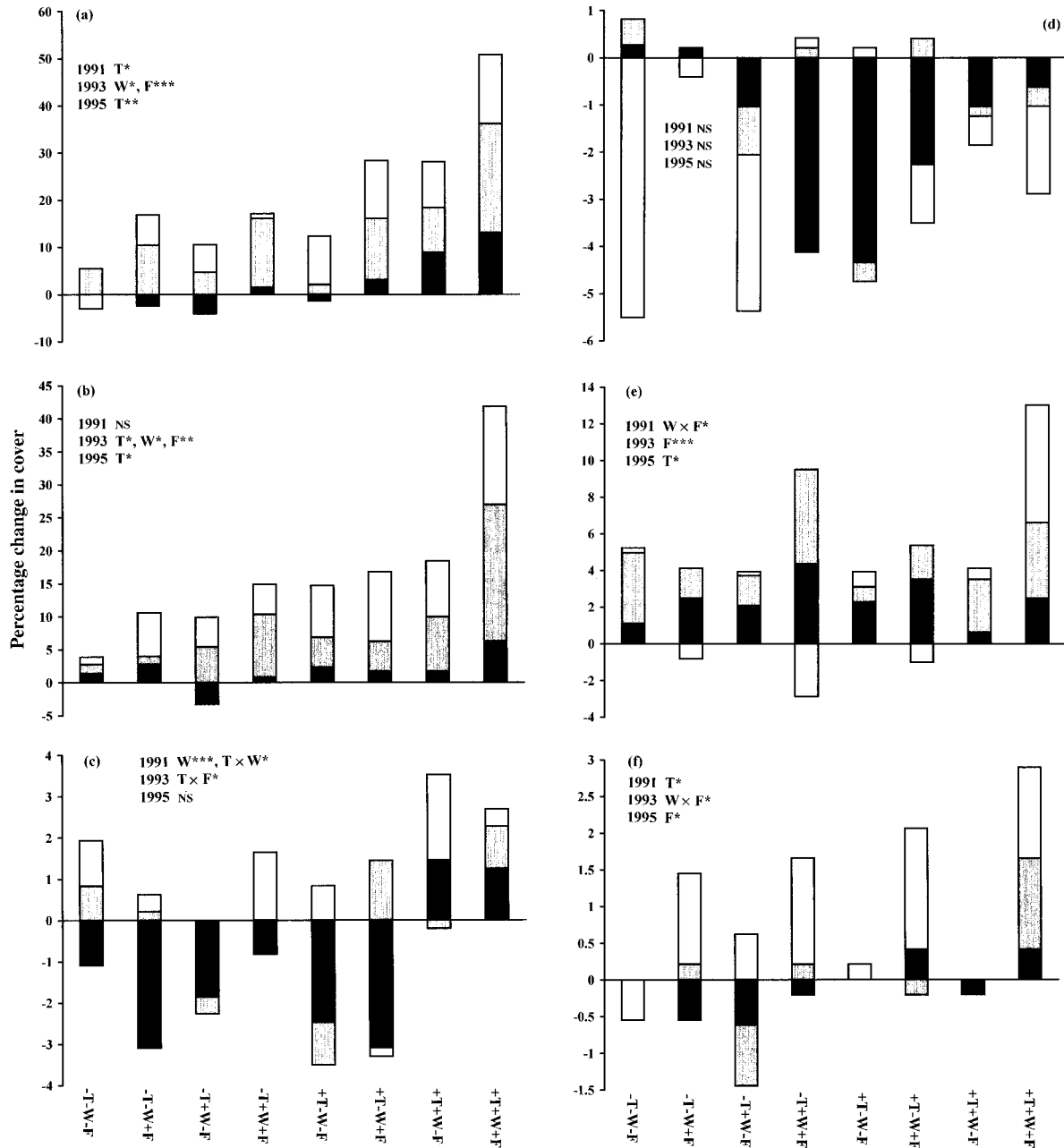


FIG. 1. Mean ($n = 4$) percentage change in cover within years with treatment for living (a) total cover, (b) *Dryas octopetala*, (c) *Saxifraga oppositifolia*, (d) lichens, (e) bryophytes, (f) *Salix polaris*, and (g) *Polygonum viviparum*, together with (h) total dead cover and (i) total bare ground. Closed bars refer to changes within the 1991 season, shaded bars to changes within the 1993 season, and open bars to changes within the 1995 season. Each total bar represents the sum of the changes in cover of the three sample periods, i.e., the split bars are additive. T = tents, W = water application, F = fertilizer; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant (General Linear Model), $n = 16$ for main effects.

