

Responses of carbon and nitrogen concentrations in high arctic plants to experimental warming

Anne Tolvanen and Gregory H.R. Henry

Abstract: We studied total carbon (C) and nitrogen (N) concentration in five arctic plant species, *Cassiope tetragona* (L.) D. Don (evergreen dwarf shrub), *Dryas integrifolia* Vahl (semi-evergreen dwarf-shrub), *Salix arctica* Pall. (deciduous, dioecious dwarf shrub), *Oxyria digyna* (L.) Hill (forb), and *Carex stans* Drej. (graminoid, sedge), after five growing seasons of experimental increase in temperature. The experiments were established in different habitats along a moisture gradient in a coastal lowland at Alexandra Fiord, Ellesmere Island (79°N). Sampling was conducted three times during the growing season. The seasonal patterns of C and N concentration were similar across all investigated species, even though the absolute concentrations differed. Nitrogen concentrations were high early in the season during the active growth period but declined later in the season. Warming decreased the N concentration and increased the C/N ratio in the three woody species, whereas N concentrations in the forb and the sedge were not affected. Although not measured directly in our study, the differences in concentrations may be due to the slower response in nutrient uptake and growth in the dwarf shrubs but increased nutrient uptake and growth in the forb and the sedge. Among-site differences were only significant in C concentrations of old tissues of *Cassiope tetragona* and *S. arctica*. Male and female *S. arctica* did not differ in their responses to warming. Differences among plant species in their plastic responses may relate to survival during rapid environmental change. Slow-responding dwarf shrubs may be under increased risk of competition from more responsive and faster growing species, such as forbs and graminoids.

Key words: allocation, climate change, dwarf shrub, forb, graminoid, ITEX, Ellesmere Island.

Résumé : Les auteurs ont étudié la teneur en carbone et en azote chez cinq plantes arctiques, *Cassiope tetragona* (L.) D. Don (arbuste nain sempervirent), *Dryas integrifolia* Vahl (arbuste nain semi-sempervirent), *Salix arctica* Pall. (arbuste nain dioïque décadu), *Oxyria digyna* (L.) Hill (herbe non-graminoïde) et *Carex stans* Drej. (carex graminioïde), après cinq saisons de croissance sous des températures expérimentalement accrues. Ces expériences ont été effectuées dans différents habitats le long d'un gradient d'humidité dans les basses terres littorales du fjord Alexandra, sur l'île d'Ellesmere (79°N). Des échantillonnages ont été effectués à trois reprises au cours de la saison de croissance. Les patrons saisonniers de la teneur en carbone et en azote sont demeurés semblables chez toutes les espèces étudiées, bien que les teneurs absolues diffèrent. Les teneurs en azote sont plus élevées au début de la saison au cours de la période de croissance active, mais diminuent plus tard en saison. Le réchauffement diminue la teneur en azote et augmente le rapport C:N chez les trois espèces ligneuses, alors que les teneurs en azote ne sont pas affectées chez le carex et l'herbe non-graminoïde. Bien que les auteurs ne les aient pas mesurées directement dans leur étude, les différences des teneurs pourraient être dues à la réaction moins rapide de l'absorption des nutriments et de la croissance chez les arbustes nains, et à un accroissement de l'absorption des nutriments et de la croissance chez le carex et l'herbacée non-graminoïde. Les différences entre les sites ne sont significatives que pour les teneurs en carbone des tissus âgés chez les *Cassiope tetragona* et *S. arctica*. Les réactions au réchauffement des plants mâles et femelles du *S. arctica* ne diffèrent pas. Les différences de réaction plastique entre les espèces végétales peuvent avoir des conséquences sur la survie au cours de changements environnementaux rapides. En compétition, les arbustes nains à réaction lente pourraient être plus à risque que les espèces à croissance rapide réagissant plus fortement, telles que les carex et les herbes non-graminoïdes.

Mots clés : allocation, changement climatique, arbuste nain, plante graminioïde, herbacée non-graminoïde, île d'Ellesmere.

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A. Tolvanen¹ and G.H.R. Henry. Department of Geography, University of British Columbia, Vancouver, BC V6T 1Z2, Canada.

¹Corresponding author. Present address: Department of Biology/Botany, University of Oulu, P.O. Box 3000, FIN-90014 Oulun yliopisto, Finland. (e-mail: Anne.Tolvanen@oulu.fi).

