ESSAY REVIEW

Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments

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Summary

1. The effects of global climate change are predicted to be strongest in the Arctic. This, as well as the suitability of tundra as a simple model ecosystem, has led to many field experiments investigating consequences of simulated environmental change.

2. On the basis of 36 experiments reviewed here, minor light attenuation by clouds, small changes in precipitation, and increases in UV-B radiation and atmospheric CO_2 concentrations will not affect arctic plants in the short term. However, temperature elevation, increases in nutrient availability and major decreases in light availability will cause an immediate plant-growth response and alter nutrient cycling, possibly creating positive feedbacks on plant biomass. The driver of future change in arctic vegetation is likely to be increased nutrient availability, arising for example from temperature-induced increases in mineralization.

3. Arctic plant species differ widely in their response to environmental manipulations. Classification into plant functional types proved largely unsatisfactory for generalization of responses and predictions of effects.

4. Nevertheless, a few generalizations and consistent differences between PFTs were detected. Responses to fertilization were the strongest, particularly in grasses. Shrubs and grasses were most responsive to elevated temperature.

5. Future studies should focus on interactive effects of environmental factors, investigate long-term responses to manipulations, and incorporate interactions with other trophic levels. With respect to plant functional types, a new approach is advocated, which groups species according to their responses to environmental manipulations.

Key-words: Biomass, global environmental change, nitrogen concentration, ozone, UV-B

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Introduction

The climatic effects of global change are expected to be most pronounced in the Arctic (Cattle & Crossley 1995; IPCC 1990; 1998; Maxwell & Barrie 1989). Many experiments have investigated the potential responses of this biome to environmental change (Henry & Molau 1997). They have generally focused on plant responses, with some accounts of soil processes (Hobbie 1996; Jonasson *et al.* 1993; Jonasson *et al.* 1999; Nadelhoffer *et al.* 1991; Robinson *et al.* 1995) and invertebrates (Hodkinson *et al.* 1996; Hodkinson *et al.* 1998; Strathdee *et al.* 1993). Ecosystem processes have also been studied (Billings *et al.* 1983; Billings *et al.* 1984; Oechel *et al.* 1994; Oechel *et al.* 1994, 1998), but detailed investigations linking plant growth and ecosystem function are rare (Hobbie & Chapin 1998b; Shaver *et al.* 1998). This review attempts to distil generalizations about the responses of arctic plants to environmental manipulations, as the basis for a predictive framework.

To predict the changes to vegetation that might occur within the Arctic, it is essential to understand the mechanisms and pathways of plant responses to altered environmental conditions. Physiological aspects of responses to temperature, CO_2, UV-B, etc. are well understood (Bazzaz 1990; Taulavuori *et al.* 1998), but our knowledge of how these act in concert and how they affect the performance of different species in the field is poor. It is this knowledge, however, that is needed to estimate climate change effects on other trophic levels (e.g. soil micro-organisms or herbivores) and to predict ecosystem functioning by means of mechanistic modelling (Reynolds & Leadley 1992).

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GLOBAL CLIMATE CHANGE: MODELS AND PREDICTIONS

For the Arctic, consistent predictions from transient-CO_2-increase-global circulation models for the middle of this century have been made. These are: (i) winter temperature to increase by 5–10 °C (IPCC 1998), but summer air temperature probably elevated by only 1–5 °C (Cattle & Crossley 1995; Rowntree 1997); (ii) winter and summer precipitation to increase by 0·25–5 mm day^{-1}, but may be locally less than at present, e.g. on the Taimyr Peninsula (Rowntree 1997). Such variability will result in more dry days in much of the Canadian and Alaskan Arctic, but more precipitation-days in Greenland and over the Arctic Sea. Soils will become drier because soil moisture is determined more by temperature (i.e. evapotranspiration) than by rainfall (Rowntree 1997).

However, these predictions are still uncertain: cloud–radiation interactions are complex and different assumptions about their effects can influence the predicted temperature rise; ocean–atmosphere coupling is modelled on too coarse a scale; and the effects of aerosols, potentially resulting in radiative forcing, are only poorly understood (IPCC 1990; Rowntree 1997). Prediction of future trends in UV-B exposure is similarly confounded by the effects of pollutants within the troposphere, and the uncertainties associated with prediction of future patterns of cloud amount and type (Madronich *et al*. 1998).

During the past few decades, environmental conditions have changed in arctic regions (Chapman & Walsh 1993; Serreze *et al*. 2000), and increased vegetation growth as well as northwards migration of the tree line have been predicted (Emanuel *et al*. 1985; Epstein *et al*. 2000). Over the past 40 years temperatures have risen by 0·2–0·3 °C, but locally trends exceed 0·5 °C per decade (Serreze *et al*. 2000). Moreover, snow cover area has declined by ≈ 10% since 1972, and precipitation (rain and snow) in northern Canada has increased by 20% over the past 40 years (Serreze *et al*. 2000). There are, however, insufficient data to detect trends in cloud cover in arctic regions. Ozone depletion in the Arctic has become more severe in recent years (Sinnhuber *et al*. 2000), and UV-B exposure appears to have increased (Madronich *et al*. 1998; Searles *et al*. 2001). This trend is predicted to intensify over the next two decades (Shindell *et al*. 1998).

PLANT FUNCTIONAL TYPES

Experiments at different locations within a biome inevitably involve different plant species. To generalize, and to incorporate plant responses into vegetation process models, it is not necessary to distinguish the responses of each species. Instead, the concept of plant functional types (PFT) can be used, with a PFT defined as a grouping of species sharing the same response to a perturbation (Gitay & Noble 1997).