air (5.4°C) and soil (6.1°C) temperatures (50 mm depth) in 1991 were increased by 3.5° and 0.7°C in comparison with ambient open plots, using open-topped polythene tents based on the design of Havström et al. (1993). These tents were in place from 22 June to the end of August in the years 1991–1995. Photon flux density was reduced by the presence of open-topped tents at

this site by 6%, and relative humidity was consistently lower beneath them. However, the magnitude of the reduction in humidity was generally less than 15%, and was probably driven by the warming of air within the tents (Wookey et al. 1993). Soil moisture contents at 5 cm depth under the tents were unchanged, although litter moisture was periodically reduced, compared

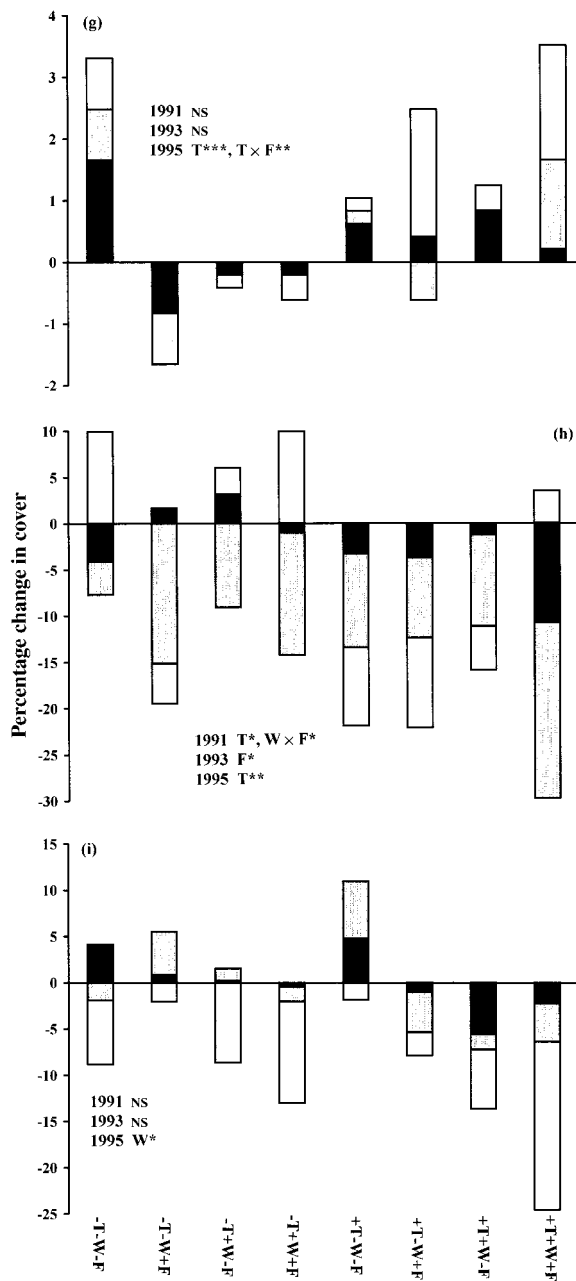


FIG. 1. Continued.

with control plots (Robinson et al. 1995, 1997). Full details of the research site and tent microclimate are provided in Wookey et al. (1993) and Robinson et al. (1995).

Water additions to watered plots (+W) were made six or seven times during each of the five seasons at a rate equivalent to a nominal 50% increase in average natural summer precipitation (a total addition of 45 mm). The enhanced precipitation treatment significantly increased the moisture content of litter for only a few hours after its application, and there were no

significant differences in soil moisture between watered and control plots, even 24 h after watering with 9 mm (the equivalent of 21 L) per watered plot (Robinson et al. 1995, 1997).

In the fertilizer (+F) treatment, the solutes nitrogen, phosphorus, and potassium were supplied in solution at total rates of 5, 5, and 6.3 g·m⁻²·yr⁻¹, respectively (as NH₄NO₃, KH₂PO₄, and KC1). Solutes were added four times during each of the five growing seasons to provide the total added annual nutrient flux. Since the solutes were added in small water volumes, equivalent amounts of water minus solutes were added to all the non-fertilized (-F) plots. The fertilizer concentrations were analogous to those used at a Canadian high arctic site by Henry et al. (1986).

The differences in methodology between our study and the International Tundra Experiment are as follows: (1) ITEX chambers, although open-topped like the polythene tents, are of a different design, being made of fiberglass and having a larger opening (0.6–1.5 m diameter, Marion et al. 1997); (2) ITEX chambers are permanent structures that are left in place throughout the year, whereas our plots are permanent but the tents are only in place during the summer season; and (3) the primary emphasis of the ITEX is the effect of global warming on tundra plant species, whereas we have also studied the effects of increased precipitation and nutrient availability on vegetation and soil processes.

