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Authors: Campioli, Matteo, Leblans, Niki, and Michelsen, Anders

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Matteo Campioli‡*

Niki Leblans and*

Anders Michelsen†

*Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium
†Department of Biology, University of Copenhagen, Oester Farimagsgade 2D, DK-1353 Copenhagen K, Denmark
‡Corresponding author: Research Group of Plant and Vegetation Ecology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium
matteo.campioli@ua.ac.be

Abstract

Our knowledge of stem secondary growth of arctic shrubs (a key component of tundra net primary production, NPP) is very limited. Here, we investigated the impact of the physical elements of the environment on shrub secondary growth by comparing annual growth rates of model species from similar habitats at contrasting altitude, microtopography, latitude, geographical location, and soil type, in both the sub- and High Arctic. We found that secondary growth has a modest sensitivity to the environment but with large differences among species. For example, the evergreen *Cassiope tetragona* is affected by altitude, microtopography, and latitude, whereas the evergreen *Empetrum hermaphroditum* has rather constant secondary growth in all environments. Deciduous species seem to be most affected by microtopography. Furthermore, the impact of the environment on secondary growth differed from the impact on primary growth (stem apical growth, stem length, and apical growth of stem plus leaves), in some cases even with opposite responses. Thus caution should be taken when estimating the impact of the environment on shrub growth from apical growth only. Integration of our data set with the (very limited) previously published information on secondary growth provides an overview of its contribution to NPP and annual growth rates for 9 arctic species at 18 sites in Sweden, Greenland, Svalbard, Alaska, and the Alps.

Introduction

Net primary production (NPP) is a process that governs the structure of terrestrial ecosystems and their exchange of matter and energy with the environment. Moreover, NPP of terrestrial ecosystems has received increasing attention in recent years because the uptake of atmospheric CO_2 in plant biomass provides a negative feedback to the greenhouse effect (Denman et al., 2007).

Despite the large cover of tundra ecosystems (5.6×10^6 km^2; Bliss and Matveyeva, 1992) and their high sensitivity to climate change (Callaghan et al., 2005), our knowledge of NPP for typical arctic plant communities is very limited. One of the primary knowledge gaps is the limited information on stem secondary growth of shrubs, one of the main growth forms of arctic ecosystems. In fact, woody stems of arctic shrubs produce new biomass through apical growth but also, and substantially, through cambial growth or secondary growth in diameter (Shaver, 1986). The very few studies that have investigated stem secondary growth in arctic shrubs (Shaver, 1986; Bret-Harte et al., 2002; Campioli et al., 2009) have reported annual growth rates of about 10–35% y^{-1}. These studies have documented the important contribution of stem secondary growth to ecosystem NPP and its sensitivity to changes in environmental conditions. For example, Shaver (1986) found that stem secondary growth accounted for 13–49% of aboveground NPP for individual species in Alaskan tundra. Campioli et al. (2009) found that stem secondary growth contributed about 20% of total vascular NPP in subarctic heaths in Sweden. Bret-Harte et al. (2002) found that secondary growth can increase up to threefold in tussock tundra shrubs following fertilization.

Neglecting the contribution of stem secondary growth of shrubs leads to a significant underestimation of the tundra carbon (C) sink capacity. In fact, not only the ecosystem C uptake is underestimated but also the residence time of C in the ecosystem as woody biomass represents a longer term C storage than leaves, particularly for deciduous shrubs (Hobbie, 1996).

One of the most important knowledge gaps of stem secondary growth of tundra shrubs is dependence on the physical constraints of the environment. Data are critically needed to understand and model the response of tundra ecosystems to climate change at broad spatial scales. A second important issue is to clarify whether the response of stem secondary growth to different environmental variables is the same as the response of apical stem growth and leaf growth. This issue is of high practical relevance as, until now, most of the studies focused on the impact of the environment on shrub growth have used apical stem growth (expressed in biomass- or length increment) or leaf growth as indicators of the total aboveground shrub growth (e.g. Wielgolaski et al., 1981; Parsons et al., 1994; Graglia et al., 1997; Arft et al., 1999; Phoenix et al., 2001; Fletcher et al., 2010). Therefore, this study addressed two main questions: (1) What is the impact of environmental variables on stem secondary growth of tundra shrubs? and (2) Is the response of secondary growth of tundra shrubs to environmental variables correlated to responses of apical growth? Further, we also sought to review the existing data on stem secondary growth, to provide ancillary information on secondary growth rate for species and plant communities never investigated for this purpose, and to provide an overview of the relative importance of secondary growth to total aboveground vascular growth based on individual shrubs and ecosystem level assessments.

TABLE 1

Geographical and climatic characteristics of the regions and altitudinal zones considered (Abisko, Zackenberg, Ny Ålesund, Fontainemore: original research results; Toolik Lake, Eagle Creek: review of published results).

Region	Abisko, Sweden	Zackenberg, Greenland	Toolik Lake, Alaska	Eagle Creek, Alaska	Ny Ålesund, Svalbard	Fontainemore, Italy
Coordinates	68°21'N, 18°49'E	74°30'N, 21°00'W	68°38'N, 149°34'W	65°10'N, 145°30'W	78°54'N, 12°06'E	45°39'N, 7°54'E
Climate zone	subarctic-alpine	High Arctic	Low Arctic	subarctic-alpine	High Arctic	subalpine
Annual precipitation (mm)	304	222	225	600 [a]	433	1070
Growing season	early June–early Sept.	end June–mid Aug.	mid June–late Aug.	early June–late Aug.	end June–mid Aug.	late May–mid Sept.
Altitude (m)	550–720 1150	40–100 470	720	730	10	2030
Annual temperature (°C)	−1.0 −4.8	−9.0 −8.0	−10	−3 [b]	−4.2	0.5
January temperature (°C)	−11 n.a.	−18 −16	−24	−17 [b]	−9.8	−4.6
July temperature (°C)	12 7.2	6.4 7.3	14	14 [b]	5.8	11

Sources: Abisko (Havström et al., 1993; Schimdt et al., 2002; Campioli et al., 2009; http://www.linnea.com/~ans/), Zackenberg (Klitgaard et al., 2007; Jensen and Rasch, 2009, 2010), Toolik Lake (Shaver and Chapin, 1991; http://ecosystems.mbl.edu/arc/), Eagle Creek (Wein and Bliss, 1974; Fetcher and Shaver, 1982; http://www.wunderground.com/), Ny Ålesund (http://met.no/), and Fontainemore (Freppaz et al., 2008, unpublished). [a] and [b]: sparse data or from regional climatic maps with large uncertainty; [a]: ±100 mm and [b]: up to ±3 °C. n.a.: data not available.

A common way to study the influence of a given environmental variable on plant growth is by investigating its impact along toposequences (Shaver et al., 1996) or gradients (Fletcher et al., 2010). However, lack of knowledge about the main environmental drivers of stem secondary growth made this approach (requiring many sampling points and large effort) inefficient. Instead, we tested the impact of a given environmental variable by examining the stem secondary growth of model species growing in two similar habitats but differing in this particular environmental variable. This approach is similar to examining the impact of an environmental manipulation by comparing plant responses in control and modified plots (Chapin et al., 1995; Jonasson et al., 1999). Thus, our first question was addressed by investigating the impact of environmental factors possibly influencing secondary growth, such as altitude, microtopography, latitude, geographical distribution, and soil type, on the secondary growth of model shrubs species growing in similar habitats but differing in one of these environmental factors. Our second question was addressed by comparing the impact of altitude, microtopography, latitude, distribution, and soil type on secondary growth, with the impact that the same variables had on apical stem biomass growth, apical stem length increment, and total apical growth (i.e. apical stem plus leaves). The ancillary objectives were addressed by presenting relevant original data and by reviewing and re-analyzing data from the sparse literature.