One approach to PFT classification, used by Chapin *et al*. (1996) for arctic plants, uses cluster analysis of plant traits such as leaf longevity, typical soil moisture and photosynthetic rate. Their aim was to predict plant effects on ecosystems. The result was a dichotomous key, which first splits vascular and non-vascular plants, then splits the vascular into woody and herbaceous groups. Woody plants are then separated into evergreen and deciduous, and the herbaceous species are differentiated into aerenchymous (sedges and rushes) and non-aerenchymous species (grasses and herbs).

Here we use the PFT concept to integrate findings from Arctic field studies which have manipulated important components of climate change. Specifically, we ask: (i) what are the patterns of plant response to different climate-change factors in manipulative field experiments? and (ii) does the PFT concept provide a useful generalization of plant responses? Although meta-analyses of temperature elevation experiments within the International Tundra Experiment (ITEX) project, and of a broader set of ecosystem warming experiments, have been performed recently (Arft *et al*. 1999; Rustad *et al*. 2001), ours is the first systematic analysis incorporating a range of environmental manipulations.

Materials and methods

THE DATABASE

This review includes Arctic field studies north of the polar circle, published before 2001, in which abiotic components of expected climate change were manipulated, such as cloudiness (shading), atmospheric CO_2 concentration, nutrient availability (fertilization), soil water availability (watering), temperature and UV-B. Fertilization is the most commonly manipulated factor in Arctic field experiments, and so only those in which fertilization was considered in combination with at least one other factor were included. The only exception was the study of Shaver & Chapin (1986), which includes data on grasses which were otherwise poorly represented amongst the experiments reviewed. Some studies had to be excluded: Hartley *et al*. (1999) and Starr *et al*. (2000) reported from soil warming experiments, where treatments were unfortunately confounded with air warming and season length manipulations, respectively. Shirazi *et al*. (1998) and Phoenix *et al*. (2000) were excluded because they manipulated disturbed vegetation. In total, 41 articles, reporting 36 separate experiments, form the database for analysis (Table 1).

We included data for all species (or genera or species groups), years and treatments reported in the original papers, but excluded those manipulations that had no direct bearing on climate change (e.g. neighbour removal, clipping). Only main factors were included in the database, as no interaction was reported in

Table 1. Summary of experimental factors manipulated. In many cases more than one study is reported from one site

Factor	No. of sites	Prediction	Level of treatment	Studies	Comments
CO_2	2	700 µmol mol^{-1}*	680 µmol mol^{-1}	1–3	
Fertilization (N)	14	0–5 g m^{-2} year^{-1}†	1–25 g m^{-2} year^{-1}	4–27	Experimental fertilizer inputs often greatly exceed natural inputs; N often applied in combination with P and K
Light availability	8	–10–20% ‡	–50%	6–13, 15–27	Uncertain prediction of cloud cover
UV-B	2	5% depletion§	15% depletion	3, 28–30	Spring maximum higher than annual average; (O$_3$ depletion) uncertain predictions
Warming	23	2–5 °C‡	2–5 °C	6–12, 15–26 31–41	Summer only warming by greenhouses (for critique see Kennedy 1995; Marion *et al.* 1997)
Watering	5	+10–25% year^{-1}‡	10–60% (summer)	4, 13–19, 41	Watering treatments representing controls for fertilizer solution applications not included

*IPCC (1990).
†Nadelhoffer *et al.* (1991).
‡IPCC (1998).
§Madronich *et al.* (1998).
Studies:
1: Tissue & Oechel (1987); 2: Moorhead & Linkins (1997); 3: Gwynn-Jones *et al.* (1997); 4: Henry *et al.* (1986); 5: Shaver & Chapin (1986); 6: Chapin & Shaver (1985); 7: Shaver *et al.* (1986); 8: Chapin *et al.* (1986); 9: Chapin *et al.* (1995b); 10: Chapin & Shaver (1996); 11: Shaver *et al.* (1998); 12: Molau & Shaver (1997); 13: McGraw (1985); 14: Karlsson (1985); 15: Wookey *et al.* (1995); 16: Parsons *et al.* (1994); 17: Parsons *et al.* (1995); 18: Potter *et al.* (1995); 19: Press *et al.* (1998); 20: Havström *et al.* (1993); 21: Michelsen *et al.* (1996a); 22: Graglia *et al.* (1997); 23: Jonasson *et al.* (1999); 24: Wookey *et al.* (1993); 25: Wookey *et al.* (1994); 26: Welker *et al.* (1993); 27: Baddeley *et al.* (1994); 28: Johanson *et al.* (1995); 29: Taulavuori *et al.* (1998); 30: Gehrke (1999); 31: Stenström *et al.* (1997); 32: Jones *et al.* (1997); 33: Hobbie & Chapin (1998a); 34: Hobbie *et al.* (1999); 35: Hobbie & Chapin (1998b); 36: Mølgaard & Christensen (1997); 37: Welker *et al.* (1997); 38: Alatalo & Totland (1997); 39: Stenström & Jónsdóttir (1997); 40: Molau (1997); 41: Shevtsova *et al.* (1997).

more than five studies, with the exception of the temperature × fertilization interaction. Combining the six experiments that manipulated fertilization and temperature provided no evidence for any overall pattern of interaction (data not shown).

