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RESISTANCE AND RESILIENCE OF FLOATING MAT FENS IN INTERIOR ALASKA FOLLOWING AIRBOAT DISTURBANCE

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Abstract: The floating mat fens of the Tanana Flats in interior Alaska are productive wetlands near the urban center of Fairbanks. Airboat traffic has created a network of trails through the floating vegetation mats. We established protected areas along established trails, which allowed for measurement of plant community resistance to airboat traffic and resilience following cessation of traffic. The fen plant community was resistant to airboat traffic for two growing seasons, but productivity declined dramatically by the third year. Woody plants, grasses, and most forbs were eliminated in new airboat trails. Aboveground biomass and species diversity in plots protected from airboat traffic re-grew to undisturbed levels after four years. However, woody plants and many forbs did not re-grow in protected areas. Fen vegetation was therefore not resilient following cessation of traffic, as re-grown communities differed in both plant community composition and canopy structure. The loss of woody vegetation in particular has ramifications for possible alterations of ecosystem function. Airboats also reduced the amount of live belowground biomass and changed the vertical distribution of live roots.

Key Words: aboveground biomass, belowground biomass, community structure, diversity, peat, Tanana Flats

INTRODUCTION

Anthropomorphic disturbance on peatlands occurs at a wide range of intensities. Extensive losses to agriculture, forestry, peat harvesting, and urbanization have resulted in the worldwide loss of 0.1% of active peatlands annually (Chapman et al. 2003). However, localized impacts such as trampling, trail development, and small-scale peat mining are not well understood or documented (Racine et al. 1998, Chapman et al. 2003) but could produce significant cumulative effects (Beanlands et al. 1986, Forbes and Jefferies 1999, Forbes et al. 2001). Small-scale disturbance in northern wetland systems could result in long-term increases (Chapin and Shaver 1981) or decreases (Forbes 1992) in total plant biomass, localized increases or decreases in plant species diversity (Chapin and Shaver 1981, Chapin et al. 1988, Kevan et al. 1995), increased landscape heterogeneity (Forbes et al. 2001), non-native plant species invasions (Rose and Hermanutz 2004), substrate compaction (Chapin and Shaver 1981, Monz 2002) and alteration of water flow patterns (Racine et al. 1998).

In interior Alaska, there are extensive peat producing floating mat fens in the Tanana Flats between the Alaska Range and the Tanana River. The area provides habitat for large populations of moose, bear, waterfowl, and other migratory birds. The Tanana Flats fens are important to the nearby community of Fairbanks because they provide a relatively pristine, ecologically rich environment close to the city, and are used extensively for hunting, snowmachining, skiing, and other recreational activities. Human use of the Tanana Flats fens has impacted the ecosystem, particularly through airboats used during fall hunting. Airboats create trails by damaging aboveground vegetation, which may lead eventually to channelization of water flow (Racine et al. 1998). Although 345 km of trails had been mapped throughout the fens by 1998 (Racine et al. 1998), ecosystem effects of airboats are presently unknown.

Community responses to disturbance can be discussed in terms of both resistance and resilience. Community resistance is evaluated by the ability of individual species and functional groups of vegetation to survive an initial perturbation (Cole 1995, Hirst et al. 2003), with the community response measured soon following the disturbance. Resilience can be measured as the time required for a system to recover from disturbance to the same fundamental community structure and function (Mitchell et al. 2000). The goals of this four-year study were 1) to quantify the effects of airboats on fen vegetation by comparing above- and belowground biomass and plant diversity on active trails and undisturbed areas, 2) to measure resistance of fen vegetation to

