Regulation of Fine Root Dynamics by Mammalian Browsers in Early Successional Alaskan Taiga Forests

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REGULATION OF FINE ROOT DYNAMICS BY MAMMALIAN BROWSERS IN EARLY SUCCESSIONAL ALASKAN TAIGA FORESTS

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Abstract. The effects of browsing by moose and snowshoe hares on fine root production, mortality, and decomposition in early successional forest ecosystems along the Tanana River floodplain in interior Alaska were studied over a 3-yr period using minirhizotrons placed inside and outside large permanent exclosures. Fine root production and mortality varied seasonally, with greatest rates of production occurring during June each year, and greatest rates of mortality occurring in fall and over winter. Annual production and mortality during 1993, a year of unusually low precipitation, were significantly higher than during either 1992 or 1994.

Aboveground herbivory significantly reduced monthly rates of fine root production, and on an annual basis, fine root production of browsed plots (311.4 ± 31.7 mm·tube^{-1}·yr^{-1}) was significantly less than that of unbrowsed plots (453.8 ± 49.8 mm·tube^{-1}·yr^{-1}) when averaged over 3 yr. Because herbivory had less of an effect on monthly or annual rates of fine root mortality, fine root turnover was higher for browsed stands. Browsed plants had a higher percentage of annual production in surface soil layers. Production on all plots shifted to deeper soil layers as the growing season progressed; this shift occurred deeper in the profile for unbrowsed plants than for browsed plants.

We used a parameter estimation program (Program MARK) to generate fine root survival and decomposition estimates from models testing the direct and interactive effects of time period, cohort (i.e., when the root first appeared) age of the root, browsing, and site on fine root longevity and decomposability. Cohort effects showed that survival of fine roots was greatest for roots that first appeared in May, and that survival progressively declined for roots first appearing during subsequent time periods, while age-based estimates showed a rapid decline in survival over the interval following first appearance. Survival and decomposition estimates were inversely correlated within a growing season, with the lowest survival but highest decomposition occurring over winter. Two-factor models indicated that time-dependent survival and decomposition rates of fine roots differed significantly between browsed and unbrowsed stands, among the 10 fine root age groups, and among the three study sites. Browsing significantly reduced fine root survival, but this effect varied among sites. Fine root decomposition rates were consistently lower (-21%) in browsed stands.

Two important features distinguish fine root dynamics in our stands from temperate and more southerly boreal ecosystems: (1) low overwinter survival of fine roots, and (2) a substantial time lag between leaf-out and maximum fine root growth, suggesting greater reliance on aboveground stores for spring regrowth. Herbivores appear to play an important role in linking these two events, first by exacerbating overwinter mortality, and second by consuming a substantial amount of aboveground stores. Thus, not only do herbivores have pronounced direct effects on carbon and nutrient cycling processes, but climatically driven effects on fine root processes may be linked with herbivory in complex ways that define fundamental latitudinal patterns in plant growth and allocation to defense against herbivory.

Key words: Alaska; browsing; fine roots; herbivory; longevity; nutrient cycling; production; turnover.

INTRODUCTION

Grazing and browsing mammals have substantial direct and indirect effects on the structure and function of terrestrial ecosystems. These effects are manifested through changes in vegetation composition and plant community dynamics (McNaughton 1983, 1985, Huntly 1991, Mulder et al. 1996, Weltzin et al. 1997), above-

ground net primary production (du Toit et al. 1990, Hik and Jefferies 1990, Coughenour 1991, Frank and McNaughton 1992, Milchunas and Lauenroth 1993), and nutrient cycling processes (McNaughton et al. 1988, Pastor et al. 1993, Ruess and Seagle 1994, Frank and Evans 1997). Other than the direct return of excretory carbon and nutrients to the system (Ruess and McNaughton 1984, Ruess 1987, Day and Detling 1990, Frank and Evans 1997), herbivores also modify the quality and turnover of plant litter. For example, winter

browsing by moose and snowshoe hares in the Alaskan interior often reduces aboveground biomass and primary production of riparian and early successional deciduous shrubs; however, the quality of leaves for both vertebrate (Danell and Huss-Danell 1985, Bryant et al. 1991) and invertebrate (Roininen et al. 1997) herbivores is higher in browsed plants, as is the decomposition rate of leaf litter in both terrestrial (Kielland et al. 1997) and aquatic habitats (Irons et al. 1991).

The effect of aboveground herbivory on fine root growth has been identified as a critical link to understanding herbivore-mediated influences on ecosystem nutrient cycling processes (Holland and Detling 1990, Merrill et al. 1994, Ruess and Seagle 1994, Holland et al. 1996). Yet despite the recent appreciation for the significance of fine roots in ecosystem function (Nadelhoffer et al. 1985, Gower et al. 1992, Hendrick and Pregitzer 1992, 1993a, b, 1996, Hendricks et al. 1993, Pregitzer et al. 1993, Fahey and Hughes 1994, Haynes and Gower 1995, Ruess et al. 1996), the effects of aboveground vertebrate herbivory on fine root processes have never been explicitly studied in any ecosystem. Research to date has focused primarily on the effects of aboveground pathogens and insect herbivory on root biomass (Jackson 1945, Redmond 1959, Moran and Whitham 1990, Vranjic and Gullan 1990), the influence of belowground vertebrate or invertebrate herbivory on root biomass and aboveground net primary production (Cantor and Whitham 1989, Ingham and Detling 1990, Klepzig et al. 1991, Wightman et al. 1994), and plant growth responses to mycophageous arthropods grazing on mycorrhizae (Harris and Boerner 1990, Klironomos and Kendrick 1995, McGonigle 1995, Setala, 1995, Larsen and Jakobsen 1996). Additional studies have shown that belowground herbivory can influence levels of aboveground herbivory. For example, Brown and Gange (1989) demonstrated that root-feeding insects can substantially alter plant growth and community composition, and that elevated leaf nitrogen contents due to water stress following root feeding may increase the growth rate of foliage feeding insects (Gange and Brown 1989). Very few of these types of studies have used direct observation methods to describe root processes. Richards (1984) used a root periscope to describe root length growth of two *Agropyron* species following simulated grazing, and using minirhizotrons, Kosola et al. (1995) found that fine root longevity of citrus trees was lower when populations of root pathogens were high. However, none of these studies used direct observations to characterize root production, mortality, and decomposition in response to levels of aboveground or belowground herbivory.

The effects of aboveground browsing on fine root dynamics may be of particular significance to nutrient cycling processes in Alaskan interior forests where a significantly higher proportion of total ecosystem carbon fixed is allocated belowground relative to temperate forests (Ruess et al. 1996). This results in approximately three times as much nitrogen cycled through fine roots compared with aboveground litterfall, and a disproportional amount of soil carbon and soil respiratory fluxes derived from fine root turnover. Early successional stands dominated by deciduous shrubs show the highest ratio of root to aboveground litterfall C allocation, suggesting that fine root turnover is even more important to the C and N cycling of these stands (Ruess et al. 1996). Because winter browsing by moose and snowshoe hares is most intensive in these early successional forest stands (Bryant 1987), herbivory impacts on fine root dynamics may have substantial effects on the rate of soil carbon and nutrient accumulation.

The purpose of this study was to characterize the effects of aboveground browsing on rates of fine root production, mortality, and decomposition in early successional forest stands in interior Alaska. Data presented are from a long-term study of fine root dynamics using minirhizotrons placed inside and outside large exclosures. We hypothesized that browsing would have a negative effect on fine root production. We also predicted that, analogous to the effects of browsing on aboveground processes, herbivory would decrease fine root longevity but increase fine root decomposition rates. To answer these questions, we combined minirhizotron techniques with a parameter estimation program, which provided an opportunity to study these processes in situ. Our results demonstrate that (1) herbivores have pronounced effects on belowground growth dynamics, (2) these effects strongly influence the cycling of nutrients and carbon at the ecosystem level, and (3) seasonal patterns of fine root growth, mortality, and decomposition in taiga ecosystems are substantially different from temperate forests.

