



Development of *Alnus tenuifolia* stands on an Alaskan floodplain: patterns of recruitment, disease and succession

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Summary

1. We investigated the population dynamics of the keystone symbiotic N-fixing species *Alnus tenuifolia* (thinleaf alder) and the patterns of primary succession on the Tanana River floodplains of interior Alaska, USA. The goals of this study were to characterize (i) the variation in the population structure of thinleaf alder and its influence on ecosystem function; (ii) the role of a fungal disease outbreak in driving the population dynamics of thinleaf alder; (iii) the patterns of landscape-scale thinleaf alder recruitment; and (iv) the variation in successional pathways across the landscape.
2. Soil N concentrations and pools increased tenfold with thinleaf alder stand age due to the accumulation of N-rich organic material. Alder stem density varied threefold among early successional stands, and was directly related to soil N.
3. The current outbreak of a fungal disease caused widespread branch dieback and mortality of alder. Young stems were disproportionately susceptible to disease-induced mortality. Overall disease incidence and mortality of young stems were positively related to alder stem density.
4. Thinleaf alder age structures revealed that landscape-scale recruitment was pulsed over time.
5. Multiple pathways of primary succession were found using indirect gradient analysis and associated environmental characteristics were described.
6. *Synthesis.* The population dynamics of thinleaf alder and the inter-relationship with disease-driven disturbance can strongly influence soil N accumulation and ecosystem function in primary succession on an active glacial floodplain. The temporal pattern of thinleaf alder recruitment across the landscape appears to reflect the influence of the hydrologic regime on silt bar development and alder dispersal limitation and population dynamics. Differential life history traits explain the predominant successional pathway, but an alternative successional pathway suggests this pattern can be altered by stochastic events, disturbance, environmental variation or other factors.

Key-words: alder, *Alnus incana*, boreal forest, disease, nitrogen fixer, plant population and community dynamics, population dynamics, primary succession

Introduction

The floodplain landscape is a complex, dynamic mosaic shaped by interactions between disturbance and succession (Kalliola *et al.* 1991; Malanson 1993). Hydrologic processes structure the physical environment of active floodplains through erosion and deposition, thereby controlling the template for plant establishment. The timing, magnitude and scale of fluvial disturbance determine the overall pattern of flood-

plain colonization (Bendix & Hupp 2000; Cooper, Andersen & Chimner 2003; Dixon 2003). Variability in disturbance regimes and successional pathways is intrinsic to most systems (Walker & del Moral 2003), and for floodplain landscapes, the distribution and abundance of plant communities shifts with time as the variation in river discharge interacts with processes of succession (Hughes 1997; Whited *et al.* 2007).

The initial colonization pattern is an important determinant of successional trajectory during primary succession, and factors influencing the arrival, establishment and survival of species have long-term consequences for vegetation

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development and ecosystem function (Egler 1954; Noble & Slatyer 1980; Walker & Chapin 1987). Life-history traits related to reproduction, dispersal, growth and stress tolerance affect the colonizing ability of a species and strongly influence observed patterns of succession (Drury & Nisbet 1973; Glenn-Lewin 1980; Noble & Slatyer 1980; Walker, Zasada & Chapin 1986). Differences in landscape context (e.g. proximity to propagule source) influence the ability of a species to colonize and can contribute to variation in successional trajectories (Fastie 1995; Lanta & Lepš 2009; del Moral, Saura & Emenegger 2010). There is also a large stochastic element to community assembly – for example, the timing of seed arrival in relationship to suitable conditions for germination (Horn 1976; Walker & Chapin 1987; del Moral, Titus & Cook 1995; Dixon 2003; Robbins & Matthews 2009). Differential population-level responses to the changing competitive environment and to disturbances like flooding, disease outbreaks and herbivory further influence the course of succession (Peet & Christensen 1980; Cooper, Andersen & Chimner 2003; Bouchard, Kneeshaw & Bergeron 2006; Taylor & Chen 2010). Thus, life history traits constrain the realm of successional possibilities, whereas stochastic factors, landscape context and disturbance promote successional variation.

The functional role of N-fixers is especially important in primary succession where productivity is N-limited (Marrs *et al.* 1983; Vitousek 1990; Walker & del Moral 2003). By altering the supply of a limiting nutrient, N-fixers can strongly influence community- and ecosystem-level processes (Van Cleve, Viereck & Schlentner 1971; Vitousek & Walker 1989; Vitousek & Howarth 1991; Chapin 2003; Walker *et al.* 2003; Hughes & Denslow 2005). Variations in the presence, abundance and persistence of N-fixers can leave legacies that persist beyond their lifetimes (Hobbie 1992; Mitchell & Ruess 2009). For example, studies of invasive N-fixers have shown that the population dynamics of a single species can mediate variation in ecosystem function and community structure at the landscape scale (Vitousek & Walker 1989; Hughes & Denslow 2005). In interior Alaska, *Alnus incana* ssp. *tenuifolia*, hereafter *Alnus tenuifolia* (thinleaf alder), commonly dominates early successional floodplain stands where dense thickets can contribute $> 100 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to the initially nutrient-poor alluvial soils, substantially altering soil chemistry, microbial processes and plant nutrient availability (Van Cleve, Viereck & Schlentner 1971; Klingensmith & Van Cleve 1993; Uliassi & Ruess 2002).

Climatic constraints on the biota of the northern boreal forest create limited redundancy within vascular functional groups, magnifying the importance of species effects of potential successional dominants on ecosystem properties. Here, we investigate the population dynamics of thinleaf alder, a keystone symbiotic N-fixing species, and the patterns of primary succession on the Tanana River floodplains of interior Alaska. The goals of this study were to characterize (i) the variation in the population structure of thinleaf alder and its influence on ecosystem function; (ii) the role of a fungal disease outbreak in driving the population dynamics of thinleaf alder; (iii) the patterns of landscape-scale thinleaf

alder recruitment; and (iv) the variation in successional pathways across the landscape.