Introduction

The limits to biotic function of the arctic environment are temperature, nutrient availability, and extremes in soil water content (e.g., Callaghan and Emanuelsson 1985), and changes in these factors may have a considerable impact on survival of organisms. Climate-change scenarios based on general circulation models predict an increase of 1.9–5.2°C in the mean global temperature, whereas winter temperature increases of 12°C are predicted in arctic regions by 2050 (Mitchell et al. 1990; Maxwell 1992; Houghton et al. 1996). Thus, climate warming impacts may become evident in arctic ecosystems sooner than elsewhere. Plant physiological and growth responses to environmental change depend on genetic variation and phenotypic plasticity of the existing genotypes. Since climate change is predicted to occur faster than the potential for adaptation, biotic response will greatly depend on phenotypic plasticity of plants to these changes.

Over the past two decades, warming experiments in arctic terrestrial ecosystems have shown that variation in plant growth is related to the plant species (Arft et al. 1999; Chapin and Shaver 1985; Baddeley et al. 1994; Parsons et al. 1994), functional groups (Arft et al. 1999; Bowman et al. 1995; Molau 1997; Henry and Molau 1997; Molau and Alatalo 1998; Press et al. 1998), habitat characteristics (Bowman et al. 1995) including the region within the geographical range of the plants (Arft et al. 1999; Havström et al. 1993; Wookey et al. 1993; Jones et al. 1997; Stenström et al. 1997; Welker et al. 1997), and sex in dioecious plants (Jones et al. 1997, 1999). However, carbon (C) and nitrogen (N) concentrations have not generally been measured in these perturbation studies, except for *Eriophorum vaginatum* L. in arctic Alaska (Chapin et al. 1986) and for *Dryas octopetala* L. in Svalbard (Welker et al. 1997). Because of increased photosynthesis and respiration rates, changes in C and N concentrations of plant tissues are a potential response to increased temperature. The changes in concentrations may have long-term feedbacks for nutrient availability of the habitat and for plant–herbivore interactions, since the C/N ratio correlates positively with the tissue decomposition rates and with the value of plant tissue to herbivores (Bryant and Reichardt 1992). Since the range of responses within a species may vary depending on habitat or sex (in dioecious plants), it is also important to compare intraspecific responses to get realistic estimates of a species' response to climate change (Jones et al. 1999).

The present study aims to supplement information on the responses of arctic plant species to a warmed environment. We investigated whether total C and N concentrations have changed in five plant species in response to five growing seasons of increased temperature in the high Arctic. The questions we asked were (i) do seasonal carbon and nitrogen concentrations vary among plant species under ambient and warmed conditions; (ii) does habitat influence the response of species to warming; and (iii) is there a difference in the response to increased temperature between sexes in a dioecious plant? The research is part of the International Tundra Experiment (ITEX), which compares responses of circumpolar plants to global climate change across arctic and alpine habitats (Arft et al. 1999; Henry and Molau

1997). The five species investigated are included among the primary ITEX species (Murray 1997). The species measured in this study were *Cassiope tetragona* (L.) D. Don (evergreen dwarf shrub), *Dryas integrifolia* Vahl (semi-evergreen cushion plant), *Salix arctica* Pall. (deciduous, dioecious dwarf shrub), *Oxyria digyna* (L.) Hill (perennial forb), and *Carex aquatilis* ssp. *stans* Drej. (i.e., *Carex stans*, sedge), which are dominant species of their life form. We expected considerable differences in concentrations between the species because of their different rates of photosynthesis (Johnson and Tieszen 1976), growth, and nutrient absorption (Kielland and Chapin 1992).

Material and methods

The experiment was carried out at a coastal lowland adjacent to Alexandra Fiord (78°53'N, 75°55'W), on the eastern coast of central Ellesmere Island, Canada, between 1992 and 1996. The site is a well-vegetated polar oasis, with warmer, longer growing seasons and more soil moisture than the surrounding polar semidesert landscapes (Svoboda and Freedman 1994). The warming experiments were established in four sites of differing vegetation types arrayed along a moisture gradient (Table 1): a mesic dwarf shrub-cushion plant community dominated by *Cassiope tetragona* (Cassiope site), a similar community dominated by *D. integrifolia* (Dryas site), a dry, deciduous dwarf shrub – graminoid community dominated by *S. arctica*, *Luzula confusa* Lindeb., and *O. digyna* (Salix site), and a wet meadow community dominated by sedges, e.g. *Carex stans* (wet meadow site). The vegetation classification follows Muc et al. (1989). The soils are poorly developed Static Cryosols in all sites (Muc et al. 1989). Carbon content of the soils vary as expected from 30–50% in the organic surface horizons of the wet meadow to 1–4% in the surface mineral horizons of the Salix and Dryas sites (Marion et al. 1997; data not shown). However, C/N ratios in the surface horizons are not significantly different among sites (J.M. Welker and G.H.R. Henry, unpublished data).

