Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change

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Summary

1 Shrubs are among the tundra plants most responsive to environmental change. We measured primary and secondary stem growth in a retrospective analysis of ramets of three codominant shrubs (Betula nana, Salix pulchra, and Ledum palustre ssp. decumbens) exposed to long-term field treatment with greenhouses and N + P fertilizers at Toolik Lake, Alaska.

2 Ramets of Salix had the greatest primary stem growth under control conditions, because of their relatively high branching rate. Under fertilization, however, Betula produced much more primary stem growth than the other species, because axillary buds that would have grown as short shoots in control ramets were instead stimulated to produce long shoots (structural branches). There appeared to be a trade-off between allocation to length per stem segment and number of stem segments produced in a given year, for both Betula and Ledum.

3 Although secondary growth in stems is the largest component of above-ground net primary production in forests, it is often ignored in shrub-dominated ecosystems. We derived an expression for secondary growth in shrubs based on distributions of stem mass and length with age, and allowing for experimentally induced changes in secondary growth rate.

4 There was good agreement between measured ramet stem mass and calculated values for all three species, validating our mathematical analysis of secondary growth.

5 Fertilization greatly increased the relative rate of secondary growth only in Betula, consistent with observed accumulations of its stem mass in ecosystem-level quadrat harvests. Secondary growth of Betula was a major component of ecosystem NPP in fertilized plots and probably contributes significantly to ecosystem carbon storage.

6 The increase in its secondary growth enabled Betula to become dominant under fertilization, whereas the inability of older stems of Ledum to respond in this way prevented it from growing into the canopy.

Key-words: arctic tundra, Betula nana, carbon storage, elevated temperature, nitrogen and phosphorus fertilization

Introduction

The slow-growing, clonal, and long-lived growth patterns seen in many arctic plants may be advantageous for survival in a harsh physical environment (Callaghan 1988). Recruitment of seedlings into mature life stages is rare, however (McGraw & Shaver 1982; McGraw & Fetcher 1992), and vegetation response to changing environmental conditions is often driven by the differential growth of individual plants. Analysis of growth may therefore give insight into the mechanisms underlying ecosystem response to environmental perturbation.

Anthropogenically induced climate change is expected to be most pronounced at high latitudes (Houghton et al. 1996). Their potential to respond to climate change makes arctic shrubs of particular importance for tundra ecosystems. Tundra responds...
strongly to manipulations of nutrient availability and temperature that simulate climate change, in both eco-
system properties such as net primary production and in the growth of individual species (Chapin et al. 1995; Chapin & Shaver 1996; Bret-Harte et al. 2001). In Alaskan moist tussock tundra, increased dominance of Betula nana is one of the most striking changes under increased nutrient availability (Fig. 1; Bret-Harte et al. 2001; Chapin et al. 1995). Betula’s dominance results from increased growth of individuals present at the start of the experiment, rather than recruitment of new individuals (Bret-Harte et al. 2001). Although more nutrients were added in this experiment (four times the annual N requirement for above-ground vascular production and 20 times the annual P requirement in this site (Shaver & Chapin 1991)) than would be expected to be associated with climate change over the short term, Betula did increase on the Alaskan North Slope during the last warm period, about 9000 yr, as seen in long-
term pollen records (Brubaker et al. 1995).

Ecologists have successfully applied a demographic approach to retrospective analysis of plant growth in individuals of a variety of species (e.g. Svensson & Callaghan 1980; Maillette 1982; Callaghan et al. 1986; Maillette 1987; Ebert & Ebert 1989). Although this approach gives insight into the patterns of growth and mortality of populations of meristems, it does not pro-
provide a direct measure of changes in biomass with time or under an experimental treatment. In particular, one cannot easily address changes in secondary growth by woody species, such as tundra shrubs, using this method.

Secondary growth of woody stems is essential to supply mechanical strength for supporting an aerial can-
opy and for hydraulic transport of water to foliage. In single trees and forests, secondary growth usually greatly exceeds primary stem growth and leaf produc-
tion (Grier et al. 1981; Whittaker et al. 1979) and is often used to estimate forest biomass and production (e.g. Phillips et al. 1998). For shrubs and mixed vegeta-
tion of low stature, however, secondary growth is still frequently considered negligible or is ignored. For example, a recent calculation of carbon-13 exchanges between atmosphere and biosphere ignored the contribution of wood in tundra ecosystems (Fung et al. 1990).
In the previous attempt to estimate the contribution of secondary growth to productivity in arctic tundra, Shaver (1986) determined distributions of mass per unit length with age for stem segments of tussock tundra. This approach assumed a constant relative rate of secondary growth and could not accommodate any changes in growth caused by experimental manipulations. Also, it used terminal bud scars to determine the age of stem segments, and thus excluded species such as Betula nana, which do not produce these persistently visible markers, from being analysed.

In this study, we retrospectively analysed the primary and secondary growth of Betula nana and two other common tundra shrubs exposed to long-term manipulations of nutrient availability and temperature. We expanded Shaver’s (1986) approach and used a mathematical analysis to derive an expression for secondary growth that could be evaluated from distributions of mass and length with age. Our derivation took into account the geometry of stem growth and the effects of experimental treatment on secondary growth.

Our objectives were (1) to quantify primary and secondary stem growth in these species; (2) to understand how primary and secondary growth change under altered environmental conditions; and (3) to understand how the patterns of growth of Betula nana allow it to achieve dominance under increased nutrient availability. Our analysis gives insight into the contribution of secondary growth to shrub growth and response to environmental change.

Materials and methods

SITE AND TREATMENTS

We conducted this study in moist tussock tundra (Bliss & Matveeva 1992) near Toolik Lake at the arctic Long-term Ecological Research (LTER) site in the northern foothills of the Brooks Range of arctic Alaska (68°38’ N, 149°34’ W; elevation 760 m). Vegetation on the site is characterized by approximately equal biomass of graminoids (mainly Eriophorum vaginatum and Carex bigelowii), deciduous shrubs (mainly Betula nana, with less Salix pulchra), evergreen shrubs (mainly Ledum palustre ssp. decumbens and Vaccinium vitis-idaea), and mosses (mainly Hylocomium splendens, Aulacomnium turgidum, Dicranum spp. and Sphagnum spp.) (Shaver & Chapin 1991). Nomenclature follows Hultén (1968).