Materials and methods

STUDY AREA

The study area encompasses an 80 km reach of the Tanana River floodplain in interior Alaska, USA, between Fairbanks (64.9°N, 147.9°W) and Nenana (64.5°N, 148.7°W) (see Fig. S1 in Supporting Information). 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 continued deposition creates new silt bars and increases terrace elevations. A common sequence of primary succession on this floodplain shifts in dominance from *Salix* to *A. tenuifolia*, to *Populus balsamifera*, to *Picea glauca*; but the dominant successional pathway varies among interior Alaskan floodplains (Viereck, Dyrness & Foote 1993; Hollingsworth *et al.* 2010). 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.* 1993). Mean annual precipitation is 269 mm in Fairbanks, and average annual temperature is -3.3°C , with mean daily temperatures ranging from -24.9°C in January to 16.4°C in July.

VEGETATION SAMPLING AND LABORATORY PROCEDURES

In 2006, we established 45 transects in alder-dominated stands that represented a wide range of stand structure. Our purpose was to understand the variation in thinleaf alder community dynamics; therefore, we haphazardly chose sites with the only criterion being thinleaf alder dominance and without any particular regard for alder density or vegetation composition that may have biased our conclusions regarding stand development. Each $50 \times 5 \text{ m}$ transect, set perpendicular to the course of the river, was subdivided into ten $5 \times 5 \text{ m}$ plots, which, after initial vegetation sampling, were pooled into zones of homogeneous vegetation (see below).

Community structure

Within each $5 \times 5 \text{ m}$ plot ($n = 450$ plots), the d.b.h. of all trees and shrubs $> 2 \text{ m}$ tall were measured and the stem density and basal area of each species were calculated. All woody plants $< 2 \text{ m}$ were counted in one $1 \times 1 \text{ m}$ quadrat randomly placed within each plot. The percentage cover of all herbaceous species in each quadrat was estimated visually. The presence or absence of moose and snowshoe hare faeces in each quadrat were recorded as measures of potential herbivory.

After initial vegetation sampling, multivariate analyses of community structure for each transect were conducted in order to aggregate plots 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 the abundance or cover 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). Vegetation nomenclature follows Hultén (1968).

Stand age and age structures

Twenty-eight sites were randomly selected to represent the full range of terrace heights, and presumably, surface ages. We collected disks at ground level from up to 10 live alder stems for each of three size classes based on d.b.h. (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 measured on a sliding bench micrometer to a precision of 0.001 mm. Three to four radii were sampled from each disk and averaged. Stand age was estimated by the age of the oldest alder in each site.

Disease survey

At each site, every alder ramet > 2 m tall was scored for severity of canker infection ($n = 11\,481$ stems). Alder stems were classified as either: (i) *live without canker* – no visible cankers; (ii) *live with canker* – visible cankers on branches or the main ramet; (iii) *dead without canker* – standing dead with no visible cankers; or (iv) *dead with canker* – standing dead with visible cankers. All of the standing dead stems we sampled were infected with canker.

Foliar chemistry

In mid-July 2007, alder leaf samples were collected from a randomly chosen subsample of 38 sites. Leaves from five trees (pooling four leaf samples per tree) were sampled at each site ($n = 190$ pooled leaf samples). Whole leaves, with petioles removed, were oven-dried at 45 °C, ground, and analysed for C, N and P. Total C and N were analysed with a LECO TruSpec CN Analyzer (St. Joseph, MI, USA), and total P was analysed 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 levelling at 5-m intervals along each transect, and averaged for each site. Hourly Tanana River gage height readings from the US Geological Survey (USGS) site in Fairbanks (#15485500) were used as benchmark elevations (<http://waterdata.usgs.gov/nwis/>). The gage datum at this USGS site was 121.92 m a.s.l., and mean summer gage height (May–September) from 1991 to 2007 was 6.42 m. Terrace height is reported as the elevation above the mean summer gage height.

Soil properties

The surface litter layer was removed prior to soil sampling in each site. Five soil cores (2 cm diameter by 10 cm deep) were collected and pooled from each site. The thicknesses of surface and buried organic layers (ranging from 0 to 4 buried layers) were recorded before organic and mineral layers were combined for chemical analyses. We refer to the total thickness of all organic layers as organic depth, and the thickness of the surface organic layer as surface organic depth. Soils were oven-dried at 45 °C, 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 analysed following the methods for the plant samples. 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 at three evenly spaced points spanning the length of each site (Lemmon 1956).

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 & Mefford 1999). Statistical significance was determined at $\alpha = 0.05$, except as otherwise noted below. The raw datasets used for these analyses are available online at http://www.lter.uaf.edu/data_b.cfm.

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 analyse relationships among alder population structure, environmental variables and foliar leaf nutrient status, and used partial correlation analyses to determine the inter-correlations among predictor variables.

Alder population dynamics and disease

Landscape-level recruitment patterns were characterized using the measured age distribution of live alder stems across all sites. Because dead stems were not included, this age distribution underestimates actual recruitment. A historical sequence of aerial images from 1949 to 2007 was used to visually characterize the spatial aspect of shrub establishment on silt bars. Visual estimates of % shrub cover and % of available colonizable area were made at a subsample of sites for each year that imagery was available.

Site-level patterns of alder establishment and disease-related mortality were characterized through age reconstructions. Relationships between stem diameter and age of live stems were applied to the size structure of both living and standing dead stems to reconstruct age distributions. Standing dead stems with evidence of canker were assumed to be recently killed by the current disease outbreak. Dead stems that were no longer standing were not included in this analysis; therefore, recruitment was likely underestimated. 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. Relationships between stand structure and canker infection were further analysed using logistic regression.

Community structure

Plant community structure was assessed through indirect gradient analysis using DCA (Hill 1979; Gauch 1982). Stem densities of trees and shrubs > 2 m in height were grouped by d.b.h. 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. Percentage 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 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. Correlations between the abundance of young successional dominants and the surface organic depth were conducted to infer whether recruitment was limited by the development of a forest floor.

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 (McCune & Grace 2002) 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.

Results

VARIATION IN ENVIRONMENTAL CHARACTERISTICS

Stand ages ranged from 13 to 56 years (Table S1) and were correlated with a number of physical and chemical environmental characteristics (Table S2). Stand age, organic depth and terrace height emerged as important predictors of soil chemical properties (Table S2). A partial correlation analysis 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). 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 (8.2–5.5) (Table S1) and declined significantly with stand age (Table S2). 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.

Concentrations and pool sizes of soil C varied by an order of magnitude across all sites, with C concentrations ranging from 0.56 to 8.88% of total dry mass and pool sizes ranging from 502 to 4663 g C m⁻² (Table S1). Soil C concentration and pool size both increased with stand age (Table S2). Organic depth was a good predictor of soil C concentration and could be used as a covariate ($r^2 = 0.67$, $P < 0.0001$).

