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LEAF CARBON-ISOTOPE DISCRIMINATION AND VEGETATIVE RESPONSES OF DRYAS-OCTOPETALA TO TEMPERATURE AND WATER MANIPULATIONS IN A HIGH ARCTIC POLAR SEMIDESERT, SVALBARD

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Leaf carbon isotope discrimination and vegetative responses of *Dryas octopetala* to temperature and water manipulations in a High Arctic polar semi-desert, Svalbard

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Abstract. Integrative ecophysiological and vegetative responses of *Dryas octopetala* were measured in response to field perturbations of temperature, precipitation and their interactions in a polar semi-desert in Svalbard, Norway (79°N, 12°E). Leaf carbon isotope discrimination (Δ), total leaf nitrogen concentration and leaf development were determined for photosynthetic leaves collected during the last week of August 1991, after one season of manipulations. Individual leaf weight and the total mass of leaf tissue were significantly lower when water was added, irrespective of temperature regime. Leaf carbon isotope discrimination and estimated long-term c_i/c_a values (the ratio of CO_2 concentration in leaf intercellular spaces to that in the atmosphere) were significantly higher under all three field manipulation treatments, and Δ was significantly reduced when *Dryas* was grown under drought conditions in a related greenhouse study. Nitrogen concentrations of plants from the field experiment were significantly lower under warmed conditions regardless of water regime. Our results indicate that changes in environmental conditions in high arctic settings will result in alterations of *Dryas* leaf gas exchange, as expressed by increases in carbon isotope discrimination, which may be accompanied by shifts in leaf nitrogen content and leaf biomass.

Key words: Arctic physiological ecology – Carbon isotope discrimination – Climate change – Water-use efficiency – Polar semi-desert

Air temperature and water availability to plants vary across the Arctic biome (Bliss and Malveyeva 1992).

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Plants at the northern end of the Arctic, where low temperatures and soil moisture are most extreme, have attributes which enhance survival and growth (Warren Wilson 1957; Savile 1972; Billings 1992; Chapin et al. 1992). For example, a thick boundary layer above compact, low-growing plants facilitates the development of leaf temperatures above ambient air (Körner and Larcher 1988). Mechanisms by which high arctic plants respond to changes in soil water conditions include fluctuations in stomatal conductance, depending on moisture availability, as well as increases in the concentration of solutes in plant sap when soil water content is low (Terri 1973; Svoboda 1977; Dawson and Bliss 1989).

Flexibility in the absolute rates at which plants use resources and shifts in the relative efficiency with which water, carbon and/or nutrients are used may become important determinants of plant growth and fitness as environmental conditions change in cold, dry environments (Mitchell et al. 1990; Ehleringer et al. 1992; Gates et al. 1992; McGraw and Fetcher 1992; Oberbauer and Dawson 1992). As water becomes limiting, it would be expected that water-use efficiency in plants adapted to low water availability would increase, through a suite of mechanisms including reductions in stomatal conductance and/or shifts in carbon allocation (Cohen 1970; Cowan 1982). Conversely, if water becomes more available, water-use efficiency might decrease while absolute rates of assimilation increase (Toft et al. 1989; Ehleringer et al. 1992). Consequently, species-specific flexibility of water-use may to some extent determine the interaction among semi-arid species, and the interaction between semi-arid species and those from more mesic habitats (Ehleringer et al. 1991, 1992).

Number of leaves per ramet and leaf mass in *Dryas octopetala*, a dominant species of extreme arctic environments, increase when plants from relatively dry areas were transplanted into wet areas (McGraw 1985a, b). Associated modelling studies indicated that vegetative growth and flowering intensity may be inversely related because reductions in vegetative growth appeared to be a "cost" associated with flowering (McGraw and An-

tonovics 1983). The direct effects of changes in temperature and soil moisture on leaf development, physiological performance or flowering were not assessed in situ as part of this research. We do, however, expect that the combination of higher air temperatures and changes in soil moisture conditions predicted for the Arctic may have significant impacts on the form and physiological function of arctic plants, such as leaf development, and the flux of water and CO_2 between plants and atmosphere.