Methods

Study sites

We studied the effects of mammalian browsing on fine root processes at three sites situated along a 10-km stretch of the Tanana River, ~30 km south of Fairbanks, Alaska (64°48′ N, 147°52′ W). Floodplain forest succession develops rapidly following alluvial bar formation (Van Cleve et al. 1991, Viereck et al. 1993a), and browsing is concentrated within young (10–20 yr), open willow stands where up to 100% of the current annual shoots can be browsed during the subsequent winter by moose and snowshoe hares (McAvinchey 1991, Kielland et al. 1997). Our study sites constituted a subset of a larger network of replicated sites established by the Bonanza Creek Long-Term Ecological Research Program (BNZ LTER) to study the effects of browsing by moose and snowshoe hares on community and ecosystem processes. Vegetation at the three sites is dominated by four willow species (*Salix alaxensis*, *S. interior*, *S. novae-angliae*, and *S. brachicharpa*), which contribute >80% of the stem density at the sites

TABLE 1.   (A) Number of live ramets/m² for each species averaged across the three study sites and (B) percentage of twigs (≥4 mm) browsed by moose and snowshoe hares averaged over winters of 1988–1992.

A) Live ramets (no./m²)

Species	Unbrowsed	Browsed
Salix novae-angliae	4.61 ± 1.50	2.80 ± 0.66
Salix alaxensis	1.84 ± 0.48	1.44 ± 0.30
Salix brachycarpa	0.98 ± 0.38	0.90 ± 0.26
Populus balsamifera	0.59 ± 0.19	0.50 ± 0.18
Salix interior	0.48 ± 0.23	0.18 ± 0.14

B) Twigs browsed (%)

Species	A1	A2	C
Salix alaxensis	74.2 ± 5.9	91.2 ± 5.9	71.0 ± 6.6
Salix interior	70.8 ± 13.6	82.8 ± 15.4	71.6 ± 13.4
Salix novae-angliae	42.8 ± 4.0	51.6 ± 9.8	44.0 ± 3.5
Salix brachycarpa	28.8 ± 3.1	18.6 ± 3.3	7.4 ± 0.92
Populus balsamifera	12.0 ± 3.5	14.2 ± 5.1	6.8 ± 3.6

Notes: (A) Data are means (±1 SE) measured during 1993 from 24 permanent plots (1 × 2 m) distributed both inside and outside exclosures. (B) Data are means (±1 SE) from five permanently tagged plants located throughout the unexclosed plot at each of the three study sites that were between 1.5 and 2.0 m tall when first tagged in 1987.

(Table 1). Subdominant woody species include *Alnus tenuifolia, Populus balsamifera,* and *Picea glauca.* Soils are in the Goldstream series and are classified as Histic Pergelic Cryaquepts (Van Cleve et al. 1993). Designations used here for our three study sites (A1, A2, and C) are abbreviations of official BNZ LTER site locations (FP1A1, FP1A2, and FP1C2, respectively). More detailed characterizations of soil processes, vegetation, and climate in these early successional forests have been described elsewhere and are available on the BNZ LTER website[3] (Van Cleve et al. 1993; Viereck et al. 1993*a, b*).

One large exclosure (30 × 50 m), paired with an unexclosed plot of the same size, was established at each site in 1987, at which time the vegetation was ~10 yr old. Each exclosure consisted of high tensile strength wire secured to wooden posts extending 5 m above the ground surface and covered with 5-cm mesh chicken wire. While the three sites represented replicates within the context of BNZ LTER experimental design (see the BNZ LTER website), there were differences among stands in soil water availability and the intensity of browsing, which we will discuss in more detail below.

Regional climate is characterized by an intensely cold snow period averaging 214 d, and annual temperature extremes ranging from −50 to 35°C. Average daily temperatures range from −24.9°C in January to 16.4°C in July, with an average annual temperature of −3.3°C. Potential evapotranspiration (466 mm) exceeds annual precipitation (269 mm), 65% of which falls during the growing season, which typically extends from mid-May to early September (Viereck et al. 1993*b*).

[3] URL = ⟨http://www.lter.alaska.edu⟩

Fine root production and mortality

Fine root production and mortality were measured using a minirhizotron system (Hendrick and Pregitzer 1992). Five clear butyrate plastic minirhizotron tubes (2 m in length, 5 cm ID), each etched with 120, 1.4 × 1.4 cm frames along the length of the tube, were installed at a 40° angle to the soil surface, inside and outside the exclosure at each site at the end of August 1991. To drill a smooth hole for the minirhizotron tube without compacting the soil, we used a gasoline powered auger that spun within a drilling tube equipped with a reverse tapered cutting bit the same diameter as the minirhizotron tube. The drilling unit slid within a stationary frame at a preset angle to the soil surface. Approximately 15 cm of tube extended above the soil surface, which was painted black, then white to prevent light penetration and heat buildup inside the tubes. Tubes were capped except during measurement periods. The pattern of tube installation, an array positioned perpendicular to the Tanana River, was identical for all plots. Beginning the following summer (June 1992), monthly images of roots were taken throughout the growing season using a color microvideo camera (Bartz Technology, Santa Barbara, California) and stored on SVHS video tape. Because study sites were accessed by boat, we began imaging tubes only after river breakup in late May, ~2–3 wk following leaf out. Images were digitized using the ROOTS program (Michigan State University) as described by Hendrick and Pregitzer (1992). The program allows for the identification and tracking of individual roots over time by storing the length and diameter tracings of each root from each time period to a database file. We then used a database program to independently calculate production and mortality based on the extension growth and/or death

of new and preexisting roots for each minirhizotron tube for each of 5 depths (0–20, 20–40, 40–60, 60–80, and 80–100 cm). This program is described in more detail, and can be downloaded from the BNZ LTER website. Here we report monthly production and mortality throughout the growing season as millimeters fine root per tube per 30 days to adjust for slightly different sampling intervals. We assumed that all fine root production between the fall and spring sampling periods occurred in the spring, and report this early season growth as millimeters fine root per tube per 30 days based on number of days between leaf out and our first sampling period. Overwinter mortality was assumed to be that occurring between the fall and spring sampling periods, and is reported as millimeters fine root per tube per period. Annual values for fine root production and mortality were simply the sum of gross growth and mortality across all actual sampling intervals throughout the year.

Fine root survival and decomposition

Estimation of survival probability of vertebrates has received considerable attention (e.g., Seber 1982) in which a sample of the population of interest is marked, and their fate is tracked through time. The data arising from such an experiment are categorical, with exhaustive, and mutually exclusive fates (multinomial). More recently (Lebreton et al. 1992), these Cormack-Jolly-Seber models have been extended to partition sources of variation in survival among temporal, treatment, and other attributable effects. This analytical procedure allows the investigation of survival probabilities to mimic an analysis of variance approach, akin to a log-linear modeling analysis. We used MARK, a program available on the World Wide Web[4] (White and Burnham, *in press*), to generate fine root survival estimates (noted as ϕ) after carefully constructing models incorporating direct effects of time, age, cohort (when roots first appeared), and browsing along with their interactions on fine root longevity. The most parsimonious models were found using the information-theoretic Akaike's Information Criterion (AIC), and likelihood ratio tests (LRT). The identification of models follows the notation of Lebreton et al. (1992). For example, a model including both treatment (browsed vs. unbrowsed) and time effects (abbreviated as $\phi_{t\times browsing}$) can be compared with a model including only time effects (ϕ_t), which can be compared to the most simple model (ϕ). In this manner, the effects of time, cohort, age of the root, browsing, site, and their interactions were evaluated. The model with the lowest AIC is the most parsimonious model.

MARK estimates survival rates and recapture probabilities for all time intervals. Encounter history files were created that included a listing for each individual

root, coded for every time period as either "1" (alive), or "0" (dead or missing). Data sets were modeled as "live recaptures" with all recapture parameters fixed at 1, since we were assured of "recapturing" a root unless it had decomposed. We were confident in this known-fate approach, because it is highly unlikely that many roots would appear, die, and completely decompose between sampling periods. In addition to modeling fine root longevity, we also estimated the probability that dead fine roots would decompose between any two time periods by modeling the "survival" of dead roots. This was accomplished by recoding the data to create encounter history files which identified dead roots as 1, and roots at time of first disappearance as 0. Fine root decomposition estimates were then simply taken as 1 minus dead root survival. A similar model selection approach to that used for fine root longevity was used to determine factors affecting fine root decomposition.