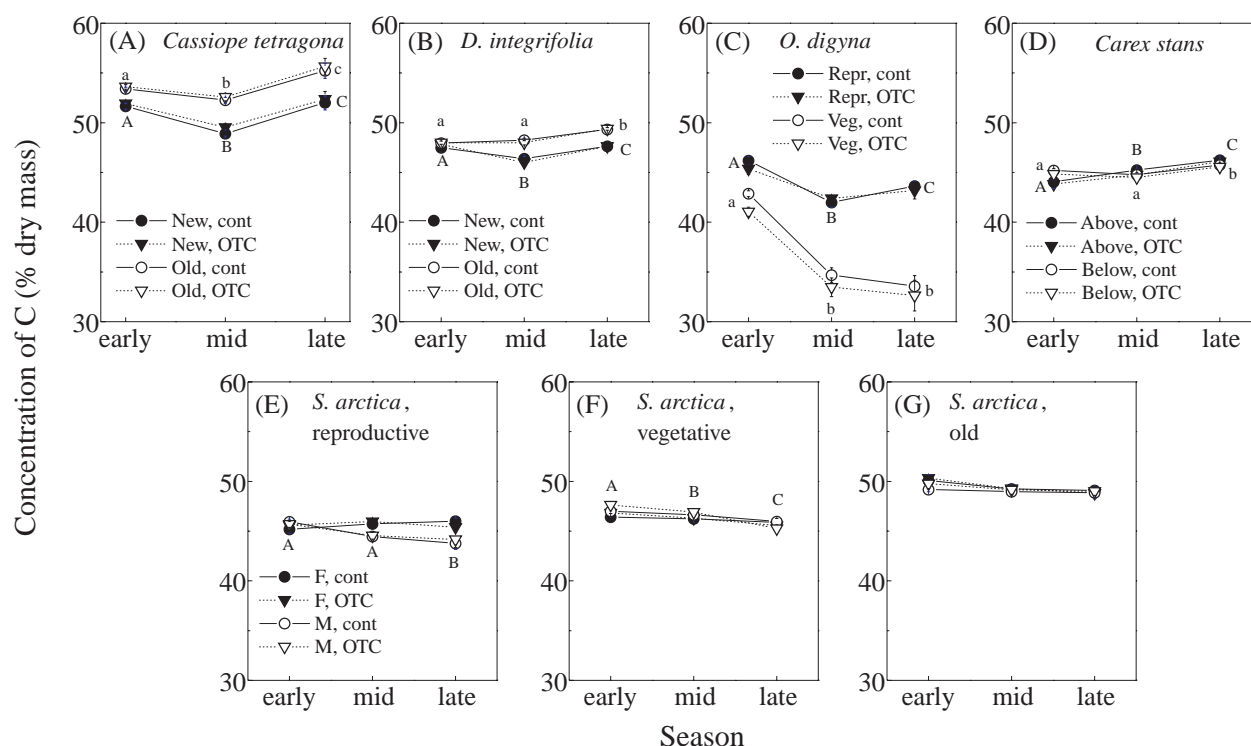
At each site, two treatment levels were applied in 1992: control and increased temperature. Air and soil temperatures were increased passively by open-top chambers (OTCs) made of transparent SunLite™ HP fibreglass (Solar Components Corp., Manchester, N.H.). The hexagonal OTCs have inclined sides, 0.5 m high, which enclose a surface of 1.8 m², although the experimental plots in each OTC and control was 1 m². Equal numbers of OTCs and control plots were established in each community type ($n = 10$ –18 per site). A large part of the temperature enhancement of the OTCs is related to increasing daily maximums, which are on average 3.5°C higher than the control. The mean near-surface air temperature was increased on average by 1.2°C relative to ambient temperature, and the change in the mean soil temperature (–3 cm) ranged from –0.2°C to 1.3°C in 1993 (Marion et al. 1997). All passive temperature-enhancing systems also slightly alter light conditions and wind patterns around plants (Marion et al. 1997), which are unwanted effects of the treatment.

Five plant species representing five different life forms were collected from the experimental and control plots in 1996 (Table 1). Sampling of the dioecious *S. arctica* was done separately for each sex at the same time periods. Three or four shoots of each species were harvested in five plots per treatment (for each sex in *S. arctica*). Sampling was carried out at three phenological stages of the plants: (i) at the beginning of vegetative growth (early season, June 21–22); (ii) during the flowering peak (midseason, July 13–15); and (iii) during seed dispersal (late season, Aug. 2). The dwarf shrub species were sampled from two experimental sites (Table 1). After harvest, samples were dried at 40°C for 48 h and stored at room temperature. The plants were separated into parts

Table 1. Plant species, life forms, sampling sites (see explanation in the text), and plant parts analysed for carbon and nitrogen.