Measurements of leaf function in relation to features of the Arctic environment have mainly focused on instantaneous gas exchange and mineral nutrition (Tieszen 1973; Chapin and Shaver 1985; Tissue and Oechel 1987; Berendse and Jonasson 1992). However, in general, integrative measurements of ecophysiological processes of arctic plants over time are rarely made. One such measure is the carbon isotope discrimination Δ (the ratio of ^{13}C to ^{12}C), which provides an integrative measure of water-use efficiency over time (Farquhar et al. 1982; Farquhar and Richards 1984; Farquhar et al. 1989; Welker 1992). Leaf carbon isotope discrimination is related to photosynthetic gas exchange because it is partially determined by c_i/c_a, (the ratio of CO_2 concentration in the leaf intercellular spaces to that in the atmosphere) (Farquhar and Richards 1984). This ratio, c_i/c_a, differs between plants in response to changes in soil water or changes in nitrogen availability because resource abundance may affect stomatal opening (affecting the supply rate of CO_2) and/or the chloroplast demand for CO_2. Consequently, measuring the stable carbon isotope composition of plant leaf material provides a long-term average estimate of c_i/c_a which can be used to estimate long-term water-use efficiency without an estimate of conductance (Ehleringer et al. 1992). When the isotopic measures are then combined with tissue nitrogen analysis (increasing N may suggest higher assimilation rates) one can begin to attribute the changes in Δ as being due to independent changes in conductance or assimilation, or simultaneous shifts in both the diffusional and biochemical limitations to carbon gain and water use (Farquhar et al. 1989).

In order to assess some of the likely impacts of climate change (reflected in the limitations of soil water and temperature to vegetative growth and ecophysiological processes) on a dominant high arctic plant, *D. octopetala*, we measured aspects of leaf development, integrative physiological function, and nitrogen concentration in response to experimental increases in temperature and precipitation.

Materials and methods

Field study

Study site. In June 1991 a research site was established 3 km to the west of Ny-Ålesund in northwestern Spitsbergen (78°56.12′N, 11°50.4′E, at an elevation of 22 m a.s.l.) within a polar semi-desert community of the Svalbard *D. octopetala* zone (Brattbakk 1986; Rønning 1969; Wookey et al. 1993). *D. octopetala,* an evergreen

genus which expands clonally, developing a mat-forming growth habit, is the dominant species at the site and typifies *Dryas*-dominated polar semi-desert communities throughout the high Arctic (Hultén 1968; Bliss 1977). Individual shoots (ramets) produce 2–5 new leaves each year, with leaves produced in one growing season regreening in their second year. Leaves which overwinter are the first photosynthesise in the subsequent growing season (Mayo et al. 1973; Svoboda 1977; McGraw 1985a, b).

The basic experimental design in this study uses a subset of four treatments within a 3 × 3 factorial experiment described in detail by Wookey et al. 1993. The four treatments had natural "ambient" (−T) and elevated (+T) temperatures, and ambient water availability (−W) and added water (+W). These were allocated randomly to experimental plots measuring 1.5 × 1.5 m. Six replicates of each treatment (−T −W, −T +W, +T −W, +T +W) were established. Temperature was increased using open-top polythene tents [based on the design of Havström et al. (1993), and water additions were made six times during the season to provide a total of 45 mm, which is equivalent to a 50% increase in growing season precipitation.

Polythene tents were used for simulating climate warming because they provide a vertical temperature profile more similar to the natural environment than can be obtained with heating cables on or below the soil surface. Tents of optically neutral, 0.05-mm-thick polythene sheet were supported over two lengths of 15 mm o.d. flexible PVC tubing, each stretching to diametrically opposite corners of the research plots with an apex of 70 cm. At the sides of the plots the polythene sheet was kept 5 cm above the soil surface with twine so as not to inhibit wind flow at the ground surface. A 10-cm opening at the top of the tent was cut to provide additional ventilation aimed at keeping humidities similar between open and tented conditions. The water supply for precipitation additions were obtained from a nearby small lake ("Trehyrningen Vatna") situated on a ridge (40 m a.s.l.) overlooking the site. On average, tents resulted in air temperatures being 3.5° C higher than ambient. Leaf temperatures were 1.1° C higher and soil temperature at 5 cm depth wee 0.7° C higher than plots in the open. Photosynthetic photon flux density was 6% lower under tents, and relative humidity averaged 78% in the open and 67% under tents (Wookey et al. 1993).

