COMMUNITY, POPULATION, AND GROWTH DYNAMICS OF *ALNUS TENUIFOLIA*: IMPLICATIONS FOR NUTRIENT CYCLING ON AN INTERIOR ALASKAN FLOODPLAIN

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 2008

ABSTRACT

This study describes the community, population, and growth dynamics of *Alnus tenuifolia* (thinleaf alder) and implications for nutrient cycling on the Tanana River floodplains. Through symbiotic N-fixation inputs, alder contributed to soil N accumulation with time. N-fixation itself was likely limited by soil P. Soil N was positively related to alder stem density in early successional stands. Community structure varied along a temporal gradient of changing environmental characteristics, but variations in successional patterns were found. Landscape scale alder recruitment varied temporally and was apparently linked to interactions between geofluvial processes, seed production and dispersal, and herbivory. A widespread stem canker outbreak has resulted in high alder mortality and likely reductions in N-fixation inputs. Disease incidence and mortality were positively related to stem density. Alder radial growth was sensitive to drought during June and August. Alder growth was positively related to river level, suggesting that fluctuation in hyporheic flow is important to alder water balance, especially on lower terraces. The sensitivity of alder growth to meteorological drought was heightened with increasing terrace elevation. Long-term climatic trends suggest that drought will become more common and severe, resulting in reductions in alder-mediated ecosystem N inputs.

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ACKNOWLEDGEMENTS

This research was supported by the Bonanza Creek LTER program (funded jointly by NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952-231) and by a University of Alaska Fairbanks (UAF) Center for Global Change Student Award. The UAF Department of Biology and Wildlife also supported this project by providing teaching assistantships.

I would first like to thank my co-advisors Roger Ruess and Teresa Hollingsworth, who were mentors that challenged and encouraged me throughout their active involvement in this project. Their friendship and guidance have truly helped to make my graduate research a rewarding, educational, and enjoyable experience. I also thank my advisory committee member Knut Kielland for all of his thoughtful advice and feedback.

I thank Dorothy Walker, an undergraduate research technician, for all of her many contributions to this project in the field and in the lab. Several friends associated with the Boreal Ecology Cooperative Research Unit (BECRU) contributed to this project, and I thank them for their assistance in the field: Mark Winterstein, Gretchen Garcia, Brian Charlton, and Emily Tissier. Jamie Hollingsworth and Brian Charlton provided me with logistical support and technical advice throughout the last three years. I extend huge thanks to my friends and family who graciously volunteered their time to help me in the field: Steve Brown (Volunteer of the Year), Sarah Nossov (Best Big Sister Ever), Wanda Nossov (Best Mom in the World), Laura Gutierrez, and Emily Bernhardt. Fellow student Steve Winslow gave me endless mentoring on tree ring analysis, and discussions with

Glenn Juday have helped to guide my climate sensitivity project. Lola Oliver of the Forest Soils Lab trained me in the procedures for chemical analyses and assisted with the C/N analyses. The staff of the Department of Biology and Wildlife and the Institute of Arctic Biology have given me much appreciated assistance along the way.

I am grateful for the many individuals and organizations whose support has made this research possible and for all of my friends and family who have been there for me throughout this process. I especially thank my mom, Wanda Nossov, who braved the cold and dark Fairbanks winters with no running water just to be near me, Steve Brown, whose warm companionship has kept me smiling, and Sarah Nossov, whose strength and determination will always inspire me.

INTRODUCTION

Nutrient limitation constrains the productivity of most terrestrial ecosystems (Vitousek and Howarth 1991, Reich et al. 1997, Chapin et al. 2002). Plant species have differential effects on nutrient cycling which feed back to influence species composition (Binkley and Giardina 1998, Miki and Kondoh 2002, Chapman et al. 2006). By supplying a commonly limiting nutrient to ecosystems through the fixation of atmospheric dinitrogen, symbiotic nitrogen (N)-fixers often assume an integral role in community dynamics and ecosystem function (Vitousek 1990). N-fixation is the primary pathway of N input into most natural terrestrial ecosystems, although industrial and agricultural N inputs are becoming increasingly important sources of N throughout the world (Vitousek et al. 1997, Chapin et al. 2002). Symbiotic N-fixers frequently dominate the characteristically N-deficient early successional seres, and drastically change soil quality through rapid N accumulation (Van Cleve et al. 1971, Chapin et al. 1994, Walker and del Moral 2003). The availability of limiting nutrients, in turn, influences community dynamics, mediating inter-specific interactions, species composition, and habitat quality (Chapin et al. 1997, Miki and Kondoh 2002, Chapman et al. 2006). The spatial and temporal variations in the presence, abundance, and activity of N-fixers, therefore, are likely to have important consequences for ecosystem function and community structure.

Alnus incana ssp. *tenuifolia*, hereafter *Alnus tenuifolia* (thinleaf alder), is the dominant N-fixing plant species in interior Alaskan floodplains of the boreal forest.

Along the Tanana River floodplain, symbiotic N-fixation mediated by thinleaf alder shrubs accounts for up to 70% of all accumulated N throughout two centuries of succession (Van Cleve et al. 1971, Van Cleve et al. 1991). Dense stands of thinleaf alder shrubs in early floodplain succession are capable of contributing up to 60 kg N ha^{-1} year^{-1}, thereby strongly influencing soil chemistry, microbial processes, plant nutrient availability, and successional dynamics (Van Cleve et al. 1971, Walker and Chapin 1986, Klingensmith and Van Cleve 1993, Van Cleve et al. 1993, Viereck et al. 1993, Uliassi and Ruess 2002).

Through decades of research on primary succession in the Tanana River floodplains of interior Alaska, the fundamental role of thinleaf alder in influencing ecosystem processes and community dynamics is fairly well understood. Much of this research, however, has focused on cross-stage comparisons of a particular successional chronosequence (Viereck et al. 1993, Chapin et al. 2006), and has not necessarily captured the range of ecological variability in thinleaf alder stands that exists at broad spatial or temporal scales. The current study aims to address this deficiency by explicitly examining the temporal and spatial variability in patterns of soil development, community structure, population dynamics, and plant growth across a wide array of thinleaf alder stands along a broad reach of the Tanana River floodplain.

This thesis is organized in two main research chapters. The first chapter addresses patterns of soil development, alder community, and population dynamics; the second examines climate sensitivity of alder growth. In Chapter 1, I address the following questions and their implications: (1) How does thinleaf alder influence soil physical and chemical properties over time, and does alder stand structure mediate soil nutrient status?, (2) How does the community structure of thinleaf alder stands vary temporally and in relationship to environmental variation?, and (3) What are the stand-level and landscape-level patterns of thinleaf alder recruitment, incidence of disease, and disease-related mortality? In Chapter 2, I analyze the sensitivity of thinleaf alder radial growth to inter-annual variation in meteorology and hydrology in order to predict the future response of this keystone N-fixer to a changing climate. Specifically, I ask: (1) What are the most likely periods of thinleaf alder vulnerability to drought stress? (2) Is there evidence that annual radial growth is sensitive to moisture limitation? (3) Does the climate sensitivity of alder growth vary across the landscape?, and (4) How are climate and hydrology changing in the long term, and what are the implications for alder-mediated ecosystem N inputs?

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CHAPTER 1: PATTERNS OF SOIL DEVELOPMENT, PLANT COMMUNITY STRUCTURE, AND POPULATION DYNAMICS IN THINLEAF ALDER STANDS ON AN INTERIOR ALASKAN FLOODPLAIN[1]

INTRODUCTION

Plant community structure strongly influences ecosystem function by mediating flows of energy, nutrients, and water, particularly when individual species exert strong controls over ecosystem processes (Chapin et al. 1997, Hooper et al. 2005). Since nutrient limitation constrains the productivity of nearly all terrestrial ecosystems (Vitousek and Howarth 1991, Chapin et al. 2002), plant species which directly or indirectly impact nutrient supply are likely to strongly influence community and ecosystem level processes (Chapin 2003). By providing fixed atmospheric N to N-limited systems, symbiotic N-fixers often play an especially important role in altering nutrient cycling, productivity, and the competitive balance between species (Vitousek 1990). Variations in the presence, abundance, and persistence of functionally important species can strongly influence ecosystem and community level processes, sometimes leaving legacies on the landscape that persist beyond their lifetimes (Hobbie 1992, Robles and Chapin 1995). The distributions of plants and the patterns of succession are mediated by the dynamic interplay between the abiotic environment, species life history traits,

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[1] Nossov, D.R., T.N. Hollingsworth, and R.W. Ruess. In preparation. Patterns of soil development, plant community structure, and population dynamics in thinleaf alder stands on an interior Alaskan floodplain. Canadian Journal of Forest Research.

population dynamics, species interactions, and chance (Walker and Chapin 1987, Chapin et al. 1994, Walker and del Moral 2003). The temporal and spatial variation in some of these controls, and their interactions, are likely to lead to variations in successional rates and pathways, which may be reflected in variations of ecosystem function (del Moral and Wood 1993, McCook 1994, Fastie 1995).

The N-fixing shrub *Alnus incana* ssp. *tenuifolia*, hereafter *Alnus tenuifolia* (thinleaf alder), commonly dominates early successional stands in the boreal forest floodplains of interior Alaska, where it contributes substantial quantities of nitrogen (N) to the initially nutrient poor alluvial soils, altering soil chemistry, microbial processes, and plant nutrient availability (Van Cleve et al. 1971, Klingensmith and Van Cleve 1993, Van Cleve et al. 1993, Uliassi and Ruess 2002). As the only dominant vascular N-fixer in this ecosystem, the processes that regulate thinleaf alder population structure could therefore be extremely important to long term soil development, community dynamics, and future plant productivity. The overall goal of this study was to assess the temporal and spatial variation in alder-mediated soil properties, community patterns, and population dynamics, in order to place our present knowledge into the context of a heterogeneous landscape influenced by processes that may change with time.

Research on primary succession in interior Alaskan floodplains has focused on a hypothesized sequence of floristic change that has become a classic paradigm of succession; however, variations from this pathway are likely to occur, with important implications for community and ecosystem dynamics (Viereck et al. 1993a, Fastie 1995, Chapin et al. 2006). Focusing on thinleaf alder-dominated stands, we analyzed the distribution of all potential successional dominants and understory plant species in relationship to stand age and environmental characteristics in order to characterize the predominant changes in alder community structure over time, identify variations from the prevailing successional pattern, and infer the potential causes and consequences of the variations.

Two important and potentially related observations inspired an investigation of the implications of landscape-scale thinleaf alder population dynamics. First, scientists working with the Bonanza Creek Long Term Ecological Research (LTER) program noticed an increase in thinleaf alder abundance on the Tanana River floodplain in the early 1990s (RW Ruess, personal observation), and secondly, a widespread outbreak of a fungal stem canker (*Valsa melanodiscus*) causing branch dieback and mortality of thinleaf alder was reported (USDA 2006, 2008). These observations have brought attention to the need to understand the dynamics of alder recruitment and mortality at broad spatial and temporal scales. We therefore investigated the temporal and spatial variation in alder recruitment and considered the roles of geofluvial processes, dispersal dynamics, competition, and herbivory in influencing these patterns. We examined the patterns of disease incidence and disease-induced mortality across the landscape, and discussed how the current outbreak might influence population, community, and ecosystem level processes.

In this study, we sampled a wide variety of thinleaf alder stands over a broad reach of the Tanana River floodplains, and investigated the temporal and spatial patterns of soil development, alder population dynamics, and community structure to assess their potential controls and consequences. Our specific objectives were (1) to quantify the changes in the physical and soil chemical environment that occur throughout the course of alder stand establishment and decline, characterize the influence of alder stand structure on soil nutrient status, and assess the implications for plant nutrient acquisition; (2) to analyze patterns of plant community structure in relationship to time and environmental variation to gain an understanding of the breadth of successional patterns; and (3) to investigate patterns of alder recruitment, incidence of disease, and disease-induced mortality and suggest implications for future community and ecosystem level processes.

METHODS

Study area

The study area encompasses a 80-kilometer reach of the Tanana River floodplain in interior Alaska, between Fairbanks (64.9° N, 147.9° W) and Nenana (64.5° N, 148.7° W) (Fig. 1.1). The Tanana River is a meandering, glacially fed river that drains the north slope of the Alaska Range into the Yukon River. The Tanana River carries a high sediment load, and through the annual rise and fall of river levels, continued deposition creates new surfaces upon which primary succession may begin.

The primary successional pathway which has received the most study is described in detail in Viereck et al. (1993a). This successional sequence consists of the early colonization by several species of *Salix* (willow) which form an open shrub community that is replaced by a closed shrub stand dominated by *Alnus tenuifolia* (thinleaf alder). The fast-growing deciduous tree *Populus balsamifera* (balsam poplar) emerges in the canopy, and the slow-growing conifer *Picea glauca* (white spruce) eventually dominates, and may be replaced in late succession by *Picea mariana* (black spruce).

The climate of this region is strongly continental with low precipitation and humidity, and is characterized by extreme seasonal variation in day length and temperature and a short growing season (Viereck et al. 1993b). Mean annual precipitation is 269 mm in Fairbanks, and annual temperature averages -3.3°C, with mean daily temperatures ranging from -24.9°C in January to 16.4°C in July.

In 2006, we established 45 transects in alder-dominated stands that represented a wide range of stand structure. Each 50 m x 5 m transect, set perpendicular to the course of the river, was subdivided into 10 5 m x 5 m plots, which, after initial vegetation sampling, were pooled into zones of homogeneous vegetation (see below).

Vegetation sampling and laboratory procedures

Community structure

Within each 5 m x 5 m plot (n = 450 plots), the diameter at breast height (dbh) of all trees and shrubs > 2 m tall were measured and the stem density and basal area of each species were calculated. All woody plants < 2 m were counted in one 1 m x 1 m quadrat randomly placed within each plot. The percent cover of all herbaceous species in each quadrat was estimated. The presence or absence of moose and snowshoe hare feces were recorded as measures of potential herbivory.

After initial vegetation sampling, multivariate analyses of community structure were conducted in order to aggregate plots from each transect into larger zones of homogeneous vegetation for further sampling. The plots were grouped using detrended correspondence analysis (DCA), based on the size structure and stem density of thinleaf alder, willow, balsam poplar, and white spruce, and on the abundance of all other vegetation, classified by growth form (shrub, forb, graminoid, moss, and lichen). In the field, some of the aggregated plots were subdivided to account for physical heterogeneity, e.g. an abrupt rise in terrace height. These aggregated plots from each transect are referred to as sites (n = 89 sites).

Tree ring sampling

27 sites were subsampled for alder age distributions by collecting disks at ground level from up to 10 live alder stems for each of three size classes based on dbh (0 - 2.9 cm, 3 - 4.9 cm, and ≥ 5 cm). Disks were oven-dried and sanded with 400-600 grit sandpaper, and growth rings were counted and measured on a sliding bench micrometer to a precision of 0.01 mm. Three to four radii were sampled from each disk and averaged to ensure accuracy of dating and growth measurements. Disks which could not be dated consistently were excluded from subsequent analyses (n = 547 disks). Stand age was estimated by the age of the oldest alder in each site.

Disease survey

At each site, every alder stem > 2 m tall was scored for severity of canker infection (n = 11,481 stems). In the early stages of canker infection, many spore-containing perithecia can be seen along the branches of the host. Diseased branches eventually die and may fall from the tree. As the infection progresses towards the main ramet, thick bands of perithecia wind down the trunk of the tree. At this point, branch dieback is severe. Alder stems were classified as either: 1) *live without canker* – no visible cankers; 2) *live with canker* – visible cankers on branches or the main ramet; 3) *dead without canker* – standing dead with no visible cankers; or 4) *dead with canker* – standing dead with visible cankers.

Foliar chemistry

In mid-July 2007, alder leaf samples were collected from a randomly chosen subsample of 38 sites. Leaves from 5 trees (pooling 4 leaf samples per tree) were sampled in each site (n = 190 pooled leaf samples). Whole leaves, with petioles removed, were oven-dried at 60 ºC, ground, and analyzed for C, N, and P. Total C and N were analyzed with a LECO TruSpec CN Analyzer (St. Joseph, Michigan, USA), and total P was analyzed with a Bran+Luebbe AA3 Autoanalyzer following acid digest (Bran and Luebbe, Norderstedt, Germany). Duplicate analyses of each sample were conducted.

Environmental sampling and laboratory procedures

Terrace height

The relative heights of terraces above the river level were determined through differential leveling at 5 m intervals along each transect, then averaged for each site. Hourly Tanana River gage height readings from the U.S. Geological Survey (USGS) site in Fairbanks (#15485500) were used as benchmark elevations (waterdata.usgs.gov/nwis/). The mean terrace height of each zone is reported as the elevation above the gage datum (121.92 m above sea level) for the Fairbanks USGS site.

Soil properties

The surface litter layer was removed prior to soil sampling in each site. Five soil cores (1.9 cm diameter by 10 cm deep) were collected and pooled from each site. The thicknesses of both surface and buried organic layers were recorded before organic and mineral layers were combined for chemical analyses. Soils were oven dried at 60 ºC, passed through a sieve, homogenized, and ground. Soil pH was measured in a 5:1 slurry of deionized water and 10 g soil. Total soil C and N were analyzed with a LECO TruSpec CN Analyzer (St. Joseph, Michigan, USA), and total P was analyzed with a Bran+Luebbe AA3 Autoanalyzer following acid digest (Bran and Luebbe, Norderstedt, Germany). Duplicate analyses of each sample were conducted. Results are expressed on a concentration basis and on a pool-size basis to a depth of 10 cm.

Light availability

Light availability was estimated by measuring canopy cover with a spherical densiometer (Lemmon 1956). The means of the canopy cover measurements from three evenly spaced points within each site were used in data analysis.

Data analysis

Distributions of all variables were examined for normality using normal quantile plots and the Shapiro Wilk test. Strong deviations from normality were corrected using the appropriate data transformation (Zar 1996). Nonparametric analyses were employed with variables that could not be transformed to approximate normal distributions. All statistical analyses were conducted using JMP IN 5.1.2 (SAS Institute 2004), with the exception of the multivariate plant community analyses, which were conducted with PC-ORD v.5 (McCune and Mefford 1999). Statistical significance was determined at $\alpha = 0.05$, except as otherwise noted below.

Environmental variation

Spearman's rank correlation analyses were used to assess relationships between stand age and environmental parameters due to the non-normal distribution of stand age. We used simple linear regression to analyze relationships among alder population structure, environmental variables, and foliar leaf nutrient status, and used partial correlation analyses to tease apart the inter-correlations among predictor variables.

Community structure

Plant community structure was assessed principally through indirect gradient analysis, utilizing the detrended correspondence analysis (DCA) method of ordination (Hill 1979, Gauch 1982, McCune and Grace 2002). Stem densities of trees and shrubs > 2 m in height were grouped by dbh size class to improve our ability to characterize successional time. Stem densities of trees and shrubs < 2 m tall were used to assess patterns of recruitment. Percent covers of forbs (by species), mosses, and lichens were included in the ordination. Species that occurred in less than 5% of the sample units were removed. All vegetation parameters were square root transformed to minimize skewness and kurtosis, and data were then relativized by a power of 2 to account for variations in units of measurement used among different plant growth forms. Axis length was used as a measure of the compositional change represented in the sample (beta diversity) and was calculated using Hill's scaling, in which the ordination axis is scaled using the average standard deviation of species turnover. The proportions of variance represented by the DCA axes were calculated using relative Euclidean distance. The species score represents the position of a species along an axis, while the species rank represents its position in relationship to other species. Species scores, ranks, and correlations of species abundance with the axes were used to assess variation in the recruitment of young successional dominants, the abundance of mature successional dominants (by size class), and the associated understory vegetation. Correlations between the abundance of young successional dominants and the thickness of the upper layer of organic soil were conducted to determine the extent to which recruitment was limited by the development of an organic layer.