Material and Methods

STUDY SITES AND SAMPLING PERIODS

We report data from six areas with typical arctic or alpine tundra: Abisko (northern Sweden), Zackenberg (North-East Greenland), Ny Ålesund (Svalbard), Toolik Lake (northern Alaska), Eagle Creek (central Alaska), and Fontainemore (northwestern Italian Alps). Geographical and climatic characteristics of each area are reported in Table 1. Data from Abisko, Zackenberg, Ny Ålesund, and Fontainemore were collected by the authors between 2005 and 2010 in late summer, when most of the annual growth had occurred (late July–early August in Zackenberg and Ny Ålesund) or totally ceased (late August–early September in Abisko; early October at Fontainemore). Data from Eagle Creek and Toolik Lake have been published (Shaver, 1986; Bret-Harte et al., 2002), but are reviewed here for completeness. The temperature data in Table 1 confirm that the growing season meteorological conditions at the high altitude subarctic site (Abisko) are similar to the growing season conditions at high arctic sites (Zackenberg and Ny Ålesund) (Havström et al., 1993). On the other hand, the temperature of the low altitude site was lower than the temperature of the high altitude site at Zackenberg (Table 1). This is likely due to the fact that the more southern aspect of the latter has a larger impact on temperature than the moderate altitudinal variation between sites.

Five model species were investigated: *Cassiope tetragona* (L.) D. Don, *Empetrum hermaphroditum* L. (also referred to as *Empetrum nigrum* L.), *Betula nana* L., *Salix polaris* Wahlenb., and *Salix arctica* Pall., which were growing at 13 dry-mesic tundra sites dominated by shrubs and dwarf shrubs at Abisko, Zackenberg, and Ny Ålesund. Overall, we present data for 18 plant communities (Table 2) and 9 species, i.e. the 5 model species plus *Ledum palustre* L., *Vaccinium uliginosum* L., *Salix glauca* L., and *Salix pulchra* Cham. (Table 3).

TABLE 2

List of communities investigated (at Abisko, Zackenberg, Ny Ålesund, Fontainemore) or reviewed (at Toolik Lake, Eagle Creek) for stem secondary growth of tundra shrubs. Microtopography and most common plant types are reported for each community (dominant species are marked with an asterisk), with relevant references. For communities at Abisko Paddustieva and Nissunsnuohkki additional information about the soil characteristics is reported.

Community	Microtopography	Common shrubs species and other plant types	References
Abisko, Paddustieva — 550 m — mesic (no permafrost), bedrock of base-rich mica schists, pH ~ 7, organic mat 20–25 cm			
tree-line heath	exposed NW-facing slope with medium/ shallow snow cover	*C. tetragona*, E. hermaphroditum, B. nana, V. uliginosum,* herbs, bryophytes	1, 2, 3
tree-line depressions	microdepressions NW-facing slope with winter accumulation of snow	*C. tetragona*, B. nana, Salix* spp., bryophytes	—
tree-line *Betula* shrubs	level terrain / NW-facing slope	*B. nana*, E. hermaphroditum, Salix* spp., bryophytes	—
Abisko, Nissunsnuohkki — 720 m — mesic (no permafrost), bedrock of hard shale, pH = 4–5, organic mat 10–20 cm			
open *Empetrum* heath	exposed NW-facing slope and ridge top with shallow snow cover	*E. hermaphroditum*, V. uliginosum,* bryophytes, cryptogamic crust	4, 5, 6
closed *Empetrum* heath	level terrain	*E. hermaphroditum*, B. nana, V. uliginosum,* bryophytes	3, 4
Betula shrubs	depressions with large snow accumulation	*B. nana*, E. hermaphroditum, Vaccinium* spp., bryophytes	3, 5
Salix shrubs	depressions with large snow accumulation	*Salix* spp*., *E. hermaphroditum, B. nana*	4, 5
Abisko — Slåttatjåkka 1150 m			
subarctic fellfield	exposed NW-facing slope with shallow winter snow cover	*C. tetragona*, V. vitis-idaea, Salix polaris, Salix herbacea,* bryophytes, cryptogamic crust	1, 2, 3
Zackenberg — 40–100 m			
Cassiope heath	level terrain	*C. tetragona*, S. arctica,* bryophytes, cryptogamic crust	7, 8
Salix heath	level terrain	*S. arctica*,* herbs, bryophytes, cryptogamic crust	7, 8
south slope heath	S-facing slope with snow accumulation	*C. tetragona*, V. uliginosum,* bryophytes	8
Zackenberg — 470 m			
snowbed	S-facing slope	*S. arctica*,* bryophytes, cryptogamic crust	8
Toolik Lake			
tussock tundra	gentle N-facing slope with deep snow cover	*Eriophorum vaginatum*, B. nana, L. palustre, V. vitis-idaea,* mosses	9
deciduous shrubs	sheltered river bars with large snow accumulation	*Salix* spp.*, *B. nana,* mosses	9
evergreen heath	exposed ridge top with shallow snow cover	*Loiseleuria procumbens, V. vitis-idaea, L. palustre, V. uliginosum,* lichens	9
Eagle Creek			
cottongrass-tussock	gentle N-facing slope with deep snow cover	*Eriophorum vaginatum*, V. vitis-idaea, L. palustre, V. uliginosum,* mosses	10
Ny Ålesund			
beach ridge heath	level terrain	*C. tetragona*, S. polaris, D. octapetala,* bryophytes, cryptogamic crust	1
Fontainemore			
alpine heath	N facing slope with medium snow cover	*V. uliginosum*, R. ferrugineum,* herbs	—

References: 1. Havström et al. (1993), 2. Schmidt et al. (2002); 3. Campioli et al. (2009), 4. Fox et al. (2008), 5. Street et al. (2007), 6. Hartley et al. (2010), 7. Ellebjerg et al. (2008), 8. Bay (1998), 9. Shaver and Chapin (1991), 10. Shaver (1986).

SEPARATION OF SHRUBS IN LEAVES AND STEM/ BRANCH SEGMENT COHORTS OF THE SAME AGE

Individual shrubs of average size were collected in each community. The stem was cut below the moss- or turf layer but above the first major adventitious root. Replicates varied from 5 to 15 for each plant community. For evergreen shrubs, stem and branches were divided into segment cohorts of the same age with the leaves attached, whereas leaves were detached from the stem/ branches and treated separately for deciduous shrubs (see below). The age of the stem/branch segments of *E. hermaphroditum, S.*

artica, S. polaris, and *S. glauca* was determined by counting the apical bud scars (Shaver, 1986). For *B. nana* and *V. uliginosum* bud scars were difficult to identify and thus segment age was identified by counting the annual growth rings in thin stem/branch cross sections after staining with 0.5% phloroglucinol in 10% HCl (Bret-Harte et al., 2002). For *C. tetragona,* stem segments of different age were identified from the size of the attached leaves, which is smaller for leaves formed at the beginning and the end of the growing season (Callaghan et al., 1989). Each stem/branch segment cohort was dried at 70 °C for 48 h, leaves were detached (for evergreen

TABLE 3

Stem secondary growth, stem apical growth, and leaf growth for different tundra shrubs expressed as growth rate (current year's new secondary stem biomass as a percentage of 15-year-old standing stem biomass; % y^{-1}) and per unit ground surface (g biomass m^{-2}).