Leaf development. Five arbitrary sub-samples of *Dryas* mats were collected throughout each treatment plot on 28 and 29 August 1991. Each sub-sample consisted of approximately 25 ramets. Intact individual ramets with photosynthetically active tissue were then removed from all samples and five arbitrary ramets possessing intact leaf sequences were used for further analysis. Three leaf cohorts could be identified on each ramet: (1) leaves emerging and photosynthetic in 1991; (2) leaves produced/emerged in 1990 but also photosynthetic in 1991 (1990/1991); (3) leaves which senesced in 1990. Leaves from each cohort per ramet were counted, dried at 70° C for 48 h, weighed and ground into a fine powder with a mortar and pestle.

Carbon isotope discrimination measurement. The estimation of carbon isotope discrimination (Δ) was calculated from measures of the carbon isotope composition of ground plant leaf material which was combusted and analysed on a mass spectrometer (ANCA-MS) using a Europa Scientific Roboprep-Tracermass system (Welker 1992). Ratios of $^{13}C/^{12}C$ were expressed as "delta" (δ) units [parts per thousand (‰); Farquhar et al. 1989] and the carbon isotope discrimination Δ was then calculated using the formula proposed by Farquhar and Richards (1984), assuming an air $\delta^{13}C$ value of −7.9‰. However, because carbon isotope discrimination is related to photosynthetic gas exchange and Δ is in part determined by c_i/c_a, an estimate of a mean c_i/c_a was obtained using the models of Farquhar et al. (1982):

$$c_i/c_a = (\Delta - a)/(b - a)$$

where Δ is the difference between foliar $\delta^{13}C$ and $\delta^{13}C$ of atmospheric CO_2, a is the discrimination factor associated with stomatal

diffusion of CO_2 (4.4‰) and b is the estimated discrimination factor associated with carboxylation (27.0‰) (Farquhar et al. 1989).

Greenhouse study

A second analysis of the carbon isotope discrimination responses of *D. octopetala* to alterations in water supply was conducted in a greenhouse situated in Ny-Ålesund. Plant material was collected in June 1992 from ten plants which were excavated from sites within 50 m of our field perturbation experiment. Small plants were separated with intact roots, and planted in 15×10 cm containers filled with a vermiculite/compost potting mixture. All plants were watered to field capacity three times a week for four weeks to facilitate establishment, after which time plants (in containers) were randomly assigned to two treatments. Eight (well watered) plants were watered to field capacity three times a week, while a second sample of eight (water stressed) plants were exposed to two drought periods, one lasting 14 days and the second lasting 10 days, separated by a period of watering to field capacity. Soil moisture (% dry weight) was determined immediately before plant removal at the end of the second drought period. Plants were then removed from the containers, roots were cleaned off and plants were allowed to air dry for two days before refrigerating. Leaves which emerged and were photosynthetic in 1992 were removed from 10 ramets per container, air dried at 70° C for 48 h, ground and analysed for carbon isotope discrimination as described for the field plant material.

Statistical analysis

Field study. A complete factorial analysis of variance statistical model with leaf cohort, temperature and water as the independent variables was initially tested for significance ($P < 0.05$) using a general linear model for a factorial design (SAS 1985). All response variables, including leaf mass, leaf number, total mass of leaves, leaf nitrogen concentration, leaf carbon isotope discrimination, and c_i/c_a exhibited a significant ($P < 0.05$) leaf cohort effect, principally in their absolute values. However, all responses were in the same direction and thus for simplicity of presentation, cohort attributes were combined. Treatment effects (water, tents or water by tent) were tested for significance ($P < 0.05$) on pooled values using a general linear model for a full factorial design.

Greenhouse study. Student's t-test was used to test for significant ($P < 0.05$) differences in carbon isotope discrimination between *Dryas* plants which were either well watered or water stressed, and also between the soil moisture contents in plant growth containers from the two treatments (SAS 1985).