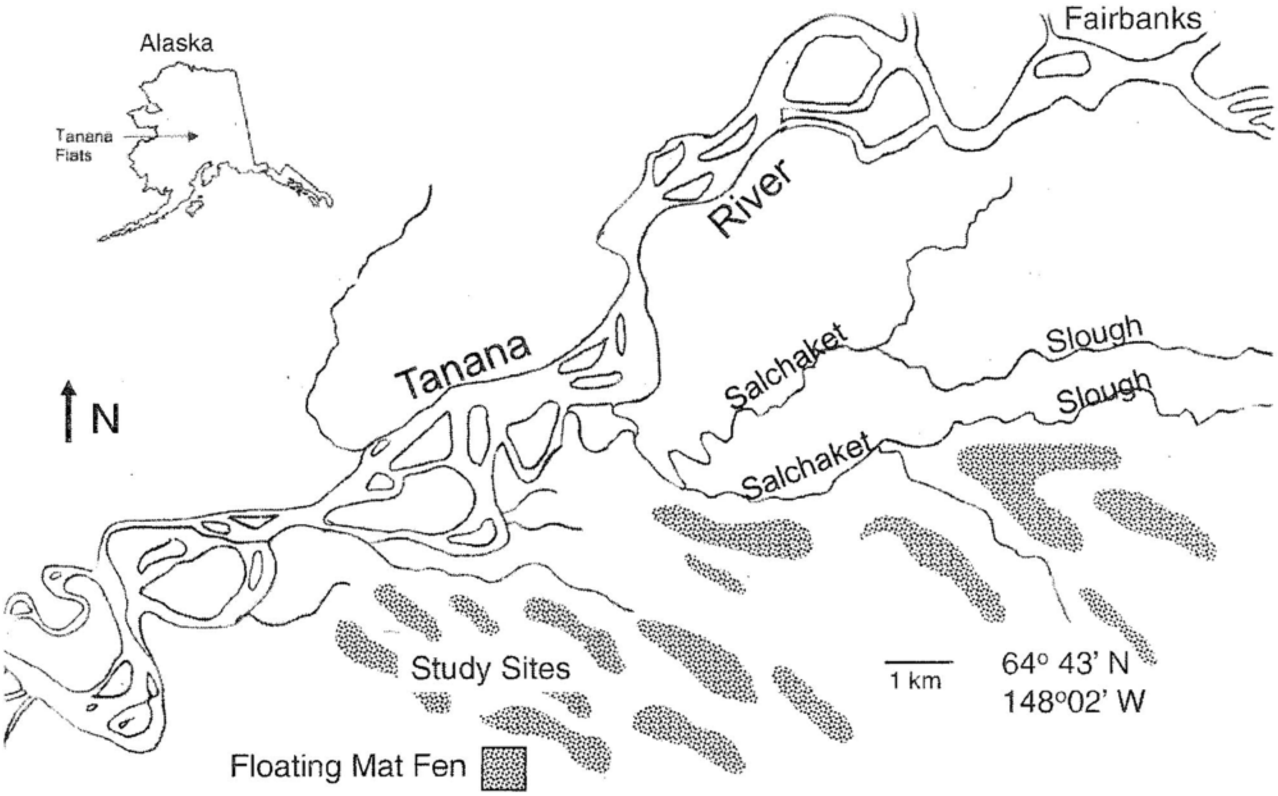

Figure 1. The study site on the Tanana Flats study site (Alaska).

disturbance by examining the effects of airboats on previously undisturbed areas, and 3) to measure resilience of the fen community by eliminating airboat traffic from some trails and documenting re-vegetation.

METHODS

Study Site Description

Research sites were located in a northern portion of the Tanana Flats, approximately 1.5 km south of the confluence of Sa1chaket Slough and the Tanana River (64°43' N, 148° 02' W; Figure 1), 10 km SW of Fairbanks, Alaska. The Tanana Flats are located in the eastern section of the Tanana Lowland, between the Alaska Range to the south and the Tanana River to the north (Figure 1). The fens are described as linear collapse-scar fens that formed through permafrost degradation of forested areas of *Picea mariana* (black spruce), *Populus tremuloides* (quaking aspen), or *Betula papyrifera* (paper birch; Jorgenson and Osterkamp 2005). Currently, fen wetlands on the Flats are expanding, as permafrost melts in forested areas (Jorgenson and Osterkamp 2005).

