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Leaf isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and nitrogen contents of *Carex* plants along the Eurasian Coastal Arctic: results from the Northeast Passage expedition

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Abstract We conducted surrogate in-situ physiological performance measures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of *Carex* plants from 15 Eurasian Coastal Arctic sites. Leaf carbon isotope discrimination (LCID) of *Carex* plants exhibited significant differences between sites (populations). Additionally, LCID was inversely correlated with mean annual temperature and stomatal density, and to a lesser extent, with the depth of thaw. Leaf $\delta^{15}\text{N}$ values of *Carex* plants exhibited significant differences between sites without differences among ramet age classes, and the leaf $\delta^{15}\text{N}$ values were inversely correlated with mean annual precipitation. These ranges of *Carex* leaf gas exchange and mineral nutrition across the Eurasian Arctic may contribute to *Carex*'s dominance in coastal tundra systems. Also, the inverse correlation between LCID, precipitation, and temperature indicates that, as precipitation increases and temperatures continue to warm in Eurasia, leaf gas exchange may actually be lower in the future, leading to reductions in shoot growth and lower above-ground biomass production.

Introduction

Understanding the physiological performance of arctic plants and populations is an important part of global-change research in northern latitudes (McGraw and Fetcher 1992; Callaghan and Carlsson 1996; Welker et al. 2000). Leaf gas exchange and mineral nutrition are

the basis of the carbon and nitrogen cycles of arctic ecosystems (Shaver et al. 1992; Chapin et al. 1995) and may be altered by warmer temperatures, changes in precipitation, alterations of irradiance, or shifts in atmospheric N deposition (Welker et al. 1993; Wookey et al. 1993, 1995; Chapin et al. 1995; Jones et al. 1998). Most studies of leaf gas exchange and mineral nutrition in arctic plants have been conducted in Alaska, Greenland, north Sweden, and on Svalbard (Shaver et al. 1979; Jonasson 1983, 1989; Welker et al. 1997; Christensen et al. 2000; Jones et al. 2000). To date no studies exist from locations along the Eurasian Coastal Arctic, even though this region represents ~one-third of the circumarctic landscape (Bliss and Matveyeva 1992). Detailed studies of plant gas exchange and mineral nutrition of vegetation in Eurasia are especially important today as it is now clear that precipitation is increasing and temperatures are warming dramatically in this region, resulting in greater rates of river discharge (Peterson et al. 2002; Polyakov et al. 2002).

Studies of in-situ physiological performance of widely distributed arctic plant populations or taxonomically similar genera with overlapping ecological niches, such as *Carex* spp. and their responsiveness to the environment, have been few because of logistical and instrumental constraints, even though modern gas analyzers are portable (Vourlitis et al. 1993; Jones et al. 2000). These constraints have been overcome in Eurasia recently as a joint Swedish-Russian expedition along the Eurasian Arctic Coast occurred in 1994, with vegetation collections at 17 different sites across 140° of longitude and 10° of latitude (Hedberg et al. 1999; Jónsdóttir et al. 1999). Surrogate in-situ physiological measures were made possible at these sites by quantifying the isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) characteristics of leaves from these plants, providing an integrative measure of gas exchange and mineral nutrition (Farquhar et al. 1989; Welker et al. 1993; Nadelhoffer et al. 1996; Michelsen et al. 1998; Robinson 2001).

The leaf carbon isotope discrimination (LCID) (Δ) characteristics of plant leaves are an integrative measure

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of carbon fixation and CO₂ diffusion (Farquhar et al. 1982, 1989; Dodd et al. 1998; Alstad et al. 1999; Gebauer and Ehleringer 2000). Leaf carbon isotope discrimination is an ecophysiological trait that is affected by soil and leaf mineral nutrition, soil and plant water status, precipitation, and irradiance (Ehleringer et al. 1991; Welker et al. 1993), and is also an indicator of population differences in habitat conditions and physiological performance (Rice et al. 1993). Typically, under abundant water supplies or higher rainfall regimes, LCID is greater than under conditions where water supplies are limited, due to higher intercellular CO₂ concentrations associated with greater rates of stomatal conductance (Ehleringer and Cooper 1988; Welker et al. 1993; Dodd et al. 1998; Alstad et al. 1999). In contrast, under conditions of higher soil and plant N contents, LCID is lower than under nutrient-deficient conditions due primarily to lower intercellular CO₂ concentrations associated with higher rates of photosynthesis. However, cold soil temperatures in the Arctic can limit hydraulic and stomatal conductance, and warm temperatures can increase soil and air dryness (atmospheric drought), effectively lowering the LCID of arctic plants (Dawson and Bliss 1993; Welker et al. 1993, 1995).