Species	Community	Growth rate (% y^{-1})			Biomass growth (g m^{-2})		
		stem secondary	stem apical	leaves	secondary stem	apical stem	leaves
C. tetragona	tree-line heath (Abisko)	13	5.2	29	15	5.9	47
	tree-line depressions (Abisko)	9.4	6.6	—	—	—	—
	subarctic fellfield (Abisko)	9.0	5.5	37	3.1	0.6	10
	Cassiope heath (Zackenberg)	7.7	1.5	25	3.6	0.7	11
	South slope heath (Zackenberg)	7.0	3.0	24	—	—	—
	beach ridge heath (Ny Ålesund)	8.8	4.3	30	—	—	—
E. hermaphroditum	tree-line heath (Abisko)	15	8.5	50	—	—	—
	open *Empetrum* heath (Abisko)	16	8.3	55	15	4.4	40
	closed *Empetrum* heath (Abisko)	18	6.9	37	25	10	84
	subarctic fellfield (Abisko)	19	6.0	40	—	—	—
	South slope heath (Zackenberg)	18	10	44	—	—	—
B. nana	tree-line heath (Abisko)	15	0.4	20	6.2	1.1	18
	subarctic fellfield (Abisko)	16	2.5	8.9	—	—	—
	tree-line *Betula* shrubs (Abisko)	19	—	—	—	—	—
	Betula shrubs (Abisko)	23	—	—	99	18	110
	tussock tundra (Toolik Lake) [a] [b]	16	—	—	5.3	4.0	12
L. palustre	cottongrass-tussock (Eagle Creek) [c]	15	—	—	—	—	—
	tussock (Toolik Lake) [a] [c]	7.9	—	—	5.9	4.1	15
	exposed heath (Toolik Lake) [c] [1]	8.9	—	—	0.6	0.8	3.3
S. arctica	*Salix* heath (Zackenberg)	14	4.5	44	12	6	32
	snowbed (Zackenberg)	15	3.7	23	—	—	—
S. polaris	subarctic fellfield (Abisko)	9.1	5.8	56	0.6	0.9	9.3
	beach ridge heath (Ny Ålesund)	11	8.6	—	—	—	—
V. uliginosum	cottongrass-tussock (Eagle Creek) [c] [2]	36	—	—	—	—	—
	alpine heath (Fontainemore)	18	2.5	—	—	—	—
S. pulchra	*Salix* shrubs (Toolik Lake) [c] [1]	30	—	—	23	3.7	20
	tussock tundra (Toolik Lake) [a] [c]	18	—	—	0.8	0.07	1.4
S. glauca	*Salix* shrubs (Abisko)	18	3.7	—	117	34	171

—: data not available; [a] Bret-Harte et al. (2002), [b] Shaver and Chapin (1991), [c] Shaver (1986), [1] for 20-year-old ramets, [2] for 10-year-old ramets.

shrubs), the number of stem/branch segments of each cohort was recorded, as well as the total length and dry weight (Shaver, 1986).

SECONDARY GROWTH RATE

We defined 'stem secondary growth' as the production of current year's new secondary stem biomass as a percentage of old standing stem biomass. We followed the method of Bret-Harte et al. (2002), modified from the approach of Shaver (1986). For each individual shrub, the basic data required were: (i) the number of stem/branch segments of the same age, (ii) the biomass (in mg) of each stem/branch segment cohort, and (iii) the length (in mm) of each cohort (Shaver, 1986). The method is based on geometrical considerations, assuming that a stem/branch

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segment is cylindrical and that the annual increment in stem/branch radius is constant (Bret-Harte et al., 2002). We present here only the key equations for the calculation of the secondary growth on a yearly basis. For details, we refer the readers to Bret-Harte et al. (2002).

First, we estimated the mass (m) of a stem/branch segment cohort of a certain age n (in years) of an individual shrub as:

$$m = l(\alpha^2(n-1)^2 + 2\alpha(n-1)c + c^2), \qquad (1)$$

where l is the length of the stem/branch segment cohort, c equals $\sqrt{m/l}$ of the current-year stem and α the slope of a linear relationship $\sqrt{m/l}$ vs. n. Second, we calculated the annual mass increment due to secondary growth (Δm) of a stem/branch segment cohort as:

$$\Delta m = l(2\alpha^2(n-1) + \alpha^2 + 2\alpha c). \qquad (2)$$

Third, we calculated the mass (M) of the individual shrub as the sum of m for all the segment cohort age classes and the annual mass increment due to secondary growth (ΔM) as the sum of Δm for all the segment cohort age classes:

$$M = \sum_{i=1}^{n} m \qquad (3)$$

$$\Delta M = \sum_{i=1}^{n} \Delta m \qquad (4)$$

Finally, the annual stem secondary growth rate equals $\Delta M/M$. To test statistically the difference in secondary growth of a model species between plant communities, we determined the stem secondary growth for each of 5–15 replicate ramets separately.

Because of this geometrical approach and its underlying assumptions, the age of the ramet has an important impact on the value of stem secondary growth rate, as older segments have larger standing biomass and therefore result in lower relative annual production. We consider the estimates of stem secondary growth derived from 15-year-old ramets as the most relevant for studying aboveground NPP of tundra shrubs as 15-year-old ramets (i) commonly represent the aboveground part of the shrubs, (ii) have stable annual stem secondary growth (Bret-Harte et al., 2002), and (iii) do not have major adventitious roots affecting the secondary growth dynamics (Shaver, 1986). For species for which the sampled ramets did not reach 15 years (e.g. *B. nana* at the tree-line heath) or for which it was difficult to separate the old stem sections in segments of the same age (e.g. not visible bud scars for old stem sections of *E. hermaphroditum*), we modeled m and Δm for the missing oldest stem segment age classes using Equations 1 and 2, assuming constant l. On the other hand, we needed original (not modeled) data sets for statistical comparison of secondary growth between plant communities (see below). Therefore, for these comparisons, we used stem secondary growth rate based on 7-year-old ramets, which were available for all species-plant community combinations.

APICAL GROWTH AND LENGTH INCREMENT

We defined 'apical growth' as the production of current year's new apical biomass as a percentage of old standing stem biomass. Apical growth was determined separately for stem, leaves, and stem plus leaves. 'Length growth' was defined as the total length of the current-year stem or branch segments expressed as a percentage of the total accumulated length of the stem or branch segments older than one year. As for the secondary growth, estimates of apical growth were reported for both 15- and 7-year-old ramets.

AREA-BASED ESTIMATES OF SECONDARY AND APICAL GROWTH

Production of current-year apical stem, current-year leaves, and older (non-current year) standing stem biomass were determined by quadrat harvest (Shaver and Chapin, 1991) for a subset of 8 plant communities between late July and early September. Vegetation was harvested in randomly selected replicate plots (varying from 0.01 to 0.16 m^2 accordingly to cover heterogeneity; n = 5–28), separated at species level in (i) current-year stem, (ii) current-year leaves, and (iii) non-current-year aboveground stem up to the first major adventitious root. Evergreen leaves older than one year were separated from the stems and discarded. Samples were subsequently dried (70 °C, 48 h) and weighed. More details about this methodology can be found in Campioli et al. (2009). Apical stem growth and leaf growth were directly derived from the quadrat harvest results, whereas ground area-based secondary growth (SG_a in g m^{-2}) was determined as:

$$SG_a = M_a - M_a/(1 + SG_r/100), \qquad (5)$$

were M_a is the biomass of the non-current year stem (g m^{-2}) and SG_r the secondary growth rate in % y^{-1} (Shaver, 1986).