A second matrix was used as an overlay and correlation analyses were conducted to examine relationships between plant community structure, environmental variables, and stand age. Correlations between the DCA axes and vegetation and environmental parameters greater than $r^2 = 0.195$ were considered ecologically relevant and are presented in a joint biplot, where vectors indicate the direction and strength of the correlations. Patterns of moose and hare herbivory were assessed through logistic regressions with axis scores and willow density.

Alder population dynamics

The distributions of stem ages were used to analyze patterns of alder stand development, to examine the long term trends in alder recruitment across the landscape, and to assess the role of canker infection in shaping future stand structure. For each site, alder stem diameter was regressed against age using linear and polynomial models to predict age distributions. The suitability of linear or polynomial models was assessed based on comparisons of adjusted r^2 and AIC values. Models significant at the alpha = 0.1 level were used to estimate the age structures of live and dead stems based on stem diameter measurements. Relationships between stand structure and canker infection were further analyzed using logistic regression.

Landscape-level recruitment patterns were characterized using the measured age distribution of alder stems across all sites. The role of geofluvial processes in influencing recruitment patterns was characterized through examination of a historical sequence of aerial images of the study area from 1949-2007. Visual estimates of % shrub cover and % of available colonizable area were made at a subsample of sites for each year that imagery was available. The influence of seed dispersal dynamics was inferred by examining the spatial pattern of shrub expansion in the aerial image sequences, and by analyzing the site-level age reconstructions of stand establishment.

RESULTS

Variation in environmental characteristics

Stand and soil characteristics showed a large variation across all sites (Table 1.1). Stand age ranged from 13-56 years old (Table 1.1), and was correlated with a number of physical and chemical environmental characteristics (Table 1.2). Stand age, organic depth, and terrace height emerged as important predictors of soil chemical properties (Table 1.2). Due to the covariation among these predictor variables (Table 1.2), we conducted a partial correlation analysis, which revealed that stand age was independently correlated with both terrace height and organic depth (partial $r_s = 0.64$, $p < 0.001$; partial $r_s = 0.55$, $p < 0.01$, respectively), two variables that were not related when stand age was held constant (partial $r_s = -0.03$, $p = 0.87$). This analysis suggests that either terrace height or organic depth may be a useful proxy for stand age, but they are not interchangeable and interpretation may vary as they each relate more closely to different processes (i.e., geofluvial vs. biotic processes).

Soil pH varied from alkaline to acidic (8.2 to 5.5) (Table 1.1), and declined significantly with stand age (Table 1.2). A partial correlation analysis showed that terrace height and organic depth were each inversely related to soil pH when the other was held constant (partial $r = -0.62$, $p < 0.0001$; partial $r = -0.57$, $p < 0.0001$, respectively). The strong inverse relationship between soil pH and stand age was therefore likely due to both the accumulation of organic matter and the elevation of terrace height, which is closely related to flooding frequency.

Soil C concentration and pool size varied by an order of magnitude across all sites, with C concentration ranging from 0.56 to 8.88% of total dry mass and pool size ranging from 502 to 4,663 g C m^{-2} (Table 1.1). Soil C concentration and pool size both increased with stand age (Table 1.2). Organic depth was a good predictor of soil C concentration and could be used as a covariate ($r^2 = 0.67$, $p < 0.0001$, $\log(y) = 0.04 + 0.32x$).

Soil N concentration ranged from 0.03 to 0.45% and pool size ranged from 26 to 235 g N m^{-2}, varying approximately tenfold across all sites (Table 1.1). Soil N concentration and pool size both increased with stand age (Table 1.2, Fig 1.2). Soil N (%) was tightly linked with organic depth ($r^2 = 0.63$, $p < 0.0001$, $\log(y) = 2.69 + 0.29x$) and soil C (%) ($r^2 = 0.97$, $p < 0.0001$, $\log(y) = -2.74 + 0.92 \log(x)$), affirming the importance of the biotic influence on soil N. Soil P concentration ranged from 0.05 to 0.08% and P pool size ranged from 27 to 71 g P m^{-2} (Table 1.1). Soil P concentration was not related to stand age (Table 1.2), although soil P pool size significantly decreased with time (Table 1.2, Fig 1.2). Soil P pool size was negatively related to organic depth ($r^2 = 0.61$, $p <$

0.0001, $y = 62.16 - 4.82x$), and positively related to soil mass (g) ($r^2 = 0.78$, $p < 0.0001$, $y = 6.48 + 0.42x$). The low bulk density of organic material influenced the declines in soil P with time, as evidenced by the significant positive relationship between soil mass and soil P pool size when stand age was held constant in a partial correlation analysis (partial $r_s = 0.87$, $p < 0.0001$); however, soil P pool size still significantly decreased with stand age when soil mass was partialed out (partial $r_s = -0.67$, $p < 0.0001$).

The increase in soil N (%) drove an increase in soil N:P ratios with time (Table 1.2). Mean soil N:P was very low (2.66), while mean alder leaf N:P was consistently above the Redfield ratio (19.69) (Table 1.1, Fig. 1.3). Leaf N:P ratio was not related to any environmental characteristics (data not shown).

Alder stem density (9,600-27,200 stems ha^{-1}) in young sites (<25 years old) varied threefold, with large impacts on soil nutrient status. Soil N pool size and concentration increased linearly with alder stem density in young sites (Fig 1.4). We did not detect an effect of alder stem density on soil P pool size ($p > 0.05$).

Variation in community structure

The first two axes of the DCA ordination represented 43% of the total variance in alder plant community structure, with Axis 1 accounting for 29% of the variation and Axis 2, 14% (Fig 1.5, Fig. 1.6). The length of Axis 1 was 2.95 SD units, indicating a complete change in species composition and size structure across the sites (McCune and Grace 2002).

Changes in community structure along Axis 1 were strongly correlated with stand age and a suite of associated environmental variables (Table 1.3, Fig. 1.5). Soil pH and soil P pools declined along Axis 1, while terrace height, organic depth, soil N and C concentrations and pools, and soil N:P ratios all increased. Axis 2 was not correlated with any environmental variables measured (Table 1.3). Leaf N:P was not correlated with either Axis 1 or Axis 2 (Table 1.3).

Small (< 2 m tall) willows and balsam poplar ranked low on Axis 1, followed by small alder, then white spruce (Table 1.4). Stem densities of small *Salix pseudomyrsinites, Salix interior,* and *Populus balsamifera* were negatively correlated with Axis 1, while young alder and spruce occurred throughout the gradient and were not linearly correlated with Axis 1 (Table 1.3, Figs. 1.5 and 1.6). The relationships between the abundance of small stems of each these species and the depth of the surface organic layer were analyzed to determine the extent to which the development of a forest floor inhibits stem initiation. Stem densities of young willow and poplar declined as surface organic depth increased, while alder and spruce recruitment were not significantly correlated with surface organic depth (Table 1.5). Both alder and spruce tended to have higher recruitment when stem densities of parent species were higher ($p = 0.05$ and $p = 0.09$, respectively).

For the mature successional dominants (> 2 m tall), scores and ranks progressed along Axis 1 from willow (0–3 cm), to alder (all diameter classes), to balsam poplar (0–3 cm to > 4 cm), to white spruce (0-3 to > 4 cm) (Table 1.4). Alder stem densities and relative dominance declined while white spruce stem densities and relative dominance increased along Axis 1 and with stand age (Table 1.3, Figs. 1.5 and 1.6).

Equisetum variegatum cover was negatively correlated with Axis 1 (Table 1.3, Fig. 1.5), and was associated with other herbaceous species with low Axis 1 scores such as *Solidago canadensis*, *Achilles siberica*, *Equisetum pratense*, and *Equisetum hyemale* (Table 1.4). Total moss cover as well as shrub abundance significantly increased along Axis 1, primarily due to *Rosa acicularis* and *Rubus ideaus* (Table 1.3, Fig. 1.5). Table 1.4 details the rankings and scores along this Axis 1 for all other species considered in this analysis.

Along Axis 2 there was a decrease in large (> 4 cm dbh) balsam poplar density which was associated with an increase in understory vegetation cover (Table 1.3, Figs. 1.5 and 1.6). The abundance of *Rubus ideaus* (shrub), *Arenaria lateriflora* (forb), and *Calamagrostis canadensis* (graminoid) significantly increased with Axis 2, while *Equisetum hyemale* (forb) cover declined (Table 1.3, Fig 1.5). The overall variation in community structure along Axis 2 was not correlated with canopy cover, an index of light availability. The abundance of the *Rubus ideaus*, however, was inversely correlated with canopy cover, suggesting a tendency for the upper Axis 2 communities to have greater light availability than their counterparts ($r_s = -0.26$, $p = 0.01$).

Logistic regressions showed that presence of moose feces was not related to either Axis 1 or Axis 2 scores ($p = 0.27$, $p = 0.19$, respectively), but was positively related to willow density ($p = 0.0003$). The presence of snowshoe hare feces was positively related to Axis 1 scores (p = 0.0006), weakly inversely related to Axis 2 scores (p = 0.059), and unrelated to willow density (p = 0.95).

Alder population dynamics

Site-level recruitment patterns

Significant relationships between stem diameter and age were described by either linear or quadratic regression equations for 25 out of the 27 sites sampled (Table 1.6). Significant regression equations were used to predict site-level alder age distributions of all stems based on stem diameter measurements. The resulting age reconstructions show several patterns of stand development (Figs. 1.7 and 1.8).

63% of the sites sampled were less than 25 years old, colonized after 1983, and the vast majority of these young sites were colonized in the early 1990s. Among the young sites (< 25 years of age), the dominant pattern of alder establishment (14 of 16 sites) was characterized by a rapid pulse in annual stem recruitment that peaked within 1-4 years of initial site colonization, with subsequent recruitment rate declining with time (Fig 1.7). Note that 'initial site colonization' refers to colonization within the boundaries of the sampling area, and not the entire stand. The pattern of stand development in the remaining young sites (2 of 16 sites) contrasted with the dominant pattern in that annual stem recruitment increased more gradually with time, peaking 7-10 years after initial colonization (Fig 1.7, sites DN04:0-2 and DN12:0-2).

Older sites (> 25 years of age), that were initially colonized by alder from 27-56 years ago (1951-1980) comprised 37% of the stands sampled for age. Some of the age distributions of these sites were wide, with alder stem recruitment continuing for up to 53 years (Fig 1.8, site DN43:0-2). Most of the age distributions were skewed with a greater proportion of younger age classes (6 of 9 sites), indicative of self-replacing stands (Fig. 1.8). A minority of the age distributions were skewed with a greater proportion of older age classes (2 of 9 sites), suggesting stand decline (Fig. 1.8, sites DN26:0-9 and DN12:6-8). One of the older sites had a bimodal age distribution (Fig. 1.8, site DN28:3-5).

Landscape-scale recruitment patterns

The age structure of all alder stems sampled for age across all sites exhibited a bimodal distribution, suggesting that there were two waves of alder recruitment at the landscape scale (Fig 1.9). The older wave in alder recruitment occurred from approximately 1960-1980, reaching a peak roughly around 1970. The recent period of alder recruitment occurred from approximately 1981-2003, with alder stem initiation increasing steadily to a peak in 1993 and subsequently declining. The rate of decline, however, was probably slower than it appears, since the sample does not include stems < 2 m tall. The recent peak in recruitment appears much larger than the previous peak, but this pattern is influenced by the mortality of older stems and the bias in sampling currently alder-dominated stands.

Patterns of stand development using aerial imagery

A historical sequence of aerial imagery of a subsample of alder sites that were established during the most recent wave of recruitment were visually analyzed, with one representative site pictured in Fig 1.10a. In 1949, most of the currently colonized area had not yet been formed, but the silt bar area had grown close to their current sizes by 1978-1983. The majority of shrub cover expansion occurred between 1978 and 1998. By 1998, the silt bars were 90-100% covered with vegetation, leaving only 0-10% of the siltbar area available for further colonization. From 1998-2007, shrub cover expansion was minimal. By 2007, nearly 100% of the colonizable silt bars were covered with vegetation. Several of the sites that were established in the previous wave of recruitment were also considered, although a large gap in available imagery precluded the dating of siltbar formation and plant colonization. Nevertheless, the recruitment patterns of these two periods appeared qualitatively similar in that silt bars were densely covered by deciduous shrubs within 20 years of initial siltbar colonization (Fig 1.10b).

Patterns of disease incidence and plant mortality

Of all standing alder stems sampled, 70% were infected with canker and 29% were dead with canker. Incidence of canker colonization tended to increase with stem diameter; however, canker-induced mortality tended to decrease with size, and presumably age (Fig 1.11). A logistic regression confirmed that the probability of canker-induced stem mortality was inversely related to age ($p < 0.0001$). The proportion of stems dead with canker for the youngest age class (1-10 yrs old) increased markedly with stem density (Fig 1.12). The overall incidence of canker infection was also positively related alder stem density (Fig 1.13).

DISCUSSION

Influence of thinleaf alder on soil properties

Alder stand age was strongly correlated with a suite of physical, chemical, and biological variables which are linked to processes associated with succession in the Tanana River floodplains (Table 1.2). Terrace heights slowly rise with time, primarily due to alluvial deposition caused by the regular flooding of the glacially fed Tanana River, and secondarily due to the gradual accumulation of organic material from vegetation (Viereck et al. 1993a). The rise in terrace height above the river with time results in an increased distance between the soil surface and the hyporheic flow, reduced flooding frequency and alluvial deposition, and a change in the particle size distribution of alluvial deposits (Viereck et al. 1993a). We found that alder stand age was correlated with both the elevation of terraces in relationship to the river and the accumulation of organic material, two physical characteristics which substantially influence the soil physical and chemical environment (Table 1.2).

Early successional soils in this ecosystem are typically alkaline as a result of the high calcite concentrations of the poorly weathered alluvial material (Marion et al. 1993). As organic matter accumulates, $CaCO_3$ solubility increases and soil pH declines (Marion et al. 1993, Van Cleve et al. 1993). Alder in particular is known to foster high rates of nitrification and rapid soil acidification (Crocker and Major 1955, Van Miegroet and Cole 1985, Marion et al. 1993, Van Cleve et al. 1993, Kielland et al. 2006). In the alder stands studied, soil pH declined rapidly with stand age (Table 1.2). Increases in terrace height and organic layer depth were each negatively related to soil pH when the other was held constant, suggesting that both the accumulation of organic material and the reduction in calcite deposition (due to decreased flooding frequency with increased terrace height) contributed to the acidification of these soils. Through the acidification of alkaline soils, both biotic and fluvial processes tend to increase the availability of nutrients to plants with time.

Thinleaf alder enriches the nutrient poor alluvial soils characteristic of early succession through substantial N-fixation inputs (Van Cleve et al. 1971, Walker 1985, Van Cleve et al. 1993, Uliassi and Ruess 2002). Soil C and N concentrations and pools increased with stand age (Table 1.2, Fig. 1.2). Across all sites, both soil C and N (concentrations and pool sizes) varied by an order of magnitude (Table 1.1.). The thickness of the organic soil layers, which increased with stand age, largely accounted for the tenfold variation in soil C and N accumulation. The tight links between soil N (concentration and pool size) and quantity of organic material illustrate the strong influence of alder N-fixation on soil nutrient status with time.

Total soil P pool size declined with stand age and with the accumulation of organic material (Table 1.2, Fig. 1.2), even when the effects of the intercorrelation between age and organic depth were removed, which we attribute to both the uptake of P in plants and the decreasing bulk density of soil. This finding supports the notion that plant P uptake exceeds the rate of chemical weathering and P supply, diminishing total P supplies with stand age, within the time scale of this study (Walker and Syers 1976). The availability of P to plants, however, may be constrained by the relatively high soil pH found in these soils, which inhibits the solubility of P compounds (Marion et al. 1993). While total P declines with succession, acidification increases the concentrations of extractable P (Van Cleve et al. 1993). Alder foliar nutrient status (N:P ratio), however, was not significantly related to any of the measured soil characteristics, suggesting perhaps that alder P acquisition is more closely tied to mycorrhizal dynamics than to total soil P (Mejstrik and Benecke 1969, Liu et al. 2005).

The ratios of soil N:P (to a depth of 10 cm) were well below 14 (Table 1.1), implying that most plants are likely N-limited in early succession. Soil N accumulated in alder stands more rapidly than P declined, theoretically leading to an attenuation of plant N-limitation with time (Fig. 1.2). While the growth of most vegetation in this ecosystem is thought to be limited by N, the growth and N-fixation rates of thinleaf alder and other N-fixers are often constrained by P availability (Vitousek and Howarth 1991, Huss-Danell 1997, Uliassi et al. 2000, Wall et al. 2000). Indeed, alder leaf N:P ratios in this study were consistently high, with site means ranging from 15-24, indicating the likelihood that alder is P-limited across all sites (Table 1.1, Fig. 1.3). The tight coupling of N and P via symbiotic N-fixation is such that the availability of P may limit N-fixation and ecosystem N inputs and ultimately constrain forest productivity.

Alder-mediated N fixation inputs decline throughout the course of primary succession on the floodplains (Van Cleve et al. 1971, Uliassi and Ruess 2002). Uliassi & Ruess (2002) suggested this decline could be attributed to a decrease in N-fixation rate of alder with stem age, a shift in the controls over N fixation, and/or reductions in alder abundance. We did find a decrease in alder abundance with time, and confirmed that early alder population structure had substantial legacy effects on total soil N accumulation. The young early successional alder stands (< 25 years) varied nearly threefold in stem density (9,600-27,200 stems ha^{-1}) with strong impacts on soil N pools and concentrations. As alder stem density increased in early successional stands of similar age, mean soil N pool size increased linearly from approximately 70-120 g N m^{-2} (Fig. 1.4). The stem density of *Alnus viridis* in a secondary successional sequence in the boreal forest uplands was similarly found to be associated with increases in soil N (Mitchell 2006).

Variation in plant community structure and successional dynamics

Most of the variation in overall community structure observed within thinleaf alder stands was represented by the first axis of the DCA ordination, which was strongly correlated with stand age and all of the environmental characteristics related to floodplain successional processes discussed above (Figs.1.5 and 1.6). Axis 1 was positively correlated with terrace height, organic depth, soil C and N (% and pool), and soil N:P ratios, and was inversely correlated with soil P (pool) and soil pH. Axis 1 thus appears to represent a gradient of community structure across successional time. There was a complete turnover in community composition along Axis 1, indicating that community structure of alder stands varied temporally along a gradient of changing environmental characteristics. The variation in plant community structure found along this gradient likely influenced and responded to the changes in soil properties with time.

Variations among the dominant successional species in seed weight and dispersal capabilities, germination requirements, and flooding tolerance largely account for the general pattern of colonization found on the Tanana River floodplains (Walker et al. 1986). Willow and balsam poplar are often the first woody plants to colonize silt bars, owing to the far wind-dispersal of their lightweight (and frequently abundant) seeds, and may be followed by alder and white spruce, with a lagged dispersal due to their heavier seeds. Our ordination results illustrated the tendency of this general colonization pattern, as young (< 2 m tall) willow and poplar were associated with early succession, followed in rank and score by alder and white spruce (Table 1.4). The inability of white spruce seedlings to withstand flooding and silt deposition contrasts the relative tolerance of willow, balsam poplar, and alder seedlings to this disturbance, and likely influenced this sequence of colonization (Walker et al. 1986).