Similar to LCID, the $\delta^{15}\text{N}$ values of plant leaves provide a measure of mineral nutrition that reflects a host of processes, especially differences in N sources (Michelsen et al. 1996; Nadelhoffer et al. 1996; Robinson 2001), variation in mycorrhizal infection (Michelsen et al. 1998), and differences in soil mineralization processes (Gebauer and Ehleringer 2000; Robinson 2001), but at undisturbed sites, leaf $\delta^{15}\text{N}$ reflects the ¹⁵N abundance of available nitrogen in the soil layers where the density of roots are greatest (Gebauer et al. 1994). This measure of ecophysiological performance is especially germane to our study, as differences in the leaf $\delta^{15}\text{N}$ values of ramet generations may indicate the degree of physiological integration of connected ramets (Welker et al. 1987, 1991; Welker and Briske 1992), as well as differences in N sources.

Differences in the average $\delta^{15}\text{N}$ values of *Carex* leaves between populations may be indicative of unique N source combinations (NH₄⁺, NO₃⁻, or amino acids) or site-specific soil mineralization/immobilization processes that occur across the Eurasian Coastal Arctic. For instance, if plant parts or plant populations are using a greater proportion of ammonium than nitrate, the leaf $\delta^{15}\text{N}$ values would be slightly enriched compared to those that are using a greater fraction of nitrate. In addition, if plants are acquiring organic sources of N from the soil via mycorrhizal associations, the leaf $\delta^{15}\text{N}$ values would be enriched compared to plants or populations that are only using inorganic N sources (Emmertson et al. 2001a, 2001b). However, because of considerable ¹⁵N fractionation associated with mycorrhizal assimilation, the leaf $\delta^{15}\text{N}$ values of plants that are infected with ericoid or ectomycorrhizal mycorrhiza are unlikely to directly reflect the $\delta^{15}\text{N}$ of the original soil N sources (Emmertson et al. 2001b). *Carex* species

are not mycorrhizal, simplifying our interpretation of $\delta^{15}\text{N}$ values. While it is typically assumed that changes in plant $\delta^{15}\text{N}$ values are the result of changes in the combination of natural sources (Emmertson et al. 2001a, 2001b), industrial sources of atmospheric N may influence the isotopic characteristics of vegetation (Ammann et al. 1999). However, because of the remoteness of our study sites from any anthropogenic N source, we expect the $\delta^{15}\text{N}$ values of these plants to reflect natural sources.

It has become increasingly clear that the modular nature of clonal plants in arctic and temperate habitats confers physiological and ecological benefits (Callaghan 1976; Welker et al. 1985, 1987; Jónsdóttir and Callaghan 1988, 1989, 1990; Welker and Briske 1992; Jónsdóttir and Watson 1997; Hertefeldt and Jónsdóttir 1999). Physiologically, the ability to transport resources among interconnected ramets that may differ in age and assimilative ability (especially from mature ramets to fast-growing juveniles), allows portions of the clone, under favorable microenvironments, to provide carbon, nitrogen, or water to shaded, partially grazed ramets, or to ramets that retain active roots without leaves (Welker et al. 1985; Jónsdóttir and Callaghan 1988). This division of labor may result in a divergence of environmental sensitivity among ramet generations, especially with regard to carbon fixation and soil N acquisition. One might expect that because juvenile ramets are typically at the leading edge of clones and may be sampling the nature of the microclimate, they would be the most responsive to the environment, especially in their gas-exchange characteristics. In contrast, mature ramets that typically transport N into developing ramets (Jónsdóttir and Callaghan 1990; Welker et al. 1991) and retain established root systems, may have the most responsive mineral nutrition attributes to environmental variation.

There are no studies in the Eurasian Arctic that simultaneously examine the patterns and processes that affect LCID, $\delta^{15}\text{N}$, and N content of clonal arctic plants. In this study, we address three main questions. First, are there differences in the ecophysiological performance of *Carex* plants located across a range of sites (populations) along the Eurasian Coastal Arctic? Second, are there differences in the physiological performance of *Carex* ramet generations (i.e., juvenile vegetative ramets, mature ramets, and reproductive ramets) within a clone? Third, to what degree is the physiological performance of *Carex* ramet generations responsive to environmental parameters such as temperature, precipitation, soil organic matter, and depth of thaw? And, fourth, to what degree are ecophysiological traits of *Carex* plants correlated with plant growth and anatomical traits?

We recognize that our sampling involved three species of *Carex* across a range of sites. Thus, some of our observed differences could be attributed to species-specific traits and physiological performance. However, since two of the species are members of the circumpolar complex *Carex bigelowii* (Murray 1994), all three species grow clonally with very similar shoot, rhizome, and root morphology (Jonsdottir et al. 1999; Stenstrom 2000),

and because these species exhibit consistent overlap in their ecological niches, we focus on general attributes. In addition, since *Carex* species have similar physiology (Lambers and Van Der Werf 1988; Hirose et al. 1989), sedge-dominated meadows are often characterized by genus as opposed to species (Henry et al. 1990), and sedges respond similarly to abiotic conditions (Nosko and Courtin 1995), our emphasis is on genera attributes. Species differences are given consideration where appropriate in our data interpretation.