Species	Life form	Sampling sites	Separate plant parts
<i>Cassiope tetragona</i>	Dwarf shrub, evergreen	Cassiope Dryas	Current (shoot, leaves, flowers produced in current year), old (shoot, leaves produced in previous years)
<i>D. integrifolia</i>	Dwarf shrub, semi-evergreen	Cassiope Dryas	Current (shoot, leaves, flowers), old (shoot, leaves)
<i>S. arctica</i>	Dwarf shrub, deciduous	Dryas Salix	Reproductive (current catkin: shoot, leaves, flowers), vegetative (current shoot, leaves), old (shoot), for each sex
<i>O. digyna</i>	Forb	Salix	Reproductive (inflorescence), vegetative (leaves)
<i>Carex stans</i>	Graminoid sedge	Wet meadow	Aboveground (leaves), belowground (rhizome)

Fig. 1. Concentration of carbon in plant tissues of different species. Cont, control; OTC, increased temperature, F, female; M, male (in *Salix arctica*); early, early season (June 21–22); mid, midseason (July 13–15); late, late season (Aug. 2). Different uppercase letters indicate significant difference in new, reproductive, and aboveground tissues between harvest times ($p < 0.05$, repeated measures ANOVA), whereas the different lowercase letters indicate differences in old, vegetative, and belowground tissues between harvest times ($p < 0.05$, repeated measures ANOVA). For simplicity, results for the different sites are pooled and presented together for *Cassiope tetragona*, *Dryas integrifolia*, and *S. arctica* ($n = 10$, otherwise $n = 5$). ANOVA results, in which also site was used as a factor, are shown in Table 2.



before analyses (Table 1). The current vegetative shoots of *Cassiope tetragona* could be distinguished by the short internode length, i.e., leaves located densely at the border between the current and previous year's growth (Johnstone and Henry 1997). New shoots of *D. integrifolia* could be identified with the smaller leaf size at the border of old and new growth and the lighter colour of new leaves. In *S. arctica*, current shoots could be easily distinguished, as they are the only shoots to have leaves. Both vegetative shoots and reproductive catkins carry leaves. *Oxyria digyna* has only new leaves, or a new flower stalk, and old parts which are belowground were not excavated. *Carex stans* was separated into green aboveground leaves and belowground rhizomes, which were excavated with a tiller.

Samples were ground using the Fritish Pulverisette® mill at the Department of Forest Resources Management, University of

British Columbia (UBC), Vancouver. Samples were further dried at 50°C for 36 h and weighed before analysis. Carbon and N concentrations were determined with a Carlo Erba NA-1500 Analyzer at the Department of Oceanography, UBC. Concentrations were calculated as a percentage of dry weight of the analyzed material.

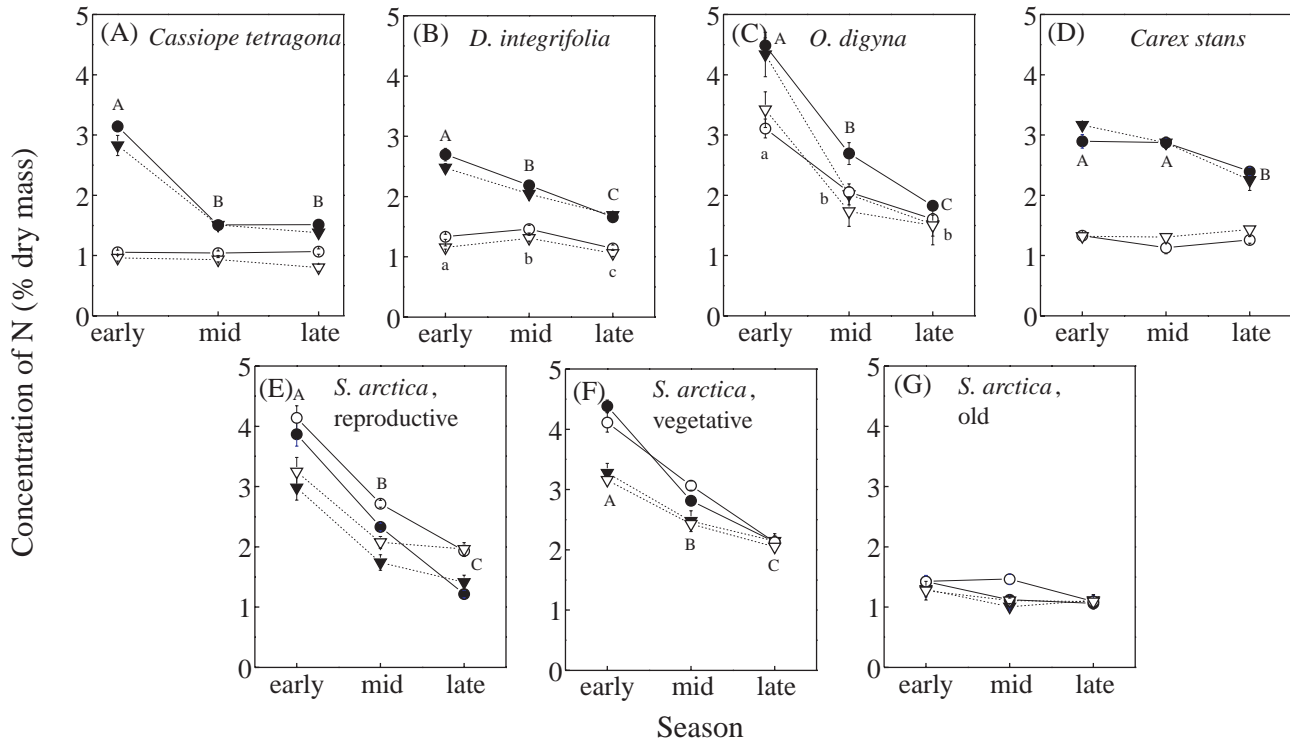
Analysis of variance with repeated measures (ANOVA) was used to compare the C and N concentrations between sites for dwarf shrubs that were sampled at more than one site (Table 1), or for treatments and sexes (*S. arctica*) over time (Zar 1984). Testing was done separately for each species and plant part. The data did not directly satisfy the Huynh–Feldt condition required for univariate testing in the repeated measures ANOVA, so the Huynh–Feldt-adjusted F values were used (Potvin et al. 1990; SAS Institute Inc. 1990). Multiple comparisons were made using the PROFILE transformation, which compares the successive differences in time, in