In most experiments, more than one response variable was measured. We selected those most commonly assessed and assigned them to one of five groups: biomass; leaf; reproductive; physiological; and chemistry measurements (details of grouping available from the authors or at www.abdn.ac.uk/pss/woodin.hti). Not all data given in an article could be incorporated: the root : shoot ratio, for example, was not included into the biomass group as it reflects relative rather than absolute change. The leaf group includes only parameters relating to individual leaves, not to leaf number or total leaf biomass. Also, as this study centres on plant functional types, only data relating to individual plants were included. Cover data (e.g. Robinson *et al.* 1998), ecosystem parameters (e.g. Shaver *et al.* 1998), and other measurements per plot were not used. Clearly, not all parameters within a designated group would necessarily be expected to show the same directional responses to any particular environmental perturbation. In fact, there were two instances in which opposite responses occurred, but these had no effect on the overall results.

Averaging over all response variables within each group yielded one value per response group per

species, treatment, year and experiment. This means, for example, that a study reporting the above-ground biomass and photosynthetic responses of four species to two treatments over 4 years generated a total of $2 \times 4 \times 2 \times 4 = 64$ data points.

Responses of species to treatments were recalculated from data presented in tables and graphs to make the different species and treatments comparable. The value in the meta-analysis database (X) was calculated as:

$$X = \log_{10}\left(\frac{\text{mean of response variable for treatment}}{\text{mean of response variable for control}} \cdot 100\%\right)$$

This transformed absolute into relative (percentage of control) values, correcting for size differences between species. Where data for a treatment were not given because they were not significant (e.g. Chapin & Shaver 1985 for elevated temperature), a value of 100% (= no change) was entered for analysis. We followed the approach recommended by Hedges *et al.* (1999) and $\log_{10}$-transformed the ratio for all analyses.

For analysis of treatment effects on PFTs, only biomass and leaf nitrogen concentration were used, as no other response variables provided sufficient data. All PFTs qualified for analysis of biomass responses, but only three (sedges, deciduous and evergreen shrubs) provided enough data to justify analysis of leaf nitrogen concentration responses.
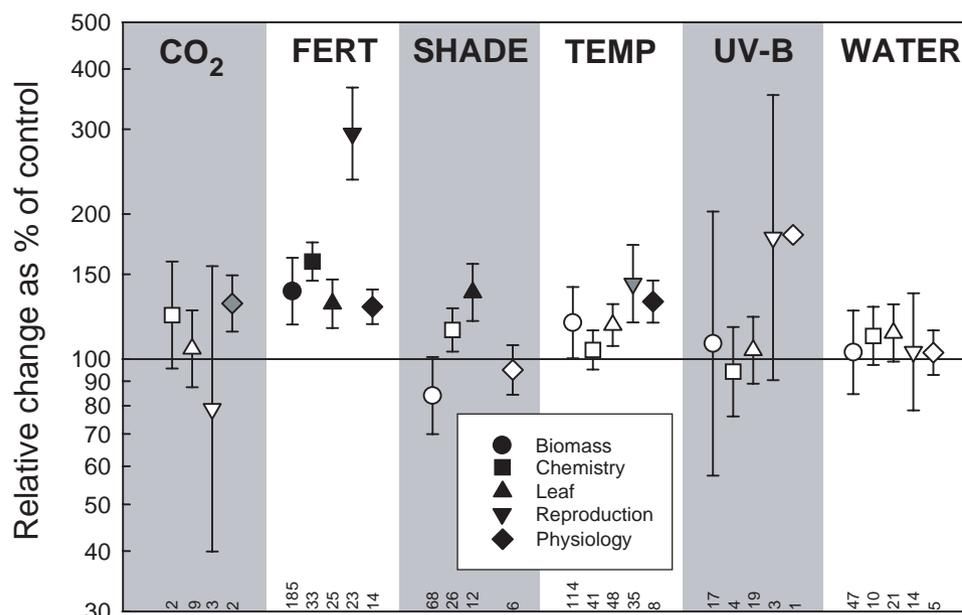
Fig. 1. Response of plants to environmental perturbations. Values are means ± SE, depicted as percentage of untreated controls. Black and grey symbols indicate that means differ significantly from 100% ($P < 0.05$ and $0.1 > P > 0.05$, respectively; two-tailed t-test). Treatments are: elevated CO_2, fertilization (FERT), light attenuation (SHADE), elevated temperature (TEMP), elevated UV-B radiation, and irrigation (WATER). The y axis is scaled logarithmically. Numbers at the bottom refer to corrected sample size (df + 1).

STATISTICAL ANALYSIS

Although it would have been desirable to follow a strict meta-analytical approach (expressing effects as multiples of standard deviations: Arft *et al*. 1999; Goldberg *et al*. 1999; Gurevitch & Hedges 1993; Gurevitch & Hedges 1999; Gurevitch *et al*. 1992), we regarded this as inappropriate for two reasons. First, too few articles reported sample size, sums of squares, *F* values etc., making it impossible to extract estimates of sample variation. In some cases where results were not significant, not even the treatment effect on the mean was reported. Also, most experiments were factorial designs including two or more treatments, and the measures of variance presented often did not represent the variance of the main effect. To exclude all such articles from analysis would have made the sample size vanishingly small. Second, we found the software (METAWIN 2, Sinauer Associates, Sunderland, MA, USA) used in recent meta-analyses (Goldberg & Novoplansky 1997; Gurevitch *et al*. 2000; Searles *et al*. 2001) unable to take account of the complicated structure of the data (especially nesting and non-linear repeated measurements). Its usage would have led to a bias towards sites/studies with many factors and/or species.

We incorporated data from different years as repeated measurements. Because few studies reported data from more than 2 years, a linear repeated measurement structure could not be applied (SAS Institute Inc. 1989). Duration was nested within site to account for multiple measurements within one experiment (which is equivalent to a repeated measurement with an unspecified covariance matrix). Latitude, elevation, average annual temperature and average July temperature, and numbers of replicates and subsamples, were considered as covariates. The different treatment manipulations were nested within site, while the species reported from an experiment were nested within treatment.