Materials and methods

The Swedish-Russian Tundra Ecology 1994 Expedition occurred between June and August along the Eurasian Coastal Arctic from the Kola Peninsula in the west to Wrangel Island in the east (Fig. 1) with the use of the Russian ice breaker, the *R/V Akademik Fedorov* (Hedberg et al. 1999). The vessel was equipped with two helicopters that allowed field parties to visit tundra sites for periods of 2–3 days, performing scientific studies ranging from vegetation collections and analysis (Jónsdóttir et al. 1999) to trace gas fluxes (Christensen et al. 1999). A total of 17 field sites were visited covering 140° of longitude with a latitudinal range from 67°N to 77°N (Hedberg et al. 1999). Field parties visited most types of Arctic Eurasian environments and tundra types, ranging from the southern Arctic where dwarf birch is present to the high-Arctic, semi-polar desert-like habitats of Cape Chelyuskin. Common to all regions are mesic and wet tundra dominated by *Carex* species. These ecosystems often constitute >50% of the landscape and,

thus, provide important forage and habitat for migratory birds, herbivores, and small rodents (Alerstam and Jonsson 1999; Danell et al. 1999; Stenstrom et al. 2002).

At each site, samples of one or two dominating *Carex* taxa were collected from mesic tundra for later analysis in the laboratory. The targeted taxa were *Carex ensifolia* Krecz. ssp. *arctisibirica* Yurtsev (here called *C. ensifolia*), *C. lugens* Holm, and *C. stans* Drej. Along 80- to 120-m transects, ten randomly chosen clonal segments were carefully removed from the soil, and preserved in a plant press. Clonal segments consisted of interconnected ramets, including vegetative juvenile (<2 years old) and mature vegetative ramets along with reproductive ramets (as indicated by the presence of an inflorescence). The material was allowed to air-dry and stored under cool temperatures.

In the autumn of 1999, replicate clonal segments were examined from all sites, and interconnected juvenile, mature, and reproductive ramets were severed. *C. ensifolia* samples available for laboratory analysis were from sites 2, 3, 4, 5, 6, 8, 9, 10, and 12a (Fig. 1, Table 1). *C. stans* samples were collected at sites 12b, 13, 14, and 16a, and *C. lugens* samples from sites 16b and 17 (Fig. 1, Table 1). Our sample size (*N*) was equal to 5 for all sites except sites 3, 4, 6, and 10, where *N* was equal to 4. Intact plant material with discernible ramet sequences was not available from all ten replicates because the material had been used in companion studies or was broken during storage and transport (Stenstrom 2000).

Green leaf material was separated from dead leaves and oven-dried at 60°C for 48 h, ground to a fine powder, and analyzed by combustion for total C and N on a Carlo Erba CHN analyzer. The combusted samples were then passed into an Isoprime Stable Isotope Mass Spectrometer under continuous flow, and the $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios of the CO_2 and N_2 gas, respectively, were measured (Farquhar et al. 1989; Welker et al. 1993; Hogberg 1997; Robinson 2001). The isotopic ratios were then converted to “delta units” (δ) in parts per thousand (‰) following the formula of Farquhar et al. (1982, 1989):

$$\delta = (R_{\text{sample}}/R_{\text{standard}} - 1)1000$$

where *R* is the molar ratio of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$). The standard was PDB for carbon and atmospheric air for nitrogen. Leaf carbon isotope discrimination (Δ , LCID) (Welker et al. 1993; Alstad et al. 1999; Gebauer and Ehleringer 2000) values were calculated from the leaf carbon isotope ratios using the

Fig. 1 Route map of the Tundra Ecology-1994 Expedition across the Eurasian Coastal Arctic and the spatial distribution of the three *Carex* species used in this study. For our study, no samples were used from site 7 and only samples from site 13.1 were used. Note that the eastern sites, such as NE Taymyr Peninsula (13), were actually sampled earlier in the summer (~ Julian day 160) compared to the Kanin Peninsula (2) that was sampled on Julian day 213). The specific sites are listed in Table 1