Willow and balsam poplar recruitment both declined along Axis 1, but neither alder nor spruce recruitment were correlated with this axis (Table 1.5, Fig. 1.5). This suggests that abundant willow and poplar recruitment were limited to very early successional sites, while alder and spruce recruitment occurred sporadically throughout succession. Experimental research has indicated that the germination of willow (some species), poplar, and alder seeds requires moist seedbeds of mineral soil characteristic of early successional sites, while spruce seeds are capable of germinating on the forest floor of mid-late successional sites (Walker et al. 1986). We found that willow and poplar recruitment significantly declined with increasing depth of the surface organic layer, confirming the importance of mineral seedbeds to the successful recruitment of these species (Table 1.5). It is important to note that willow and alder species may also reproduce vegetatively, and resprouting has been found to be a particularly important mode of reproduction for alder as succession advances (Walker et al. 1986). Alder recruitment was not related to the depth of the surface organic layer, perhaps demonstrating the importance of both sexual and vegetative reproduction for alder, or the potential ability of alder seeds to germinate without a mineral seedbed. Spruce recruitment was also unrelated to organic depth, and was therefore not limited to any particular successional stage; instead, recruitment tended to increase with mature spruce density, reflecting the importance of a local seed source to this heavy-seeded species with substantial dispersal limitations.

After initial colonization, the traits of potential successional dominants, such as growth rate and longevity, further influence the course of succession (Walker et al. 1986). The generalized model of early-mid primary succession that has been developed for the Tanana River floodplain describes a sequence of stages shifting through time from willow, to alder, to poplar, to white spruce dominance (Viereck et al. 1993a). The preferential browsing of willow by moose and snowshoe hares has been shown to accelerate the transition from willow to alder stages (Kielland et al. 2006), and indeed we found greater evidence of moose browsing, although not snowshoe hare, with increasing willow density. The ranking of these four successional dominants generally followed the sequence outlined by Viereck et al. (1993a) along Axis 1 (Table 1.4); however, the stem densities of mature balsam poplar were highly variable and independent of stand age (Table 1.3, Figs. 1.5 and 1.6), suggesting either a highly variable rate of succession from alder to poplar-dominated stages or the possibility of a successional trajectory in which a poplar-dominated stage is absent (see below).

The understory floristics of the alder stands varied along a continuum of stand age. Our indirect gradient analysis allowed us to identify several understory floristic indicators of the relative age of an alder stand and its associated environmental characteristics. The frequently-flooded young sites on low terraces, with alkaline soils, low organic matter content, and low N:P ratios were best characterized by the relatively high % cover of *Equisetum variegatum* (Fig. 1.5). The older alder stands situated on higher terraces, with more acidic soils, increased organic material, and higher soil N:P ratios were differentiated by their increased cover of mosses and high abundance of shrubs, in particular, *Rosa acicularis* and *Rubus ideaus* (Fig. 1.5). The temporal shift in stand structure towards white spruce emergence is associated with a decline in deciduous litterfall, allowing the development of a moss layer, which inhibits the recruitment of other plant species (Viereck et al. 1993a). This shift in community composition also impacts ecosystem processes, as the recalcitrance of both moss litter and evergreen needles slows the rates of decomposition and nutrient cycling (Flanagan and Van Cleve 1983, Van Cleve et al. 1993).

There was evidence of variation in community structure, represented by Axis 2 of the DCA ordination, which was unrelated to stand age and all of the environmental variables measured that changed with time (Fig. 1.5). This axis, therefore, represents the variation within, and perhaps deviation from, the successional sequence described by Viereck et al. (1993a) (Fig. 1.5, Fig. 1.6). The variation in overstory stand structure was characterized by a gradient in the abundance of mature balsam poplar (> 4 cm dbh). Balsam poplar density varied widely along this axis, and was entirely absent from almost 25% of the sites which had an emerging white spruce canopy. Since mature balsam poplar density varied widely, independent of stand age, and the recruitment of young balsam poplar was similarly low among these sites, this suggests that the absence of an emerging poplar-dominated stage characterizes an alternative successional pathway or, at the least, a delayed successional transition from alder to poplar stages.

Because the variation in mature poplar density was not associated with any current abiotic differences between the sites, we attribute this variation to either biotic or stochastic processes related to the establishment and survival of poplar. There was no consistent variation in white spruce abundance among these sites, and since white spruce recruitment is limited more by its flooding intolerance than by shading or an organic layer (Walker and Chapin 1986), the rate of transition from these sites to a potentially white spruce-dominated stage cannot be predicted. The timing of the emergence of a white spruce-dominated stand is limited by the slow growth rate typical of this species. The timing of the decline of an alder-dominated canopy is thought to be controlled by the emergence of a quickly growing poplar canopy (Chapin et al. 2006). If this is true, then when poplar density is low, the period of alder dominance is likely to be prolonged; and the period of poplar dominance, if any, is likely to be shortened, dependent on when spruce-dominance is slowly achieved.

The understory vegetation also varied markedly along this gradient of mature poplar density (Fig. 1.5). The communities associated with high poplar stem density were characterized by their minimal herbaceous cover, while the communities associated with low poplar stem density were distinguished by their lush understory, in particular, the high % cover of *Arenaria lateriflora* (forb) and *Calamagrostis canadensis* (graminoid), and the increased abundance of *Rubus ideaus* (shrub). These community types did not vary in age, but were quite distinct from each other. The overall variation in community structure along Axis 2 was not correlated with canopy cover, an index of light availability; however, there were species-specific responses to canopy cover, suggesting a tendency for the low poplar density/lush understory communities to have greater light availability than their counterparts, which might explain some of the current variation in the community structure. This highly vegetated understory characteristic of low poplar density stands may further slow the rate, and perhaps alter the pathway, of succession. *Calamagrostis canadensis* is an especially competitive species which has been found to inhibit the successful establishment of white spruce and suppress the growth of deciduous trees in the boreal forest uplands (Lieffers et al. 1993, Landhäusser and Lieffers 1998), and may play a similar role in delaying successional turnover in this floodplain ecosystem.

This variation in successional rates and pathways could have important implications for community dynamics and ecosystem function, as well as the way we study succession on the Tanana River floodplain. The prolonged period of alder dominance in the low poplar density stands, and the lessened inter-specific competition between alder and poplar for light and soil resources, may allow for the functional traits of alder to dominate ecosystem properties for a longer period of time, contributing to increases in total N-fixation inputs in the long term. The emergence of a poplar canopy has been considered a turning point in floodplain succession (Chapin et al. 2006), so the delay, absence, or shortening of a poplar stage also has important ecosystem consequences. Balsam poplar leaf litter contains tannins that inhibit microbial activity, thus reducing rates of nitrification and denitrification and tightening the nitrogen cycling between vegetation and soils (Schimel et al. 1996, Chapin et al. 2006). The large inputs of leaf litter that last throughout the period of poplar dominance can prevent the establishment of other plant species, including mosses, which play an important role in influencing decomposition rates and soil thermal insulation (Viereck et al. 1993a). The temporal and spatial variation in the recruitment patterns of potential successional dominants contributes to the complexity of successional pathways and its ecosystem consequences. The variety of successional pathways is frequently overlooked in chronosequence-based studies, where it is sometimes falsely assumed that the current pattern of stand types on the landscape is representative of a temporal trajectory of successional development (Fastie 1995, Johnson and Miyanishi 2008).

Patterns of thinleaf alder recruitment

The distribution of all alder stems, pooled across sites, exhibited a somewhat bimodal structure, supporting observations of long term variation in alder recruitment (Fig. 1.9). Two waves of alder recruitment have apparently occurred on the Tanana floodplains since 1950: an earlier wave peaking around 1970 and a recent wave peaking in 1993. The timing of this long term trend in alder recruitment concurs with observations reported in several studies on the Tanana floodplains near Fairbanks. Van Cleve et al. (1971) reported finding numerous alder seedlings in this area in 1968-1969, while Walker et al. (1986) found no alder seedlings in the early 1980s. The discrepancies of these previous findings are consistent with the long-term variability in alder recruitment observed here.

The current age structure of surviving alder stems showed a much higher peak in alder stems established during the recent wave of recruitment relative to the older wave. The disparity in alder stem densities between these two periods is likely to be strongly influenced by the mortality of the older stems as well as by a bias that limited our sampling to alder-dominated stands, precluding the use of mid-late successional stands which may contain more evidence of historic alder recruitment events. Whether these two waves of recruitment were quantitatively and qualitatively similar remains unknown; however, a crude examination of historic aerial photography revealed an apparently similar pattern (Figure 1.10). In both periods of alder recruitment, the peak was preceded by approximately 10 years of steadily increasing alder stem density, and followed by 10 years of decline. The gradual build up and decline in alder recruitment evident in both these periods suggests that the long term recruitment dynamics of alder are linked to other cyclical or periodic processes. Sedimentation and siltbar formation (Chapin et al. 2006, Takagi et al. 2007), alder seed production and dispersal (Walker and Chapin 1986, Yarie and Van Cleve 2006), and herbivore population dynamics (Rextad and Kielland 2006, Kielland et al. 2006, Butler et al. 2007) are potential controls on recruitment of alder that themselves fluctuate with time and vary spatially, and could interact to contribute to the variation in alder abundance throughout the landscape.

Fluvial geomorphological processes, driven by the fluctuations in river discharge, strongly influence the structure and dynamics of floodplain plant communities through effects on plant establishment, competitive ability, and mortality (Bendix and Hupp 2000, Yarie et al. 1998). The sedimentation that occurs as floodwaters recede creates new colonizable surfaces upon which primary succession may proceed, but may also alter competitive interactions between plants due to species-specific variations in tolerance to flooding and sedimentation (Walker and Chapin 1986). Abiotic disturbance (i.e., flooding) is widely believed to be the primary driver of successional dynamics (Chapin et al. 2006), although there is growing evidence that the interactions between abiotic and biotic disturbance (i.e., sedimentation and herbivory) drive successional dynamics at the landscape scale (Butler et al. 2007).

The sequence of aerial imagery of developing siltbars clearly shows the influence of flooding patterns and topography on the spatial distribution of colonizing shrubs, as the location of vegetation closely follows the contours of the elevated terraces (Fig. 1.10). The submergence of low terraces precludes alder establishment until additional terrace aggradation could make these surfaces colonizable. Terrace aggradation of silt bars on the Tanana River floodplain may occur rapidly, rising 1-2 m above mean river height within a decade (Yarie et al. 1998). The initial colonization of low terraces has a positive feedback on further terrace aggradation, as plants stabilize soils, slow the local velocity of river flow during flooding, and trap greater quantities of sediment (Chapin et al. 2006).

River discharge and sediment load vary at many temporal scales, with important implications for sedimentation, aggradation, and succession. The frequency of large floods was positively related to the instability of channel distribution and land cover along the Brahmaputra River in Bangladesh (Takagi et al. 2007). Balsam poplar recruitment along the Nyack River in Montana increased after large floods created expansive areas for recruitment, and decreased in periods of low disturbance when the availability of colonization sites was limited (Whited et al. 2007). Deposition rates within the Tanana River floodplain have also exhibited temporal variation (Adams 1999), and thus the recruitment patterns of thinleaf alder may similarly reflect a legacy of geofluvial processes.

The historical sequences of aerial imagery suggest that the recent peak in alder recruitment can largely be attributed to increases in colonizable area (Fig. 1.10). In 1949, the majority of the area of the siltbars which were colonized during the recent wave of recruitment had yet to be formed. In 1978, large portions of these islands were still submerged underwater. The above-water surfaces did not approximate their current sizes until 1978-1983, concurrent with the beginning of the period of major shrub cover expansion between 1978 and 1998. This shrub expansion reduced the area available for colonization as the sites were 90-100% covered with vegetation by 1998, which logically led to only minor increases in shrub cover from 1998-2007. By 2007, the siltbars were all nearly 100% covered by vegetation.

It is also important to note that geofluvial disturbance patterns likely vary spatially across different reaches of the river as a result of variable stream gradient, discharge, velocity, and bedload, affecting the occurrence of landforms available for colonization (Bendix and Hupp 2000). An increase in stream gradient, for example, is often associated with a shift to a braided channel pattern in bedload-laden streams, resulting in unstable, shifting islands and bars (Graf 1988). The stream gradient of the Tanana River varies among its reaches, as does its discharge (Ott et al. 2001), so patterns of vegetation dynamics should also vary at larger spatial scales than considered in this study. Further study of the spatial and temporal dynamics of siltbar aggradation would help clarify the trends in thinleaf alder recruitment and landscape evolution represented here and more broadly throughout the Tanana River basin.

Initial colonization patterns are likely strongly related to seed availability, which is influenced by the proximity to a seed source, the abundance of seed, and seed dispersal. The reconstructed site-level age distributions showed that the vast majority of recently-established alder stands filled in rapidly, with most stem recruitment occurring within just 1-4 years (Fig. 1.7). Differences in alder establishment rates and population densities are likely affected by the proximity to, or size of, a seed source (Harper 1977, Chambers and MacMahon 1994, Clark et al. 1999). If the initial seed source is sparse or distant, future recruitment may lag until the colonizing plants mature and produce seed themselves, becoming the nucleus of future stand development. If seed rain is high and environmental conditions are suitable, a stand may become stocked rather quickly. The influence of seed dispersal dynamics evident in the site-level age reconstructions is consistent with the spatial pattern of nucleation apparent in aerial imagery, where alder stand area expands outward from the colonizing seed trees with time (Fig. 1.10a). A study of primary succession during glacial retreat illustrated how the distance of a colonizable site from a seed source could have great consequences for ecosystem function, as the arrival of alder was completely precluded by landscape position in one of the successional pathways found at Glacier Bay (Fastie 1995).

The reconstructed alder age distributions in older sites all showed continual alder recruitment (Fig. 1.8). The wide age distributions found in many of the older sites (> 25 years old) illustrate the potentially long persistence of alder stands and longevity of individual ramets. The skewed age distributions found in the majority of our older sites are typical of self-replacing stands (Harper 1977). It is interesting to note the degree to which recent alder recruitment occurred even in these established stands on older terraces. A net increase in alder population size from 1993-1998 was also detected in late successional sites in this area, and was attributed to root sprouting in canopy gaps (Yarie and Van Cleve 2006). Large scale disturbance events that open the canopy, such as the record snowfall event in 1992 that caused widespread stem breakage, could have also contributed to this recent increase in alder recruitment (R.W. Ruess, personal observation). It is unclear whether the high level of recent stem recruitment in the older stands is indicative of a landscape-scale pulse in recruitment, or whether it is simply a characteristic of normal alder stand development. However, the recruitment of young alder stems in older sites on established terraces shows that the creation of new siltbars, while overwhelmingly important, was not the sole cause of the recent peak in alder recruitment.

The preferential browsing of willow by moose and snowshoe hares has been shown to reduce the competitive ability and longevity of willow and favor the establishment of alder, thereby accelerating the transition from willow to alder stages, and influencing the relative abundance of alder to willow communities at the landscape scale (Bryant et al. 1985, Kielland and Bryant 1998, Kielland et al. 2006, Butler and Kielland 2008). Although long term alder recruitment trends did not closely track the fluctuation in mammalian herbivore population sizes, alder recruitment may have been responsive to threshold peaks or prolonged periods of high density in herbivore populations (Fig. 1.9, Dale and Zbigniewicz 1997). The most recent wave of alder recruitment on the Tanana (in the early 1990s) was preceded by both a major increase in moose population size that stabilized in the mid-1980s (Rexstad and Kielland 2006) and a moderate peak in snowshoe hare population size that occurred in 1990 (Flora 2002). Similarly, the previous wave of alder recruitment that began in the mid-1960s occurred as moose population size was beginning a rapid decline from very high estimated densities (Gasaway et al. 1983), and as snowshoe hare population size approached a major peak in 1971 (Flora 2002, Wolff 1980, Rexstad and Kielland 2006). The interactions between siltbar formation, seed production and dispersal, and herbivory are likely controls on the long-term variation in thinleaf alder recruitment throughout the Tanana River floodplains.

Patterns of disease incidence and plant mortality

Our disease survey data from 2006 confirmed that the current outbreak of the fungal pathogen causing stem canker infection throughout Alaska is also widespread in the Tanana River floodplain (Fig. 1.11). At least 70% of all standing alder stems sampled were infected with canker, and 29% of all stems were dead with evidence of the disease. This branch dieback and mortality of thinleaf alder associated with canker infection is likely decreasing N-fixation inputs through reductions of nodule biomass (Ruess et al. submitted).

At the landscape scale, the proportion of alder colonized with canker increased with increasing stem size and age; yet, the proportion of standing alder that were dead with canker decreased, suggesting either that young stems were disproportionately susceptible to canker-induced mortality, or that older stems could withstand infection longer (Fig. 1.11). This age-related pattern of disease-related mortality varied with alder population structure, where the proportion of young alder dead with canker was positively related to alder stem density (Fig. 1.12). In addition, incidence of canker colonization overall increased with alder stem density (Fig. 1.13). Alder stem density in early successional stands was tightly linked with total soil N, so the immediate effects of the reduction in alder abundance in high density stands will likely reduce total ecosystem N inputs, and may accelerate the rate of succession. In the older, low density stands, canker-induced mortality was less common in young alder stems, allowing the persistence of these alder stands at lower abundances; however, many of the older stems in these sites were suffering branch-dieback and severe infection which likely reduced their N-fixation inputs.

Conclusions

Thinleaf alder strongly influenced soil development and nutrient cycling over time in the Tanana River floodplains. Through symbiotic N-fixation inputs, thinleaf alder likely attenuated the N limitation of other plants; yet alder N-fixation itself appeared to be limited by P throughout succession. The population structure of thinleaf alder in early successional stands drove the nutrient status of these soils, as increasing alder stem density caused linear increases in soil N. Alder community structure varied as expected along a temporal gradient of changing environmental characteristics, but interesting variations in the dominant successional trajectory were found, which are likely to influence community and ecosystem level processes. Landscape scale alder recruitment occurred in waves over the long term, and was likely linked to interactions between geofluvial processes, seed production and dispersal, and herbivory. The current outbreak of a stem canker is causing widespread branch dieback and mortality of alder stems, with mortality of young stems and overall disease incidence positively related to alder stem density, most likely causing landscape scale declines in N-fixation inputs.

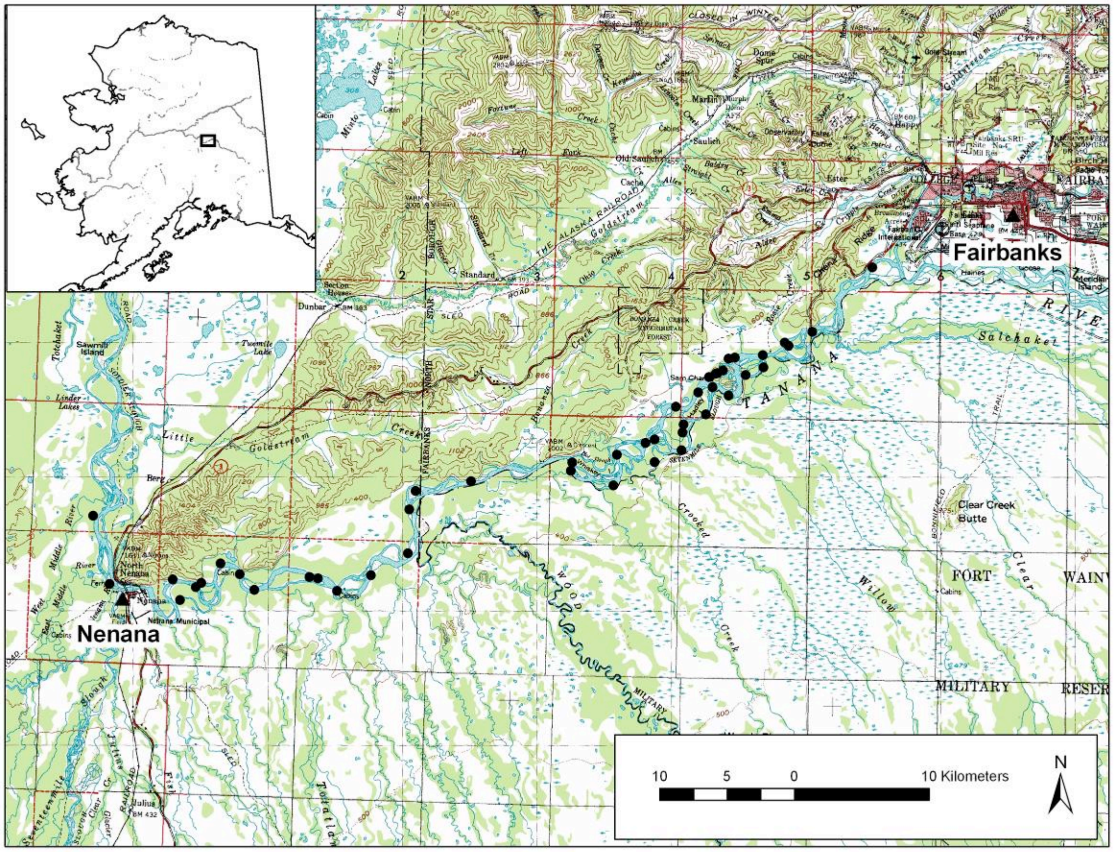

Fig. 1.1. Map of study area and transects. Inset shows location of study area in interior Alaska. Circles represent study transects along the Tanana River. Triangles show nearby population centers.