Results

Field study

Leaf demographic and developmental responses to manipulations. The total number of leaves in the two combined cohorts was unaffected by experimental manipulation (Fig. 1a). The total number of leaves in the combined cohorts ranged between four and five leaves per ramet, half of which were, on average, produced in 1990 and were photosynthetic again in 1991, and two and a half of which only emerged and were photosynthetic in 1991.

The average mass of individual *Dryas* leaves was significantly lower ($P < 0.006$, $F = 9.73$) in water-treated plots with no tent by water interaction (Fig. 1b). *Dryas* leaves which developed under ambient temperature con-
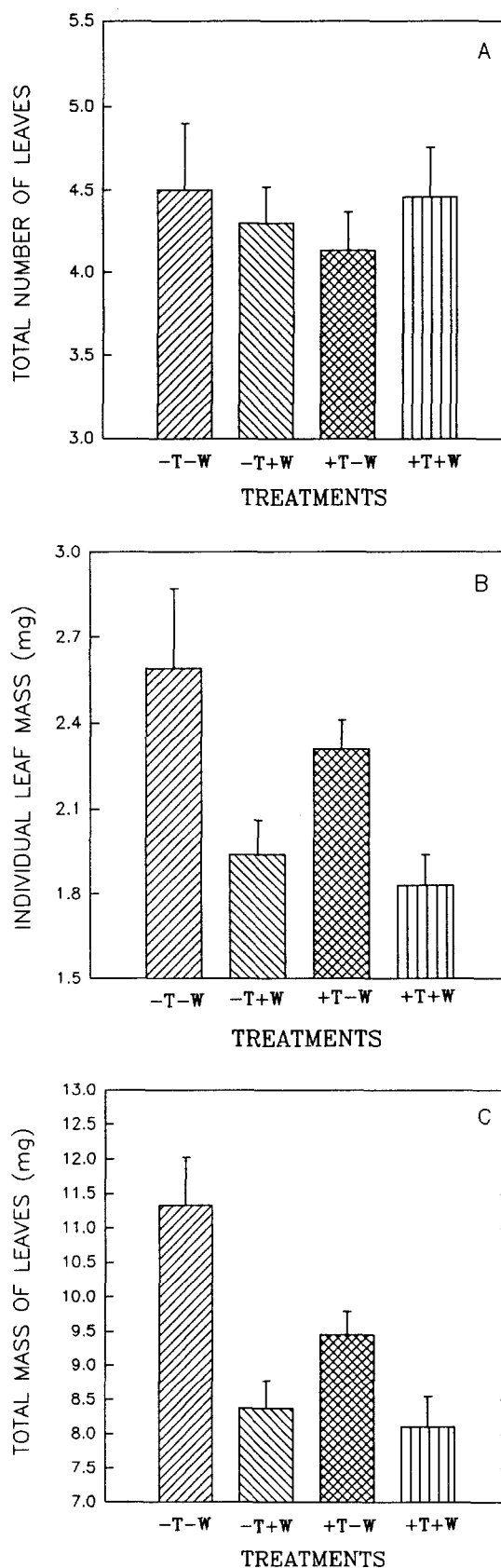
Fig. 1A–C. Numbers of *Dryas octopetala* leaves for combined cohorts (A) individual leaf mass (B) and the total mass of leaf tissue in the combined cohorts (C) in response to four treatments: control $(-T, -W)$, water only added $(-T, +W)$, tented only $(+T, -W)$, tented and watered combined $(+T, +W)$. *Bars* represent the mean and standard error
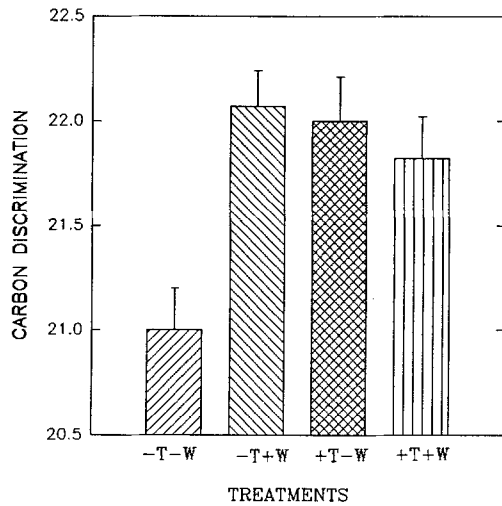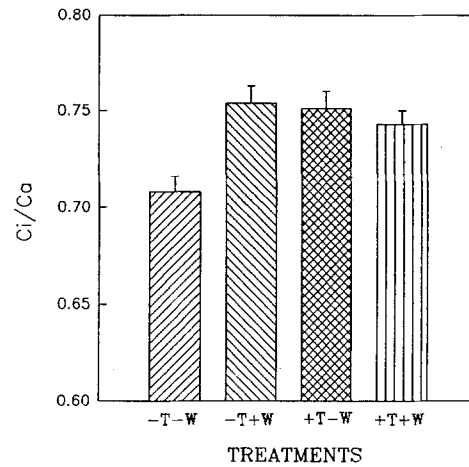
Fig. 2. *Dryas octopetala* leaf carbon isotope discrimination (‰) in the combined leaf cohorts in response to four treatments: control $(-T, -W)$, water only added $(-T, +W)$, tented only $(+T, -W)$, tented and watered combined $(+T, +W)$. Bars represent the mean and standard error