Statistical analyses

Variations in fine root production and mortality due to site, browsing, and time period (interval period or annual) were analyzed by ANOVA (SAS 1996) using a split-plot design with minirhizotron tube location within each treatment plot (browsed or unbrowsed) treated as a subplot (Potvin 1993). The whole-plot mean square error (site × treatment) was used to test for site, treatment, time, time × treatment, and site × time effects, with subplot mean error computed as treatment × tube location. Differences between site means were computed using a *t* test and established standard error calculations for split-plot designs (Petersen 1985). Data were square-root transformed where necessary to meet ANOVA assumptions. Linear regression was used to define relationships between production and mortality, mortality and survival, and survival and decomposition. Unless otherwise stated, data presented represent means ± 1 standard error.

RESULTS

Climate and site characteristics

Precipitation data from the BNZ LTER climate database ("FP1A" rain gauge) show that for the period of greatest plant growth (1 June to 4 August), precipitation totaled 123.0, 62.8, and 107.5 mm for 1992, 1993, and 1994, respectively. All three study sites received the same precipitation; however, proximity to the main river channel, seasonal sloughs, and subsurface water uniquely influenced soil moisture at each site. Although soil moisture was not measured regularly at our study plots, C was the driest site, and A1 was by far the wettest site, particularly during late May, when both browsed and unbrowsed plots were typically under 20 cm of water for several weeks (R. W. Ruess, *unpublished data*; see BNZ LTER website for available soil moisture data).
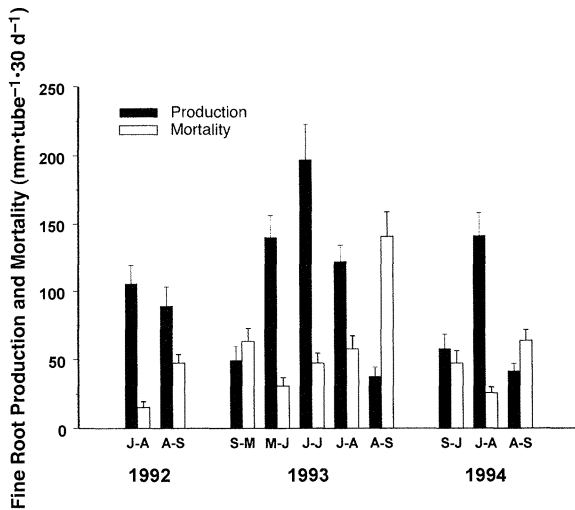
FIG. 1. Fine root production and mortality measured over 10 time intervals from 1992 through 1994, averaged across all sites and browsed and unbrowsed stands (J = June in both 1992 and 1994). All values are expressed as mm root length per minirhizotron tube per 30 d (+1 SE), except overwinter values, which are expressed per actual period length.

Browsing intensity was greatest at the A2 site and least at the C site (Table 1). Species composition was similar among sites, and the proportion of dominant species was similar inside vs. outside the exclosures (J. P. Bryant, *unpublished data*). A comprehensive characterization of vegetation at all the BNZ LTER exclosure plots can be found on the BNZ LTER website.

Seasonal and annual patterns of fine root production and mortality

Fine root production and mortality varied significantly throughout the season each year of the study (both $P < 0.001$). During 1993, production was greatest in June and steadily declined throughout July and August (Fig. 1). Data from 1992 and 1994 indicate a similar pattern. Monthly rates (millimeters fine root per tube per 30 days) of fine root production (FRPROD) and mortality (FRMORT), when averaged across all sites, treatments, and tubes, were inversely correlated, with greatest rates of mortality occurring in fall and winter (winter mortality entered as per period):

$$FRMORT = 229.6 - 39.55 \times \ln(FRPROD)$$

($r^2 = 0.44$, $P < 0.05$). Overwinter mortality was higher during 1992–1993 compared with 1993–1994.

Annual production and mortality averaged 385.06 ± 30.74 and 197.52 ± 16.0 mm·tube^{-1}·yr^{-1}, respectively, across all treatments, sites, and years. Annual fine root production and mortality varied significantly among years (both $P < 0.0001$), due to the fact that production and mortality during 1993, a year of unusually low precipitation, were significantly higher than during ei-
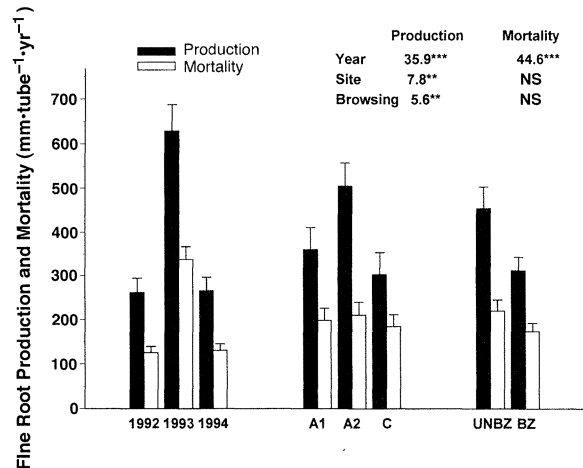

FIG. 2. The effects of year, site, and browsing on annual fine root production and mortality. All values are expressed as mm root length per minirhizotron tube per year (+1 SE). ANOVA inset lists percentages of variance explained by main effects: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

ther 1992 or 1994 (Fig. 2). Annual fine root production and mortality were positively correlated across treatments, sites, and tubes, and in all but a few individual tubes, annual production exceeded mortality (Fig. 3). The ratio of annual production to mortality averaged 2.3 ± 0.2, and did not vary among years ($P = 0.37$).

Annual fine root production varied among sites ($F_{2,2} = 23.2$, $P = 0.04$), principally due to a higher production at the A2 site (Fig. 2). These site patterns in production did not vary among years ($F_{\text{years} \times \text{site}} = 0.89$, df = 4, 69, NS), and annual fine root mortality did not vary among sites ($P = 0.86$).

Effects of herbivory on fine root production and mortality

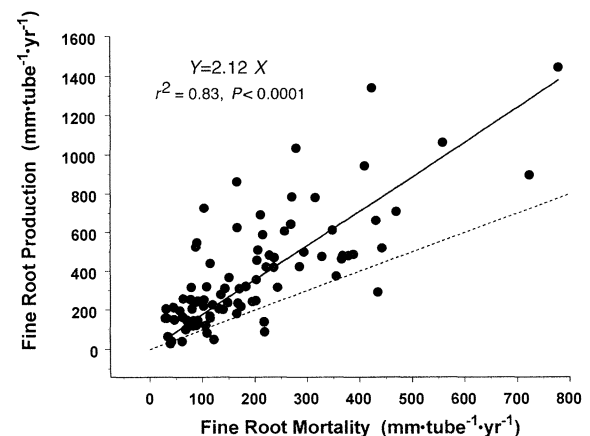Aboveground herbivory significantly reduced monthly rates of fine root production, which averaged