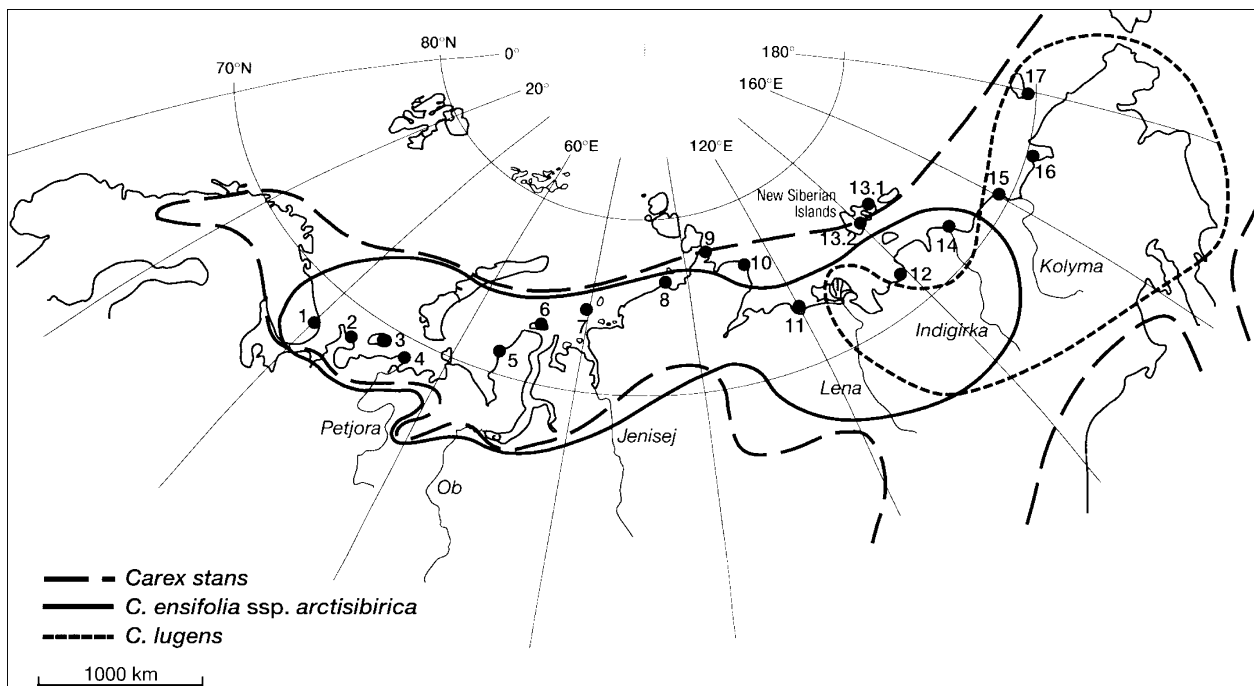


Table 1 Sites and associated abiotic traits along the Eurasian Coastal Arctic expedition from which we analyzed *Carex* plant ecophysiological, anatomical, and growth attributes. *Site numbers* are associated with the locations on the map in Fig. 1. These data are from Jonsdottir et al. (1999) based on Goryachkin et al. (1994)

Study site	Mean annual temperature (°C)	Mean July temperature (°C)	Mean annual precipitation (mm)
Kanin Peninsula (2)	-2.2	7.3	346
Kolguyev Island (3)	-5.6	7.6	341
Pechora Bay (4)	-5.6	8.6	338
W. Yamal Peninsula (5)	-8.3	6.6	307
N. Yamal Peninsula (6)	-10.0	4.1	258
NW Taymyr Peninsula (8)	-13.8	3.4	240
Chelyuskin Peninsula (9)	-14.5	1.5	209
NE Taymyr (10)	-15.3	3.0	190
Yana Delta (12a)	-13.5	4.4	179
Yana Delta (12b)	-13.5	4.4	179
Faddeyevsky Island (13)	-14.9	2.3	169
Indigirka Delta (14)	-15.2	7.1	236
Kolyma Delta (15)	-12.7	6.7	209
Ayon Island (16a)	-13.0	4.3	299
Ayon Island (16b)	-13.0	4.3	299
Wrangel Island (17)	-11.0	3.6	175

formula of Farquhar and Lloyd (1993) with the $\delta^{13}\text{C}$ of the atmosphere assumed to be -8.0‰ .

In this study, we used a General Linear Model (GLM) (SAS 1999) to test whether LCID, total leaf N and leaf $\delta^{15}\text{N}$ values were significantly ($P < 0.05$) different between sites and ramet age class, and their interaction. We also used GLM procedures to test whether there was a significant ($P < 0.05$) covariant (sample date) effect on LCID, total leaf N, and leaf $\delta^{15}\text{N}$ values since we were not able to simultaneously sample all the sites. We used a least square means separation test to evaluate significant ($P < 0.05$) differences in ecophysiological traits when there was a main effect of site (e.g., for LCID and leaf $\delta^{15}\text{N}$), and when there was a site by ramet age class interaction (e.g., for % N). We used a correlation analysis (Pearson's r) (SAS 1999) to examine whether *Carex* plants or *Carex* ramet age classes responded to the range of abiotic and soil properties that exist along the natural gradient of environmental conditions found among our sampling locations. The abiotic parameters used in our analysis were mean annual temperature (MAT), mean July temperature (MJT), mean annual precipitation (MAP) (Jónsdóttir et al. 1999), soil temperature at the time of our plant collections (ST, 10 cm), soil organic carbon (SOC), and depth of thaw at time of collection (DOT) (Goryachkin et al. 1994; Christensen et al. 1999). Because the same plants were used in the evaluation of growth (shoot height—Sheight), and anatomical traits (stomatal size—Stsize and stomatal density—Stdensity), we were also able to examine whether LCID, N content, and $\delta^{15}\text{N}$ values were correlated with these parameters (Stenstrom 2000).