The data set was analysed using the MIXED procedure of SAS (SAS Institute Inc. 1989). Denominator degrees of freedom were calculated using the Satterthwaite option. After the full model was tested (covariates entered first), it was simplified by stepwise removal of interactions and covariates, with a removal threshold of $P = 0.1$ (Crawley 1993). This procedure eliminated all covariates, leaving only main effects in the model.

Residuals were tested for assumptions of ANOVA, namely that the transformed data were normally distributed and groups had homogeneous variances (Sokal & Rohlf 1995). *Post hoc* comparisons were performed using Tukey's honest significant difference test (SAS Institute In*c*. 1989; Sokal & Rohlf 1995). Error bars represent standard errors of means according to the output of the statistical model and are thus corrected for blocking and repeated measurements.

Results

TREATMENT EFFECTS

Fertilization

Biomass of plants in fertilized plots was, on average, 141% of controls, with a similar magnitude of response in leaf measures (135% of controls; Fig. 1). Element contents in leaves and physiological parameters responded more strongly, to 162 and 151% of controls,
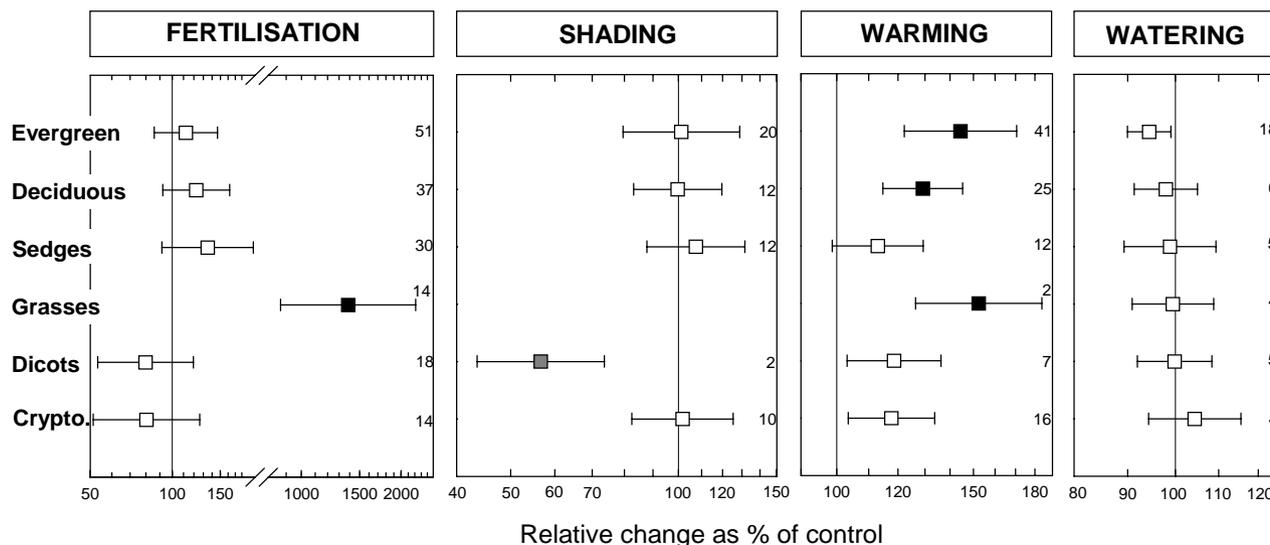
Fig. 2. Biomass response of plant functional types (PFT) to (a) fertilization; (b) shading; (c) elevated temperature; and (d) irrigation as percentage of untreated controls (see Table 2). Solid symbols indicate that means differ significantly from 100% (two-tailed *t*-test on $\log_{10}$-transformed data). Response of grasses to fertilization differs from all other PFTs (Tukey's HSD, $P < 0.05$); response of dicotyledons to shading is almost significantly different from the other PFTs (Tukey's HSD, $P = 0.094$). Note differences in scaling and that the *x* axis is scaled logarithmically. Numbers refer to sample size.

respectively. The dramatic boost in reproductive measures (294% of controls) indicates nutrient limitation of reproduction through seeds or bulbils in the Arctic. Factorial application of nitrogen and phosphorus identified phosphorus to be the limiting factor to reproduction in most cases (Henry *et al.* 1986; Shaver & Chapin 1986).

PFTs differed in their biomass response to fertilization (Table 2), with grasses profiting significantly, by more than 15-fold (Parsons *et al.* 1995; Shaver & Chapin 1986), and no other PFT showing any statistically detectable response (Fig. 2). Leaf nitrogen

concentration tended to increase in response to fertilization in the three PFTs analysed, most significantly so in evergreen shrubs (Fig. 3; Table 3).