Soil N varied approximately tenfold across all sites, with concentrations ranging from 0.03 to 0.45% and pool sizes ranging from 26 to 235 g N m⁻² (Table S1). Soil N concentration and pool size both increased with stand age (Table S2; Fig. 1). Soil N (%) was correlated with organic depth ($r^2 = 0.63$, $P < 0.0001$) and soil C (%) ($r^2 = 0.97$, $P < 0.0001$), suggesting a 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 S1). Soil P concentration was not related to stand age (Table S2), although soil P pool size significantly decreased with time (Table S2, Fig. 1). The increase in soil N (%) drove an increase in soil N:P ratios with time (Table S2). Mean soil N:P (2.66) was low, while mean foliar N:P (19.69) of alder was consistently above the Redfield ratio (Table S1).

Alder stem density in new stands (< 25 years old) varied threefold (9600–27 200 stems ha⁻¹), and was strongly related to soil nutrient status. Soil N pool size and concentration increased linearly with alder stem density in young sites (Fig. 2). We did not detect a relationship between alder stem density and soil P pool size ($P > 0.05$).

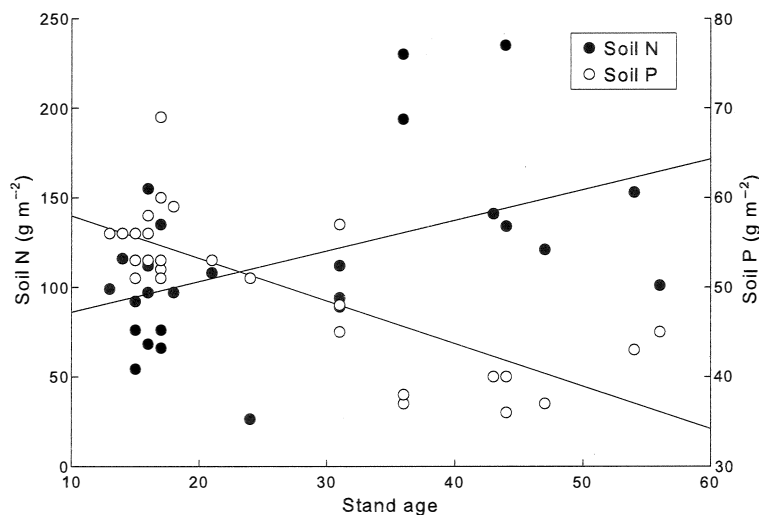


Fig. 1. Correlations of soil nutrient pool sizes with age of thinleaf alder stands. Pool sizes are to a depth of 10 cm, $n = 28$ sites. (Soil N: $y = 69.0 + 1.7x$, $r^2 = 0.24$, $P = 0.0087$; Soil P: $y = 62.75 - 0.48x$, $r^2 = 0.60$, $P < 0.0001$).

PATTERNS OF THINLEAF ALDER RECRUITMENT,
DISEASE INCIDENCE AND MORTALITY

Sixty percent of the sites were colonized after 1983 (< 25 years old at time of sampling), and the vast majority of these sites were colonized in the early 1990s. Older stands (> 25 years of age) that were initially colonized by alder between 1951 and 1980 comprised 40% of the stands sampled for age. The age structure of live alder stems across all sites suggests a recent pulse in alder recruitment (Fig. 3). Alder recruitment increased from 1983 to a peak in 1993, and subsequently declined until 2004. The rate of decline, however, was probably slower than it appears, because the sample does not include stems < 2 m tall and

survivorship of young stems was reduced due to disease. Recruitment into new stands accounted for the majority of the recent pulse in alder abundance, although recruitment into old stands also increased during this period. There may have also been a pulse in recruitment that peaked around 1970, but this is less clear due to the expected mortality of older stems. This age distribution does not account for stems that have died, and therefore underestimates past recruitment.

Historical sequences of aerial imagery of a subsample of new alder stands were visually analysed, with one representative stand pictured in Fig. 4. 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

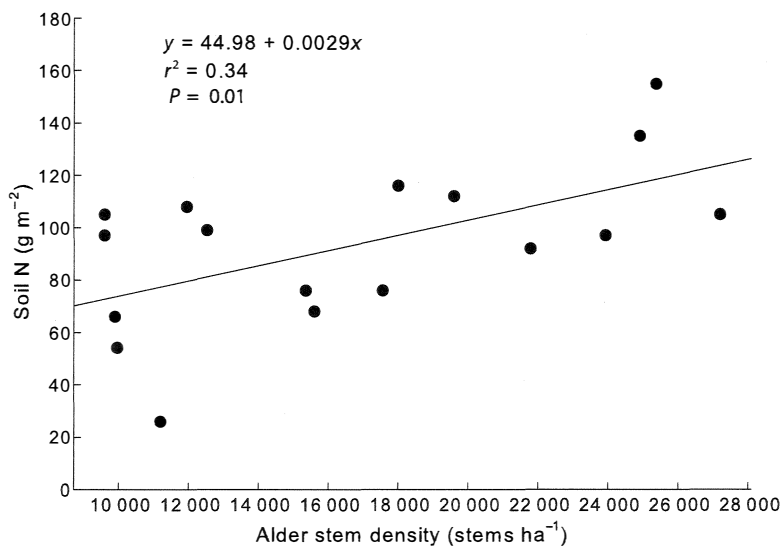


Fig. 2. Regression of alder stem density versus soil N pool size in all new stands (< 25 years old), $n = 17$ sites.