Fig. 3. The ratio of intercellular to ambient CO_2 concentrations (c_i/c_a) in combined leaf cohorts of *Dryas octopetala* in response to four treatments: control $(-T, -W)$, water only added $(-T, +W)$, tented only $(+T, -W)$, tented and watered combined $(+T, +W)$. Bars represent the mean and standard error

ditions and received supplemental water $(-T, +W)$ were 26% lighter than leaves of "control" plants $(-T, -W)$. Mean mass per leaf of *Dryas* plants under tented conditions but which also received water additions $(+T, +W)$ were 21% lighter than those from plants which were only tented $(+T, -W)$.

When the changes in mass are considered within the context of leaf numbers per ramet (leaf numbers × individual leaf weights), lower total mass of leaves $(P<0.01, F=8.32)$ was observed with water additions with no overall tent effect and no tent by water interaction (Fig. 1c). The total mass of leaves in the combined cohorts was 26% lower when water was added under ambient conditions $(-T +W)$. Lower total leaf masses per ramet were observed when tented plots were watered $(+T, +W)$, the decrease in weight was 28% below that observed for the unmanipulated plots $(-T -W)$.

Leaf carbon isotope discrimination responses to manipulation. The effect of water additions on *Dryas* leaf carbon isotope discrimination, Δ, depended on temperature treatments $(P<0.002, F=11.14)$ (Fig. 2). Leaves on plants which were watered and under ambient temperature conditions $(-T, +W)$ exhibited 1.0‰ higher discrimination in comparison to the $-T -W$ plants. This indicates greater rates of stomatal conductance and/ or lower rates of carboxylation and less conservative water use. Carbon discrimination was also higher in plants which were under tents with and without water additions $(+T -W, +T +W)$, and plants under these conditions exhibited shifts in Δ which were similar to those observed when water was added under ambient conditions $(-T +W)$.

Intercellular/ambient CO_2 concentration ratios (c_i/c_a). The effects of water additions on estimated *Dryas* c_i/c_a values depended on temperature treatments $(P<0.002, F=11.14)$ (Fig. 3). *Dryas* plants which were watered
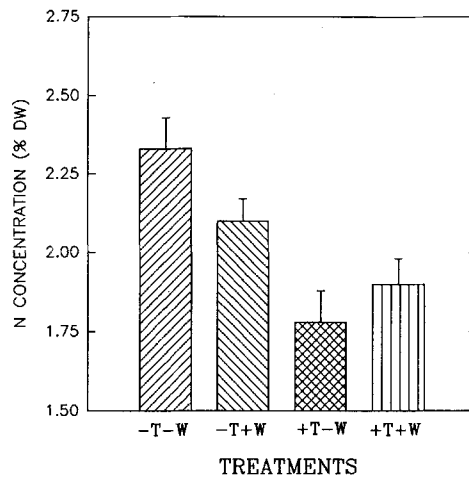
Fig. 4. *Dryas octopetala* leaf nitrogen concentration (% dry weight) in the combined leaf cohorts in response to four treatments: control $(-T, -W)$, water only added $(-T, +W)$, tented only $(+T, -W)$, tented and watered combined $(+T, +W)$. Bars represent the mean and standard error

under ambient conditions $(-T +W)$ had c_i/c_a ratios which were 7% higher than plants under unmanipulated conditions, while plants watered under tented conditions $(+T +W)$ exhibited no change in the ratio above that of the tented plots $(+T -W)$ when water was added. The ratio in plants from the $+T +W$ treatment was higher than those of the unmanipulated plants $(-T -W)$.