Changes in cover

Percentage cover of each cover category was recorded, using a point-frame, in a 550 × 550 mm area of each of four replicate plots in each treatment in exactly the same position at the start of the field season in 1991, 1993, and 1995, and at mid-season (peak biomass) in the same years. The point-intercept method was used, with records obtained at 50-mm intervals, giving a total of 121 points per replicate plot. This method was ideally suited to the single-layered, low (~3 cm height) canopy.

Seedling establishment

The numbers of seedlings of previously unrecorded plant species were counted on 2 August 1993, 29 July 1994, and 26 July 1995 in each of the six replicate plots of each treatment.

Statistical analysis

Main effects (*n* = 16) of tent, water, and nutrient treatments were evaluated by multifactorial General Linear Models (GLMs). All measured variables were subjected to a test for homogeneity of variance prior to performing statistical analyses, and appropriate data transformations were made when necessary. *F* values and degrees of freedom for the Type III sums of squares (SAS Institute 1988) were used as the basis for statistical comparisons between treatments, their interactions, and main effects. Changes in plant cover (i.e.,

percentage cover at one sampling minus percentage cover at a previous sampling) were analyzed, since the responses of the treated plots (e.g., +T) can be compared with the appropriate untreated controls (e.g., -T), without the confounding effects of naturally occurring (rather than treatment-induced) changes in vegetation cover, which would occur if actual percentage cover values were analyzed. Moreover, it is the changes in cover, rather than cover values per se, that are most important in characterizing the extent of vegetation responses (e.g., colonization of bare ground) as a result of climate change.

RESULTS

The effects of the experimental manipulations on vegetation cover between mid-season 1991, 1993, and 1995 are arguably the most important to follow with respect for inclusion in future GCMs. These are summarized in Table 3 in response to fertilizer, since the other treatments had little effect on vegetation cover between seasons (see Fig. 2).

Changes in cover within a season

1. *Early to mid-season 1991.*—There was no effect of any treatment from early to mid-season 1991 (i.e., within the first year of treatment) on the major cover categories of living *D. octopetala*, lichens, or bare ground (Fig. 1b, d, and i). In contrast, change in percentage total live cover was significantly greater in the tented than untented treatments (Fig. 1a), and change in percentage total dead cover was lower in this treatment (Fig. 1h). Small significant changes in cover with treatment were observed for *Saxifraga oppositifolia* (Fig. 1c) and *Salix polaris* (Fig. 1f).

2. *Early to mid-season 1993.*—Change in percentage total live cover was significantly greater in the fertilized than unfertilized treatments (Fig. 1a), and in the watered compared to unwatered plots. Cover of *D. octopetala* increased in response to all three of the experimental factors over the season (Fig. 1b). Bryophyte cover was increased (Fig. 1e) and total dead cover (Fig. 1h) decreased in the fertilized treatment compared with the appropriate (-F) controls.

3. *Early to mid-season 1995.*—Change in percentage total live cover was significantly greater in the tented than untented treatments (Fig. 1a). Within the season, the tent treatment also increased the cover of *D. octopetala* (Fig. 1b), *Polygonum viviparum* (Fig. 1g), and bryophytes (Fig. 1e), and decreased the percentage of dead cover (Fig. 1h).

Changes in cover between years in early season

1. *Early season 1991 to early season 1993.*—There was no effect of any treatment on changes in percentage cover in the major cover categories of total live cover, total dead cover, bryophytes, lichens, or bare ground. Change in percentage living cover of *D. octopetala* was significantly greater in the fertilized treatments than in

the unfertilized treatments (Table 2a), although by contrast, change in percentage living cover of *S. oppositifolia* was significantly lower in the fertilized treatment (Table 2a).

2. *Early season 1991 to early season 1995.*—The direction and magnitude of changes in vegetation cover from 1991 to 1995 with treatment were different to the changes from early season 1991 to 1993, although again there was no effect of any treatment on changes in percentage total living cover; changes in *S. oppositifolia* cover in the fertilized treatment were as above (Table 2b). For example, in 1995, change in percentage *D. octopetala* cover was significantly more negative in the fertilized than in the unfertilized treatments (Table 2b). Also, unlike the 1991–1993 period, change in bryophyte cover was greater in the watered and fertilized treatments, both alone (fertilizer) and interacting together, and changes in percentage lichen cover and bare ground were significantly more negative in the fertilized than in the unfertilized treatments (Table 2b). Similarly, unlike the previous measurement period, changes in dead vegetation cover were significantly greater in the fertilized treatment (Table 2b). Changes in percentage dead and lichen cover were significantly greater and more negative in the tented vs. untented treatments, respectively (Table 2b).