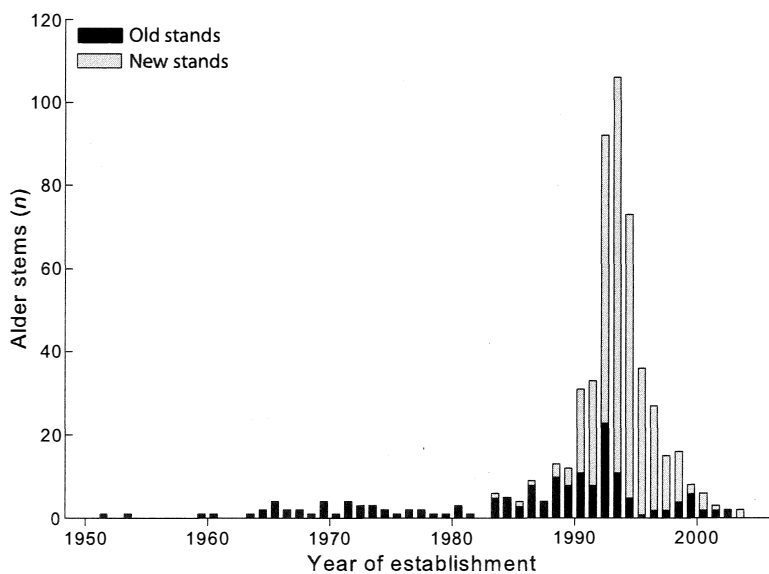


Fig. 3. Age distribution of thinleaf alder in old and new stands at the landscape scale, based on the measured ages of all live stems sampled.

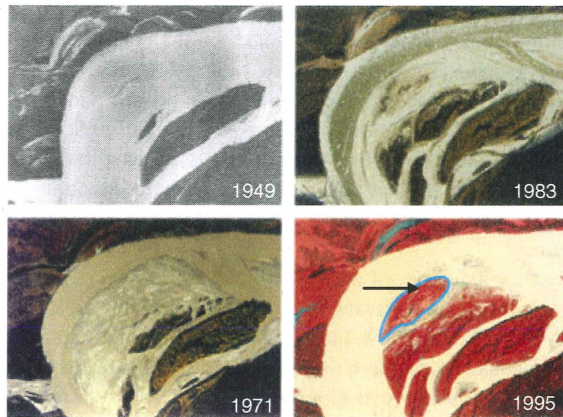


Fig. 4. Sequence of aerial imagery showing development of a thinleaf alder stand on an aggrading silt bar. The area outlined in blue is currently dominated by thinleaf alder. Note that the images from 1971 and 1983 were captured when river levels were very low, exposing parts of the silt bar that were likely underwater for most of the growing season.

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 silt bar area available for further colonization. From 1998 to 2007, shrub cover expansion was minimal. By 2007, nearly 100% of the colonizable silt bars were covered with vegetation.

Significant relationships between alder stem diameter and age were described by either linear or quadratic regression equations for 25 sites (Table S3). These equations were used to predict site-level alder age distributions of live and dead stems based on diameter measurements of standing stems. The resulting age reconstructions show several patterns of alder recruitment and recent disease-related mortality (Figs 5 and 6). Among the new stands (< 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 declining with time (Fig. 5a–c). Disease-related mortality was high in these stands, and survivorship of young stems was disproportionately low (Fig. 5a–c). The pattern of stand development in the remaining new stands (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. 5d). Disease-related mortality was relatively low in these stands (Fig. 5d). Some of the age distributions in the old stands were wide, with alder stem recruitment continuing for up to 53 years (Fig. 6a). Most of the age distributions in the old stands (6 of 9 sites) had a greater proportion of younger age classes, indicative of self-replacing stands (Fig. 6a–c). A minority of the age distributions in the old stands had a greater proportion of older age classes (2 of 9 sites), suggesting stand decline (Fig. 6d). One of the older

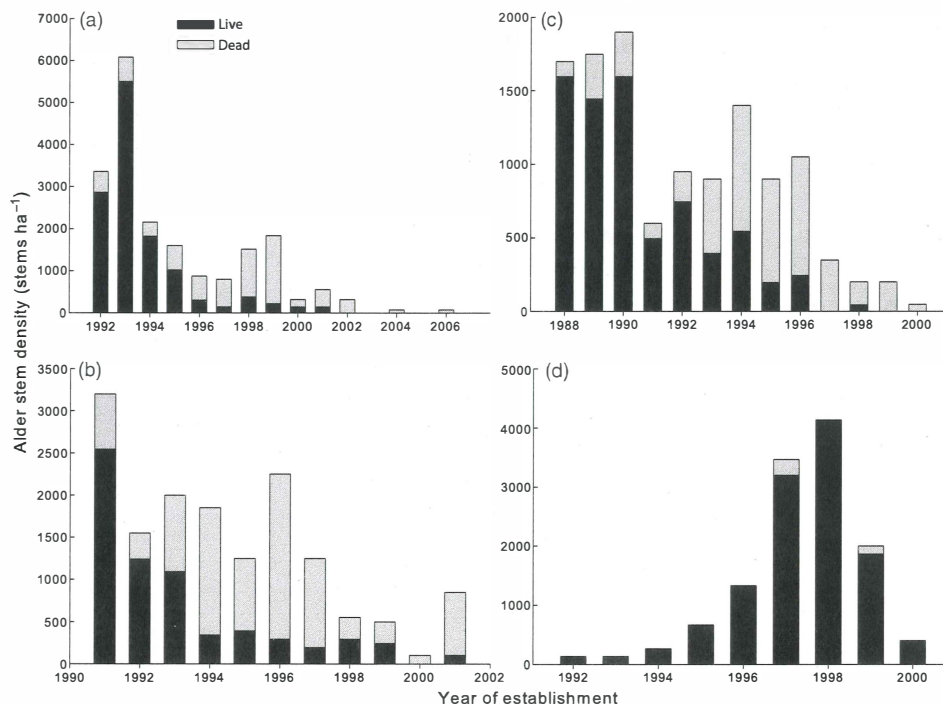


Fig. 5. Age reconstructions of thinleaf alder stems in representative new stands (< 25 years old), based on regression analyses between size and age. Note differences in scale.