Temperature

Elevated temperature increased reproductive and physiology measures (144 and 132% of controls, respectively; Fig. 1), but the other parameters were unaffected. These data provide no evidence for significantly increased growth or dilution of soluble cell compounds due to increase in biomass, as might have been expected.
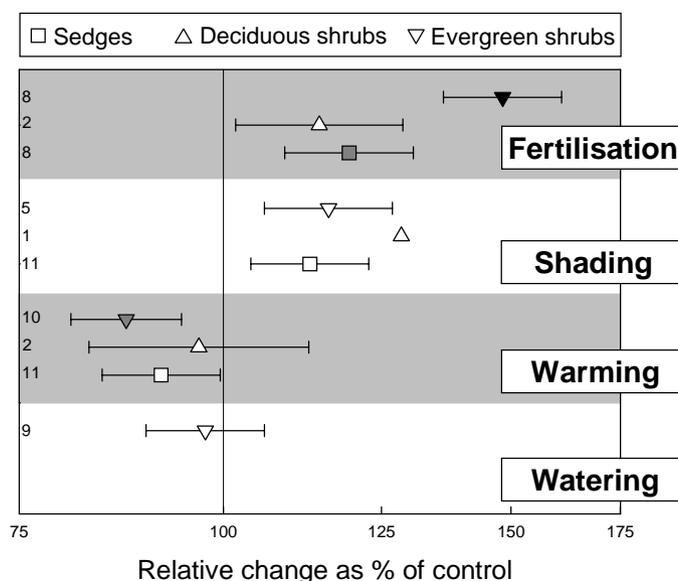
Fig. 3. Leaf nitrogen concentration of three PFTs in the different treatments (see Table 3). Black and grey symbols indicate that means differ significantly from 100% ($P < 0.05$ and $0.1 > P > 0.05$, respectively; two-tailed *t*-test). Symbols without error bars are represented by one value only (numbers refer to corrected sample size). The *x* axis is scaled logarithmically.

Table 2. Differences between plant functional types in terms of above-ground biomass in the different treatments (see Fig. 2)

Treatment	df	F	P
Fertilization	5,25	4·94	0·0018
Shading	5,43	2·00	0·0981
Warming	5,93	2·28	0·0424
Watering	5,31	0·15	0·9960

No covariate (latitude, elevation, mean annual temperature, mean July temperature, duration, replication) or covariate interaction was significant below the threshold of $P < 0.1$ used for incorporation into the final model for any treatment.

Table 3. Analysis of leaf nitrogen concentration (see Fig. 3)

Effect	df	F	P
Treatment type	3,13	12·80	0·0004
Plant functional type	2,8	0·25	0·7874
Interaction	4,34	2·60	0·0535

Cryptogams, dicots and sedges were unaffected by elevated temperature, but the biomass of deciduous and evergreen shrubs and grasses was significantly increased (Fig. 2). Although there was no overall effect of warming on tissue chemistry parameters (Fig. 1), among the three individual PFTs analysed there was a tendency to reduced tissue nitrogen concentration that was marginally significant in evergreen shrubs (Fig. 3).

Shading

Leaf measures increased significantly in shaded plots and chemical parameters tended to increase (to 138 and 115%, respectively; Fig. 1), but there was no significant effect of shading on biomass. No data were found on the effect of shading on reproductive performance, and no other reported measurements showed any significant response.

Dicots were negatively affected by shading, but none of the other PFTs, among which grasses were not represented, showed a significant biomass response to shading (Fig. 2). Also, there were no significant differences in response between PFTs (Table 2). Leaf nitrogen was not affected by shading in any of the three PFTs analysed, although the consistent trend was for increased concentration.

Elevated CO_2

The few data points available indicate a significant increase in physiological process rates in response to elevated CO_2 (130% of controls; Fig. 1). There was no overall effect of CO_2 on leaf, chemistry or reproductive parameters, and no biomass data were available. The lack of data prevented analysis of PFT responses to CO_2, and prevents a reasonable assessment of long-term impacts of elevated CO_2 on arctic vegetation.

UV-B

The impact of UV-B on plant performance has been addressed in only two field experiments (Table 1). In these, UV-B had no significant influence on biomass, leaf, chemical or reproductive measurements, but increased physiological parameters (132% of control; Fig. 1). Overall, plants responded to the increased radiation by protecting their leaves with increased contents of UV-B and radical-absorbing substances (Taulavuori *et al.* 1998) without any further effects on their performance.

Watering

Irrigation did not affect any of the response groups (Fig. 1). This is mainly because some studies did not give data, but stated the non-significance of watering, which resulted in many 100% points in this analysis. PFTs showed no significant difference in their responsiveness (Table 2; Fig. 2). Evergreen shrubs tended to

show a negative biomass response, but too few data points for almost all PFTs prevented a more sensitive analysis. There was no effect of watering on the leaf nitrogen concentration of evergreen shrubs, the only PFT with sufficient data for analysis.

DURATION OF EXPERIMENTS

One reason for our present poor understanding of plant responses to climate change is the generally short duration of field experiments. Chapin *et al.* (1995b) stated that short-term (3-year) responses generally differ from long-term (9-year) responses. Therefore we incorporated duration as a covariate in the statistical model, but it was never significant ($P > 0.1$). This does not say that long-term effects are the same as short-term effects, only that the database was insufficient to detect a change in effects.

EFFECTS OF LATITUDE AND ALTITUDE

No effects of latitude, altitude, or their interaction were detectable in biomass responses to any manipulations. In the Low Arctic, vegetation occurs over a wide altitudinal range, and at altitudes above 1000 m the biomass response to warming treatments increased markedly (from ≈120% of controls to ≈260%). However, all these data are from one area (near Abisko, Sweden), and site-specific effects cannot be disentangled from an altitudinal effect.

Discussion

The responses of plants to environmental manipulations differed greatly within and between the response groups and factors manipulated (Fig. 1). Despite the huge scatter in the data, a response group was significantly ($P < 0.1$) affected by a treatment in nine out of 28 cases. Fertilization increased the parameters in all five response groups assessed, but most noticeably in reproductive measures (294% of control). Elevated temperature significantly increased the mean reproduction and physiology responses (143 and 135% of controls, respectively). Shading increased leaf parameters (to 140% of controls), but biomass was not significantly affected. Elevated CO_2 and increased UV-B caused a significant increase in physiological parameters, but did not significantly influence any other response group. Watering had no significant effect on any response group assessed.