Table 2. ANOVA table by species and plant tissue for concentrations of carbon, nitrogen, and the C/N ratio.

Species	Plant tissue	Factor ^a	df	Carbon (%)		Nitrogen (%)		C/N ratio	
				<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
<i>Cassiope tetragona</i>	New	Site	1	4.09	ns ^b	1.15	ns	0.02	ns
		Time	2	28.02	0.0001	173.37	0.0001	158.55	0.0001
		Treatment	1	0.95	ns	16.68	0.0001	31.06	0.0001
	Old	Site	1	6.11	0.0294	1.78	ns	0.22	ns
		Time	2	25.97	0.0001	1.36	ns	4.77	0.0184
		Treatment	1	0.62	ns	19.58	0.0008	14.95	0.0022
		Site × time	2	5.47	0.0129	—	—	—	—
<i>D. integrifolia</i>	New	Site	1	2.35	ns	3.28	ns	0.62	ns
		Time	2	80.49	0.0001	265.47	0.0001	274.29	0.0001
		Treatment	1	6.25	0.0280	6.25	0.0279	4.38	ns
		Time × treatment	2	8.87	0.0013	5.37	0.0118	—	—
	Old	Site	1	0.03	ns	1.08	ns	0.74	ns
		Time	2	63.31	0.0001	25.39	0.0001	33.33	0.0001
		Treatment	1	0.12	ns	6.70	0.0237	6.38	0.0267
<i>S. arctica</i>	Reproductive	Site	1	2.67	ns	0.16	ns	1.05	ns
		Time	2	4.22	0.0244	164.75	0.0001	110.71	0.0001
		Treatment	1	0.08	ns	30.26	0.0001	10.82	0.0031
		Sex	1	28.72	0.0001	24.74	0.0001	59.82	0.0001
		Time × treatment	2	—	—	11.30	0.0001	8.79	0.0006
		Time × sex	2	9.10	0.0007	—	—	17.01	0.0001
	Vegetative	Site	1	0.67	ns	0.35	ns	0.18	ns
		Time	2	21.81	0.0001	176.99	0.0001	63.63	0.0001
		Treatment	1	0.09	ns	22.27	0.0001	8.82	0.0001
		Sex	1	3.58	ns	0.19	ns	0.51	ns
		Time × treatment	2	3.49	0.0386	16.64	0.0001	4.21	0.0207
		Site	1	9.62	0.0049	1.02	ns	3.02	ns
	Old	Time	2	3.51	0.0421	10.20	0.0008	14.57	0.0001
		Treatment	1	0.56	ns	0.31	ns	7.29	0.0125
		Sex	1	2.22	ns	6.96	0.0144	9.98	0.0042
		Site × time × sex	2	3.90	0.0308	—	—	—	—
	Reproductive	Time	2	23.56	0.0001	102.04	0.0001	23.48	0.0006
		Treatment	1	0.49	ns	2.48	ns	2.89	ns
	Vegetative	Time	2	83.98	0.0001	58.69	0.0001	19.50	0.0002
		Treatment	1	1.76	ns	0.04	ns	0.78	ns
<i>Carex stans</i>	Aboveground	Time	2	46.74	0.0001	24.5	0.0001	26.20	0.0001
		Treatment	1	0.70	ns	0.29	ns	0.00	ns
	Belowground	Time	2	7.97	0.0174	1.96	ns	1.06	ns
		Treatment	1	1.07	ns	1.39	ns	1.74	ns
						6			

