

Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons

J.M. WELKER^{1,2}, U. MOLAU³, A.N. PARSONS², C.H. ROBINSON⁴ and P.A. WOOKEY⁵

¹Department of Rangeland Ecology and Watershed Management, University of Wyoming, Laramie, WY 82071 USA

²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80523 USA

³Department of Systematic Botany, University of Gothenburg, Carl Skottsbergs Gata 22, 413 19 Gothenburg, Sweden

⁴Division of Life Sciences, King's College, University of London, Campden Hill Road, London W8 7AH, UK

⁵Institute of Earth Sciences, Physical Geography, Uppsala University, Norbyvägen 18B, S-752 36, Uppsala, Sweden

Abstract

We have examined organismic responses of *Dryas octopetala* to simulated changes in the summer climate at four tundra sites as part of the International Tundra Experiment (ITEX). Our study sites are located in the High Arctic, on Svalbard, Norway, in the Low Arctic at Abisko, Sweden, and at Toolik Lake, Alaska, USA and our temperate alpine site is at Niwot Ridge, Colorado, USA. These sites represent a range of tundra temperature and precipitation regimes, being generally cold and dry in the High Arctic and warmer and wetter at Toolik Lake and Niwot Ridge. Results from our studies indicate organismic attributes such as flowering shoot length varies by 30% between low and high arctic populations and that experimental warming results in significant increases in shoot height at three of four sites. We find that phenological development of *Dryas* is accelerated under experimentally warmed conditions which corresponds with a lengthening of the growing season in autumn, greater degrees of seed set and a higher likelihood of colonization of bare ground. We also observe that *Dryas* dominated ecosystems which are exposed to experimental manipulations are capable of exhibiting net carbon sequestration in late autumn, and that *Dryas* photosynthesis and green leaf biomass is significantly greater under warmer as opposed to ambient temperature conditions. *Dryas* leaf nitrogen is also significantly lowered under warmer conditions resulting in senescent leaves having a higher C:N ratio than those under ambient conditions. Together these findings indicate that *Dryas* phenology and carbon flux may be altered to the greatest degree in spring and again in autumn by higher summer temperatures and that simultaneously both positive and negative feedback effects may result from changes in plant and ecosystem performance.

Keywords: tundra, climate change, dwarf shrub, Arctic, alpine, comparative studies, ITEX

Introduction

Developing broad-based ecological theorems about how tundra plants and ecosystems will respond to changing climates requires studies of the same species in alpine, low and high arctic settings. There are, however, very few tundra species which have a circumpolar distribution and are also found in the alpine tundra of lower latitudes (Hultén 1959; 1968). *Dryas octopetala* is one exception; this species is found as far south as the Rocky Mountains of Colorado, USA (Komarkova & Webber 1978) while also

being widely distributed in the Low Arctic in Alaska (McGraw 1985) and Scandinavia with High Arctic populations found on Svalbard, Norway, Greenland, and Russia (Hultén 1959, Rønning 1969). Because parent material, time since deglaciation, soil nutrient status, hydrology and local weather vary greatly across tundra occupied by *Dryas octopetala*, accurate generalizations may only be accomplished if a broad level of variability is included in comparative studies. In addition, using a cross-site comparison broadens the inferences which can be drawn and facilitates our ability to identify common attributes and to identify those which are unique or site specific.

Correspondence: J.M. Welker, fax: +1 307 766 6403; e-mail: jeff@uwyo.edu

Recently, a concerted international effort has begun whereby arctic research teams from the circumpolar countries (United States, Canada, Denmark, Sweden, Norway, Finland, Russia) and the United Kingdom have agreed to establish similar environmental manipulation experiments in an array of tundra sites (Molau & Mølgaard 1996; Henry & Molau 1997). The principal justification for this programme, The International Tundra Experiment (ITEX) was: the need to perform comparative studies across tundra types so that generalizations regarding the physiology, growth and phenology of tundra species in response to natural variation in weather could be ascertained, and to quantify the extent to which tundra species and ecosystems from an array of sites might respond to similar directional changes in climate, especially warmer summer conditions (Henry & Molau 1997).

Dryas octopetala is a mat-forming species from the Rosaceae family which is typically found on sites where snow cover is thin in winter (Elkington 1965, 1971; Rønning 1969). Leaves on this species are photosynthetic for multiple years similar to true evergreen species. However, during winter, the chlorophyll in active leaves breaks down, the leaves become brown. In spring the these same leaves again become photosynthetic, giving rise to the term 'wintergreen'. Because of its 'wintergreen' nature and the landscape position it occupies, this species may be predisposed to increases in spring, summer and autumn temperatures compared with tundra habitats dominated by deciduous species or those with strong photoperiodic controls on growth.

For example, higher temperatures in early summer may accelerate floral development, and possibly increase leaf carbon gain in part because plants in these habitats will have been snow-free for several weeks. Modified plant performance in the spring may also be matched by altered organismic and ecosystem processes in the autumn because the 'wintergreen' nature of this species provides active leaf tissue to either gain carbon while other life forms may be senescent, or capture soil nutrients when other root systems may be inactive (Karlsson 1985a, b). Thus, this species and its associated ecosystem processes may be especially sensitive to changing conditions and because of its broad distribution, *Dryas octopetala* provides a strong comparative framework using the ITEX programme.

In this paper we have synthesized findings from four main research sites where ITEX studies of *Dryas octopetala* have been ongoing for several years. We report both original data and incorporate findings from previously published work necessary for our conceptual models and generalizations. We have not, however, attempted to completely summarize all the research on this species but do provide a broad representation of the research to date. Our findings will range from reporting abiotic

conditions resulting from the warming chambers, to leaf, seed and flowering attributes as well as measures of carbon assimilation.

Methods

Sites

This paper examines the response of *Dryas octopetala* to increases in air temperature at four sites. There are two alpine sites, one at Niwot Ridge in Colorado, USA, and a second in the subarctic near Abisko in Sweden called Latnjajaure (Latnja). The third site is in the low Arctic at Toolik Lake, Alaska, USA and one site is in the high Arctic near the settlement of Ny-Ålesund, Svalbard, Norway. Our studies cover almost 40° of latitude and 100° of longitude and represent the broad range of distribution exhibited by this arctic-alpine species. Specific details of each study site can be found in earlier works: Niwot Ridge is described by Isard (1986), the alpine site at Latnja Field Station in Sweden is described by Stenström and Molau (1992), the Toolik Lake area is described by Walker *et al.* (1989), and the Svalbard site is referred to in Wookey *et al.* (1993).

Dryas growth characteristics

Dryas octopetala has a circumpolar distribution in arctic and subarctic habitats and is also found in alpine regions of North America, Europe and Asia (Hultén 1959, Murray 1997). This species dominates the vegetative cover in what are typically very severe habitats, flourishing in polar semi-deserts and alpine fell-field communities which have thin snow cover in winter and well-drained soil in summer (Rønning 1969, Isard 1986). Individual clones of *Dryas* often grow in isolated patches separated by rocks and lichens and some clones may be in excess of 100 years old (Kihlman 1890) although continuous carpets of *Dryas* are observed in some locales.