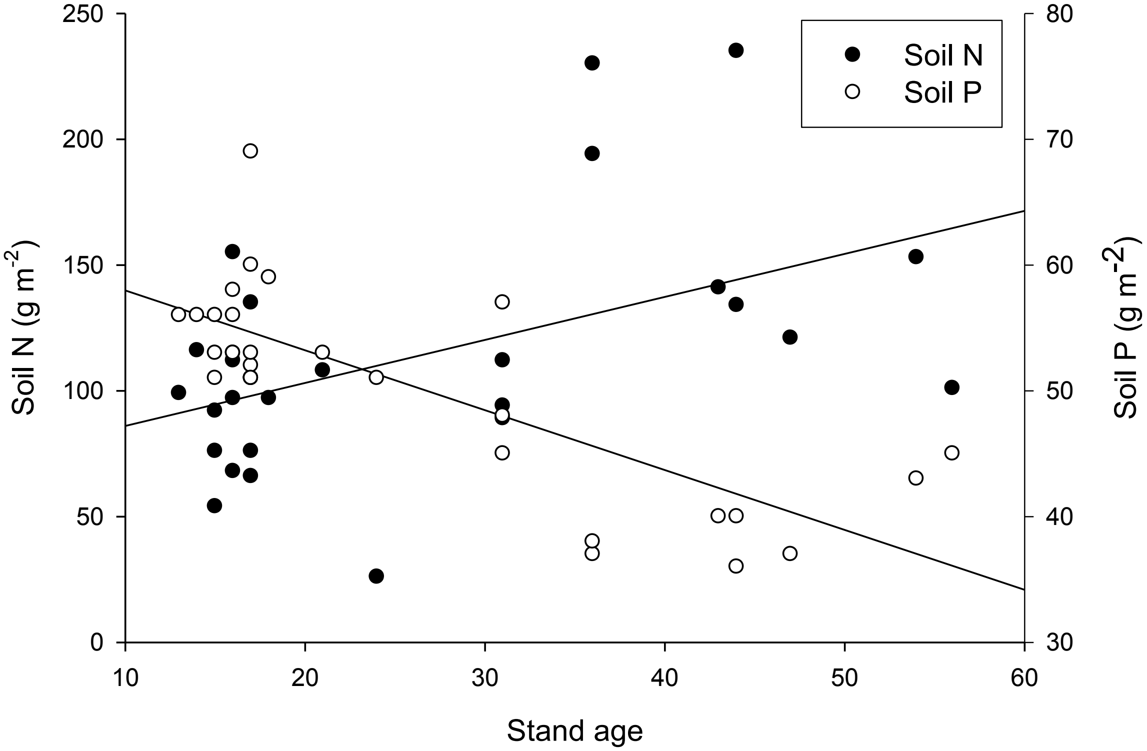

Fig. 1.2. Correlations of soil nutrient pool sizes with age of thinleaf alder stands. Pool sizes are to a depth of 10 cm, n = 28 sites. (Soil N: $y = 69.0 + 1.7x$, $r^2 = 0.24$, $p = 0.0087$; Soil P: $y = 62.75 - 0.48x$, $r^2 = 0.60$, $p < 0.0001$).

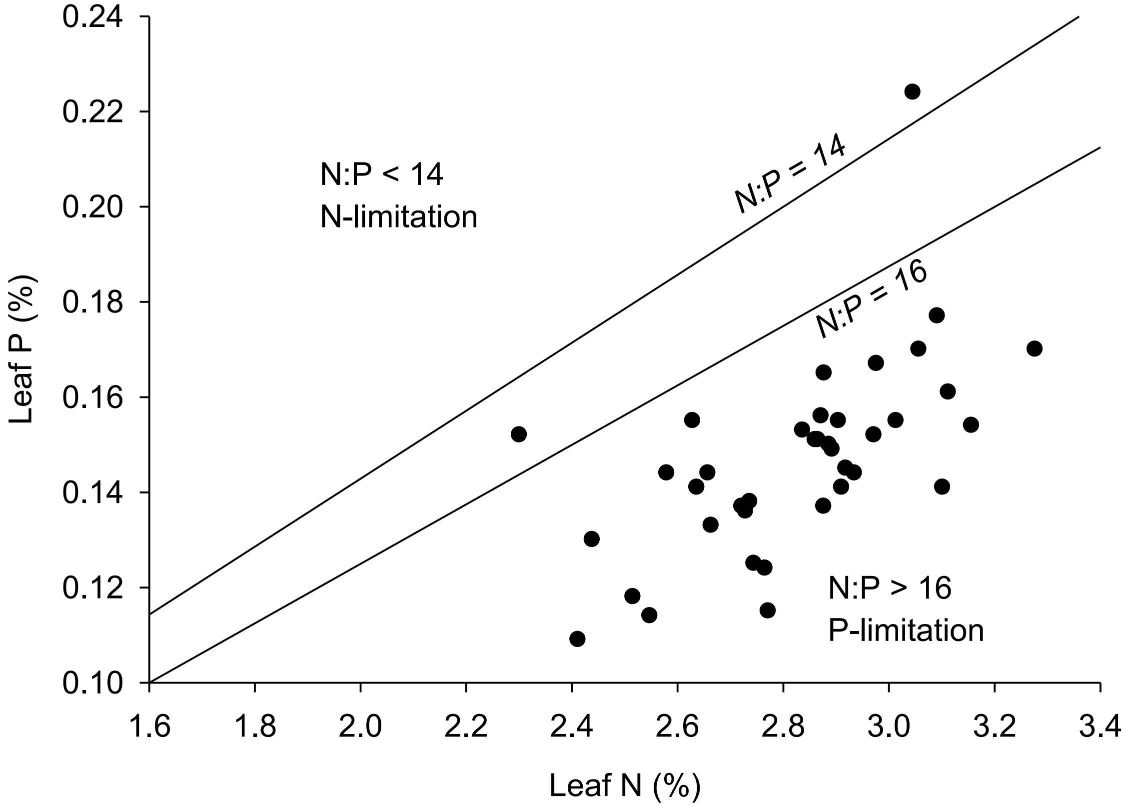

Fig.1.3. Thinleaf alder foliar N:P ratios. Points represent site means, n = 38 sites. Lines show N:P ratios of 14 and 16. Foliar N:P ratios < 14 suggest N-limitation; foliar N:P ratios > 16 suggest P-limitation.

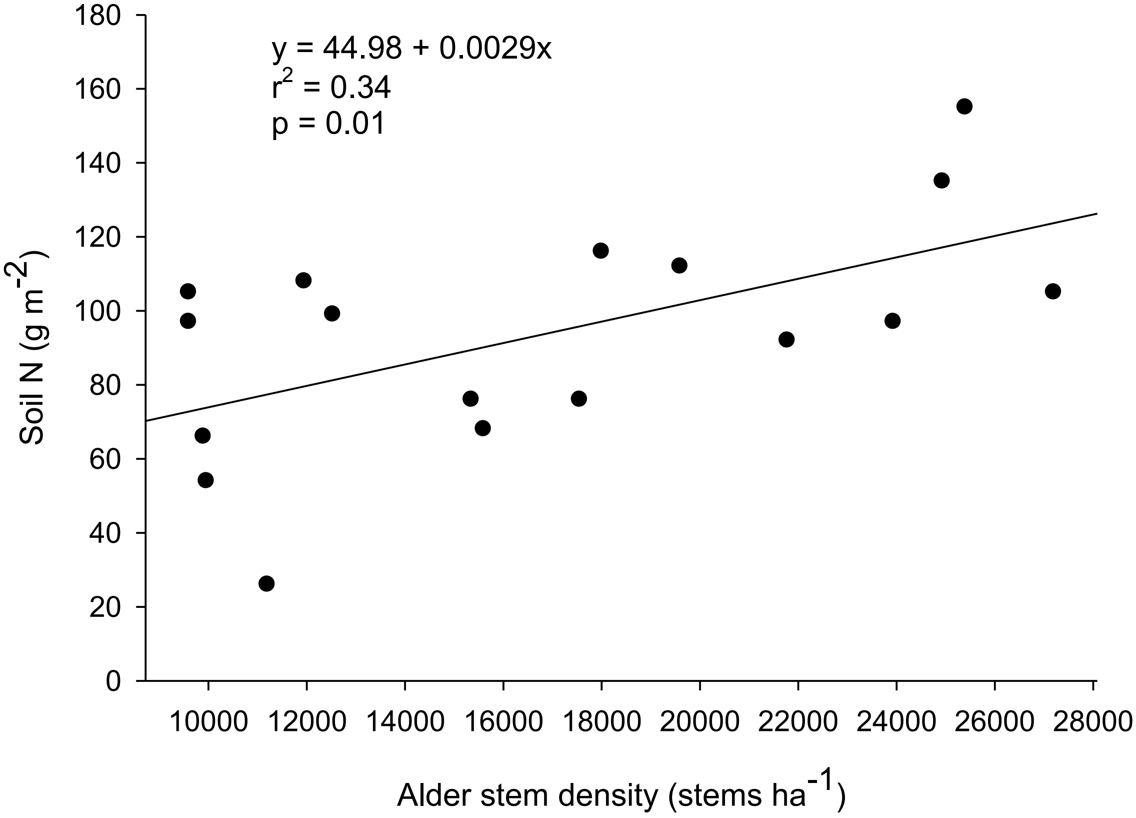

Fig. 1.4. Influence of alder stem density on soil N pool size. Regression of alder stem density versus soil N content in all young stands (<25 years old), n = 17 sites.

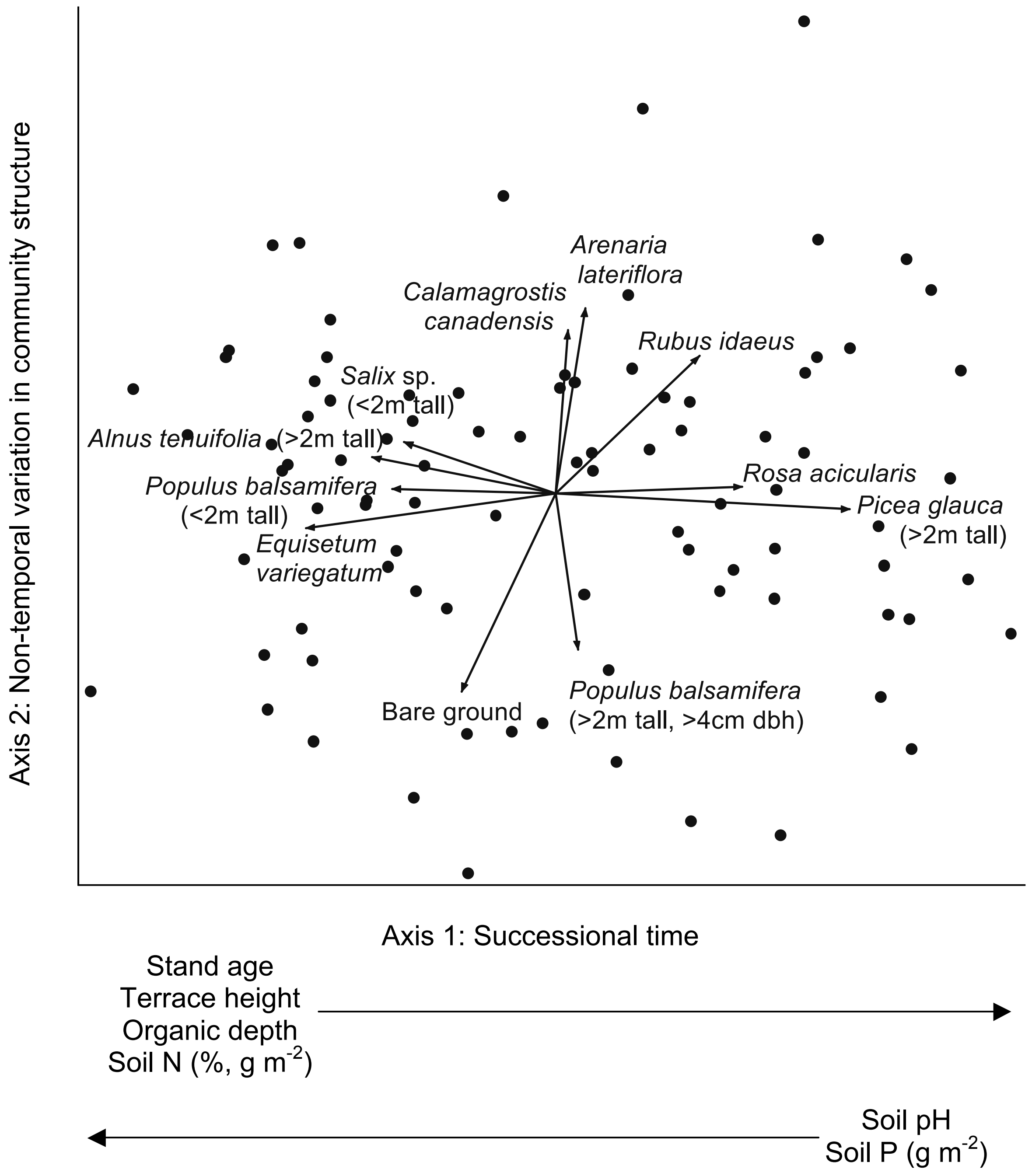

Fig. 1.5. DCA ordination of thinleaf alder community structure and relationships with selected site characteristics. Points represent site community structure, n = 89 sites. Vectors (scaled 150%) represent the direction and strength of correlations. Arrows below Axis 1 show the direction of the relationships between community structure and site characteristics.

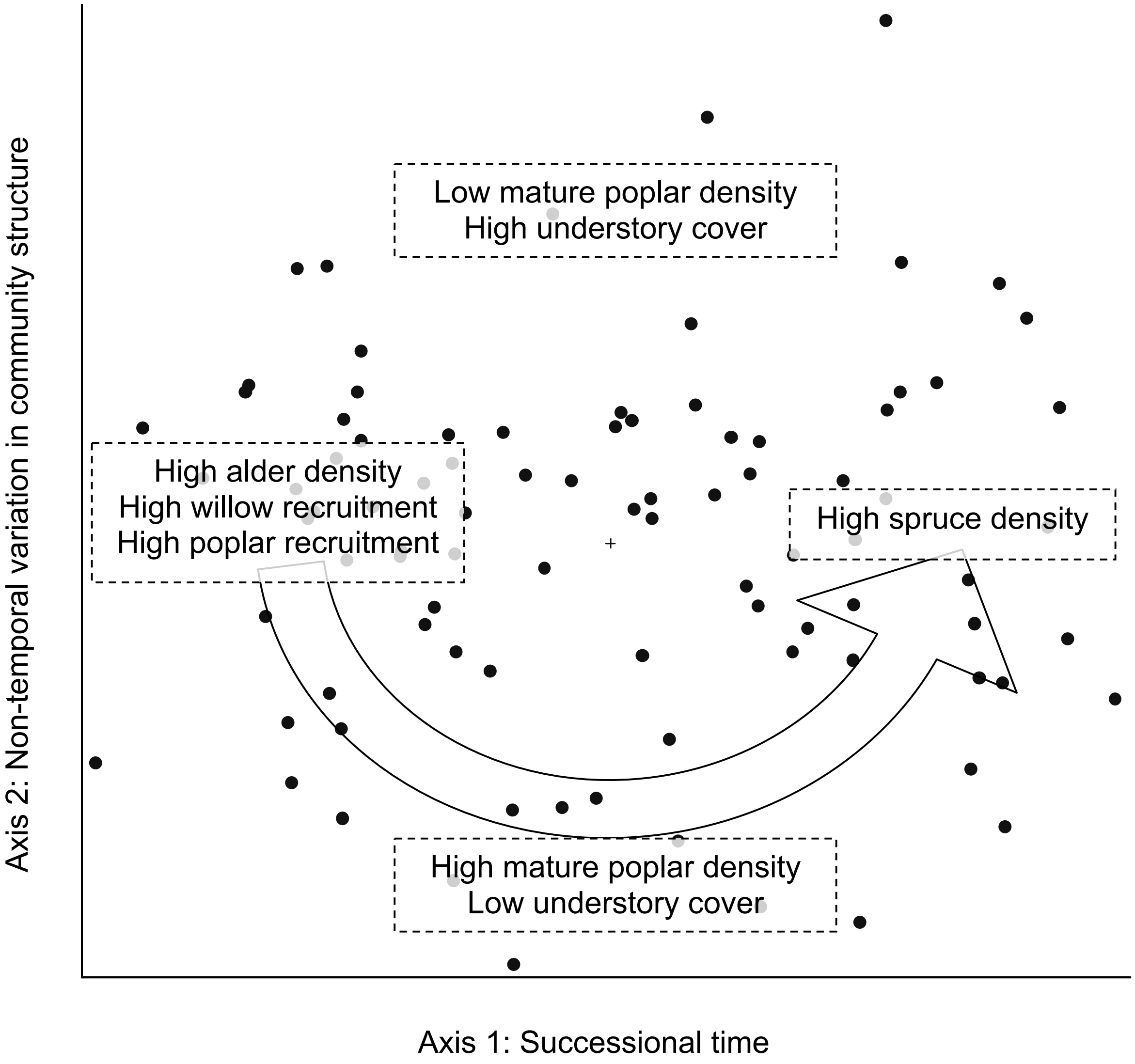

Fig. 1.6. Conceptual diagram of successional patterns within thinleaf alder stands overlain onto DCA ordination. The text boxes describe general community characteristics for each region of the ordination. The arrow shows the traditional successional trajectory described in Viereck et al. 1993a. The ‘low poplar density’ community type represents variation within, or deviation from, the traditional successional trajectory.