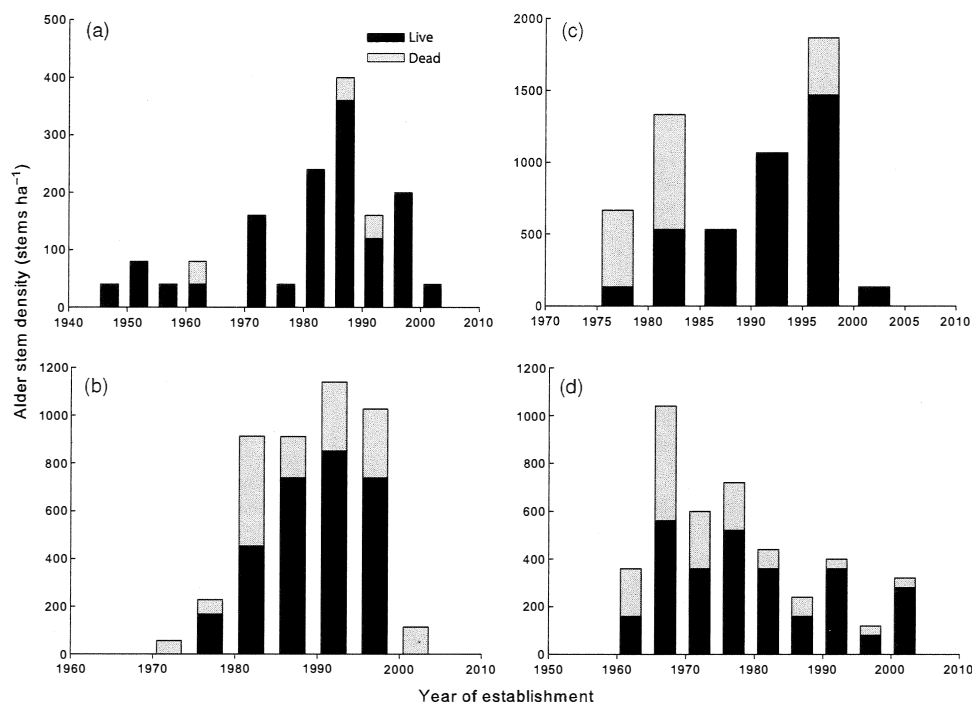


Fig. 6. Age reconstructions of thinleaf alder stems in representative old sites (> 25 years old), based on regression analyses between size and age, grouped by 5-year age classes. Note differences in scale.

sites had a bimodal age distribution (data not shown). When age-related patterns of disease mortality were found in the older stands, older stems tended to be more susceptible (Fig. 6c,d).

Of all standing alder stems sampled, 70% were infected with canker and 29% were dead with canker. Incidence of canker colonization was positively related to alder stem density ($r^2 = 0.05$, $F_{(1,86)} = 4.79$, $P < 0.03$). Incidence of canker colonization tended to increase with stem diameter; however, canker-induced mortality tended to decrease with stem diameter, and presumably age (Fig. 7). A logistic regression confirmed that the probability of canker-induced stem mortality decreased from 0.87 to 0.25 with increasing stem size ($\chi^2_{(1,1481)} = 371.27$, $P < 0.0001$). The probability of canker-induced mortality for 1- to 10-year-old alder stems (from age reconstructions) was also positively related to alder stem density (Fig. 8, $\chi^2_{(1,821)} = 91.3$, $P < 0.0001$).

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 for 14% (Fig. 9). The length of Axis 1 was 2.95 SD units, indicating a complete change in species composition and size structure across the sites (McCune & Mefford 1999).

Changes in community structure along Axis 1 were strongly correlated with stand age and a suite of associated environ-

mental variables (Table S4; Fig. 9). 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. Leaf N:P was not correlated with either Axis 1 or Axis 2 (Table S4).

Small (< 2 m tall) willows and balsam poplar ranked low on Axis 1, followed by small alder, then white spruce (Table S5). 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 S4; Fig. 9). The relationships between the depth of the surface organic layer and the abundance of small stems of *Salix* spp., *P. balsamifera*, *A. tenuifolia* and *P. glauca* were analysed to infer whether the development of a forest floor inhibits stem initiation, as suggested by experimental studies. Stem densities of young willow and poplar declined as surface organic depth increased ($P < 0.0001$ and $P < 0.05$, respectively), while alder and spruce recruitment were not significantly correlated with surface organic depth ($P > 0.05$). 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 to > 4 cm), to white spruce (0–3 to > 4 cm) (Table S5). Alder stem densities and relative dominance declined while white spruce stem densities and relative dominance increased along Axis 1 and with stand age (Table S4; Fig. 9).

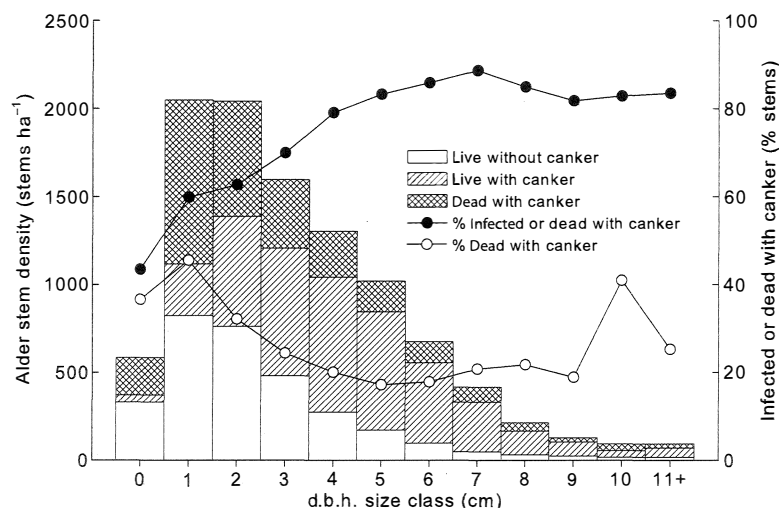


Fig. 7. Patterns of disease incidence and disease-related mortality by alder size class. Bars represent stem density and levels of canker incidence and related mortality; dots represent the % of ramets infected or dead with canker. $n = 11\,481$ stems.

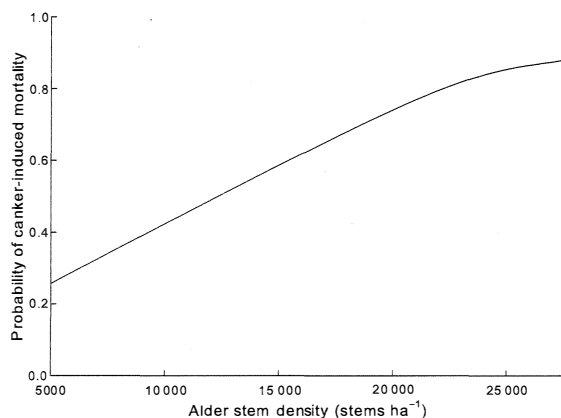


Fig. 8. Logistic probability plot of canker-induced mortality of 1- to 10-year-old alder stems by site-level alder stem density. Based on predicted age reconstructions and canker survey data, ($n = 821$, $\chi^2 = 91.3$, $P < 0.0001$).