STATISTICAL ANALYSIS

Differences in secondary-, apical-, and length growth between individuals living in two plant communities were tested by performing a one-way ANOVA (factor: plant community) combined with Tukey's test for each species and growth component, separately. If prerequisites for analysis of variances (normality, checked with Shapiro's test at W > 0.90 and homoscedasticity, checked with Levene's test at p > 0.05; we assume that our experimental setup prevented dependency among data) were lacking, we performed the Kruskal-Wallis test combined to pairwise Wilcoxon test with Bonferroni correction instead. All analyses were performed in R (R Development Core Team, 2010).

Results

SECONDARY GROWTH PER SPECIES AND PLANT COMMUNITY

The shrubs examined presented stem secondary growth varying between 7 and 36% y^{-1} across species and plant community (Table 3). The evergreen shrubs showed overall lower values of secondary growth: 7–13% y^{-1} for *C. tetragona*, 15–19% y^{-1} for *E. hermaphroditum*, and 9–15% y^{-1} for *L. palustre*. The deciduous shrubs presented larger values and variability: 16–23% y^{-1} for *B. nana*, 9–30% y^{-1} for *Salix* spp., and 18–36% y^{-1} for *V. uliginosum* (Table 3). Remarkable differences were observed between *Salix* species sharing the same growth form and habitat. For instance, the high-statured *S. pulchra* growing in sheltered high shrub vegetation in low arctic Alaska, had secondary growth nearly twice as large as the high-statured *S. glauca* growing in similar habitat in subarctic Sweden (Table 3).
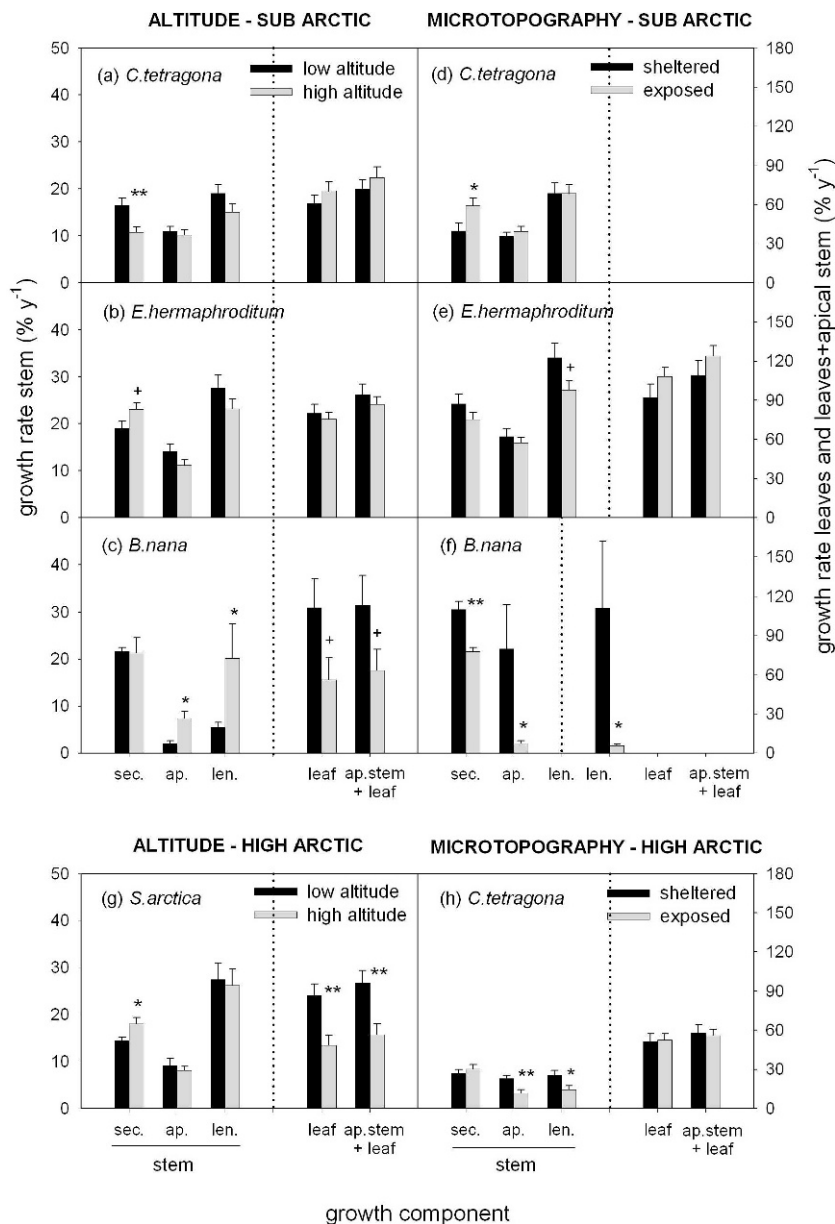
FIGURE 1. Growth rate of the major components of the above-ground growth of tundra shrubs (*sec.*: stem secondary growth; *ap.*: stem apical growth; *leaf*: leaf growth; *ap.stem+leaf*: total apical growth; and *len.*: stem length growth) for four model species (*C. tetragona*, *E. hermaphroditum*, *B. nana*, and *S. arctica*) at selected pairs of dry-mesic tundra contrasting in altitude and microtopography (wind exposure) in the sub- and High Arctic. In reference to Table 2, the pairs of compared plant communities are: (a), (b), and (c) tree-line heath vs. subarctic fellfield (Abisko); (d) tree-line depressions vs. tree-line heath (Abisko); (e) closed *Empetrum* heath vs. open *Empetrum* heath (Abisko); (f) tree-line *Betula* shrubs vs. tree-line heath (Abisko); (g) *Salix* heath vs. snowbed (Zackenberg); and (h) south slope heath vs. *Cassiope* heath (Zackenberg). Growth rate is expressed as current year's new biomass (or length) as a percentage of 7-year-old standing stem biomass (or length) (average plus 1SE; $n = 5$–15; $\%\ y^{-1}$). Significant difference is indicated by asterisks (** for $p < 0.01$, * for $p < 0.05$), whereas a trend ($0.05 < p < 0.10$) is indicated by a plus (+). In each subpanel, scale of y-axes is 0–50 for variables on the left of the dotted line and 0–180 for variables on the right of the dotted line (for panel (f), note that *len.* is on the right of the dotted line because of the exceptionally large stem length growth of *B. nana* at the sheltered subarctic location).

At the ramet level, average secondary growth was equivalent to 5.2 times the apical stem growth and 0.5 times the leaf growth and represented about 27% of the total ramet growth (Table 3). The proportion of secondary stem growth was more important for deciduous shrubs (e.g. 60% for *B. nana* at the subarctic fellfield, 36% for *S. arctica* at a high arctic snowbed) than for evergreen shrubs (e.g. on average 22% and 25% for *C. tetragona* and *E. hermaphroditum*, respectively), but with exceptions (e.g. the proportion of secondary growth for *S. polaris* at the subarctic fellfield was only 13%) (Table 3). These data, calculated at the ramet level, are very similar to the estimates obtained from quadrat harvest (Table 3). In dry-mesic shrub tundra, secondary growth of belowground stem is equivalent to only 3–4% of the total aboveground vascular NPP (Campioli et al., 2009).

