



# Interactive controls of herbivory and fluvial dynamics on landscape vegetation patterns on the Tanana River floodplain, interior Alaska

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## ABSTRACT

**Aim** We examined the interactive effects of mammalian herbivory and fluvial dynamics on vegetation dynamics and composition along the Tanana River in interior Alaska.

**Location** Model parameters were obtained from field studies along the Tanana River, Alaska between Fairbanks (64°50.50' N, 147°43.30' W) and Manley Hot Springs (65°0.0' N, 150°36.0' W).

**Methods** We used a spatially explicit model of landscape dynamics (ALFRESCO) to simulate vegetation changes on a 1-year time-step. The model was run for 250 years and was replicated 100 times.

**Results** Increases in herbivory decreased the proportion of early successional vegetation and increased the proportion of late successional vegetation on the simulated landscape. Erosion and accretion worked as antagonists to herbivory, increasing the amount of early successional vegetation and decreasing the amount of late successional vegetation. However, the interactive effects of herbivory and erosion/accretion were especially important in determining system response, particularly in early seral vegetation types. High erosion rates, when coupled with low herbivory, greatly increased the proportion of willow on the landscape. When coupled with high herbivory, however, they greatly increased the proportion of alder on the landscape. At low levels of herbivory, alder abundance peaked at intermediate levels of erosion/accretion.

**Main conclusions** Neither erosion/accretion nor herbivory produced consistent landscape patterns that could be predicted independently of the other. These findings underscore the importance of the interactive effects of biotic and abiotic disturbances in shaping large-scale landscape vegetation patterns in boreal floodplain ecosystems – systems traditionally thought to be driven primarily by abiotic disturbance alone.

## Keywords

Alaska, boreal forest, fluvial dynamics, herbivory, landscape dynamics, spatially explicit models, succession.

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## INTRODUCTION

The landscape pattern of vegetation communities is of fundamental importance to ecologists and biogeographers because it establishes the biotic template upon which large-scale ecological processes occur. Landscape vegetation patterns within boreal forests are thought to be driven strongly by abiotic disturbance processes (i.e. fire in uplands, floods in

floodplains) coupled with the extremely cold climate of boreal regions (Chapin *et al.*, 2006a,b). Biotic interactions (e.g. competition among plants, herbivore–plant interactions) are usually thought to be most important at the community level of organization (e.g. species composition) and in plant successional patterns (Kielland *et al.*, 2006).

Boreal forest floodplains are highly active environments where physical disturbance is frequent and obvious. Floods

occur annually, driven mostly by glacial melt waters during the relatively warm summer (Oswood *et al.*, 2006). Floodplains of interior Alaska are highly dynamic systems, with established plant communities being lost to erosion and new mineral soils being created, via flood deposits, as river channels shift or dry up (Viereck *et al.*, 1993; Yarie *et al.*, 1998). Erosion alters landscape vegetation patterns by removing plants from any stage of succession. Flooding deposits new alluvium on the inside of point bars, which then become the surfaces on which primary succession commences. Primary successional substrates expand as a result of repeated sedimentation and build-up of terrace height (Yarie *et al.*, 1998).

Willow species (*Salix* spp.) are the first colonizers of these newly formed alluvial surfaces as a result of their fast growth and high seed production (Walker *et al.*, 1986). Once established, willows dominate the open shrub stage of primary succession and are replaced by alder (*Alnus tenuifolia*) during the closed shrub stage. Shrub communities are replaced by later successional species such as balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*) (Van Cleve *et al.*, 1993). The succession theory of boreal floodplains has emphasized the temporal response of vegetation to changes initially triggered by abiotic disturbance or erosion/accretion. However, the extension of succession theory at the stand-level scale to large-scale landscape pattern has seldom been undertaken in field studies or in modelling.

Several studies have examined the influence of herbivores on willow communities and found changes in physical and chemical properties of the stands (Bryant, 1987; Kielland *et al.*, 1997; Kielland & Bryant, 1998). Herbivores have also been linked to a reduction in the longevity of willow communities, thus influencing the rate of successional change (Walker *et al.*, 1986; Bryant, 1987). These findings indicate that herbivory can influence early successional communities and may have consequences for vegetation patterns at the landscape level. Thus, we can hypothesize that the large-scale landscape vegetation pattern of boreal floodplains is driven by both the abiotic disturbance of erosion/accretion and the biotic disturbance of herbivory. But to what extent might the *interaction* of those two factors determine the system response? Does the interaction of herbivory and erosion/accretion result in differences in landscape patterns from what might be predicted on the basis of either alone?

