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Ecology of Invasive *Melilotus albus* on Alaskan Glacial River Floodplains

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Abstract

Melilotus albus (white sweetclover) has invaded Alaskan glacial river floodplains. We measured cover and density of plant species and environmental variables along transects perpendicular to the Nenana, Matanuska, and Stikine Rivers to study interactions between *M. albus* and other plant species and to characterize the environment where it establishes. *Melilotus albus* was a pioneer species on recently disturbed sites and did not persist into closed canopy forests. The relationships between *M. albus* cover and density and other species were site-specific. *Melilotus albus* was negatively correlated with native species *Elaeagnus commutata* at the Nenana River, but not at the Matanuska River. *Melilotus albus* was positively correlated with the exotic species *Crepis tectorum* and *Taraxacum officinale* at the Matanuska River and *T. officinale* on the upper Stikine River. However, the high density of *M. albus* at a lower Stikine River site was negatively correlated with *T. officinale* and several native species including *Lathyrus japonicus* var. *maritimus* and *Salix alaxensis*. Glacial river floodplains in Alaska are highly disturbed and are corridors for exotic plant species movement. *Melilotus albus* at moderate to low densities may facilitate establishment of exotic species, but at high densities can reduce the cover and density of both exotic and native species.

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Introduction

High latitude regions were considered to be relatively immune to establishment of alien plant species due to cold temperatures and short growing seasons, but this perception is changing. Rejmanek and Randall (1994) studied the proportion of alien species in various floras and found the Alaska flora of the early 1960s contained a low proportion of aliens in the flora (10.5%) compared to more tropical areas such as southern Florida (24.1%) and Hawaii (47.7%). However, Carlson and Shephard (2007) determined that the rate of new introductions of alien taxa in Alaska's flora increased from roughly one species per year from 1941 to 1968 to three species per year from 1968 to 2006, mirroring the threefold increase in human population in Alaska since 1968 as well as the increase of goods shipped to the state. Richness of alien plant species at high latitudes may increase further if temperatures warm as predicted by climate models (Meehl et al., 2007).

Alien species are one of the major factors contributing to loss of biological diversity (D'Antonio, 1997), but few studies have been conducted to determine the effects of alien plant species on diversity and ecosystem function of the boreal ecosystem, even though this is the largest terrestrial biome (Pielou, 1988). In one of the few studies of alien plant invasions in the boreal forest, Rose and Hermanutz (2004) found that alien plants were establishing in naturally disturbed areas away from human influence in Gros Morne National Park (Newfoundland, Canada). Forests, riparian areas, fens, and meadows were most susceptible to invasion. Invasions were associated with disturbance and high soil pH.

Melilotus albus (white sweetclover), a biennial legume native to Asia and Europe, was brought to Alaska in 1913 as a potential forage and nitrogen (N) fixing crop (Irwin, 1945). This species is the most winter hardy legume forage crop for high latitude

agriculture (Klebesadel, 1992). *Melilotus albus* has escaped from cultivation and formed numerous dense populations ($>400\text{ m}^{-2}$) on roadsides, disturbed urban areas, and glacial-fed river floodplains of the Stikine (Fig. 1), Matanuska, and Nenana Rivers (Conn et al., 2008). In Alaska, it is found from southeastern Alaska to above the Arctic Circle in the Brooks Range (55.34 to 67.15°N). *Melilotus albus* is also spreading in western Greenland (Polunin, 1959), Canada, and northern conterminous U.S.A. (Turkington et al., 1978), and at Rocky Mountain National Park in Colorado (Wolf et al., 2003).

In Alaska, *M. albus* does not extend appreciably from roadsides into undisturbed adjacent upland natural vegetation (Conn et al., 2008). Upland soils in interior Alaska are generally acidic with pH values ranging 4.5 to 5.6 (Van Cleve et al., 1983), whereas the optimum pH for *M. albus* growth and symbiotic N fixation is neutral to basic (Smith et al., 1986; Sparrow et al., 1993). However, extensive populations of *M. albus* occur on the glacial floodplains of the Nenana, Matanuska, and Stikine Rivers where soil pH averaged 8.1 and along roads where the average pH was 7.3 (Conn et al., 2008).

Melilotus albus populations may affect native plant communities by altering the soil environment or through interactions with other species. Nitrogen-fixing plant species may facilitate invasion by other exotic plant species (Vitousek and Walker, 1989). *Melilotus* species form N-fixing root nodules with *Rhizobium* bacteria, and *Melilotus officinalis* (yellow sweetclover) can fix up to 100 kg N ha⁻¹ in subarctic Alaska (Sparrow et al., 1993, 1995), dramatically increasing soil N levels. *Melilotus albus* and *M. officinalis* have been shown to increase the number of exotic species and decrease native species in montane grasslands (Wolf et al., 2003), whereas *M. officinalis* either facilitated or competed with native plant species depending on the vegetation type in South Dakota, U.S.A. (Van Riper and Larson, 2009).



FIGURE 1. *Melilotus albus* growing on a sand island, the “Stump Patch” (location of ST2), located at the mouth of the Stikine River in southeast Alaska (photo by Michael Shephard).

Melilotus albus populations on the Nenana River near the Rex Bridge are recent, dating from the summer of 2002 (Roseann Densmore, personal observation). The Matanuska River infestation was also recently discovered in 2002. *M. albus* has been on the Stikine River just downstream from Telegraph Creek since at least 1935–1940 (Conn et al., 2008) and may have originated at Telegraph Creek when it was a stopover for gold miners on their way to the Cassiar and Klondike gold fields (Loken, 1979).

Melilotus albus has the potential to invade other large glacier-fed braided river floodplains in Alaska. These rivers are critically important because they are pathways for salmon migration and support large mammals such as moose, both of which are important subsistence foods for indigenous peoples. These braided rivers are characterized by frequent flooding, high sediment loads, steep gradients, sediment deposition, shifting channel locations (Wooster, 2002), and ice scouring (Scrimgeour et al., 1994) that continually produce new soil substrate for plant colonization. *Melilotus albus* is well adapted to this environment; its seeds disperse readily in water (Turkington et al., 1978) and can remain viable in soil for at least 20 years (Stoa, 1933).

Little is known about the ecology of braided rivers (Milner and Petts, 1994; Tockner et al., 2009) where *M. albus* has invaded. In fluvial systems, plant distributions are determined largely by the tolerance of species to geomorphic processes in areas of frequent flooding and by competition with other riparian species where the geology is more stable (Hupp and Osterkamp, 1996). To understand the importance of an invasive species such as *M. albus* in a riparian system it is critical to determine the relationship between this species and the hydrogeomorphological variables

that govern species distributions in riparian plant communities (Tickner et al., 2001).

It is important to assess the impact of *M. albus* on the ecosystems of the currently infested Alaska floodplains to determine whether the impacts are great enough to warrant expensive control efforts and an intensive campaign to prevent it from invading other floodplains. The objectives of this study were to (1) determine where *M. albus* grows in relation to other species and environmental factors on the Nenana, Matanuska, and Stikine River floodplains, (2) characterize plant communities where *M. albus* grows, and (3) evaluate the relationships between *M. albus* cover and density on other species and overall species richness.

Methods

STUDY LOCATIONS

Transects were established along three rivers where *M. albus* had invaded: the Nenana River in interior Alaska, near Denali National Park; the Matanuska River in south-central Alaska, near Palmer; and the Stikine River in southeast Alaska, northeast of Wrangell (Fig. 2). The study locations selected were typical of invaded areas and were accessible by boat or vehicle.