Vegetative growth of *Dryas* occurs primarily by the extension and branching of individual ramets, produced acropetally, each ramet having between two and five leaves which are photosynthetic in any given year (McGraw & Antonovics 1983; Welker *et al.* 1993). However, leaves of *Dryas* are 'wintergreen' and usually have a 2-year life-span, after which they may stay attached for another 2–4 years. As individual shoots lengthen, and clones expand, secondary growth occurs resulting in significant woody tissue above ground with each clone often having at least one tap-like root. These tap roots appear to be able to grow to considerable depth, reaching in some cases 2 m in length (J Welker pers. obs.). Fine roots are produced from meristems along the basal portions of the woody stems above ground and are

present at greater depths branching from woody, main roots.

Genetics and sexual reproduction

Dryas populations are typically gynodioecious composed of a mixture of hermaphrodite and purely female clones. *Dryas* is an exclusive outbreeder, the level of autodeposition of pollen and subsequent self-compatibility being very low. The flowers are open, bowl-shaped and rather unspecialized in terms of pollination biology with the most frequent pollinators being small flies. The gynoecium is apocarpous and the fruits are one-seeded nutlets with a long, slender barbed awn, effective for wind dispersal. This species is relatively early-flowering, attributed in part to the lack of snow cover in winter, and 'wintergreen' leaves facilitating early season carbon gain, growth and reproduction.

The extent of flowering and sexual reproduction appears to vary from year to year in *Dryas*, thus there is significant inter-annual variability in seed production and the possibility for colonization of bare ground. Floral buds of *Dryas* are pre-formed in the year preceding emergence and elongation (Kjellberg *et al.* 1982); thus two favourable growing seasons back-to-back may be necessary for significant floral displays, seed filling and dissemination.

Experimental protocol

The principal ITEX experiment uses mini greenhouses (termed chambers) to warm the local microenvironment (Marion *et al.* 1997) establishing about a 1–3°C increase in air temperature compared with nonmanipulated conditions and about a 1–2°C increase in soil temperature at 5 cm depth. At our sites portions of the tundra have been exposed to warming treatments alone, while at two of our sites (Niwot and Svalbard), supplemental summer water was combined with higher temperatures, and at Svalbard a nutrient (NPK) application was also added. Chambers are placed on the same plots year after year and are usually installed in late May to early June and left in place until late August to early September, removed and stored over winter until spring deployment. When water applications have been implemented, they amounted to approximately a 50% increase in summer rainfall applied four to six times over the course of the summer. Nutrient applications were applied as NPK fertilizer in aqueous form four times during the growing season (Wookey *et al.* 1993).

Abiotic monitoring

The environmental conditions inside the chambers and in unmanipulated plots were quantified using thermo-

couples or thermistors for air (10 cm above the leaf canopy) and soil temperatures (5 cm below the soil surface), relative humidity sensors for atmospheric water vapor, quantum sensors for photosynthetic photon flux densities (PPFDs) at 10 cm above the leaf canopy and in some cases anemometers were used to measure wind speed. These measurements were made for periods lasting 2–6 weeks during the summer to characterize conditions inside and outside the chambers, with readings taken every 5 min, averaged every 60 min and stored on data loggers.

Organismic measurements

Patterns of plant and leaf phenology and flowering have been recorded in manipulated and in unmanipulated plots by either tagging individual shoots or dividing plots into quadrants and scoring the stage of development (Wookey *et al.* 1993, 1995). For *Dryas*, the following developmental stages were recognized and recorded: the greening of leaves, the appearance of petals, the dissemination of seeds and the gradual yellowing and browning of leaves in autumn. Developmental stages have in some cases been bracketed to include pre-floration time, the time between thawing and anther dehiscence, and post-floration, the time from flowering to seed dispersal.

Attributes of the reproductive inflorescences were measured after shoots had been collected in the autumn, and transported back to the laboratory. Length of the pedicel (inflorescence height) was measured to the nearest mm, and individual seed masses quantified after air drying. Seed number per inflorescence was quantified at two of our sites by counting the number of seeds on inflorescences before dissemination. Seed germination was also tested for seeds collected from our Latnja site. Four replicates of 20 randomly selected seeds were placed on moist filter paper and kept in the dark at 5°C. Germination was considered successful when roots had appeared.

Vegetative growth characteristics, including photosynthetic leaf numbers per ramet, the mass of individual leaves and the total leaf mass per ramet have also been quantified (Welker *et al.* 1993). In the autumn, vegetative subsamples from throughout the plots were collected, air-dried and brought back to the laboratory. Ramets were separated with forceps and photosynthetic leaves removed and counted. Leaves were then oven-dried at 60°C for 48 h, and weighed. This allowed for measures of individual leaf masses and estimates of the total mass of leaves per ramet. In some cases leaves were ground and total carbon and total nitrogen quantified using a LECO CHN-1000 analyser (LECO Corp., St Joseph, MI, USA).

At the end of the second experimental season (1994) at Niwot Ridge, we also assessed coloration of leaves in October as a measure of growing season extension. In this case, a 50 cm line transect (N–S direction) was established across individual *Dryas* clones either exposed to experimental warming only or grown in ambient temperature conditions. At 10-cm intervals the colouration of the nearest *Dryas* leaf was recorded, being either green (>75% of the leaf), yellow or brown. Leaf colouration transects were assessed in three replicate plots per treatment.

Carbon flux

At our polar semi-desert site on Svalbard we measured photosynthetic rates of detached *Dryas* leaves (Wookey *et al.* 1995) and conducted preliminary measures of ecosystem carbon flux by quantifying CO₂ characteristics in *Dryas* canopies. The individual leaf measures were carried out in year 3 of the experimental manipulations at this site and the carbon flux measures were conducted in year 2 of the study. Details of the leaf photosynthesis techniques can be found in Wookey *et al.* (1995). The carbon flux measurements used vertical stratification as an indicator of changes in ecosystem carbon dynamics, such as soil respiration and photosynthetic processes, by measuring CO₂ concentrations at the soil surface and in the leaf canopy (Bazzaz & Williams 1991). Depletion of CO₂ concentrations in the canopy to below ambient atmospheric concentrations indicates net carbon gain even though absolute flux rates are not measured (Bazzaz & Williams 1991).

Carbon dioxide concentrations were measured at the soil surface beneath actively growing mats of *Dryas* (0 cm), in the leaf canopy, (approximately 5 cm above the soil surface) and at 1.5 m. Measurements were taken on two days in late August, one with stable low irradiance (PPFD 110–190 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (20 August) and one with stable moderate irradiance (PPFD 356–433 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (25 August). Samples at the different positions were taken by placing a polypropylene tube of 2 mm inside diameter at each location drawing air through an infra-red gas analyser (IRGA) (LCA-2, ADC Ltd, Hoddesdon, UK) at a flow rate of 150 mL min⁻¹. After a 4 min equilibration period, the CO₂ concentration in the air stream was recorded from the IRGA. Three samples from the different treatment plots were randomly selected over a 6-h sampling period with bulk air readings at 1.5 m height taken periodically. The effects of treatment and canopy location on CO₂ concentrations were first analysed using a two-way analysis of variance (2-way ANOVA) with a treatment by layer interaction term for the late August sampling dates. Treatment differences were considered significant