Our study examined changes in vegetation communities on a simulated landscape to evaluate the relative effects of herbivory, erosion, and accretion along the Tanana River in interior Alaska. The general hypothesis of this study was that the combined effects of herbivory, erosion, and accretion alter landscape vegetation patterns by changing the transition time between successional stages. Herbivory primarily alters the duration of the willow stage by increasing plant mortality and reducing the competitive capacity of willow, resulting in more rapid replacement by alder (Kielland *et al.*, 1997). At high levels of browsing, herbivores influence the quantity of available forage by decreasing the above-ground biomass of forage plants and by decreasing the proportion of willow

communities on the landscape. Erosion and accretion alter successional patterns by removing communities of all successional stages and initiating primary succession. We expected the interaction of biotic (herbivory) and abiotic (erosion/accretion) disturbances to yield results at large spatial (landscape) and temporal (decadal) scales that might not be predicted by consideration of either factor alone.

To examine these ideas, we incorporated data from previous process studies at the plot level into a spatially explicit model of interior Alaska vegetation dynamics (ALFRESCO) in order to assess if the effect of herbivory in the willow stage of succession can alter landscape vegetation patterns and future willow biomass production. The model incorporated fluvial processes and the effect of herbivory by moose (*Alces alces* Grey) and snowshoe hares (*Lepus americanus* Erxleben) on willow communities to determine the interactive effects of biotic and abiotic factors on vegetation communities at the landscape and successional scales of space and time.

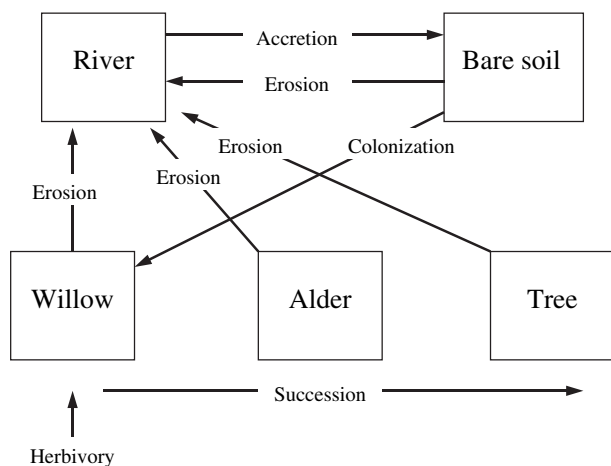
## METHODS

### Study area

The intention is that our model simulations should represent the ecological interactions resulting from biotic and abiotic processes found along a 250-km stretch of the Tanana River in interior Alaska between Fairbanks (64°50.50' N, 147°43.30' W) and Manley Hot Springs (65°0.0' N, 150°36.0' W). The Tanana River forms at the junction of the Chisana and Nabesna rivers and flows *c.* 850 km before entering the Yukon River at the village of Tanana (65°10.4' N, 152°5.5' W). The active floodplain of the Tanana River ranges in width from 300 to 2000 m (Collins, 1990) and extends 824 km through boreal forest communities (Ott *et al.*, 2001) exposed to a wide range of herbivory levels. Primary succession along the Tanana River was described by Van Cleve *et al.* (1993), who reported a transition from bare soil to a willow stage followed by an alder-dominated stage, a poplar-dominated stage, and culminating in white and black spruce forests.

### Model overview

ALFRESCO was originally developed to simulate the response of subarctic vegetation to a changing climate and disturbance regime (Rupp *et al.*, 2000a,b). Previous research has highlighted both direct and indirect (through changes in fire regime) effects of climate on the expansion rate, species composition, and extent of the tree line in Alaska (Rupp *et al.*, 2000b, 2001). Additional research, focused on boreal forest vegetation dynamics, has emphasized that fire-frequency changes – both direct (climate-driven or anthropogenic) and indirect (as a result of vegetation succession and species composition) – strongly influence landscape-level vegetation patterns and associated feedbacks to future fire regimes (Rupp *et al.*, 2002; Chapin *et al.*, 2003; Turner *et al.*, 2003), as well as the



**Figure 1** Conceptual diagram of the model showing interrelationships of model states and processes across successional stages.

availability of wildlife habitat (Rupp *et al.*, 2006). A detailed description of ALFRESCO can be obtained from the literature (Rupp *et al.*, 2000a,b, 2001, 2002, 2006). For the purposes of this study we will focus our description on details relevant to this research (see Appendix S1 in Supplementary Material for equations and additional details).

The simulation landscape represented a typical  $1 \times 2$  km stretch of the Tanana River, composed of  $10 \times 10$  m pixels. The model simulated vegetation transitions among four successional stages (bare soil, willow, alder, and mature trees; Van Cleve *et al.*, 1993; Fig. 1). Because transition to a new stage of succession was determined by the colonization and growth of the new plant community, the model simulated and monitored those factors and processes important to the development of plants that would define the next successional stage. Successional change was dictated by annual changes in species density for most successional stages and by annual changes in the biomass ratio of poplar and alder to willow during the willow stage.