TRANSECTS

Transects were established perpendicular to the river edge and were variable in length, ranging from 70 to 370 m depending on

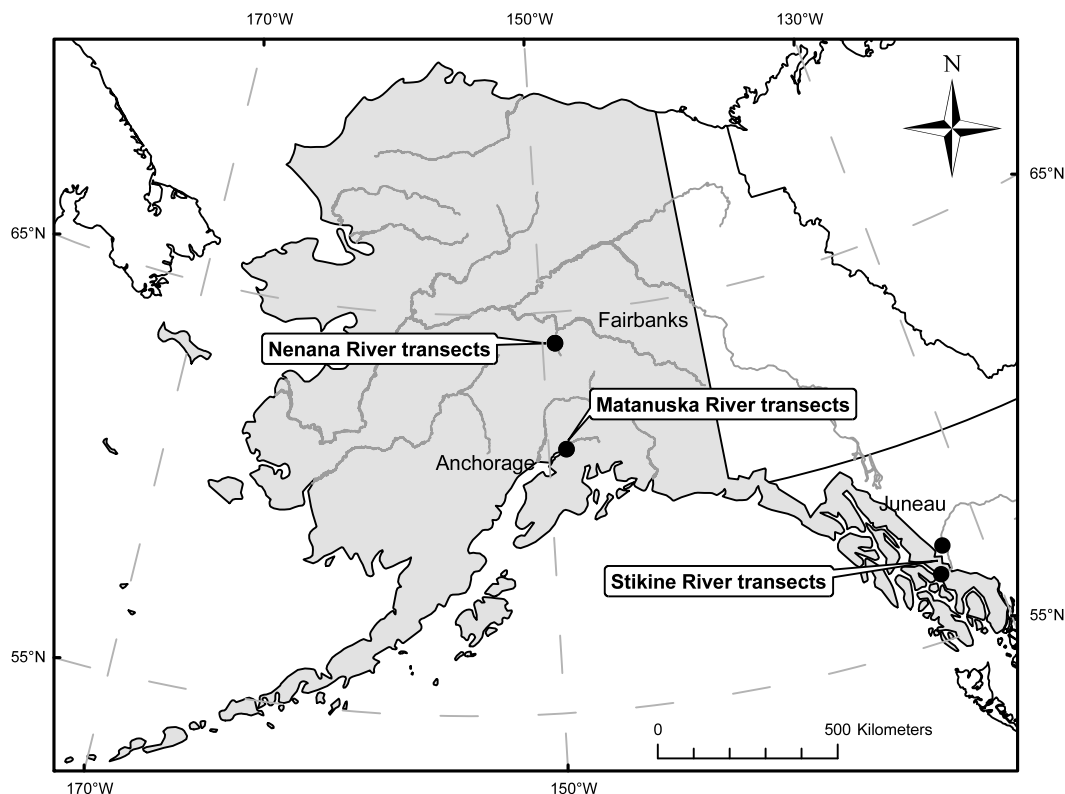


FIGURE 2. Locations of the Nenana, Matanuska, and Stikine River transects in Alaska.

floodplain width and elevation gradient. Three transects were established on the Nenana River, each ending 15 to 29 m inside a closed-canopy forest. Two transects were established on the Matanuska River, each ending at the foot of a 25-m-tall bluff. On the Stikine River, two transects were created that extended over islands with no adjacent forest. All transects were established and measured during July and early August 2005.

Along each transect, a series of belts were established at 5-m intervals. At each interval, a belt of six contiguous 1-m² quadrats was established perpendicular to the transect with three quadrats on each side. If the elevation difference from a previous belt was less than 5 cm, belt locations were skipped until the 5-cm elevation difference criteria was met. Usually this meant skipping just one potential belt location, but there were several instances on the Matanuska and Nenana Rivers where the topographic gradients were so small that three contiguous belt locations were skipped. The location (determined by GPS) and elevation of each transect, transect length, and number of belts are shown in Table 1.

In each 1-m² quadrat we visually measured percent cover, density of each plant species, and percent of surface covered by rock. For each belt we measured terrace height using a surveyor's

level. We collected stem cross sections from the three largest woody plants within 5 m of the transect at the belt terrace elevation and counted annual rings to estimate the terrace age since the last flood removed all vegetation at that belt (Nanson and Beach, 1977; Hupp, 1988). A composite soil sample was collected from each belt by combining a 15-cm-deep soil sample from each quadrat. Organic matter depth was determined for each soil sample. At the Stikine River transects, woody plants were located too far from belts, so stem cross sections were not collected. Instead, height above river was used since this has been found to be associated with flooding frequency (Hupp, 1988) and sedimentation (Nanson and Beach, 1977). At each study location, measurements of terrace height above river were equilibrated between transects and sampling days by using a reference stake driven into the soil at the river's edge on the first day of sampling.

Nenana River

Transects on the Nenana River were located just downstream of the Rex Bridge/Parks Highway crossing, approximately 64 km north of Denali National Park. All three transects were located on

TABLE 1
Locations and descriptions of river transects.

River	Transect	Latitude (°N)	Longitude (°W)	Elevation (m)	Length (m)	Belts (No.)
Nenana	NT1	64.2202	149.2789	212	80	17
	NT2	64.2216	149.2785	212	170	29
	NT3	64.2230	149.2781	211	270	41
Matanuska	MT1	61.5673	149.0631	38	370	57
	MT2	61.5631	149.0701	37	250	34
Stikine	ST1	57.2872	131.8617	59	145	23
	ST2	56.6188	132.3450	7	70	15

the west side of the river and were accessed by foot from the Parks Highway. Transects proceeded from the river edge over a bench, through a flowing slough and into a mixed *Populus balsamifera*–*Picea glauca* forest. Dominant vegetation on the bench consisted primarily of *M. albus*, *Elaeagnus commutata*, *Hedysarum alpinum*, and *Populus balsamifera* seedlings.

Matanuska River

Two transects were located on the large dissected floodplain on the north side of the Matanuska River, southwest of Palmer, and were accessed by foot. The transects originated at the river and continued north through a series of benches (dominated by *M. albus*, *E. commutata*, *Oxytropis campestris*, and immature *Populus trichocarpa*) and small dry sloughs, to a large bluff with mature *P. trichocarpa*.

Stikine River

The Stikine River sites were reached by boat from Wrangell. Transect 1 (ST1) was located approximately 100 km from the river mouth and extended over a large mid-stream island. Transect 2 (ST2) was located at the “Stump Patch,” a small island at the end of the river, and extended from one side of the island to the other. In addition to *M. albus*, these transects were dominated by *Leymus mollis*, *Equisetum variegatum*, and *Lathyrus japonicus* var. *maritimus*.

SOIL ANALYSIS

A composite soil sample from each belt was analyzed at Soiltest Farm Consultants (Moses Lake, Washington, U.S.A.) using standard soil chemical methods (Gavlak et al., 2003). Soils were air-dried and sieved (<2 mm) prior to analysis. Soil particle distribution was determined by the hydrometer method, pH, and electrical conductivity by electrode with a 1:1 soil water ratio; organic matter by a Walkley-Black titration; and total N by combustion. Nitrate and ammonium were extracted with KCl and concentrations determined by flow injection analysis. Phosphorus and potassium were extracted using the Mehlich-3 method and analyzed by inductively coupled plasma.