FERTILIZATION

Reports on fertilization experiments in the Arctic are abundant, but as their variance shows, the results are not straightforward. The general trend of fertilization stimulating plant growth is complicated by the reduced performance of some species. Although experimental evidence is still lacking (Hobbie *et al.* 1999), this

growth suppression can be attributed to shading by taller plants (Chapin *et al*. 1995a; Havström *et al*. 1993; but see Jonasson 1992; McGraw & Chapin 1989; Mulder & Ruess 1998). Individually, vascular plants generally respond to fertilization with increases in all measured parameters, including nitrogen accumulation (Chapin *et al*. 1986; Shaver *et al*. 1998), photosynthesis (Oberbauer *et al*. 1986) and colonization efficiency (Klokk & Rönning 1987). In the studies analysed here, fertilization increased total vegetation biomass to an average of $193 \pm 134\%$ of control plots, $n = 13$. Nutrient availability is probably the main factor limiting vascular plant processes in arctic ecosystems, and any change in availability due to climate change is likely to have considerable influence on the vegetation.

TEMPERATURE

Only shrubs and grasses increased biomass in response to warming. It has been argued that increasing shrub biomass and cover competitively reduces the performance of other members of the community. However, Hobbie & Chapin (1998a); Hobbie, Shevtsova & Chapin (1999) and Shevtsova *et al*. (1997) found few negative responses to selective plant removal, and concluded that it is not competition that prevents some other PFTs responding to elevated temperature in the short term. The net effect of the different responses to warming of individual PFTs was no change in the total vegetation biomass ($125 \pm 23\%$ of controls, $n = 50$).

Generally, plant physiological processes have a Q_{10} of ≈ 2 (a 100% increase in process rate over 10 °C). With temperature manipulations of +4 °C in the field, we would expect to see approximately 40% increases in physiological parameters, and the mean increase of 44% (Fig. 1) was exactly as expected. So other factors such as nutrient availability or product inhibition seem not to limit physiological responses to temperature. However, overall biomass and leaf responses do not parallel the trend in physiological measures, and this is probably because of nutrient limitation. Decreases in the leaf nitrogen concentration of plants in warmed plots are likely because temperature manipulations affect air temperature more than soil temperature (Hobbie & Chapin 1998b). Nutrient uptake could not have been increased greatly by the treatments (Atkin & Cummins 1994). This is supported by the fact that evergreen shrubs showed some dilution of foliar nitrogen as their biomass increased in elevated temperature treatments, although there was no overall response of chemical or biomass measures to warming. Thus soil temperature may constrain the response to air temperature, although this is contrary to the data of Kummerow & Ellis (1984) who showed that colder air limited growth of the sedges *Carex bigelowii* and *Eriophorum vaginatum* more than did colder soil.

Arft *et al*. (1999) reported a general trend of stronger vegetative responses to elevated temperature in the Low Arctic and reproductive responses in the High Arctic. This distinction was not made in our analysis (due to the few studies that assessed reproduction in the High Arctic), and so we cannot judge whether the apparent similarity in reproductive and leaf parameter responses opposes their findings or, more likely, is the result of pooling data from the Low and High Arctic.

SHADING

Plant species react idiosyncratically to shading (Chapin & Shaver 1985; Shaver *et al*. 1998). A frequent response is leaf and/or internode elongation, which is commonly interpreted as an attempt to escape the zone of shading (Grime 1979). Such elongation may be outweighed by a reduction in leaf width or thickness. None of the studies included in this analysis assessed both parameters simultaneously, but the overall pattern was for increase in leaf parameters without concomitant increase in plant biomass. Shading tends to cause nutrient accumulation in leaves, as growth is often reduced due to limited availability of assimilates, while nutrient uptake is maintained (Chapin & Shaver 1996). Light reduction of about 60% corresponds with that experienced by understorey plants in boreal forests (Michelsen *et al*. 1996a), while reduction due to increased cloudiness will probably be less severe. However, as shading effects might accumulate over time, a conservative growth form, i.e. storage-based with long-lived leaves, may eventually gain relative profit from these conditions.

ELEVATED CO$_2$

The field data that are available suggest that impacts of elevated CO_2 on arctic plants may be limited. An increase in tiller production by *Eriophorum* was not related to higher leaf growth rate, leaf area did not differ between CO_2 treatments, and transpiration and CO_2 uptake were not significantly affected (Tissue & Oechel 1987). Elevated CO_2 will not necessarily translate into increased biomass, as plants can acclimatize to a new CO_2 environment within weeks (Tissue & Oechel 1987), this acclimation probably being due to sink limitation imposed by low nutrient availability (Oechel *et al*. 1997).

Similar evidence comes from laboratory experiments in which Oberbauer *et al*. (1986) found no effects of CO_2 on biomass, despite a positive effect on photosynthesis. But they also showed, for three plant species, that responses to elevated CO_2 were not nutrient-limited. Sonesson *et al*. (1992) found that the moss *Hylocomium splendens* responded strongly to a doubling of atmospheric CO_2 concentration, by doubling its net rate of light saturated photosynthesis. Lichens, on the other hand, showed hardly any response to elevated CO_2 (Sonesson *et al*. 1995). It has also been argued that the CO_2 concentrations encountered by arctic plants in the field are generally

above ambient, because the shoots of many species lie close to the soil surface, and to CO_2 generated by soil respiration. It is therefore possible that CO_2 is not limiting to their growth (Crawford 1989; Sonesson *et al.* 1992), although this alone cannot explain the limited importance of CO_2 as an ecological factor in the Arctic. Evidence is accumulating, at the ecosystem level, that elevated CO_2 concentrations increase carbon translocation into arctic soils (Billings *et al.* 1983; Grulke *et al.* 1990). However, it has also been convincingly argued that this is only a short-term effect (Oechel *et al.* 1994) and that, without an increase in nutrient availability to overcome carbohydrate sink limitation, it is unlikely that elevated CO_2 alone will increase long-term carbon accumulation (Oechel *et al.* 1997).