Equisetum variegatum cover was negatively correlated with Axis 1 (Table S4; Fig. 9), and was associated with other herbaceous species with low Axis 1 scores such as *Solidago canadensis*, *Achillea sibirica*, *Equisetum pratense* and *Equisetum hyemale* (Table S5). Total moss cover as well as shrub abundance significantly increased along Axis 1, primarily due to *Rosa acicularis* and *Rubus idaeus* (Table S4; Fig. 9). Table S5 details the rankings and scores along Axis 1 for all other species.

Axis 2 was not correlated with stand age or any environmental variables measured (Table S4). Densities of large balsam poplar (> 4 cm d.b.h.) varied widely along Axis 2 (Fig. 9). Balsam poplar of all sizes were entirely absent from almost 25% of the sites that had an emerging white spruce canopy. Recruitment of small (< 2 m tall) willow, thinleaf alder, balsam poplar and white spruce were unrelated to Axis 2 (Table S4). The decrease in large balsam poplar densities along

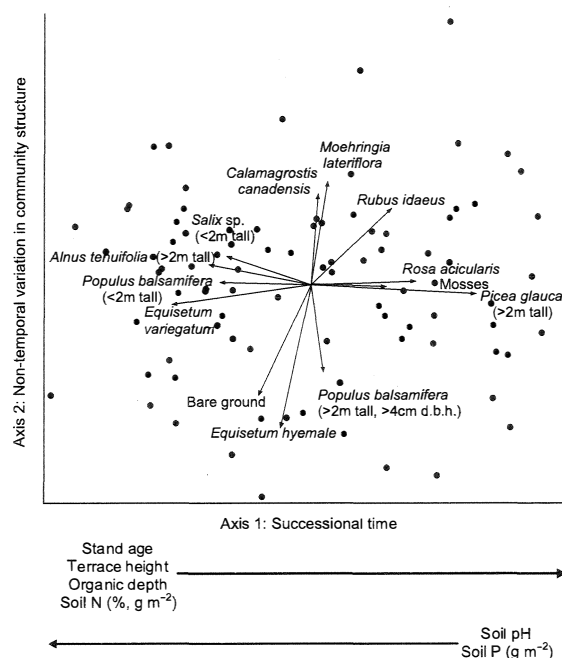


Fig. 9. Detrended correspondence analysis ordination of thinleaf alder community structure and relationships with selected site characteristics. Points represent site community structure, $n = 89$ sites. Vectors (scaled 150%) represent the direction and strength of correlations. Arrows below Axis 1 show the direction of the relationships between community structure and site characteristics.

Axis 2 was associated with an increase in understorey vegetation cover (Table S4; Fig. 9). The abundance of *R. idaeus* (shrub), *Moehringia lateriflora* (forb) and *Calamagrostis canadensis* (graminoid) significantly increased with Axis 2, while *E. hyemale* (forb) cover declined (Table S4; Fig. 9). The abundance of the *R. idaeus* was inversely correlated with canopy cover ($r_s = -0.26$, $P = 0.01$).

Logistic regressions showed that presence of moose faeces 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 faeces 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 ($P = 0.95$).

Discussion

INFLUENCE OF ALDER POPULATION STRUCTURE ON SOIL NITROGEN

This study confirmed the strong influence of thinleaf alder on soil N accumulation at the site-level throughout successional time on the Tanana River floodplains (Van Cleve, Viereck & Schlentner 1971; Walker & Chapin 1987; Van Cleve *et al.* 1993; Uliassi & Ruess 2002); furthermore, we found that wide variability in alder population structure contributed to the spatial variation in soil N accumulation across the landscape. Alder stem density varied nearly threefold (9600–27 200 stems ha^{-1}) and accounted for a linear increase in mean soil N pool size from approximately 70–120 g N m^{-2} across the newly established stands (< 25 years old). Studies of invasive N-fixers have shown that the population dynamics of a single species can mediate variation in ecosystem function at the landscape level (Vitousek & Walker 1989; Hughes & Denslow 2005). Our study suggests that variability in the population structure and dynamics of a native N-fixer within a successional stage could have important long-term effects on ecosystem function. The mediation of the impact of alder on soil N accumulation by alder stem density underscores the importance of the temporal and spatial patterns of recruitment and mortality that control the variation in alder abundance.

When abundant in early primary successional seres, symbiotic N-fixers often alter productivity and the competitive balance between species by increasing the N supply to N-limited systems (Vitousek 1990; Walker & del Moral 2003). The net effect of N-fixers on other species usually depends on the balance of both competitive and facilitative interactions (Walker & Chapin 1986, 1987; Walker *et al.* 2003). For example, N-fixers may either inhibit the establishment and growth of other plant species through competition for light and soil resources or facilitate their growth by increasing soil N supply. Within the *Alnus* genus, both facilitation and competition have been observed. A net facilitative effect of *Alnus sinuata* on the nutrient status and growth of *Picea sitchensis* seedlings was found on a glacial moraine (Chapin *et al.* 1994); while a net competitive effect of thinleaf alder on willow, balsam poplar and white spruce seedlings was found in the Tanana River floodplain (Walker & Chapin 1986). The balance of facilitative and competitive interactions can be complex and dynamic (McCook 1994; Berkowitz, Canham & Kelly 1995; Walker *et al.* 2003). For example, dense alder thickets may have a negative effect on seedling growth or establishment beneath

the canopy, while the additions to soil N may have a positive effect on mature trees, or a legacy effect that lasts beyond the lifetime of the individual plants.

