

RESPONSES OF TUNDRA PLANTS TO EXPERIMENTAL WARMING: META-ANALYSIS OF THE INTERNATIONAL TUNDRA EXPERIMENT

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Abstract. The International Tundra Experiment (ITEX) is a collaborative, multisite experiment using a common temperature manipulation to examine variability in species response across climatic and geographic gradients of tundra ecosystems. ITEX was designed specifically to examine variability in arctic and alpine species response to increased temperature. We compiled from one to four years of experimental data from 13 different ITEX sites and used meta-analysis to analyze responses of plant phenology, growth, and reproduction to experimental warming. Results indicate that key phenological events such as leaf bud burst and flowering occurred earlier in warmed plots throughout the study period; however, there was little impact on growth cessation at the end of the season. Quantitative measures of vegetative growth were greatest in warmed plots in the early years of the experiment, whereas reproductive effort and success increased in later years. A shift away from vegetative growth and toward reproductive effort and success in the fourth treatment year suggests a shift from the initial response to a secondary response. The change in vegetative response may be due to depletion of stored plant reserves, whereas the lag in reproductive response may be due to the formation of flower buds one to several seasons prior to flowering. Both vegetative and reproductive responses varied among life-forms; herbaceous forms had stronger and more consistent vegetative growth responses than did woody forms. The greater responsiveness of the herbaceous forms may be attributed to their more flexible morphology and to their relatively greater proportion of stored plant reserves. Finally, warmer, low arctic sites produced the strongest growth responses, but colder sites produced a greater reproductive response. Greater resource investment in vegetative growth may be a conservative strategy in the Low Arctic, where there is more competition for light, nutrients, or water, and there may be little opportunity for successful germination or seedling development. In contrast, in the High Arctic, heavy investment in producing seed under a higher temperature scenario may provide an opportunity for species to colonize patches of unvegetated ground. The observed differential response to warming suggests that the primary forces driving the response vary across climatic zones, functional groups, and through time.

Key words: arctic tundra; experimental warming; global change; global warming; International Tundra Experiment; ITEX; meta-analysis; plant response patterns; spatiotemporal gradients; tundra plants.

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INTRODUCTION

Global air temperatures are predicted to increase 1–4.5°C over the next century, with the greatest increases expected in the Arctic (Mitchell et al. 1990, Maxwell 1992, Intergovernmental Panel on Climate Change 1996). Field experiments designed to simulate this warming incorporate variation in growth, reproductive, and phenological responses among species as well as by latitude and habitat (Havström et al. 1993, Wookey et al. 1993, Chapin et al. 1995, Henry and Molau 1997, Welker et al. 1997). Little is known about the nature of variation in response to these experiments, yet understanding it is critical to our ability to adequately predict and understand ecosystem response to a changing climate. A common assumption is that patterns of experimental response can be directly extrapolated to the geographic range of the species, to other species within the same functional type, or across years, but rarely have ecologists explicitly tested these assumptions.

Tundra ecosystems are globally important in relation to the rise in atmospheric CO₂ concentrations because they contain large stores of soil carbon, and shifts in balance between photosynthesis and respiration, therefore, potentially could have a major impact on carbon fluxes between the ecosystem and atmosphere (Oechel et al. 1993). Arctic tundra stores between 250 and 455 Pg of C below ground on a global basis (Oechel and Billings 1992). In tundra ecosystems where mean growing-season temperatures are near zero, an increase of a few degrees can produce a significant increase in the total warmth available to plants and decomposers. There is considerable current interest in understanding how this biome will respond to warming.

We examined the responses of a set of tundra vascular plant species that were subjected to experimental warming at 13 sites located throughout the circumpolar Arctic and in north temperate alpine regions (although there remains a lack of coverage in Russia). The data were collected as part of the International Tundra Experiment (ITEX), a collaborative, global experiment based on a common warming manipulation treatment (Henry and Molau 1997). ITEX was designed specifically to examine variability in arctic and alpine species response across climatic and geographic gradients (Henry and Molau 1997). The experiment is based on a common experimental design, a common set of species, and quantifying common environmental parameters (Molau and Mølgaard 1996). By using geographically widespread experimentation, a broad spectrum of species, and multiple years of sampling, ITEX incorporates controlled variability in time, space, and functional groups. In the present analysis, time represents the duration of the experiment; space represents a complex of climate and site factor variables (climatic zones); and functional groups are plant growth forms

traditionally recognized by arctic ecologists. By compiling and integrating the initial four years of data from these sites, we were able to examine how the response of tundra plants to experimental warming varied within and among temporal, spatial, and functional groups.

We examined three specific scientific hypotheses:

1. *Most species will exhibit measurable, significant increases in vegetative growth due to warming in the early years of experimentation.*—Most of the live biomass of tundra vegetation occurs below ground (Kjellvik and Kärenlampi 1975, Webber 1977, Jonasson 1982, Miller et al. 1982, Ellenberg 1988, Henry et al. 1990, Shaver and Kummerow 1992). Much of this belowground biomass consists of stems or rhizomes that function primarily as storage tissues (Shaver and Cutler 1979, Bliss 1981). These carbon and nutrient reserves are important resources when growth requirements cannot be met by current uptake of nutrients (Berendse and Jonasson 1992, Shaver and Kummerow 1992). Thus, short-term temperature-enhanced vegetative growth may occur at the expense of stored plant reserves. The long-term cost of increased shoot growth, however, will be a decline in production if plants are not allowed to recover and restore reserves. Chapin and Shaver (1996) found that arctic species that responded to increased temperature with earlier leaf expansion (*Betula* and *Ledum*) had reduced total nitrogen and phosphorus pools after three years, suggesting that earlier phenology may have depleted stored plant reserves.

2. *Vegetative growth will be greater at warmer, low arctic sites, whereas sexual reproduction will be greater at colder, high arctic sites.*—Relative shifts in vegetative growth and reproduction will be a function of competition and nutrient availability. The change from a complete to an incomplete canopy cover along a gradient of summer temperature corresponds with a gradient from combined biotic and abiotic controls to purely abiotic controls (Svoboda and Henry 1987, Walker 1995). Thus, as the size of the flora, canopy cover, and biomass decrease, competitive interactions decrease as well. Within the polar barrens, there is little evidence that competition occurs at all; in most areas, average plant cover is <1% (Bliss and Peterson 1992). In the Low Arctic, an increase in nutrients translates into increased vegetative growth, but not increased reproduction (Walker et al. 1995, Chapin and Shaver 1996), which we have interpreted as a response to competition. In the High Arctic, an increase in nutrients results in an increase in both vegetative growth and reproduction (Wookey et al. 1994, 1995). The more extreme resource limitations in the High Arctic may limit an increase in vegetative growth (Bliss and Peterson 1992). In addition to constraints on growth imposed directly by soil nutrient availability, the response of high arctic vegetation might be constrained by its developmental or evolutionary history; if the vegeta-

tion has adapted to an environment in which reproduction is favored, perhaps it will respond to more favorable conditions with more reproduction, rather than increased vegetative growth.

3. *Although species will exhibit individualistic responses to increased summer temperature, there will be high similarity of response within functional groups.*—The response of each species to warming depends on inherent physiological pathways, reproductive structures, and leaf morphology (Billings 1992). Although these characteristics vary widely among species, similarities within functional groups contribute to a similar response within these groups. Chapin et al. (1996) developed a hierarchical classification of functional types for arctic plant species, based on environmental gradients and the relative impact of different traits on ecosystem processes. Within the vascular plant group, plants were broadly divided into woody or herbaceous forms. Woody plants differ from herbaceous plants in the maximum canopy height that they can achieve, and in the high lignin and low nitrogen content of wood. Within the woody form, deciduous plants differ from evergreens in their shorter period of photosynthetic activity, greater resource requirements, higher leaf turnover, and higher quality of leaf litter. Deciduous shrubs within the Arctic tend to dominate nutrient-rich sites, whereas evergreen shrubs dominate dry and infertile heath sites (Chapin et al. 1996). Herbaceous forms include sedges, grasses, and forbs. Within the Arctic, sedges tend to dominate waterlogged soils, whereas the belowground meristems of grasses allow them to be effective colonizers following disturbance, and forbs reach their greatest abundance and diversity in dry and moist nutrient-rich sites (Chapin et al. 1996). Plant functional types such as these have been widely used in arctic research to describe patterns of response to environmental change (Webber 1978, Henry et al. 1986, Walker et al. 1989) and have been proposed as a key tool for developing predictive models of plant responses to changing environments.

Although many of these hypotheses have been examined in specific research contexts, our objective was to determine how well they held up across a variety of sites and conditions. The nature and strength of the ITEX network, a circumpolar series of arctic and alpine sites with similar sampling protocols, provided a unique opportunity to synthesize our data using meta-analysis techniques. Meta-analysis permits the statistical analysis of a set of primary studies (usually taken from the scientific literature), and has only recently been applied to ecological data (Gurevitch et al. 1992). This is the first quantitative assessment of ITEX, following the more qualitative synthesis of Henry and Molau (1997).