We simulated river pixels on the landscape as a cosine wave that moved across the model landscape at rates that corresponded to erosion/accretion rates observed along the Tanana River (Ott *et al.*, 2001). The simulated river had a fixed width of 60 m. While this is a lower value than the average total width of the Tanana River's active floodplain as a whole, it was used to represent an active channel along this braided river. As the river moved across the landscape it 'eroded' pixels of any type and left pixels of bare soil in its wake. Erosion and accretion rates were assumed to occur at equal annual rates, resulting in a stable active floodplain. Erosion rates were derived from a study of bank erosion along the Tanana River during a 20-year interval comparing aerial photographs taken in 1978 with Landsat Thematic Mapper images from 1998 (Ott *et al.*, 2001).

We assumed that colonization of soil was not an obstacle to community establishment because seeds are easily distributed from nearby communities by the river and by wind (Wolff &

Zasada, 1979), that erosion equalled accretion in every year of the model, and that succession always followed the trajectory described by Van Cleve *et al.* (1993). Bare soil was colonized by willow according to patterns observed at field sites along the Tanana River (Viereck *et al.*, 1993). Once the willows reached a critical density within a pixel, the pixel transitioned to willow. The transition from willow to alder was based on the ratio of the above-ground biomass of willow to that of alder-plus-poplar (willow AGB ratio, Kielland & Bryant, 1998). Willow AGB was modelled using a logarithmic equation based on transect field data from willow stands along the Tanana River (Butler, 2003). Similarly, alder and poplar above-ground biomass were modelled with data obtained along the Tanana River. The exponential growth equation reflected the continued growth trends following the transition to alder (see Supplementary Material).

As with the willow and alder vegetation stages, the model transitioned into the tree frame at a specified density of trees (see Supplementary Material). Initial and critical transition densities reflected those reported by Van Cleve *et al.* (1993). The mature tree type represented stands dominated by poplar and spruce. For the purposes of this research we did not simulate fire, even though it can be an important factor, particularly in older spruce stands.

The effects of herbivory on willow biomass were derived from exclosure and transect studies along the Tanana River (Kielland & Bryant, 1998; Butler, 2003). We compared willow communities affected by high levels of herbivory (69% of current annual growth browsed) with those affected by low levels of herbivory (15%) to obtain estimates of the effect of herbivory on biomass and density in stands of various ages. The differences were summarized in one herbivory variable reflecting the proportion of available twigs browsed, which could be altered in the model to simulate the effect of varying levels of herbivory. A similar comparison was performed for later successional species (alder and poplar) found in willow communities that were used in the willow AGB ratio for transition from willow to alder.

Our model was an extremely simple system compared with the extremely complex system of the actual Tanana River. For example, we did not model the spatial complexities of islands and sloughs, mainstream vs. back channels, or intermediate levels of erosion whereby vegetation might be only partially removed (e.g. within a model pixel) rather than completely removed. We did not model interactions between plant species (e.g. competition), or cause-and-effect mechanisms affecting life-history events (e.g. germination, establishment, mortality). This is because we viewed our analysis as a first step in exploring and elucidating the *interactive* effects of two major factors (erosion/accretion and herbivory) that had heretofore been studied only in isolation. Our interests were in the general nature of the interactive response, especially at a large spatial scale, rather than in the detailed modelling and analysis of site-specific mechanisms and patterns. We considered our level of analysis to be a logical precursor to more detailed, in-depth study.

## Model experiments and data analysis

We considered four general modelling experiments to investigate the potential effect of herbivory, erosion/accretion, and the interactions between the two on landscape-level successional patterns.

1. The Time Model (T) was the simplest model, replicating only the passing of successional time based on changes in plant density and biomass within pixels.
2. The Time and Herbivory Model (T\*H) incorporated a herbivory variable, which affects the willow, alder, and poplar biomass within willow pixels, as well as successional processes from the Time Model.
3. The Time and Erosion Model (T\*E) allowed the river to move across the landscape, simulating erosion and accretion effects in addition to successional processes.
4. The Time, Herbivory, Erosion Model (T\*H\*E) was a global model that incorporated all of the processes from the other models.

The simulated landscape compositions were compared with vegetation compositions observed by Ott *et al.* (2001) and transect data from two study areas along the Tanana River that differed in herbivory levels and erosion/accretion levels (Butler, 2003). The study area near Manley Hot Springs had low levels of herbivory and a moose density of 0.2 moose km<sup>-2</sup> (Alaska Department of Fish & Game, 1998); 15% of the available stems had been browsed by moose/snowshoe hares; and the erosion/accretion rate was 4.2 ha km<sup>-1</sup> year<sup>-1</sup>. The high-herbivory area near Fairbanks had a moose density of about 1.0 moose km<sup>-2</sup> (Alaska Department of Fish & Game, 1998); 69% of forage plant stems had been browsed by moose and hares; and the erosion/accretion rate was 6.1 ha km<sup>-1</sup> year<sup>-1</sup>.