Results

Environmental conditions

The environmental conditions across the study sites ranged from being relatively warm and wet in the southern tundra sites (Kanin Peninsula, site 2 and Pechora Bay, site 4) (Table 1) to being colder and drier at sites that were farther east and north, such as Taymyr Peninsula (site 10) and Wrangel Island (site 17). These abiotic parameters have been measured at these sites

Table 2 Summary of statistical analysis of LCID, %N, and $\delta^{15}\text{N}$ of *Carex* vegetation, F -values and P -values from GLM analysis, respectively (*ns* no significant effect)

Main effects	LCID	%N	$\delta^{15}\text{N}$
Population (P)	2.11, 0.022	ns	8.2, 0.001
Ramet age class (RA)	ns	ns	ns
$P \times \text{RA}$ interaction	ns	1.92, 0.036	ns
Covariant (sample date)	6.20, 0.018	ns	4.7, 0.039

for > 10 years, and have been reported and published elsewhere by Goryachkin et al. (1994), and are thus suitable for our analysis. In addition to long-term abiotic conditions, a series of measurements were taken at the time of plant-material collection and trace gas measurements (Christensen et al. 1999; Jonsdottir et al. 1999). While these measurements are only single point-in-time, they are our best estimates of site-site variation in conditions and appear to reflect general trends that would be expected based on latitude and longitude.

Soil temperatures were warmest at Kanin Peninsula and Kotelny Island, averaging $\sim 8^\circ\text{C}$ when the field party visited the sites, while temperatures were coldest at Wrangel Island, NE Taymyr, and Chelyuskin, averaging $\sim 0.5^\circ\text{C}$ (see Christensen et al. 1999). The soil organic-matter contents were almost 100% at the Kanin Peninsula site, $\sim 60\%$ at the Kolyma site, and $< 10\%$ at the Chelyuskin site. The depth of thaw ranged from 100 cm at Kolguyev Island to < 30 cm at the NE Taymyr location.

Leaf Carbon Isotope Discrimination

The LCID of *Carex* plants exhibited significant ($F = 2.11$, $P < 0.022$) site differences even when considering the significant ($F = 6.2$, $P < 0.018$) sampling date covariant (Table 2). *Carex* plants at NE Taymyr Peninsula (10), NW Taymyr Peninsula (8), Faddeyevsky Island (13), and Indigirka Delta (14) all had LCID values that were generally higher (21.8‰ average) than those of plants from the other populations, especially populations at the Yana Delta (12) that had values of 19.6‰ (Fig. 2A).

Leaf N content

The leaf N content of *Carex* plants exhibited a significant ($F = 1.92$, $P < 0.036$) site by ramet age class interaction, and when the covariant (sample date) was considered, only the N content of juvenile and mature ramets was significantly ($P < 0.02$) different between sites (Figs. 2B, 3). Juvenile ramets from the NW Taymyr (8), Chelyuskin (9), Faddeyevsky (13), and Ayon Island (16a, 16b) sites had the highest amount of leaf N, while plants from the West Yamal (5) and North Yamal (6) sites had the lowest (Fig. 3A). The leaf N content of mature ramets was consistently highest in the *Carex*