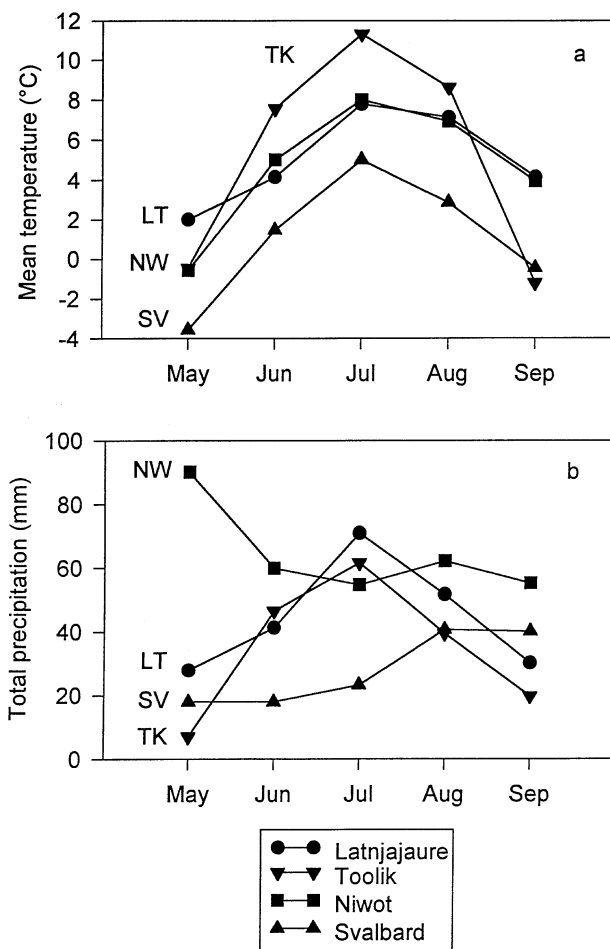


Fig. 1 Mean (a) air temperatures and (b) total precipitation for the months May, June, July, August and September from Toolik Lake (TK), Latnjajaure (LT), Niwot Ridge (NW) and Svalbard (SV). Means are based on 5–15 years of data from each site.

when $P < 0.05$ and treatment mean differences were determined using a least significant difference test.

Results

Abiotic conditions at the four sites

The average monthly temperatures of the four sites are presented in Fig. 1a. In May, Latnja (LT) was the warmest of the sites while Niwot (NW) and Toolik (TK) were almost identical with Svalbard (SV) being the coldest. Throughout the course of the growing season Svalbard remained the coldest site while in June, July and August, average temperatures at Toolik were the highest. Both Latnja and Niwot did however, stay warm in autumn as the temperature difference between July and September was only a 4°C decrease while at Toolik the air temperature decreased by 12°C between July and September.

The differences in total monthly precipitation across

the four *Dryas* sites is greatest in May when Niwot receives significant snowfall and the other sites receive little snow or rain (Fig. 1b). Over the course of the summer precipitation is lowest at Svalbard though in September both Toolik and Latnja have precipitation amounts which are less than the high arctic site. Only the Niwot site has more snowfall precipitation than Svalbard.

Organismic attributes

Phenological development as measured by the appearance of flowering shoots was accelerated by warming at both Svalbard and at Latnja (Fig. 2). The frequency of the appearance of open flowers and floral buds was greater early in the season under temperature increases though by the middle of the season, floral development was similar between warmed and ambient temperature conditions on Svalbard (Fig. 2a). Seed setting, as indicated by styles elongating was consequently further developed under warmed conditions at Svalbard (Fig. 2b). At Latnja, a similar observation of accelerated phenology was observed in both 1993 and in 1994. In this case, pre-floration, the time between thawing and anther appearance, was accelerated under warmed conditions, on average by over 2 weeks (Fig. 2c).

The length of the pedicel (flower stalk) of *Dryas* under ambient temperature conditions ranged between 32 and 48 mm, the longest being from Latnja and the shortest on Svalbard (Fig. 3). Pedicel length increased significantly ($P < 0.05$) at three of the four sites under warmer conditions by as much as 40%. Only at Toolik Lake did we observe that pedicel length was unaffected by warming. We also examined the number of seeds per flower at the Svalbard and Latnja sites. In year 1 of the experimental treatment on Svalbard, only plants under warmed conditions produced flowers with seeds. Water augmentation increased seed numbers from 40 to 50 ($P < 0.001$) per inflorescence while fertilizer applications had no effect (Fig. 4). At Latnja, plants from both warmed and ambient conditions produced flowers with seeds. At this site, we have also found that the number of seeds produced is significantly ($P < 0.01$) correlated ($r^2 = 0.46$) with the length of the flowering shoots as depicted in Fig. 5.

The mean mass of individual seeds of *Dryas* was almost identical at Latnja and Niwot Ridge, averaging about 250 μg under ambient temperature conditions (Fig. 6). Seeds from Svalbard and from Toolik were lighter, with those from Toolik Lake only averaging 100 μg each. Higher temperatures at two of the four sites, Niwot Ridge and Svalbard, resulted in significant ($P < 0.05$) increases in seed mass but temperature had no effect at Latnja or at Toolik. Seed germination was found to be size class dependent and unresponsive to higher temperatures

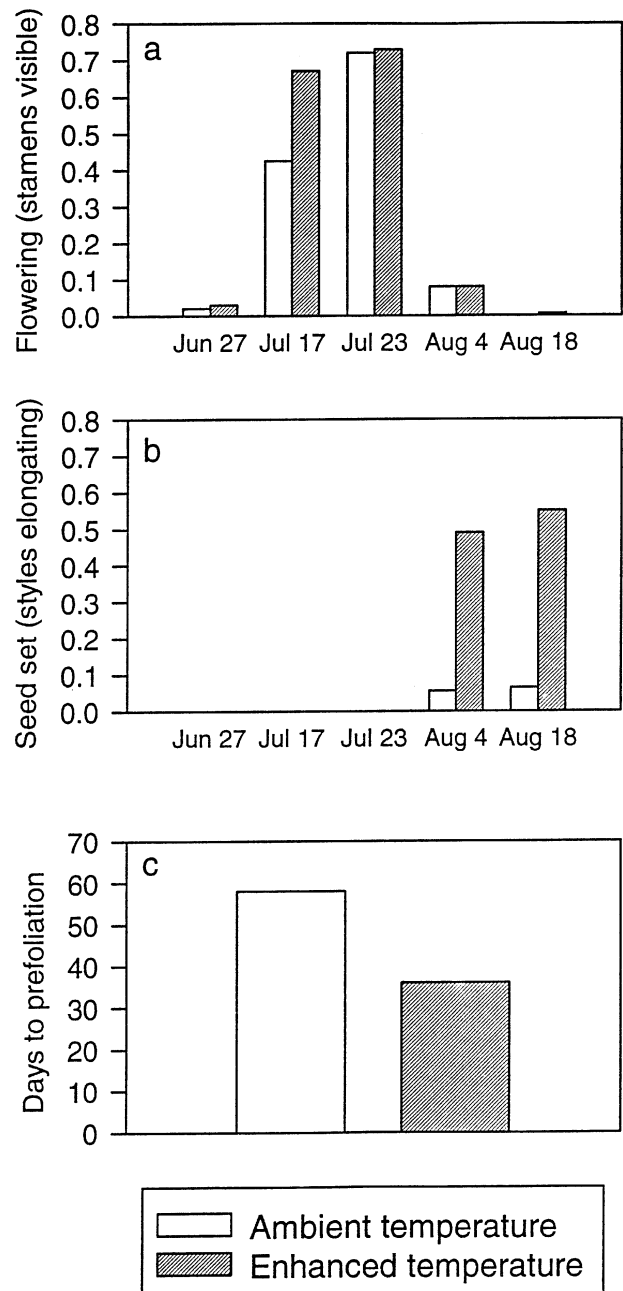


Fig. 2 Phenological patterns of *Dryas octopetala* based on measurements of the proportion of quadrants in which (a) flowering, and (b) seed set were occurring and (c) days to prefloration under ambient (\square) or warmed conditions (hatched). (a) and (b) were measured on Svalbard and the data are from Wookey *et al.* (1993), the data in (c) were collected from Latnjaure. Significant differences, $P < 0.001$, between flowering under ambient and warmed conditions occurred in early July and in August for seed setting.