DATA ANALYSIS

A total of 1290 1-m² quadrats from seven transects on three rivers were analyzed. Cover data for each species were summed over quadrats for each belt and were expressed as a percent of total cover for the belt (relative cover). Frequency for each species was determined as the number of quadrats in each belt in which the species occurred and were then expressed as a percentage of the total frequency in each belt (relative frequency). We calculated synthetic importance values for each species as the average of relative cover and relative frequency.

Ordination

We used nonmetric multidimensional scaling (NMDS) with PC-ORD (McCune and Mefford, 1999) to analyze the relationships between plant species composition in the belts and the environmental conditions we measured. Ordinations were performed for the entire data set, for each river separately, and for the two transects on the Stikine River. Uncommon species that were found in only one belt and had importance values <5% were deleted before the analysis. We arc sine transformed the species

importance values for the Matanuska River ordination to improve normality. NMDS ordinations were run in autopilot mode, allowing the program to choose the best solution of starting configurations and number of dimensions to achieve the lowest stress value (McCune and Grace, 2002). We used the Sorensen (Bray-Curtis) distance measure and random starting configurations, with 40 runs of real data and 50 runs of randomized data to perform a Monte Carlo test of significance. Correlations of environmental variables with NMS axes were made using Kendall's tau (τ). The critical values of τ for a two-tailed test were determined using the SuppDists package (Wheeler, 2008) in R (R Development Core Team, 2007). Absolute values of $\tau \geq 0.30$ ($P < 0.01$) were deemed as significantly correlated to NMDS axes for the entire data set ($n = 191$) and the Nenana, Matanuska, and Stikine Rivers analyzed separately ($n = 72, 82$, and 37 , respectively), and values of $\tau \geq 0.37$ ($P < 0.05$) were significantly correlated to NMDS axes for Stikine transects 1 and 2 ($n = 22$ and 15 , respectively). Vectors on the ordination plots show the magnitude and direction of the most strongly related environmental variables. To make interpretation and comparison among the different rivers easier, the ordinations were rotated on the average terrace age variable for the ordinations of the entire data set and the Nenana and Matanuska Rivers. The ordinations for the two transects of the Stikine River were rotated on the average terrace height variable because there were too few trees to determine terrace age based on average age of woody vegetation.

Relationship between *Melilotus albus* and Other Plant Species

Pearson correlations were calculated (PROC CORR; SAS, 2000) between percent cover and density of *M. albus* and co-occurring species. Correlations were deemed statistically significant when P values were ≤ 0.05 . Percent cover and density data were transformed (arc sine and square-root, respectively) to normalize the variance prior to correlation analysis, and belts without plants were omitted. Separate correlation analyses were made for each river and for each transect on the Stikine River because the community types were different.

To aid in the interpretation of significant species correlations, we graphed species importance values versus terrace age or height to visually determine if species importance changed along this disturbance gradient and evaluated whether correlations between species were due to interactions between species or to species occupying different habitats along the disturbance gradient. We performed an additional correlation analysis between cover and density of *M. albus* and other species on the Nenana River belts with terrace age ranging from 0 to 8 years, since this was where *M. albus* importance was highest and where this species had the greatest potential for interaction with other species. Data were arcsine transformed prior to analysis. This analysis was not performed for the Matanuska River since *M. albus* occurred on all terraces, or for the Stikine River because there was insufficient tree age data to determine terrace age.

Diversity Analysis

We used correlation analysis (PROC CORR of SAS) to study the relationship of *M. albus* cover and density to species richness of each belt. Separate analyses were performed for the Nenana and Matanuska Rivers and for each Stikine River transect. Another analysis was performed for the Nenana River to examine the effect of *M. albus* on diversity at belts with terrace age ranging from 0 to 8 years.

Results

RELATIONSHIP OF MELILOTUS ALBUS TO FLOODPLAIN ENVIRONMENT

All Rivers

A total of 68 vascular plant species were found in the combined transects from all three rivers (Table 2). Ordination of vegetation importance values from all rivers resulted in a two-dimensional solution that captured 84% of the variation in the entire data set. The first NMDS axis explained 56% of the variation in vegetation composition, with an additional 28% represented by the second axis. Latitude, longitude, elevation, and terrace age were positively correlated and soil pH was negatively correlated with axis 1 (Fig. 3, a). No environmental variables were significantly correlated with axis 2. Since there were large differences in species composition between rivers due to climate and geology, we performed ordinations for each river separately.

Nenana River

Thirty-seven vascular plant species were found in the Nenana River transects including 13 species that were not present at the other rivers (Table 2). A two-dimensional ordination explained 85% of variation in species composition, with 48% in axis 1 and an additional 37% in axis 2. Terrace age was the most important variable explaining variation in species composition along axis 1 (Fig. 3, b). Other variables that were positively correlated with axis 1 were terrace height and the following soil variables: percent organic matter, total N, and K. Surface rock cover and soil pH were negatively correlated with axis 1. Axis 1 appears to represent a primary successional gradient where soil nutrients and vegetation cover increase and soil pH declines with increasing terrace age. The graph of changes in environmental variables with increasing terrace age illustrates these successional trends (Fig. 4). Terrace height, vegetation cover, organic matter depth, and soil K and total N increased with terrace age, whereas percent rock and soil pH decreased with increasing terrace age.

Species importance values that were positively correlated ($P \leq 0.01$) with the NMDS axis 1 successional gradient were: *Elaeagnus commutata*, *Populus balsamifera*, *Erigeron* spp., *Eurybia sibirica*, and *Chamerion angustifolium* ($\tau = 0.58, 0.46, 0.37, 0.35, 0.32$, respectively). *Melilotus albus* and *Crepis elegans* were negatively correlated with axis 1 ($\tau = -0.71$ and -0.30 , respectively). *Festuca rubra* was positively correlated with NMS axis 2 ($\tau = 0.49$) and *Elymus trachycaulus* and *Elaeagnus commutata* were negatively correlated with NMS axis 2 ($\tau = -0.39$ and -0.34 , respectively).

The graph of species importance values over terrace age classes descriptively confirmed the ordination results showing that species growing in the Nenana River floodplain occupied different portions of the disturbance gradient (Fig. 5). *Melilotus albus* was the most important species in belts on terraces ≤ 8 years old. Other important species were *Chamerion latifolium* and *Elymus trachycaulus*. *Hordeum jubatum*, although uncommon ($\leq 0.1\%$ importance value), was found only at belts with terrace age ≤ 4 years. *Elymus trachycaulus* and *Festuca rubra* were early grass colonizers that also occurred on older terraces. *Hedysarum alpinum*, *M. albus*, and *Oxytropis campestris* occurred on the earliest sites, were important on 0- to 15-year-old terraces, but declined in the oldest stands. *Alnus tenuifolia* increased in importance from terraces > 2 to 15 years old, but had low importance values on the oldest terraces. *Elaeagnus commutata*, *Eurybia sibirica*, and *Populus balsamifera* were found on the youngest sites and increased in

importance through the entire chronosequence, with *P. balsamifera* and *E. commutata* dominant on the oldest belts. We found a small number of *Picea glauca* seedlings on the youngest sites, but the importance of *P. glauca* as a climax species in this region was limited until late in the chronosequence.