Detailed information on the experimental treatments and their environmental effects is given by Bret-Harte et al. (2001) and Chapin et al. (1995). Briefly, in 1988 we established four replicate blocks in homogene-
and a 17% average decrease in relative humidity during June, when the sun was highest in the sky. This 20% light reduction is less than the 30% reduction recorded by Chapin et al. (1985), who used a different plastic to cover the greenhouses. Greenhouses did not decrease soil moisture (Chapin et al. 1995). Consequences of these unintended effects were evaluated by McKane et al. (1997).

**RAMET GROWTH ANALYSIS**

In 1995 we analysed branches from two deciduous and one evergreen shrub species (*Betula nana*, *Salix pulchra*, and *Ledum palustre* ssp. *decumbens*) for growth performance prior to and during the experiment. These shrubs are long-lived and grow clonally; their supporting branches are largely prostrate and become progressively covered by moss, after which they produce adventitious roots. It is thus difficult to identify genetic individuals in the field. Three ramets (large, rooted branches) of each species were chosen randomly from each treatment in each block, giving 12 ramets per treatment except for *Salix* in the greenhouse-plus-fertilizer treatment. In that treatment, there was only enough *Salix* to collect one ramet from each of three blocks. The stem and attached branches of each ramet were pulled up and the stem was cut underground. In the laboratory, the most apical 12–15 years of growth were analysed for branch structure, mass, and length. Thus, ramets had grown for up to 9 years before the experiment began, then for another 6 years under experimental treatment. Ramets were harvested from mid-June to early August. We analysed one ramet of each species from all treatments in all blocks before collecting subsequent ramets. Changes in growth or mortality that occurred over the harvest period were thus averaged across the season in all treatments.

To determine distributions of branch number, stem biomass, and stem length with age in each ramet, a map (drawing) was made of the branch structure and ages of the most apical 12–15 years of growth, counting 1995 as year 0. Ages of branches in ramets of each species from all treatments in all blocks before experimental treatment. Ramets were harvested from mid-June to early August. We analysed one ramet of each species from all treatments in all blocks before collecting subsequent ramets. Changes in growth or mortality that occurred over the harvest period were thus averaged across the season in all treatments.

To determine distributions of branch number, stem biomass, and stem length with age in each ramet, a map (drawing) was made of the branch structure and ages of the most apical 12–15 years of growth, counting 1995 as year 0. Ages of branches in ramets of *Salix* and *Ledum* were determined by counting terminal bud scars (Shaver 1986), which are visible for many years. *Betula* does not form persistent bud scars, so branch ages were determined by cutting thin stem cross-sections by hand with a razor blade. Annual growth rings in stem cross-sections were counted at 50 × or 100 × magnification under a compound microscope, after staining with 1% phloroglucinol in 20% HCl (Fig. 2). Whenever possible, at least two stem cross-sections were cut within each year of growth. Where a stem indicated different ages at the apical and basal ends of the closest cuts, mass and length values were evenly divided among the age classes in that piece.

*Betula* has long/short shoot dimorphism. Long shoots undergo extensive primary and secondary growth, and provide many opportunities for branching by producing buds in each leaf axil. In contrast, short shoots have little internodal elongation or subsequent secondary growth, few leaves, and usually produce only one viable bud for growth in the following season; thus, they do not lead to further branching. Short shoots occasionally convert to long shoots, and secondary growth is also triggered following the conversion. Because short shoots do not branch or produce much wood, we define a ‘structural branch’ for *Betula* to include only long shoots and short shoots that have converted to long shoots. For *Salix* and *Ledum*, all branches are structural, as these plants do not make short shoots.

**IMPLEMENTATION OF ANALYSIS AND COMPARISONS WITH OTHER CALCULATIONS**

Data were summarized and calculations of secondary growth were implemented using Excel spreadsheets (Microsoft 1998). Our calculations were based on mean values of length and mass/length for stem segments of a given age and shoot type. We calculated secondary growth for the entire growing season, but assumed that measured values of mass and length represented values after half the current season’s growth had occurred, because ramets were harvested throughout the season. Different assumptions about the amount of growth experienced before harvest had little effect on calculated relative rates of secondary growth (data not shown).

Our results were compared with two other estimates of secondary growth, both of which assumed that the relative secondary growth rate is represented by the slope (h) of the logarithm-transform of mass/length vs. age (Shaver 1986). This method was developed using plants that did not experience a large change in environment during the period in which growth was analysed, but each of our ramets contained stem segments that grew both before and for 6 years after the experiment began (Fig. 2). To compare with our analysis, we therefore applied Shaver’s (1986) method by calculating h separately for stem segments formed before and after the
Stem growth in arctic shrubs


treatment began (‘Shaver 86a’), and also by calculating h only for stem segments formed after the treatments began, and applying that value to all stem segments (‘Shaver 86b’).

We estimate secondary growth in shrub ramets from a mathematical analysis that uses empirical data on mass and length of stem segments of different ages. Our expression for secondary growth is derived geometrically, assuming that a stem segment is cylindrical and that the annual increment (a) in its radius (r) is constant on average; although the radial increment may vary between years, we assume that its mean value does not change systematically with age. Our analysis allows for a change in the radial increment following a persistent environmental alteration (see Experimentally induced change in rate of secondary growth, below). All symbols used in this analysis are defined in Table 1.

The value of a can be determined from the relationship between the age of stem segments and their mass per unit length (ml/l). From the formula for the volume of a cylinder, \( \pi r^2 l \), mass/length equals \( \pi r^2 \). The radius of a cylindrical stem at time t equals the radius \( a_t \) at the end of the segment’s first year of growth, plus the years since then (s) times a. Taking the square root of this formula,

\[
(ml/l)^{1/2} = \pi^{1/2} \rho^{1/2} (a + a_t) \quad \text{eqn 1}
\]

Therefore, if a is constant on average, the square root of a segment’s mass/length should increase linearly with age. Data for control ramets (Fig. 3) conform to this expectation in the shrubs we analysed, indicating that a is indeed relatively constant, on average, over 15 years of growth. If \( \alpha \) is the slope of such a plot of \((ml/l)^{1/2}\) vs. age, then \( a = \alpha (\pi \rho)^{1/2} \).