(Table 1). Seeds which weighed less than 150 μg exhibited essentially no germination, while those seeds which were greater than 450 μg exhibited greater than 94% germination.

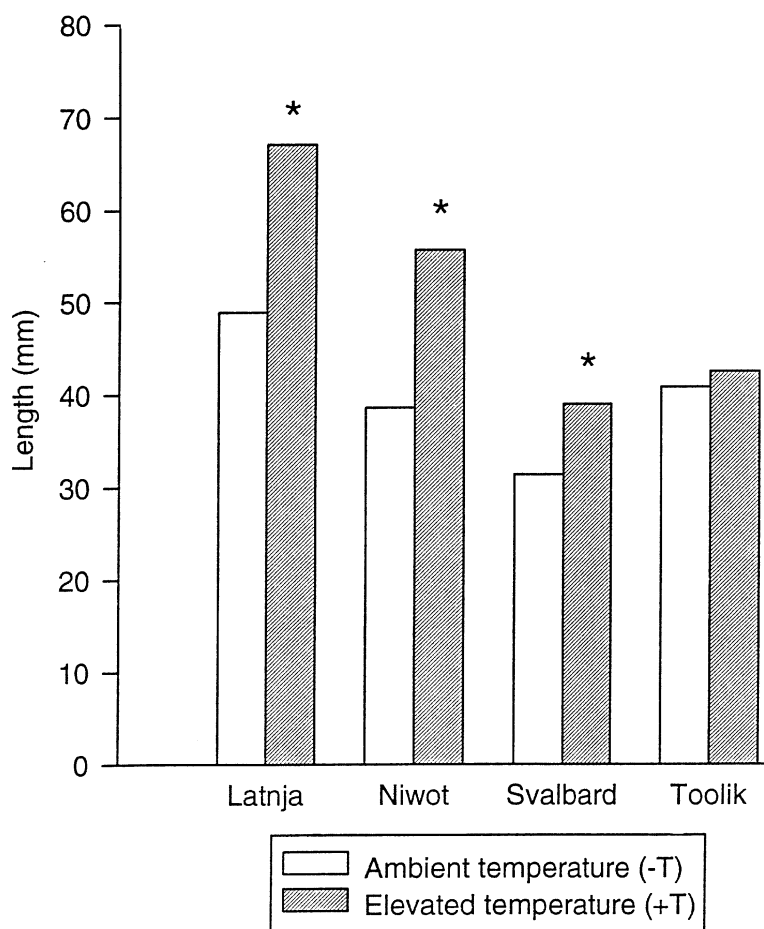


Fig. 3 Length of *Dryas octopetala* pedicels measured at the end of the growing season at four sites (Latnjaure, Niwot, Svalbard and Toolik), grown under ambient conditions (\square) or inside chambers (▨). * indicates significant effect of chamber treatment at that site ($P < 0.05$).

The number of photosynthetic leaves per ramet of *Dryas* under ambient conditions varied from three to seven leaves, the fewest being found at Toolik Lake and the most being found at Svalbard, though some year to year variability was observed (Table 2). Leaf number per ramet was only responsive to experimental warming at our Svalbard site in year 2, increasing by about one leaf per ramet. However, leaf number per ramet was fewer under watered conditions at Niwot in year 2.

The mass of individual leaves under ambient conditions ranged from 2.2 to 4.1 mg, the heaviest from Niwot and the lightest at Svalbard (Table 2). The mass of individual leaves was also observed to be responsive to experimental manipulations, weighing significantly ($P < 0.05$) less under warmed treatments at Toolik in year 1 only, and weighing less under watered treatments in year 1 at Svalbard.

Combining the leaf number per ramet with the individual leaf weights, total leaf mass per *Dryas* ramet was unaffected by experimental warming and additions of summer rainfall in year 1 or year 2 at Niwot Ridge, and were unaffected in year 1 at Toolik Lake by experimental

warming (Table 2). Svalbard plants exhibited lower leaf mass per ramet under watered conditions in year 1 due in part to lower average leaf weights. In year 2, however, total leaf mass per ramet was significantly higher under warmer conditions for plants in the high arctic. These increases in leaf mass per ramet culminated in the overall green leaf biomass of *Dryas* being significantly higher under warmed conditions, 3 years after experimental treatments had been implemented on Svalbard ($P < 0.01$) (Fig. 7).

Leaf senescence patterns also appeared to be responsive to simulated climate warming (Fig. 8). At Niwot Ridge, for instance we observed that leaves of plants exposed to elevated temperatures remained green longer (*t*-test, $P < 0.05$). In addition the proportion of leaves which had browned were significantly ($P < 0.01$) less under warmed (+T) as opposed to ambient (-T) conditions, lengthening the growing season and the period in which plants were capable of photosynthesizing. In addition, we found that the leaf nitrogen content at the end of the growing season, tended to be lower (0.8% N vs. 1.0% N) under higher compared with ambient temperature conditions and under watered as opposed to unwatered conditions at Niwot Ridge. These reductions in leaf N content, result

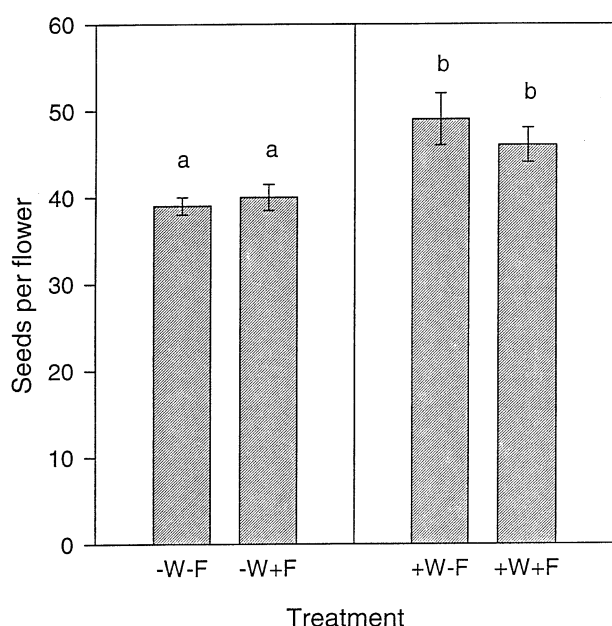


Fig. 4 The number of *Dryas octopetala* seeds per flower from plants after 1 year of experimental treatment on Svalbard. All samples were collected from plots with warming chambers, and in addition they received either no treatment (-W-F), NPK fertilizer (-W+F), additional water (+W-F) or both added water and fertilizer (+W+F). Different letters indicate that watered plants had a significantly ($P < 0.05$) greater number of seeds than those under ambient water conditions. There was no significant effect of fertilizer.