Changes in cover between years in mid-season

1. *Mid-season 1991 to mid-season 1993.*—Change in percentage total live cover was significantly greater in the fertilized than in the unfertilized treatments (Fig. 2a), and correspondingly, change in percentage bare ground was significantly lower in the fertilized treatment (Fig. 2i). There was a significantly greater increase in percentage *D. octopetala* cover in the watered plus fertilized treatments (Fig. 2b), but no effect of any treatment on changes in cover of *S. oppositifolia* (Fig. 2c), lichens (Fig. 2d), bryophytes (Fig. 2e), *S. polaris* (Fig. 2f), *P. viviparum* (Fig. 2g) or total dead cover (Fig. 2h).

2. *Mid-season 1991 to mid-season 1995.*—The direction and magnitude of changes in vegetation cover from 1991 to 1995 with treatment were very different to the changes from mid-season 1991 to 1993 outlined above. For example, in 1995, change in percentage total live cover and in percentage *D. octopetala* cover were significantly more negative where the watered and fertilized treatments were present together (Fig. 2a, b). Also, unlike the 1991–1993 period, change in percentage dead cover was greater in the watered and fertilized treatments, both alone and interacting together (Fig. 2h), and change in percentage *S. oppositifolia* cover was significantly more negative in the fertilized than in the unfertilized treatments (Fig. 2c). Similarly, unlike in the previous measurement period, changes in cover of bryophytes (mainly as *Bryum caespitium* Hedw. and *Tetraplodon mniodes* (Hedw.) B.&S.), *Salix polaris* and *Polygonum viviparum* were signifi-

TABLE 2. Mean percentage change in cover between years at the early sampling for each significant factor ($n = 16$, General Linear Model), or combination of factors. All values refer to living cover, unless specifically stated otherwise.

Cover type	T	W	F	TW	TF	WF	TWF
a) Early 1991 to early 1993							
Live cover
<i>Dryas octopetala</i>	4.79*
			-4.25				
<i>Saxifraga oppositifolia</i>	-5.47**
			-2.53				
<i>Salix polaris</i>
<i>Polygonum viviparum</i>
Lichens
Bryophytes
Dead cover
Bare ground
b) Early 1991 to early 1995							
Live cover
<i>Dryas octopetala</i>	-4.2***
			1.8				
<i>Saxifraga oppositifolia</i>	-5.8**
			-2.4				
<i>Salix polaris</i>
<i>Polygonum viviparum</i>
Lichens	-10.1*	...	-9.8*
	-5.4		-5.8				
Bryophytes	9.9***	11.8*	...
			0.1			1.2	
Dead cover	5.4	...	7.0**
	-1.8		-3.5				
Bare ground	1.6*
	-9.5

Note: The upper number of each pair of means in a column refers to the value with application of the treatment (e.g., +F), whereas the lower refers to the value in its absence (e.g., -F). T = tents, W = water application, F = fertilizer.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

cantly greater in the fertilized treatment (Fig. 2e, f, g). However, as between 1991 and 1993, change in percentage "bare" cover was significantly more negative in the fertilized than in the unfertilized treatments (Fig. 2i). There was no effect of any treatment on change in lichen cover (Fig. 2d). The changes outlined above resulted in marked differences in the floristic composition of the fertilized compared with the unfertilized plots, and these differences are summarized in Table 3 for mid-season 1991, 1993, and 1995.

Seedling establishment

On fertilized plots, species characteristics of bird-fertilized sites were present since 1993 (Table 4). None of these species was found on plots that had not been fertilized. Individuals of all the species established as seedlings in 1993 survived the winter 1993–1994, and *Cochlearia officinalis* and *Saxifraga cernua* appeared for the first time in 1994. Two grass "seedlings" had also established in 1994 for the first time on plots that had received fertilizer, and more had established by mid-season 1995 (Table 4).

DISCUSSION

Treatment artifacts

For this project, as for the ITEX (see Marion et al. 1997), temperature manipulation devices had to

meet the following criteria: (1) be simple systems for use in extremely remote sites, (2) be sufficiently robust to withstand high winds and cold temperatures, (3) give a temperature enhancement in line with GCMs, and (4) minimize unwanted ecological effects. These criteria were met by an open-topped tent design. There is a wealth of information on the limitations of using such greenhouses for manipulating field temperature in high-latitude ecosystems. These problems have been reported from our own specific study (Wookey et al. 1993, Robinson et al. 1995, Wookey and Robinson 1997), from the ITEX (Marion et al. 1997), and more generally (Kennedy 1995). In our study, the effects of the tents on light quality, relative humidity, and soil and litter moisture contents, as outlined in the *Methods* section, were relatively small. The mean daily increase in air temperature of 3.5°C produced here was at the high end of the range of temperature increases produced in the ITEX (1°–2°C, Marion et al. 1997).