Matanuska River

Twenty-nine vascular plant species were found in transects on the Matanuska River floodplain, including 5 species that were not present at the other rivers such as the endemic *Salix setchelliana* and the exotic species *Bromus inermis*, *Chenopodium album*, *Crepis tectorum*, *Elymus repens*, and *Polygonum aviculare* (Table 2). The first two axes of the NMDS ordination accounted for 85% of the variation in species composition. Terrace age was the only environmental variable significantly correlated with axis 1 and there were no significant correlations of environmental variables with axis 2 (Fig. 3, c). Transect data from the Matanuska River did not exhibit the decrease in soil pH or increases in soil N, K, and organic matter associated with the flooding disturbance gradient seen at the Nenana River. *Populus trichocarpa* was positively correlated with axis 1 ($\tau = 0.63$), whereas *M. albus* was negatively correlated ($\tau = -0.58$). *Elymus trachycaulus* and *Elaeagnus commutata* were positively correlated with axis 2 ($\tau = 0.62$ and 0.32 , respectively) and *M. albus* was negatively correlated ($\tau = -0.47$).

Melilotus albus was the most important species on terraces 0 to 6.5 years old, but its importance decreased and while *Populus trichocarpa* increased at older sites (Fig. 6). *Salix setchelliana* and *Crepis tectorum* were early colonizers, occurring primarily on terraces ≤ 4 years old. The grass, *Elymus trachycaulus*, was important on 0- to 6.5-year-old terraces but declined on older terraces. *Elaeagnus commutata* and *P. trichocarpa* importance increased throughout the chronosequence.

Stikine River

Forty-one vascular plant species were found at the Stikine River transects, including 21 species not found on the Nenana or Matanuska Rivers (Table 2). The first two axes of the NMDS ordination explained 80% of the variability in species composition. Longitude was strongly positively correlated and elevation was strongly negatively correlated with NMDS axes 1 and 2, clearly separating the two transects in the ordination space, with belts from ST2 clustered to the right of the ordination (Fig. 3, d). ST2 was located near the river end and was lower in elevation and greater in longitude than ST1. Percent rock was negatively correlated with axis 1, also separating the two transects, as large amounts of rock were found at ST1 but were absent from ST2. Terrace height and soil nitrate were positively correlated to NMDS axis 1. Terrace age, percent clay, and soil ammonium were negatively correlated to NMDS axis 2. Due to the differences between the transects in species composition attributable to differences in longitude and elevation, we performed separate NMDS ordinations for each transect.

Stikine River Transect 1

Thirty-four vascular plant species were found at ST1, including 11 species not found in other transects (Table 2). The first two axes of the NMDS ordination explained 72% of the variation in species composition. Terrace height was positively correlated and soil electrical conductivity was negatively correlated with NMDS axis 1. Percent rock was positively correlated with

TABLE 2

Vascular plant species found in quadrats from the Nenana, Matanuska, and Stikine Rivers. Abbreviations: C = common; U = uncommon; NP = not present.

Scientific name	Nenana	Matanuska	Stikine T1	Stikine T2
<i>Achillea millefolium</i> L.	U	U	NP	U
<i>Achillea sibirica</i> Ledeb.	NP	NP	C	NP
<i>Agrostis scabra</i> Willd.	U	NP	NP	NP
<i>Alnus fruticosa</i> Rupr.	NP	NP	U	NP
<i>Alnus sinuata</i> (Regel ex DC.) Rydb.	NP	NP	U	C
<i>Alnus tenuifolia</i> Nutt.	C	C	NP	NP
<i>Anemone</i> spp. L.	U	NP	NP	NP
<i>Arabis holboellii</i> Horneum.	NP	NP	U	NP
<i>Artemisia tilesii</i> Ledeb.	U	U	U	NP
<i>Astragalus alpinus</i> L.	C	NP	U	NP
<i>Astragalus</i> spp. L.	NP	NP	U	NP
<i>Bromus inermis</i> Leyss.	NP	U	NP	NP
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	U	U	C	NP
<i>Calamagrostis purpurascens</i> R. Br.	U	NP	NP	NP
<i>Calamagrostis stricta</i> subsp. <i>inexpansa</i> (Gray) C.W. Greene	U	NP	NP	C
<i>Chamerion angustifolium</i> (L.) Holub	C	U	NP	NP
<i>Chamerion latifolium</i> (L.) Holub	C	C	U	NP
<i>Chenopodium album</i> L.	NP	U	NP	NP
<i>Cornus sericea</i> L.	NP	NP	U	NP
<i>Crepis elegans</i> Hook.	C	NP	NP	NP
<i>Crepis tectorum</i> L.	NP	C	U	NP
<i>Deschampsia caespitosa</i> (L.) Beauv.	NP	NP	NP	C
<i>Dryas octopetala</i> L.	NP	U	C	NP
<i>Elaeagnus commutata</i> Bernh. ex Rydb.	C	C	NP	NP
<i>Elymus repens</i> (L.) Gould	NP	U	NP	NP
<i>Elymus sibiricus</i> L.	U	U	NP	NP
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	C	C	C	U
<i>Equisetum arvense</i> L.	NP	U	NP	C
<i>Equisetum pretense</i> Ehrh.	U	U	NP	NP
<i>Equisetum variegatum</i> Schleich. ex F. Weber & D.M.H. Mohr	NP	NP	C	C
<i>Erigeron</i> spp. L.	C	U	U	NP
<i>Eurybia sibirica</i> (L.) Nesom	C	NP	NP	NP
<i>Festuca rubra</i> L.	C	U	C	NP
<i>Geocaulon lividum</i> (Richards.) Fern.	U	NP	NP	NP
<i>Hedysarum alpinum</i> L.	C	U	U	NP
<i>Hordeum jubatum</i> L.	U	C	NP	NP
<i>Lathyrus japonicus</i> var. <i>maritimus</i> (L.) Kartesz & Gandhi	NP	NP	NP	C
<i>Leymus mollis</i> (Trin.) Pilger	NP	NP	NP	C
<i>Lupinus arcticus</i> S. Wats.	U	NP	NP	NP
<i>Melilotus albus</i> Medik.	C	C	C	C
<i>Melilotus officinalis</i> (L.) Lam.	U	NP	NP	NP
<i>Oxytropis campestris</i> (L.) DC.	C	C	U	NP
<i>Packera pauciflora</i> (Pursh) A. & D. Löve	C	NP	NP	NP
<i>Picea glauca</i> (Moench) Voss	C	U	NP	NP
<i>Platanthera dilatata</i> (Pursh) Lindl. ex Beck	NP	NP	U	U
<i>Poa palustris</i> L.	NP	NP	C	NP
<i>Poa</i> spp. L.	U	U	NP	NP
<i>Polemonium pulcherrimum</i> Hook.	NP	NP	U	NP
<i>Polygonum aviculare</i> L.	NP	U	NP	NP
<i>Populus balsamifera</i> L.	C	NP	NP	NP
<i>Populus trichocarpa</i> Torr. & A. Gray	NP	C	C	NP
<i>Pyrola asarifolia</i> Michx.	NP	NP	U	NP
<i>Rosa acicularis</i> Lindl.	U	NP	NP	NP
<i>Rubus idaeus</i> L.	NP	NP	U	NP
<i>Salix alaxensis</i> (Anderss.) Coville	C	NP	U	C
<i>Salix bebbiana</i> Sarg.	NP	NP	U	U
<i>Salix hookeriana</i> Barratt ex Hook.	NP	NP	C	C
<i>Salix interior</i> Rowlee	C	NP	C	C
<i>Salix setchelliana</i> Ball	NP	C	NP	NP
<i>Salix sitchensis</i> Sanson ex Bong.	NP	NP	C	U
<i>Salix</i> spp. L.	U	U	NP	NP
<i>Shepherdia canadensis</i> (L.) Nutt.	U	NP	C	NP
<i>Solidago canadensis</i> var. <i>salebrosa</i> (Piper) M.E. Jones	NP	NP	C	NP
<i>Solidago multiradiata</i> Ait.	NP	NP	NP	C

TABLE 2
Continued.