FIG. 3. Relationship between annual fine root production and mortality (dashed line indicates equality). Each point represents one minirhizotron tube for one year.
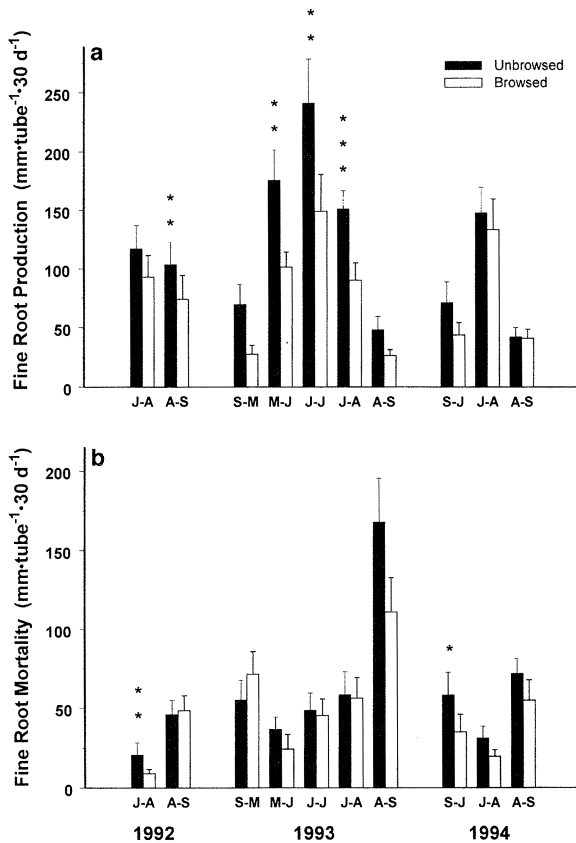
FIG. 4. Fine root production (a) and mortality (b) for browsed and unbrowsed stands measured over 10 time intervals from 1992 through 1994, averaged across sites. All values are expressed as mm root length per minirhizotron tube per 30 d (+1 SE), except overwinter values, which are expressed per actual period length. Asterisks identify significant effects of browsing by time period: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

33% less in browsed plots compared with unbrowsed plots over the 3 yr of study ($P = 0.03$, Fig. 4a). The greatest effects occurred during 1993, when monthly production was reduced in May (-43%, $P = 0.05$), June (-38%, $P = 0.07$), and July (-40%, $P = 0.005$) by browsing. Herbivory had less of an effect on monthly rates of fine root mortality, which averaged 17% less in browsed plots relative to unbrowsed plots (NS; Fig. 4b).

On an annual basis, fine root production of browsed plots (311.4 ± 31.7 mm·tube^{-1}·yr^{-1}) was also significantly less than that of unbrowsed plots (453.8 ± 49.8 mm·tube^{-1}·yr^{-1}) when averaged over 3 yr (Fig. 2). These effects were greatest during 1993 ($F_{browsing \times year} = 4.1$, df = 2, 69, $P = 0.02$), and were similar across sites ($F_{browsing \times site} = 1.2$, df = 2, 69, NS). Annual fine root mortality of browsed plots was not significantly different from that of unbrowsed plots ($P = 0.34$). However, when annual mortality per tube was regressed

against annual production, browsed plots had a significantly steeper slope than unbrowsed plots ($P < 0.05$), indicating that fine root longevity was reduced when plants were browsed.

Profile characterization of fine root production and mortality

There were distinct soil profile patterns of fine root production among treatments and both within and among years of the study. Annual fine root production and mortality declined significantly with increasing soil depth ($P < 0.001$). As a percentage by depth, annual production and mortality averaged: 0–20 cm, 43.0 ± 2.2 and $45.5 \pm 2.5\%$; 20–40 cm, 26.2 ± 2.1 and $23.3 \pm 2.3\%$; 40–60 cm, 16.6 ± 1.7 and $15.7 \pm 1.7\%$; 60–80 cm, 10.5 ± 1.1 and $10.9 \pm 1.5\%$; 80–100 cm, 3.8 ± 0.9 and $4.7 \pm 1.2\%$, respectively. The percentage of annual production within each depth varied among treatments ($F_{browsing \times depth} = 2.78$, df = 4, 48, $P = 0.02$) and years ($F_{years \times depth} = 3.21$, df = 8, 48, $P = 0.002$), but not among sites ($F_{site \times depth} = 1.23$, df = 8, 48, $P = 0.29$). Browsed plots had a higher percentage of production in the 0–20 cm ($45.6 \pm 3.5\%$ vs. $40.5 \pm 2.8\%$, $P = 0.09$) and 20–40 cm ($28.5 \pm 3.3\%$ vs. $24.0 \pm 2.7\%$, $P = 0.18$) layers, and less in the 40–60 cm layer ($12.5 \pm 2.3\%$ vs. $20.4 \pm 2.5\%$, $P = 0.13$) compared with unbrowsed plots. This was particularly evident at the A2 site, where $36.3 \pm 3.5\%$ of the annual fine root production occurred in the top 20 cm of the unbrowsed plot, compared with $55.3 \pm 5.9\%$ at the same depth in the browsed plot. The most notable difference among years was a lower percentage of production above 20 cm and a greater percentage of production below 20 cm in 1994 compared with the two previous years.

The proportion of fine root production by depth varied significantly within the growing season each year ($P < 0.0001$) due to progressive declines in percentage fine root production in the 0–20 cm layer, and progressive increases in the proportion of growth lower in the profile throughout the summer. Differences between browsed and unbrowsed plots in patterns of root growth by depth were particularly apparent during 1993. For unbrowsed plots, monthly fine root production (percentage by depth) steadily declined in the 0–20 cm layer from 58.3% in May, to 23.6% during August, over which time production in the 60–80 cm layer increased from 5.8 to 25.7%. For browsed plots, production in the 0–20 cm layer decreased from 63.2% in May to 40.3% in August; however, the most notable subsurface increase occurred in the 20–40 cm layer (25.6% in May to 38.3% in August) (Fig. 5a, b).

Modeling fine root survival and decomposition

Fine root survival was affected significantly by time period (ϕ_t), cohort, i.e., when the root first appeared (ϕ_{cohort}), age of the root (ϕ_{age}), browsing ($\phi_{browsing}$), and site (ϕ_{site}) (Table 2). These single-factor models cannot be compared statistically with one another directly, but
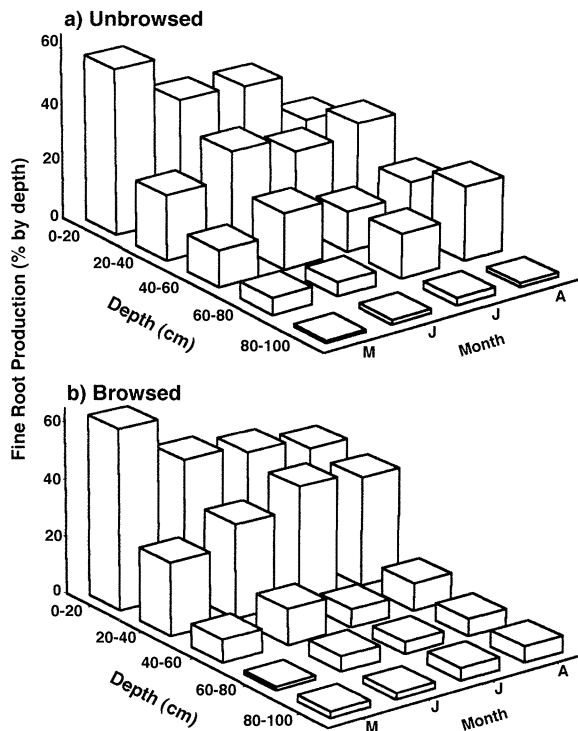
a) Unbrowsed

b) Browsed

FIG. 5. Proportion of monthly fine root production occurring in five soil depths during the 1993 growing season for (a) unbrowsed and (b) browsed stands.

based on Akaike's Information Criterion (AIC) scores, the time model was the most parsimonious of the five. However, other single-factor models provided insight into factors regulating fine root survival. For example, the cohort model showed that, during the 1993 growing season, survival was highest for fine roots that first appeared in May and lowest for those that first appeared during fall and over winter (Table 3). The age-dependent model indicated that survival declined most rapidly over the interval following first appearance (Table 3). Two-factor models including both time and treatment ($\phi_{t \times browsing}$) (LRT, $\chi^2_{10} = 164.7$, $P < 0.0001$), time and age ($\phi_{t \times age}$) (LRT, $\chi^2_{43} = 188.2$, $P < 0.0001$), and time and site ($\phi_{t \times site}$) (LRT, $\chi^2_{20} = 272.1$, $P < 0.0001$), were all significantly different from the reduced single-factor model (ϕ_t). This indicates that time-dependent survival rates of fine roots varied significantly between browsed and unbrowsed stands, among the 10 age groups, and the three sites. Using AIC as a tool for model selection, results indicate that the $\phi_{t \times site}$ model is a more parsimonious model than the $\phi_{t \times browsing}$ model, which is superior to the $\phi_{t \times age}$ model, although these conclusions cannot be tested statistically (Lebreton et al. 1992). To account for these site differences, we modeled browsing effects separately for each site and found that the effects of browsing on fine root longevity varied among sites (data not shown). Based on single-factor model results for each site ($\phi_{browsing}$), browsing significantly decreased fine root longevity at the A2 (0.58 ± 0.01 vs. 0.45 ± 0.01; LRT, $\chi^2_{10} = 279.7$, $P <$

TABLE 2. Results of MARK survival modeling, and comparisons between models for (a) fine root survival and (b) fine root decomposition (1−[dead root "survival"]).