We analysed 56 distinct model scenarios representing naturally occurring variation in combinations of erosion/accretion (eight levels; 0–30 ha km<sup>-1</sup> year<sup>-1</sup>) and herbivory (seven levels; 0–80%). Each scenario was run for 250 years and replicated 100 times. The duration of 250 years was set *a priori* using a coefficient of variation analysis on model outputs to determine when landscape parameters had stabilized. The herbivory, erosion/accretion, and interaction effects were evaluated on the basis of percentage landscape cover of each vegetation type, residence time, total willow AGB (kg ha<sup>-1</sup>) on the landscape, and mean willow AGB density (g m<sup>-2</sup>). We defined residence time as the length of time a pixel was in a particular vegetation type, total willow AGB as the total amount of willow above-ground biomass on the landscape, and mean willow AGB as the average amount of willow above-ground biomass within a willow pixel. Residence time was used to distinguish between changes in landscape proportions that resulted from changes in successional transition rates and those that resulted as a consequence of another vegetation type becoming a larger or smaller percentage of the landscape. Total willow AGB represented the quantity of forage available on the landscape. Mean willow AGB was used as an indication of the amount of forage biomass available to a herbivore within a

willow stand regardless of the size of the stand or the proportion of willow on the landscape.

A two-way ANOVA was used to test the significance of herbivory (seven levels), fluvial dynamics (eight levels), and an interaction term on model parameters, and was verified using stepwise regression. Multivariate regression models indicated whether the factors had a positive or negative influence on model parameters. All data were analysed using SAS statistical software (SAS Institute Inc., 2001) at an  $\alpha$  level of 0.05.

## RESULTS

The model accurately simulated landscape processes and successional dynamics observed along the Tanana River. The model results reflected changes in the landscape that conformed to theoretical expectations, even though the individual replicate runs did not always reflect the landscapes that existed on the river during our study. Models T and T\*H both resulted in a landscape composed of 100% trees, as was expected. This series of scenarios served primarily as a model validation exercise. Both models performed as expected on a theoretical landscape without erosion and accretion. Without abiotic factors producing bare soils for colonization, the landscape would be expected to be composed entirely of late successional stages. Model T\*E performed better than all other scenarios in the low-herbivory field-study area (Table 1). However, in the high-herbivory areas (Table 2) it overestimated the proportion

**Table 1** Comparison of the observed landscape proportions in the low-herbivory study area with the equivalent simulation data used to validate the model. Standard errors were < 0.007 in all cases, making differences < 0.2 significant.

	Observed	Model T	Model T*H	Model T*E	Model T*H*E
Bare soil	0.1	0	0	0.2	0.2
Willow	12.7	0	0	13.9	10.1
Alder	6.6	0	0	5.7	5.7
W:A ratio	1.9	N/A	N/A	2.4	1.8
Tree	80.6	100	100	80.2	83.9
$\chi^2$ , d.f. = 3		24.1	24.1	0.3	0.9

**Table 2** Comparison of the observed landscape proportions in the high-herbivory study area with the equivalent simulation data used to validate the model. Standard errors were < 0.007 in all cases, making differences < 0.2 significant.

	Observed	Model T	Model T*H	Model T*E	Model T*H*E
Bare soil	6.2	0	0	0.4	0.4
Willow	5.3	0	0	20.7	7.0
Alder	6.8	0	0	8.2	8.6
W:A ratio	0.8	N/A	N/A	2.5	0.8
Tree	81.6	100	100	70.7	84.0
$\chi^2$ , d.f. = 3		22.4	22.4	51.9	6.5

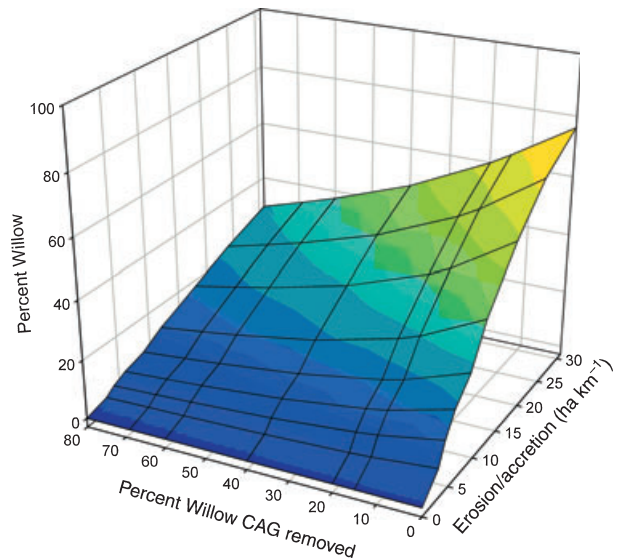
of willow by about 15% (T\*E model, 20.7% vs. observed, 5.3%) and the willow:alder ratio (W:A ratio) by 1.7% (8.2 vs. 6.8). It also underestimated the proportion of bare soil by 5% (0.4 vs. 5.8) and of late successional-stage trees by 11% (70.7 vs. 81.6). The results of model T\*H\*E were reasonable in the low-herbivory area (Table 1). The greatest difference between the simulations and observed data was in the overestimation of trees by 3% (83.9 vs. 80.6). This scenario also performed reasonably well in the high-herbivory area (Table 2). The greatest difference in that area was in the proportion of bare soil on the landscape, which was underestimated by 6% (0.4 vs. 6.2). No significant differences were detected in the W:A ratio in comparisons of model T\*H\*E and the observed field data.