Scientific name	Nenana	Matanuska	Stikine T1	Stikine T2
<i>Solidago simplex</i> subsp. <i>simplex</i> Kunth	C	NP	NP	NP
<i>Spiranthes romanzoffiana</i> Cham.	NP	NP	U	NP
<i>Taraxacum ceratophorum</i> (Ledeb.) DC.	U	NP	NP	NP
<i>Taraxacum officinale</i> G.H. Weber ex Wiggers	NP	C	C	C

axis 2. As with the Nenana River, the NMDS axes appear to represent a flooding disturbance gradient related to terrace height and associated flooding frequency. *Polemonium pulcherrimum* and *M. albus* were positively correlated ($\tau = 0.42$ and 0.37) and *Populus trichocarpa* was negatively correlated with NMDS axis 1 ($\tau = -0.77$). *Polemonium pulcherrimum* was positively correlated with axis 2 ($\tau = 0.40$), and *Equisetum variegatum*, *M. albus*, and *Elymus trachycaulus* were negatively correlated with axis 2 ($\tau = -0.64$, -0.54 , and -0.43 , respectively).

The lack of woody vegetation at this site made it difficult to estimate terrace age at many of the belts, so we used terrace height to describe vegetation changes over time. *P. trichocarpa*, *Equisetum variegatum*, and *Salix hookeriana* were the most important species from 0 to 0.5 m terrace height (Fig. 7). *Melilotus albus* grew at 0.6 m and higher terrace height and was the most important species above 1 m. The highest sites on this island were occupied primarily by *M. albus* and *Dryas octopetala*. The exotic *Taraxacum officinale* occurred at low levels at all terrace heights. The lack of old *P. trichocarpa* (oldest was 14 years) and the presence of large driftwood suggest that the island was completely submerged during recent flooding events.

Stikine River Transect 2

Eighteen species grew at this site including four species that did not grow along other transects: *Deschampsia caespitosa*, *Lathyrus japonicus* var. *maritimus*, *Leymus mollis*, and *Solidago multiradiata* (Table 2). NMDS ordination found a one-dimensional solution explaining 94% of the variation in vegetation composition. Total soil N and percent silt were positively correlated, whereas terrace height and percent sand were negatively correlated to NMDS axis 1. *Melilotus albus* was negatively correlated to axis 1 ($\tau = -0.82$). Six species were positively correlated to axis 1: *Lathyrus japonicus* var. *maritimus* ($\tau = 0.64$), *Alnus sinuata* ($\tau = 0.61$), *Taraxacum officinale* ($\tau = 0.61$), *Solidago multiradiata* ($\tau = 0.55$), *Calamagrostis stricta* subsp. *inexpansa* ($\tau = 0.47$), and *Salix alaxensis* ($\tau = 0.47$).

Melilotus albus was the most important species at all terrace heights (Fig. 8). The importance of *Leymus mollis* and *Equisetum variegatum* were generally constant across all terrace heights. *Alnus sinuata* importance declined with increased terrace height. *Lathyrus japonicus* var. *maritimus* increased in importance on terraces 0.6 to 2.6 m, and then declined on higher terraces.

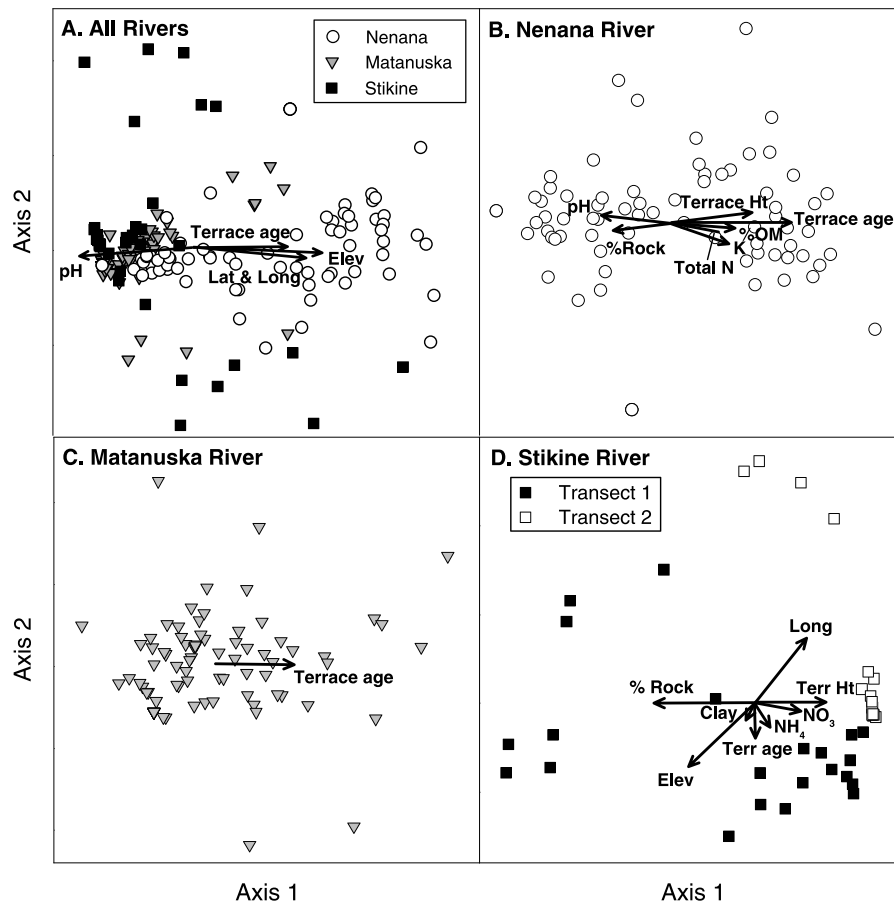


FIGURE 3. Nonmetric multidimensional scaling ordination of transect belts for (A) all rivers combined, (B) Nenana River, (C) Matanuska River, and (D) Stikine River. Vectors show the magnitude and direction of significant correlations with environmental variables ($|\tau| > 0.30$, $P < 0.01$).

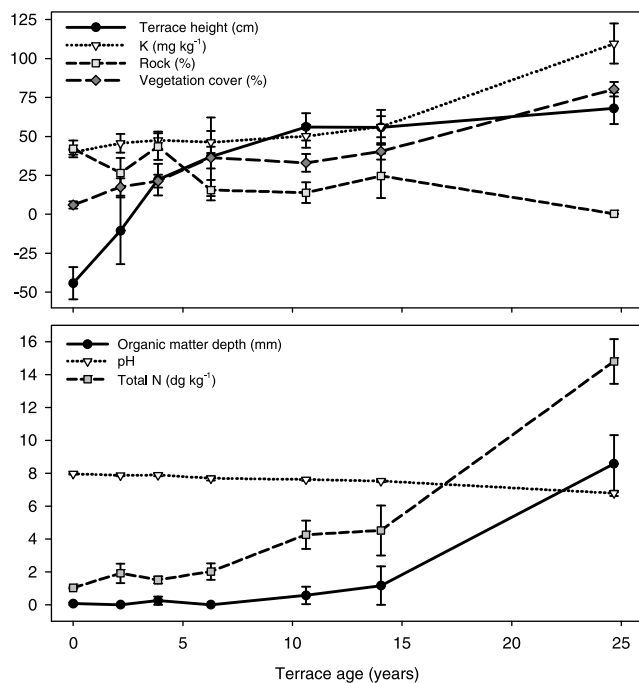


FIGURE 4. Changes in environmental variables with increasing terrace age on the Nenana River.