Model	np	AIC	LRT comparison
a) Fine root survival rate			
(1) ϕ	1	16 185	
(2) ϕ_{age}	10	15 908	(2) vs. (1): $\chi^2_9 = 295.6$, $P < 0.0001$
(3) ϕ_{cohort}	10	15 940	(3) vs. (1): $\chi^2_9 = 263.4$, $P < 0.0001$
(4) $\phi_{browsing}$	2	16 170	(4) vs. (1): $\chi^2_1 = 8.4$, $P < 0.01$
(5) ϕ_t	10	14 371	(5) vs. (1): $\chi^2_9 = 1832.3$, $P < 0.0001$
(6) ϕ_{site}	3	16 154	(6) vs. (1): $\chi^2_2 = 34.8$, $P < 0.0001$
(7) $\phi_t \times$ site	30	14 139	(7) vs. (5): $\chi^2_{20} = 272.1$, $P < 0.0001$
(8) $\phi_t \times$ browsing	20	14 226	(8) vs. (5): $\chi^2_{10} = 164.7$, $P < 0.0001$
(9) $\phi_t \times$ age	55	14 269	(9) vs. (5): $\chi^2_{45} = 188.2$, $P < 0.0001$
(10) $\phi_{cohort \times browsing}$	20	15 868	(10) vs. (3): $\chi^2_{10} = 91.3$, $P < 0.0001$
(11) $\phi_{age \times browsing}$	20	15 870	(11) vs. (2): $\chi^2_{10} = 57.8$, $P < 0.0001$
b) Fine root decomposition rate			
(1) ϕ	1	10 768	
(2) ϕ_{age}	10	9 519	(2) vs. (1): $\chi^2_9 = 1267.1$, $P < 0.0001$
(3) ϕ_{cohort}	10	9 142	(3) vs. (1): $\chi^2_9 = 1644.3$, $P < 0.0001$
(4) $\phi_{browsing}$	2	10 637	(4) vs. (1): $\chi^2_1 = 132.7$, $P < 0.0001$
(5) ϕ_t	10	9 225	(5) vs. (1): $\chi^2_9 = 1560.7$, $P < 0.0001$
(6) ϕ_{site}	3	10 336	(6) vs. (1): $\chi^2_2 = 436.1$, $P < 0.0001$
(7) $\phi_t \times$ site	30	8 815	(7) vs. (5): $\chi^2_{20} = 450.2$, $P < 0.0001$
(8) $\phi_t \times$ browsing	20	9 099	(8) vs. (5): $\chi^2_{10} = 146.3$, $P < 0.0001$
(9) $\phi_t \times$ age	55	8 103	(9) vs. (5): $\chi^2_{45} = 1212.7$, $P < 0.0001$
(10) $\phi_{cohort \times browsing}$	20	9 037	(10) vs. (3): $\chi^2_{10} = 124.7$, $P < 0.0001$
(11) $\phi_{age \times browsing}$	20	9 454	(11) vs. (2): $\chi^2_{10} = 81.3$, $P < 0.0001$

Notes: For each model we list the number of estimated parameters (np) and the Akaike Information Criterion (AIC). Comparison of nested models uses the likelihood ratio test (LRT) and lists χ^2_{df} and the P value. For model notation, see *Methods: Fine root survival* and refer to Leberton et al. (1992).

TABLE 3. Estimates (± 1 SC) of fine root survival and decomposition rates (from MARK) for single-factor models separately evaluating the effects of time period (ϕ_t), cohort, (i.e., when the root first appeared; ϕ_{cohort}), age of the root (ϕ_{age}), browsing ($\phi_{browsing}$), and site (ϕ_{site}).

A) ϕ_t

Time interval	Survival	Decomposition
J-A	0.51 $\pm$ 0.03	0.50 $\pm$ 0.05
A-S	0.69 $\pm$ 0.02	0.51 $\pm$ 0.03
S-M	0.40 $\pm$ 0.02	0.77 $\pm$ 0.02
M-J	0.68 $\pm$ 0.02	0.32 $\pm$ 0.02
J-J	0.76 $\pm$ 0.01	0.29 $\pm$ 0.02
J-A	0.67 $\pm$ 0.01	0.44 $\pm$ 0.02
A-S	0.59 $\pm$ 0.01	0.41 $\pm$ 0.02
S-J	0.09 $\pm$ 0.01	0.88 $\pm$ 0.01
J-A	0.62 $\pm$ 0.02	0.46 $\pm$ 0.02
A-S	0.45 $\pm$ 0.01	0.63 $\pm$ 0.02

B) ϕ_{cohort}

Cohort	Survival	Decomposition
J-A	0.58 $\pm$ 0.02	0.32 $\pm$ 0.02
A-S	0.59 $\pm$ 0.01	0.49 $\pm$ 0.02
S-M	0.58 $\pm$ 0.02	0.64 $\pm$ 0.02
M-J	0.62 $\pm$ 0.03	0.28 $\pm$ 0.02
J-J	0.60 $\pm$ 0.01	0.33 $\pm$ 0.02
J-A	0.53 $\pm$ 0.01	0.59 $\pm$ 0.02
A-S	0.43 $\pm$ 0.01	0.63 $\pm$ 0.02
S-J	0.14 $\pm$ 0.03	0.89 $\pm$ 0.02
J-A	0.52 $\pm$ 0.02	0.47 $\pm$ 0.02
A-S	0.48 $\pm$ 0.01	0.86 $\pm$ 0.02

C) ϕ_{age}

Age group	Survival	Decomposition
1	0.60 $\pm$ 0.01	0.76 $\pm$ 0.01
2	0.44 $\pm$ 0.01	0.40 $\pm$ 0.01
3	0.46 $\pm$ 0.01	0.27 $\pm$ 0.02
4	0.48 $\pm$ 0.02	0.30 $\pm$ 0.02
5	0.63 $\pm$ 0.03	0.28 $\pm$ 0.03
6	0.50 $\pm$ 0.04	0.28 $\pm$ 0.04
7	0.40 $\pm$ 0.06	0.26 $\pm$ 0.05
8	0.67 $\pm$ 0.09	0.79 $\pm$ 0.07
9	0.71 $\pm$ 0.11	0.75 $\pm$ 0.22
10	0.00 $\pm$ 0.00	1.00 $\pm$ 0.00

D) ϕ_{site}

Site	Survival	Decomposition
A1	0.50 $\pm$ 0.01	0.55 $\pm$ 0.01
A2	0.53 $\pm$ 0.01	0.75 $\pm$ 0.01
C	0.57 $\pm$ 0.01	0.48 $\pm$ 0.01

E) $\phi_{browsing}$

Treatment	Survival	Decomposition
Unbrowsed	0.54 $\pm$ 0.01	0.67 $\pm$ 0.01
Browsed	0.52 $\pm$ 0.01	0.53 $\pm$ 0.01