### Model simulations

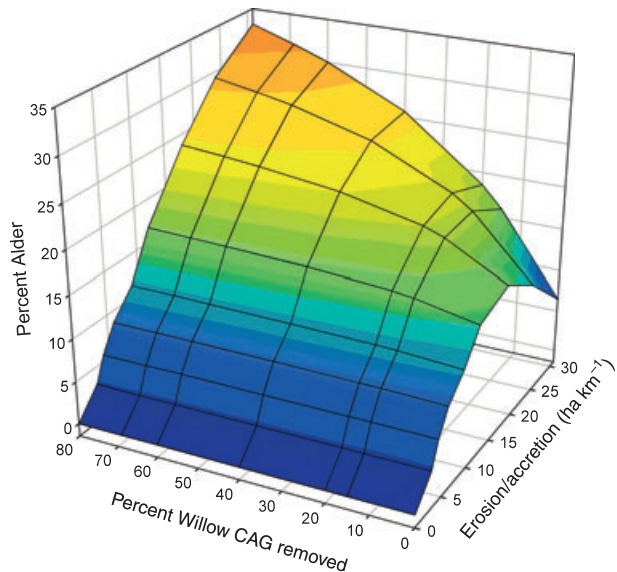
Because model T\*H\*E was the most robust in comparison with observed landscapes exposed to high and low levels of herbivory, it was used to test the effects of erosion/accretion and herbivory on the proportion of vegetation in the simulated landscape. In model T\*H\*E, erosion/accretion had a positive effect on the proportion of bare soil in the landscape ( $F_{7,5544} = 4.68 \times 10^5$ ,  $P < 0.001$ ), with increases in erosion/accretion rate increasing the proportion of bare soil. On the other hand, herbivory and the interaction between herbivory and erosion/accretion did not significantly affect the proportion of bare soil ( $F_{6,5544} = 0.14$ ,  $P = 0.992$  and  $F_{42,5544} = 1.29$ ,  $P = 0.102$  respectively). This effect was not surprising, as bare soil originates from erosion/accretion, while herbivory only affects transitions between vegetation types.

There were significant effects of erosion/accretion, herbivory, and their interaction on willow ( $F_{7,5544} = 1.78 \times 10^8$ ,  $P < 0.001$ ;  $F_{6,5544} = 1.70 \times 10^7$ ,  $P < 0.001$ ; and  $F_{42,5544} = 2.36 \times 10^6$ ,  $P < 0.001$  respectively; Fig. 2) and on all of the subsequent successional stages. The number of willow pixels in the simulated landscape decreased non-linearly with increasing herbivory and decreasing erosion/accretion (Fig. 2). The interaction of the two factors resulted in a peaked abundance of willow at the combination of lowest herbivory rates and highest erosion/accretion rates. Although the significant interaction was important in terms of the magnitude of effects, the general pattern was not surprising, given the roles played by herbivory and erosion/accretion.

Alder abundance, on the other hand, increased with increasing erosion/accretion and the interaction term, and then decreased as the erosion/accretion rate increased further at low levels of herbivory ( $F_{7,5544} = 1.46 \times 10^7$ ,  $P < 0.001$ ;  $F_{42,5544} = 3.71 \times 10^5$ ,  $P < 0.001$ ; and  $F_{6,5544} = 5.17 \times 10^5$ ,  $P < 0.001$  respectively; Fig. 3). The proportion of alder was positively related to herbivory (because herbivory speeds the transition from willow to alder), but the sharp decrease in alder abundance at low levels of herbivory combined with high erosion/accretion rate was not expected. At high erosion/accretion rates, alder is lost to erosion when herbivory rates are low, but when herbivory rates are high, it is replenished from the willow stage more quickly than it is lost to erosion.