We can find the increment in mass (\( \Delta m \)) of a stem segment due to secondary growth during a period \( \Delta x \) (expressed in number of growing seasons and fractions thereof) from the radii at the beginning and end of the period \( \Delta x \). The beginning radius is \( a_1 + a_x \), the end radius is \( a_1 + a_x + \Delta a \), and \( \Delta m \) is the segment mass at the end minus its mass at the beginning. Squaring these radii, substituting them into the equation for mass/length above, multiplying by length to give mass, and substituting \( \alpha (\pi \rho)^{1/2} \) for a, gives \( \Delta m \) as

\[
\Delta m = \frac{\Delta x}{2a^2 c}\Delta a + \alpha^2 (\Delta x)^2 \left[ 1 + \frac{\Delta a}{2a\Delta x} \right] \quad \text{eqn 2}
\]

where \( c = a (\pi \rho)^{1/2} \). Since stem mass/length after the first year of growth equals \( c^2 \), equation 2 can be evaluated from empirical data. However, equation 2 describes the increment in mass for only one age class of stem segments over the time interval \( \Delta x \). The increment in stem mass of the whole ramet (M) due to secondary growth is the sum over all age classes of segments.
Symbols used in the mathematical analysis and their definitions

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>Annual radial increment under control conditions (mm y$^{-1}$)</td>
</tr>
<tr>
<td>$a_i$</td>
<td>Radius of stem segment after 1st year of secondary growth (i.e. radius of primary growth + 1 year) (mm)</td>
</tr>
<tr>
<td>$b$</td>
<td>Annual radial increment under experimental conditions (mm y$^{-1}$)</td>
</tr>
<tr>
<td>$b_i$</td>
<td>Radius of stem segment after 1st year of secondary growth under experimental conditions (i.e. radius of primary growth + 1 year) (mm)</td>
</tr>
<tr>
<td>$c$</td>
<td>Square root of mass/length of segments after 1 year of growth under control conditions (mg$^{1/2}$ mm$^{-1/2}$)</td>
</tr>
<tr>
<td>$c_i$</td>
<td>Square root of mass/length of segments after 1 year of growth under experimental conditions (mg$^{1/2}$ mm$^{-1/2}$)</td>
</tr>
<tr>
<td>$f$</td>
<td>Years since treatment began (y)</td>
</tr>
<tr>
<td>$g$</td>
<td>Age when treatment began minus 1 (y)</td>
</tr>
<tr>
<td>$h$</td>
<td>Slope of the natural log of (mass/length) vs. age</td>
</tr>
<tr>
<td>$i$</td>
<td>Length of stem segments in a given age class (mm)</td>
</tr>
<tr>
<td>$m$</td>
<td>Mass of stem segment (mg)</td>
</tr>
<tr>
<td>$M$</td>
<td>Mass of whole ramet (mg)</td>
</tr>
<tr>
<td>$M_l$</td>
<td>Old stem biomass per m$^2$ (g m$^{-2}$)</td>
</tr>
<tr>
<td>$n$</td>
<td>Age of the whole ramet (y)</td>
</tr>
<tr>
<td>$p$</td>
<td>Primary stem growth in the current year (g m$^{-2}$)</td>
</tr>
<tr>
<td>$r$</td>
<td>Radius of stem segment (mm)</td>
</tr>
<tr>
<td>$R$</td>
<td>Relative rate of secondary growth compounded continuously (y$^{-1}$)</td>
</tr>
<tr>
<td>$t$</td>
<td>Time (y)</td>
</tr>
<tr>
<td>$v$</td>
<td>Volume of a cylinder (mm$^3$)</td>
</tr>
<tr>
<td>$x$</td>
<td>Age of stem segment minus 1 (y)</td>
</tr>
<tr>
<td>$z$</td>
<td>Stem biomass lost from the above-ground biomass compartment in 1 year due to mortality or engulfment by moss (g m$^{-2}$)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Slope of the square root of (mass/length) vs. age for control stem segments (mg$^{1/2}$ mm$^{-1/2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>$\alpha_i$</td>
<td>Slope of the square root of (mass/length) vs. age for control stem segments (mg$^{1/2}$ mm$^{-1/2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Slope of the square root of (mass/length) vs. age under experimental conditions for segments formed before the treatment took effect (mg$^{1/2}$ mm$^{-1/2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>$\beta_i$</td>
<td>Slope of the square root of (mass/length) vs. age under experimental conditions for segments formed after the treatment took effect (mg$^{1/2}$ mm$^{-1/2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Density of biomass in stem segments (mg/mm$^3$)</td>
</tr>
<tr>
<td>$\Delta x$</td>
<td>Increment in time over which secondary growth is occurring (y)</td>
</tr>
<tr>
<td>$\Delta M$</td>
<td>$\sum_{i=1}^{n} \left(2\pi x_i^2 \Delta x + \alpha (\Delta x)^2 + 2\pi x_i \Delta x \right)$ eqn 3</td>
</tr>
</tbody>
</table>

where $n$ is the age of the ramet, and $i$, the age of any particular class of segments at the start of the interval, equals $x + 1$ (from the definition of $x$, above).

The mass $M$ of one age class of stem segments (neglecting the mass of any short shoots of Betula) is $np\alpha x + \alpha \Delta x$, and the stem mass of the whole ramet is thus

$M = \sum_{i=1}^{n} \left(2\pi x_i^2 + 2\pi x_i \Delta x + \alpha \Delta x \right)$ eqn 4

Comparing mass calculated from this equation with measured values of stem mass provides a check on our analysis (see Results). The fractional increase $\Delta M/M$ in stem mass of the whole ramet due to secondary growth over the time interval $\Delta x$ is equation 3 divided by equation 4.

Experimentally induced change in rate of secondary growth

The shrub ramets that we analysed grew for 12–15 years, the last 6 of which were under experimental treatments. Some of these treatments caused a dramatic increase in secondary growth, even in stem segments formed before the treatment began (Fig. 2). To account mathematically for an experimental treatment that causes a step-change in the rate of secondary growth, we assume that the average value of the radial increment prior to treatment ($a$) increases to a new value following treatment ($b$), which applies to stem segments of all ages.