Calamagrostis stricta subsp. *inexpansa*, *Salix alaxensis*, and *T. officinale* importance was higher in belts where *M. albus* importance was lower, suggesting a competitive negative interaction. Mean *M. albus* cover and density were much higher at this location than at the other transects (Table 3).

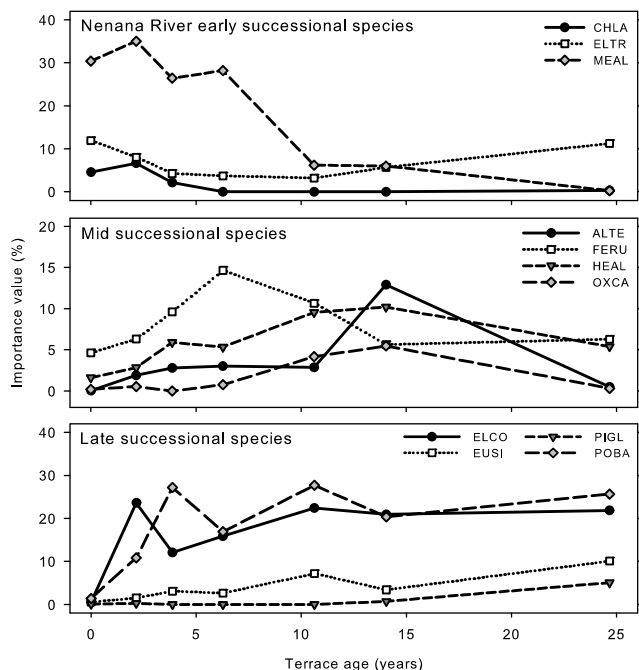


FIGURE 5. Changes in importance of plant species with increasing terrace age on the Nenana River. Species abbreviations: ALTE = *Alnus tenuifolia*; CHLA = *Chamerion latifolium*; ELCO = *Elaeagnus commutata*; ELTR = *Elymus trachycaulus*; EUSI = *Eurybia sibirica*; FERU = *Festuca rubra*; HEAL = *Hedysarum alpinum*; MEAL = *Melilotus albus*; OXCA = *Oxytropis campestris*; PIGL = *Picea glauca*; POBA = *Populus balsamifera*.

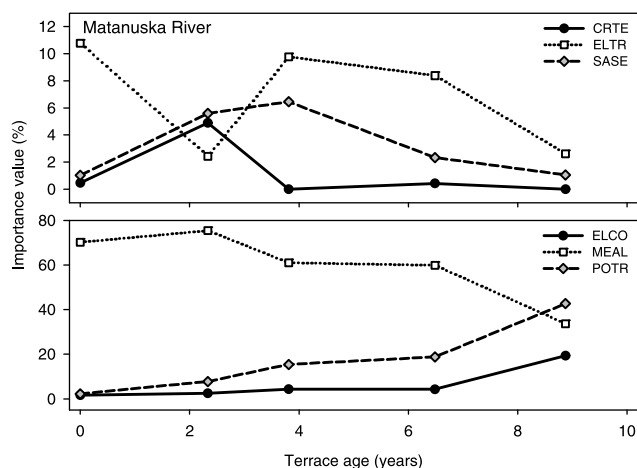


FIGURE 6. Changes in importance of plant species with increasing terrace age on the Matanuska River. Species abbreviations: CRTE = *Crepis tectorum*; ELCO = *Elaeagnus commutata*; ELTR = *Elymus trachycaulus*; MEAL = *Melilotus albus*; POTR = *Populus trichocarpa*; SASE = *Salix setchelliana*.

EFFECTS OF MELILOTUS ALBUS ON OTHER SPECIES AND DIVERSITY

Because the rivers differed in species composition, population density, and duration of interaction with *M. albus*, we studied correlations between *M. albus* cover and density and that of other species and overall species richness separately for each river.

Nenana River

Cover of *M. albus* was negatively correlated with *Elaeagnus commutata*, *Populus balsamifera*, *Alnus tenuifolia*, *Erigeron* spp., and *Picea glauca* ($r = -0.48, -0.30, -0.27, -0.25$, and -0.24 , respectively). Density of *M. albus* was negatively correlated with *Elaeagnus commutata* ($r = -0.34$) and positively correlated with *Crepis elegans* ($r = 0.46$). Neither *M. albus* cover nor density was significantly correlated with species richness at the Nenana River study site.

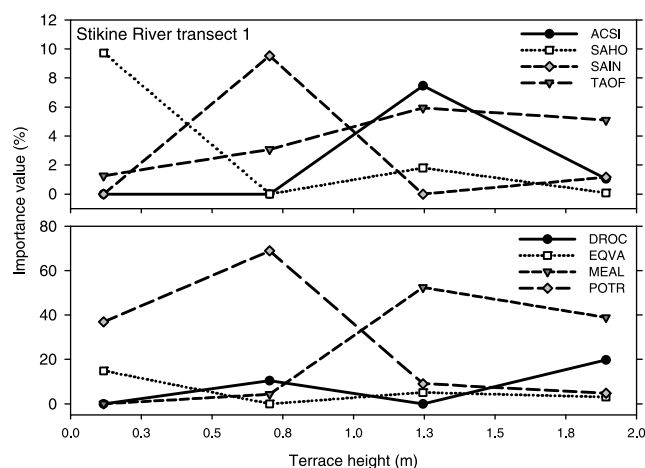


FIGURE 7. Changes in importance of plant species with increasing terrace height on Stikine River transect 1. Species abbreviations: ACSI = *Achillea sibirica*; DROC = *Dryas octopetala*; EQVA = *Equisetum variegatum*; MEAL = *Melilotus albus*; POTR = *Populus trichocarpa*; SAHO = *Salix hookeriana*; SAIN = *Salix interior*; TAOF = *Taraxacum officinale*.

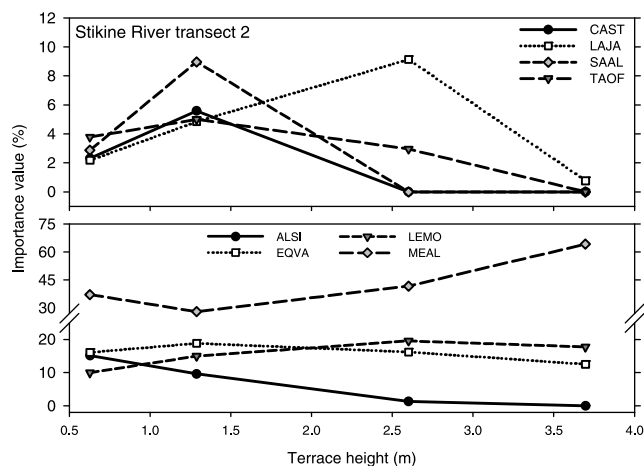


FIGURE 8. Changes in importance of plant species with increasing terrace height on Stikine River transect 2. Species abbreviations: ALSI = *Alnus sinuata*; CAST = *Calamagrostis stricta* subsp. *inexpansa*; EQVA = *Equisetum variegatum*; LAJA = *Lathyrus japonicus* var. *maritimus*; LEMO = *Leymus mollis*; MEAL = *Melilotus albus*; SAAL = *Salix alaxensis*; TAOF = *Taraxacum officinale*.