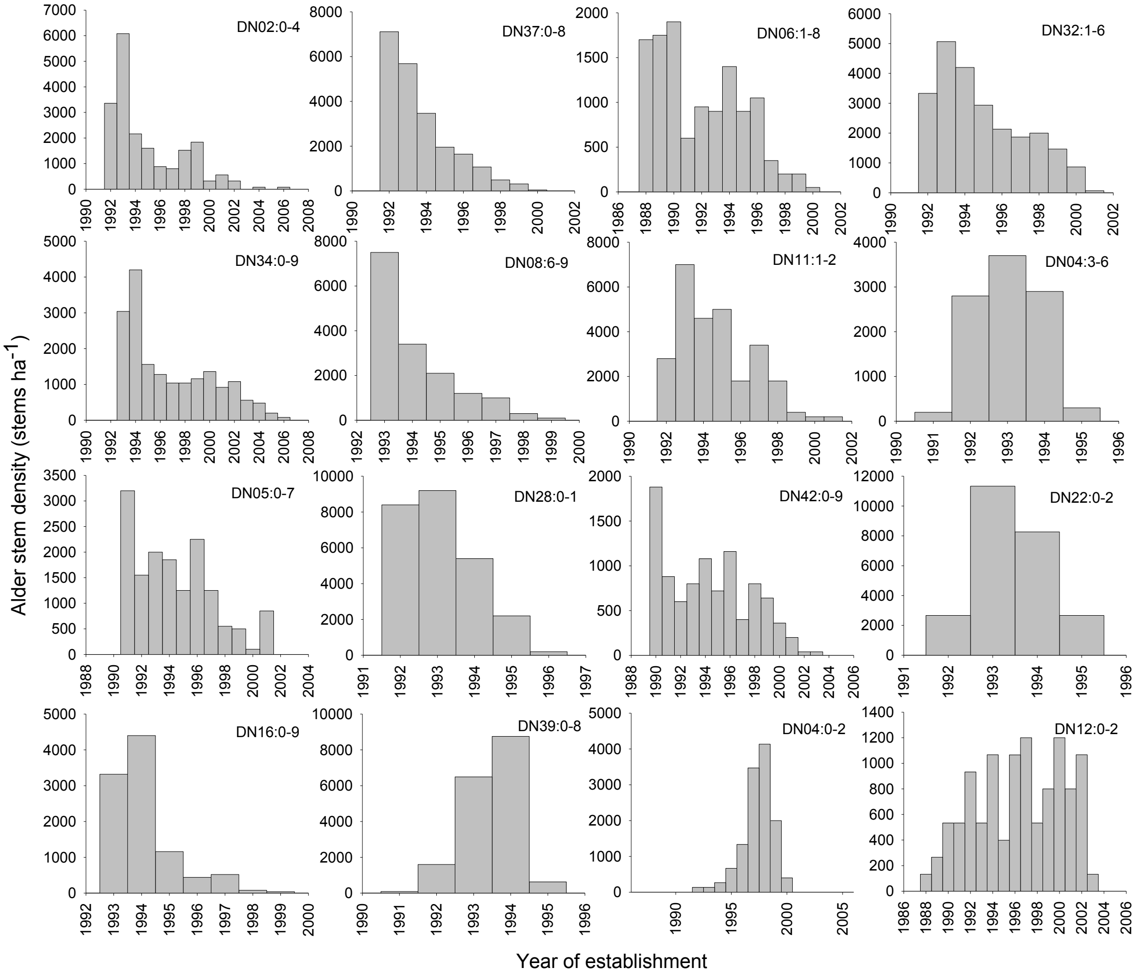

Fig. 1.7. Age reconstructions of thinleaf alder stems at young sites (< 25 years old), based on regression analyses between size and age.

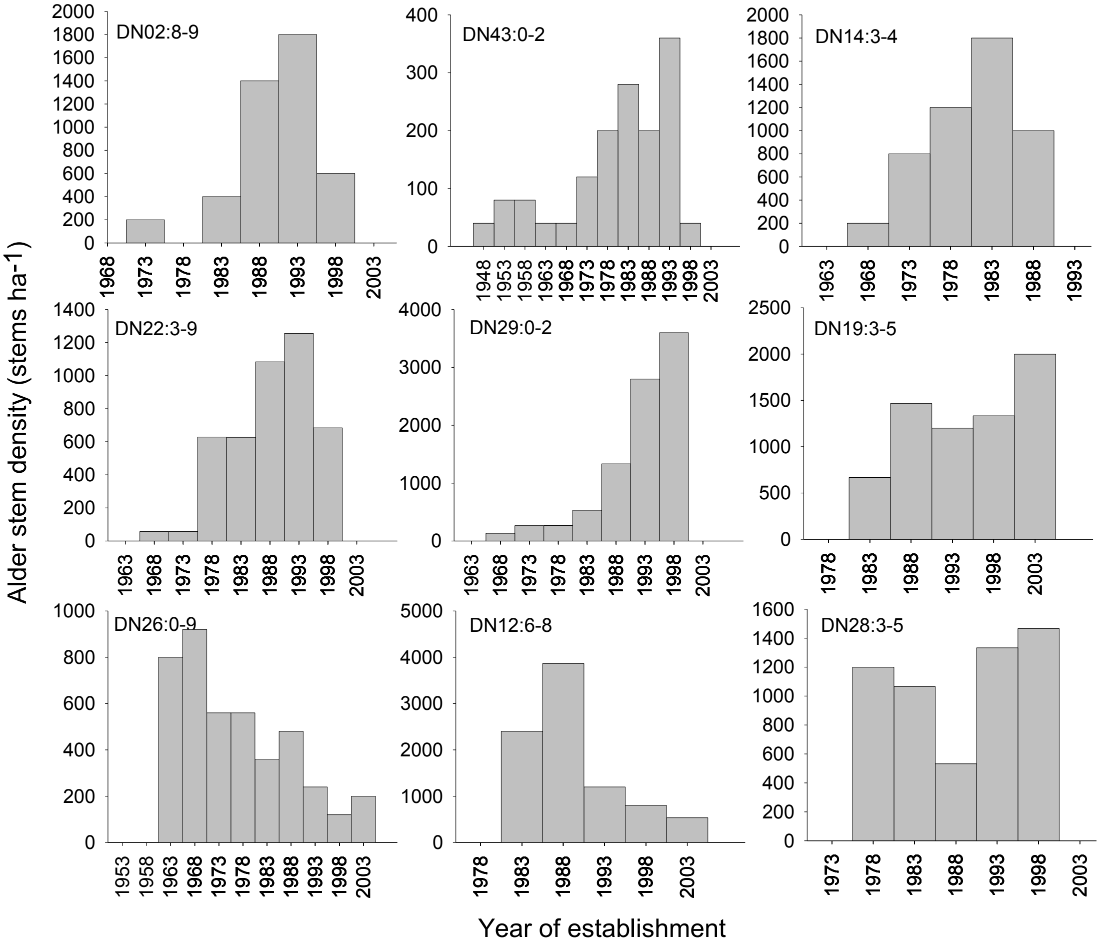

Fig. 1.8. Age reconstructions of thinleaf alder stems at old sites (> 25 years old), based on regression analyses between size and age. Stem recruitment is grouped by 5-year age classes.

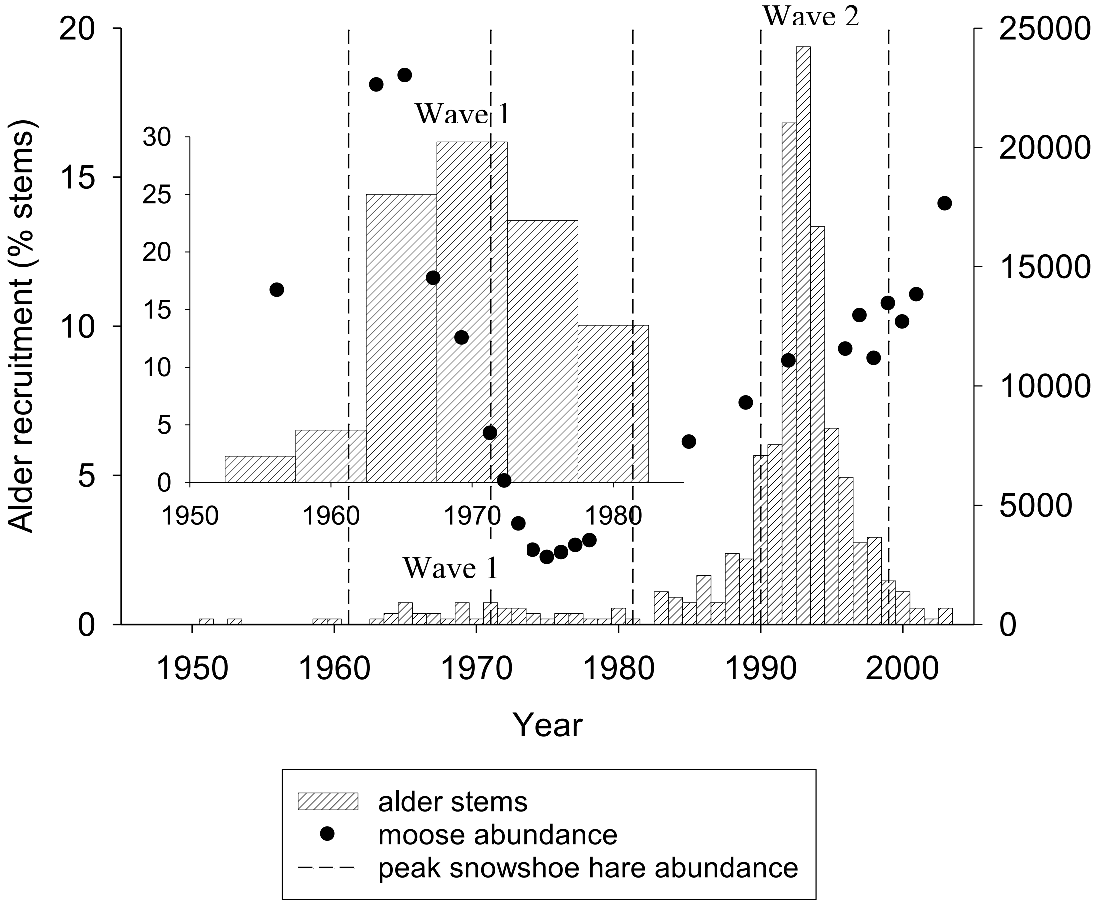

Fig. 1.9. Temporal patterns of thinleaf alder recruitment and mammalian herbivore abundance at the landscape scale. Two waves of alder recruitment were identified. The inset shows alder recruitment data only from 1950-1985, scaled by 5-year age classes, while the larger graph extends from 1950-2005 and is scaled by 1-year age classes. The frequency distribution of alder establishment is based on the actual ages of all stems sampled (n = 547 stems). Moose abundance estimates are from Gasaway et al. 1983, Boertje et al. 1996, Young 2002, and Young 2004. Snowshoe hare abundance data are from Trapp 1962, Ernest 1974, Wolff 1980, Hodges et al. 2001, and Flora 2002.

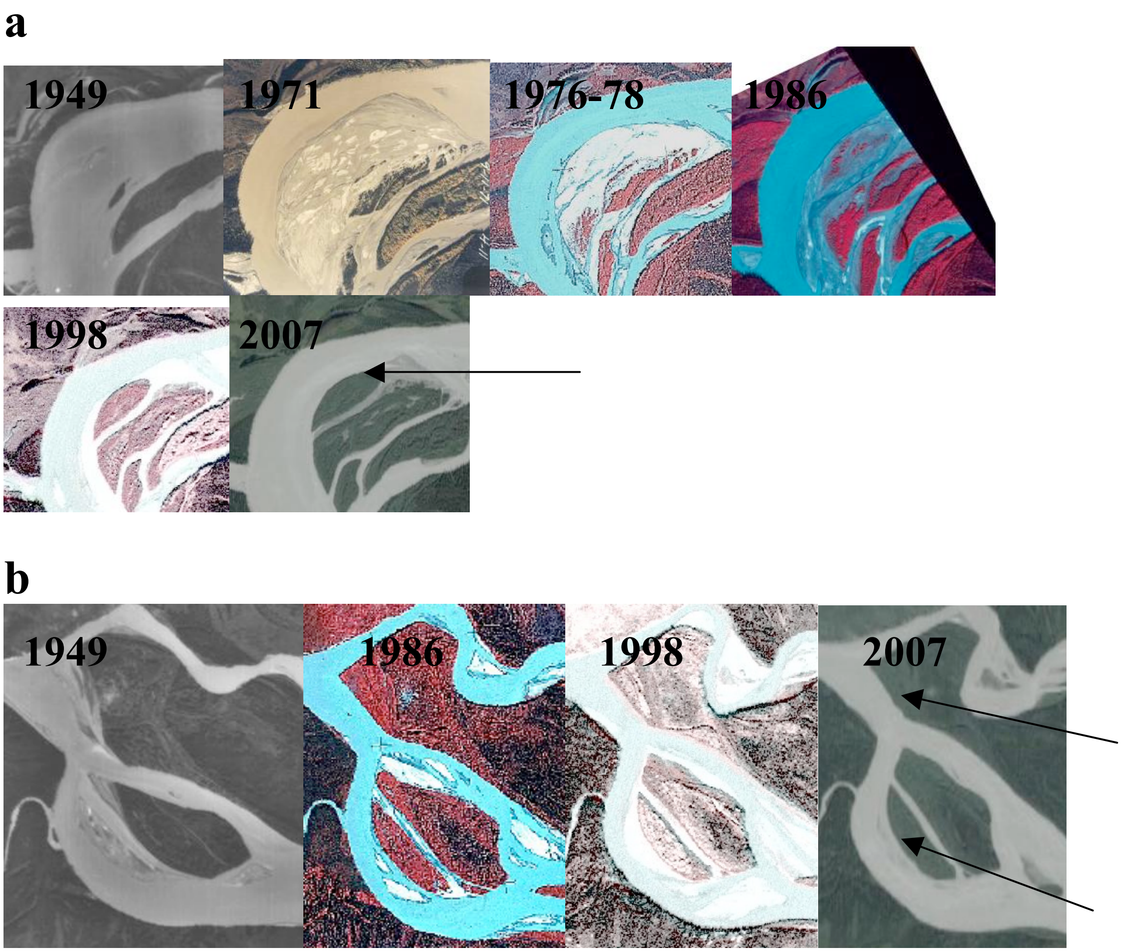

Fig. 1.10. Sequence of aerial imagery showing thinleaf alder stand development during (a) a recent wave of recruitment, and (b) a previous wave of recruitment. Images are labeled with the year of photography. Arrows point to the approximate locations of study sites. Note that the images were captured during different months of the year, and river levels are highly variable. The image from 1971 was taken when river levels were very low, exposing parts of the silt bar that were likely underwater for most of the growing season.

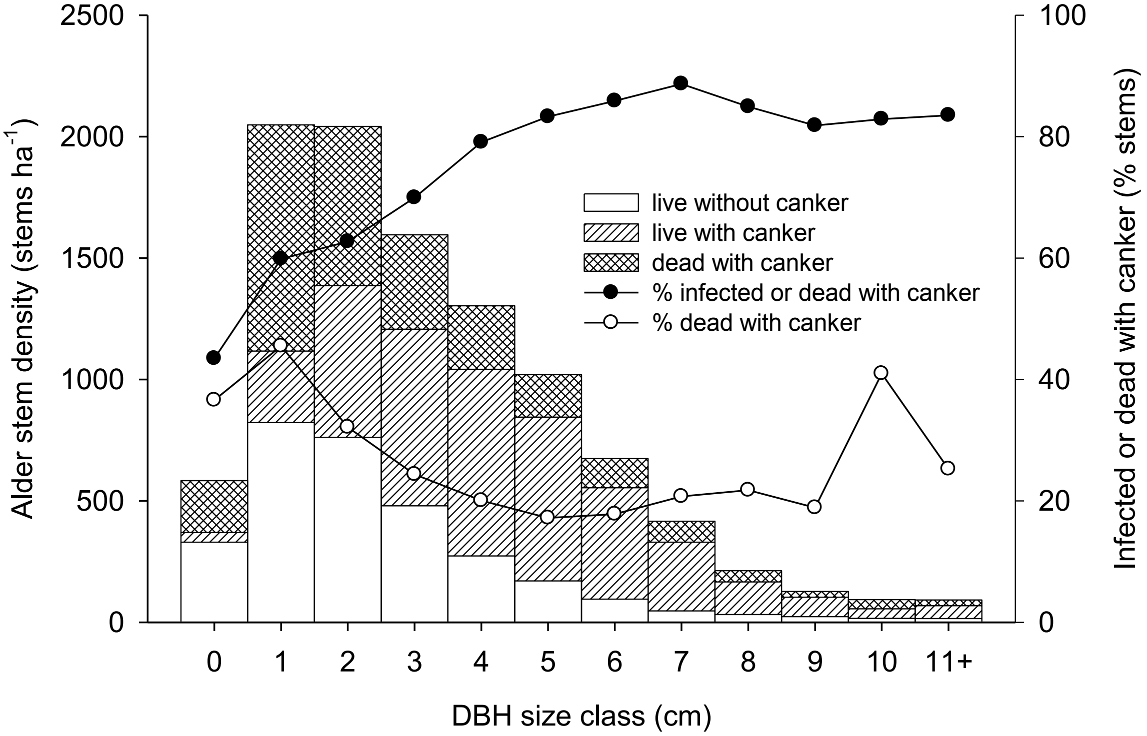

Fig. 1.11. Patterns of disease incidence and disease-related mortality by alder size class. Bars represent stem density and levels of canker incidence and related mortality; dots represent the % of ramets infected or dead with canker. n = 11,481 stems.

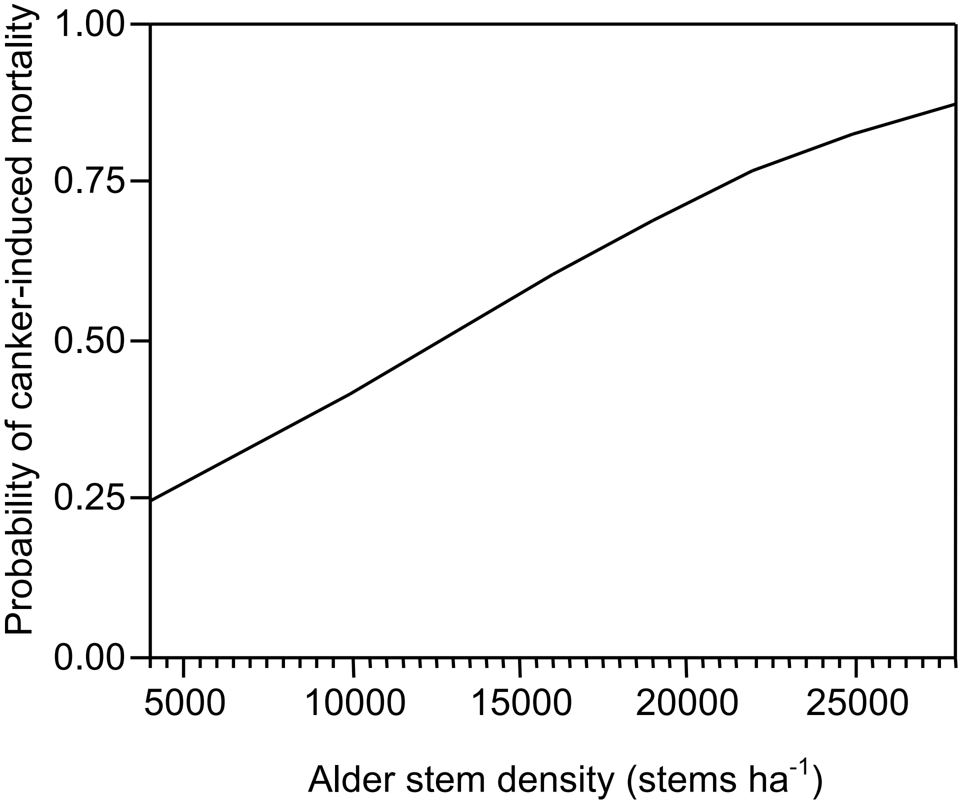

Fig. 1.12. Relationship between disease-related mortality of young stems (1-10 years old) and alder stem density. Logistic regression, based on age reconstructions and disease survey, n = 821 stems, $p < 0.0001$.