The Tanana Flats fens are characterized by a floating mat of vegetation, 0.5-1.5m thick, consisting of roots, rhizomes, and peat. Species at our sites consisted primarily of the forbs *Menyanthes trifoliata* and *Equisetum fluviatile,* the dwarf woody plant *Potentilla palustris,* and the sedges *Carex gynocrates,* C. *utriculata,* C. *diandra,* C. *magellanica,* and C. *aquatilis* (following Hulten 1968, Tande and Lipkin 2003). The mat floats above silt on either water or loose peat mixed with water (Racine and Walters 1994). The height of the water table above the silt fluctuates annually and seasonally with the mat rising and falling with the water. The fens are continuously flooded during the growing season, although the height of the water above the mat varies. There is little open water except for airboat trails, some upwelling areas, and a few creeks (Racine and Walters 1994). Ground- and surface water flow slowly (averaging 2 cm s^{-1}) across the fens from the Alaska Range in the southeast toward the northwest, where the water is discharged into the Tanana River (Racine and Walters 1994). In early July 2003, water from the surface of the mat averaged 22°C and contained 2.78 mg 1^{-1} dissolved oxygen, while water at 40 cm depth averaged 5°C with 0.65 mg1^{-1} dissolved oxygen. Water pH

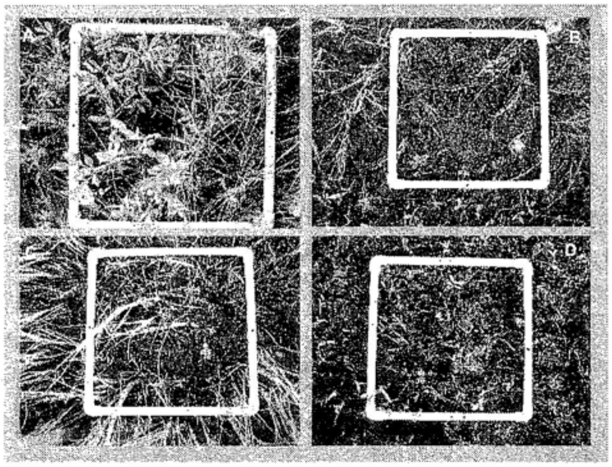

Figure 2. Photos from a representative site on August 12, 2004: A) undisturbed, B) active trail, C) exclosed, and D) new trail plots. The area of the quadrat is 0.0625 m^2.

averaged 6.7. The silt below the mat contained no permafrost, at least to a depth of 4 m (Jorgenson et al. 2001).

Airboat traffic in the Tanana fens occurs throughout the growing season from late May through October, with a large spike in activity during the September moose hunting season. Although the exact number is unknown, the Alaska Department of Fish and Game and the Interior Alaska Airboaters' Association estimate between 25 and 50 airboats use the fens. Airboat traffic, as estimated by moose harvest reports, has been generally consistent over the last 7 years; however, the extent of the airboat trails has been expanding over the years as boaters use new routes (Racine et al. 1998).

Experimental Design and Sampling

In March 2002 we established eight study sites extending along approximately 4 km of airboat trail. Sites were separated by a minimum of 200 m. At each site there were four treatment plots situated as closely as possible to each other, depending on conditions. The undisturbed or control plots (U) had no evidence of airboat traffic at any time in the past (Figure 2A). The active trail plots (AT) showed clear evidence of airboat traffic, probably for several years. Active trails cut through thickly vegetated areas and appeared as linear paths of crushed, damaged, or missing vegetation (Figure 2B). We constructed exclosed plots (E) in March 2002 by erecting tripods of birch logs over active trails. Exclosures forced airboat traffic around the plots, removing disturbance for the remainder of the study (Figure 2C). The purpose of these plots was to follow recovery of vegetation after the removal of the disturbance. As airboats bypassed the tripods and the exclosed plots, they created new disturbed areas, which we labeled new trail plots (NT; Figure 20). The purpose of the new trail plots was to follow the effects of airboat traffic on previously undisturbed areas.