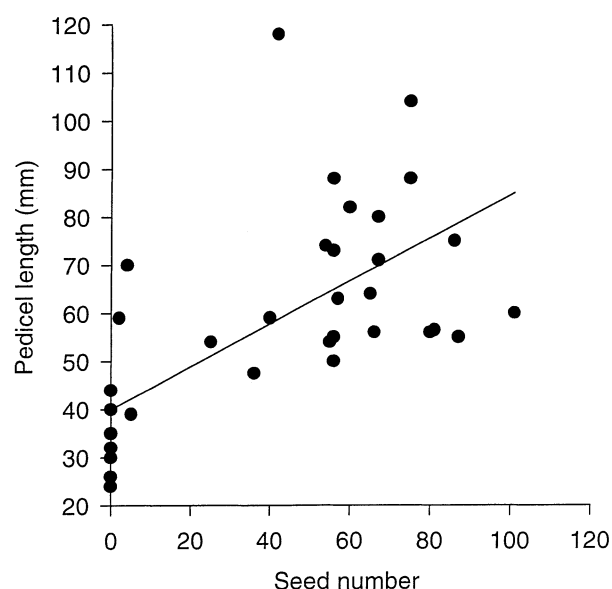


Fig. 5 Association between *Dryas octopetala* pedicel length (mm) and seed number per flowering shoot on plants from Latnja, Sweden. The relationship is significant ($P < 0.05$) with an r^2 of 0.45.

in senescing leaves that have a higher C:N ratio possibly slowing decomposition and modifying nutrient cycling under manipulated conditions (Fig. 9).

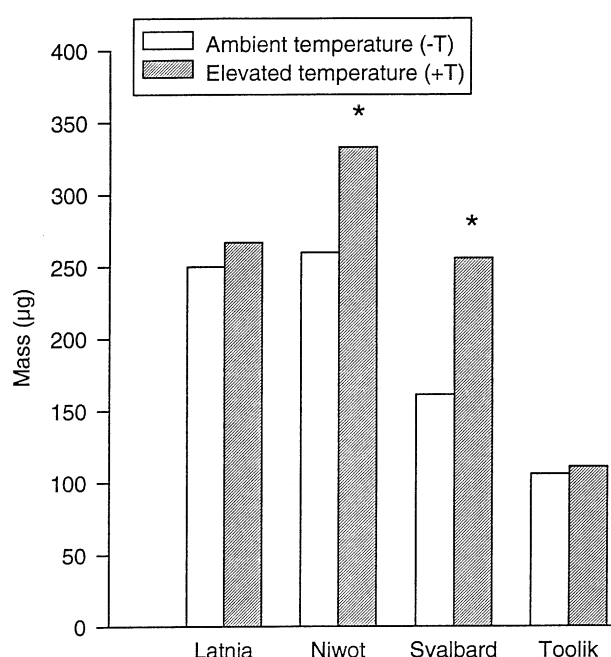


Fig. 6 The mass (μg) of individual *Dryas octopetala* seeds at four sites (Latnja, Niwot, Svalbard and Toolik), grown under ambient conditions (\square) or inside chambers (hatched). * indicates significant effect of chamber treatment at that site ($P < 0.05$).

Table 1 Germinability (%) of *Dryas octopetala* seeds collected from plants at the Latnja field site in northern Sweden at the end of the 1993 growing season. Each value is the mean of four replicates with each replicate consisting of 20 seeds.

Seed weight class	Germinability (%)
< 150 μg	0.0
150–300 μg	2.5
301–450 μg	50.5
> 450 μg	94.8

Individual leaf photosynthesis was significantly ($P < 0.001$) greater under higher as opposed to ambient temperature conditions at Svalbard (Fig. 10). Carbon gain by these leaves was approximately 10% higher increasing from 14 to 16.5 $\text{mmol m}^{-2} \text{s}^{-1}$. Ecosystem carbon flux was also responsive to experimental conditions (Fig. 11). For instance, under low irradiance ($< 400 \mu\text{mol m}^{-2} \text{s}^{-1}$), CO_2 concentrations at the soil surface beneath *Dryas* mats in the High Arctic averaged 368 ppm under unamended or 'control' conditions while averaging 391 ppm under fertilized conditions (+F, TWF) ($P < 0.001$) (Fig. 11). On the second day of analysis, soil surface CO_2 concentrations were again significantly ($P < 0.02$) higher in plots which were warmed, watered and fertilized (TWF) as opposed to the control plots (Fig. 12).

The CO_2 concentrations in *Dryas* leaf canopies (5 cm height) were significantly ($P < 0.0001$) lower in plots which

Table 2 Cross-site comparison of *Dryas octopetala* leaf attributes from Niwot Ridge, Toolik Lake and Svalbard. Treatments are either ambient temperatures and ambient rainfall (–T–W), ambient temperatures and 50% additional summer rainfall (–T+W), experimentally warmed and ambient summer rainfall (+T–W) and experimentally warmed and additional summer rainfall (+T+W). Different letters represent significant ($P < 0.05$) differences between treatments as tested by a 2-way analysis of variance and LSD test for mean separations for the Niwot site in years 1 and 2 and for the Toolik Lake and Svalbard site in year 1.

Year*	Leaves/ ramet		Leaf mass (mg)		Leaf mass/ ramet (mg)	
	1	2	1	2	1	2
Niwot Ridge						
–T–W	3.2 ^a	4.8 ^a	4.0 ^a	4.1 ^a	12.5 ^a	19.8 ^a
–T+W	3.7 ^a	3.7 ^b	4.4 ^a	4.7 ^a	16.5 ^a	17.8 ^a
+T–W	3.9 ^a	4.8 ^a	4.8 ^a	4.1 ^a	18.9 ^a	19.8 ^a
+T+W	3.8 ^a	4.1 ^b	4.9 ^a	4.4 ^a	19.2 ^a	18.3 ^a
Toolik Lake						
–T–W	3.0 ^a		4.1 ^a		12.3 ^a	
+T–W	3.3 ^a		3.2 ^b		10.8 ^a	
Svalbard						
–T–W	4.5 ^a	7.3 ^a	2.6 ^a	2.2 ^a	11.2 ^a	15.7 ^a
–T+W	4.3 ^a	7.1 ^a	1.9 ^b	2.3 ^a	8.3 ^b	16.6 ^a
+T–W	4.1 ^a	8.1 ^b	2.3 ^a	2.3 ^a	9.5 ^a	18.7 ^b
+T+W	4.5 ^a	8.4 ^b	1.8 ^b	2.5 ^a	8.2 ^b	21.1 ^b

* The 1 and 2 here represent the first and the second year in which the experimental treatments were applied.

were warmed, watered and fertilized (TWF) than those of the other treatments (Figs 11 & 12). CO₂ concentrations in the canopies of the other treatments were not different to those of the bulk air (358 ppm) and because the control and the warmed only leaf canopy CO₂ concentrations were not significantly different, no 'structural' warming chamber effect altering wind conditions and plant boundary layer were found.