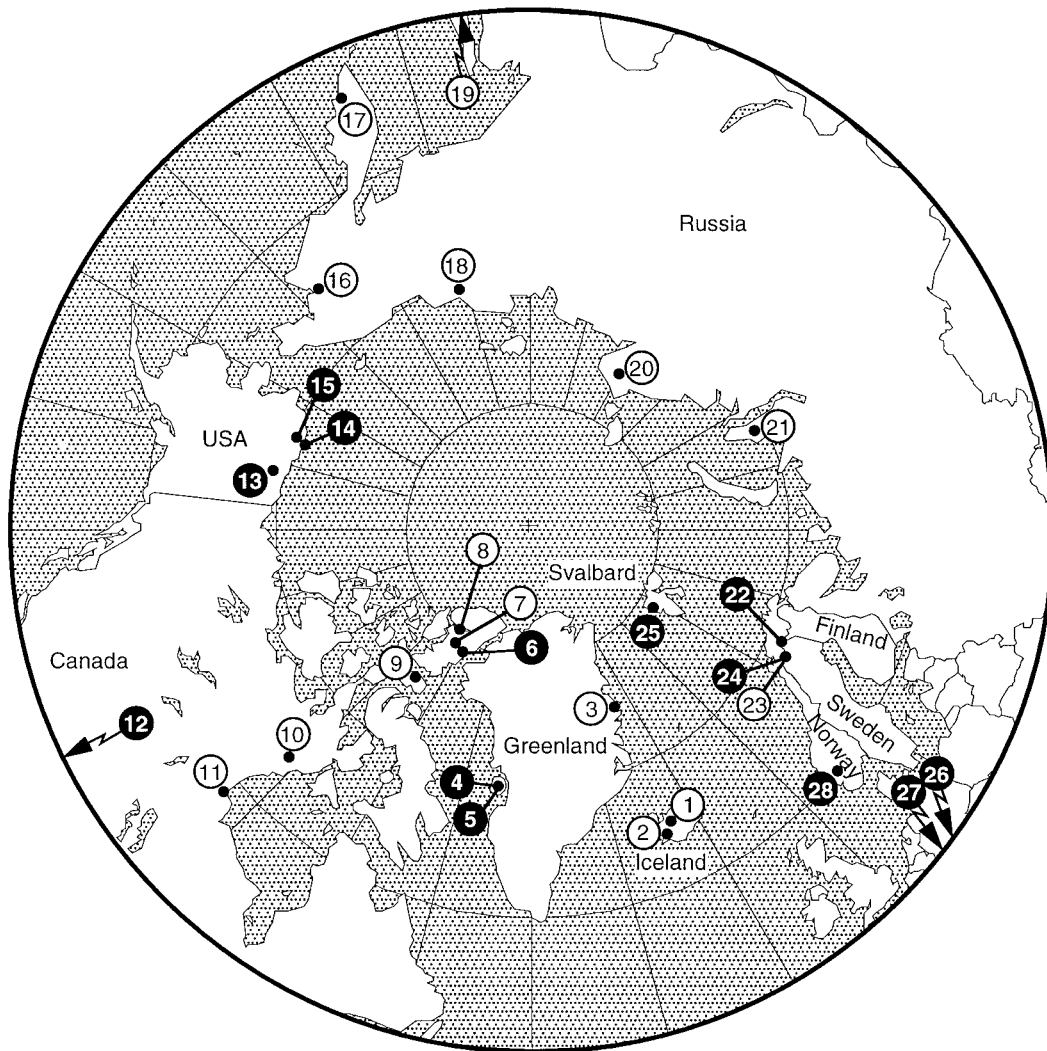
METHODS

The data for this analysis came from 13 circumpolar and alpine ITEX sites (Fig. 1). Although all studies

used similar methods, the timing and duration of the studies varied, with studies beginning as early as 1989 and with duration ranging from one to four years. We assumed that experimental duration was more important than calendar year. Each site was classified as alpine, high arctic, or low arctic, based upon the divisions described by Bliss and Matveyeva (1992). These divisions are based upon latitude, vegetation, temperature, and precipitation. The data set includes five high arctic, four low arctic, and four alpine sites (Table 1). We included a total of 61 plant species from 13 sites (Table 2). We classified each species into a broad functional type (woody or herbaceous) and a narrow functional type (deciduous shrub, evergreen shrub, forb, or graminoid) using the functional type classification scheme of Chapin et al. (1996).

The ITEX experiment uses open-topped chambers (OTCs) or corners (open walls at 90° angles) with transparent walls made from greenhouse fiber glass, plexiglass, or polycarbonate to passively warm the local microenvironment (Marion 1996, Marion et al. 1993, 1997). Marion et al. (1997) have conducted detailed studies on ITEX chambers at six sites in the Arctic and Antarctic, including three sites in the present study (Alexandra Fiord, Canada; Fortunebay, Greenland; and Latnjajaure, Sweden). They found that the mean daily near-surface air and soil temperatures increased by 1.2° to 1.8°C in warmed plots, whereas the effect on snow accumulation was variable, with one site showing no difference in snow melt date and another site at which snow melt occurred 1–2 wk earlier. At some sites, OTCs were removed from the plots during the winter months because of high winter wind velocity. Although the degree of warming differed across climatic zones, particularly between arctic and alpine sites, we were not able to adjust for these differences using ANCOVA, because the statistical theory has not been developed for meta-analysis. Although OTCs significantly alter air temperature, unwanted side effects such as altered light, moisture, and/or gas exchange are minimized. A randomized-block design with equal numbers of control and experimental plots in each plant community was used; however, different numbers of plots were established at different sites. Individual plants within each plot were marked for quantitative growth analysis (Molau and Edlund 1996). Methods of selection varied among studies and included an array of approaches including random, systematic, or all-plants approaches. Phenology was recorded from the same individuals or was based on individuals within the entire plot (Molau and Edlund 1996).

Standard ITEX plant response variables, both vegetative and reproductive, are grouped in two main categories, phenological and quantitative (Molau and Møgaard 1996). Many of the studies used in the synthesis included more than one measure of vegetative growth or reproduction. To eliminate redundancies in the data set and to be able to compare among different



- | | |
|----------------------------------|----------------------------|
| 1 Audkuluheidi, Iceland | 15 Atkasuk, USA |
| 2 Thingvellir, Iceland | 16 Anadyr, Russia |
| 3 Zachenberg, Greenland | 17 Petropavlovsk, Russia |
| 4 Fortune Bay, Greenland | 18 Lower Kolyma, Russia |
| 5 Fjeldspindersletten, Greenland | 19 Taisetsu Mts., Japan |
| 6 Alexandra Fjord, Canada | 20 Taimyr, Russia |
| 7 Sverdrup Pass, Canada | 21 Yamal, Russia |
| 8 Hot Weather Creek, Canada | 22 Kilpisjärvi, Finland |
| 9 Truelove Lowland, Canada | 23 Abisko, Sweden |
| 10 Baker Lake, Canada | 24 Latnjajaure, Sweden |
| 11 Churchill, Canada | 25 Ny-Ålesund, Svalbard |
| 12 Niwot Ridge, USA | 26 Val Bercla, Switzerland |
| 13 Toolik Lake, USA | 27 Furka Pass, Switzerland |
| 14 Barrow, USA | 28 Finse, Norway |

FIG. 1. The ITEX network of sites. Sites included in the meta-analysis are shown with black circles.

species, we consolidated the original variables into three phenological (leaf bud burst, anthesis, and senescence) and three quantitative variables (vegetative growth, reproductive effort, and reproductive success; Table 3). Not all of the variables listed in Table 3 were

measured in all plants or at all sites. For each individual study, the original phenology variables were consolidated by using the earliest of the original variables available. For example, anthesis date is considered to be the first date on which glumes or flowers are open,

TABLE 1. Classification, investigator(s), reference, and location of the 13 circumarctic and alpine ITEX sites included in the synthesis.

Site	Classification	Investigator(s)	References for site description	Latitude/longitude
Alexandra Fiord, Canada	high arctic	G. H. R. Henry, M. H. Jones	Svoboda and Freedman (1994), Stenström et al (1997), Henry (1998), Marion et al. (1997)	78°53' N, 75°45' W
Barrow, United States	high arctic	R. D. Hollister, L. J. Walker, P. J. Webber	Tieszen (1978)	71°19' N, 156°37' W
Fjeldspindlersletten, Greenland	high arctic	P. Mølgaard		69°17' N, 53°28' E
Fortunebay, Greenland	high arctic	P. Mølgaard		69°16' N, 53°50' E
Ny-Ålesund, Norway	high arctic	T. V. Callaghan, J. A. Lee, M. C. Press, C. H. Robinson, J. M. Welker, P. A. Wookey	Wookey et al. (1993), Robinson et al. (1998)	78°56' N, 11°50' E
Atkasuk, United States	low arctic	R. D. Hollister, L. J. Walker, P. J. Webber	Komárková and Webber (1980)	71°29' N, 157°25' W
Kilpisjärvi, Finland	low arctic	K. Laine, U. Nordenhäll	Lohiluoma (1995)	63°03' N, 20°50' E
Latnajaure, Sweden	low arctic	J. Alatalo, I. S. Jónsdóttir, U. Molau, U. Nordenhäll, A. Stenström, M. Stenström	Stenström and Molau (1992), Molau and Alatalo (1998)	68°20' N, 18°30' E
Toolik Lake, United States	low arctic	A. M. Arft, M. S. Bret-Harte, M. H. Jones, G. R. Shaver, M. D. Walker, J. M. Welker	Walker et al. (1994)	68°38' N, 149°38' W
Finse, Norway	alpine	Ø. Totland	Totland (1997)	60°37' N, 7°32' E
Furka, Switzerland	alpine	M. Diemer, P. Bockmühl	Körner et al. (1996)	46°35' N, 8°23' E
Niwot Ridge, United States	alpine	P. L. Turner, M. D. Walker, J. M. Welker	Isard (1987)	40°3' N, 105°36' W
Val Bercla, Switzerland	alpine	F. Gugerli	Stenström et al. (1997)	46°29' N, 9°35' E

Notes: Classifications are based on the divisions described by Bliss and Matveyeva (1992). Specific details of sites can be found in the earlier works referenced.

or either stigmas or anthers are visible. This consolidation was necessary to make interspecific comparisons among species with different morphology or life history. Quantitative variables were consolidated by priority ranking of the original variables and use of the highest priority variable available (Table 3). Reproductive estimates were divided into those measuring reproductive effort (i.e., the potential or amount of energy put into reproduction) and those measuring reproductive success (i.e., actual production of seeds or fruits). We use the term "reproductive effort" to represent the best available quantitative measure of effort put into reproduction, which we took to be the number of flowers or inflorescences, when available. This is in contrast to the more classical definition, which specifically refers to the proportion of biomass dedicated to reproductive structures. We did not have adequate information to assess this. When flower counts were not available, we used other information as outlined in Table 3.

We used meta-analysis to analyze responses of plant

phenology, growth, and reproduction to temperature warming. Meta-analysis is the quantitative synthesis of a set of independent studies (see, e.g., Arnqvist and Wooster 1995). Meta-analysis depends upon estimating an effect size (i.e., the magnitude of the experimental effect) for each independent experiment (Gurevitch et al. 1992, Rosenberg et al. 1997). Although the effect may be measured with different units in each study, the metric used to calculate effect size standardizes them to a single scale. A seeming alternative might be to combine experimental results by simply counting up the number of statistically significant results in the various studies (Gurevitch et al. 1992, Rosenberg et al. 1997). This "vote-counting" approach, however, has serious flaws, because statistical significance depends not only on the magnitude of the effect, but also on its sample size (Gurevitch et al. 1992, Rosenberg et al. 1997). Studies with small sample sizes are less likely to be statistically significant than those with large sample sizes, even if both have the same effect. In addition, "vote-counting" is not a reliable indication of whether

TABLE 2. Species, families, functional groups, and sites included in the meta-analysis.