As expected, the age of the ramets had an important impact on the absolute values of secondary growth rates, with larger values for younger ramets. For example, for *C. tetragona* secondary growth of 7-year-old ramets (8–16% y^{-1}) was about 1–3% y^{-1} larger than the secondary growth of 15-year-old ramets (7–13% y^{-1}), whereas for *E. hermaphroditum* this difference was 4–5% y^{-1} and for *B. nana* it was up to 12% y^{-1} (Figs. 1–4; Table 3).

IMPACT OF ENVIRONMENTAL VARIABLES ON SECONDARY GROWTH AND BRANCHING

Stem secondary growth was not greatly affected by environmental drivers. Significant variation ($p < 0.05$) was observed between populations differing in (i) altitude for *C. tetragona* in the subarctic (decrease of 6% y^{-1} with increase in altitude; Fig. 1, part a) and for *S. arctica* in the High Arctic (increase of 4% y^{-1} with altitude; Fig. 1, part g); (ii) microtopography for *C. tetragona* (increase of 5% y^{-1} with exposure; Fig. 1, part d) and *B. nana* (decrease of 9% y^{-1} with exposure; Fig. 1, part f), both in the subarctic; and (iii) latitude, for *C. tetragona* between subarctic and High Arctic (decrease of 8% y^{-1} with increase in latitude; Fig. 2, part a). In addition, the secondary growth of *E. hermaphroditum* showed a tendency ($p < 0.1$) to increase about 4% y^{-1} with altitude (Fig. 1, part b). The number of branches of *C. tetragona* was largest at a subarctic tree-line heath, intermediate at subarctic tree-line depressions, and lower at the colder sites (subarctic high altitude fellfield and high arctic heaths), with the lowest number of branches for populations from Greenland (Fig. 5, part a). By contrast, *E. hermaphroditum* presented the largest number of
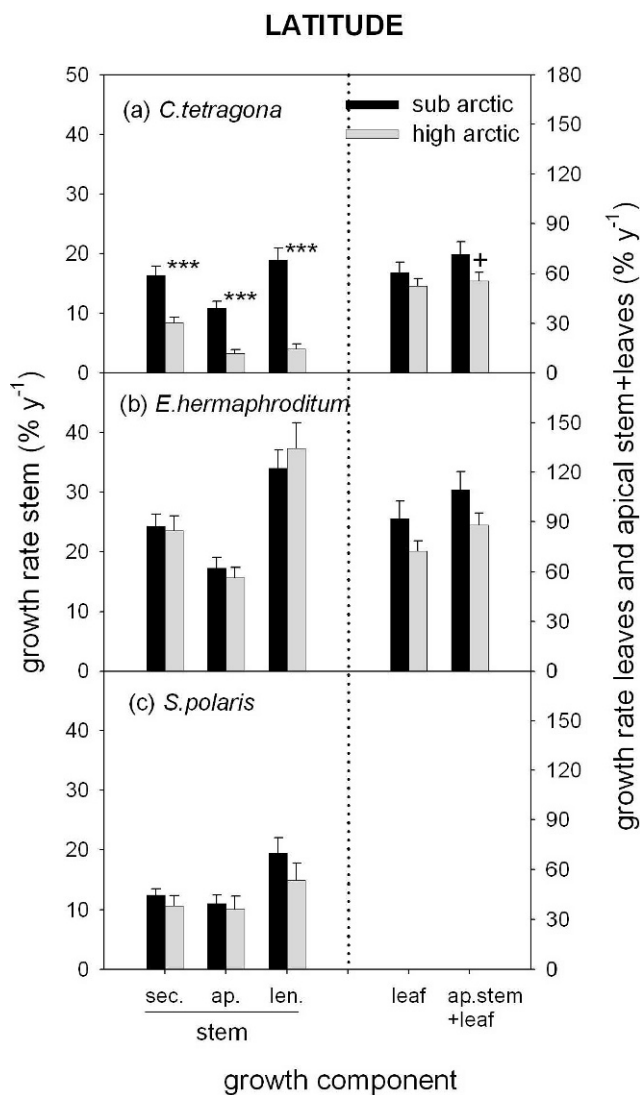
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LATITUDE

FIGURE 2. Growth rate of the major components of the above-ground growth of tundra shrubs (*sec.*: stem secondary growth; *ap.*: stem apical growth; *leaf*: leaf growth; *ap.stem+leaf*: total apical growth; and *len.*: stem length growth) for three model species (*C. tetragona*, *E. hermaphroditum*, and *S. polaris*) at selected pairs of dry-mesic tundra at different latitudes. In reference to Table 2, the pairs of compared plant communities are: (a) tree-line heath (Abisko) vs. *Cassiope* heath (Zackenberg), (b) closed *Empetrum* heath (Abisko) vs. south slope heath (Zackenberg), and (c) subarctic fellfield (Abisko) vs. beach ridge heath (Ny Ålesund). Growth rate is expressed as current years new biomass (or length) as a percentage of 7-year-old standing stem biomass (or length) (average plus 1SE; $n = 6$–12; % y^{-1}). Significant difference is indicated by asterisks (*** for $p < 0.001$) whereas a trend ($0.05 < p < 0.10$) is indicated by a plus (+). In each subpanel, scale of *y*-axes is 0–50 for variables on the left of the dotted line and 0–180 for variables on the right of the dotted line.

branches at a high arctic heath in Greenland and least at the subarctic tree-line heath, with other subarctic plant communities presenting intermediate values (Fig. 5, part b).

SECONDARY GROWTH VS. APICAL- AND LENGTH GROWTH

As for secondary growth, apical stem growth showed a modest sensitivity to environment with (i) decreased growth with exposure for high arctic *C. tetragona* (Fig. 1, part h) and subarctic
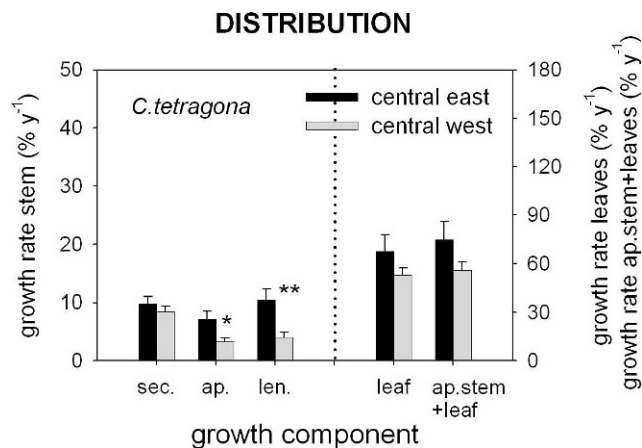
DISTRIBUTION

FIGURE 3. Growth rate of the major components of the above-ground shrub growth (*sec.*: stem secondary growth; *ap.*: stem apical growth; *leaf*: leaf growth; *ap.stem+leaf*: total apical growth; and *len.*: stem length growth) for the model species *C. tetragona* at a beach ridge heath at Ny Ålesund (central-east distribution of the species) and at a *Cassiope* heath at Zackenberg (central-west distribution of the species). Growth rate is expressed as current year's new biomass (or length) as a percentage of 7-year-old standing stem biomass (or length) (average plus 1SE; $n = 8$–12; % y^{-1}). Significant difference is indicated by asterisks (** for $p < 0.01$, * for $p < 0.05$). Scale of *y*-axes is 0–50 for variables on the left of the dotted line and 0–180 for variables on the right of the dotted line.