Note: Sites from where the species were collected are presented in Table 1.^aTreatment, control versus increased temperature; time, early, middle and late season. (*n* = 5). Values for interactions are given only if they are significant.^bns, not significant (*p* > 0.05).

Fig. 2. Concentration of nitrogen in plant tissues of different species. Cont, control; OTC, increased temperature; F, female; M, male (in *Salix arctica*); early, early season (June 21–22); mid, midseason (July 13–15); late, late season (Aug. 2). Different uppercase letters indicate significant difference in new, reproductive, and aboveground tissues between harvest times ($p < 0.05$, repeated measures ANOVA), whereas the different lowercase letters indicate differences in old, vegetative, and belowground tissues between harvest times ($p < 0.05$, repeated measures ANOVA). For simplicity, results for the different sites are pooled and presented together for *Cassiope tetragona*, *Dryas integrifolia*, and *S. arctica* ($n = 10$, otherwise $n = 5$). ANOVA results, in which also site was used as a factor, are shown in Table 2.



this case early season versus midseason and midseason versus late season (general linear methods procedure, SAS Institute Inc. 1990).

Results

All species had similar temporal patterns of C and N concentrations, despite differences in the absolute concentrations. Carbon concentration decreased significantly between early and midseason harvest times in all tissues of *Cassiope tetragona* and *O. digyna*, new tissues of *D. integrifolia*, and vegetative tissues of *S. arctica* (Fig. 1). Only in old parts (stems) of *S. arctica* did the C concentration remain unchanged throughout the growing season (Fig. 1G; Table 2). Nitrogen concentrations in tissues of most species decreased during the growing season (Fig. 2). The N concentration was relatively constant over time in old tissues of *Cassiope tetragona*, *S. arctica*, and *Carex stans*. The C/N ratio increased during the growing season for all species (Fig. 3). Except for belowground parts of *Carex stans* and old parts of female *S. arctica* (Figs. 3D and 3G), the C/N ratio was at its maximum late in the growing season, during seed maturation.

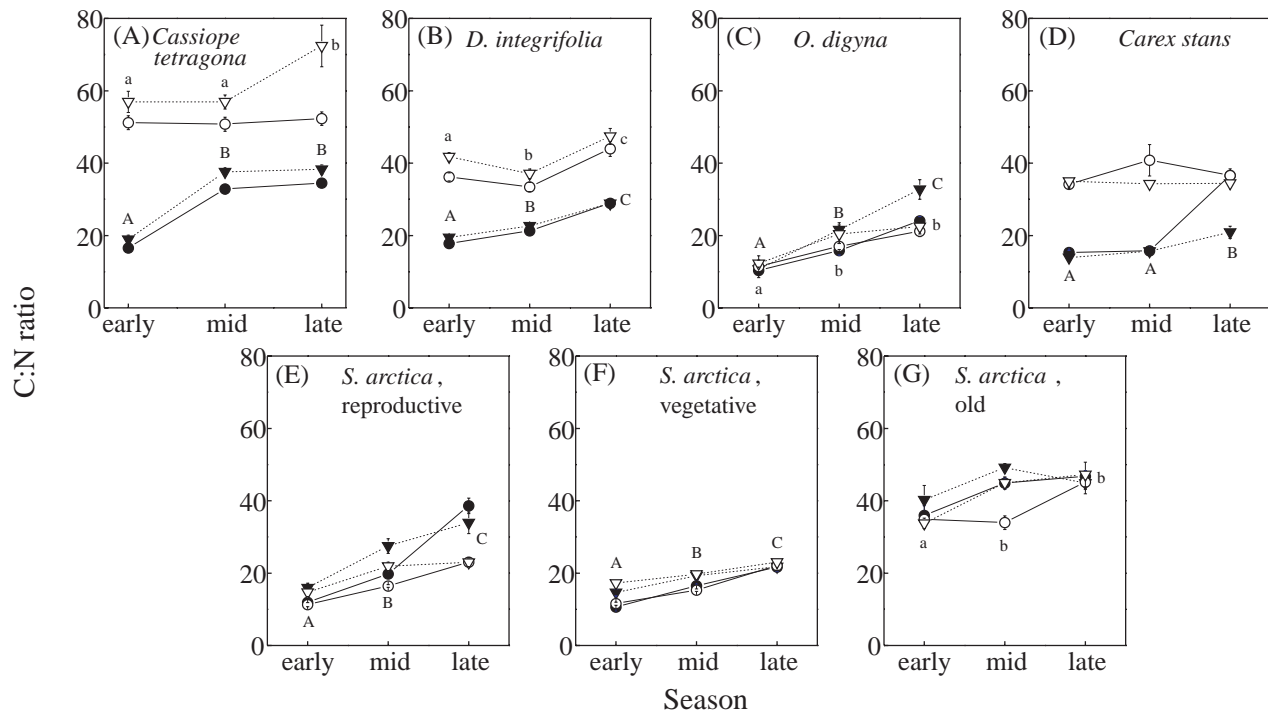
The warming treatment (OTC) increased the carbon concentration in the new parts of *D. integrifolia* but had no effect on other species (Fig. 1; Table 2). The N concentrations decreased in all tissues of *Cassiope tetragona* and *D. integrifolia*, and in reproductive and vegetative parts of *S. arctica*, but concentrations in *O. digyna* and *Carex stans* were not affected by the warming treatment (Fig. 2; Ta-