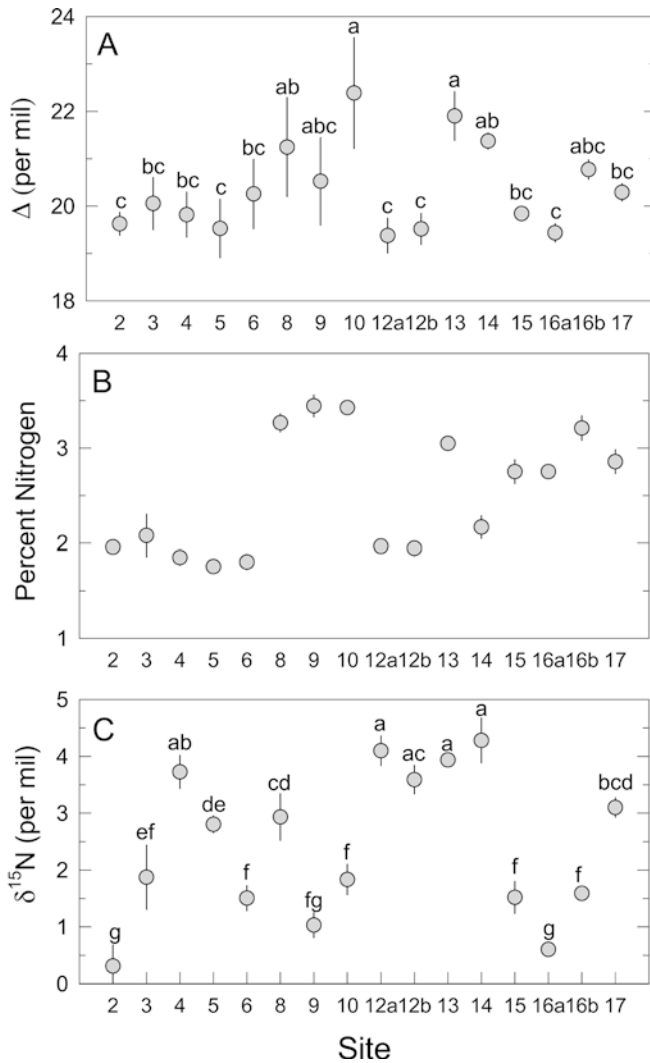


Fig. 2A–C Population differences in the leaf carbon isotope discrimination (LCID) (A), total leaf N (B) content, and leaf $\delta^{15}\text{N}$ values (C) of *Carex* plants sampled along the Eurasian Coastal Arctic. The LCID and the leaf $\delta^{15}\text{N}$ values were significantly different between populations, even when the covariant (date of sampling) was considered, though the leaf N content exhibited a significant ($P < 0.05$) population by ramet age class interaction and, thus, a mean separation test was not performed to distinguish population differences. Each value represents the mean and one standard error. $N = 5$ for all sites, except for sites 3, 4, 6, and 10 where $N = 4$.

plants from the Chelyuskin (9) and the NW Taymyr Peninsula (10) sites (Fig. 3B).

Leaf $\delta^{15}\text{N}$ values

The leaf $\delta^{15}\text{N}$ values of *Carex* plants were significantly ($F = 8.2$, $P < 0.001$) different between sites (Table 2). The leaf $\delta^{15}\text{N}$ values of plants at the Yana Delta (12a), Faddeyevsky (13), and Indigirka Delta (14) were significantly higher (4.2‰ average) than those of plants from other sites (Fig. 2C). The leaf $\delta^{15}\text{N}$ values were most depleted in plants from Kanin Peninsula (2),

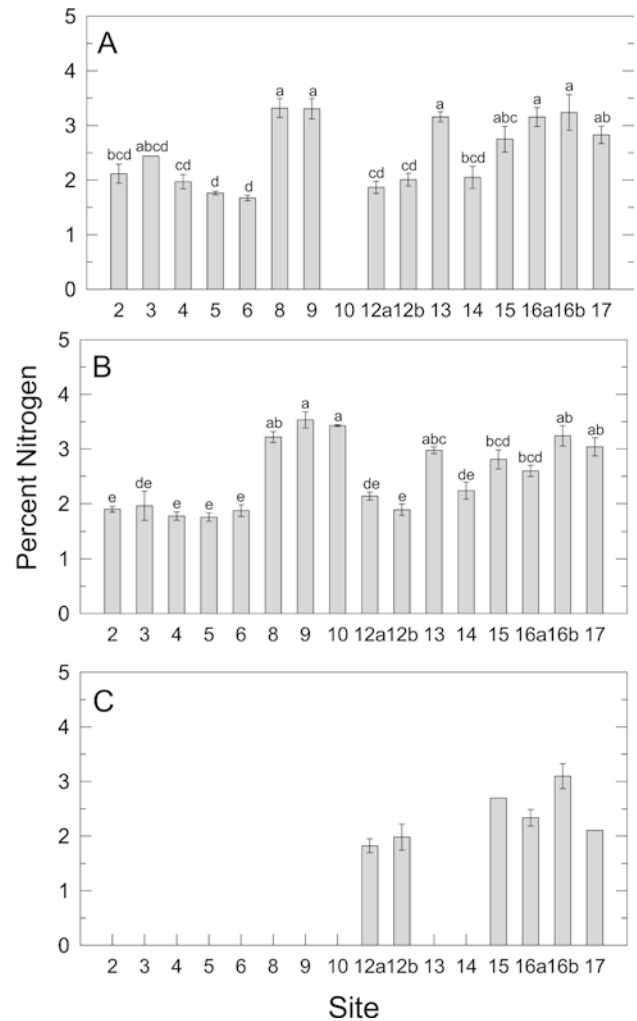


Fig. 3A–C Leaf N content of *Carex* populations for juvenile (A), mature (B), and reproductive (C) ramet age classes collected along the Eurasian Coastal Arctic. Sites are the same as in Fig. 1

Chelyuskin (9), and Ayon Island (16a) sites where the values averaged 0.8‰. These similarities in N mineral nutrition between *C. ensifolia* and *C. stans* further substantiate the ecological and physiological similarity across the *Carex* species sampled in this study.