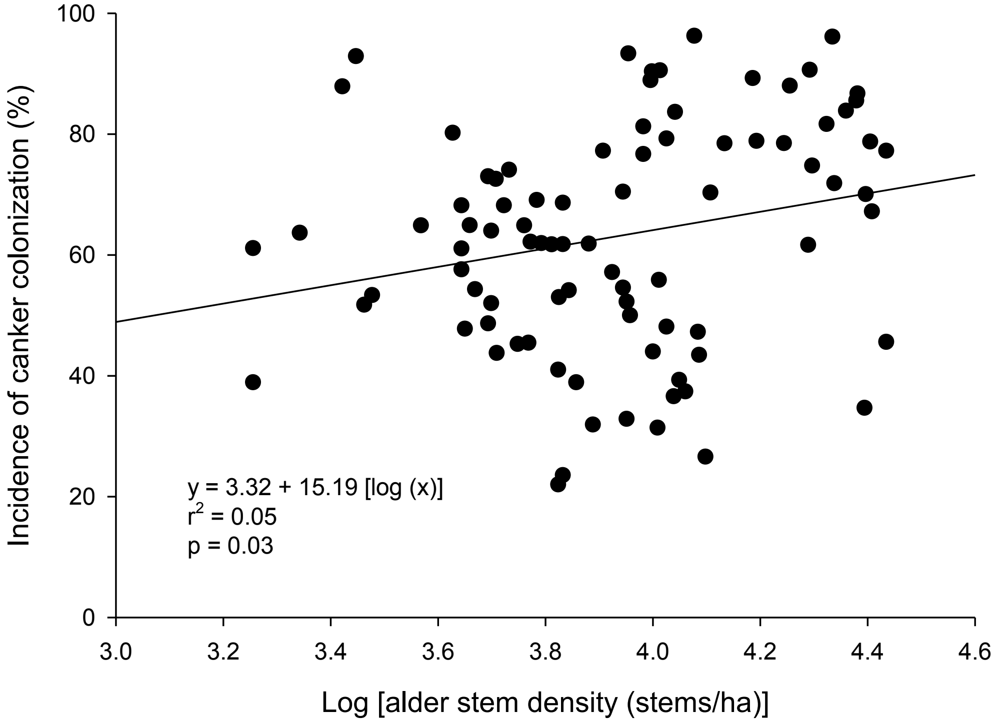

Fig. 1.13. Relationship between disease incidence and alder stem density. Regression, n = 87 sites.

Table 1.1. Descriptive statistics for site characteristics.

Site characteristics	n	Mean ± SE (Min, Max)
Stand age (yrs)	28	26.3 ± 2.5 (13, 56)
Terrace height (m)	89	7.66 ± 0.04 (6.70, 8.86)
Organic depth (cm)	89	3.0 ± 0.2 (0.2, 6.3)
Soil pH	89	6.99 ± 0.07 (5.55, 8.18)
Soil C (%)	89	3.19 ± 0.19 (0.56, 8.88)
Soil N (%)	89	0.18 ± 0.01 (0.03, 0.45)
Soil P (%)	89	0.07 ± 0.00 (0.05, 0.08)
Soil C (g/m^2)	89	2014 ± 83 (502, 4663)
Soil N (g/m^2)	89	118 ± 4 (26, 235)
Soil P (g/m^2)	89	48 ± 1 (27, 71)
Soil N:P	89	2.66 ± 0.13 (0.51, 6.18)
Leaf N:P	38	19.69 ± 0.31 (14.89, 24.42)

Table 1.2. Correlations between selected site characteristics. Pearson product-moment correlation coefficients are shown (r), except with stand age, in which Spearman's rank correlation coefficients (r_s) are displayed. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Site characteristics		n	Correlation coefficient	p-value
Stand age (yr)	Terrace height (m)	28	0.74***	<0.0001
Stand age (yr)	Organic depth (cm)	28	0.68***	<0.0001
Stand age (yr)	Soil pH	28	-0.72***	<0.0001
Stand age (yr)	Soil C (%)	28	0.54**	0.0027
Stand age (yr)	Soil N (%)	28	0.51**	0.0055
Stand age (yr)	Soil P (%)	28	-0.31	0.1144
Stand age (yr)	Soil C (g m^{-2})	28	0.57*	0.0016
Stand age (yr)	Soil N (g m^{-2})	28	0.46*	0.0139
Stand age (yr)	Soil P (g m^{-2})	28	-0.69***	<0.0001
Stand age (yr)	Soil N:P	28	0.61***	0.0005
Terrace height (m)	Organic depth (cm)	89	0.46***	<0.0001
Terrace height (m)	Soil pH	89	-0.72***	<0.0001
Terrace height (m)	Soil C (%)	89	0.26*	0.0131
Terrace height (m)	Soil N (%)	89	0.19	0.0717
Terrace height (m)	Soil P (%)	89	-0.28**	0.0091
Terrace height (m)	Soil C (g m^{-2})	89	0.26*	0.0148
Terrace height (m)	Soil N (g m^{-2})	89	0.16	0.1429
Terrace height (m)	Soil P (g m^{-2})	89	-0.39***	0.0002
Organic depth (cm)	Terrace height (m)	89	0.46***	<0.0001
Organic depth (cm)	Soil pH	89	-0.68***	<0.0001
Organic depth (cm)	Soil C (%)	89	0.82***	<0.0001
Organic depth (cm)	Soil N (%)	89	0.79***	<0.0001
Organic depth (cm)	Soil P (%)	89	0.14	0.1919
Organic depth (cm)	Soil C (g m^{-2})	89	0.73***	<0.0001
Organic depth (cm)	Soil N (g m^{-2})	89	0.70***	<0.0001
Organic depth (cm)	Soil P (g m^{-2})	89	-0.78***	<0.0001

Table 1.3. Pearson correlation of selected site and community characteristics with DCA axes. Correlations with $r^2 > 0.195$ are considered ecologically significant and are displayed in **bold**.

	Axis 1 r	Axis 2 r
Site characteristics		
Stand age	**0.736**	-0.014
Terrace height	**0.516**	-0.071
Organic depth	**0.697**	0.160
Soil pH	**-0.712**	-0.012
Soil C (%)	**0.660**	0.076
Soil C (g m^{-2})	**0.620**	0.071
Soil N (%)	**0.644**	0.121
Soil N (g m^{-2})	**0.572**	0.125
Soil P (g m^{-2})	**-0.596**	-0.066
Soil N:P	**0.648**	0.114
Leaf N:P	0.154	0.096
Successional dominants, > 2 m tall		
Alnus tenuifolia (Relative dominance)	**-0.572**	0.382
Alnus tenuifolia (< 2 cm dbh)	**-0.464**	0.186
Alnus tenuifolia (2-4 cm dbh)	**-0.515**	0.230
Alnus tenuifolia (> 4 cm dbh)	**-0.492**	0.258
Picea glauca (Relative dominance)	**0.599**	-0.148
Picea glauca (< 4 cm dbh)	**0.608**	-0.268
Picea glauca (> 4 cm dbh)	**0.653**	-0.156
Populus balsamifera (> 4 cm dbh)	0.182	**-0.477**
Successional dominants, < 2 m tall		
Salix pseudomyrsinites	**-0.468**	0.272
Salix interior	**-0.443**	-0.094
Populus balsamifera	**-0.485**	0.080
Understory vegetation		
Equisetum variegatum	**-0.601**	-0.225
Moss spp.	**0.450**	-0.086
Shrub abundance	**0.591**	0.326
Rosa acicularis	**0.521**	0.098
Rubus idaeus	**0.456**	**0.445**
Equisetum hyemale	-0.292	**-0.628**
Calamagrostis canadensis	0.134	**0.486**
Arenaria lateriflora	0.209	**0.519**
Bare ground	-0.371	**-0.536**

Table 1.4. Species scores and ranks for Axis 1 of DCA ordination, by growth form and size class.

Species	Growth form	Size class (dbh)	Score	Rank
Successional dominants, < 2 m tall				
Salix hastate	shrub	.	-90	2
Salix interior	shrub	.	-71	4
Salix alexensis	shrub	.	-63	5
Salix pseudomyrsinites	shrub	.	-2	8
Populus balsamifera	tree	.	6	9
Alnus tenuifolia	tree/shrub	.	40	11
Picea glauca	tree	.	90	16
Successional dominants, > 2 m tall				
Salix spp.	shrub	<4 cm	70	12
Alnus tenuifolia	tree/shrub	1-4 cm	79	13
Alnus tenuifolia	tree/shrub	<1 cm	82	14
Alnus tenuifolia	tree/shrub	>4 cm	88	15
Populus balsamifera	tree	<4 cm	115	17
Salix spp.	shrub	>4 cm	171	21
Populus balsamifera	tree	>4 cm	172	22
Picea glauca	tree	<4 cm	314	32
Picea glauca	tree	>4 cm	340	35
Understory vegetation				
Solidago canadensis	forb	.	-135	1
Achillea sibirica	forb	.	-80	3
Equisetum variegatum	forb	.	-54	6
Equisetum pretense	forb	.	-27	7
Equisetum hyemale	forb	.	9	10
Fragaria virginiana	forb	.	116	18
Calamagrostis canadensis	graminoid	.	159	19
Equisetum arvense	forb	.	164	20
Epilobium angustifolium	forb	.	218	23
Arenaria lateriflora	forb	.	225	24
Cornus stolonifera	shrub	.	225	25
Moss spp.	moss	.	232	26
Rosa acicularis	shrub	.	265	27
Pyrola secunda	forb	.	265	28
Pyrola asarifolia	forb	.	266	29
Lichen spp.	lichen	.	275	30
Viburnum edule	shrub	.	297	31
Cornus canadensis	forb	.	334	33
Rubus idaeus	shrub	.	335	34
Mertensia paniculata	forb	.	408	36

Table 1.5. Correlation of recruitment density of successional dominants with the depth of the surface layer of organic soil. Spearman's rank correlation. n = 89 sites.

Stem density of successional dominants < 2 m tall	r_s	*P*
Willow	-0.431	<.0001
Poplar	-0.232	0.029
Alder	-0.122	0.254
Spruce	-0.038	0.723

Table 1.6. Summary of regression equation statistics for reconstructing site-level age distributions of thinleaf alder, based on relationships between age and stem diameter at breast height.

Site	r^2	adjusted r^2	N	P	Regression equation
DN02:0-4	0.586	0.531	18	0.0013	$age = (3.17 + 0.07\sqrt{dbh} -0.09(\sqrt{dbh}-6.99)^2)^2$
DN02:8-9	0.321	0.236	10	0.0876	$age = (1.86 + 0.36\sqrt{dbh})^2$
DN04:0-2	0.236	0.173	14	0.0779	$age = (2.13 + 0.17\sqrt{dbh})^2$
DN04:3-6	0.489	0.438	12	0.0114	$age = (3.13 + 0.08\sqrt{dbh})^2$
DN05:0-7	0.695	0.663	22	<.0001	$age = (2.84 + 0.15\sqrt{dbh} -0.03(\sqrt{dbh}-6.73)^2)^2$
DN06:1-8	0.657	0.600	15	0.0016	$age = (2.78 + 0.16\sqrt{dbh} -0.03(\sqrt{dbh}-7.77)^2)^2$
DN08:6-9	0.253	0.182	24	0.0465	$age = (3.57 + 0.03\sqrt{dbh} -0.04(\sqrt{dbh}-6.32)^2)^2$
DN11:1-2	0.523	0.486	29	<.0001	$age = (2.86 + 0.12\sqrt{dbh} -0.05(\sqrt{dbh}-6.12)^2)^2$
DN12:0-2	0.645	0.620	16	0.0002	$age = (1.44 + 0.34\sqrt{dbh})^2$
DN12:6-8	0.259	0.194	26	0.032	$age = (3.25 + 0.22\sqrt{dbh} -0.16(\sqrt{dbh}-6.01)^2)^2$
DN14:3-4	0.396	0.329	11	0.038	$age = (3.72 + 0.19\sqrt{dbh})^2$
DN16:0-9	0.236	0.180	30	0.0262	$age = (3.12 + 0.06\sqrt{dbh} -0.04(\sqrt{dbh}-6.4)^2)^2$
DN19:3-5	0.605	0.552	18	0.0009	$age = (1.86 + 0.4\sqrt{dbh} -0.2(\sqrt{dbh}-6.28)^2)^2$
DN22:0-2	0.229	0.199	28	0.0100	$age = (3.15 + 0.07\sqrt{dbh})^2$
DN22:3-9	0.553	0.534	25	<0.0001	$age = (1.09 + 0.49\sqrt{dbh})^2$
DN26:0-9	0.627	0.569	16	0.0017	$age = (2.64 + 0.42\sqrt{dbh} -0.06(\sqrt{dbh}-7.39)^2)^2$
DN27:3-4	0.318	0.148	6	0.2434	$age = (3.73 + 0.22\sqrt{dbh})^2$
DN28:0-1	0.407	0.360	28	0.0014	$age = (3.26 + 0.07\sqrt{dbh} -0.01(\sqrt{dbh}-6.15)^2)^2$
DN28:3-5	0.489	0.425	19	0.0046	$age = (2.17 + 0.36\sqrt{dbh} -0.03(\sqrt{dbh}-5.92)^2)^2$
DN29:0-2	0.868	0.853	21	<0.0001	$age = (1.08 + 0.38\sqrt{dbh} +0.05(\sqrt{dbh}-6.51)^2)^2$
DN32:1-6	0.454	0.410	28	0.0005	$age = (2.54 + 0.16\sqrt{dbh} -0.04(\sqrt{dbh}-6.33)^2)^2$
DN34:0-9	0.531	0.475	20	0.0016	$age = (2.72 + 0.13\sqrt{dbh} -0.1(\sqrt{dbh}-7.11)^2)^2$
DN37:0-8	0.704	0.678	26	<0.0001	$age = (3.02 + 0.1\sqrt{dbh} -0.04(\sqrt{dbh}-6.41)^2)^2$
DN39:0-8	0.528	0.503	21	0.0002	$age = (3.21 + 0.07\sqrt{dbh})^2$
DN41:0-9	0.047	0.007	26	0.2886	$age = (3.25 + 0.04\sqrt{dbh})^2$
DN42:0-9	0.683	0.653	24	<0.0001	$age = (2.5 + 0.21\sqrt{dbh} -0.04(\sqrt{dbh}-6.58)^2)^2$
DN43:0-2	0.691	0.666	14	0.0002	$age = (1.37 + 0.50\sqrt{dbh})^2$

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CHAPTER 2: CLIMATE SENSITIVITY OF THINLEAF ALDER GROWTH IN INTERIOR ALASKA: IMPLICATIONS FOR N-FIXATION INPUTS TO RIVER FLOODPLAINS[2]

INTRODUCTION

Increased levels of greenhouse gases are causing rapid climate warming in the circumboreal north (Serreze et al. 2000), and the rate of warming has accelerated over the last 30 years (Chapin et al. 2005). The temperature-induced increase in summer drought is one of the most important and rapidly changing features of the physical environment of the boreal forest (Oechel et al. 2000). Increased summer air temperatures in interior Alaska have accelerated evapotranspiration rates and led to a net reduction in soil moisture, with summer water deficits increasing 6.5 cm decade^{-1} (Oechel et al. 2000). Some coniferous and deciduous boreal tree species sensitive to the increased summer water deficit exhibit drought stress, growth suppression, and susceptibility to disease (Barber et al. 2000, Brandt et al. 2003, Lloyd and Bunn 2007, Hogg et al. 2008, Winslow 2008, Juday et al. 2005). This study addresses the patterns of climate sensitivity in the growth of the N-fixing shrub *Alnus incana* ssp. *tenuifolia*, hereafter *Alnus tenuifolia* (thinleaf alder), on the Tanana River floodplains of interior Alaska. The response of this keystone N-fixer to a warmer, drier climate could have major implications for ecosystem function in the boreal forest floodplains.

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[2] Nossov DR, Ruess RW, Hollingsworth TN (In preparation). Climate sensitivity of thinleaf alder growth in interior Alaska: Implications for N-fixation inputs to river floodplains. *Global Change Biology*.

Thinleaf alder is the dominant N-fixing species in interior Alaskan floodplains, with dense thinleaf alder stands contributing up to 60 kg N ha^{-1} $year^{-1}$ (Uliassi and Ruess 2002). Up to 70% of the N accumulated over the 200 years of floodplain succession is fixed by thinleaf alder during the relatively short phase of its dominance (Van Cleve et al. 1971, Van Cleve et al. 1991). Therefore, factors that limit the ability of alder to fix N also have profound effects on ecosystem processes. Because symbiotic N-fixation is controlled by plant N demand (Wall and Huss-Danell 1997), high rates of thinleaf alder growth are synonymous with high rates of N-fixation input in early successional environments where soil N is nearly non-existent (Uliassi and Ruess 2002). Thus, if alder growth is limited by drought stress, ecosystem N inputs through N fixation will also be reduced.

Surface soil moisture in the Tanana River floodplains is influenced by the depth of hyporheic flow, which is a function of river level (Viereck et al. 1993b). River level is controlled indirectly by air temperature, primarily through the rate of glacial melt (Swanson et al. 1998), as the Tanana River derives 85% of its water from glacially-fed tributaries (Yarie et al. 1998). Interestingly, while increased summer air temperatures would be predicted to *decrease* soil moisture through increased evapotranspiration (Oechel et al. 2000), warmer summer temperatures would also be predicted to *increase* floodplain soil moisture by increasing glacial melt (Woo et al. 2008) and the height of hyporheic flow (Viereck et al. 1993b, Clilverd et al. 2008). These opposing consequences of warming on floodplain soil moisture are separated in time within the growing season, where drought stress may be more likely to occur before river levels and hyporheic flow peak. Evaporation rates are highest in June and July, but river levels of the Tanana do not typically peak until mid-July (Viereck et al. 1993b), and the capillary rise of hyporheic water does not reach the rooting zone of willow until late June (Clilverd et al. 2008). If air temperature is high and precipitation is low in June, then increased glacial melt later in the season may not offset the effect on plants of low soil moisture experienced earlier in the growing season. Thus, floodplain vegetation may be quite vulnerable to moisture stress in years of early season meteorological drought, despite the late-season increase in hyporheic flow.

The goal of this study was to understand the patterns in the growth sensitivity of thinleaf alder to climate warming in order to assess the importance of potentially long-term controls on N-fixation inputs in the Tanana River floodplains. Our specific objectives were to (1) analyze the monthly variation in climate and hydrology to identify key periods of potential vulnerability to drought stress, (2) determine the influence of monthly meteorological and hydrological variables on annual alder radial growth, (3) assess the variability in alder climate sensitivity across the landscape due to variations in the distance to hyporheic flow, and (4) explore the long-term trends in climate and hydrology and the implications for future alder growth and N-fixation inputs.

METHODS

Study area

The study area encompasses an 80-km reach of the Tanana River floodplain in interior Alaska, between Fairbanks (64.9° N, 147.9° W) and Nenana (64.5° N, 148.7° W). The climate of this region is strongly continental with low precipitation and humidity, and is characterized by extreme seasonal variation in day length and temperature and a short growing season (Viereck et al. 1993b).

In 2006, 45 transects (50 m x 5 m) were established in alder-dominated stands representing a large range in alder stand structure and terrace heights. Each transect was subdivided into 10 5 m x 5 m plots. After initial vegetation sampling, multivariate analyses of community structure were conducted to aggregate plots of each transect into larger zones of homogenous vegetation that were then used for subsequent sampling (Nossov et al., in preparation). We refer to the aggregated plots from each transect as sites. Of the 89 sites established for a larger study, we subsampled 27 sites for the purpose of this climate sensitivity project.

Tree ring sampling

At each site we collected disks at ground level from up to 10 live alder stems for each of three size classes based on diameter at breast height (dbh) (0-2.9 cm, 3-4.9 cm, and ≥ 5 cm). The disks were oven-dried and sanded with 400-600 grit sandpaper. Tree rings were counted and measured on a sliding bench micrometer to a precision of

0.01 mm. Three to four radii were sampled from each disk and averaged to ensure accuracy of dating and growth measurements. Due to the difficulty of cross-dating the relatively short series typical of our samples, stems that could not be dated consistently were excluded from subsequent analyses.