Species	Family	Functional group	Site													
			6	15	14	28	5	4	27	22	24	12	25	13	26	
<i>Acomastylis rossii</i>	Rosaceae	forb										X				
<i>Alchemilla pentaphyllea</i>	Rosaceae	forb								X						
<i>Andromeda polifera</i>	Ericaceae	evergreen shrub													X	
<i>Arctostaphylos alpina</i>	Ericaceae	evergreen shrub													X	
<i>Arctagrostis latifolia</i>	Poaceae	graminoid				X										
<i>Betula nana</i>	Betulaceae	deciduous shrub													X	
<i>Carex bigelowii</i>	Cyperaceae	graminoid										X			X	
<i>Carex chordorrhiza</i>	Cyperaceae	graminoid													X	
<i>Carex curvula</i>	Cyperaceae	graminoid								X						
<i>Carex foetida</i>	Cyperaceae	graminoid								X						
<i>Cardamine pratensis</i>	Brassicaceae	forb				X										
<i>Carex rotundata</i>	Cyperaceae	graminoid													X	
<i>Carex saxatilis</i>	Cyperaceae	graminoid		X												
<i>Carex stans</i>	Cyperaceae	graminoid		X	X											
<i>Cassiope tetragona</i>	Ericaceae	evergreen shrub	X	X	X							X			X	
<i>Diapensia lapponica</i>	Diapensiaceae	forb		X											X	
<i>Dryas integrifolia</i>	Rosaceae	evergreen shrub	X		X											
<i>Dryas octopetala</i>	Rosaceae	evergreen shrub										X	X	X	X	
<i>Dupontia fisheri</i>	Poaceae	graminoid				X										
<i>Empetrum nigrum</i>	Empetraceae	evergreen shrub													X	
<i>Eriophorum angustifolium</i>	Cyperaceae	graminoid		X												
<i>Eriophorum russeolum</i>	Cyperaceae	graminoid				X										
<i>Eriophorum triste</i>	Cyperaceae	graminoid				X										
<i>Eriophorum vaginatum</i>	Cyperaceae	graminoid										X			X	
<i>Hierochloë alpina</i>	Poaceae	graminoid		X												
<i>Hierochloë pauciflora</i>	Poaceae	graminoid				X										
<i>Juncus biglumis</i>	Juncaceae	graminoid				X										
<i>Ledum decumbens</i>	Ericaceae	evergreen shrub		X											X	
<i>Leontodon autumnalis</i>	Asteraceae	forb					X									
<i>Leontodon helveticus</i>	Asteraceae	forb								X						
<i>Loiseleuria procumbens</i>	Ericaceae	evergreen shrub													X	
<i>Luzula arctica</i>	Juncaceae	graminoid		X	X											
<i>Luzula confusa</i>	Juncaceae	graminoid		X	X											
<i>Luzula lutea</i>	Juncaceae	graminoid								X						
<i>Oxyria digyna</i>	Polygonaceae	forb	X													
<i>Papaver hultenii</i>	Papaveraceae	forb				X										
<i>Papaver radicanum</i>	Papaveraceae	forb							X							
<i>Pedicularis kanei</i>	Scrophulariaceae	forb		X												
<i>Polygonum bistorta</i>	Polygonaceae	forb		X									X		X	
<i>Polygonum viviparum</i>	Polygonaceae	forb										X		X	X	
<i>Potentilla aurea</i>	Rosaceae	forb								X						
<i>Pyrola grandiflora</i>	Pyrolaceae	forb													X	
<i>Ranunculus acris</i>	Ranunculaceae	forb					X									
<i>Ranunculus glacialis</i>	Ranunculaceae	forb					X					X				
<i>Ranunculus nivalis</i>	Ranunculaceae	forb				X						X				
<i>Rubus chamaemorus</i>	Rosaceae	forb													X	
<i>Salix arctica</i>	Salicaceae	deciduous shrub	X					X	X							
<i>Salix herbacea</i>	Salicaceae	deciduous shrub									X	X				
<i>Salix pulchra</i>	Salicaceae	deciduous shrub				X									X	
<i>Salix reticulata</i>	Salicaceae	deciduous shrub													X	
<i>Salix rotundifolia</i>	Salicaceae	deciduous shrub				X										
<i>Saxifraga cernua</i>	Saxifragaceae	forb				X										
<i>Saxifraga foliolosa</i>	Saxifragaceae	forb				X										
<i>Saxifraga hieracifolia</i>	Saxifragaceae	forb				X										
<i>Saxifraga hirculus</i>	Saxifragaceae	forb				X										
<i>Saxifraga oppositifolia</i>	Saxifragaceae	forb										X			X	
<i>Saxifraga punctata</i>	Saxifragaceae	forb				X										
<i>Silene acaulis</i>	Caryophyllaceae	forb					X				X	X				
<i>Vaccinium myrtillus</i>	Ericaceae	deciduous shrub									X					
<i>Vaccinium uliginosum</i>	Ericaceae	deciduous shrub													X	
<i>Vaccinium vitis-idaea</i>	Ericaceae	evergreen shrub													X	

Notes: An "X" indicates that species phenological and/or quantitative data for that site were included in the analysis. Site numbers correspond to those in Fig. 1: 4, Fortune Bay, Greenland; 5, Fjeldspindersletten, Greenland; 6, Alexandra Fjord, Canada; 12, Niwot Ridge, USA; 13, Toolik Lake, USA; 14, Barrow, USA; 15, Atqasuk, USA; 22, Kilpisjärvi, Finland; 24, Latnjajaure, Sweden; 25, Ny-Ålesund, Svalbard; 26, Val Bercia, Switzerland; 27, Furka Pass, Switzerland; 28, Finse, Norway.

TABLE 3. Consolidation of original variables into three new groups each of (A) phenology variables and (B) quantitative variables.

A) Phenology variables	
Leaf bud burst	
Leaf/flower bud burst	
First leaf visible	
Anthesis	
Glume open	
First flower open	
First stigmas visible	
First anthers visible	
Senescence	
First leaf color change	
B) Quantitative variables	
Vegetative growth	
Leaf length	
Tiller length	
Average long shoot	
Fascicle length	
Biomass	
Length of longest shoot	
Leaf width	
Leaf mass	
No. leaves	
Annual growth	
Reproductive effort	
No. flowers or no. inflorescences	
(whichever is greater, OR if both are missing, then	
total reproductive units)	
No. bulbils/shoot	
Length of catkins	
No. female catkins	
No. male catkins	
No. ovules/flower	
No. ovules/head	
Reproductive success	
Seed yield	
Seed mass	
No. fruits	
No. seeds	
No. seeds/head	
Bulbil yield	
Bulbil mass	
No. heads in fruit	

Notes: Original variables are indented under each of the consolidated variables (e.g., leaf bud burst). Phenology variables used the earliest of the original variables for which both experimental and control values were present. Quantitative variables were also consolidated: the highest priority original variable for which both experimental and control values were present was used for the consolidated variable. Unless otherwise noted, the highest priority variable is first in the list of original variables.

an effect is significantly different from zero, whether the studies are in agreement with respect to the magnitude of the effect, or whether the effect differs among different categories of studies.

A number of different metrics may be used to calculate effect size in meta-analysis (Rosenberg et al. 1997). For our quantitative data, we used two different methods. In the first, we calculated the “*d* index” as the difference between the means of the experimental and control groups divided by the pooled standard deviation (Cohen 1969):

$$d = \left(\frac{X_e - X_c}{s} \right) J \quad (1)$$

where X is the mean for the experimental (e) and control (c) groups, s is the pooled standard deviation, J is a sample size correction factor, and d is the effect size (Hedges and Olkin 1985). The sample size correction factor, J , corrects for bias due to small sample size and is calculated as

$$J = 1 - \left(\frac{3}{4(N_e + N_c - 2) - 1} \right) \quad (2)$$

where N is the sample size for the experimental (e) and control (c) groups. Using d as the metric, the conventional interpretation is that an effect size of zero indicates no experimental effect, and effect sizes of 0.2, 0.5, and 0.8 indicate small, medium, and large effect sizes, respectively (Cohen 1969). Values above zero indicate a “positive” effect, i.e., the manipulation caused an increase in the measured variable, and values below zero indicate a negative effect or decrease in the variable. Both positive and negative effects can be significant; the statistical significance of d is based upon analysis of confidence intervals.

Although the statistical properties of the d index are well understood and it has been commonly used in meta-analysis, some ecologists have questioned the biological validity of the d index (Osenberg et al. 1997). Because calculation of d (Eq. 1) requires division by a standard deviation, the effect size could vary substantially simply based on the standard deviation. This property is not unique to d ; it is shared by many commonly used statistics such as the Student’s t parametric and ANOVA. To provide a more robust analysis, we used a second metric, the natural logarithm of the response ratio, to calculate effect size. The response ratio is the ratio of the experimental mean to the control mean. Use of the natural logarithm linearizes the metric and provides a more normal sampling distribution in small samples (L. V. Hedges, J. Gurevitch, and P. Curtis, *unpublished manuscript*). The natural logarithm of the response ratio is calculated as

$$L = \ln \left(\frac{X_e}{X_c} \right) \quad (3)$$

where L is the effect size and X is the mean for the experimental (e) and control (c) groups.

The phenological data presented a special challenge because they are interval data only, i.e., they have no true zero and no reliable variance, so neither d nor L could be calculated for them. We recorded phenology data as the calendar day on which a particular event occurred, and we used the simple difference between experimental and control groups to calculate the effect size (PD) for the phenological data using a variance of 1.0 for all studies:

$$PD = X_e - X_c \quad (4)$$

We justified using the simple difference because the phenological data are already on the same scale (calendar days). In contrast, the response ratio would not

TABLE 4. Total number of studies (with number of sites in parentheses) included in each meta-analysis and within each category.