UV-B

Some plants can make use of high-energy input for photosynthesis (Björn *et al.* 1997; Gwynn-Jones & Johanson 1996), but UV-B radiation is usually associated with negative effects such as photo-oxidative damage, enzyme destruction by radicals, and reduced growth due to higher allocation to protective structures and molecules (Taulavuori *et al.* 1998). Laboratory studies provide clear evidence that UV-B radiation can influence plant growth (Gwynn-Jones & Johanson 1996; Gwynn-Jones *et al.* 1997; Sonesson *et al.* 1995; Sonesson *et al.* 1996). However, a reduction in biomass of two subarctic grasses was not evident at high, but rather at intermediate UV-B doses (Gwynn-Jones & Johanson 1996). Reduced biomass was ascribed to the costs of producing UV-B-absorbing compounds. In this analysis there are too few data points from field experiments on UV-B radiation to enable wider extrapolation, but the indication is of increased physiological activity, possibly related to UV-B defences, without any concomitant reduction in biomass. The recent meta-analysis of UV-B studies by Searles *et al.* (2001) also concluded that UV-B radiation primarily causes increases in the concentration of UV-B absorbing substances, but only modest growth reduction. In contrast to this, the bryophyte *Hylocomium splendens* showed strong impairment of biomass production under increased UV-B ($\approx 50\%$ of control; Sonesson *et al.* 1996), while lichens were again hardly affected (Sonesson *et al.* 1995).

WATER

Despite frequent claims that water limits plant growth in the Arctic (Billings 1987; Bliss & Gold 1999; Gold & Bliss 1995; Hodkinson *et al.* 1999), only very few positive responses to watering occur in our dataset. Negative responses were at least as common (e.g. Welker *et al.* 1993), despite the fact that only vegetation in dry habitats was chosen for irrigation treatments.

Soil moisture is regularly reported to influence the distribution of Arctic plants (Bliss *et al.* 1994; Kincheloe & Stehn 1991; Walker *et al.* 1994), however, the relationship is not straightforward. Rainfall reduced the number of leaves of *Cassiope tetragona* in the European Arctic (Callaghan *et al.* 1989), but had no such effect in eastern Canada (Johnstone & Henry 1997). The timing of precipitation seems crucial, as it might affect photosynthesis only in the drier late season (Enquist & Ebersole 1994). Oberbauer & Miller (1982) provide evidence that several tundra species profit from waterlogged soils, in contrast to which Oechel *et al.* (1998) found a lower water table to slightly increase primary production. Water movements in the soil, increasing nutrient availability and productivity (Chapin *et al.* 1988), further complicate the picture. No clear-cut view on the present or future role of water in arctic ecosystems has yet emerged (Kane 1997).

DURATION OF EXPERIMENTS

Of the studies included in this analysis, experimental manipulations lasting more than 3 years were reported from only two sites (Toolik Lake, Alaska; Abisko, Sweden). Shaver & Jonasson (1999) compared the experiments at these two sites, concluding that environmental factors affecting the carbon and/or nitrogen cycle will affect plant growth in the longer term. For example, 6 years of shading had no effect on vegetation biomass at Abisko (Jonasson *et al.* 1999), and it was 9 years before a marked decline in biomass occurred in Alaska (Chapin *et al.* 1995b).

In a meta-analysis of the International Tundra Experiment (ITEX), Arft *et al.* 1999 reported a transient response of plants to warming in experiments of 4 years' duration. Woody plants showed a positive vegetative growth response in only the first 2 years. Herbaceous plants, on the other hand, demonstrated a sustained increase in their reproductive effort, but without any apparent increase in their reproductive success. However, even 4 years is a relatively short duration for arctic plant communities, and as rather few of the ITEX studies actually contributed data from the fourth year, the meta-analysis findings have to be interpreted with caution.

EFFECTS OF LATITUDE AND ALTITUDE

Arft *et al.* (1999) also report a greater response of vegetative measures to temperature elevation in the Low Arctic, and of reproductive measures in the High Arctic. As only biomass measures were used in the present analysis, our data cannot corroborate their statements, but rather indicate that it is not only the Low versus High Arctic distinction which is important, but also the effect of altitude at any given site within the Arctic.

PLANT FUNCTIONAL TYPES

The enormous variation depicted in Fig. 1 is not surprising, as the data represent plants of various morphological and taxonomic groups, from deciduous trees to lichens. We tested the arctic PFT concept of Chapin *et al.* (1996) using the biomass group responses.

There are generally few differences between arctic PFTs in their responses to individual treatments. The significant effect of PFT in fertilization treatments (Table 2) is due to the strong responsiveness of grasses compared to the absence of response in all other PFTs (Fig. 2). Similarly, the negative biomass response of one PFT (dicots) to shading causes a marginal significance of PFT. Responses to warming are significantly related to PFT, with three PFTs showing similar, positive responses and three showing none (Table 1; Fig. 2). All PFTs showed a similar lack of response to watering.