Terrace height sampling

Terrace height, the elevation of the soil surface relative to the gage datum (121.92 m above sea level) for the Tanana River at the Fairbanks USGS site (#15485500), was used as an index for the vertical distance between the soil surface and the height of hyporheic flow at each site. Terrace heights were surveyed and calculated through differential leveling at 5 m intervals along transects, and were then averaged for each site. Hourly Tanana River gage height readings from the Fairbanks USGS site were used as benchmark elevations.

Data analysis

The raw tree ring-width series from each alder disk was individually detrended to remove age-related growth trends in order to isolate the climatic signal (Fritts 1971). A flexible cubic spline was fit to each series after truncating the early growth data to maximize the fit of the growth curve (Cook and Peters 1981). Residuals from each growth curve were arithmetically averaged by site for each year with at least five data points to build standardized site-level ring-width chronologies (Cook and Peters 1997). Mean series intercorrelation, the average correlation of each individual chronology with the site chronology, was 0.575, indicating the presence of a fairly strong climate signal common to most stems sampled. The site-level ring-width chronologies were averaged to develop a master ring-width chronology representing growth data for 547 stems across all 27 sites.

The use of individually fit flexible splines in detrending removes the long term variation in tree growth history, potentially removing climatically-driven growth trends in addition to age-related growth trends; however, the short length of alder tree-ring series precluded the use of other detrending methods (Cook and Peters 1981). Therefore, the results presented here are conservative estimates of the growth response to climate anomalies, and are interpreted at the inter-annual time scale.

We identified key periods of potential vulnerability to drought through examination of the variation in monthly mean values of meteorological and hydrological variables likely to influence soil moisture from May-September. The variables we considered were temperature, precipitation, the Palmer Drought Severity Index (PDSI), and Tanana River discharge and gage height. Temperature and precipitation data were from the Fairbanks International Airport for the period 1930-2006 (www.climate.gi.alaska.edu). Hydrological data for the Tanana River were obtained from U.S. Geological Survey (USGS) website (waterdata.usgs.gov/nwis/) for sites in Fairbanks (#15485500) and Nenana (#15515500). Tanana River gage height data from Fairbanks (1991-2006) were used as direct measurements of river levels; however, due to the short period of record, gage height data were supplemented with river discharge data from Nenana (1962-2006). The PDSI data from 1960-2006 were obtained from the Bonanza

Creek Long-Term Ecological Research (LTER) program based in Fairbanks, Alaska (McGuire 2006).

The PDSI is a standardized index of meteorological drought which approximates the departure from the local mean atmospheric moisture supply and demand at the soil surface (Palmer 1965). The water balance approach of the PDSI utilizes temperature, precipitation, and local soil available water content data to estimate evapotranspiration, soil recharge, runoff, and moisture loss (Thornthwaite 1948, Palmer 1965). Despite the limitations of this index (Alley 1984), the PDSI provides a useful approximation of relative meteorological drought that is typically a stronger predictor of soil moisture than either temperature or precipitation alone (Dai et al. 2004), and is commonly correlated with ring widths of drought-stressed trees (Cook et al. 1999). Although the PDSI was developed to estimate meteorological drought, this index is frequently correlated with river discharge (Dai et al. 2004, MacDonald et al. 2007); therefore, the PDSI functions as a hydrometeorological index for our application with riparian vegetation.

Distributions of all variables were examined for normality using normal quantile plots. Strong deviations from normality were corrected using the appropriate data transformation prior to correlation and regression analyses (Zar 1996). The influence of meteorological and hydrological variation on overall alder radial growth was assessed through correlation analyses with the standardized tree-ring widths from the master chronology spanning 1968-2006. To address the variation in alder climate sensitivity in relationship to terrace height, standardized ring widths from the site-level chronologies from 1998-2005 were correlated with monthly temperature, precipitation, and gage height for the key period of growth sensitivity. The resulting site-level correlation coefficients were regressed against terrace height to identify spatial trends in climate sensitivity. Long-term trends in the climate and hydrological variables that were most limiting to alder radial growth were assessed using simple linear regression. Results were considered statistically significant at $\alpha = 0.05$. All statistical analyses were conducted with JMP IN 5.1.2 (SAS Institute 2004).

RESULTS

Intra-seasonal variation in climate and hydrology

Local climate and hydrological variables varied widely throughout the course of the growing season (May-September) (Fig. 2.1). Mean monthly temperature from 1960-2006 approached its peak in June and reached its maximum in July (Fig. 2.1a). Mean monthly precipitation followed a similar pattern, but peaked in July and August (Fig. 2.1a). Tanana River discharge and gage height rapidly increased from May through July, and decreased from July through September (Fig. 2.1b). The monthly PDSI fluctuated considerably among years, but also showed a seasonal pattern with means below 0 from June through August, indicating relatively dry conditions during this period (Fig. 2.1c). The timing of the seasonal variation of these climate and hydrologic variables suggests that floodplain plant communities are likely to be most vulnerable to drought stress from May through June, a time when temperatures increased faster than precipitation, when PDSI was below 0 (June), and before river discharge and gage height reached their peak.

Thinleaf alder leaf-out typically does not occur until late May or early June on the Tanana River floodplains, so we considered June to be the key period of vulnerability to drought stress.

Influence of meteorological and hydrological variation on alder growth

Mean monthly climate and hydrological series were correlated with the master ring-width chronology, representing growth data from 547 alder stems across 27 sites. The strength and direction of the correlations of alder ring-width with meteorological and hydrological data exhibited intra-seasonal patterns, with the strongest relationships occurring in June (Fig. 2.2). June PDSI was the strongest predictor of alder ring width ($r = 0.420$, $p = 0.008$, Figs. 2.2 and 2.3d), but June discharge was also significantly correlated with ring width ($r = 0.367$, $p = 0.02$, Figs. 2.2 and 2.3c), suggesting that alder annual growth was sensitive to both atmospheric and hydrologic conditions during this key period of vulnerability. June PDSI and June discharge, however, were highly inter-correlated ($r = 0.609$, $p < 0.0001$), complicating interpretation. Alder growth was also subjected to moisture limitation during August, as suggested by the significant positive correlation between alder ring width and August discharge ($r = 0.324$, $p = 0.04$, Fig. 2.2). Monthly mean temperatures and ring width were not significantly correlated (Figs. 2.2 and 2.3a), but July temperature did have a weak positive relationship with ring-width ($r = 0.309$, $p = 0.06$, Fig. 2.2), suggesting that alder growth was not limited by drought during this month. Monthly mean precipitation values were not correlated with alder ring width (Figs. 2.2 and 2.3b).

Spatial variation in climate sensitivity of alder growth

Site-level ring widths were correlated with monthly mean temperature, precipitation, and river gage height for June and August to evaluate the influence of terrace height on variation in alder climate sensitivity. Due to the short series length used (n = 8 years) and the relatively low sample size of stems comprising the site ring-width chronologies (n < 30 stems), the correlations of meteorological and hydrological variables with the site-level ring widths were generally weaker than with the landscape-level ring widths; however, consistent trends in the strength and direction of the correlations by terrace height were apparent (Fig. 2.4a,b). In June and August, both the negative relationship between temperature and ring width, and the positive relationship between precipitation and ring width, were strengthened with increasing terrace height (Fig. 2.4a,b). On lower terraces, alder ring width was not related to temperature or precipitation, but exhibited significant positive relationships with gage height, in contrast with alder on higher terraces (Fig. 2.4a,b). The remarkable consistency in the spatial variation of the growth responses to temperature, precipitation, and gage height between June and August suggests that the mechanisms of moisture limitation early in the growing season are similar to those late in the growing season.

Long term trends in climate and hydrology

Fairbanks climate data showed that both June and August mean temperatures increased linearly from 1930-2006 (Fig. 2.5a). In addition, mean August precipitation declined from 1930-2006, although mean June precipitation showed no significant trend,

(Fig. 2.5b). June PDSI also decreased linearly from 1960-2006, although August PDSI did not change predictably (Fig. 2.5c). From 1962-2006, mean discharge of the Tanana River in June and August did not exhibit a temporal trend (Fig. 2.5d).

DISCUSSION

Intra-seasonal variation in climate and hydrology

Seasonal patterns of plant water availability on the floodplains of the glacial Tanana River are complex due to the seasonality and timing of climatic and hydrological processes. The Palmer Drought Severity Index (PDSI), based on meteorological and soil data, indicates a generally dry period from June through August (Fig. 2.1c), with evaporation rates at their highest in June and July (Viereck et al. 1993b). However, the level of hyporheic flow, which is directly related to river discharge and gage height (Viereck et al. 1993b, Clilverd et al. 2008), typically peaks in July and remains relatively high through August, potentially alleviating drought conditions for vegetation (Fig. 2.1c, Viereck et al. 1993a, Viereck et al. 1993b). In June, mean air temperatures are relatively high and precipitation low, with PDSI indicating drier conditions, while river discharge and gage height have yet to reach their seasonal peak (Fig. 2.1a,b,c). We found that the timing of the variation in climate and hydrology does indeed suggest that plants in the glacial floodplains of interior Alaska are likely most vulnerable to drought stress early in the growing season.

Influence of meteorological and hydrological variation on alder growth

Our results show that thinleaf alder radial growth was most sensitive to inter-annual variation in climate early in the growing season, before the seasonal peak in river levels, but was also vulnerable to moisture limitation later in the season, after river levels began to subside (Figs. 2.2 and 2.1b).

Alder ring width was most strongly correlated with the mean Palmer Drought Severity Index (PDSI) for June, indicating that radial growth was most limited by and responsive to inter-annual variation in soil moisture during this month (Fig. 2.2). The relationship of alder radial growth with PDSI showed the tendency for alder growth to increase in years when June weather was cooler and wetter, and decrease in years with warmer and drier June weather. The radial growth of drought-stressed trees frequently shows a positive correlation with the PDSI (Cook et al. 1999). June PDSI was a better predictor of alder annual growth than either temperature or precipitation alone, perhaps because PDSI takes into account both variables to more accurately approximate soil moisture (Palmer 1965, Dai et al. 2004).

The co-occurrence of meteorological and hydrological drought in June explains the sensitivity of alder radial growth to the inter-annual variation in river discharge during this month (Fig. 2.2). In other words, when alder growth was moisture-limited due to meteorological drought, growth responded positively to the fluctuations in river levels and the height of hyporheic flow (Fig. 2.2). Alder ring width was also responsive to the variation in river discharge during August (Fig. 2.2), despite the relatively high monthly mean river level in comparison with June levels (Fig. 2.1), suggesting that alder radial growth can also be sensitive to moisture limitation late in the growing season. The weak, positive relationship between July temperature and alder ring width provided evidence that temperature-induced drought stress was not likely in July (Fig. 2.2), when river levels were at their peak (Fig. 2.1).

The suppression of tree growth and susceptibility to disease have been linked to moisture stress in several deciduous and coniferous species native to the boreal forest (Barber et al. 2000, Brandt et al. 2003, Lloyd and Bunn 2007, Hogg et al. 2008, Winslow 2008, Juday et al. 2005). Dendroecological studies of moisture limitation have traditionally focused on upland environments, where sensitivity to meteorological drought is expected to be greater due to the presumably reduced access to groundwater (Fritts 1971). However, recent studies such as this are beginning to show that some riparian plant species are vulnerable to drought stress, despite their relative proximity to subsurface water (Dawson and Pate 1996, Leffler and Evans 1999, Horton et al. 2001, Cooper et al. 2003, Li et al. 2007, Winslow 2008). Because subsurface flow is often important to riparian plant water balance (Busch et al. 1992, Leffler and Evans 1999, Li et al. 2007), it is not surprising to find that the growth of thinleaf alder was most sensitive to meteorological drought during periods of low hyporheic flow. In predicting the future response of floodplain vegetation to a changing climate, it will be important to consider this demonstrated temporal variation in drought sensitivity.

Spatial variation in climate sensitivity of alder growth

The deposition of alluvium with flooding causes terrace heights to rise as primary successional stands develop along the Tanana River floodplains (Viereck et al. 1993b). The rise in terrace height above the river with time results in an increased distance between the soil surface and hyporheic flow (Viereck et al. 1993b, Clilverd et al. 2008). Our results show that the sensitivity of alder growth to inter-annual variation in meteorology and hydrology consistently varied across the landscape in relationship to terrace height, and therefore, distance to hyporheic flow (Fig. 2.4).

During both months of sensitivity to moisture limitation (June and August), the negative response of alder radial growth to increased temperatures and decreased precipitation intensified with increasing terrace height, while the strong positive relationship of ring width with river level diminished (Fig. 2.4). The spatial variation in the strength of the response of alder growth to temperature, precipitation, and river level suggests that alder growth is more susceptible to drought stress on higher terraces, where distance to hyporheic flow is greater and soil moisture replenishment through river level fluctuation is less likely. The strong response of alder growth on low terraces to variation in gage height suggests that alder growth is moisture-limited in these sites, but hyporheic flow plays an important role in alleviating or exacerbating soil moisture deficits on low terraces.

Thinleaf alder growth responded negatively to meteorological drought throughout our study area on the Tanana River floodplains (Fig. 2.2), but the strength of this growth response was heightened at sites where the distance to hyporheic flow was greater (Fig.

2.4). Alder N-fixation rates tend to decrease from early to mid-succession (Uliassi and Ruess 2002), and our results suggest that the increased vulnerability of alder to drought stress on high terraces could contribute to this decline. This successional pattern is likely to become more striking with continued warming (Fig. 2.5a). The dependence of alder on atmospheric moisture versus subsurface flow varied even within this relatively minimal gradient in floodplain terrace height (range of < 2 m). The spatial variation we found in alder water source utilization was expected. While we are unaware of any other studies explicitly examining the effect of elevation on the vulnerability of plant growth to drought stress within a riparian landscape, our findings are conceptually analogous to those derived from the examination of wide elevation gradients (Li et al. 2007) and variable levels of subsurface flow (Leffler and Evans 1999, Horton et al. 2001, Cooper et al. 2003).

Different plant species and growth forms vary in their water source utilization, and consequently experience meteorological drought differently (Ehleringer et al. 1991). Therefore, spatial and temporal variations in moisture availability are likely to alter the competitive interactions between species and perhaps facilitate changes in community structure (Fowler 1986, Ehleringer et al. 1991). The community structure of alder stands along the Tanana River floodplains varies markedly along a gradient of terrace height, and could be partially attributed to the differential abilities of plant species to utilize subsurface water (Nossov et al., in preparation). If the competitive ability of alder is weakened through the increased distance to hyporheic flow, this could be a potential mechanism facilitating the shift in successional dominance.

Long term trends in climate and hydrology: implications for N-fixation inputs

With annual alder radial growth most sensitive to climate and hydrological variation during June and August, we examined the long term trends of temperature, precipitation, PDSI, and river discharge during these months to predict the future response of alder to a changing climate (Fig. 2.5). From 1930-2006, mean June and August temperatures in Fairbanks increased linearly with time. Mean precipitation decreased for August, but showed no pattern for June. June PDSI for Fairbanks declined linearly during this period, suggesting a long-term trend of increasing drought severity, while August PDSI showed no trend. Although annual discharge rates of the Tanana River have significantly increased from 1962-2006 (Hinzman et al. 2005, Woo et al. 2008), this was attributable solely to changes in winter discharge (data not shown); and no significant change in Tanana river discharge rates for June or August were detected. If temperature continues to increase without concurrent increases in precipitation or river discharge, alder growth suppression and drought stress will likely become more common and severe.

Because of the tight connection between alder growth and N-fixation (Wall and Huss-Danell 1997, Uliassi and Ruess 2002), a warming climate can be expected to reduce ecosystem N-fixation inputs through alder growth suppression. Many studies have shown that moisture deficits may cause declines in N-fixation rates and nodulation (Dalton and Zobel 1977, Dixon and Wheeler 1983, Harrington and Seiler 1988, Hennessey et al. 1989, Huss-Danell 1997), and with acute drought stress an almost complete inhibition of N-fixation was observed in *Alnus incana* (Sundström and Huss-Danell 1987). Because most soil N in this N-limited ecosystem is derived through thinleaf alder N-fixation (Van Cleve et al. 1971, Van Cleve et al. 1991, Uliassi and Ruess 2002), a reduction in alder N-fixation rates is likely to have large consequences for ecosystem function and community interactions.

In addition to growth suppression and reduced N-fixation rates, drought stress can increase the vulnerability of plants to disease through the induction of biochemical changes in the host that decrease active resistance mechanisms or the stimulation of the metabolism and growth of pathogens (Boyer 1995). There is evidence for drought-stress induced predisposition to fungal stem canker infection in diverse host-pathogen relationships (Schoeneweiss 1975, Desprez-Loustau et al. 2006), including black alder and the fungal canker *Phomopsis alnea* (Moricca 2002).

Widespread outbreaks of a fungal canker pathogen (putatively *Valsa melanodiscus*, anamorph *Cytospora umbrina*) have recently caused considerable branch dieback and ramet mortality in thinleaf alder throughout south-central and interior Alaska (USDA 2006, 2008), causing stand-level reductions in N-fixation inputs through declines in nodule biomass (Ruess et al., submitted). The incidence of canker infection and canker-induced mortality are high throughout the Tanana River floodplains, with over 70% of thinleaf alder colonized by the pathogen, and 29% of all standing alder dead with the disease (Nossov et al., in preparation). This outbreak could potentially be influenced by the stress-induced predisposition of the host or the stimulated growth of the pathogen due to drought. The spatial variation of the incidence of the disease and mortality within the landscape, however, appears to be controlled by alder stem density, rather than by alder drought sensitivity (Nossov et al., in preparation). It is uncertain to what extent the current outbreak is related to climate, but if drought does increase the vulnerability of alder to disease, a warming climate may be expected to further reduce N-fixation inputs through disease-related dieback and mortality.

Conclusions

The response of thinleaf alder, a keystone N-fixer, to a changing climate could substantially impact ecosystem function in the boreal forest floodplains of interior Alaska. We found that thinleaf alder radial growth was most sensitive to moisture limitation at two key points in the growing season. During June and August, meteorological drought tends to be severe, while the river level and the height of hyporheic flow tend to be low, relative to their seasonal peaks. Alder growth responded positively to increases in river levels during these months, suggesting that fluctuation in hyporheic flow plays a large part in either alleviating or exacerbating drought stress, especially on lower terraces where the availability of subsurface water is greater. The sensitivity of alder growth to meteorological drought was heightened with increasing terrace elevation, due to the greater distance to hyporheic flow. The long-term meteorological and hydrologic trends in this region suggest that drought will become more common and severe in this region, resulting in reductions in alder-mediated ecosystem N inputs through further growth suppression, drought stress, and, perhaps, vulnerability to disease infection.