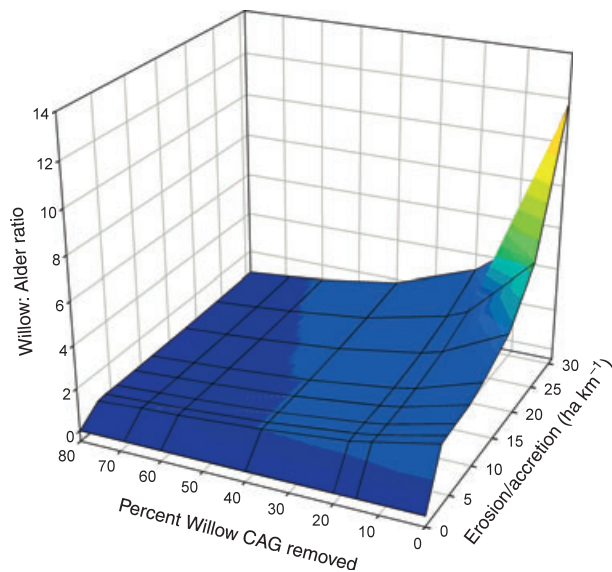


**Figure 2** Percentage of the simulated landscape in the willow stage during year 250 of the model resulting from various combinations of erosion/accretion and herbivory (percentage willow CAG removed). CAG refers to current annual growth in terms of mass of new shoots produced. Radial growth of main stem of shrub was not considered in this context.



**Figure 3** Percentage of the simulated landscape in the alder stage during year 250 of the model resulting from various combinations of erosion/accretion and herbivory (percentage willow CAG removed). CAG refers to current annual growth in terms of mass of new shoots produced.

The mature tree type was negatively correlated with erosion/accretion rate, and was positively correlated with herbivory and the interaction term ( $F_{7,5544} = 1.97 \times 10^7$ ,  $P < 0.001$ ;  $F_{6,5544} = 6.42 \times 10^6$ ,  $P < 0.001$ ; and  $F_{42,5544} = 5.61 \times 10^5$ ,  $P < 0.001$ , respectively). This vegetation type was affected more by changes in erosion/accretion than by herbivory.

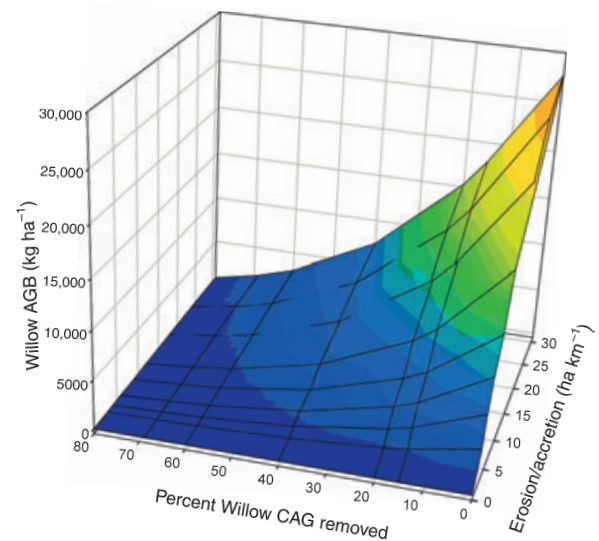


**Figure 4** Ratio of willow to alder in the simulated landscape during year 250 of the model resulting from various combinations of erosion/accretion and herbivory (percentage willow CAG removed). CAG refers to current annual growth in terms of mass of new shoots produced.

Although herbivory and the interaction term were statistically significant, the magnitudes of their effects were relatively minor in comparison to that of erosion/accretion. With the long residence time of the tree stage in the successional sequence, its proportion on the landscape was primarily governed by the rate at which it was lost to erosion rather than recruited from alder.

The ratio of willow to alder (W:A ratio) was significantly affected by erosion/accretion, herbivory and the interaction term ( $F_{7,5544} = 1.29 \times 10^6$ ,  $P < 0.001$ ;  $F_{6,5544} = 2.22 \times 10^6$ ,  $P < 0.001$ ; and  $F_{42,5544} = 4.63 \times 10^5$ ,  $P < 0.001$ ; Fig. 4). Erosion/accretion was positively correlated with the ratio, while herbivory and the interaction term were negatively correlated with it. The strongest interactive effect occurred at high erosion/accretion and low levels of herbivory, yielding a surprisingly sharp and pronounced peak in the W:A ratio (Fig. 4). Although high erosion rates (restarting the successional sequence) and low herbivory rates (favouring willow) would be expected to yield high W:A ratios, the shape of the response surface was not expected.

The residence time of all vegetation types was significantly affected by erosion/accretion, herbivory, and the interaction between the two ( $P < 0.001$ ), with the exception of bare soil, for which only erosion/accretion significantly influenced residence time ( $F_{7,5544} = 951.99$ ,  $P < 0.001$ ). Erosion/accretion had a negative effect on residence time after erosion/accretion levels were increased to a sufficient level to produce bare soil in the simulated landscape. Whereas herbivory decreased the residence time of willow it had negligible effects on the residence time of alder and mature trees (because of its simple effect of advancing the successional sequence). The



**Figure 5** Total willow aboveground biomass during year 250 of the model resulting from various combinations of erosion/accretion and herbivory (percentage willow CAG removed). CAG refers to current annual growth in terms of mass of new shoots produced.

residence time in all model scenarios averaged 1.2 years (SE = 1.0) for bare soil, 43.7 years (SE = 2.8) for willow, 31.7 years (SE = 0.6) for alder, and 118.7 years (SE = 8.1) for mature trees. Tree residence time increased as the number of years modelled increased, and is given here only as a reference point for the other vegetation types.