Variables†	Treatment year 1	Treatment year 2	Treatment year 3	Treatment year 4
Vegetative growth				
Total	28 (6)	30 (10)	27 (9)	9 (3)
HA, LA, AL	14 (2), 6 (2), 8 (2)	14 (3), 6 (3), 10 (4)	11 (4), 14 (3), 2 (2)	7 (2), 2 (1), 0
W, H	6 (4), 22 (6)	5 (4), 25 (9)	16 (7), 11 (7)	5 (2), 4 (3)
DS, ES, F, G	0, 5 (4), 12 (5), 10 (3)	0, 4 (3), 15 (8), 10 (4)	5 (3), 11 (6), 6 (5), 5 (3)	3 (2), 2 (1), 4 (3)
Reproductive effort				
Total	17 (6)	17 (6)	20 (7)	5 (2)
HA, LA, AL	8 (2), 6 (2), 3 (2)	7 (3), 6 (1), 4 (2)	6 (4), 12 (2), 2 (1)	4 (1), 0, 0
W, H	6 (4), 11 (6)	5 (3), 12 (5)	13 (5), 7 (3)	4 (1), 0
DS, ES, F, G	0, 5 (4), 8 (5), 3 (2)	0, 4 (4), 10 (5), 2 (2)	3 (2), 10 (5), 6 (3), 0	2 (1), 2 (1), 0, 0
Reproductive success				
Total	18 (8)	17 (7)	20 (9)	4 (3)
HA, LA, AL	0, 7 (2), 10 (4)	0, 10 (2), 6 (4)	3 (3), 13 (3), 4 (3)	2 (1), 0, 0
W, H	5 (4), 13 (4)	5 (3), 12 (6)	12 (7), 8 (4)	3 (2), 0
DS, ES, F, G	2 (2), 3 (3), 11 (6), 2 (2)	2 (2), 3 (3), 11 (6), 0	0, 11 (7), 7 (4), 0	0, 3 (2), 0, 0
Leaf bud burst				
Total	28 (6)	38 (7)	15 (5)	8 (3)
HA, LA, AL	23 (3), 4 (2), 0	23 (2), 12 (3), 3 (2)	8 (2), 7 (3), 0	5 (1), 3 (2), 0
W, H	8 (4), 20 (3)	15 (5), 23 (5)	6 (3), 9 (3)	6 (3), 2 (2)
DS, ES, F, G	5 (3), 3 (2), 10 (3), 10 (1)	9 (4), 6 (3), 13 (5), 10 (1)	3 (2), 3 (2), 6 (3), 3 (1)	3 (2), 3 (2), 2 (2), 0
Anthesis				
Total	34 (8)	49 (10)	37 (8)	10 (3)
HA, LA, AL	18 (3), 9 (2), 7 (3)	21 (3), 20 (3), 8 (4)	8 (3), 27 (3), 8 (2)	4 (1), 6 (2), 0
W, H	8 (5), 26 (5)	16 (6), 33 (6)	20 (5), 17 (6)	7 (3), 3 (1)
DS, ES, F, G	2 (2), 6 (4), 13 (5), 13 (3)	5 (3), 11 (6), 18 (6), 15 (2)	5 (3), 15 (5), 10 (6), 7 (3)	3 (2), 4 (2), 2 (1), 0
Senescence				
Total	11 (4)	16 (6)	29 (3)	2 (1)
HA, LA, AL	2 (1), 4 (2), 5 (1)	4 (1), 7 (3), 5 (2)	0, 29 (3), 0	0, 2 (1), 0
W, H	6 (2), 5 (3)	6 (3), 10 (4)	20 (3), 9 (2)	0, 0
DS, ES, F, G	4 (2), 2 (1), 2 (2), 3 (3)	4 (3), 2 (2), 7 (3), 3 (2)	7 (3), 13 (2), 5 (2), 4 (1)	0, 0, 0, 0

Note: Categories with only one study were not included in the analysis.

† Abbreviations: HA, high arctic; LA, low arctic; AL, alpine; W, woody forms; H, herbaceous forms; DS, deciduous shrubs; ES, evergreen shrubs; F, forbs; G, graminoids.

be a good phenological metric, because it would change based on when the event occurred during the season (e.g., if the mean between experimental and control groups differed by 5, the response ratio might be (135/140) at the beginning of the season and (205/210) later in the season. Note that Eq. 1 collapses down to Eq. 4 if s and J are set equal to 1.

The initial four years of data from 13 circumarctic and alpine ITEX sites were analyzed using SAS and Metawin 1.0, a statistical software program for meta-analysis (Rosenberg et al. 1997). Data were analyzed using treatment years (i.e., the year since initiation of experimental manipulation) and not calendar years. The total number of studies included in each meta-analysis is shown in Table 4. We chose to analyze each year separately, even though by doing so we may have created a problem of non-independence. We felt that the alternative of using a single year or only studies with four full years of data resulted in the loss of too much data.

Means and confidence intervals for the average effects of warming on various groups of studies were estimated using a mixed model and standard, weighted

meta-analytic parametric methods for the d index and natural logarithm response ratio (Hedges and Olkin 1985; Hedges and Olkin, *in press*, Gurevitch and Hedges 1999). Effect sizes were weighted by the inverse of the estimated sampling variance, as is conventional. For the phenological analyses, we used an unweighted mixed model (i.e., all weights = 1) and bias-corrected bootstrapping to calculate means and confidence intervals, because parametric weights have not been defined for this measure (Adams et al. 1997).

The homogeneity statistic, Q , was used to test whether the various effect sizes within and among spatial, temporal, and functional groups differ only by sampling error, vs. the alternative hypothesis that there are true differences in effect among studies (Hedges and Olkin 1985, Gurevitch et al. 1992, Rosenberg et al. 1997). The total homogeneity can be partitioned into within-class homogeneity, Q_w , a measure of the variability among individual studies within a particular class, and between-class homogeneity, Q_b , a measure of the variability among classes of studies in the analysis. We used parametric, weighted homogeneity tests for variables measured using the d index and natural

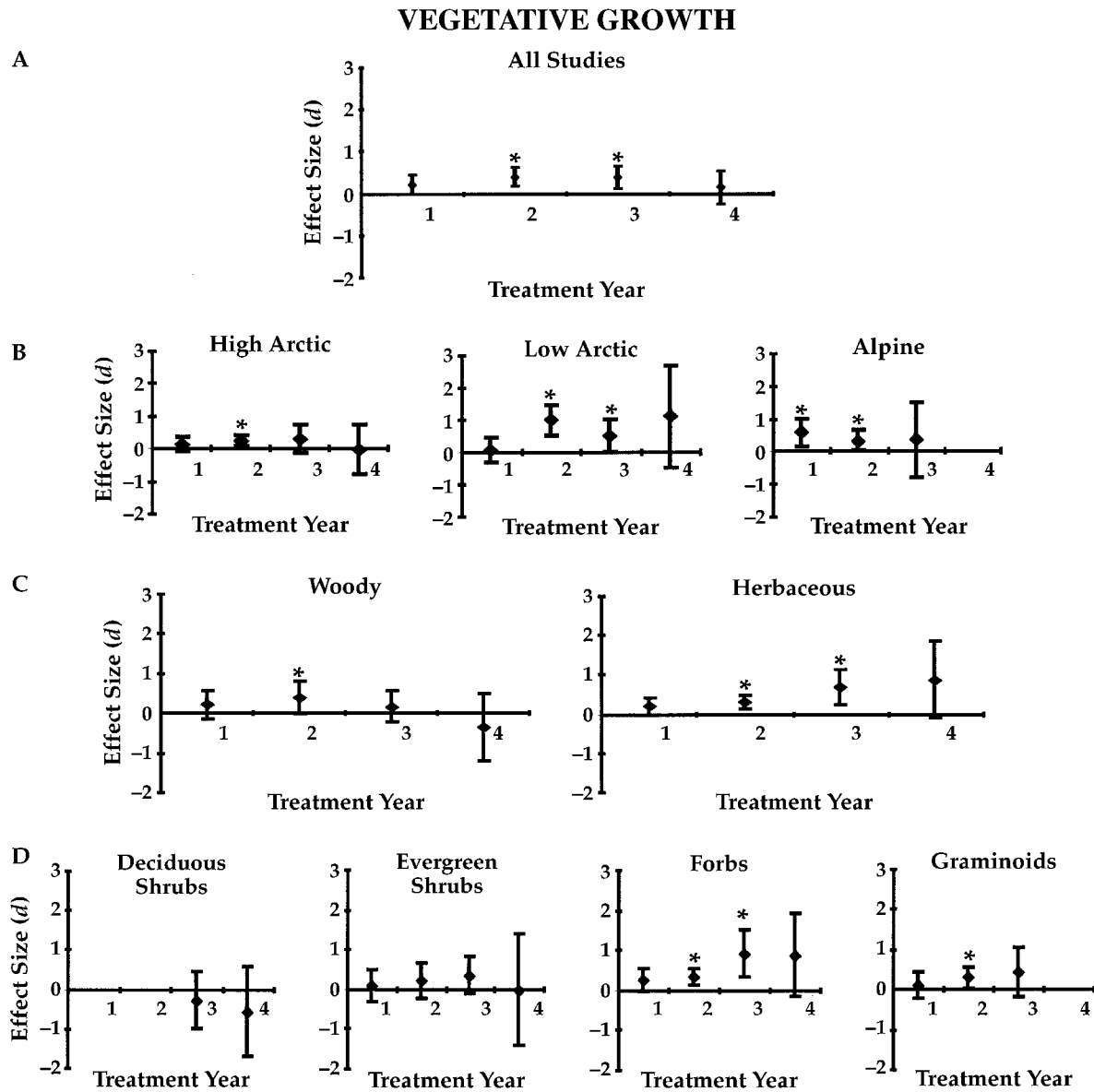


FIG. 2. Effect size (d index) of experimental warming over a 4-yr period for vegetative growth. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized by (B) geographic zone (high arctic, low arctic, and alpine), (C) broad functional types (woody and herbaceous), and (D) narrow functional types (deciduous shrubs, evergreen shrubs, forbs, and graminoids). An asterisk (*) indicates that the effect is significantly different from zero at $P \leq 0.05$.

log response ratio metrics, and unweighted, resampling tests to evaluate the homogeneity statistic for the phenological difference metric (Rosenberg et al. 1997, Gurevitch and Hedges 1999).

RESULTS

Vegetative growth

Short-term experimental warming had a small-to-moderate positive effect on vegetative growth (Fig. 2; see Table 5 for a summary of the results). Positive mean effect sizes for all treatment years indicate a trend of

greater vegetative growth in warmed plots relative to controls for both the d index and response ratio (Fig. 2A). For both metrics, vegetative growth in treatment years 2 and 3 was significantly greater than zero; however, in treatment year 4 it was not. Growth responses in treatment year 1 were significantly greater than zero for the response ratio, but not for the d index. Increased variability was observed with years across both climatic zones and functional groups.

Vegetative growth response differed among climatic groups (Fig. 2B) in treatment year 2 (d index, $Q_b =$

TABLE 5. Summary of quantitative and phenological responses across temporal, spatial, and functional group categories, for the d index only. Responses are indicated in sequence for treatment years 1–4.

Category	Vegetative growth	Reproductive effort	Reproductive success	Leaf bud burst	Anthesis	Senescence
Temporal	0++0	0000	0000	----	0---	0+00
Spatial						
High arctic	0+00	0++0	nn00	---0	---	00nn
Low arctic	0++0	000n	000n	0-00	0---	0000
Alpine	++0n	0-0n	000n	n0nn	000n	+0nn
Broad functional group						
Woody	0+00	0000	0000	--0-	0---	000n
Herbaceous	0++0	00+n	000n	----	----	+00n
Narrow functional group						
Deciduous shrubs	nn00	nn00	00nn	--00	0000	000n
Evergreen shrubs	0000	0000	00nn	0-00	0---	n00n
Forbs	0++0	000n	000n	00--	00--	+00n
Graminoids	0+0n	00nn	00nn	000n	0--n	+00n

Notes: The sequences of four symbols indicate significance of the effect size over each of the four treatment years; +, the effect size for all studies within the specific year and category was significantly greater than zero; -, the effect size was significantly less than zero; 0, the effect size did not differ significantly from zero; n, data were not available.