Notes: The 10 periods listed for ϕ_{time} and ϕ_{cohort} models correspond to actual time intervals shown in Fig. 1, while the 10 values for ϕ_{age} correspond to age classes independent of time interval. Summary information and model comparisons for these and the more parsimonious two-factor models are listed in Table 2.
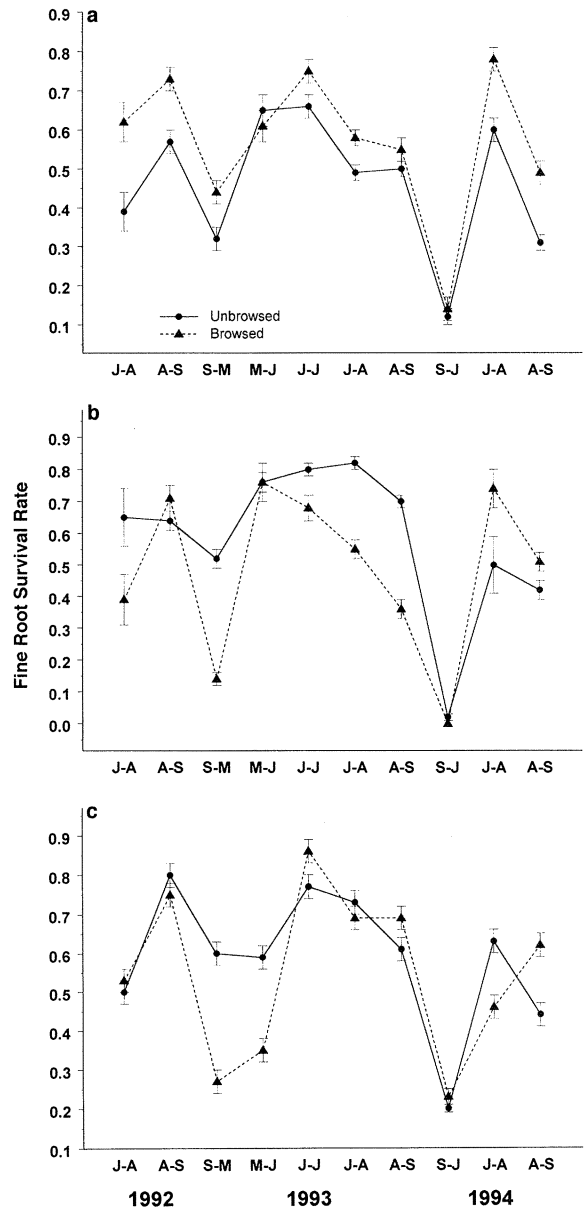

FIG. 6. Estimates (± 1 SE) of fine root survival (from MARK) for each of the 10 time intervals from 1992 through 1994. Data are results from two-factor models that included time and treatment ($\phi_{t \times browsing}$), modeled separately for the (a) A1, (b) A2, and (c) C sites. For each site, time and treatment models ($\phi_{t \times browsing}$) were significantly different from the reduced single-factor model (ϕ_t) as follows: (a) LRT, χ^2_{10} = 52.5, $P < 0.0001$, (b) LRT, $\chi^2_{10} = 279.7$, $P < 0.0001$, and (c) LRT, $\chi^2_{20} = 51.2$, $P < 0.0001$. See *Methods: Fine root survival* and *Results: Modeling fine root survival* for model notations, and Tables 2 and 3 for other model results.

0.001) and C sites (0.58 $\pm$ 0.01 vs. 0.54 $\pm$ 0.01; LRT, χ^2_{10} = 154.7, $P < 0.001$), but significantly increased fine root longevity at the A1 site (0.44 $\pm$ 0.01 vs. 0.56 $\pm$ 0.01; LRT, χ^2_1 = 40.3, $P < 0.001$). However, at all sites, the two-factor model $\phi_{t \times browsing}$ provided a sig-

nificantly more parsimonious representation of herbivory effects (Fig. 6).

Fine root decomposition was affected significantly by time period, cohort, age, site, and browsing (Table 2). Roots that first appeared later in the growing season,
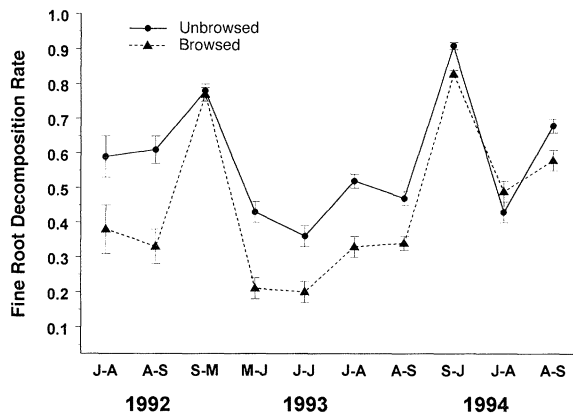
FIG. 7. Estimates (± 1 SE) of fine root decomposition (from MARK) for each of the 10 time intervals from 1992 through 1994. Data are results from the two-factor model that included time and treatment ($\phi_{t \times browsing}$), modeled across sites. The time and treatment model ($\phi_{t \times browsing}$) was significantly different from the reduced single-factor model (ϕ_t) (LRT, χ^2_{10} = 146.3, $P < 0.0001$). See Methods: Fine root survival and Results: Modeling fine root survival for model notations, and see Tables 2 and 3 for other model results.

including those that first appeared in fall and over winter, had a significantly higher probability of decomposing than roots that first appeared earlier in the growing season (Table 3). Among all time periods, decomposition rates were highest during the first and second overwinter periods. Rates of decomposition declined significantly with age, most notably over the first three age groups. Browsing decreased fine root decomposition by 21%, and decomposition estimates for the A2 site were significantly higher than those at either the A1 or the C sites (Table 3). Similar to fine root survival, several two-factor models were significantly different from reduced single-factor models; however, there were distinct differences in the relative degree to which these factors affected survival and decomposition. For example, time and site ($\phi_{t \times site}$) (LRT, χ^2_{20} = 450.2, $P < 0.0001$, AIC = 8815), and time and treatment ($\phi_{t \times browsing}$) (LRT, χ^2_{10} = 146.3, $P < 0.0001$, AIC = 9099) were both significantly different from the reduced single-factor model (ϕ_t). However, unlike fine root survival, the effect of browsing on fine root decomposition was consistent across sites (Fig. 7). Moreover, the age of a dead root was the most parsimonious determinant of decomposition at a given time period ($\phi_{t \times age}$) (LRT, χ^2_{43} = 1212.7, $P < 0.0001$), as indicated by the AIC score for this model.

DISCUSSION

The influence of herbivores on fine root production

Browsing by moose and snowshoe hares decreased annual fine root growth of early successional willow stands an average of 31.4% over 3 yr, and had significant effects on the seasonal patterns of fine root longevity, decomposition, and the depth distributions of

production and mortality. These results are the first we know of documenting the effects of aboveground herbivory on fine root production, mortality, and decomposition. Until now, all research on the effects of aboveground herbivory on root dynamics has focused on root biomass. Many of these field and laboratory studies have reported negative effects of aboveground herbivory on root biomass (Jameson 1963, Holland and Detling 1990, Pandey and Singh 1992, Chaieb et al. 1996, Thornton and Millard 1996, Vare et al. 1996). However, this generalization is clearly not universal, and is highly dependent on the timing, intensity, and frequency of herbivory (Davidson and Milthorpe 1966, McNaughton and Chapin 1985, Milchunas and Lauenroth 1989, Hik and Jefferies 1990, Coughenour 1991, Milchunas and Lauenroth 1993). Coughenour (1991) found that nearly 30 years after elk had been excluded from grazing Yellowstone National Park's northern winter range, there was no difference in root biomass between exclosed and unexclosed plots. Clearly, the removal of senescent herbaceous vegetation during winter by grazers is substantially different from the impacts of winter browsing on live, dormant aboveground biomass of woody plants. Moreover, few of these previous studies have separated live from dead root biomass. Most importantly, static measures of root biomass are a poor surrogate for root growth, since root production and mortality occur simultaneously (Hendrick and Pregitzer 1992, Pregitzer et al. 1995, Steele et al. 1997), and because many factors can alter fine root longevity as we have shown.