To overcome criticisms of artifacts in tent design, Kennedy (1995) recommended two amendments to methodology: (1) to design greenhouse apparatus for a tightly defined aim, and (2) to have multiple controls that address individual environmental factors. This may represent a way to improve our current

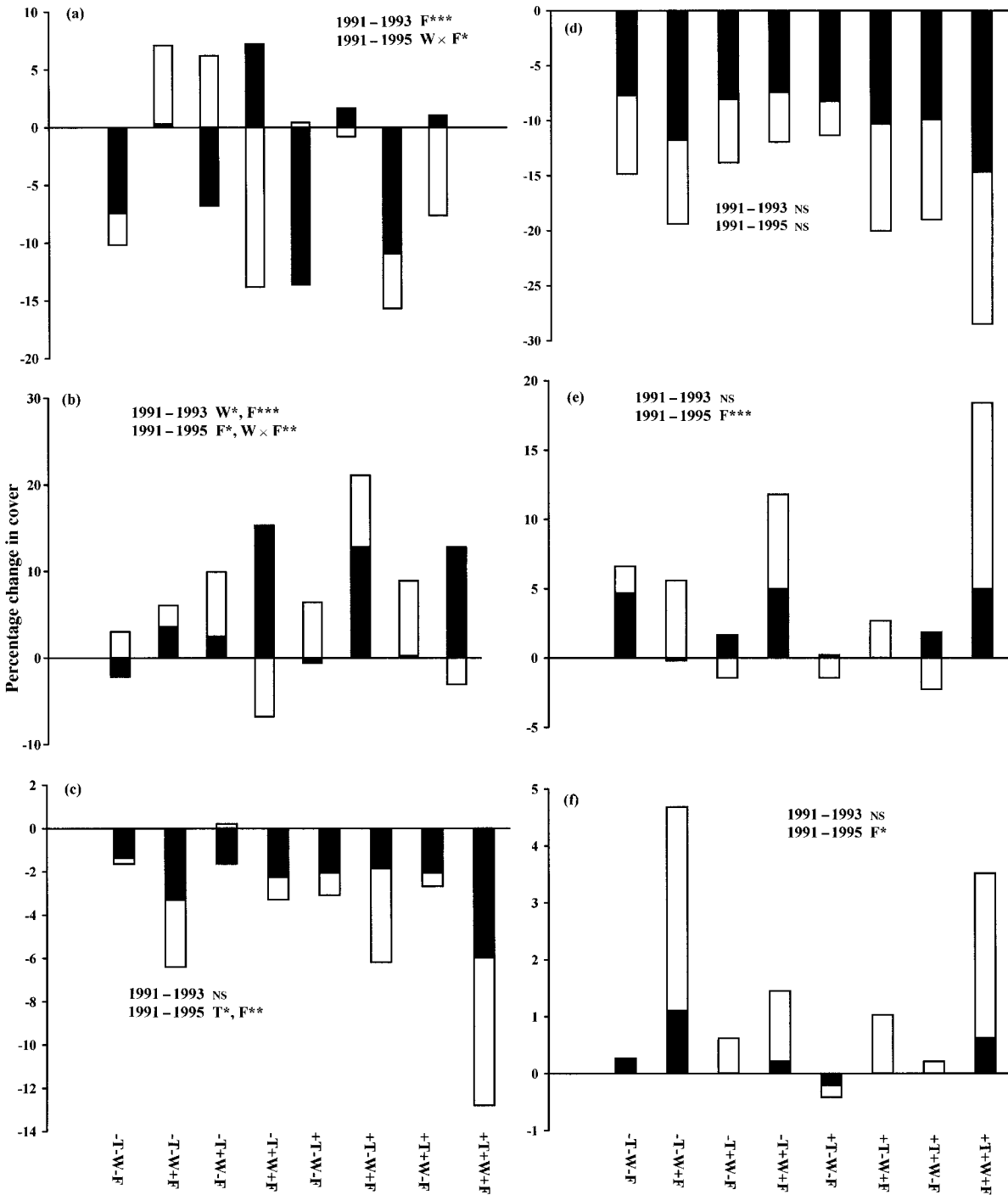


FIG. 2. Mean ($n = 4$) percentage change in cover between years with treatment at the mid-season sampling for living (a) total cover, (b) *Dryas octopetala*, (c) *Saxifraga oppositifolia*, (d) lichens, (e) bryophytes, (f) *Salix polaris*, and (g) *Polygonum viviparum*, together with (h) total dead cover and (i) total bare ground. Closed bars refer to changes between mid-season 1991-1993, and open bars to changes between mid-season 1991-1995. Each total bar represents the sum of the changes in cover of the two sample periods, i.e., the split bars are additive. T = tents, W = water application, F = fertilizer; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant (General Linear Model), $n = 16$ for main effects.