For stem segments formed after the treatment began to affect secondary growth, the previous analysis applies because $b$ can be substituted for $a$ in equations 1 and 2. Thus, for these segments, there should be a linear relationship between the square root of mass/length and age, and if $\beta$ is the slope of that relationship, $b = \beta (np)^{1/2}$. If $c_i = (np)^{1/2}h_i$, and $h_i$ is the stem radius after the first year of growth under the treatment (analogous to $a_i$), then by equation 2,

$\Delta m = l(2\beta^2 \pi \Delta x + \beta^2 (\Delta x)^2 + 2\beta \pi c \Delta x) \quad$ eqn 5

For stem segments formed before the treatment began, let $f/2$ be the number of years since the treatment began to affect secondary growth, and $g + 1$ be the segment age when the treatment took effect. Thus $x = g + f$, and $n = f + g + 1$, where $n$ is the age of the segment. The stem radii at the beginning and end of the interval $\Delta x$ are then $a_i + ag + bf$ and $a_i + ag + bf + h_i \Delta x$. As in the derivation of equation 2, $\Delta m$ can be calculated from these stem radii in terms of both $a$ and $b$.

As before, we can use the empirical relationship between mass/length and age of stem segments to
obtain values to substitute for \(a\) and \(b\). Because \(b\) is the same for all age classes of stem segments, we can substitute \(b = \beta(np)^{1/2}\), as above. For stem segments formed before the treatment began to affect secondary growth, \(ml = np(a + ag + bf)^2\). Although \(f\) increases with time following treatment, it is constant for all segments harvested at the same time. Only \(g\) varies with age in this equation, giving a linear relationship between square root of mass/length and age, whose slope is \(\alpha\). Thus, a plot of square root of mass/length vs. age for ramets from an experimental treatment should consist of two straight lines with slopes \(\alpha\) and \(\beta\), with the breakpoint between the lines occurring when the treatment began to affect secondary growth.

Substituting \(\alpha\), \(\beta\), and \(c\) as in the derivation of equation 2 gives an expression for the increment in mass due to secondary growth in segments formed before the treatment took effect. That can be evaluated from empirically determined mass/length data.

\[
\Delta m = \rho \left[ 2\beta x + 2\alpha + 2\beta^2 \Delta x + \beta^2 (\Delta x)^2 \right] \quad \text{eqn 6}
\]

Equation 6 reduces to equation 2 if \(\alpha = \beta\).

The absolute increment in mass due to secondary growth for the whole ramet is obtained by adding equations 5 and 6 and summing over all age classes of stem segments.

\[
\Delta M = \sum_{x=1}^{n} \left( 2\beta x + 2\alpha + 2\beta^2 \Delta x + \beta^2 (\Delta x)^2 \right) + \\
\sum_{x=1}^{n} \left[ 2\beta x + 2\alpha + 2\beta^2 \Delta x + \beta^2 (\Delta x)^2 \right] \quad \text{eqn 7}
\]

In this equation \(x_i = i - 1, \ g_i = i - f - 1, \ \text{and} \ c_i = (np)^{1/2} h_i\) is the square root of mass/length of 1-year-old segments from experimentally treated ramets. The first sum in equation 7 gives secondary growth in the current year in segments formed after the treatment took effect, while the second sum gives secondary growth in the current year in segments formed before the treatment took effect. Both \(c\) and \(c_i\) must be known to calculate \(\Delta M\) from equation 7. We assumed that \(c\) for treated ramets was the same as for control ramets.

The mass of stem segments formed after the treatment affected secondary growth (i.e. \(x < f\)) is \(m = n(\rho x + h_j)^2\). The mass of segments formed before the treatment took effect is \(m = n(\rho x + ag + bf)^2\).

Expanding and modifying these expressions as in the derivation of equation 4, adding them together, and summing over all age classes in a ramet gives its total stem mass as

\[
M = \sum_{x=1}^{n} \left[ (\beta x_i^2 + 2\beta c_i x_i + c_i) + \\
\sum_{x=1}^{n} \left[ c_i^2 + 2\alpha x_i + x_i^2 \right] \right] \\
= \sum_{x=1}^{n} \left[ 2\beta x_i + 2\alpha x_i + \beta^2 \Delta x_i + \beta^2 (\Delta x_i)^2 \right] \quad \text{eqn 8}
\]

where conventions for subscripts are the same as for equation 7. As before, this result may be compared with empirical values to check our analysis. The fractional increase in mass of the experimentally treated ramet caused by secondary growth is equation 7 divided by equation 8.

For both control and experimentally treated ramets, the fractional increase in biomass is calculated for a finite time interval. The true relative rate of secondary growth (compounded continuously), \(R = dM/Mdt\), is related to a finite fractional change by

\[
1 + \frac{\Delta M}{M} = e^{R \Delta t} \quad \text{eqn 9}
\]

If the growth interval was one growing season, \(\Delta t = 1\).
Correction for reduced \( b \) in older segments

In experimentally treated ramets, the slope of square root of mass/length vs. age of stem segments formed before the treatment took effect should equal \( \alpha \). If that value, which we will call \( \alpha_r \), is less than \( \alpha \) in control ramets (e.g. F vs. C treatments, Fig. 3), either \( a \) or \( b \) must be less in older segments than in segments formed after the treatment began. Since \( a \) applies to pre-treatment growth, it is more reasonable that \( b \) is less in older segments than in younger ones.

An average correction to \( b \) for older segments can be calculated as follows. Assume that \( b \) is constant for a given age class of segments but declines with age; this reduced average \( b \) in older segments will be called \( b_r \). Mass/length of older segments is

\[
\frac{m}{l} = \pi(p\alpha + ag + b_r f) / l
\]

Substituting in \( a \) and \( c \), and letting \( \beta = (\pi p)^2 / \pi \), the square root of mass/length is

\[
\left(\frac{m}{l}\right)^{\frac{1}{2}} = c + ag + \beta f, \quad \text{eqn 10}
\]

To find \( \beta_r \), let \( \alpha_r \) be the slope of the line through the square root of mass/length vs. age for segments formed before the treatment took effect. The equation for this line is

\[
\left(\frac{m}{l}\right)^{\frac{1}{2}} = \alpha_r (g + 1) + \beta_r (f - 1) + c, \quad \text{eqn 11}
\]

The first term in equation 11 is the mass/length that resulted from growth of older segments in the years before treatment. Since \( g \) is defined as age prior to treatment minus one, \( (g + 1) \) is the number of years that each of these segments grew before the treatment affected their growth. The second and third terms in equation 11 together equal the square root of mass/length of segments formed in the first year that the treatment took effect, which is the breakpoint of the curve. Since \( c \), is the square root of mass/length after the first year of growth under treatment, these segments grew for an additional \((f - 1)\) years, with results governed by coefficient \( \beta \). Assuming that \( c \) and \( \alpha_r \) are the same as for control segments, we can set equations 10 and 11 to be equal and solve for \( \beta_r \),

\[
\beta_r = \beta + \frac{(\alpha_r - \alpha)g + c_r - c + \alpha_a - \beta}{f}, \quad \text{eqn 12}
\]

\( \beta_r \) is substituted for \( \beta \) in the second sum terms in equations 7 and 8.