The severe winter browsing sustained by many early successional stands in interior Alaska substantially decreases the number of active buds and reserves of carbon and nutrients (Bryant 1987). The rate at which plants restore leaf area and replenish reserves used for tissue reconstruction following browsing determines the rate of regrowth relative to unbrowsed plants, and ultimately the frequency with which plants can tolerate browsing. Richards (1984) found that following clipping, root length growth was reduced by half in the grazing tolerant bunchgrass, Agropyron desertorum, but not in the grazing intolerant species A. spicatum. It was argued that in grazing tolerant species, reductions in root growth may represent an adaptation for more rapid regrowth of aboveground tissues following herbivory. The rapid regrowth of many hardwood trees following short-rotation coppicing (Blake 1980, Kauppi and Kiviniitty 1990) provides some insight into how woody plants may respond to single or multiple browsing events, but differs substantially from sustained browsing effects by large mammals. For example, Dickmann et al. (1996) studied aboveground and belowground growth responses of two hybrid poplar clones to coppicing and found no detectable effect on fine root production or mortality the year following coppicing. However, Bedeneau and Auclair (1989) found decreased root growth in hybrid poplar treated

with annual rotation coppicing compared with 3-yr rotation coppice. Under intensive browsing, such as occurs in our system, it is reasonable that plants would preferentially allocate resources to aboveground growth at the expense of root growth in order to reestablish a functional balance between root and shoot growth. If total productivity is also reduced by browsing, root growth would likely scale back to a level that meets aboveground demand for soil resources.

Seasonality of fine root production and mortality

Several aspects concerning the seasonal patterns of fine root production and mortality distinguish our sites from temperate and southern boreal ecosystems. First, the seasonal peak in fine root production at our sites occurred in midsummer, following a gradual increase during spring and early summer. Maximum leaf out occurred on 3 May, 30 April, and 3 May during 1992, 1993, and 1994, respectively. Thus, the period of maximum root growth lagged behind leaf out by ~6 wk. This delay was likely a function of the time required for surface and subsurface soils to thaw and subsequently warm to the temperature optimum for root growth. Tyron and Chapin (1983) also found that root elongation of Alaskan taiga tree species peaked in mid-July, and closely followed the seasonal pattern of soil temperature. Steele et al. (1997) reported that soil temperature explained >90% of the variation in fine root growth for three species growing at two Canadian boreal forest sites, and that fine root growth began earlier at their more southerly site. Hendrick and Pregitzer (1996) found that fine root production was greatest in early spring soon after leaf out for northern hardwood forests. Thus, there appears to be a general trend towards delayed maximum fine root growth relative to leaf out with increasing latitude, supporting the notion that spring regrowth in high latitude ecosystems is comparatively more dependent on aboveground nutrient and carbon stores. This pattern also has consequences for the impacts of winter browsing on spring regrowth, and may partially explain why there is also a general trend towards increased concentrations of chemical defenses in current annual shoots of woody plants at higher latitudes (Bryant et al. 1994, Swihart et al. 1994).

Second, there was an inverse relationship between fine root production and mortality within a year, but a strong positive relationship between these two processes among years. This within-season asynchrony was a function primarily of the pronounced seasonal peak of production in midsummer, coupled with increasing mortality and declining survival rates towards fall and over winter. As far as we are aware, no other study has found overwinter mortality to contribute significantly to annual fine root processes (Persson 1980, Hendrick and Pregitzer 1993b, Steele et al. 1997). Our survival modeling estimates indicate that, across all sites and treatments, overwinter survival averaged 0.40

± 0.02 and 0.09 ± 0.01 during the 1992–1993 and 1993–1994 winters, respectively. Several factors could account for such low survival rate over winter, including the breakage of fine roots during soil freezing. An additional factor may be dessication, which is a potential cause of fine root overwinter mortality in pine seedlings (Sutinen et al. 1996). It is important to recognize, however, that mortality on a mass or length basis may not necessarily be inversely correlated with longevity ($r^2 = 0.01$, $P = 0.45$). This is simply because a few roots with low survival rate would translate into a low absolute mortality rate, and vice versa. We cannot identify any factor or set of factors accounting for the dramatic differences in survival between our two winter periods. Nor is there any clear reason why fine-root overwinter survival in browsed plots (0.27 ± 0.02) was so much lower than in unbrowsed plots (0.50 ± 0.02) the first year. Perhaps the higher percentage of roots in surface layers of browsed plants increased the vulnerability of these roots to overwinter mortality. Irrespective of cause, such low overwinter survival has serious consequences for spring regrowth and adds to the importance of aboveground reserves since uptake of soil resources must rely entirely on the growth of new fine roots, or existing coarse roots. Low overwinter survival of fine roots may also partially explain why Alaskan taiga forests appear to have disproportionately more carbon allocated belowground relative to temperate forests (Ruess et al. 1996).

Third, we found a pronounced variation in annual fine root production among years, and significant sequential increases in deeper root growth within the growing season, both of which appear to be related to soil moisture availability. Differences in fine root production and mortality among years accounted for the largest proportion of explained variation in fine root production and mortality (Fig. 3), with production and mortality being ~2.5 times greater in 1993 compared with 1992 and 1994. While we can't rule out the possibility that low production levels during 1992 may have been partially a result of delayed root colonization on the minirhizotron tubes, 1992 and 1994 production values were nearly identical, and other data suggest a strong climatic influence on this interannual pattern. As mentioned above, precipitation during 1993 was unusually low, the BNZ LTER climate database shows that river levels were also lower, and air temperatures during May and June were notably warmer during 1993 compared with 1992 and 1994. Aboveground production was not measured at our sites, but is available for balsam poplar/green alder (25 yr old) and white spruce (150 yr old) stands that occur close by on similarly positioned terraces relative to river level. Annual diameter growth increments for 1992, 1993, and 1994 for balsam poplar (0.42 ± 0.04, 0.18 ± 0.10, and 0.45 ± 0.07 cm/yr, respectively) and white spruce (0.22 ± 0.04, 0.14 ± 0.02, and 0.23 ± 0.04 cm/yr, respectively) indicate significantly lower aboveground production

during 1993. Litterfall at contiguous BNZ LTER sites (early successional willow stage) was greater in 1994 relative to 1992 and 1993. Together, these data suggest that the higher rates of fine root growth during 1993 represent an increase in belowground vs. aboveground production in response to a warmer, drier growing season. Virtually all studies on fine root dynamics to this point have focused on one or at the most two years. Substantially more carbon and nitrogen are cycled annually through fine roots in taiga ecosystems, resulting in a disproportionate percentage of soil respiration derived from fine roots relative to litterfall (Ruess et al. 1996). Therefore, it is expected that large interannual variation in belowground carbon allocation would have significant effects on net ecosystem production beyond what would be predicted simply from variations in aboveground growth.

The progressive seasonal increase in fine root production at deeper soil depths that we found is similar to that reported by other studies (Fernandez 1975, Persson et al. 1995, Day et al. 1996). For example, Hendrick and Pregitzer (1996) observed that episodic periods of deep root production coincided with intervals of low soil water availability during late summer. At our sites, this seasonal shift in production to deeper soil layers occurred deeper in the profile for unbrowsed plants compared with browsed plants (Fig. 5a, b). Browsed plants had a higher percentage of annual production in surface layers, perhaps to exploit nutrients cycled more rapidly at the soil surface by herbivores (Ruess 1987, Kielland et al. 1997). Rodriquez et al. (1995) also cited this explanation for their observation that relative to ungrazed communities, grazed grasslands had a higher concentration of root biomass near the soil surface. Given that willow plant density and height were greater inside the exclosures, the increased demand for soil resources likely stimulated deeper exploration and uptake of both water and nutrients. Root proliferation into deeper soil layers would allow unbrowsed plants to access subsurface river water, which typically rises in early July as the snowmelt in the Alaska Range recharges river levels in the Tanana River basin. This subsurface water may also be an important source of soluble organic and inorganic nutrients for plants (Chapin et al. 1988, Yarie et al. 1993).