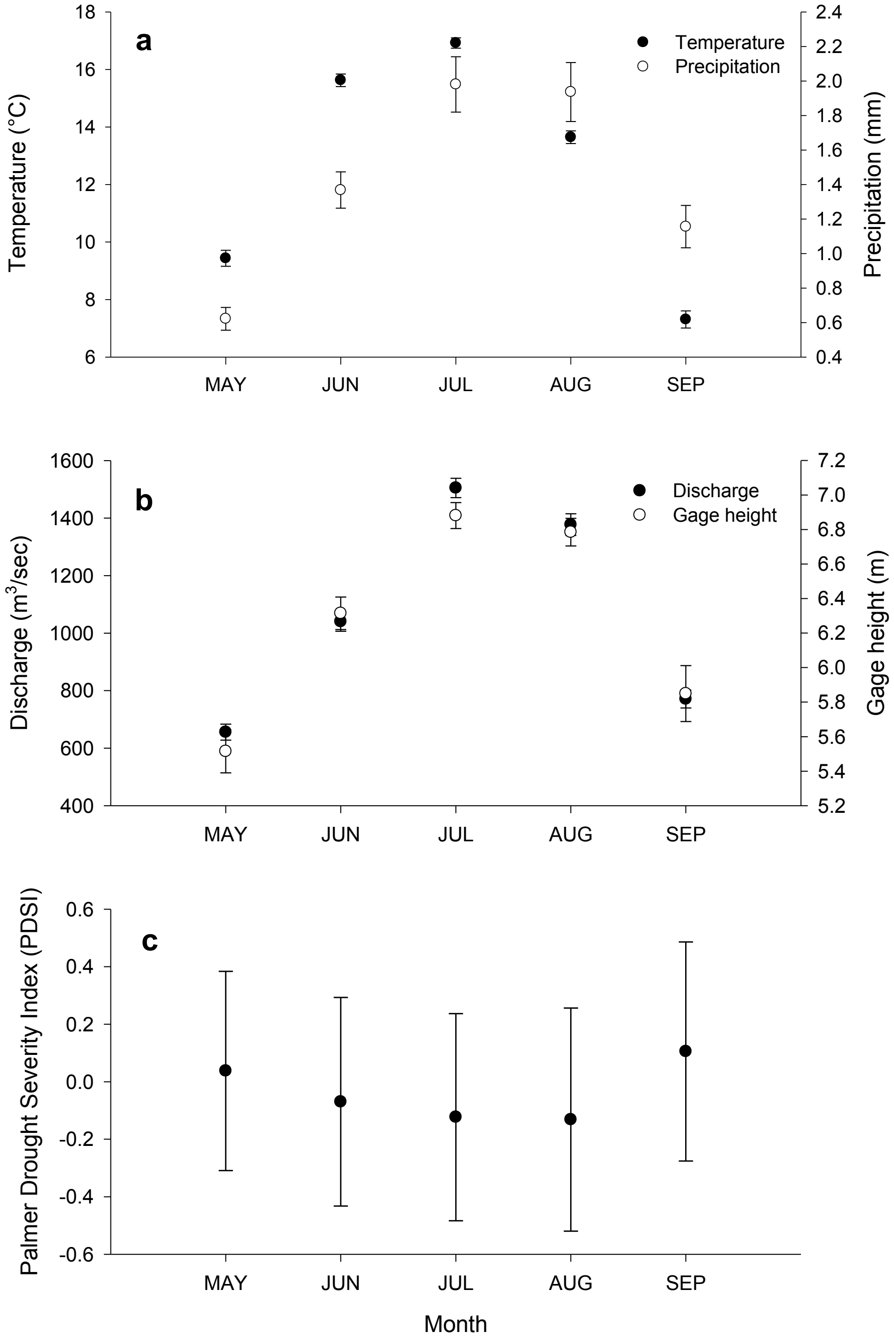


Fig. 2.1. Intra-seasonal variation (May – September) in (a) air temperature and precipitation in Fairbanks, AK (1930-2006), (b) Tanana River discharge in Nenana, AK (1962-2006) and gage height in Fairbanks, AK (1991-2006), and (c) PDSI in Fairbanks, AK (1960-2006). Data are monthly means ± SE.

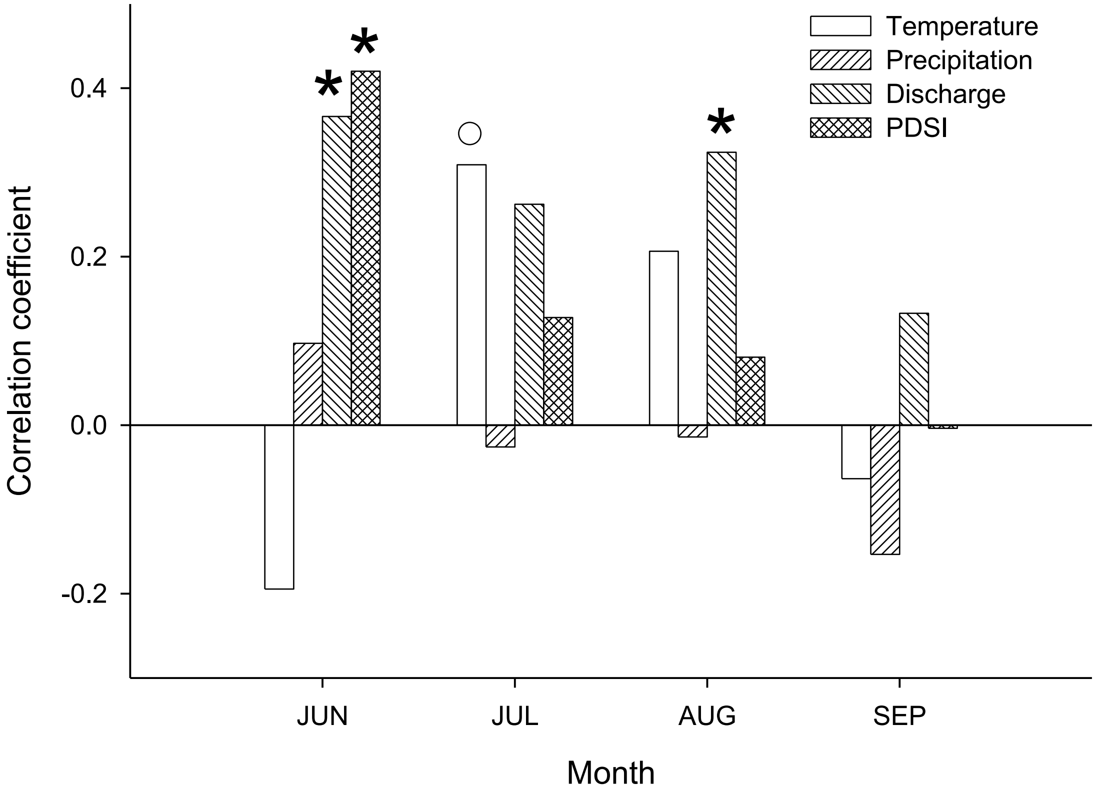


Fig. 2.2. Correlation of alder ring widths with monthly mean temperature, precipitation, discharge, and PDSI from June-September. Pearson product-moment correlations, n = 39 years. Asterisks indicate correlations significant at $p < 0.05$; circles indicate weak correlations with $p < 0.10$.

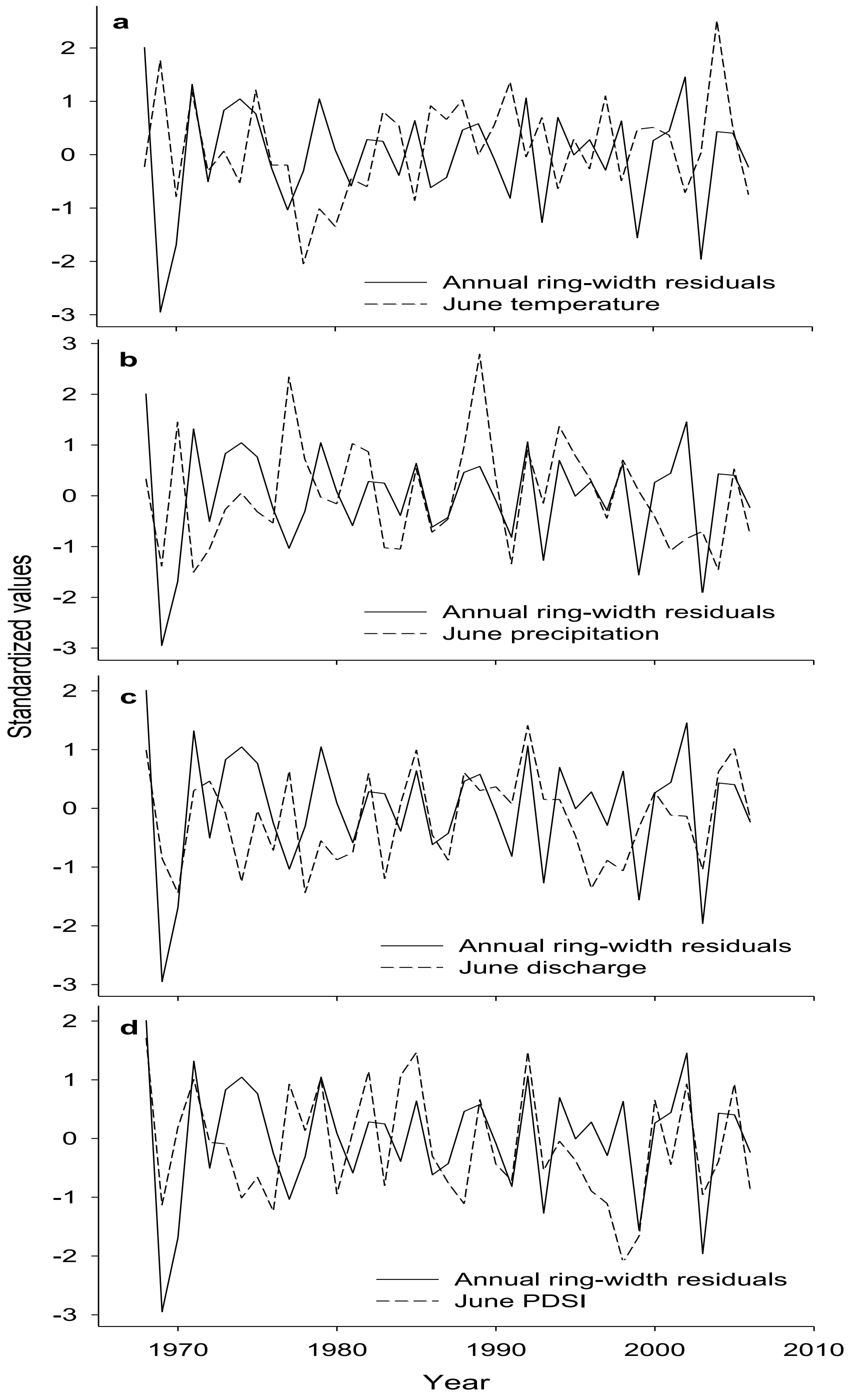
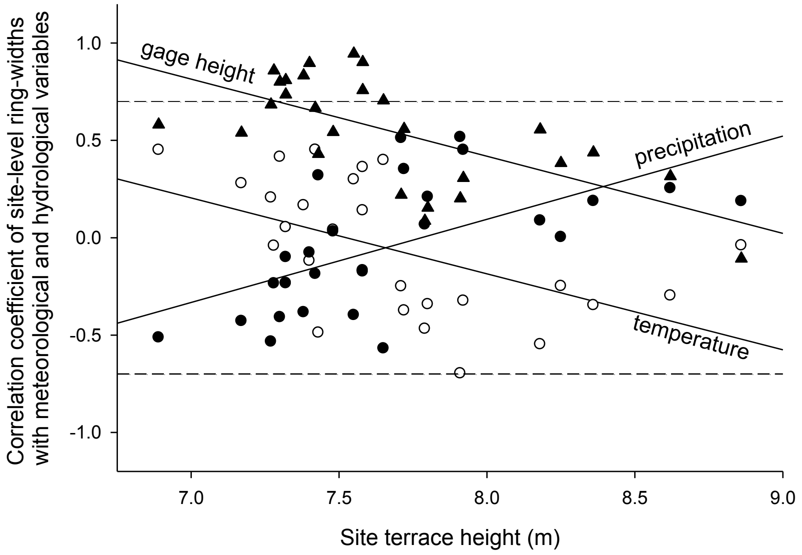


Fig. 2.3. Annual ring-width residuals in relationship to mean June (a) temperature, (b) precipitation, (c) river discharge, and (d) PDSI. All values are standardized.


(a) JUNE

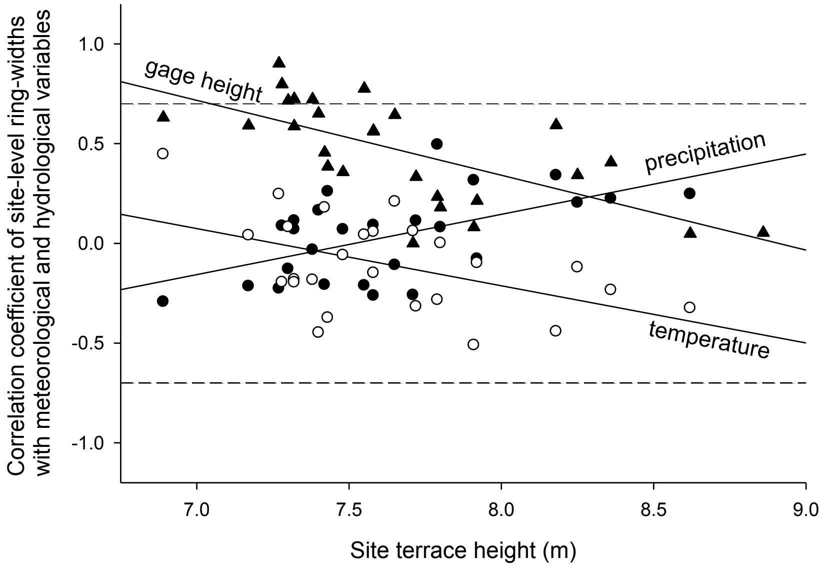

(b) AUGUST

Fig. 2.4. Correlations of alder radial growth with meteorological and hydrological inter-annual variation during (a) June and (b) August, as they varied by terrace height. (Pearson product-moment correlations, n = 8 years; Regressions of correlation coefficients with terrace height, n = 27 sites). Ring-width correlations with gage height = triangles, with temperature = open circles, with precipitation = solid circles. Points above the upper and below the dashed lower dotted reference lines are statistically significant correlations. All regression lines are statistically significant ($p < 0.05$).

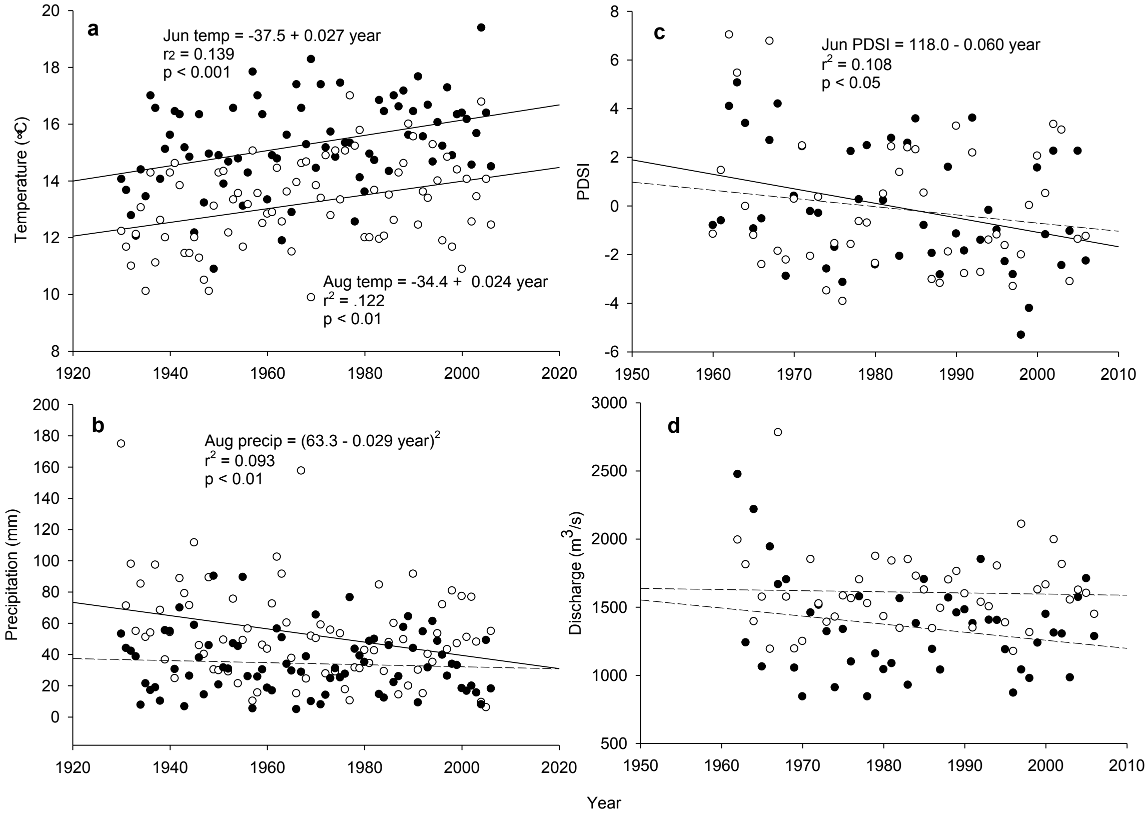


Fig. 2.5. Long-term trends in June and August (a) temperature, (b) precipitation, (c) PDSI, and (d) Tanana River discharge. Fairbanks temperature and precipitation data are from 1930-2006, Fairbanks PDSI data are from 1960-2006, and discharge data from Nenana are from 1962-2006. Statistically significant regression lines are solid with regression statistics displayed. Dashed lines show regressions which were not statistically significant. Solid circles represent June; open circles represent August.

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CONCLUSIONS

The results of this study show the temporal and spatial variation in community structure, population dynamics, and growth of thinleaf alder along the Tanana River floodplains of interior Alaska, and how these patterns are likely to influence current and future successional and ecosystem level processes.

As thinleaf alder stands aged, organic material accumulated, alkaline soils were acidified, soil N content increased by an order of magnitude, and soil P content declined. Soil N:P ratios increased with thinleaf alder stand age, suggesting an attenuation of N-limitation of most plants with time. Consistently high foliar N:P ratios of thinleaf alder imply that symbiotic N-fixation itself was limited by P throughout succession. The population structure of thinleaf alder similarly influenced the spatial variation in soil nutrient status. In early successional stands, increasing alder stem density led to strong linear increases in soil N content.

Much of the temporal variation in alder community structure varied as expected along a gradient of changing environmental characteristics, and floristic indicators of the dominant successional pathway were identified. Interesting variations in, or deviation from, the dominant successional trajectory were also found. Most notably, the abundance and presence of mature balsam poplar, was highly variable and independent of stand age, suggesting either (a) variable rates of successional turnover to a poplar dominated stage, or (b) a somewhat common successional trajectory in which poplar never dominates. The variation in mature poplar density was associated with variation in the understory plant community. The communities with low mature poplar abundance contrasted the communities with high mature poplar abundance in that the former were characterized by a dense understory of graminoid, forb, and shrub species, which could limit the recruitment success of the potentially dominant successional tree species and further slow the rates of succession.

The landscape-scale recruitment of alder occurred in waves over the long term, with a large recent pulse in the early 1990s and a previous pulse around 1970. Evaluation of aerial imagery and site-level age distributions suggests that these patterns of alder recruitment were likely to be driven primarily by geofluvial processes which govern the area available for colonization and by the dynamics of alder seed production and dispersal. The site-level age distributions also highlighted the rapidity of initial stand establishment as well as the continued recruitment in, and potentially long persistence of, mature alder stands. The effects of a current outbreak of a fungal stem canker (*Valsa melanodiscus* anamorph *Cytospora umbrina*) on alder were severe and widespread throughout the study area, and will likely reduce the ecosystem N inputs across the landscape. The incidence of canker colonization was linearly related to alder stem density, and young stems had disproportionately high mortality rates in high density alder stands.

The annual radial growth of thinleaf alder radial growth was sensitive to moisture limitation during two key periods of the growing season. During June and August, meteorological drought tended to be severe, while the river levels and the height of hyporheic flow tended to be low, relative to their seasonal peaks. Alder growth responded positively to increases in river levels during these months, suggesting that the fluctuation in hyporheic flow plays a large part in either alleviating or exacerbating drought stress, especially on lower terraces where the availability of subsurface water is greater. The susceptibility of alder growth to drought stress was heightened with increasing terrace elevation, due to the greater distance to hyporheic flow. The long-term meteorological and hydrologic trends in this region suggest that drought will become more common and severe in this region, resulting in reductions in alder-mediated ecosystem N inputs through further growth suppression, drought stress, and, perhaps, vulnerability to disease infection.