A significant negative correlation could be due to an interaction between the species or species having different niches. Since the species along the Nenana transect are part of flooding disturbance gradient, it is possible that the negative correlation between *M. albus* and late successional species such as *Picea glauca* may be due to the species being temporally or spatially separated on this gradient and not due to an interaction.

To further test this, an additional correlation analysis was performed for belts with average terrace age ≤ 8 years where *M. albus* populations were highest. When only these belts were included in the analysis, cover of *M. albus* was still negatively correlated with *Elaeagnus commutata* ($r = -0.32$) and positively correlated with *Elymus trachycaulus* ($r = 0.51$). Density of *M. albus* was positively correlated with *Crepis elegans*, *Astragalus alpinus*, and *Elymus trachycaulus* ($r = 0.47$, 0.40 , and 0.30 , respectively). Neither *M. albus* cover nor density was significantly correlated with species richness at the Nenana River study site.

Matanuska River

Cover of *M. albus* was positively correlated with *T. officinale* ($r = 0.61$), *Crepis tectorum* ($r = 0.60$), *Elymus trachycaulus* ($r = 0.31$), *Hordeum jubatum* ($r = 0.22$), and *Salix setchelliana* ($r = 0.21$). Density of *M. albus* was positively correlated with *C. tectorum* ($r = 0.51$) and *S. setchelliana* ($r = 0.24$). Species richness was positively correlated with both cover and density of *M. albus* ($r = 0.24$ and 0.31 , respectively).

Stikine River

At ST1, cover of *M. albus* was positively correlated to *Solidago canadensis* var. *salebrosa* and *Taraxacum officinale* ($r = 0.74$ for both), and *Populus trichocarpa* ($r = 0.49$). Density of *M. albus* was positively correlated with *T. officinale* ($r = 0.79$), *S. canadensis* var. *salebrosa* ($r = 0.65$), *Artemisia tilesii* ($r = 0.61$), *Erigeron* spp. ($r = 0.59$), and *Achillea sibirica* ($r = 0.55$). Species richness was positively correlated with both cover and density of *M. albus* ($r = 0.44$ and 0.52).

At ST2, all significant correlations between *M. albus* and other species were negative. Cover and density of *M. albus* were negatively correlated with *T. officinale* ($r = -0.74$ and -0.76), *Lathyrus japonicus* var. *maritimus* ($r = -0.68$ and -0.65), *Alnus sinuata* ($r = -0.60$ and -0.53), and *Calamagrostis stricta* subsp. *inexpansa* ($r = -0.53$ and -0.53). Density of *M. albus* was also negatively correlated with *Solidago multiradiata* ($r = -0.58$) and *Salix alaxensis* ($r = -0.53$). Similarly, species richness was negatively correlated with *M. albus* cover and density ($r = -0.67$ and -0.59 , respectively).

Discussion

MELILOTUS ALBUS DISTRIBUTION ON FLOODPLAINS

There were differences in species composition between the rivers related to geographic location. This was expected because the rivers are draining watersheds with different geologies and climates. The Stikine River sites were located at latitude 56 to 57°N with a more moderate maritime climate compared to the Matanuska River at 61°N (also maritime) and the Nenana River at 64°N with an inland location. Agricultural fields occupy much of the land above the Matanuska River, which may account for the high number of exotic species there compared to the Nenana and Stikine Rivers.

Although the rivers differed in species composition, *M. albus* was always found on sites that had been recently disturbed. It did not persist or invade into lower disturbance successional stages dominated by woody species such as *Alnus sinuata*, *A. tenuifolia*, *Populus balsamifera*, or *P. trichocarpa*. *Melilotus albus* is thought to be shade intolerant (Turkington et al., 1978), which could explain its absence on the older sites that were dominated by woody species.

The extent of the *M. albus* infestation was largely explained by topography. The Nenana and Matanuska floodplains were wide, low, and frequently flooded. They supported large communities of *M. albus*. Similar areas exist on the Stikine River as well, such as at ST1. However, other areas of the Stikine are of lower gradient with a single channel and steeper banks where only narrow bands of *M. albus* occurred. The "Stump Patch" at ST2 was quite different than ST1 and the other rivers. This is a sand island with frequent disturbance due to wind erosion and

TABLE 3
Percent ground cover and density of *Melilotus albus* along the Nenana, Matanuska, and Stikine River transects.

Transect	Belts (No.)	Ground cover		Density	
		Mean \pm SE	Maximum	Mean \pm SE	Maximum
		——(%)——		——(Plants m ⁻²)——	
Nenana	87	3 \pm 1	34	10 \pm 3	170
Matanuska	91	6 \pm 1	90	121 \pm 31	2085
Stikine T1	23	13 \pm 4	70	239 \pm 94	1823
Stikine T2	15	31 \pm 7	83	660 \pm 192	2963

deposition that supported a high density of *M. albus* over the entire island (Fig. 1).

Flooding disturbance gradients, where soil nutrients and vegetation cover increased and soil pH declined with increasing terrace height, were found at the Nenana and ST1 sites, but not at the Matanuska or ST2 site. A possible explanation is that the range of average terrace age in belts on the Matanuska River was much smaller (0 to 10 years) than at the Nenana River (0 to 26 years) and the ST2 site is subject to wind rather than water deposition of sediments. At ST2, the percent of sand increased while percent of silt declined with increasing terrace height. However, there were no discernable changes in plant cover or soil nutrients that are characteristic of primary succession. ST2 is a sand island at the mouth of the Stikine River and is subject to high winds, evidenced by numerous vegetation “blowouts.” This constant disturbance may inhibit the progress of primary succession.

There was a general tendency at all sites (except ST2) for soil P and N to increase with terrace height and age. Similar changes in soil nutrients during primary succession have been found at other locations in the interior (Viereck, 1966; Viereck et al., 1993) and southeast Alaska (Crocker and Major, 1955).

Studies of primary succession on the Tanana River floodplain of interior Alaska showed that pioneer species (such as *Salix* spp. and *Populus balsamifera*) are wind dispersed and germinate quickly (Walker et al., 1986). Though general stages of succession have been recognized and related to flooding frequency on the Tanana floodplain (Viereck et al., 1993), the trajectories of succession may change from site to site or with time due to founder effects, herbivory, disease, climate change, and differences between sites in geomorphology or species-specific population dynamics (Hollingsworth et al., 2010). Studies of primary succession at Glacier Bay, Alaska, showed that the direction and speed of successional trajectories were greatly influenced by which species initially colonized, which depended on distance to seed source (Chapin et al., 1994; Fastie, 1995).