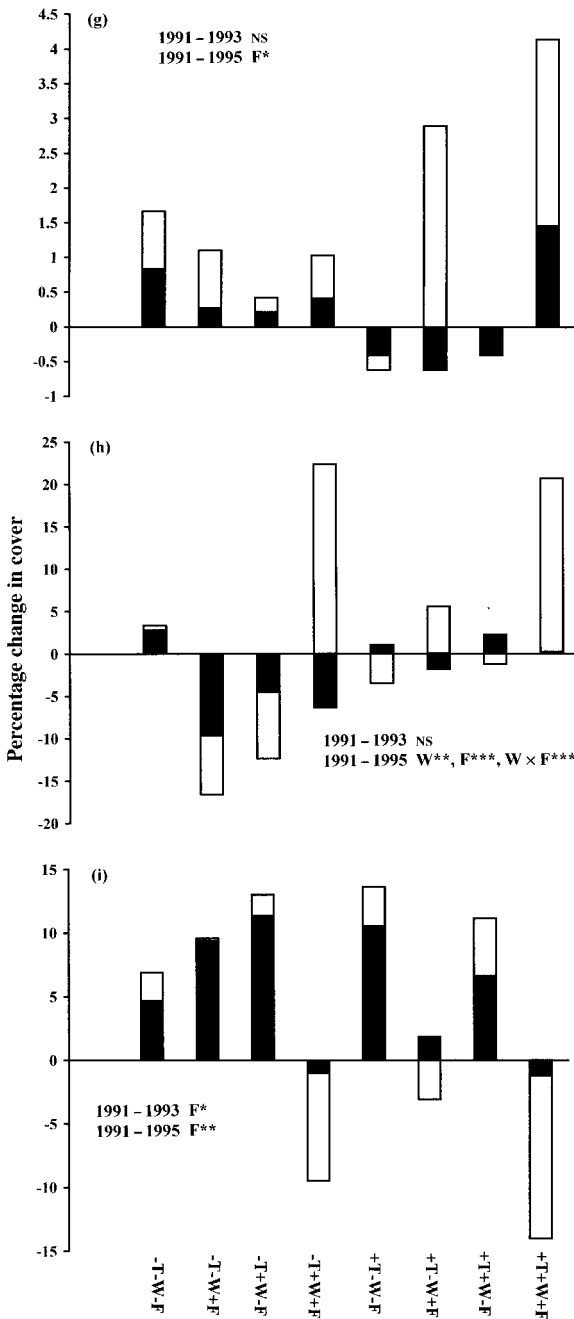


FIG. 2. Continued.

methodology, along with standardizing experimental treatments in as many sites as possible, as has occurred in the ITEX. Similarly, although applying fertilizer at the soil surface may not truly mimic changes in nutrient concentrations throughout a soil profile that could be induced by warming, better comparisons can be made by standardizing (small) application rates and methods among experiments in different ecosystems.

Vegetation responses

The response of high arctic vegetation to simulated environmental change was rapid, with an increase in live cover in the tented treatment within the first season. The vegetation thus showed considerable plasticity in response to environmental manipulations, even though the polar semi-desert can be termed a low-resource, or “stressful” environment that should impose and maintain traits associated with stress resistance syndrome (SRS) as described by Chapin et al. (1993). These characteristics putatively include low rates of growth, photosynthesis, and nutrient uptake. Within the three seasons of sampling at our site, the year-specific responses to the individual aspects of simulated climate change may reflect vegetation responses to inter-annual variability in temperature, rainfall, and nutrient supply.