ble 2). The C/N ratios increased in all tissues of the dwarf shrubs (*Cassiope tetragona*, *D. integrifolia*, and *S. arctica*) in the warming treatment, whereas the herbaceous species (*O. digyna* and *Carex stans*) were not affected. There was a significant interaction between treatment and harvest time in the nitrogen level and the C/N ratio of reproductive and vegetative *S. arctica* shoots. The concentration of N decreased more slowly in the OTCs than in the control plots (Figs. 2E and 2F) leading to a more gradual increase in the C/N ratio in the OTCs than in the control plots (Figs. 3E and 3F).

Among-site differences were only significant in C concentrations of old tissues of *Cassiope tetragona* and *S. arctica* (Table 2). In these tissues there was also a significant site \times time or site \times time \times sex interaction, respectively. On average, the C concentrations were slightly higher at the Dryas site than at the Cassiope site in *Cassiope tetragona* (54.3 ± 0.2 vs. $53.3 \pm 0.3\%$ per dry mass, respectively; mean \pm SE). In *S. arctica*, C concentrations were slightly greater at the Dryas site than at the Salix site (49.7 ± 0.3 vs. $48.9 \pm 0.2\%$ per dry mass, respectively). Since the largest differences in C concentrations between sites were only 1.5% units at respective harvest times and sexes, the sites were combined in figures for clearer presentation of data.

Concentrations of C and N differed between the sexes in the reproductive (catkins) and old parts of *S. arctica* but not in the current vegetative parts. The concentration of C and the C/N ratio were higher in females than in males, whereas the situation for N was the reverse. There was a significant

Fig. 3. Carbon/nitrogen (C/N) ratio in plant tissues of different species. Cont, control; OTC, increased temperature; F, female; M, male (in *Salix arctica*); early, early season (June 21–22); mid, midseason (July 13–15); late, late season (Aug. 2). Different uppercase letters indicate significant difference in new, reproductive, and aboveground tissues between harvest times ($p < 0.05$, repeated measures ANOVA), whereas the different lowercase letters indicate differences in old, vegetative, and belowground tissues between harvest times ($p < 0.05$, repeated measures ANOVA). For simplicity, results for the different sites are pooled and presented together for *Cassiope tetragona*, *Dryas integrifolia*, and *S. arctica* ($n = 10$, otherwise $n = 5$). ANOVA results, in which also site was used as a factor, are shown in Table 2.



interaction between harvest time and sex in the reproductive parts of *S. arctica*: the C concentration remained unchanged in females, but it decreased during the growing season in males (Fig. 1E). Moreover, the C/N ratio increased faster in females than males (Fig. 3E). There was no difference between the sexes in response to the warming treatment (interaction between the treatments and sex was not significant, $p > 0.05$).

Discussion

Our study adds additional information on the response patterns of arctic plants under increasing temperature. Earlier studies have shown that aboveground growth and reproduction increased with increasing temperature in almost every species studied in the tundra, including the species studied here but less in dwarf shrubs than in forbs and sedges (Arft et al. 1999; Henry and Molau 1997). Our results show that differences in growth responses also reflect differences in C and N concentrations of plant tissues.

The seasonal patterns of C and N tissue concentrations were similar across all species, even though the absolute concentrations differed. Nitrogen concentrations were high early in the season during the active growth period, but declined later in the season, a pattern common to most plants in temperate and high latitudes. There is an increase in structural material in plants that causes N concentrations to decline late in the season, although the total aboveground standing crop of N can be increasing (Chapin 1980). Carbon

concentrations did not show large seasonal changes. Changes in sugars can be balanced by changes in polysaccharides (Chapin and Shaver 1988), and much of the C is inert in plant structures.