Discussion

Shifts in the patterns of *Dryas octopetala* phenological development whereby floral and vegetative development occurs earlier in the growing season is one of the most consistent responses we have observed under simulated summer climate warming. The acceleration of phenology in spring appears to result in a general lengthening of the growing season, resulting in taller reproductive flowers which in turn have a larger number of seeds. This early season development may contribute to the increase in the green leaf area we observed under manipulated

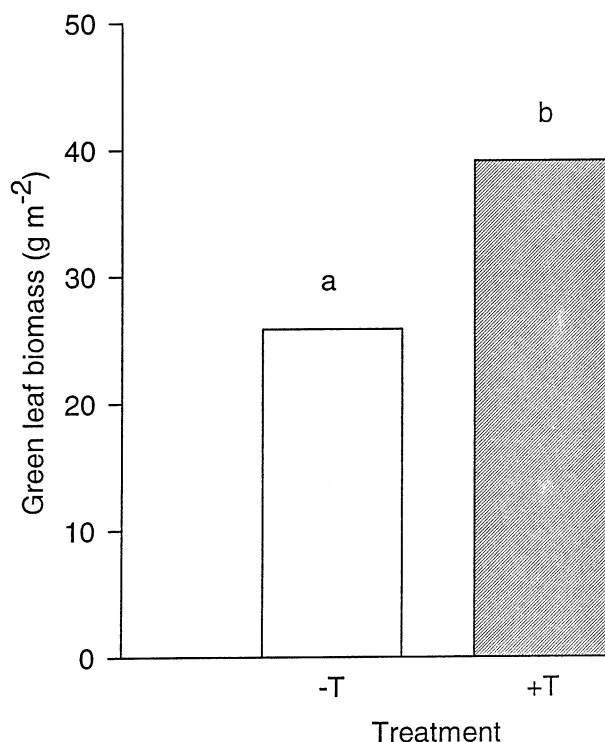


Fig. 7 The green leaf biomass (g m⁻²) of *Dryas octopetala* at Svalbard, grown under ambient temperature (–T) conditions (□) or under experimentally warmed (+T) (▨) conditions. Different letters above the bars represent significant treatment differences ($P < 0.01$) as tested with a multifactorial analysis of variance (Wookey *et al.* 1995).

conditions. In addition, we find that the growing season is prolonged, extending the period in which this species and possibly the entire ecosystem is capable of sequestering carbon. Thus, changes in environmental conditions in habitats dominated by *Dryas* may result in shifts in plant performance both early and late in the season (Fig. 13).

These changes in *Dryas* performance are however, only possible in part because of its 'wintergreen' nature and the presence of green leaves shortly after snowmelt along with the maintenance of green leaves into the autumn. These characteristics allow *Dryas* to be somewhat opportunistic in its growth, optimizing the potential ecological benefits of warmer conditions over the entire course of the snow-free period (Chapin *et al.* 1993). This is counter to what might be expected from deciduous species, such as dwarf shrubs which are more reliant on photoperiodic cues for vegetative initiation. Because deciduous species have a much more fixed schedule of leaf display (Karlsson 1985a, b) they may be less responsive to changes in conditions, or responsive to a different degree than evergreen species such as *Dryas octopetala* (Parsons *et al.* 1994).

The long-term ecological consequences of changes in

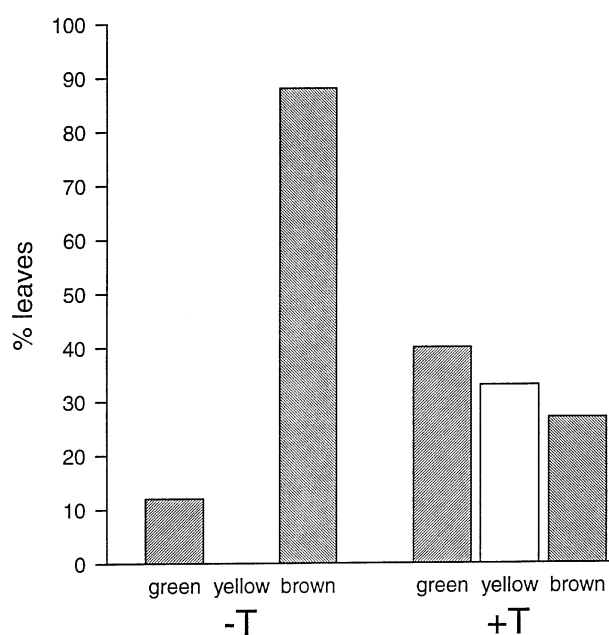


Fig. 8 The proportion (%) of *Dryas octopetala* leaves which were categorized as being green, yellow or brown at the end of the growing season after 2 years of experimental treatment at Niwot Ridge. Plants were either in ambient conditions (-T) or grown inside chambers (+T).

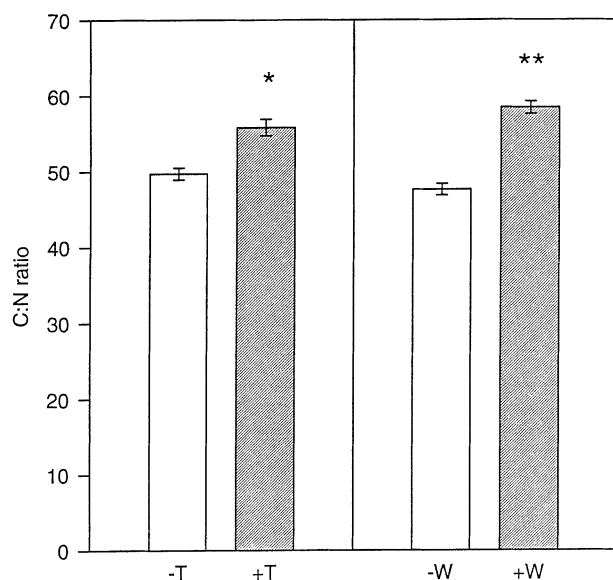


Fig. 9 The carbon to nitrogen ratio (C:N) of senescing *Dryas octopetala* leaves harvested in October at the end of the second year of experimental manipulations at Niwot Ridge. Plants had been grown in ambient conditions (-T, -W), in chambers (+T) or with an enhanced water supply (+W). * indicates a significant ($P < 0.05$) effect of warming, ** indicates a significant ($P < 0.01$) effect of water addition on leaf C:N ratios as tested with a two-way factorial analysis of variance.