8.02, $P = 0.02$; response ratio, $Q_b = 10.16$, $P = 0.01$), with species in the Low Arctic exhibiting the strongest response to experimental warming. Although mean effect size for vegetative growth in the low arctic studies was small and not significantly different from zero in the first treatment year, mean effect size was moderate to large in subsequent years and significantly greater than zero in treatment years 2 and 3. In contrast, mean effect size in high arctic studies was negligible to small and significantly different from zero only in treatment year 2. Mean effect size in alpine studies was small to moderate for all three treatment years and significantly greater than zero in treatment years 1 and 2. Overall, low arctic plants exhibited a stronger, more consistent vegetative growth response to experimental warming than did high arctic or alpine plants.

Plant functional groups differed in their mode and strength of vegetative growth response (Fig. 2C). Herbaceous plants showed a stronger, more consistent vegetative growth effect than did woody plants in treatment year 4 (response ratio, $Q_b = 5.56$, $P = 0.02$). Herbaceous forms exhibited a small response to warming in the first two treatment years and a larger response in subsequent years. Vegetative growth within the woody forms, however, was not significantly different from zero for any treatment year or metric. Woody forms experienced a small, mean positive effect in the first three treatment years.

Within narrow functional groups, forbs showed a stronger vegetative growth response in treatment year 3 (Fig. 2D; response ratio, $Q_b = 12.87$, $P = 0.005$). Mean effect size for vegetative growth of the forbs showed a similar pattern to that of the more broadly defined herbaceous forms (i.e., small effect sizes observed in the first two treatment years and larger effect sizes during treatment years 3 and 4). Graminoids also showed positive mean effect size; however, only treatment year 2 was significantly greater than zero. Within

woody forms, evergreen shrubs experienced a small positive effect in the first three treatment years, whereas deciduous shrubs experienced negative mean effect size (although the mean effect sizes were not significantly different from zero).

Reproductive effort

Mean effect size for reproductive effort was positive in treatment years 2, 3, and 4, becoming progressively larger in later years (Fig. 3A). The magnitude of the effect was small to moderate during this time, indicating a trend toward greater reproductive effort in the warmed plots relative to control plots. The effect size was not significantly different from zero for any of the treatment years.

Reproductive effort differed across climatic zones in treatment year 2 (Fig. 3B; d index, $Q_b = 9.96$, $P = 0.01$ and response ratio, $Q_b = 27.94$, $P < 0.001$), with the high arctic studies showing a greater response than the low arctic studies, and the alpine studies showing a negative response. Mean effect size for reproductive effort in high arctic studies was small to moderate except in treatment year 1 (which was slightly, but insignificantly, negative). In treatment years 2 and 3, the warmed plots had significantly greater reproductive effort than the controls (both metrics). In contrast, none of the means differed significantly from zero for either metric for low arctic studies. Mean effect size in alpine studies was significantly different from zero only in treatment year 2 (both metrics). The mean effect in alpine studies was negative, however, indicating greater reproductive effort in the control rather than the warmed plots. Thus, in high arctic studies, the response was stronger and more consistent than in either low arctic or alpine studies in terms of reproductive effort.

No significant differences were found among either broad or narrow functional groups (Fig. 3C,D). For woody forms, the mean effect size for reproductive

REPRODUCTIVE EFFORT

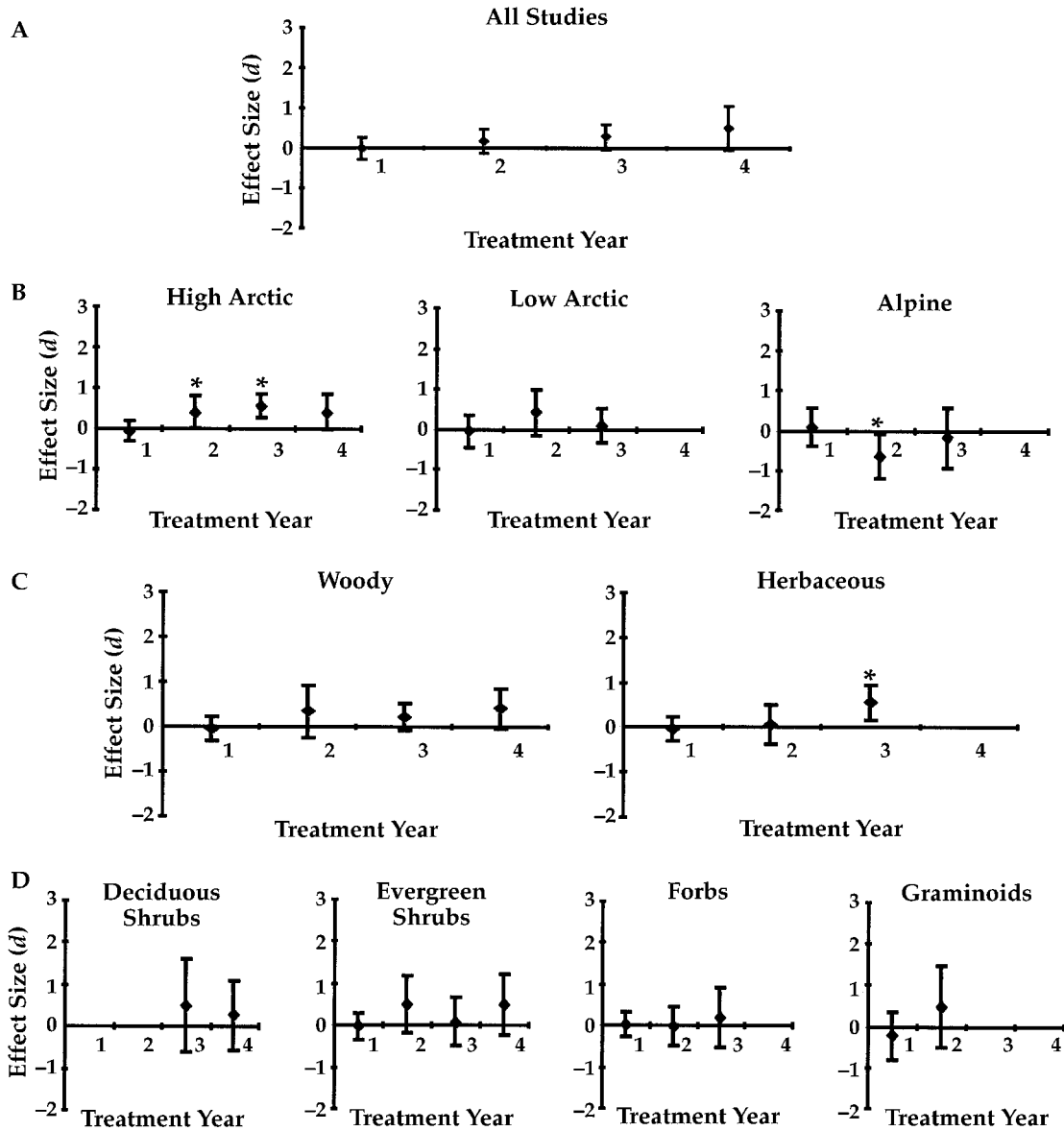


FIG. 3. Effect size (d index) of experimental warming over a 4-yr period for reproductive effort. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized as in Fig. 2. An asterisk (*) indicates that the confidence interval is significantly different from zero at $P \leq 0.05$.

effort was positive (with the exception of treatment year 1), although not significantly different from zero. In contrast, herbaceous forms exhibited a positive response to warming in treatment year three only (d index only). Within woody forms, evergreen shrubs contributed primarily to the response observed in treatment years 1 and 2 (only one study on deciduous shrubs contributed to the response of woody forms). High variability characterized both evergreen and deciduous shrubs. Forbs and graminoids displayed negligible-to-small effects during the study.

Reproductive success

Mean effect sizes for reproductive success were positive throughout the study, indicating a trend toward greater reproductive success under short-term experimental warming (Fig. 4A). The magnitude of the effect was generally small to moderate throughout the study. The mean effect sizes were significantly greater than zero for reproductive success during treatment years 1 (both metrics) and 3 (response ratio).

Reproductive success varied from negligible to large across climatic zones, with no significant difference