B. nana (Fig. 1, part f), (ii) increased growth at higher altitude for *B. nana* in the subarctic (Fig. 1, part c), and (iii) decreased growth at the coldest sites at high latitude for *C. tetragona* (Figs. 2, part a; and 3). Irrespective of the significance level, the response (positive or negative) of stem secondary growth and stem apical growth to the same environmental variable showed the same direction of response in 9 out of the 14 cases examined (Figs. 1–4). For 6 of these cases, variations in secondary and apical growth between communities were small ($<3\%$ y^{-1}), whereas for 3 cases secondary and apical growth differences between communities were larger ($>3\%$ y^{-1}).

Total apical growth (i.e. growth of apical stem plus leaves) was almost constant with significant variation only between different soil types for *E. hermaphroditum* (Fig. 4, part a) and growth reduction at higher altitude for *S. arctica* and *B. nana* (Fig. 1, parts c and g), and at higher latitude for *C. tetragona* (Fig. 2, part a). Differences in secondary growth and apical growth between communities increased when total apical growth was considered instead of only stem apical growth. The same direction of response occurred in 6 out of 12 cases, with remarkably different levels of variation for all cases. Leaf growth showed a very similar pattern as total apical growth, consistent with the fact that leaf growth represents 85–90% of total apical growth (Figs. 1–4; Table 3).

Among the different growth components examined (secondary-, apical stem-, leaf-, total apical-, and stem length growth), stem length growth was the one most affected by the environment, with generally lower values under harsher conditions except for *B. nana* at higher altitude (Fig. 1, part c). Variation in stem secondary growth and stem length growth showed the same direction of response in 7 out of 14 cases, but in 5 of these cases with much variability. The variation in stem length growth between contrasting plant communities was similar to the variation in apical stem growth (same direction of response of difference for 12 out of 14 cases), but in general it was larger in extent.
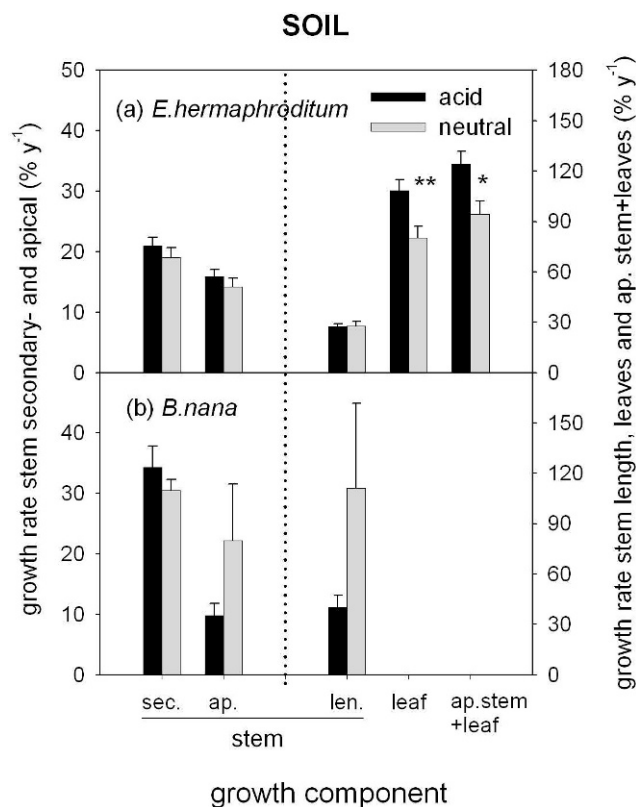
FIGURE 4. Growth rate of the major components of the above-ground growth of tundra shrubs (*sec.*: stem secondary growth; *ap.*: stem apical growth; *leaf*: leaf growth; *ap.stem+leaf*: total apical growth; and *len.*: stem length growth) for two model species (*E. hermaphroditum* and *B. nana*) at selected pairs of dry-mesic tundra with contrasting soil pH: (a) open *Empetrum* heath vs. tree-line heath (Abisko) and (b) *Betula* shrubs vs. tree-line *Betula* shrubs (Abisko). Growth rate is expressed as current year's new biomass (or length) as a percentage of 7-year-old standing stem biomass (or length) (average plus 1SE; $n = 6$–12; % y^{-1}). Significant difference is indicated by an asterisk (** for $p < 0.01$, * for $p < 0.05$). In each subpanel, scale of y-axes is 0–50 for variables on the left of the dotted line and 0–180 for variables on the right of the dotted line.

Discussion

IMPACT OF ENVIRONMENTAL VARIABLES ON SECONDARY GROWTH

Overall, the impact of environmental variables on secondary growth was rather low, but with important differences among species and functional groups (evergreen vs. deciduous). For *C. tetragona*, secondary growth was similar among high arctic populations and the subarctic high altitude site, and greater at the subarctic low altitude site, in agreement with previous studies documenting that leaf and apical growth of *C. tetragona* is limited at colder sites (Havström et al., 1993). The larger stem secondary growth of *C. tetragona* in more exposed subarctic sites (Fig. 1, part d) was unexpected, as exposed sites are characterized by higher wind and lower soil moisture and nutrients than sheltered sites, in particular depressions (Shaver et al., 1996; Darmody et al., 2004). However, moderate reduction in water and nutrient availability might have had little impact on the growth of *C. tetragona* of the subarctic population, as *C. tetragona* is a xerophyte and is subjected to less competition in more exposed locations. The positive effect of exposure on secondary growth might reflect a larger photosynthate investment to increase stem mechanical strength against wind. In the High Arctic, the positive effect of wind exposure on secondary growth might have been offset by the negative
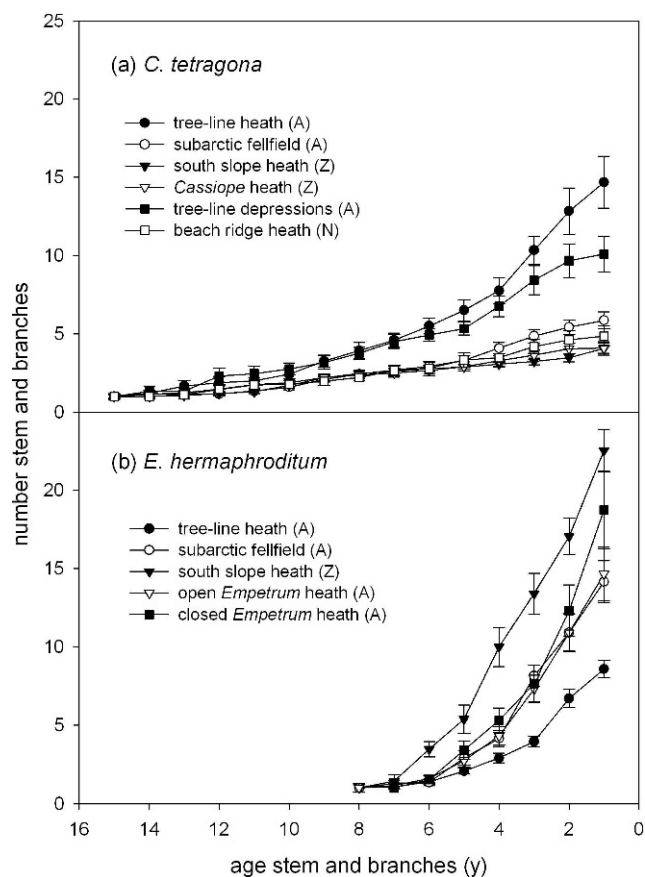