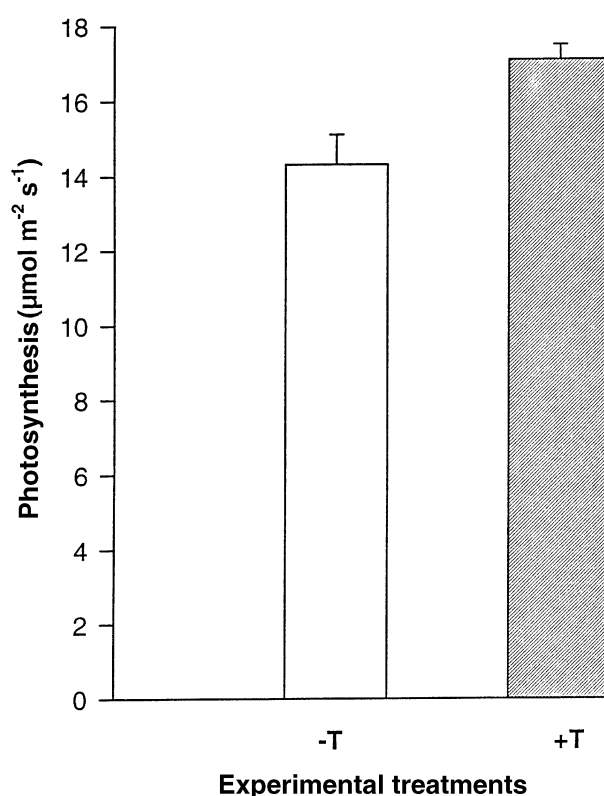


Fig. 10 Photosynthesis ($\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of *Dryas octopetala* leaves measured in July of the third year of experimental manipulations at Svalbard. Plants were growing in either ambient conditions (-T) or inside chambers (+T).

environmental conditions in *Dryas* dominated habitats is somewhat difficult to ascertain with short-term field experiments (Chapin *et al.* 1995). However, we propose that the organismic responses we observe are likely to result in both positive and negative feedback in these terrestrial habitats (Fig. 14), the balance between the two at this time being uncertain.

For instance, we find that the C:N ratio of senescent leaves is higher under warmer and wetter conditions which we would predict results in leaves which are slower to decompose, tying up nutrients and slowing down the rate of nutrient cycling in these systems (Fig. 14) (Anderson 1991; Nadelhoffer *et al.* 1992). This reduction in the rate of nutrient turnover may have a cascading effect on plant mineral nutrition, carbon sequestration and the overall carbon budget of these systems (Shaver *et al.* 1992). Because *Dryas* ecosystems have inherently low levels of soil nutrient resources (Robinson *et al.* 1996), as observed in other tundra ecosystems (Haag 1974, Svoboda 1977, Chapin *et al.* 1986, Henry *et al.* 1986, Kielland & Chapin 1992), a further constraint on the cycling of nutrients between soils and plants may result in the surpassing of an ecological threshold, curtailing the abil-

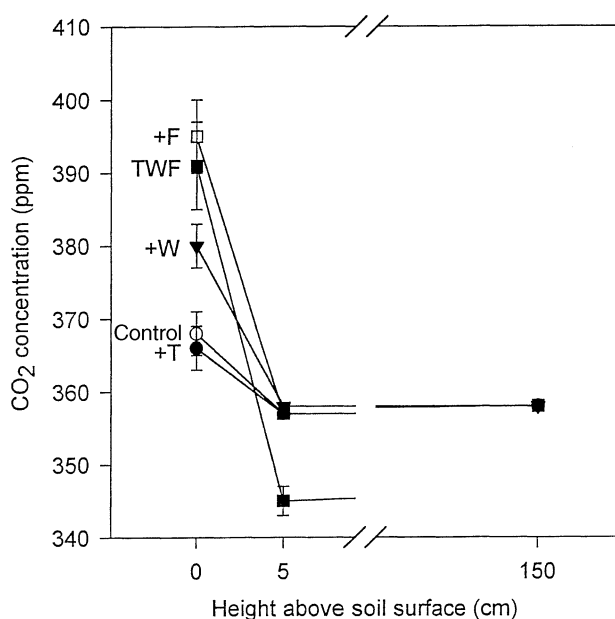


Fig. 11 Carbon dioxide concentrations (ppm) recorded on 21 August 1992 after 2 years of experimental manipulations in Svalbard. Measurements were taken at the soil surface under *Dryas* mats, in the leaf canopy and from bulk air, 1.5 m above the soil surface. Means represent the average of four replicates. The data are from five treatments: unamended (control), additional NPK fertilizer (+F), additional water (+W), inside chambers (+T) and a combination of chamber, water and fertilizer (TWF). Irradiance (PPFD) on this day averaged $184 \mu\text{mol m}^{-2} \text{s}^{-1}$ due to continuous cloud cover, with an average leaf temperature of 6.3°C under ambient conditions and an average air temperature of 5.2°C . Inside chambers, leaf temperatures averaged 6.6°C and air temperatures averaged 7.8°C .

ity of *Dryas* to occupy these habitats. The higher C:N ratio in decomposing leaves could, however, also represent a nutrient conservation strategy whereby a greater fraction of the leaf N is being resorbed for use in future years, increasing the likelihood of internal plant N cycling (Kielland & Chapin 1992, Chapin *et al.* 1993).

There are positive feedback effects that have been observed. In general, we find that *Dryas* vegetative and reproductive growth is increased under manipulated conditions which in turn leads to increases in plant cover reducing the albedo of these habitats. The subsequent increase in plant cover may in turn result in an overall increase in leaf area, increasing the ability of the system to sequester carbon from the atmosphere (Fig. 14).

Soil respiration and carbon fixation by high arctic *Dryas* plants exposed to warmer, wetter and higher nutrient conditions appear to have responded in parallel to simulated changes in climate late in the growing season as evidenced by simultaneous increases in soil surface CO_2 concentrations and canopy CO_2 depletion. Net

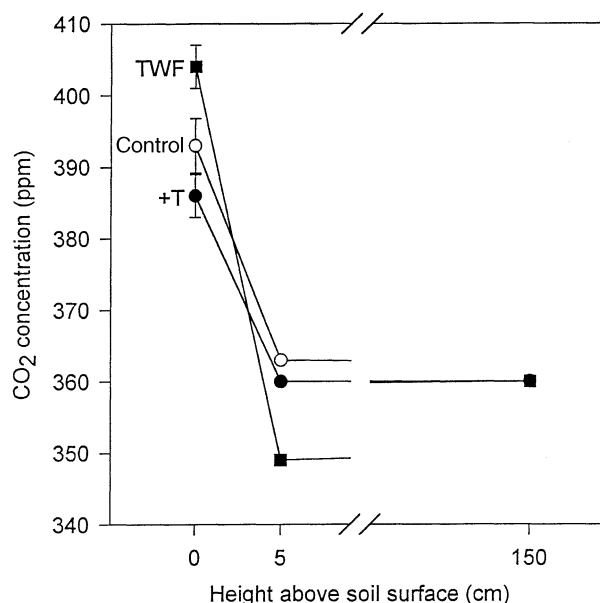


Fig. 12 Carbon dioxide concentrations (ppm) recorded on 25 August 1992 after 2 years of experimental manipulations in Svalbard. Measurements were taken at the soil surface under *Dryas* mats, in the leaf canopy and from bulk air, 1.5 m above the soil surface. Means represent the average of four replicates. The data are from three treatments: unamended (control), inside chambers (+T) and a combination of chamber, water and fertilizer (TWF). Irradiance (PPFD) on this day averaged $516 \mu\text{mol m}^{-2} \text{s}^{-1}$, with an average leaf temperature of 12.2°C under ambient conditions and an average air temperature of 6.5°C . Inside chambers, leaf temperatures averaged 12.1°C and air temperatures averaged 15.6°C .

carbon sequestering by high arctic *Dryas* plants thus appears to be occurring under conditions of low PPFD ($<400 \mu\text{mol m}^{-2} \text{s}^{-1}$) which is the rule rather than the exception in the High Arctic (Mayo *et al.* 1971; Crawford 1989). Net CO_2 gain occurred even under conditions of high apparent rates of soil CO_2 efflux as measured by CO_2 concentrations at the soil surface beneath plant mats. This was only observed in plots amended with fertilizer which support the findings of Shaver *et al.* (1992) that nutrients appear to be an important limiting factor in low and in this case, high arctic ecosystem carbon balance. Added nutrients may stimulate soil microbial processes, partially accounting for the higher CO_2 concentrations at the soil surface, and may prolong and accentuate photosynthesis in autumn, resulting in net carbon acquisition by *Dryas* systems during a period when unamended plots have already senesced.