REPRODUCTIVE SUCCESS

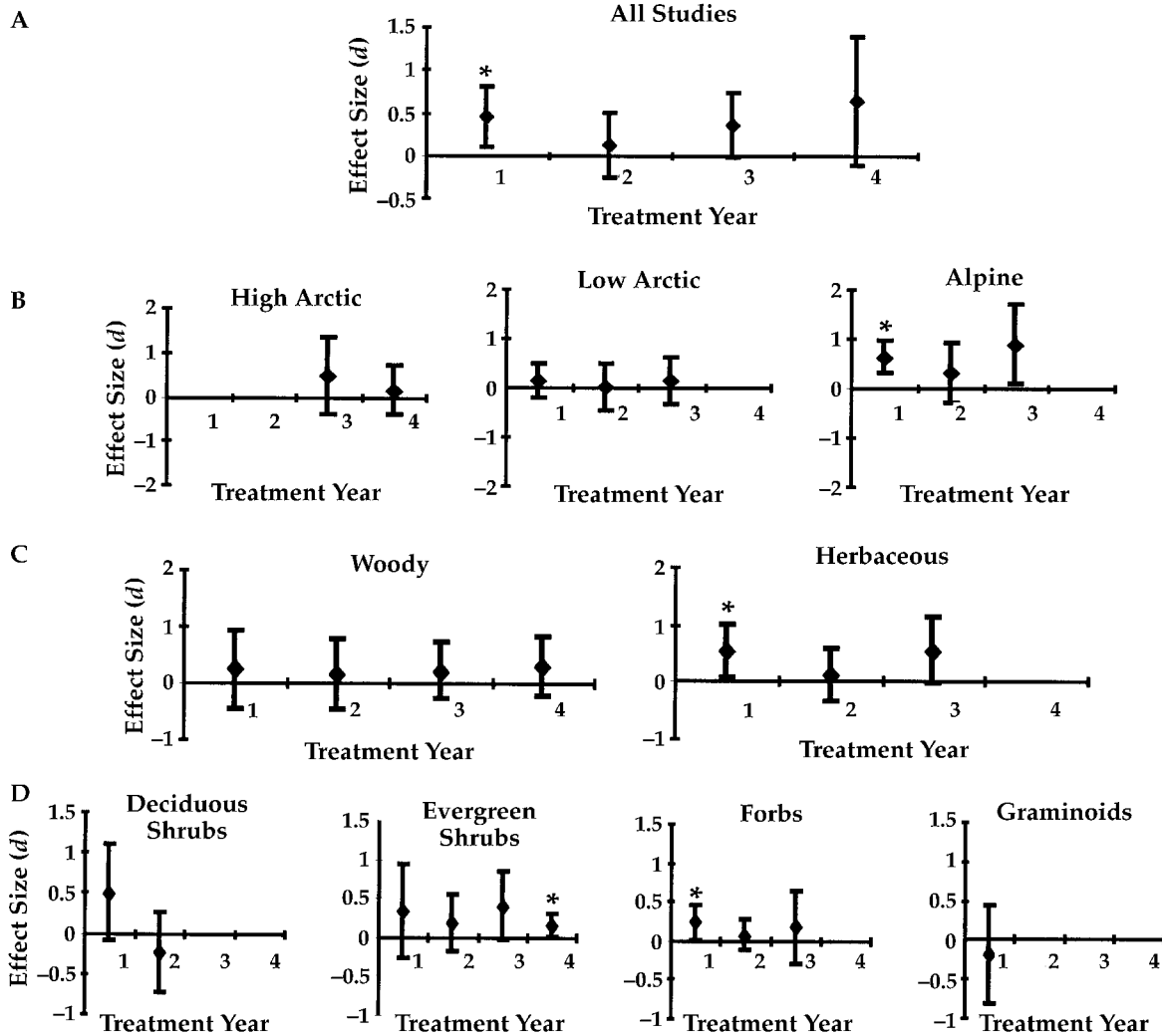


FIG. 4. Effect size (d index) of experimental warming over a 4-yr period for reproductive success. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized as in Fig. 2. An asterisk (*) indicates that the confidence interval is significantly different from zero at $P \leq 0.05$.

among zones (Fig. 4B). Confidence differed depending on which metric was used in the analysis. Using the d index as the metric, only alpine vegetation exhibited a significant positive response to experimental warming (in treatment years 1 and 3). In contrast, when the response ratio was used, only high arctic studies in treatment year 3 were significantly greater than zero.

Experimental warming produced small-to-moderate responses for both woody and herbaceous forms, although only treatment year 1 for herbaceous forms was significantly greater than zero (d index; Fig. 4C). The homogeneity statistic indicated no significant differences among forms. Upon analysis using narrow functional types, only forbs showed significantly greater

reproductive success for treatment year 1 (both metrics; Fig. 4D). The mean effect for both graminoids and deciduous shrubs was negative for reproductive success in treatment years 2 and 1, respectively. Both evergreen shrubs and forbs showed small-to-moderate positive mean effect sizes for reproductive success.

Phenology

Leaf bud burst.—Experimental warming resulted in an earlier initiation of the growing season (Fig. 5). There were small-to-moderate effects on leaf phenology during the first three treatment years, followed by a large effect in treatment year 4 (Fig. 5A). The mean effect size for leaf bud burst in high arctic plants was

LEAF BUD BURST

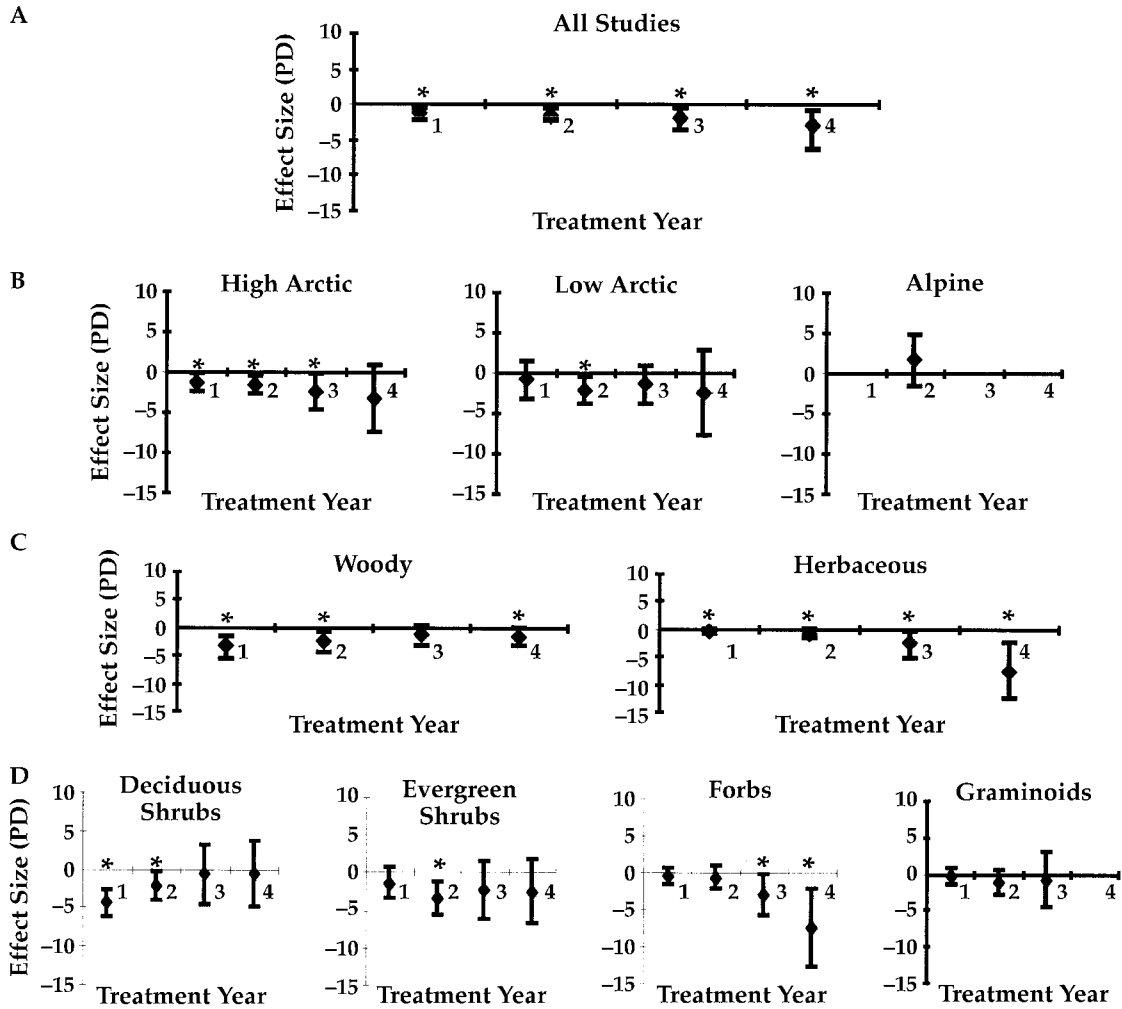


FIG. 5. Effect size (PD) of experimental warming over a 4-yr period for leaf bud burst. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized as in Fig. 2. An asterisk (*) indicates that the effect is significantly different from zero at $P \leq 0.05$.

small to moderate, with the first three treatment years significantly less than zero (Fig. 5B). Low arctic plants exhibited a small-to-moderate response throughout the study; however, only the effect in treatment year 2 was significantly greater than zero. No significant effect was observed in treatment year 2 at the alpine sites. The homogeneity statistic indicated no significant difference among zones for any of the treatment years. Leaf bud burst occurred earlier in warmed plots for both woody and herbaceous forms (Fig. 5C). The mean effect size was small in both woody and herbaceous forms, with the exception of the large effect size in treatment year 4 for herbaceous forms. The homogeneity statistic indicated a trend toward differences among broad functional types in treatment year 1 ($Q_b = 11.59, P < 0.001$). Woody plants exhibited accelerated bud burst in the first two treatment years, but it

was not until treatment year 4 that herbaceous plants exhibited an acceleration of leaf bud burst in warmed plants vs. plants in ambient temperature conditions. Differences among narrow functional types occurred only in treatment year 1, with deciduous shrubs showing the greatest effect ($Q_b = 18.09, P < 0.001$). Leaf bud burst of forbs occurred significantly earlier in the warmed plots relative to plants in ambient temperature conditions in treatment years 3 and 4 (Fig. 5D). Forbs also contributed solely to the large effect size observed in treatment year 4 for herbaceous forms. Both deciduous and evergreen shrubs experienced earlier bud burst in warmed than in control plots.

Anthesis.—Anthesis also occurred significantly earlier (negative effect size) in the warmed vs. control plots (Fig. 6A). Plants experienced moderate-to-large mean effects in flowering phenology during the first