Comparison of calculated results with ecosystem biomass accumulation

Relative rates of secondary growth calculated from our model were compared to equivalent rates calculated from quadrat harvest data on Betula abundance in long-term fertilization experiments (Chapin et al. 1995; Bret-Harte et al. 2001; Shaver et al. 2001). To make this comparison, we assumed that above-ground stem mass of Betula in control tundra is in a steady state, in which addition of new stem material by primary and secondary stem growth in one season is offset by an equal loss of stem mass. Stem loss occurs either by mortality or by engulfment of basal stems by upward growth of moss, which does not kill the stems but removes them from the above-ground stem compartment measured in these experiments. This assumption is reasonable because, over time, biomass in control tundra fluctuates around a roughly constant value (Shaver et al. 2001). We assumed that stems in experimental stem mass calculated above with observed rates of accumulation in the long-term experiments as follows. When harvests from different years were available (Shaver et al. 2001), we calculated an observed relative rate of net increase in old stem mass between harvests as

\[
\frac{\text{Old stem mass at time 2} - \text{Old stem mass at time 1}}{\text{Old stem mass at time 1}}, \quad \text{eqn 9}
\]

We compared expected relative rates of accumulation of stem mass per \( m^2 \) in an experimental treatment was calculated by expressing \( z \) as a true relative rate (equation 9) and subtracting this relative loss rate from the relative gain rate.

We computed expected relative rates of accumulation of stem mass calculated above with observed rates of accumulation in the long-term experiments as follows. When harvests from different years were available (Shaver et al. 2001), we calculated an observed relative rate of net increase in old stem mass between harvests as

\[
R = \ln M_{2} - \ln M_{1} / \Delta t, \quad \text{where} \quad M_{2} \text{is old stem mass in the experimental treatment at time 2,} \quad M_{1} \text{is old stem mass in the experimental treatment at time 1, and} \quad \Delta t \text{is the number of years between harvests.}
\]

When only one harvest was available, we used the same formula, but substituted old stem mass in control plots for \( M_{1} \); \( \Delta t \) was then the duration of the experiment prior to harvest.
Stem growth in arctic shrubs

Results

Primary stem growth in length is the product of length per stem segment times the number of stem segments formed in a given year. Under control conditions, Salix ramets produced structural branches more rapidly (approximately doubling their number every 2–3 years) than ramets of Ledum and Betula (Fig. 4). For control Betula ramets, structural branch number was nearly constant for long periods of time, because almost all auxillary buds that grew developed into short shoots rather than structural branches. Betula, and to a lesser extent, Ledum, responded to the two fertilization treatments by increasing the number of structural branches after a 3-year lag, but ramets of Salix showed no significant change in branch number under any treatment (Fig. 4).

Average length per stem segment in control ramets varied from year to year but showed no strong trend over time for any species (Fig. 5). Greenhouse treatment did not significantly increase length per stem segment for any species (Fig. 5). Both fertilization treatments strikingly increased the length of individual stem segments of Betula and Ledum for several years, but by the time of harvest (6 years after treatment began), values had nearly returned to pre-treatment levels (Fig. 5). The decrease in length per stem coincided with the increase in branching (Fig. 4).

Total primary growth in length of each age class of stems (length per stem segment times number of stem segments) is needed to calculate secondary growth. Under control conditions, Salix showed the greatest total stem length per age class (Fig. 4b, insert), because
of its greater branching rate. Under both fertilization and greenhouse plus fertilization treatments, however, there was a large progressive increase in total stem length in *Betula* and *Ledum* with time (Fig. 4, insert). The factor of increase in total stem length with fertilization was much greater for *Betula* than for the other species (Fig. 4a, insert).

**SECONDARY STEM GROWTH**

**Empirical data support our key assumptions**

A key assumption underlying our mathematical analysis of secondary growth is that annual radial increment does not change systematically with age under unchanging growing conditions, and this is supported by the linear relationships in Fig. 3. As predicted, treatments that changed secondary growth rate caused a break in the plot of square root of mass/length vs. year segments were produced, with stem segments formed before and after the treatment took effect showing different slope values (Fig. 3). This indicates that radial increment increased substantially in all stem segments following fertilization; the increase can easily be seen in stem cross-sections from fertilized *Betula* ramets (Fig. 2).

Correlation coefficients describing the linear fit of square root of mass/length with age (Fig. 3) for *Betula* were greater than 0.99 for all segments formed after the treatment began, and greater than 0.95 in all treatments (Table 2). This indicates that average inter-annual variability in radial increment was very small in the population of *Betula* ramets we sampled. The fit was slightly poorer for *Salix* and worst for *Ledum* (Fig. 3), but correlation coefficients were mostly greater than 0.93 for *Salix* and 0.8 for *Ledum* (Table 2). Deviations from constant radial increment in *Ledum* occurred because some stem segments grew consistently better than others. For example, control stem segments of *Ledum* produced in 1984 were heavier than segments produced in 1981 and 1982 (Fig. 3), which could not have resulted from poor growth throughout the ramet in any year when all these stem segments were alive.

In all three species, fertilization with or without greenhouse treatment increased the annual radial increment, as indicated by differences between treatments in the slope of square root of mass/length vs. year segments were produced (Fig. 3, Table 2). However, fertilization had a much greater effect on *Betula* than on either *Salix* or *Ledum*. There was little difference between effects of greenhouse treatment and fertilization for *Salix* ramets (Fig. 3). Ramets of *Betula* and *Ledum* from fertilizer and greenhouse plus fertilizer treatments showed a slightly less negative slope of the square root of mass:length relationship for stem segments formed before the treatment began than was seen for control ramets (Fig. 3). This indicates that radial increment increased slightly less with treatment in older stem segments than in ones formed after the treatment took effect (see Mathematical analysis of secondary growth).