Fine root survival and decomposition

Coupling minirhizotron measurements of production and mortality with survival modeling of live and dead roots using MARK provides insights into factors regulating fine root longevity and decomposition. Together, these analytical tools allow for a more detailed understanding of fine root turnover, which has traditionally been viewed as the ratio of production to biomass. Results from MARK indicated that although single-factor models were less parsimonious than most of the two-factor models, many of these more reduced models yielded useful information regarding factors controlling fine root survival and decomposition. Several of these more reduced survival models provided results consistent with other published studies. For example, cohort effects showed that during the 1993 growing season, survival of fine roots was greatest for roots that first appeared in May, and progressively declined for roots first appearing during subsequent time periods through winter (Table 3). This seasonal pattern is similar to Hendrick and Pregitzer's (1993a) findings, who showed that roots first appearing in the spring lived longer than the average for all fine roots. Weber and Day (1996) found that young roots had greater rates of senescence than older roots in a perennial dune ecosystem, and Day et al. (1996) found a similar pattern at oak–palmetto scrub sites. We also found that age-based survival declined most rapidly over the interval following first appearance.

Considerably more detail was provided by our two-factor models, which showed significant but often complex interactions among time, age, treatment, and site. For example, time and site were important factors ($\phi_{t\times\text{site}}$) due to higher fine root survival at the C site, particularly during the two overwinter periods. Patterns of overwinter survival also differed among browsed and unbrowsed plots; browsing decreased fine root survival at the A2 and C sites, but increased survival at the A1 site (Fig. 6a, b, c). We expected browsing to decrease fine root survival, given that the few previous studies seem to show trends towards increased mortality and reduced survival following disturbance (Silver and Vogt 1993, Kosola et al. 1995). Levels of herbivory were intermediate at the A1 site; thus an interaction between site conditions and herbivory must explain higher survival outside the exclosures at this site. At least two factors distinguish the A1 site from the other two sites. First, as mentioned above, A1 is by far the wettest site. The second factor is a greater density of thin-leaf alder (Alnus tenuifolia) at the A1 site, which fixes substantial amounts of atmospheric N in these early successional stands and has highly decomposable leaf litter (Kielland et al. 1997). There are contradictory data sets on the effects of nutrient availability on fine root growth and turnover (Hendricks et al. 1993, Pregitzer et al. 1993, 1995, Haynes and Gower 1995, Steele et al. 1997). Fine root production and mortality of browsed plants may respond to increased nutrient availability differently than unbrowsed plants if increased fine root longevity alleviates belowground carbon allocation in plants already C-stressed from browsing. However, if herbivores maintain nutrients cycling rapidly at the soil surface (Ruess 1987), a similar argument would predict higher turnover rates in browsed plots, as has been shown for other deciduous hardwood species following fertilization (Hendricks et al. 1993, Pregitzer et al. 1995). However, it is often difficult to establish predictive relationships linking fine root production and mortality with soil environmental factors (Hendrick and Pregitzer 1997).

Several of the single-factor models yielded similar, but more pronounced patterns of regulation over fine root decomposition compared with control on fine root survival. For example, fine root decomposition rates progressively increased for roots first appearing later in the season each year, and the initial decline in age-based decomposition was more pronounced than age effects on fine root survival (Table 3). Moreover, herbivory significantly reduced fine root decomposition rates at all sites (Fig. 7), despite the fact that herbivore effects on fine root survival varied among sites. Survival varied by 14% across sites, but decomposition rates varied by as much as 56% among sites. Even rates of decomposition during the first (0.77 ± 0.02) and second (0.88 ± 0.01) overwinter periods, were higher than average growing season values compared with patterns for fine root survival. Together, these results point to the strong influences of time and substrate quality in the regulation of fine root decomposition, with perhaps more endogenous, plant-level regulation of fine root survival (Hendrick and Pregitzer 1997). However, fine root survival and decomposition were closely coupled, as shown during 1993, when decomposition rates and survival rates for live and dead root cohorts were inversely correlated ($r = -0.94$, $P < 0.05$). Thus, roots from a late season cohort that did not survive had a significantly greater chance of decomposing than did roots from a cohort first appearing early in the growing season (ϕ_{cohort}). In contrast, younger roots that did not survive decomposed rapidly (ϕ_{age}). It may be that the youngest roots with the highest growth rates also had low C:N ratios, and thus, decomposed rapidly (Reich et al. 1992). Conn and Day (1996) attributed slower decay of fine roots from mature dune sites to higher lignin : N and lignin : P ratios, and similar arguments have been used for explaining slower decomposition rates of fine roots from tropical tree species (Bloomfield et al. 1993), and from plants grown under elevated CO_2 (Gorissen et al. 1995, Van Ginkel et al. 1996).

Similar factors could account for consistently slower fine root decomposition rates in browsed plants. For example, higher resorption of nitrogen prior to senescence (Goldfarb et al. 1990), or the presence of secondary chemicals (Muller et al. 1989, Bloomfield et al. 1993) could lower the substrate quality and thus the decomposability of fine roots from browsed plants. Additional differences in soil moisture or biotic properties between browsed and unbrowsed plots may also contribute to this pattern. We didn't measure soil water regularly at our sites, and found only a slightly lower soil water content (0–20 cm) in browsed plots (NS) when measured during the 1996 growing season (data not shown). We also have observed substantially more collembolans in surface soils of unbrowsed plots compared with browsed plots (R. W. Ruess, *personal observation*). The higher herbaceous cover (Bryant, BNZ LTER web site) and greater fine root biomass of both herbaceous and woody species of unbrowsed plots like-

ly cultivates a more active detrital food web, resulting in more rapid decomposition rates of fine roots.

Our estimates of in situ decomposition rates were substantially faster than many previously reported. For example, McClaugherty et al. (1984) found that root decomposition was initially rapid (10–20% loss) but slowed, and after 4 yr roots had lost between 20–60% of initial mass. Lohmus and Ivask (1995) used buried root bags and found that after 5 yr, the finest roots had lost 40% of their initial dry mass. These and many other studies have used litter bags to measure fine root decomposition rates (Fahey et al. 1988, Burke and Raynal 1994), but the rapid disappearance of fine roots observed from more direct methods (Hendrick and Pregitzer 1993b) points to the limitations of this method in assessing fine root decomposition. Fahey and Hughes(1994) found rapid disappearance of fine roots in a northern hardwood forest using ingrowth screens, and commented that the disturbance of active hyphal networks is the primary reason that litter bag studies typically underestimate decomposition rates.

CONCLUSION

Previous research on herbivore–ecosystem interactions has focused almost entirely on aboveground plant growth responses and associated nutrient cycling processes. Our results are the first we know of that measure the effects of aboveground herbivory on seasonal and annual patterns of fine root production and mortality, and characterize factors controlling fine root longevity and decomposition. These data add to the large body of previous research showing substantial influence of browsing by moose and snowshoe hares on early successional forest development in interior Alaska (Bryant 1987, Bryant et al. 1991, Kielland et al. 1997). We showed previously that, relative to other ecosystem types along the Tanana River floodplain, these heavily browsed early successional stands have the highest ratio of root to aboveground litterfall C allocation (Ruess et al. 1996). Present data suggest that herbivores may be partially responsible for this pattern, given the lower ratio of annual production to mortality, and the lower average longevity of fine roots in browsed stands. Our sense is that, although root growth was substantially lower in browsed plants, herbivory reduced aboveground growth to an even greater extent (data not presented), further increasing the ratio of root to litterfall-derived soil carbon in browsed sites. Finally, two important additional features distinguish fine root dynamics in our stands from temperate and more southerly boreal ecosystems: (1) low overwinter survival of fine roots, and (2) a substantial time lag between leaf out and maximum fine root growth, suggesting greater reliance on aboveground stores for spring regrowth. Herbivores appear to play an important role in linking these two events, first by exacerbating overwinter mortality and secondly by consuming a substantial amount of aboveground stores. Thus, not only do herbivores have

pronounced direct effects on nutrient cycling processes, but climatically driven effects on fine root processes may be linked with herbivory in complex ways that define fundamental latitudinal patterns in plant growth and allocation to defense against herbivory.

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