ALDER POPULATION DYNAMICS, DISTURBANCE AND LONG TERM CHANGE

Our disease survey data indicate that the outbreak of a fungal stem canker (*Valsa melanodiscus*) affecting thinleaf alder is widespread and severe in the middle Tanana River floodplains and is dramatically altering the population structure of alder stands. At least 70% of all standing alder stems were infected, and nearly 30% of all stems were dead with evidence of the disease. Young stems were disproportionately susceptible to canker-induced mortality, and the proportion of young stems killed by disease and the incidence of canker colonization overall were both positively related to alder stem density. Considering the strong direct relationship between alder density and soil N, and the negative effect of stem canker on N-fixation rates of alder (Ruess *et al.* 2009), the immediate effects of this disturbance will be to reduce total ecosystem N inputs. The widespread alder mortality may allow for the competitive release of the other woody species growing beneath or emerging from the alder canopy, potentially accelerating the rate of succession. Dramatic shifts in species composition have resulted from epidemics of introduced (Bradshaw & Miller 1988; Foster *et al.* 1992; Agrawal & Stephenson 1995; Abrams, Orwig & Dockry 1997) and native pathogens (Holah, Wilson & Hansen 1993; Hansen & Goheen 2000) in secondary succession, but the role of disease-driven disturbance in early primary succession and among dominant N-fixers remains relatively unexplored (Walker & Chapin 1987).

Disturbances caused by plant pathogens can drive the population dynamics of host species and mediate successional processes; and the density of host plants can, in turn, influence disease incidence and severity (Burdon & Chilvers 1982; Gilbert 2002). A recent landscape-wide pulse in alder recruitment preceded the outbreak of this pathogen, which, like many fungal diseases, is dependent on host density, in part due to increased host–pathogen encounter rates (Burdon & Chilvers 1982; Carlsson & Elmqvist 1992; Lively *et al.* 1995; Garcia-Guzman *et al.* 1996). The landscape-scale increase in high-density alder stands may have facilitated the spread of this fungal disease, which would suggest that multiple disturbance regimes are interacting to influence the abundance of this key N-fixer and its impact on ecosystem properties.

The rapid recruitment of alder into newly established stands accounts for the majority of the increase in alder abundance that peaked in the early 1990s in the middle Tanana. This pulse in recruitment appears to reflect a response to the fluvial disturbance regime that led to the development of colonizable silt bars, and to the dispersal and population dynamics of alder. We visually compared the changes in bare versus colonized silt bar area between 1978 and 1998 for our study area using the Tanana River Erosion Study GIS map, and found that bare silt bars were dramatically more abundant in 1978, and the majority of this new silt bar area had been colonized by 1998

(<http://gis.tananachiefs.org/maps/erosion/viewer.htm>). Fluctuations in river discharge determine rates of silt bar formation and strongly influence the structure and dynamics of floodplain plant communities (Bendix & Hupp 2000; Cooper, Andersen & Chimner 2003; Dixon 2003; Whited *et al.* 2007). A major 100-year flood that occurred in 1967 on the Tanana River was followed by *c.* 15 years of relatively low discharge until the 1980s to early 1990s, which were characterized by relatively high discharge with the longest sustained flood period on record (Ott *et al.* 2001). The timing of the 1967 flood and the subsequent period of high discharge may have led to the aggradation of terraces that were then colonized by alder. Initial colonization patterns are also a function of seed availability, which is influenced by the proximity to a seed source, seed production and seed dispersal (Harper 1977; Chambers & MacMahon 1994). When the initial seed source is sparse or distant, future recruitment may lag until early colonists mature and produce seed, becoming the nucleus of future stand development. Our site-level age reconstructions showed the rapid establishment of most new alder stands, and the aerial imagery showed the spatial pattern of the outward expansion of alder from seed trees. Our sequence of aerial imagery of developing silt bars emphasizes the influence of flooding patterns and terrace aggradation on the distribution of colonizing shrubs, and suggests that the recent peak in alder recruitment was influenced by increases in colonizable area interacting with the dispersal and population dynamics of alder.

It is unknown whether this pulse in alder recruitment signifies a change in the abundance of alder relative to other species in early succession. Other studies have concluded that the preferential browsing of willow by moose alters the competitive relationship between willow and alder, thereby accelerating the establishment and dominance of alder (Kielland & Bryant 1998) and increasing the relative abundance of alder communities (Butler & Kielland 2008). Given the rapid tripling of moose densities in this area from the 1980s to the present (Gasaway *et al.* 1983; Boertje, Valkenburg & McNay 1996; Young 2002, 2004), the increased browsing pressure on willow may have indirectly facilitated the establishment and dominance of alder.

VARIATION IN SUCCESSIONAL PATHWAYS

Most of the variation in plant community structure observed within thinleaf alder stands was strongly correlated with stand age and a suite of physical, chemical and biological variables linked to processes associated with succession and alder stand development – the rise in terrace height above the river, the accumulation of organic material, the decline in soil pH and the increase in soil N. In our community ordination, the strong relationship of Axis 1 with these environmental variables and stand age indicates that this axis represents a gradient of community structure across successional time and shows the dominant successional pathway seen on this landscape. The strong temporal patterning along Axis 1 of this ordination allowed us to visualize the variation in successional patterns in Axis 2.

Interspecific differences in seed weight, dispersal capabilities, germination requirements and flooding tolerance can explain the most common sequence of colonization (Walker, Zasada & Chapin 1986). Abundant willow and poplar recruitment were limited to very early successional sites with mineral seedbeds, while alder and spruce recruitment occurred throughout succession. Willow and poplar often colonize early via wind dispersal of their lightweight seeds. Alder recruitment was not related to surface organic depth, perhaps demonstrating the importance of both sexual and vegetative reproduction, or the ability of alder seeds to germinate without a mineral seedbed. Spruce recruitment was also unrelated to surface organic depth; instead, recruitment increased with mature spruce density, reflecting the importance of a local seed source to this heavy-seeded species with substantial dispersal limitations. After initial colonization, differences in growth rate and longevity further explain the common sequence of successional dominance from willow, to alder, to poplar, to white spruce. The ranking of the mature successional dominants along Axis 1 followed the sequence outlined by Viereck, Dyrness & Foote (1993); however, variation from the predominant successional pathway is suggested by the community patterns along Axis 2. A conceptual diagram of these successional patterns is presented in Fig. 10.