The warming treatment decreased the N concentration and increased the C/N ratio in the three dwarf shrubs (*Cassiope tetragona*, *D. integrifolia*, and *S. arctica*) but had no effect on concentrations in the forb (*O. digyna*) and the sedge (*Carex stans*). Although not measured in our study, differences in the inherent growth rate and the rate of nutrient uptake between species may account for the observed differences in concentrations. Air and soil temperatures limit the rate at which resources become available to and can be acquired by plants (Chapin 1983), and hence, relatively small temperature increases become important with regard to plant metabolic processes. When temperature increases, photosynthetic and respiration rates also increase. Increased photosynthesis can lead to higher growth rates provided that nutrient uptake is also enhanced (e.g., Berendse and Jonasson 1992). If not, photosynthates are stored in tissues rather than allocated to new tissue construction (Bryant et al. 1983). Therefore, elevated temperature may increase the C/N ratio, if growth does not increase. It is possible that *O. digyna* and *Carex stans* were able to adjust to warmed conditions by taking up more nutrients to meet the needs of an increased growth rate, resulting in an uniform C/N ratio. Allocation to roots may have also increased, as faster growth leads to greater soil N demand. Dwarf shrubs have slower inherent growth rates with smaller demand for nutrients (Chapin 1980), and they rely on

stored reserves to a greater extent than fast-growing species (Kielland and Chapin 1992). Hence, the inherently low growth rate and low demand for nutrients may limit the response of high arctic dwarf shrubs to increased temperature.

A shift in the C/N ratio may have implications for decomposition rates and plant–herbivore interactions (Bryant and Reichardt 1992). In our study, this would mean reduced rate of decomposition and reduced value of dwarf shrub tissues for herbivores under increased temperature. However, the change in the C/N ratio was very small, as we only manipulated temperature in the present study. Warming is suggested to slowly increase decomposition and mineralization rates, which may decrease nutrient constraints for growth, and, consequently, the C/N ratio of plant tissues (Bryant and Reichardt 1992). Five growing seasons of passive temperature manipulation may not have been long enough to influence decomposition rates in our study. Mineralization rates were increased after 9 years of experimental warming in tussock tundra in arctic Alaska (Chapin et al. 1995); however, decomposition was not measured.

Habitat did not have a strong influence on C or N concentrations in the dwarf shrubs of our study. This may be due to similarity in soil moisture and nutrient content between the sites where the dwarf shrubs dominate (Muc et al. 1989).

The decrease in nitrogen concentrations was similar between the sexes of *S. arctica* in response to warming. Although there are intersexual differences in the physiology of *S. arctica* under the same experimental regime (Jones et al. 1999), temperature does not significantly influence the sex ratio (Dawson and Bliss 1989a, 1989b). Hence, climate warming may not have a strong influence on the performance of different sexes in *S. arctica*. The C/N ratio of the reproductive parts was generally higher in females than males. This is apparently due to higher net assimilation rates in females, measured after 2 years of experimental warming (Jones et al. 1999; but see Dawson and Bliss 1993). The N concentration was always lower in the reproductive parts of the females than males. Males appear to lose N in the short-lived catkins, whereas females allocate only the required amount of C and N to reproductive components and are able to allocate more to plant growth. The results do support the hypothesis that sex-specific life-history traits have evolved to meet significantly different costs of reproduction and survival for males and females (Dawson and Bliss 1989a, 1989b; Dawson and Ehleringer 1993; Gehring and Monson 1994; Delph and Meagher 1995). Dioecy may increase the ability of the species to occupy a wider ecological range of habitats than could otherwise be possible (Dawson and Bliss 1989b), and it may be one reason why *S. arctica* is so common in arctic and alpine areas.

Conclusions

Plant survival in the arctic requires a high degree of phenological control so that a significant C gain can be made within the short period available for photosynthesis and growth. Climate change may have strong effects due to disturbance of phenological responses (Crawford et al. 1993; Henry and Molau 1997). Warmer growing seasons will alter the C and nutrient concentrations in tundra plants, and the magnitude and direction of the changes will be species and growth-form specific. A prolonged growing season length-

ens the time for C assimilation and nutrient absorption in plants, which may also affect C and N concentrations. The difference between species in physiological and growth responses to rapid environmental changes may determine their survival in the habitat. Unless slow-growing species are able to disperse and establish at new sites, they may be under increased risk of competition from more responsive and faster growing species, such as forbs and graminoids.

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