Ecophysiological traits and responses to the Eurasian environmental gradient

Overall response

Carex LCID was inversely ($P < 0.01$) correlated with mean annual temperature and stomatal density (Table 3), and to a lesser extent, with the depth of thaw. Leaf carbon isotope discrimination was typically enriched in *Carex* leaves of plants from colder sites and was depleted at sites where temperatures were warmer and possibly drier. We also found that LCID was significantly ($P < 0.05$) correlated with shoot height,

Table 3 Pearson correlation coefficients (r) for *Carex* plant eco-physiological, abiotic, and anatomical traits ($N=16$). The morphological and anatomical (shoot height, stomatal density, and stomatal size) traits are based on analysis by Stenstrom (2000) for a separate sub-set of plants collected at each site (MAT mean annual temperature, MJT mean July temperature, MAP mean annual precipitation, DOT depth of thaw, OC organic C content)

All Tillers combined	N content (%)	$\delta^{15}\text{N}$	LCID
MAT	-0.32	-0.24	-0.42**
MJT	-0.37*	-0.02	-0.30
MAP	-0.07	-0.38*	-0.22
DOT	-0.22	-0.34*	-0.35*
OC	-0.15	-0.42**	-0.14
Shoot height	0.03	0.21	0.38*
Stomatal density	-0.38*	-0.20	-0.42**
Stomatal size	0.35*	-0.06	0.19

* $P < 0.05$; ** $P < 0.01$.

Table 4 Pearson correlation coefficients (r) for *Carex* plant eco-physiological, abiotic, and anatomical traits by each ramet age class ($N=16$) (MAT mean annual temperature, MJT mean July temperature, MAP mean annual precipitation, DOT depth of thaw, OC organic C content)

Tiller category	N content (%)	$\delta^{15}\text{N}$	LCID
Juvenile tillers	-	-	MAT -0.64**
	-	-	MJT -0.49*
	-	-	DOT -0.56*
	-	-	$STSize$ 0.60**
Mature tillers	MAT -0.61*	-	$STdensity$ -0.63**
	MJT -0.70**	-	$Sheight$ 0.76**
	DOT -0.52*	-	-
	$STdensity$ -0.59*	-	-
Reproductive tillers	-	OC -0.88*	$STSize$ -0.86*

* $P < 0.05$, ** $P < 0.01$.

indicating that under conditions of higher rates of gas exchange, plant growth is greater, and the converse.

Correspondingly, *Carex* leaf $\delta^{15}\text{N}$ values were inversely ($P < 0.05$) correlated with mean annual precipitation. Under wetter conditions, leaf $\delta^{15}\text{N}$ values were depleted compared to plants that were found under lower rainfall conditions across the Eurasian Coastal Arctic. In addition, lower leaf $\delta^{15}\text{N}$ values were found in *Carex* leaves of plants growing in soil where organic matter content was higher. Plant N content was inversely correlated with mean July temperatures ($P < 0.05$) and with stomatal density.

Ramet age class responses

Only in juvenile vegetative ramets did LCID appear to be responsive to the environment (Table 4). Leaves of juvenile ramets had consistently higher LCID under colder conditions, and their LCID was significantly ($P < 0.01$) correlated with stomatal size and inversely correlated with stomatal density. Neither the N content nor the leaf $\delta^{15}\text{N}$ values of juvenile ramets were

correlated with any of our environmental, growth, or anatomical traits. In contrast, the leaf N content of mature ramets was inversely correlated with air temperature, depth of thaw, and stomatal density.

Discussion

The isotopic attributes we measured in *Carex* plants along the Eurasian Coastal Arctic are within the range of values reported for *Carex* and other tundra species in the Arctic (Welker et al. 1993; Michelsen et al. 1996, 1998; Nadelhoffer et al. 1996). However, we discovered several important findings regarding *Carex* site (population) and ramet generation differences in leaf isotopic traits across 140° of longitude and 10° of latitude. *Carex* plants from different sites along the Eurasian Coastal Arctic from mesic habitats did not have identical gas exchange attributes as measured by LCID. An LCID range of $\sim 3.0\text{‰}$ represents a difference of ~ 45 ppm in the intercellular CO_2 concentrations of *Carex* leaves between our two extreme populations (NE Taymyr and Yana Delta—both *C. ensifolia*). The differences in physiology between these *Carex* populations may be due to differences in photosynthetic capacity, their rates of stomatal conductance, or a combination of both (Ehleringer et al. 1991; Rice et al. 1993; Alstad et al. 1999). Since we found that *Carex* LCID values were positively correlated with leaf N content ($r = 0.30$, $P < 0.09$ —data not shown), it is likely that photosynthetic processes (carboxylation) are partially involved in the differences between the populations we observed. However, *Carex* LCID is reduced under warmer temperatures (negative correlation— $P < 0.01$), and this may be the result of decreases in stomatal conductance in response to drier soils, larger vapor pressure deficits, or increases in the rates of transpiration. Decreases in stomatal conductance in *C. stans* have been reported by Nosko and Courtin (1995) over the course of the summer as soil and air drought progressed on Devon Island, NWT (latitudes similar to those we sampled from in this study). Thus, differences in the rates of stomatal conductance likely account for the majority of population (site) variations in LCID across the Eurasian Coastal Arctic.