**Agreement with measured mass and mass/length data**

A second test of our analysis is how well calculated mass and mass/length agree with empirical data. Calculated values of mass/length mostly fell within the

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**Table 2**

Slopes and correlation coefficients (R-values) from plots of square root of mass/length vs. year segments produced. Correlation coefficients are calculated for a linear fit through square roots of mean values of mass/length.

<table>
<thead>
<tr>
<th>Species and treatment</th>
<th>Pre-treatment</th>
<th>Post-treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>Correlation coefficient</td>
</tr>
<tr>
<td><em>Betula</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-0.140</td>
<td>0.996</td>
</tr>
<tr>
<td>F</td>
<td>-0.087</td>
<td>0.954</td>
</tr>
<tr>
<td>GH</td>
<td>-0.183</td>
<td>0.988</td>
</tr>
<tr>
<td>GHF</td>
<td>-0.106</td>
<td>0.974</td>
</tr>
<tr>
<td><em>Salix</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-0.210</td>
<td>0.982</td>
</tr>
<tr>
<td>F</td>
<td>-0.193</td>
<td>0.975</td>
</tr>
<tr>
<td>GH</td>
<td>-0.162</td>
<td>0.978</td>
</tr>
<tr>
<td>GHF</td>
<td>-0.153</td>
<td>0.844</td>
</tr>
<tr>
<td><em>Ledum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-0.041</td>
<td>0.935</td>
</tr>
<tr>
<td>F</td>
<td>-0.027</td>
<td>0.805</td>
</tr>
<tr>
<td>GH</td>
<td>-0.048</td>
<td>0.937</td>
</tr>
<tr>
<td>GHF</td>
<td>-0.016</td>
<td>0.516</td>
</tr>
</tbody>
</table>

Pre-treatment, stem segments formed before the treatment took effect; post-treatment, stem segments formed after the treatment took effect; C, control; F, fertilized with 10 g/m² N and 5 g/m² P; GH, warmed with plastic greenhouses; GHF, fertilized as in F and warmed with plastic greenhouses.
SEs of measured values for *Salix*, *Betula*, and *Ledum* (Fig. 6). The average difference between calculated and measured values was within 0.1–9% of measured values for different treatments of *Ledum*, within 1–15% for *Salix*, and within 5–12% for *Betula*.

Calculated mass for each age class of stem segments incorporates stem length. For *Salix* and *Ledum*, calculated mass was usually within the SEs of measured values (Fig. 7), as it was for *Betula*, except for ramets from the greenhouse plus fertilizer treatment (Fig. 7). Here, the biggest difference was in the youngest age classes of *Betula* (Fig. 7), even though their calculated and measured mass/length ratios agreed well (Fig. 6). Multiplication of calculated mass/length by very large length values (Fig. 4a, insert) may have magnified small differences between calculated and measured mass/length. For the whole ramet, calculated mass was within 0.2–23% of measured mass for *Betula*, 0.8–21% for *Salix*, and 0.8–12% for *Ledum*.

The response of whole ramet mass to the two fertilization treatments in *Betula* was dominated by the youngest age classes, because of extensive branching (Figs 4 and 7), even though mass/length was greater in the older age classes (Fig. 6). This was less true for *Salix* and *Ledum*.

**Secondary Growth Rates**

Relative rates of secondary growth for control ramets ranged from 8% y⁻¹ for *Ledum* to 18% y⁻¹ for *Salix* (Fig. 8). In both fertilizer and greenhouse plus fertilizer treatments, however, *Betula* experienced a greater increase in the relative rate of secondary growth (2.8–3.3-fold vs. 1.2–1.7-fold for *Salix*), making its secondary growth by far the greatest under these conditions (Fig. 8). Although *Ledum* also responded to fertilization, its relative rate of secondary growth was so much smaller in control ramets that the 2–3-fold increase...
only made it comparable with *Salix* (Fig. 8). For *Salix*, greenhouse treatment alone had a similar effect to fertilization on relative secondary growth rate (Fig. 8).

**Comparison with previous methods of calculating secondary growth rate**

Rates of secondary growth calculated for the whole ramet based on our analysis were fairly similar to those obtained with previous methods (Shaver 1986). Treated ramets showed the largest differences between the methods (Table 3), as expected since treatment effects were not considered previously (Shaver 1986). Because square root (as used here) and natural log (as used in Shaver 1986) plots are similar over a limited range of values, their slopes are not very different, but the correlation coefficients were higher in every case using our revised method. Assuming a constant relative rate of secondary growth among all age classes of segments (Shaver 1986) requires that the annual radial increment should increase as the segment grows larger, which is not reasonable.

The amount of secondary growth indicated for different age classes differed between our analysis and the...
Stem growth in arctic shrubs

Table 3 Relative rates of secondary growth (% y⁻¹) for the whole ramet from our analysis compared with rates calculated as previously (Shaver 1986).

<table>
<thead>
<tr>
<th>Species and treatment</th>
<th>Present analysis</th>
<th>Shaver 86a</th>
<th>Shaver 86b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>15.8</td>
<td>16.5</td>
<td>16.5</td>
</tr>
<tr>
<td>F</td>
<td>44.1</td>
<td>37.4</td>
<td>45.6</td>
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<tr>
<td>GH</td>
<td>19.8</td>
<td>19.8</td>
<td>29.1</td>
</tr>
<tr>
<td>GHF</td>
<td>51.8</td>
<td>46.2</td>
<td>55.4</td>
</tr>
<tr>
<td>Salix</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>18.1</td>
<td>19.4</td>
<td>19.4</td>
</tr>
<tr>
<td>F</td>
<td>25.1</td>
<td>22.1</td>
<td>34.6</td>
</tr>
<tr>
<td>GH</td>
<td>24.4</td>
<td>21.7</td>
<td>31.9</td>
</tr>
<tr>
<td>GHF</td>
<td>29.8</td>
<td>21.3</td>
<td>37.0</td>
</tr>
<tr>
<td>Ledum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>7.9</td>
<td>8.0</td>
<td>8.0</td>
</tr>
<tr>
<td>F</td>
<td>20.3</td>
<td>15.5</td>
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</tr>
<tr>
<td>GH</td>
<td>9.5</td>
<td>9.1</td>
<td>10.5</td>
</tr>
<tr>
<td>GHF</td>
<td>21.7</td>
<td>18.6</td>
<td>25.9</td>
</tr>
</tbody>
</table>

Shaver 86a, pre- and post-treatment slopes of regressions of ln(mass/length) vs. year segment produced were assumed to equal the relative secondary growth rates of those stem segments; Shaver 86b, post-treatment slopes of ln(mass/length) vs. year segments produced were assumed to equal the relative secondary growth rate of the whole ramet.