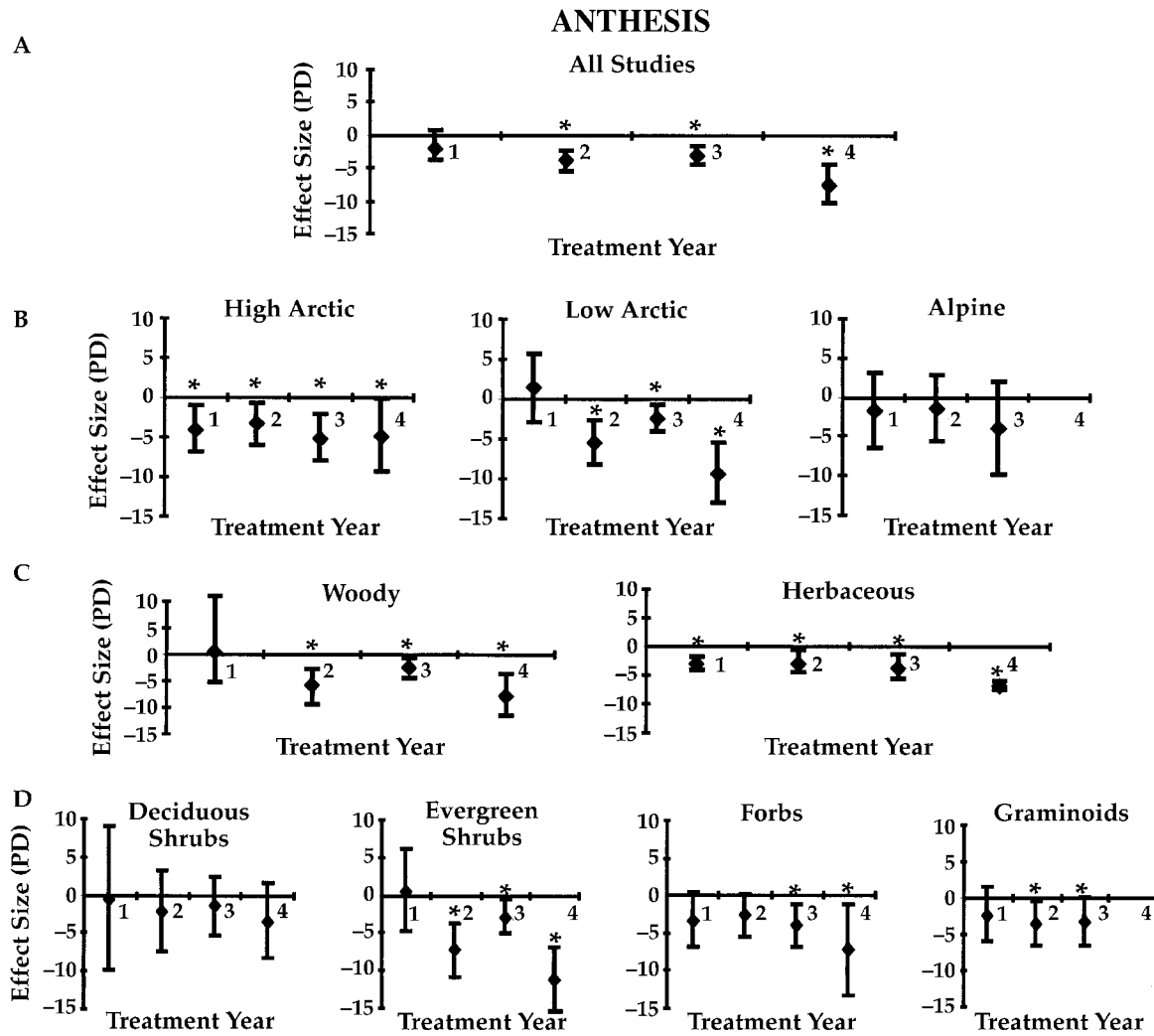


FIG. 6. Effect size (PD) of experimental warming over a 4-yr period for anthesis. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized as in Fig. 2. An asterisk (*) indicates that the effect is significantly different from zero at $P \leq 0.05$.

three treatment years, followed by a very large response in treatment year 4. No significant difference was found among zones for any of the treatment years (Fig. 6B). Mean effect size for anthesis in high arctic studies was moderate to large throughout the study. In low arctic studies, the effect sizes were moderate to large (treatment years 2–4), with a significantly greater effect in the fourth treatment year (relative to treatment year 3). A moderate mean effect size was observed in alpine studies for the first three treatment years. For both woody and herbaceous forms, anthesis occurred significantly earlier in warmed plots relative to controls; however, no significant difference was found among forms (Fig. 6C). Small-to-large effects were observed for both forms, and both forms showed significantly greater effect size in treatment year 4. Both forbs and graminoids had moderate-to-large effects within the

warmed relative to the control plots (Fig. 6D). Within the woody forms, evergreen shrubs showed a stronger response. Open flowers occurred significantly earlier in evergreen shrubs during treatment year 4 than during previous years.

Senescence.—Mean effect sizes for senescence were positive (with the exception of treatment year 4), indicating later senescence in warmed plots than in controls (Fig. 7A). Effect sizes were small for all four treatment years; however, the homogeneity statistic indicated a significant difference among zones in treatment year 1 ($Q = 7.29$, $P = 0.03$). Mean effect size for senescence in high and low arctic studies was small and not significantly different from zero (Fig. 7B). In alpine studies, warmed plants senesced significantly later than control plants, with a large mean effect size for the first treatment year; however, only one site (Fur-

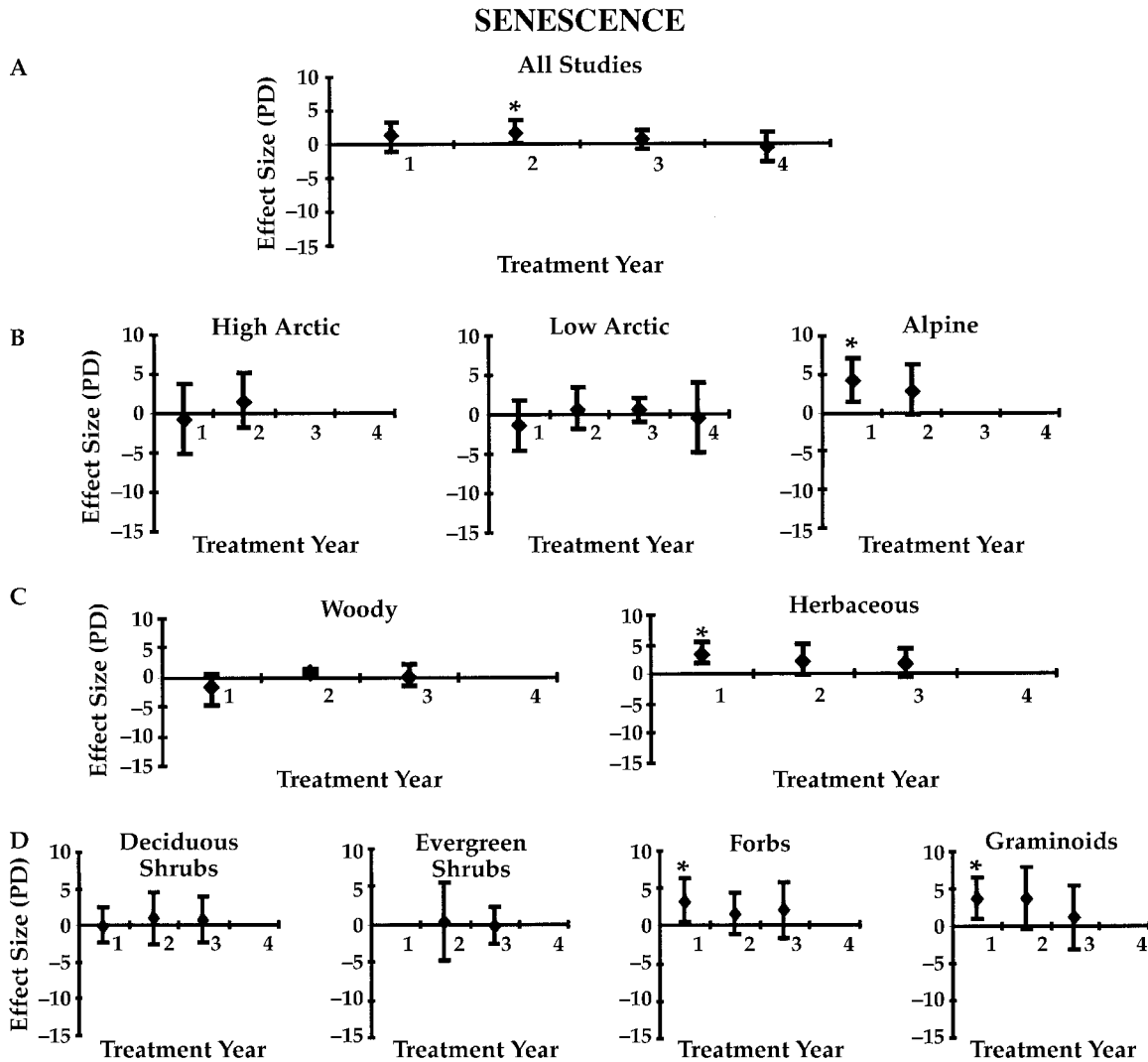


FIG. 7. Effect size (PD) of experimental warming over a 4-yr period for first color change. The mean effect size for each treatment year is indicated with a diamond and vertical bars representing the 95% CI. In the top row (A), all studies are included in the analysis. Studies are then categorized as in Fig. 2. An asterisk (*) indicates that the effect was significantly different from zero at $P \leq 0.05$.

ka, Switzerland) was included in the analysis. The mean effect size for senescence was generally positive within the herbaceous forms, indicating that individuals within warmed plots senesced later relative to control plots (Fig. 7C). The response of herbaceous forms was similar for both forbs and graminoids (Fig. 7D). Although the mean effect size for both deciduous and evergreen shrubs was negligible, the response across studies was quite variable.

Meta-analysis metrics

Results using the d index and the response ratio as the metric were quite similar overall; however, some differences were observed. Effect size confidence intervals were not significantly different from zero for both metrics in 66 cases. Both metrics produced con-

fidence intervals that were significantly different from zero in 16 cases. Instances in which the d index, but not the response ratio, produced significant confidence intervals and vice versa occurred in four and nine analyses, respectively.

The similar results obtained using either the d index or the response ratio indicate a strong pattern in our data. The differences observed between the metrics may be because of small sample sizes, the influence of variance on the d index, or some other difference in how the metrics operated.

DISCUSSION

Temporal variation

Tundra plants across our host of sites exhibited consistent increases in vegetative growth in the first years

of experimental manipulation, substantiating our hypothesis that there would be a significant increase in vegetative growth early in the experiment (see Table 5). By the fourth year, however, this effect, although positive, was more variable and not significantly different from zero. Higher variability in later years may be due to a smaller sample size and an increase in variability of individual species response with time. The initial response of tundra plants to warmer conditions is relatively consistent across the circumarctic and in the alpine of the northern hemisphere, which supports the more site-specific findings of Chapin and Shaver (1985) and others. The reduction in positive growth response of tundra plants to warming in later years may be indicative of resource limitations besides temperature (Shaver and Kummerow 1992), or it may merely be an artifact of sample size. Other potential limitations include soil nutrients (Nadelhoffer et al. 1991), or, in some cases, the meristem network of tundra plants, i.e., source-sink carbon relations (Tissue and Oechel 1987). Our studies did not include a complete analysis of plant mineral nutrition; however, one would postulate that as growth is enhanced and soil nutrients begin to constrain growth, leaf nutrient content may be reduced. Increases in C:N ratios have been found in warming experiments, especially in the dwarf shrubs (Michelsen et al. 1996, Welker et al. 1997, Tolvanen and Henry 1998).

The observed short-term growth response of tundra plants may be transient in nature, based on the limited supply of nutrients available in these harsh environments. Seastedt and Knapp (1993) described a "transient maxima hypothesis" in which a transient maxima or elevated response of key system processes will occur under non-equilibrium conditions when availability or demand for limiting resources varies. These transient responses may affect ecological processes on a time scale from annual estimates of net primary productivity through decadal or longer changes in plant succession, soil organic matter, and nitrogen dynamics (Seastedt and Knapp 1993). In our study, the relatively large effect size during the second and third treatment years and the subsequent decline in vegetative growth during the fourth treatment year may support a transient maxima as resource limitations (temperature, nutrients) vary. This trend was also observed within many of the individual studies (Henry and Molau 1997). For example, during their 4-yr ITEX experiment in Greenland, Mølgaard and Christensen (1997) found that the greatest increase in vegetative growth of the forb *Paspalum radicum* occurred during the second treatment year.