We found the range of leaf $\delta^{15}\text{N}$ values (4.8‰ – 0.05‰) to be almost identical to those for *Carex* species in the sub-arctic of Sweden, low-arctic in Alaska, high-arctic on E. Greenland, and for other graminoid species in Siberia (Nadelhoffer et al. 1996; Michelsen et al. 1998). The leaf $\delta^{15}\text{N}$ values of *Carex* plants from all sites were positive, which is indicative of non-mycorrhizal species that use inorganic nitrogen as their N source (Michelsen et al. 1996, 1998). The Eurasian plants do, however, exhibit an inverse relationship between leaf $\delta^{15}\text{N}$ values, mean annual precipitation, and soil organic carbon content. This correlation suggests that when water is in greater abundance, leaf $\delta^{15}\text{N}$ values are depleted, indicating either a change in the proportion of ammonium and nitrate used by *Carex* plants or a change

in the ratio of microbial immobilization to mineralization, and a subsequent shift in the $\delta^{15}\text{N}$ values of the soil N pool used by *Carex* plants (Handley and Raven 1992).

The responsiveness of *Carex* LCID and plant and soil nitrogen processes ($\delta^{15}\text{N}$ values) to precipitation and temperature are especially germane to the changes being observed in Eurasian climatology (Peterson et al. 2002; Polyakov et al. 2002). It is now apparent that Eurasia is getting wetter in summer and warmer throughout the year which, based on our analysis, will translate into different rates of leaf gas exchange, as well as plant N sources and/or soil mineralization/immobilization processes (Schimel et al. 2004). Warmer temperatures will likely reduce LCID during the growing season, but this effect may be counteracted by greater precipitation; the net effect of these climate scenarios are uncertain and merit further investigation with field manipulations (Welker et al. 1993). Simultaneously, greater rainfall in summer will result in increased availability of nitrate and its use by *Carex* plants. This increase would ameliorate, to some degree, the inherent nutrient limitations that curtail growth, biomass production, and carbon sequestration in sedge-dominated systems (Shaver et al. 1998). Collectively, the warming and wetter conditions developing in Eurasia will have cascading effects on *Carex* ecosystem function and structure, though field-based manipulation studies along with long-term monitoring will be necessary to fully elucidate the changes in this important vegetation type (Serreze et al. 2000; Shaver et al. 2000).

The modular nature of clonal organisms is expressed in our findings through the differential sensitivity of each ramet age class to the environment. Juvenile vegetative ramets exhibited the strongest changes in gas exchange (LCID) along this Eurasian environmental gradient. This response indicates that the youngest portions of *Carex* clones that are undergoing the greatest rates of growth have the ability to significantly alter photosynthesis and/or stomatal conductance in response to environmental fluctuations. Juvenile ramets of *Carex* are typically at the leading edge of individual clones and thus, are most likely to encounter variance in soil and canopy microclimate (Jónsdóttir and Callaghan 1988). Consequently, effective control of carbon and water exchange in juvenile ramets provides a means through which *Carex* clones can retain their resource exploitation capacity, even in the face of competition with other species or adjacent clones and with microclimatic variations in soil moisture and canopy conditions.

In contrast, gas exchange (LCID) attributes of mature vegetative or reproductive ramets were largely insensitive to the environmental gradient, maintaining a high degree of buffering capacity within *Carex* clones in the face of daily, seasonal, and annual changes in temperature and precipitation. This dichotomy of gas exchange patterns within a *Carex* clone may confer several ecological advantages. For instance, the mature and reproductive ramets provide consistency in carbon acquisition and water use, securing the existing space

from competitors. However, juvenile ramets may be opportunistic in their carbon acquisition and water use when conditions are favorable, facilitating the expansion of clones. These traits are physiologically and ecologically important, as mature vegetative ramets in *Carex* clones are the primary carbon-assimilating generation. They supply carbon to both juvenile vegetative ramets and older, non-assimilating generations that no longer have active leaf tissue, but retain roots that may supply the clone with water and nutrients (Jónsdóttir and Callaghan 1988, 1989; Welker et al. 1995; Brooker et al. 1999).

The total leaf N content of mature vegetative ramets responded to our environmental gradient, with leaf N contents being highest where temperatures were coldest. This inverse relationship indicates that under cold temperatures, growth may be lower and leaf N dilution less. Previous studies by Körner (1989) indicated that at higher altitudes and latitudes, where growing seasons were shorter and colder than lower altitudes and latitudes, leaf N was significantly higher in herbaceous and graminoid species. Thus, even along the temperature gradient that exists across the Eurasian Coastal Arctic, portions of *Carex* clones are exhibiting fundamental plant nutritional patterns that have been found at the global scale. However, this relationship is ramet generation-specific.

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