Total willow AGB in the simulated landscape ( $\text{kg ha}^{-1}$ ) and mean willow AGB per pixel ( $\text{g m}^{-2}$ ) were significantly affected by erosion/accretion, herbivory, and the interaction term ( $F_{7,5544} = 1.45 \times 10^7$ ,  $P < 0.001$ ;  $F_{6,5544} = 2.43 \times 10^7$ ,  $P < 0.001$ ; and  $F_{42,5544} = 1.16 \times 10^6$ ,  $P < 0.001$ ; and  $F_{7,5544} = 5.64 \times 10^7$ ,  $P < 0.001$ ;  $F_{6,5544} = 5.31 \times 10^7$ ,  $P < 0.001$ ; and  $F_{42,5544} = 7.50 \times 10^6$ ,  $P < 0.001$ , respectively). Total willow AGB was positively correlated with erosion/accretion and negatively correlated with herbivory and the interaction term (Fig. 5) in a pattern very similar to that of percentage willow in the landscape (Fig. 2). However, the peak in willow AGB was much sharper and more pronounced than that of percentage willow in the landscape, primarily because willow AGB declined much more quickly with increasing herbivory than was the case for percentage willow in the landscape. While erosion/accretion consistently favoured early seral (e.g. willow) communities, herbivory affected the biomass of willows (willow AGB) at a faster rate and more sharply than it affected the willow successional stage (percentage willow) and its transition to alder.

## DISCUSSION

Abiotic and biotic disturbances influence successional patterns and modify the proportions of plant communities on the landscape. The simulated abiotic disturbance of erosion/

accretion played a major role in shifting the landscape towards early successional communities, while the biotic disturbance of herbivory acted in the opposite direction, shifting the landscape towards later successional communities. Our treatment of community dynamics under fluctuating levels of herbivory and erosion was fairly simplistic, but it clearly illustrated that the interaction of these two processes results in landscape patterns that would not be predictable on the basis of either factor acting alone (see, for example, Fig. 3). It also provides insight into the large-scale effects of this push–pull nature of interacting, competing processes. Although there is a relative paucity of data from boreal ecosystems documenting long-term effects of herbivores on plant communities and successional trajectories (Jefferies *et al.*, 1994), herbivores have been shown to have significant short-term effects on vegetation and soil processes (McInnes *et al.*, 1992; Pastor *et al.*, 1993; Jefferies *et al.*, 1994; Kielland *et al.*, 1997). Our results also emphasize the short-term nature of the herbivore effect (primarily the willow–alder transition only). However, despite its short-term duration, its effect on large-scale landscape pattern can be great and long lasting, depending on its interaction with erosion/accretion (see, for example, Figs 2 and 3).

Most studies have analysed the effects of herbivores on established plant communities (e.g. Bryant & Chapin, 1986), and there is little empirical information on critical life-stage events such as germination and establishment. Our analysis falls into the former category. For example, colonization of willow on newly deposited alluvium was deterministically set at 1 year, whereas, in reality, both colonization and subsequent growth of the stand may be subject to substantial inter-annual variation. Moreover, our model does not differentiate among the several willow species typically found in the riparian zone of the Tanana River, which are differentially impacted by herbivory (Butler, 2003). For example, the biomass of barren-ground willow (*Salix brachycarpa*), a less preferred species, increased over sevenfold from our field sites near Manley Hot Springs to sites 250 km upriver near Fairbanks, despite the browsing frequency for this species (percentage of twigs browsed) increasing from about 0% near Manley Hot Springs to 15% near Fairbanks (L.G. Butler & K. Kielland, unpublished data). Thus, biotic interactions with other willow species, which we did not model, affect the distribution and abundance of barren-ground willow.

In contrast to the situation for boreal forests, several studies of temperate systems have illustrated how herbivory affects vegetation during critical life-history stages. For example, the absence of recruitment of cottonwood in selected areas of Yellowstone National Park between 1926 and 1995 has been ascribed to high rates of herbivory by resident herds of ungulates (Beschta, 2003). Moreover, stand and age structure of aspen and willow in Yellowstone have been explained as an interaction between vegetation and herbivory (Larsen & Ripple, 2003; Beschta & Ripple, 2006). These empirical observations are in agreement with our modelling of the landscape effects of herbivory.