FIGURE 5. Number (mean ± 1SE) of stem and branch segments vs. segment age (in years) for the arctic evergreen dwarf-shrubs (a) *C. tetragona* and (b) *E. hermaphroditum* at different plant communities in the subarctic (A: Abisko) and the High Arctic (Z: Zackenberg; N: Ny Ålesund).

effect of nutrient reduction which was not counterbalanced by decreased competition in these sparsely vegetated high arctic communities. By contrast, the stem secondary growth of *E. hermaphroditum* was affected neither by microtopography nor by higher latitude and even tended to increase at higher altitude. Whereas the lack of correlation between secondary growth of *E. hermaphroditum* and microtopography was confirmed by ring-width chronology (Bär et al., 2008), the reason for lack of growth reduction at colder sites is unclear (Bär et al., 2007, 2008). Branching patterns might explain this. For *C. tetragona* (in all cases examined), more branching corresponded to larger secondary growth as larger plants need larger stems to support more branches (Fig. 5, part a). *Empetrum hermaphroditum* showed similar dynamics except between subarctic and high arctic populations, for which a substantial increase in branching was associated with a non-significant decrease in secondary growth (Figs. 2, part a; and 5, part b). Whereas at subarctic low altitude, *E. hermaphroditum* is abundant and forms extensive homogeneous mats, at high arctic locations *E. hermaphroditum* is less common and is present only as small patches composed of few large plants. Therefore, lack of a relationship between latitude and secondary growth might be an artifact due to sampling, and secondary growth at high latitude might be overestimated. Compared to our model evergreen species, *L. palustre* showed intermediate characteristics, with different secondary growth between individuals at different latitudes but not with different microtopography (Table 3; Shaver, 1986; Bret-Harte et al., 2002).

For deciduous species, secondary growth did not vary with latitude (*S. polaris*) and presented different responses to altitudinal

variations, with no variation for subarctic *B. nana* and increased secondary growth with higher altitude for high arctic *S. arctica*. Because the high altitude site at Zackenberg is characterized by milder temperatures (Table 1 and Material and Methods), the increased stem secondary growth of *S. arctica* with altitude might be an indication of better growth under less harsh conditions. The substantial reduction in secondary growth of *B. nana* in less sheltered sites was due to its large growth plasticity. In contrast to evergreens, the growth form of subarctic deciduous shrubs changes substantially with microtopography, with high-statured individuals and dense stands in sheltered sites and prostrate and isolated individuals in exposed locations. High-statured deciduous shrubs in sheltered locations invest more biomass in stem secondary growth, as the need for mechanical support of erect growth forms is greater, and moist, nutrient-rich sheltered sites support larger individuals than dry, nutrient-poor exposed sites. The comparison of the secondary growth of *V. uliginosum* at an arctic site (Eagle Creek, Alaska) (36% y^{-1}) and near its southern distributional limit in an alpine environment (Fontainemore, Italy) (18% y^{-1}), and *S. pulchra* in a sheltered community (deciduous shrubs) (30% y^{-1}) and a less sheltered community (tussock) (18% y^{-1}) at the same arctic location (Toolik lake) (Table 3; Shaver, 1986; Bret-Harte et al., 2002), confirms that the secondary growth of deciduous tundra shrubs is more affected by microtopography than by the harshness of the climate. Although non-significant, the lower secondary growth of *E. hermaphroditum* and *B. nana* at the least acidic site was expected, as these species are typical of acidic soils (De Groot et al., 1997; Tybirk et al., 2000).

We should stress that the approach we used in this study to define the environmental variables differing between plant communities (and assumed to drive the growth variations) is rather simplistic. More environmental variables may vary between sites than just the variables we have used for the site characterization, and unexpected environmental conditions might occur for some sites (e.g. see the mild temperature for the high altitude site at Zackenberg; Table 1). However, the key general trends emerged in this exploratory work provide a sound base upon which more specific gradient studies can rely to further elucidate the environmental sensitivity of stem secondary growth of tundra shrubs.

*SECONDARY GROWTH VS. APICAL- AND
LENGTH GROWTH*

Stem apical growth and stem secondary growth showed the same direction of response to environmental variables in only 64% of the cases examined, whereas the magnitude of the response was similar in only 43% of the cases. Even more variation was observed between the impact of environment on secondary growth and the impact of environment on total apical growth and stem length growth. Therefore, apical growth cannot be used as an indicator of stem secondary growth when studying the impact of the environment on the growth of tundra shrubs. Furthermore, assessments of shrub growth performance based only on apical growth should not overlook potential biases caused by the inconsistent environmental sensitivity of apical and secondary growth, as secondary growth is an important component (accounting for 25–30% of NPP) of the total aboveground growth.

The different environmental responses shown by apical and secondary growth are likely due to the different (eco)physiology of these two growth components. Whereas apical growth has the unique function of intercepting light (competing with other individuals), secondary growth has different functions: (1) to sustain apical growth and the photosynthetic C uptake by e.g. producing new conduits for water and sugar transport, and storage of non-structural carbohydrate reserves, (2) to mechanically sustain the

whole plant, and (3) to protect the plant from direct and indirect adverse environmental impacts as e.g. by replacing embolized conduits and by providing enhanced mechanical support against wind. As a response to a given environmental variable, our results show that these components of the secondary growth might change in the same way (thus producing a remarkable variation in secondary growth) or counter-balance each other (thus producing a non-significant variation in secondary growth).

Conclusion

This study has revealed that the stem secondary growth of tundra shrubs has modest sensitivity to the physical environment but that large differences among species and functional groups do exist. For example, the secondary growth of *C. tetragona* was affected by altitude, microtopography, and latitude much more than the secondary growth of *E. hermaphroditum*, whereas the impact of microtopography was much larger for the deciduous species *B. nana*, which has a flexible growth form. Furthermore, we showed that the impact of the environment on stem apical growth (as well as on stem length and apical growth of stem plus leaves) differs from the impact of the environment on secondary growth, even to the extent that secondary growth and apical growth may show opposite responses. On the other hand, we confirmed that the biomass produced by stem secondary growth is much larger (5 times) than the biomass produced by stem apical growth and that it is important (25–30%) even when considering growth of apical stem plus leaves. This should not be overlooked by arctic biogeochemists as wood is a longer term C storage than leaves.

Future priority areas in the study of the stem secondary growth of tundra shrubs comprise: (i) investigating gradients for the variables found to clearly drive stem secondary growth (e.g. latitude for *C. tetragona*, microtopography for *B. nana*); (ii) translating the knowledge gained on tundra shrubs to boreal shrubs, as shrub understory plays an important role in determining NPP of boreal ecosystems; and (iii) analyzing the impact of biotic effects as competition and herbivory on secondary stem growth, which might be of importance in tundra sites with more benign environmental conditions.