As in moist tussock tundra in the Alaskan arctic (Chapin et al. 1995), short-term (1–3 yr) responses to environmental perturbations at our high arctic site were poor predictors of longer term changes in community composition. Plant growth in arctic ecosystems has often been shown to respond strongly to increased nutrient availability (e.g., Haag 1974, Chapin and Shaver 1985, Henry et al. 1986, Wookey et al. 1993, 1994, 1995, Parsons et al. 1994), and similarly, in our study, the largest changes in plant cover occurred in the fertilized treatments. After three growing seasons, *D. octopetala* plants receiving nutrient applications exhibited an increase in cover. However, more rapid above-ground growth and altered leaf morphology and chemistry, which occurred as a response to nutrient additions (Wookey et al. 1995), did not equate with an improvement in overall plant fitness, nor with greater survival potential in the longer term. *Dryas* plants in fertilized plots remained green into the autumn of 1993 (C. H. Robinson, unpublished data), and winter injury in fertilized *D. octopetala* plants was observed in spring 1994 after an autumn and early winter of exceptionally wet and mild conditions compared with the average for 1961–1990 (230 mm rainfall in November 1993 compared with the 19-yr average of 69 mm, and -2.8°C in November 1993 compared with the average of -7.0°C), suggesting that winter injury resulted from delayed hardening. By contrast to these reductions in “native” polar semi-desert clonal plants, seedlings of nitrophilous species established in the fertilized plots in 1993, and survived the 1993–1994 winter. The results suggest that the interaction between nutrient supply and tolerance of winter injury may be a major factor governing the distribution of plant communities in the high arctic. Between mid-season 1991 and 1995, the water and fertilizer interaction was, for some reason perhaps related to winter hardening, particularly detrimental to percentage live cover of *D. octopetala* and to percentage total live plant cover (Fig. 2a, b). The damaging effects of fertilizer on *Dryas* species have previously been reported (Henry et al. 1986, Fox 1992).

TABLE 3. Mean ($n = 16$) percentage cover at mid-season in each of the three years of sampling in fertilized and unfertilized plots.

Cover type	1991		1993		1995	
	+F	-F	+F	-F	+F	-F
Vascular plants						
<i>Dryas octopetala</i>						
Living	14.5	14.6	26.1***	14.6	14.5	21.2
Dead	7.3	8.9	2.6	4.2	19.4**	11.3
<i>Saxifraga oppositifolia</i>						
Living	4.6	4.3	1.2*	2.5	0.8***	3.9
Dead	0.1	0	0.2**	1.2	0.7***	2.5
<i>Salix polaris</i>						
Living	0.4	0.3	0.9*	0.3	2.5*	0.4
Dead	0.1	0	0	0	0.1	0.0
<i>Polygonum viviparum</i>						
Living	0.6	1.0	1.0	0.5	2.4*	0.7
Dead	0.1	0.1	0	0	0.1	0.1
<i>Silene acaulis</i>						
Living	0.3	0.1	0.3	0.1	0.1	0.2
Dead	0.1	0	0.2	0	0.1	0.0
Lichens	11.6	10.5	0.6*	1.9	2.7	4.2
Bryophytes	5.2*	3.1	7.6	5.2	12.3***	2.1
Litter/organic detritus	19.0	19.9	19.3*	24.0	13.1	11.9
Live cover	40.0*	34.2	43.0***	24.3	36.1	34.1
Dead cover	27.4	29.2	23.0**	29.4	37.7***	25.9
Bare ground	32.2	36.6	34.0**	45.2	26.2**	39.6

Note: +F = fertilized, -F = unfertilized.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Henry and co-workers (1986) employed single fertilizer additions of 5 and 25 g N/m² as NH₄NO₃ and 5 and 25 g/m² NPK in the 1980 field season. In July 1982, a significant reduction was observed in total biomass of *Dryas integrifolia* M. Vahl. with the high NPK addition at a mesic *Cassiope* heath site, but not at a wet meadow or a dry-mesic community. The interpretation of these results is complicated by the fact that single large additions of fertilizer were made, so that the growth reductions may have been due to direct toxicity of the fertilizer, or to the lack of frost tolerance of the plants.

After five growing seasons of fertilizer additions, the plant community in our experiment had changed substantially (Tables 3, 4). Compared with the vegetation cover in the unfertilized plots, the community was characterized by less cover of *S. oppositifolia*, by greater abundance of living *S. polaris*, *P. viviparum*, and by nitrophilous bryophytes, more angiosperm seedlings, and greater cover of dead *D. octopetala*. There was also a marked decline in the amount of bare ground with the application of fertilizer. The "new" seedlings are characteristic of bird-cliff vegetation. Hoffman (1968, as cited in Elvebakk 1994) described an *Oxyria-Saxifragetum cernuae* association from bird cliffs in eastern Svalbard, where *Oxyria digyna*, *Saxifraga cernua*, and *Cochlearia officinalis* were considered to be the species most favored by manuring. Hartmann (1980, as cited in Elvebakk 1994) studied (probably

less intensively manured) bird-cliff sites dominated by grasses. There are no records of *D. octopetala* from nutrient-rich sites in Svalbard, although bryophytes are abundant in these areas (Eurola and Hakala 1978, Elvebakk 1994).