Leaf nitrogen concentration. The nitrogen concentration of *Dryas* leaves was significantly reduced under tented conditions $(P<0.006, F=8.54)$, with no main water effect and no tent × water interaction (Fig. 4). Plants which were under tented conditions without water additions $(+T -W)$ had nitrogen concentrations which were 24% less than those from the unmanipulated plots $(-T -W)$.

Table 1. Leaf carbon isotope discrimination (‰) of *Dryas octopetala* plants and soil moisture content (SM) (% dry weight) under well-watered and water-stressed conditions in a 1992 greenhouse experiment conducted at Ny-Alesund, Svalbard, Norway (mean and SE)

		Treatment	
		Well-watered	Water-stressed
Δ	Mean	22.24[a]	20.54[b]
	SE	0.41	0.51
% SM	Mean	35.1[a]	15.5[b]
	SE	7.6	6.6

Within rows, values superscripted by different letters differ significantly ($P < 0.05$)

The fully treated plants ($+T +W$) had slightly higher nitrogen concentrations than those which were only tented, but they were still 20% less than the unmanipulated plants.

Greenhouse study

Dryas plants from the greenhouse experiment exhibited similar morphologies to plants in the field even to the extent that flowers developed in a few of the containers. In addition, all plants developed extensive fine roots after transplanting. Leaf carbon isotope discrimination in water stressed plants was significantly ($t = 2.56$, $P = 0.022$) lower than in plants which were well watered (Table 1). Lower Δ values in *Dryas* plants under water-stressed conditions corresponded to significantly ($t = 2.29$, $P = 0.040$) lower soil moisture contents in containers which were exposed to the drought treatment.

Discussion

Lower individual leaf masses and total leaf mass per ramet in response to higher water supply were unexpected (Fig. 1). Earlier studies from Alaska suggested that leaf mass and leaf area would increase if water deficits were reduced (McGraw and Antonovics 1983), though later studies found that some perturbations (nutrient additions) did result in reductions in *Dryas* vegetative growth as did root competition (McGraw 1985a, b). We observed up to a 28% decrease in leaf mass when water was added or when water was added under warmer conditions, a response not unlike the reductions in vegetative growth reported by McGraw (1985b). Because so few studies have manipulated water conditions and/or temperature in arctic habitats where *Dryas* is a dominant species, direct comparisons of our leaf mass findings with others are limited. Moisture was only one of several environmental factors which varied between the snowbed and fellfield habitats in Alaska (McGraw and Antonovics 1983; McGraw 1985b) so it is difficult to ascertain the extent to which the present study agrees or disagrees with the findings of McGraw and Antonovics (1983) or McGraw (1985b). However, Havström et al. (1993)

found that the leaves of *Cassiope tetragona* plants increased in size under tented conditions similar to ours in a high arctic ecosystem while leaf size increased as temperature decreased along a latitudinal gradient.

The lower leaf mass we observed in response to added water ($-T +W$) may be associated with a shift in biomass allocation from vegetative growth to sexual reproduction in the first year of our study. In these same plots, the number of flowering shoots of *Dryas* increased from 140 shoots m^{-2} ($-T -W$) to 210 m^{-2} ($-T +W$) (Wookey et al. 1993), although these differences were not significant and whole-plant biomass measures are not yet available. On the other hand, *Dryas* has a complex system of branching, and lighter leaves may be associated with an increase in the number of lateral branches which have smaller leaves. Our first year findings of lower leaf masses in watered plants appear to be well founded because leaves which were active in the second growing season again had lower masses under watered conditions (unpublished data).