Previous method, particularly for stem segments formed before the treatment began (Fig. 9). In Betula ramets from both fertilization treatments, these segments made up such a small proportion of the total stem mass that their contribution to secondary growth of the whole ramet was minimal (Figs 7 and 9, Table 3). Any experimental treatment that increased the relative representation of older segments would magnify differences between the secondary growth predicted by our analysis and by Shaver’s (1986) method.

Comparison with ecosystem biomass accumulation

A final test of our analysis is to compare the experimentally induced increases in secondary growth that we predict based on ramet growth with changes in Betula nana stem mass per m² seen in the same experiment in 1996 (Bret-Harte et al. 2001), and in a previous long-term fertilization experiment in tussock tundra (Chapin et al. 1995; Shaver et al. 2001). We focused on Betula because it becomes dominant in the fertilizer and greenhouse plus fertilizer treatments in these experiments (Fig. 1). To make this comparison, we assumed that above-ground stem mass in the control tundra was in steady-state and that the same proportional stem loss rate occurred in the experimental treatments as in the control (see Mathematical analysis of secondary growth). The relative loss rate of old stem mass for Betula in control tundra was 20.8% y⁻¹, which is slightly higher than the secondary growth rate in control tundra because stem material from primary growth in the current year is added to the old stem compartment in the following year (equation 13).

Fig. 9 Comparison of increase in mass/length for each age class of stem segments of Betula ramets from our analysis (constant increment), and from two alternative methods of calculating secondary growth (Shaver 86a and b; see Methods).
Expected relative rates of accumulation of old stem mass based on ramet data agreed reasonably well with observed average relative rates calculated from the two quadrat harvest data sets (Fig. 10). To compare our results with the older experiment (Shaver et al. 2001), we calculated the observed rates of relative increase in Betula stem mass in fertilized plots between harvests in 1984 and 1989. We used these harvests because the midpoint of that period (6.5 years of treatment) was similar to the 6-year time point in the current study, on which our ramet calculation was based. This average rate (Fig. 10; ‘LTER 1984-89’) was virtually identical to the rate predicted by the model for fertilized Betula (Fig. 10; ‘Expected’). The greenhouse and greenhouse plus fertilizer treatments were not harvested in 1984, so it was not possible to do the same comparison for those treatments (Shaver et al. 2001). The average rate of accumulation of stem mass between 1989 and 1995, i.e. between 9 and 15 years into the older experiment, was somewhat lower (data not shown), even as Betula biomass increased to over 12 times that of the controls after 15 years of fertilization (Shaver et al. 2001).

In the present experiment, there were no quadrat harvests of initial stem mass at the start of treatment in 1989 (Bret-Harte et al. 2001). We estimated the average relative rate of increase in Betula stem mass over the seven years of this experiment by comparing experimental values in 1996 with control values in 1990, assuming that the control value was equivalent to initial stem mass in experimental plots. This gave somewhat lower rates than expected for Betula in fertilizer and greenhouse plus fertilizer plots (Fig. 10; ‘1996 harvest’). One reason for the lower value may be that the mid-point of the calculation is only 3.5 years from the start of treatment. Accumulation of Betula stem mass by secondary growth was probably lower in the early years of the experiment because branching rates did not increase until 3 years after treatment (Fig. 4). Secondary growth in younger branches contributes disproportionately to the secondary growth of the whole ramet (Fig. 7). We may have underestimated stem mortality in the fertilized plots by assuming it occurs at the same rate as in control plots.

Overall, this comparison reveals that the secondary growth rates we calculated for ramets are reasonably consistent with the measured accumulation of above-ground Betula stem mass at the ecosystem level. This is true even though Betula in the field includes stems that are much older than our ramets, which should decrease the overall rate of secondary growth. Many older Betula stems are prostrate and may have been covered by moss, in which case they would not be included in the above-ground stem mass sampled in the ecosystem measurements. If they are part of the above-ground stem mass, they probably comprise a very small fraction of the total.

Discussion

Primary Growth

The increase over time in primary stem growth induced by the two fertilization treatments in ramets of Betula and Ledum results initially from increased stem elongation, but beyond three years of fertilization it becomes largely due to increased numbers of branches. In contrast, Salix fails to increase primary stem growth very much under any treatment because it apparently has a more rigid branching programme. In Betula and Ledum, annual elongation per stem increases transiently with fertilization, but there appears to be a trade-off between increased numbers and length per branch, because as branch production increases, length per stem segment declines toward the control level (Figs 4 and 5). Under fertilization, whole-plant photosynthesis is higher because of increased leaf area (Bret-Harte et al. 2001; Shaver et al. 2001). However, this increased carbon capture is apparently insufficient to allow allocation to both increased branch production and increased length per stem segment for either Betula or Ledum.

In Betula, production of long-shoot (structural) branches requires a much greater investment of both nitrogen, in leaves, and carbon, in stems and leaves, than production of short shoots does, although photosynthetic return from long shoots is higher than from short shoots (Maillette 1982; Bret-Harte et al. 2001). Betula normally grows along one or a few axes, each of which results from continuing elongation of a single long shoot. Betula achieves its great increase in branch production under fertilization by inducing axillary...
buds that would normally grow as short shoots to grow instead as long shoots (Bret-Harte et al. 2001). Maillette (1982) found that leader shoots in *Betula pendula* produce more long shoots than branches lower on the tree, possibly indicating that in that species also, better access to resources allows shoots to change the fate of their buds. However, unlike *Betula nana*, vegetative terminal buds of long shoots in both *Betula pendula* and *Betula cordifolia* normally aborted after one season of growth, indicating that their development was more constrained (Maillette 1982; Maillette 1987).

Clonal, perennial growth is often associated with slow-growing, determinist plants that live in harsh and nutrient-poor environments, where transfer of nutrients and carbon from older modules to younger ones is important to their survival (Callaghan 1988; Jonsdottir & Callaghan 1990). Although *Betula nana* is clonal, perennial, and relatively slow-growing in control tundra, developmental flexibility in the fate of its buds allows it to radically change its branching pattern when resource limitation is removed, in contrast to many other tundra species. Because *Betula nana* can hybridize with tree species of *Betula* and shows introgression with other shrub *Betula* species where their ranges overlap (Hultén 1968), introgression may have introduced genes for tree-like behaviour into populations of *Betula nana* remote from the present occurrence of trees.