The magnitude of the effect of herbivory on species assemblages is dependent on animal densities. We modelled this effect by varying browsing pressure. We know from field experience that there are real gradients in both the biotic and abiotic variables on the landscape. For example, rates of erosion decreased on average by about one-third across the 250-km stretch of the Tanana River from Fairbanks to Manley Hot Springs (Ott *et al.*, 2001), with a concomitant fivefold decrease in moose densities (Alaska Department of Fish & Game, 1998). However, the extent to which herbivore-affected vegetation modulates other ecological processes, such as hydrologic connectivity with the adjacent floodplain – as has been observed in smaller clearwater streams (Beschta & Ripple, 2006) – is unknown for large glacial rivers such as the Tanana River.

The W:A ratio provided the best reference for comparison of the simulated and the observed landscapes because it was the parameter least sensitive to changes in the simulated river size. Sensitivity testing (results not reported) indicated that increasing the size of the river lowered the proportion of trees in the landscape and increased the proportion of willow and alder, because all successional stages then had shorter durations in the landscape and trees must transition from only the alder stage. The W:A ratio, on the other hand, was not affected by changes in river size because it is a relative measure of the landscape and is strongly affected by the interaction of erosion and herbivory. For example, changing the width of the river from 60 to 300 m increased the willow and alder proportions by 2% and decreased the tree proportion by 4%, but it did not effect the W:A ratio at all. Moreover, the W:A ratio is a measure of habitat quality for mammalian herbivores that utilize both of these tall shrub communities for cover but only the willow for food (Collins & Helm, 1997; Weixelman *et al.*, 1998). It is, therefore, an important parameter in ecological community and population dynamics. The W:A ratio resulting from model T\*H\*E corresponded well with field observations (L.G. Butler & K. Kielland, unpublished data). We found that, on a per area basis, the W:A ratio in the high-moose-density area was 0.8; it was 1.9 in the low-moose-density area. The W:A ratios predicted for those areas in the model were 0.8 and 1.8, respectively.

Because the model calculates *relative* abundances (percentages) of successional stages, the amount of any one stage is not independent of that of the others. Whereas changes in relative abundances are biologically important, simply observing changes in the landscape does not necessarily illustrate the mechanism by which the changes occur. To determine what sequence of events initiated the change, residence time must be evaluated for changes in the duration and transition frequency of a particular vegetation type.

Erosion/accretion had a negative effect on all vegetation residence times. Herbivory had a negative effect on the residence time of willow and positive effects on the residence times of alder and mature trees. The positive effects of herbivory on alder and mature trees are attributable to the decreased duration of the willow stage, advancing the rate of

succession to subsequent stages. While erosion/accretion rate affected the residence time of willow (negatively) at low levels of herbivory, its effect at high levels of herbivory was negligible, as the effect of herbivory (also negative) was overwhelmingly dominant in shifting willow communities to alder communities (Butler, 2003).

Our modelling analysis demonstrated that the effects of erosion/accretion and herbivory are non-linear and, much more importantly, highly interactive. Although erosion/accretion always resulted in more willow communities at any given level of herbivory (Fig. 2), the magnitude of the effect depended on the level of herbivory. Similarly, although herbivory always resulted in less willow at any given level of erosion/accretion, the magnitude of the effect depended on the erosion/accretion rate (Fig. 2). The interaction of the two processes is especially interesting and counterintuitive in its effect on the percentage of the landscape in alder (rather than willow – i.e. Fig. 3). Here, at high erosion rates and low herbivory, alder communities are eroded faster than they are created, and alder peaks at an intermediate level of erosion/accretion – but only when herbivory is low. Although quite logical to us in retrospect, these interactive effects were initially surprising. Similarly, the dramatic peak in the response surface of the W:A ratio (Fig. 4) was not at all intuitive.

Thus, it is the *interactive* effect of the two types of disturbance that determines the outcome of pattern at the coarse, landscape-level scale. Our analysis also demonstrated how data from finer spatial scales (exclosures, line transects) and short time scales (5–10 years) can be combined with data from coarser spatial and time scales (aerial photogrammetry of the Tanana River) to yield insight into system dynamics at coarse spatial (landscape) and long time (successional) scales. In the Tanana River ecosystem, the interactive effects of the abiotic disturbance of fluvial dynamics and the biotic disturbance of herbivory are stronger and more important than is either process alone. The interaction of the two can have profound and unexpected consequences for ecosystem structure at both the individual stand scale and, especially, the landscape scale.

## ACKNOWLEDGEMENTS

This study was funded by the US Forest Service and received supplemental funding from the Bonanza Creek Long Term Ecological Research Program, the National Science Foundation, and the University of Alaska Fairbanks, Thesis Completion Fellowship. This study benefited greatly from erosion data provided by Tanana Chiefs Conference and the Alaska Department of Natural Resources.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online

### Appendix S1. Model framework.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01713.x> (This link will take you to the article abstract.)

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Editor: Glen MacDonald