Comparing the biomass responses of an individual PFT to different treatments, the only response of dicots was a negative one to shading. The absence of positive responses to other factors is perhaps due to the rosette form of many arctic dicots, in which an increase in leaf numbers/size would lead to self-shading. Neither sedges nor cryptogams responded to any treatment, both evergreen and deciduous shrubs showed a positive response to warming only, and grasses responded positively to warming and fertilization (Fig. 2). The response of grasses to fertilization was the strongest response. Shaver *et al.* (1997) attribute this to the modular organization of graminoids, and argue that their higher tissue turnover enables them to respond more rapidly to environmental manipulations than do other PFTs. This is not supported by the temperature data, however, which show deciduous and evergreen shrubs to be as responsive as grasses.

While there is a theoretical argument for defining PFTs (Chapin 1993; Gitay & Noble 1997; Hobbs 1997), within our data only one separation is really distinct: grasses exhibit an extraordinary biomass response to improvement in nutrient availability (Fig. 2). The support previously given to PFT groupings (Arft *et al.* 1999; Chapin *et al.* 1996) can be only partly corroborated here (see also Press *et al.* 1998). This may be because species' morphological features (growth form) and physiological characteristics are not strongly linked; similar morphotypes may have different physiological responsiveness, and *vice versa*. For example, high tissue turnover rate is common to two different morphotypes, deciduous shrubs and grasses (Chapin & Shaver 1996). On the other hand, species with very responsive and conservative growth characteristics can occur not only within the same morphotype, but also within the same family or genus (e.g. McGraw & Chapin 1989). A morphotype-based PFT classification may not be the best for predicting responses to environmental change. A desirable next step would be the creation of a PFT classification primarily based on species' responses to various environmental manipulations (e.g. Dyer *et al.* 2001). This would clarify whether responsiveness to, say, fertilization was correlated with responsiveness to other factors, for example elevated CO_2.

GAPS IN OUR KNOWLEDGE

Of the different factors contributing to environmental changes in the arctic, CO_2, and UV-B are the most expensive and difficult to study, and there is a lack of published studies of likely interactions between, for example, CO_2 and fertilization or temperature (Oechel *et al.* 1994). There is still doubt as to whether UV-B exposure will increase in the Arctic, as increasing cloudiness might offset this trend. But CO_2 concentration is certainly increasing (Maxwell 1992), and this should perhaps become the focus of closer investigation, not simply to measure biomass responses but also to assess changes in plant physiology and forage quality. On the other hand, it could be argued that CO_2 studies are less important because they have commonly shown acclimation of photosynthesis to elevated CO_2 (Bazzaz 1990), and so expected ecological consequences for the whole vegetation would be small.

Even for some commonly investigated factors such as fertilization or irrigation, experiments have sometimes not been performed appropriately. Nitrogen additions have exceeded natural inputs by up to two orders of magnitude, and might have damaged some species. These high loads might also increase plants' vulnerability to sudden temperature changes, due to loss in hardiness. Watering experiments generally suffer from infrequent application. Recruitment in dry sites is probably limited by dry soil (Billings 1987; Gold & Bliss 1995), but we are aware of only one relevant study assessing germination rate or seedling establishment (Wookey *et al.* 1995).

One prediction of GCMs is that the growing season in the Arctic will be longer in future (Maxwell 1992). Differences in season length can cause profound differences in morphology and productivity of species (Crawford & Smith 1997). However, we know of only three experimental studies addressing this effect. Walsh *et al.* (1997) measured carbon and nitrogen content of caribou forage, but did not publish biomass data. The short-term experiment of Van der Wal *et al.* (2000) showed that differences in snowmelt timing affected patch choice by reindeer, but did not affect above-ground biomass by the end of the season. Starr *et al.* (2000) showed physiological and phenological responses, but did not assess biomass. As Galen & Stanton (1993) showed in alpine systems, advanced snowmelt can have strong (mostly positive) impacts on the cover of different species, while delay to the start of the growing season was generally without short-term effect (Galen & Stanton 1995). Research in this direction should be encouraged.

The experiments that form the basis for this meta-analysis commonly investigated impacts of components of global climate change on plants and vegetation *per se*, but only recently have interactions among plants come into focus (Hobbie *et al.* 1999; Jonasson 1992; Shevtsova *et al.* 1995). Interactions with herbivores are still poorly understood (Gunn & Skogland 1997; Harrington *et al.* 1999; Van der Wal *et al.* 2000), as are effects on mycorrhizas and other intertrophic relationships (Michelsen *et al.* 1996b).

Conclusions

Of all the components of environmental change considered here, the driver for future change in arctic vegetation is likely to be increased nutrient availability. This could affect the performance of individuals and recruitment to their populations, and may also mediate plant and ecosystem responses to CO_2. Minor changes in precipitation, increases in UV-B radiation and increased atmospheric CO_2 concentration alone will have little effect on arctic plants in the short term. Temperature elevation, increases in nutrient availability and major decreases in light availability, however, will cause immediate plant-growth responses and alter nutrient cycling. In the case of increased nutrients and/or temperature, their effects on nutrient cycling may create positive feedbacks on plant biomass (Hobbie 1995, 1996).

There is wide variation in the responses of arctic plant species to environmental manipulations. While classification into plant functional types may be useful in some respects (e.g. correlation of plant morphology with environmental gradients; Diaz & Cabido 1997), we suggest that it is generally unsatisfying for generalization of responses to, and predictions of effects of, environmental change. In the absence of a better classification system, it may be that analysis at the species level is still the most useful option.

The short duration of the experiments reviewed here (generally less than 5 years) is a major obstacle to predicting the response of arctic vegetation to a changing climate. Additionally, of the many gaps in our understanding of ecological processes related to responses of plants and vegetation to a changing climate, the investigation of changes in biotic interactions across all trophic levels seems to be the most urgent and intricate challenge.

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