**SECONDARY GROWTH**

Extensive theory exists on relative growth rate, in both whole plants (Huht 1978), and in tissues and organs (Erickson & Sax 1956; Erickson 1976; Silk & Erickson 1979). Usually, however, relative rates of whole plant growth are calculated only for annual plants, while relative growth rates in tissues are calculated only for primary growth. Here we present a mathematical analysis that allows calculation of relative rates of secondary growth in perennial plants. Our results indicate that secondary growth is a significant part of biomass accumulation by tundra shrubs under control conditions. Under increased nutrient availability, secondary growth becomes the major component of biomass accumulation by tundra shrubs, as with forest trees.

**IMPLICATIONS FOR ECOSYSTEM PRODUCTION**

Inclusion of our assessment of secondary growth greatly increases our estimates of net primary production (NPP) in this fertilized ecosystem (Shaver et al. 2001). The increase in secondary growth of *Betula* under fertilization leads to a continued increase in estimated NPP with time in fertilized tundra (Shaver et al. 2001). Previously, vascular plant NPP was thought to jump up, under fertilization, to a larger but constant value over time, even though the relative contributions to NPP by different species changed with time (Chapin et al. 1995).

Because wood has a much higher C : N ratio than leaves, increased secondary growth by shrubs, especially *Betula*, causes greater carbon storage per unit of nitrogen in fertilized plots than in control plots (Shaver et al. 2001). There may be a threshold of nitrogen availability below which ecosystem carbon storage is constrained by the need to invest primarily in nitrogen-rich leaves. When the threshold is exceeded, secondary growth increases more than proportionally to increases in nitrogen availability, and tundra behaves more like a forest with respect to carbon storage, in that the C : N ratio in accumulated biomass is high.

Anthropogenically induced increases in atmospheric CO$_2$ concentration are expected to cause arctic and boreal regions to warm more than other parts of the globe (Houghton et al. 1998). Arctic and boreal soils contain roughly one-third of the global soil carbon pool (Schlesinger 1977; Gorham 1991). Decomposer activity is expected to increase as soils warm; since nutrients are mineralized from soil organic matter during decomposition, soil nutrient availability should increase (Hobbie 1996; Nadelhoffer et al. 1991). It is not yet clear whether the release of CO$_2$ by increased decomposition will be greater than nutrient-stimulated increases in plant production or vice-versa (Shaver et al. 1992; Goulden et al. 1998; Hobbie et al. 2000; Shaver et al. 2000). Our results suggest that, if warming increases soil nutrient availability, carbon storage in woody biomass in tundra may be larger than previously expected from NPP estimates that did not account fully for a changing allocation to secondary growth. Shrubs in arctic Alaska have already increased in numbers and size as warming has occurred (Sturm et al. 2001).

**HYDRAULIC AND MECHANICAL CONSIDERATIONS**

A large increase in primary stem growth such as that found in *Betula* ramets under fertilization increases both total leaf area and the mass of the canopy (leaves plus stems). Secondary growth provides both conduits for water transport and the strength to meet the mechanical demands of supporting the canopy. Most woody species operate near the tolerable limit of their xylem’s hydraulic conductance, set by its vulnerability to gas embolisms (Tyree & Sperry 1989). Thus, hydraulic demands of an increased area of transpiring leaves could not be met by increased xylem tension, but require increased secondary growth to increase xylem area.

Mechanical support of a larger canopy also requires increased secondary growth. In control ramets of *Betula* and *Salix*, both radial increment (Fig. 3) and length per stem segment (Fig. 5) were roughly constant, so branch length scales in proportion to diameter, thus, they exhibit what is termed geometric self-similarity (King & Loucks 1978; Niklas 1995). Geometric
self-similarity is seen in tree saplings (King 1990; Alvarez-Buylla & Martinez-Ramos 1992; Coomes & Grubb 1998), shrubs (Whitaker & Woodwell 1968), and non-woody plants (Niklas 1994). In contrast, large trees exhibit elastic or stress self-similarity (Niklas 1994), in which height scales as the 2/3 power or 1/2 power, respectively, of diameter (McMahon 1973; McMahon & Kronauer 1976; Niklas 1993). Bertram (1989) suggested that small branches of trees show geometric self-similarity because of hydraulic demands, whereas larger branches and trunks exhibit elastic similarity because of greater mechanical demands. Even fertilized tundra shrubs need not meet the mechanical demands of tree canopies, so their growth allometry may be set by maintenance of constant conductance for hydraulic transport, as in small tree branches.

**IMPLICATIONS OF SPECIES DIFFERENCES IN SECONDARY GROWTH**

Among the species studied, *Betula* responds to added nutrients most strongly, in both primary and secondary growth (Figs 4 (insert) and 8; Bret-Harte et al. 2001). Under both fertilization and greenhouse plus fertilization treatments, *Betula* dominates the community, whereas *Salix* and *Ledum* decline in abundance, even though ramets of all three species respond positively to fertilization (Bret-Harte et al. 2001). *Betula*’s response results from its ability to switch between producing long shoots and short shoots (Bret-Harte et al. 2001). However, more primary growth would not be advantageous to *Betula* if its secondary growth could not also be increased to meet the hydraulic and mechanical demands of the extra leaf and stem tissue. *Salix* and *Ledum* appear unable to increase their secondary growth as much as *Betula* does (Fig. 8). Secondary growth of treated *Salix* ramets does not differ much from that of controls. Fertilization increases *Ledum*’s secondary growth only in the youngest stem segments (Fig. 3). Its shoot length increases more than in proportion to stem diameter, so *Ledum* does not have even the limited mechanical reinforcement provided by geometric self-similarity. Because *Ledum* does not acquire mechanical strength in its stems that would enable it to grow upward into the canopy, it becomes confined to the understorey in both fertilization treatments, where its photosynthetic performance is light-limited by the *Betula* canopy and further growth is reduced (Bret-Harte et al. 2001). When nutrient availability increases, *Betula*’s developmental plasticity in secondary growth and flexibility in the fate of its buds contribute to its dominance, whereas the way that *Ledum*’s secondary growth is regulated puts this species at a competitive disadvantage.

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