Ecosystem responses that would help to mitigate this resource limitation (increased active layer depth, soil moisture, and nutrient mineralization rates) may not occur for many years and will depend on feedbacks coupling plant and soil processes. Chapin et al. (1995) observed a long time lag (>3 yr) between the initiation

of treatment and ecosystem response. A major effect of their 9-yr temperature warming experiment at Toolik Lake, Alaska, was an increase in nutrient availability due to changes in mineralization (Chapin et al. 1995). Other studies have found that an increase in soil temperature increased the rate of carbon and nitrogen cycling through litter and soil (Hobbie 1998, Rustad and Fernandez 1998). Warmer temperatures could result in increased mineralization of this carbon, producing a positive feedback to rising atmospheric CO₂ concentrations. In addition to direct thermal effects, decomposition may be affected indirectly through changes in species composition and litter quality (Hobbie 1998). Decreasing litter quality (increased C:N ratios) has been found for high arctic dwarf shrubs four years after ITEX warming treatments were established (Tolvanen and Henry 1998); however, there was no effect on graminoids or forbs. Hence, we may expect a shift in species composition to faster growing species that are able to maintain their nutrient uptake, a result noted by Chapin et al. (1996). Changes in canopy cover will, in turn, affect active layer depth and soil moisture regimes, which are tightly linked to soil nutrient reservoirs and availability.

The lag in reproductive effort may be due to adaptation of individual species to the short, and often unpredictable, arctic and alpine summers. In many tundra species, flower buds form one to several seasons prior to flowering (Sørensen 1941, Diggle 1997). Thus, the effects of increased temperature on reproduction may not manifest for several years and will vary by species. Preformation of buds may be an evolutionary adaptation to a short growing season. For example, the preformed buds of *Eriophorum vaginatum* are able to begin development before snow melt in the spring, providing the maximum amount of time for seed maturation. Some species, however, may be more plastic in other aspects of reproduction. The developmental processes of seed production in a high arctic *Dryas* population were highly sensitive, even within one growing season, to enhanced temperature (Wookey et al. 1993, Welker et al. 1997).

Temperature and photoperiod are key environmental factors that may initiate growth, flowering, and senescence in vascular plants (Reynolds and Leadley 1992, Shaver and Kummerow 1992, Price and Waser 1998, Thórhallsdóttir 1998). Key phenological events such as leaf bud burst and flowering occurred earlier in warmed plots throughout the study period. This early-season development may contribute to the increase in vegetative growth observed, particularly in light of plants being able to capitalize on the period of longest day length and potentially highest photon flux density. The lack of a response in senescence at the end of the season may indicate that photoperiod plays a more important role in late-season phenology, similar to many woody plant species with northern ranges (Barnes et al. 1998). Some studies have indicated short-term changes in phe-

nology, particularly delayed senescence (Christensen and Mølgaard 1995, Gugerli 1995, Jones 1995, Molau 1997, Stenström et al. 1997). There is a degree of genetic control in the timing of senescence in *Picea* species, with high-latitude plants senescing earlier when grown in a common environment (Morganstern 1996). Thus, photoperiod may indeed limit the extent to which tundra plants can capitalize on warmer temperature at the end of the season. There is potential, however, for decomposer processes to be prolonged into the autumn (if freeze-up is delayed). If decomposition continues later in the season (under a warming scenario), then increased autumn assimilation of the mineralized nutrients may be a very important process for vascular plants, even if aboveground senescence and/or frost hardening is taking place. Such responses could, to some extent, offset the increased demand for nutrients caused by increased aboveground growth in warmer conditions (although there would be significant time lags involved). Experiments on season length, day length, and snowpack also indicate significant phenological responses to warming (Johnstone and Henry 1995, Oberbauer 1995, Walker et al. 1995).

Spatial variation

The results support the hypothesis that warmer, low arctic sites will show greater increases in vegetative growth, whereas colder, high arctic sites will show greater increases in reproduction (Table 5). Warmer, low arctic and alpine sites produced the strongest vegetative growth response. Greater resource investment in vegetative growth may be a conservative strategy in the Low Arctic, where there is severe competition for light, nutrients, or water and there may be little opportunity for successful germination or seedling development (Parsons et al. 1995). In contrast, in the High Arctic, heavy investment in producing seed under a higher temperature scenario may provide an opportunity for species to colonize patches of unvegetated ground (Welker et al. 1997). The increase in reproduction in some species, however, may take several years to manifest, due to preformation of flower buds.

Seedling establishment is thought to occur rarely in the Arctic because of the short growing season, low temperatures, drought, and ice (Billings 1973). Although this is true for most species in undisturbed tundra (Freedman et al. 1982, McGraw and Shaver 1982), many kinds of natural disturbance do occur (Billings 1973, Freedman et al. 1982, McGraw and Vavrek 1989, McGraw and Fetcher 1992). Grulke and Bliss (1988) showed that establishment from seed is the predominant form of reproduction in the High Arctic. Due to the long life-spans of individual plants (Callaghan and Emanuelsson 1985, Johnstone and Henry 1995, Steinger et al. 1996, Molau 1997), successful seed set and seedling recruitment need only take place infrequently to ensure that a viable population is maintained. Jonsen et al. (1996) found that recruitment by seedlings

occurs relatively frequently, when considered in this broader context, even for long-lived clonal plants growing in closed vegetation of the Arctic and Subarctic. Wookey et al. (1993, 1995) found that the developmental processes of seed production and viability in *Dryas* were highly sensitive to specific environmental perturbations (their data are included in the present study). The high arctic response of *Dryas* supports the hypothesis that high arctic plants respond by increasing reproductive processes that may, in turn, limit their vegetative response. Johnstone and Henry (1995) found that there was a cyclical trade-off between vegetative growth and reproductive effort in *Cassiope tetragona* (an evergreen dwarf shrub). Strong vegetative growth was negatively correlated with reproductive effort in the same year, but positively correlated in the following year. Whether other arctic plants display this periodicity, and how environmental changes affect the allocation patterns is still not well known.

Increased reproduction and earlier reproductive phenology could be particularly important in light of the presence of large unvegetated areas in the High Arctic and the potential need for genetic variability to accommodate the predicted climate change. Environmental change in the High Arctic could shift the balance between clonal and sexual colonization of unvegetated areas. In contrast, the closed vegetation in the Low Arctic is dominated by species that persist predominantly vegetatively. Wookey et al. (1993) found a striking effect of temperature warming on phenology and seed-setting in *Dryas octopetala* ssp. *octopetala* at a polar semidesert, and no significant effects on fruit production of *Empetrum hermaphroditum* at the subarctic site. In fact, Chester and Shaver (1982) found that abortion of fruiting structures between flower and fruit formation was common in the Alaskan tussock tundra, particularly in *Empetrum nigrum*, possibly reducing carbon and nutrient losses.

Functional group variation

Vegetative growth and phenology results supported the hypothesis that there would be a high similarity of response within functional groups (Table 5). For reproductive responses, however, we found no differences among broad or narrow functional groups. Although considerable variability in response occurred among life-forms, herbaceous forms responded more strongly and consistently by increasing vegetative growth than did woody forms. The responsiveness of the herbaceous forms to warming may be attributed to their more flexible morphology, greater ability to scavenge nutrients, and/or greater supply of belowground resources (Shaver et al. 1997). For example, many arctic graminoids may add new leaves without forming new buds, graminoid leaf size may increase dramatically, and rapid tillering is possible. The strong vegetative growth response of evergreen shrubs and some graminoids may also be linked to their ability to more

fully utilize a longer growing season (Chapin et al. 1996, Shaver and Laundre 1997, Welker et al. 1997).

Deciduous shrubs exhibited the weakest growth response to experimental warming, which may be due to a shorter period of photosynthetic activity, greater resource requirements, and a higher leaf turnover rate (Keilland and Chapin 1992). Genera such as *Salix* and *Ledum* may have tight developmental control over meristem activity, which may limit their response or ability to respond quickly to warming. Other genera such as *Betula nana* may be more flexible in responding to warming. *Betula nana* may be unusual in that it has two types of shoots (short shoots and long shoots) that may give it an advantage in responding to increased temperature because it has a much larger pool of active meristems than do any other species (M. S. Bret-Harte, *personal communication*). Significant ecological responses may not be elicited, however, unless multiple environmental stresses are relieved, i.e., warmer temperatures and more available nutrients (mineralized or deposited in precipitation). Chapin et al. (1995, 1996) reported no net increase in *Betula* biomass after nine years of an increased temperature treatment, although *Betula* became the dominant shrub under conditions in which temperature was increased in concert with increases in nutrients applied as fertilizer.

Chapin and Shaver (1996) found that species within a growth form were similar to one another in their response to resources (light and nutrients), but were species specific in their temperature response. Thus, changes in functional groups due to increased temperature may ultimately depend, particularly in the Low Arctic, on changes in nutrient availability and how these changes affect the competitive balance between species with different abilities to take up and utilize soil nutrients (Berendse and Jonasson 1992, Keilland and Chapin 1992, Callaghan and Jonasson 1995). Species typical of nutrient-rich sites (deciduous shrubs and grasses) show a greater growth response to improved nutrient availability than do species typical of nutrient-poor sites (evergreen shrubs; Henry et al. 1986, Keilland and Chapin 1992).

Conclusions

Plants from both the arctic and alpine tundra exhibited consistent sensitivity to warmer summer temperatures, especially short-term increases in vegetative growth with gradual increases in sexual reproduction. Short-term changes in plant performance, however, may not be maintained. Although the mechanisms are still uncertain, they are probably the results of nutrient limitations (Shaver and Kummerow 1992). These changes in vegetative growth associated with experimental warming are not totally uniform across all growth forms, being most pronounced in herbaceous forbs.

Our multisite study supports the following results: (1) most species exhibited a measurable increase in

vegetative growth in the early years of the experiment; (2) warmer, low arctic and alpine sites produced the strongest vegetative growth response, whereas high arctic sites produced a greater reproductive response; (3) herbaceous forms produced a stronger vegetative growth response than did woody forms; and (4) warmer temperatures accelerated plant development in the spring, but had little impact on growth cessation at the end of the season.

Manipulation of single factors such as increased temperature may not account for all of the complex interactions between environmental factors that limit growth of tundra species. For example, long-term responses will probably be constrained by water and/or nutrients, in both the Low and High Arctic (Chapin et al. 1996, Henry and Molau 1997, Shaver et al. 1997, Robinson et al. 1998). Thus, long-term studies will be crucial for resolving how nutrients and other environmental factors affect arctic and alpine plants, because short-term experiments may miss many of the responses that are important in determining the ultimate consequence of disturbances. Whether these initial responses are maintained in the warming experiments, and how they translate to community-level changes, are the focus of ongoing research at ITEX sites.

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