Because mature balsam poplar density varied widely along Axis 2, independent of stand age, and the recruitment of young balsam poplar was consistently low among these sites, we propose that the absence of an emerging poplar-dominated stage characterizes an alternative successional pathway. Balsam poplar was entirely absent from almost 25% of the sites that had an emerging white spruce canopy. The variability in pop-

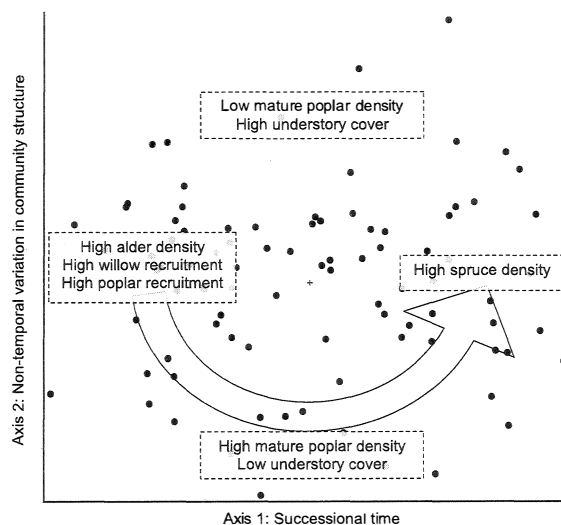


Fig. 10. Conceptual diagram of successional patterns within thinleaf alder stands overlain onto detrended correspondence analysis ordination. The text boxes describe general community characteristics for each region of the ordination. The arrow shows the predominant successional pathway described by Viereck, Dyrness & Foote (1993). The 'low poplar density' community type represents a stage from an alternative successional pathway.

lar density could be the result of a number of factors that influence its dispersal, establishment, or survival. *Populus* species are particularly sensitive to the timing and magnitude of river discharge relative to seed dispersal and germination phenology (Fenner, Brady & Patton 1985; Walker, Zasada & Chapin 1986; Scott, Auble & Friedman 1997; Mahoney & Rood 1998; Dixon 2003). Due to the extremely short period of viability of poplar seeds, successful establishment depends on the co-occurrence of dispersal with the recession of high spring water levels. The spatial heterogeneity in poplar establishment could be linked to small differences in topography that have large effects on the local influence of river discharge (Cooper, Andersen & Chimner 2003; Whited *et al.* 2007), or other stochastic factors like wind direction that influence dispersal (Walker, Zasada & Chapin 1986; del Moral, Titus & Cook 1995; Lanta & Lepš 2009). The spatial variability in balsam poplar recruitment further suggests that recruitment of this species may be particularly sensitive to temporal changes in the disturbance regime.

Among sites with low poplar density, there was no consistent pattern in white spruce abundance, and because white spruce recruitment may occur throughout succession, it is unclear whether some of these sites will eventually transition to a closed white spruce-dominated stage or diverge into a more open stand type. The differences in the structure of the understorey community between sites with high and low poplar density suggest that divergence is a possibility. The communities associated with high mature poplar stem density (predominant pathway) were characterized by minimal herbaceous cover, while the communities associated with low poplar stem density (alternative pathway) were distinguished by a relatively lush understorey, in particular, increased abundance of *R. idaeus* (shrub) and high % cover of *C. canadensis* (graminoid) and *M. lateriflora* (forb). Species-specific responses to canopy cover suggest a tendency for the sites with low poplar density to have greater light availability than their counterparts. Reduced leaf litter and increased light in the sites with low poplar density may have facilitated the establishment and growth of shrubs, graminoids and forbs, which may indirectly inhibit the establishment and growth of tree species. *Calamagrostis canadensis* is an especially competitive species which has been found to inhibit the establishment of white spruce and suppress the growth of deciduous trees in the boreal forest (Liefers, MacDonald & Hogg 1993; Landhäusser & Liefers 1998). Competition with the highly vegetated understorey could delay successional turnover or alter the trajectory of succession into an open shrub–graminoid dominated community.

The likelihood of multiple pathways in early primary succession is widely recognized (Fastie 1995; Walker & del Moral 2003; Hollingsworth *et al.* 2010; del Moral, Saura & Emenegger 2010); however, only a singular successional pathway has been thoroughly described and well-studied for the Tanana River floodplains (Viereck, Dyrness & Foote 1993). The existence of multiple pathways has important implications for ecosystem function in the boreal forest, where each of the potential dominant species can strongly influence ecosystem processes. This study helped elucidate some of the variability

in primary successional patterns found on the floodplain landscape, and two distinct pathways in early to mid-succession were identified. The predominant successional pathway found here supports the idea that life history traits largely account for the dominant pattern of primary succession (Walker, Zasada & Chapin 1986); but the alternative pathway suggests that this general pattern can be altered by other processes.

Conclusions

This study confirmed the strong influence of thinleaf alder on soil N accumulation in primary succession on the middle Tanana River floodplain, and further, we showed that ecosystem effects of this symbiotic N-fixer varied across the landscape depending on processes that control alder abundance. We demonstrated how the outbreak of disease caused by the fungal pathogen *V. melanodiscus* has substantially altered the population structure of thinleaf alder stands. The immediate effect of this disease-driven disturbance will be to reduce total ecosystem N inputs through increased alder mortality and reduced N-fixation rates, and longer-term effects on successional processes and ecosystem function are expected. We found evidence of a large landscape-scale increase in thinleaf alder recruitment that may have facilitated the spread of this density-dependent disease. We attribute the pulsed recruitment of alder primarily to the influence of the fluvial disturbance regime on the availability of colonizable silt bars, and to the dispersal and population dynamics of this species. The dynamics of fluvial disturbance, alder dispersal and recruitment, and disease each contribute to the temporal and spatial variation in the abundance of this key N-fixer and, ultimately, its impact on ecosystem properties.

Our plant community analyses revealed that multiple successional pathways are likely operating in early- and mid-primary succession on the Tanana River floodplain. The predominant successional pathway and associated gradient of environmental characteristics were consistent with previous descriptions of floodplain succession (Viereck, Dyrness & Foote 1993); however, we found a notable deviation from this pathway, in which several maturing alder stands were not succeeding to a balsam poplar-dominated stage and were distinct in their highly vegetated understorey communities. It is unclear whether these sites will eventually converge with the predominant pathway to a closed white spruce-dominated stage or if they will diverge into a more open stand type. The predominant successional pathway supports the idea that life history traits largely account for the dominant pattern of primary succession (Walker, Zasada & Chapin 1986), but the alternative pathway suggests that this general pattern can be altered by stochastic events, disturbance, environmental variation or other factors.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Map of study area and transects.

Table S1. Descriptive statistics for site characteristics.

Table S2. Correlations between selected site characteristics.

Table S3. 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.

Table S4. Pearson correlation of selected site and community characteristics with DCA axes.

Table S5. Species scores and ranks for Axis 1 of DCA ordination, by growth form and size class.

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