Succession at Glacier Bay progressed faster and differently when the heavier seeded *Alnus sinuata* reached sites early and contributed N through symbiotic N fixation. *A. sinuata* occurs along the Stikine River and *A. tenuifolia* is common at the Nenana and Matanuska River sites. Uliassi and Ruess (2002) found that *A. tenuifolia* on the Tanana River floodplain contributed 15–85 kg N ha⁻¹ yr⁻¹, up to 70% of the N accumulated during succession on the Tanana River floodplain. Since symbiotic nitrogen fixation by *Melilotus* in an agricultural setting can reach 100 kg N ha⁻¹ yr⁻¹ (Sparrow et al. (1993, 1995), we believe that dense stands of N-fixing *M. albus* on river floodplains could cause ecosystem effects similar to alder by increasing soil N status. The importance of N-fixation inputs by *M. albus* could be even more important due to the recent disease-mediated decline of *A. tenuifolia* in Alaska (Ruess et al., 2009). Lisuzzo et al. (2008) found that nitrogen was transported in saturated soils along the Tanana River and was an important source of N for early successional sites there. Thus, increased N input from *M. albus* symbiotic nitrogen fixation could have effects at some distance from where this species is growing.

EFFECTS OF MELILOTUS ALBUS ON OTHER SPECIES AND DIVERSITY

Differences between the two correlation analyses on the Nenana River made using data over the entire chronosequence versus the early portion where *M. albus* occurs (0 to 8 years), indicates that the negative correlations between *M. albus* and

Picea glauca and *Alnus tenuifolia* are due to niche differences and not due to interactions. Since *Elaeagnus commutata* was negatively correlated with *M. albus* in both analyses, it is likely that these species are interacting. Indeed, our field observations were that *M. albus* rarely grew within *E. commutata* populations.

Positive correlations between species can also be difficult to interpret. The positive correlation between *M. albus* and *Astragalus alpinus*, *Crepis elegans*, and *Elymus trachycaulis* could be due to the species having similar habitat requirements (but not interacting) or could be due to facilitation.

Similarly, positive correlations at the Matanuska River between *M. albus* and exotic species may be due to similar habitat requirements or could be a result of a positive interaction. Other symbiotic N-fixing species are known to facilitate establishment of exotic species (Vitousek and Walker, 1989). DeFerrari and Naiman (1994) also found that disturbed riparian sites on the Olympic Peninsula of Washington, U.S.A., had a relatively high proportion of exotic plant species.

The ecological impacts of *M. albus* may be different on the three rivers. *Elaeagnus commutata* appeared to suppress *M. albus* on the Nenana River, but a negative correlation between these species was not found at the Matanuska River. Several positive correlations were found between *M. albus* and native species such as *Astragalus alpinus*, *Crepis elegans*, and *Elymus trachycaulis* on the Nenana and *Salix setchelliana* and *Elymus trachycaulis* on the Matanuska Rivers. There was a positive interaction between *M. albus* and the exotic species *Crepis tectorum* and *Taraxacum officinale* on the Matanuska River and at ST1 on the Stikine River. At ST2 all significant interactions with *M. albus* were negative, including the interaction with *T. officinale*.

The relationship of *M. albus* cover and density to species richness followed similar trends, with no relationship at the Nenana River, a positive relationship at the Matanuska River and ST1, and a strongly negative correlation at ST2. A possible explanation for these differences lies in differences between the sites in *M. albus* population cover and density (Table 3). Nenana River populations of *M. albus* were sparse with low cover ($\leq 3\%$) whereas the Matanuska River and ST1 populations had somewhat higher cover (6–13%). The “Stump Patch” at ST2 differed from all of the other sites in having high mean *M. albus* cover (31%). *Melilotus albus* may facilitate growth and survival of other species at low populations, but become detrimental at high levels, even at the same river. Walker (1993) stated that small herbaceous N-fixers may increase the rate of primary succession, whereas large thicket-forming N-fixers can inhibit the rate of succession.

To test the direct influence of *M. albus* on the growth and survival of other species, Spellman (2008) removed *M. albus* from 12 sites on the Nenana River with high *M. albus* cover and compared survival of seedlings of native species to that on adjacent plots where *M. albus* was not removed. Approximately 50% fewer seedlings survived where *M. albus* was growing than where it was removed. It should be noted that the cover of *M. albus* at Spellman’s sites was high (50–90%) compared to the mean *M. albus* cover we measured on the Nenana, Matanuska, and ST1 transects (3, 6, and 13%, respectively) and even surpassed the mean cover at ST2 (31%). Spellman showed that photosynthetically active radiation is reduced in a nearly 1:1 ratio with *M. albus* cover. Dense, high-cover *M. albus* could severely shade native species, whereas low density populations would cause little shading.

Another factor to consider in the interpretation of correlations between *M. albus* and other species and species richness is that there may have been insufficient time for negative or positive interactions to manifest at the Nenana and Matanuska Rivers

since the *M. albus* infestations there were quite recent compared to those on the Stikine River.

Conclusions

Melilotus albus was always found on lower river terraces that had been recently disturbed. It did not persist or invade older or higher terraces. Hupp and Osterkamp (1996) hypothesized that vegetation patterns in fluvial systems are driven by the tolerance of species to flooding and by competition on opposite ends of the flooding disturbance gradient. *Melilotus albus* does not appear to be particularly adapted to withstand flooding, though the authors have observed the species to withstand several days of immersion under low current conditions. The success of this species on lower terraces may be due to its ability to disperse and colonize new fluvial sediments. Often when flooding occurs on the lower terraces where *M. albus* occurs, vegetation is totally removed by high energy water or by ice. Because *M. albus* seeds float and have a hard seed coat (Turkington et al., 1978), floodwaters should transport the seed to areas where sediment is being deposited. The hard seed coat would be abraded by sand and gravel while being transported and the seed would readily germinate.

Interactions between white sweetclover and other species varied within and between rivers due to differences in *M. albus* density and species composition differences between rivers. At the Nenana River, *M. albus* was negatively correlated with *Elaeagnus commutata*, but this was not the case at the Matanuska River. Positive correlations between *M. albus* and the exotic species *Crepis tectorum* and *Taraxacum officinale* were found at the Matanuska River and between *M. albus* and *T. officinale* at the Stikine River Transect 1. However, at Stikine River Transect 2, where *M. albus* densities were the highest, the correlation between *M. albus* and *T. officinale* and between *M. albus* and several native species including *Lathyrus japonicus* var. *maritimus*, *Alnus sinuata*, *Calamagrostis stricta* subsp. *inexpansa*, *Solidago multiradiata*, and *Salix alaxensis* were strongly negative. *Melilotus albus* density and cover were not correlated with species richness on the Nenana and Matanuska Rivers but were negatively correlated with species richness at Stikine River Transect 2. Differences between rivers in the effects of *M. albus* on other species may be related to *M. albus* density and length of time *M. albus* has been present in the river system.

Glacial river floodplains in Alaska are highly disturbed and are corridors for exotic plant species movement. Subsequently, herbivores such as moose could consume seed of alien plants and disperse them into communities away from river corridors (Rose and Hermanutz, 2004, Seefeldt et al., 2010). Symbiotic nitrogen-fixing *M. albus*, when growing at moderate to low density, may facilitate exotic species. At high densities, this species can reduce seedling survival, cover, and density of native species. Though the infestations on the Nenana, Matanuska, and Stikine Rivers would be difficult to eradicate (Conn and Seefeldt, 2009), preventative measures should be taken to keep *M. albus* from invading other glacial floodplains. The network model developed by Wurtz et al. (2008) could be used to identify road-river interfaces that would expose downstream public lands to invasion by *M. albus*, allowing public land managers to prioritize control of *M. albus* at road-river crossings.

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