The apparent net carbon acquisition by *Dryas* dominated ecosystems under warmer, wetter and higher nutrient conditions (TWF) when irradiance was low, may be partially the result of the low light compensation point of *Dryas* and its high light saturation (Mayo *et al.* 1971). In addition, a positive photosynthetic response to the

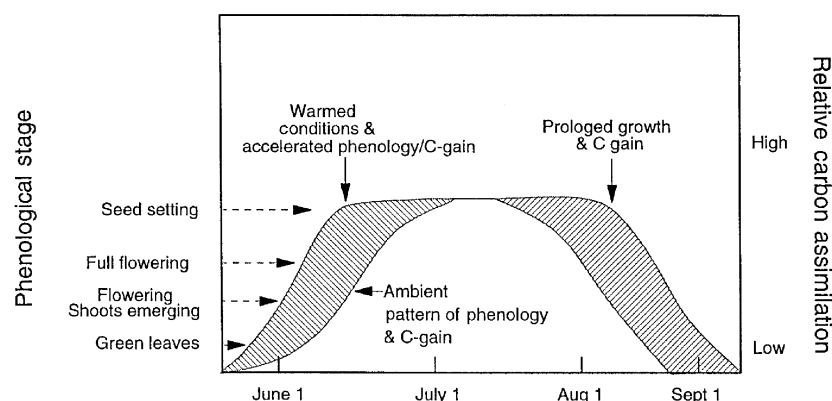


Fig. 13 A simplified conceptual diagram depicting the extent to which changes in environmental conditions may accelerate phenological development, growth and carbon gain in *Dryas octopetala* plants and ecosystems early in the growing season, and how changes in conditions may prolong phenology, growth and carbon gain late in the growing season.

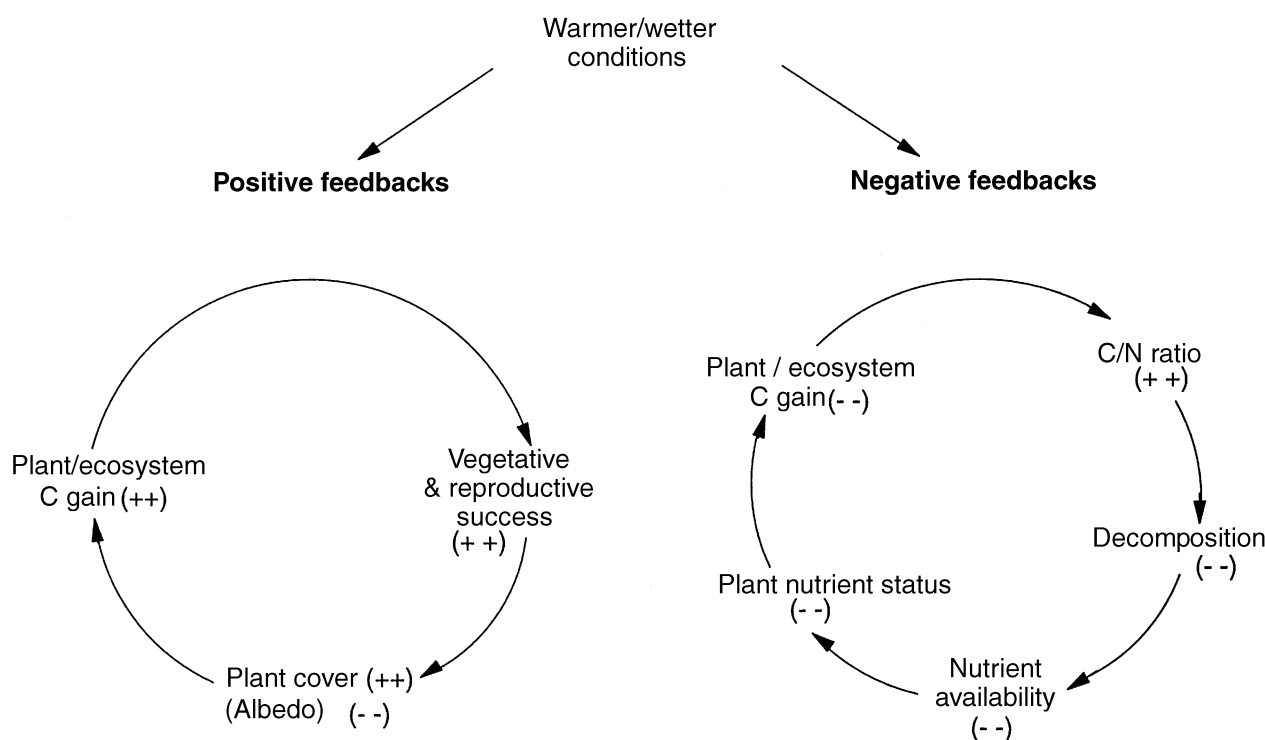


Fig. 14 A model of the extent to which the direct responses of *Dryas octopetala* plants and ecosystems to changes in environmental conditions may have both positive and negative feedback effects on the functional attributes of these habitats.

higher temperatures in the chambers as well as the alleviation of drought stress due to summer watering may have contributed to elevated carbon assimilation and net ecosystem carbon gain, even under low irradiance during a prolonged portion of the growing season (Mayo *et al.* 1971). For instance, *in situ* studies of the photosynthetic characteristics of *Dryas integrifolia* from Devon Island, Canada, indicate that under very low irradiance caused primarily by clouds and a low sun angle for a portion of the day, net carbon assimilation could occur up to a rate of $3.4 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ (Mayo *et al.* 1971).

One aim of the ITEX programme, besides developing generalizations, is also to address any site or regional differences in species traits or performance, for example, high vs. low arctic, or arctic vs. alpine populations. Based on our study we would suggest that there are some life history traits, such as flowering shoot length which are typically longer for low arctic as opposed to high arctic populations, the average for Toolik Lake and those from Latnja being 42 mm and those from Svalbard being 30 mm. The consequences of these differences may be that populations with longer pedicels will produce seeds

with the largest mass, larger seeds being the ones to exhibit higher germination rates (Table 2). Thus, one might predict that low arctic *Dryas* ecosystems may exhibit greater expansion of plant cover under changing climates, while changes in plant cover and community attributes may be slower to respond in the High Arctic.

In summary, we have observed changes in *Dryas* plant performance and in *Dryas* ecosystem processes under simulated climate changes expected in the coming decades. Because of its 'wintergreen' growth habit, this species appears to be capable of expanding its period of growth, and its period of carbon sequestration. Changes in these two processes will result in a much higher likelihood of successful seed maturation and subsequent colonization of bare ground in addition to increasing the total amount of CO₂ *Dryas* ecosystems convert to above and below ground biomass.

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