In our analogous experiment in a subarctic dwarf shrub birch heath (Press et al. 1998), the strongest response of plant cover was also to fertilizer (N, P, and K, here applied at 10, 10, and 12.6 g·m⁻²·yr⁻¹, respectively). However, the response in the subarctic was mediated by an increase in abundance of a grass, *Calamagrostis lapponica* (Wg.) Hartm., at the expense of *Empetrum hermaphroditum* Hagerup, an evergreen dwarf shrub, the original dominant species at the site. Greater grass cover and canopy density plus an accumulation of standing dead material combined to reduce the cover of subordinate understory species, particularly mosses (Potter et al. 1995), liverworts, and lichens (Press et al. 1998). These results from the subarctic ecosystem, probably mediated by competition, contrast markedly with those from the polar semi-desert site, where the response of vegetation cover to increased nutrient availability was mediated through the colonization of bare ground by both new seedlings and bryophytes, and through the interaction of nutrient supply and winter hardening on the survival of *Dryas octopetala*. In both high and subarctic ecosystems, however, species responses to perturbations are highly in-

TABLE 4. Mean (± 1 SE) number of individuals per plot ($n = 24$) of species unrecorded prior to 1993 at the Ny Ålesund site.

	+F	-F
<i>Draba corymbosa</i> R. Br.		
1993	5.30 \pm 0.89	0 \pm 0
1994	1.67 \pm 0.40	0 \pm 0
1995	2.33 \pm 0.33	0 \pm 0
<i>Minuartia stricta</i> (Swartz) Hiern		
1993	1.40 \pm 0.58	0 \pm 0
1994	0.29 \pm 0.17	0 \pm 0
1995	2.21 \pm 1.03	0 \pm 0
<i>Oxyria digyna</i> (L.) Hill		
1993	0.04 \pm 0.04	0 \pm 0
1994	0.17 \pm 0.11	0 \pm 0
1995	0.17 \pm 0.10	0 \pm 0
<i>Cochlearia officinalis</i> L.		
1993	0 \pm 0	0 \pm 0
1994	0.17 \pm 0	0 \pm 0
1995	0.08 \pm 0.06	0 \pm 0
<i>Saxifraga cernua</i> L.		
1993	0 \pm 0	0 \pm 0
1994	0.12 \pm 0.09	0 \pm 0
1995	0.21 \pm 0.13	0 \pm 0
Grass spp. (mainly <i>Phippsia algida</i> (Sol.) R. Br.)		
1993	0 \pm 0	0 \pm 0
1994	0.08 \pm 0.06	0 \pm 0
1995	1.63 \pm 1.41	0 \pm 0

Note: +F = fertilized, -F = unfertilized.

dividualistic and not readily generalized (Chapin et al. 1995).

Within the growing seasons of 1991 and 1995, total vegetation cover was significantly increased by the tent treatment. However, the effects of the tents on plant cover between seasons and on community composition were minor. These facts suggest that increases in mean summer integrated air and soil temperatures of 3.5° and 0.7°C are effective in increasing plant cover over a season, but this effect does not persist from year to year. The results also suggest that additional summer precipitation (up to 58%) that may occur by the end of the next century has little effect on vegetation cover alone, although in combination with nutrient additions, enhanced precipitation was a potent factor in the colonization of bare ground. This poses the questions, "How realistic are the fertilizer applications?" and "By what amount will soil nutrient availability be increased under a climate-change scenario?" The answers to these questions depend to a certain extent upon the actual increases in air temperature that will occur, and thus on the increases they induce in soil temperatures. In our study, the small increase in soil temperature (0.7°C) produced by the tents over the summer season did not increase nitrogen mineralization (Robinson et al. 1995). The answers to these questions also depend on the balance between gross mineralization of nutrients and their immobilization in plant or microbial biomass (Jonasson et al. 1993). Thus, the conclusion

of Chapin et al. (1995), studying moist tussock tundra, that "realistic predictions of the future distribution of vegetation with respect to climate must emphasize the indirect effects of climate on resource supply," also holds true for our study.

Conclusions

This study shows that if soil nutrient availability increases at the soil surface in polar semi-desert sites under a climate-change scenario, areas of bare ground could be colonized by both "immigrant" seedlings and bryophytes. The tent treatment and the simulated increase in summer precipitation, in comparison with the fertilizer treatment, had little effect between seasons on the plant community. While it is only possible to speculate on the precise climatic causes of winter injury in *D. octopetala* in the fertilized plots, it is probable that, over centuries, these would be repeated several times. The frequency of these "extreme events," if nutrient availability increases in arctic soils, has strong implications for the composition of the plant community of high arctic polar semi-desert ecosystems. Further work should elucidate the effect of changes in vegetation cover on ecosystem function and the consequences of changes in the plant community on feedbacks to climate change.

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