The increases in leaf carbon isotope discrimination observed when plants received added water, or when plants were exposed to warmer conditions, corresponded to a higher mean c_i/c_a ratio, indicating more CO_2 was in the intercellular spaces, and that leaves may have been fixing carbon at lower water-use efficiencies (A/E) (Figs. 2, 3). The higher Δ values and higher c_i/c_a ratios observed are most likely the result of: (1) higher stomatal conductance without a change in assimilation, (2) a greater relative increase in conductance compared to assimilation, (3) simply a reduction in assimilation (carboxylation demand) with no change in conductance or (4) a change in the relative proportion of leaf carbon derived from atmospheric as opposed to biogenic (soil CO_2) sources. In the case of plants which were watered ($-T +W$), higher Δ may reflect increases in conductance due to more favourable plant and soil water status, as well as higher humidities in the boundary layer due to watering. However, trends in nitrogen content (lower N in watered and warmed treatments) may have partially contributed to increases in c_i/c_a and increases in carbon discrimination due to lower carbon fixation rates. Recent simulation models indicate that small reductions in leaf nitrogen concentrations can result in decreases in carbon assimilation rates (higher c_i/c_a) of plants across a range of irradiance levels (Hilbert et al. 1991).

We have found, though, that other species in these same plots exhibited no change in photosynthetic rates per unit leaf area when plants were watered, warmed, or experienced the combined treatments (Wookey et al. submitted). Also, the increases in carbon discrimination observed under the three manipulated conditions are most likely not the result of changes in the relative proportion of carbon sources (atmospheric vs biogenic) assimilated by *Dryas* leaves. We conclude this because the concentration of CO_2 at the soil surface beneath plant mats, in the leaf canopies, and at 10 cm above plants was not different between the three treatment plots presented here and the unmanipulated plots (Welker et al., in preparation). These CO_2 measures were, however, taken in the second field season of our project. Havström

et al. (1993) also report that CO_2 concentrations above arctic vegetation which was warmed using the same design as ours ("tents") exhibited no significant differences compared with unmanipulated plots.

Water regulation of Δ was also observed when *Dryas* plants were subjected to water deficits in the greenhouse (Table 1): decreases in Δ are indicative of reductions in stomatal conductance. The Δ values for the well-watered plants (22.24‰) were similar to those in plants in the field grown under our $-T$ $+W$ treatment (Fig. 2) and the plants which were water stressed had values slightly smaller than plants under our unmanipulated treatment plots ($-T$ $-W$). Increases in Δ under wetter situations, and lower Δ values under drier conditions, have also been observed in plants from other xeric habitats where Δ values ranged between -23 and -17‰ (Ehleringer and Cooper 1988; Toft et al. 1989; Ehleringer et al. 1992). In these cases, not only does Δ increase under in situ application of water as we have observed (Toft et al. 1989), but Δ exhibits both temporal and spatial variation corresponding to higher and lower soil moisture conditions between microsites or over the course of a growing season. Smedley et al. (1991), for example, found that on a community-wide basis, discrimination was highest in May (-20.0‰) and increased to -18.5‰ by September which corresponded to progressive increases in soil drought.

Dryas exhibited significant fluctuations in integrative measures of leaf gas exchange as depicted by more efficient use of water during water scarcity. However, this was possibly at the cost of assimilating carbon at higher absolute rates, while sacrificing water-use efficiency when water was abundant. This ability to use water efficiently when required indicates that under a spectrum of conditions, water use by *Dryas* can be tailored not only for short-term conditions (diurnal variation in temperature, soil water potentials, light, and humidity) but for conditions which persist within and between growing seasons. Because the Arctic growing season is so short, and water is only in an available form during summer, drought avoidance by early season senescence is not ecologically feasible, unlike other cold, dry climates (Ehleringer et al. 1992). Consequently, arctic species which can effectively tolerate drought by curtailing water loss during scarcity and by using water efficiently will have a competitive advantage when the resource is scarce. However, if they sacrifice efficiency for bulk resource acquisition under abundance or temperature amelioration ["luxury consumption" in the case of nutrients (Chapin 1980)], they may be outcompeted by those species which are capable of using a plentiful resource efficiently, for example, as new climate equilibria are established. We hypothesize that the ability of *Dryas octopetala* to increase relative physiological performance partially contributes to its dominance in the polar-semi deserts of Svalbard and even to its broad circumpolar distribution.

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