References Cited

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jonsdottir, I. S., Laine, K., Levesque, E., Marion, G. M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wookey, P. A., 1999: Responses of tundra plants to experimental warming: meta-

analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.

Bär, A., Bräuning, A., and Löffler, J., 2007: Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from the Norwegian mountains. *IAWA Journal*, 28: 325–338.

Bär, A., Pape, R., Bräuning, A., and Loffler, J., 2008: Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography*, 35: 625–636.

Bay, C., 1998: Vegetation mapping of Zackenberg valley, Northeast Greenland. Copenhagen: Danish Polar Center and Botanical Museum, University of Copenhagen, 29 pp.

Bliss, L. C., and Matveyeva, N. V., 1992: Circumpolar arctic vegetation. *In* Chapin, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate. an Ecophysiological Perspective*. San Diego: Academic Press, 59–89.

Bret-Harte, M. S., Shaver, G. R., and Chapin, F. S., 2002: Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology*, 90: 251–267.

Callaghan, T. V., Carlsson, B. A., and Tyler, N. J. C., 1989: Historical records of climate-related growth in *Cassiope tetragona* from the Arctic. *Journal of Ecology*, 77: 823–837.

Callaghan, T. V., Björn, L. O., Chapin, F. S., Chernov, Y., Christensen, T. R., Huntley, B., Ims, R., Johansson, M., Riedlinger, D. J., Jonasson, S., Matveyeva, N., Oechel, W., Panikov, N., and Shaver, G. R., 2005: Arctic tundra and polar desert ecosystems. *In ACIA: Arctic Climate Impact Assessment*. New York: Cambridge University Press, 243–352.

Campioli, M., Michelsen, A., Demey, A., Vermeulen, A., Samson, R., and Lemeur, R., 2009: Net primary production and carbon stocks for subarctic mesic-dry tundras with contrasting microtopography, altitude, and dominant species. *Ecosystems*, 12: 760–776.

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A., 1995: Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, 76: 694–711.

Darmody, R. G., Thorn, C. E., and Dixon, J. C., 2004: Relationship of vegetation distribution to soil properties in Karkevagge, Swedish Lapland. *Arctic, Antarctic, and Alpine Research*, 36: 21–32.

De Groot, W. J., Thomas, P. A., and Wein, R. W., 1997: *Betula nana* L and *Betula glandulosa* Michx. *Journal of Ecology*, 85: 241–264.

Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M., Dickinson, R. E., Hauglustaine, D., Heinze, C., Holland, E., Jacob, D., Lohmann, U., Ramachandran, S., da Silva Dias, P. L., Wofsy, S. C., and Zhang, X., 2007: Couplings between changes in the climate system and biogeochemistry. *In* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.), *Climate Change 2007: the Physical Science Basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press, 501–587.

Ellebjerg, S. M., Tamstorf, M. P., Illeris, L., Michelsen, A., and Hansen, B. U., 2008: Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *Advances in Ecological Research*, 40: 249–273.

Fetcher, N., and Shaver, G. R., 1982: Growth and tillering patterns within tussocks of *Eriophorum vaginatum*. *Holarctic Ecology*, 5: 180–186.

Fletcher, B. J., Press, M. C., Baxter, R., and Phoenix, G. K., 2010: Transition zones between vegetation patches in a heterogeneous arctic landscape: how plant growth and photosynthesis change with abundance at small scales. *Oecologia*, 163: 47–56.

Fox, A. M., Huntley, B., Lloyd, C. R., Williams, M., and Baxter, R., 2008: Net ecosystem exchange over heterogeneous arctic tundra: scaling between chamber and eddy covariance measurements. *Global Biogeochemical Cycles*, 22(2): GB2027.

Freppaz, M., Celi, L., Marchelli, M., and Zanini, E., 2008: Snow removal and its influence on temperature and N dynamics in alpine soils (Vallée d'Aoste, northwest Italy). *Journal of Plant Nutrition and Soil Science*, 171: 672–680.

Graglia, E., Jonasson, S., Michelsen, A., and Schmidt, I. K., 1997: Effects of shading, nutrient application and warming on leaf growth and shoot densities of dwarf shrubs in two arctic-alpine plant communities. *Ecoscience*, 4: 191–198.

Hartley, I. P., Hopkins, D. W., Sommerkorn, M., and Wookey, P. A., 2010: The response of organic matter mineralization to nutrient and substrate additions in sub-arctic soils. *Soil Biology and Biochemistry*, 42: 92–100.

Havström, M., Callaghan, T. V., and Jonasson, S., 1993: Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high sites and sub-arctic sites. *Oikos*, 66: 389–402.

Hobbie, S. E., 1996: Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, 66: 503–522.

Jensen, L. M., and Rasch, M., 2009: *Zackenberg Ecological Research Operations, 14th Annual Report, 2008*. Roskilde: National Environmental Research Institute, Aarhus University, 116 pp.

Jensen, L. M., and Rasch, M., 2010: *Zackenberg Ecological Research Operations, 15th Annual Report, 2009*. Roskilde: National Environmental Research Institute, Aarhus University, 134 pp.

Jonasson, S., Michelsen, A., Schmidt, I. K., and Nielsen, E. V., 1999: Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. *Ecology*, 80: 1828–1843.

Klitgaard, A. B., Rasch, M., and Caning, K., 2007: *Zackenberg Ecological Research Operations, 12th Annual Report, 2006*. Copenhagen: Danish Polar Center, Danish Agency for Science, Technology and Innovation, 104 pp.

Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V., and Lee, J. A., 1994: Growth responses of four subarctic dwarf-shrubs to simulated environmental change. *Journal of Ecology*, 82: 307–318.

Phoenix, G. K., Gwynn-Jones, D., Callaghan, T. V., Sleep, D., and Lee, J. A., 2001: Effects of global change on a subarctic heath: effects of enhanced UV-B radiation and increased summer precipitation. *Journal of Ecology*, 89: 256–267.

R Development Core Team, 2010, *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Schmidt, I. K., Jonasson, S., Shaver, G. R., Michelsen, A., and Nordin, A., 2002: Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming. *Plant and Soil*, 242: 93–106.

Shaver, G. R., 1986: Woody stem production in Alaskan tundra shrubs. *Ecology*, 67: 660–669.

Shaver, G. R., and Chapin, F. S., 1991: Production-biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, 61: 1–31.

Shaver, G. R., Laundre, J. A., Giblin, A. E., and Nadelhoffer, K. J., 1996: Changes in live plant biomass, primary production and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research*, 28: 363–379.

Street, L. E., Shaver, G. R., Williams, M., and Van Wijk, M. T., 2007: What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems? *Journal of Ecology*, 95: 139–150.

Tybirk, K., Nilsson, M. C., Michelson, A., Kristensen, H. L., Shevtsova, A., Strandberg, M. T., Johansson, M., Nielsen, K. E., Rils-Nielsen, T., Strandberg, B., and Johnsen, I., 2000: Nordic *Empetrum* dominated ecosystems: function and susceptibility to environmental changes. *Ambio*, 29: 90–97.

Wein, R. W., and Bliss, L. C., 1974: Primary production in arctic cottongrass tussock tundra communities. *Arctic and Alpine Research*, 6: 261–274.

Wielgolaski, F. E., Bliss, L. C., Svoboda, J., and Doyle, G., 1981: Primary production of tundra. *In* Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems: a Comparative Analysis*. Cambridge: Cambridge University Press, 187–226.