Within our study area there was a large variation in the degree of root mat degradation in active trail plots, from areas of open water where the mat was completely removed to areas where aboveground vegetation was only slightly disturbed. We restricted our study sites to areas with enough mat integrity to support an exclosure, but where there was consistent airboat traffic. Our plots, therefore, had been impacted to a moderate degree with most above-ground biomass removed, but with a partially intact root mat (Figure 2B).

Each treatment plot was 1.0 × 3.25 m, divided into 14 sampling quadrats (25 × 25 cm) separated by 25-50 cm buffer strips. At each sampling period, all shoot vegetation, except for mosses, were clipped at the root or rhizome from a randomly selected quadrat. Because the system does not contain soil, this was considered aboveground biomass. Mosses were noted as present or absent. Shoot biomass was sampled on August 2-5 2002, July 7-10 2003, August 8-12 2004, and August 1 2005. Samples were sorted into standing live and dead biomass, with the live component sorted to species following regional nomenclature (Hulten 1968, Tande and Lipkin 2003). Samples were dried at 60°C to constant weight and weighed. A voucher collection was made and species identification was verified at the University of Alaska Museum Herbarium in Fairbanks, Alaska.

In August 2004 we sampled the roots and rhizomes in the mat using a 1.2 m long corer constructed of 10 cm diameter plastic pipe fitted with a saw blade at the bottom. We removed an intact core from the mat and cut it into segments at depths of 0-10 cm, 10-20 cm, 20-30 cm, 30-45 cm, 45-60 cm, and >60 cm, We report root data only to 60 cm depth in this paper. Deeper profiles contained primarily dead roots and detritus, and were highly unconsolidated and difficult to remove from the mat, making quantification of deep samples unreli-able.

Root cores were kept refrigerated until sorting, usually within 2-3 days. We removed an approxi-mately 2 g subsample from each segment of each core, and sorted the material to fine live (< 2 mm diameter), medium live (2-4 mm diameter), and coarse live (>4 mm diameter). For this paper, all

Table 1. Results of repeated measures analysis for the years 2002–2005 for total live shoots, standing dead shoots, forbs, woody, sedges, and the Shannon-Weaver diversity index. Treatments are undisturbed, active trail, exclosed, and new trail plots. The F values for the year and treatment effects, and their interaction, are presented, with levels of significance indicated.

	Total live shoots	Standing dead	Forbs	Woody	Sedges	Diversity
year $F_{3,84}$	0.00	0.00	0.00	0.00	0.00	0.00
treatment $F_{2,28}$	16.22****	16.46****	1.11	31.14****	6.94**	19.87****
year*treatment $F_{9,84}$	3.55***	1.86	1.37	4.01**	3.87***	4.21***

*$P<0.05$; ** $P<0.01$; *** $P<0.001$; **** $P<0.0001$.

live categories were combined into a single live root category. We did not attempt to differentiate species in the live root samples. Dead roots and rhizomes and detritus (fine dead material) were combined into a dead root category. Root subsamples were dried at 60°C to constant weight and weighed. We also dried and weighed each segment of the root core. Sorting subsamples to live and dead allowed calculation of percent live and dead material; these percentages were then multiplied by the mass of each segment of the root core to estimate total live and dead biomass within each segment of the core, within the total core, and on an area basis.

Data Analysis

Our experiment was a block design with tripod sites (blocks) as the fixed effect and treatments (U, AT, E, NT) as the random effects. We analyzed data using PROC MIXED (SAS v. 9.1), which is designed to analyze mixed models (Littell et al. 1996). We ran repeated measures analyses on the four years of above-ground biomass, including total live shoot biomass, standing dead biomass, forb biomass, woody biomass, sedge biomass, and the Shannon-Weaver diversity index ($H' = -\Sigma \ln P_i(P_i)$ where Pi is the proportional biomass of an individual species). We modeled the covariance structure within tripod sites (to allow for correlation between data points) as either autoregressive order one, unstructured, or compound symmetric covariance (Littell et al. 1996). For each analysis we selected the covariance structure with two model-fit criterion closest to zero (Akaike's Information Criterion and Schwarz's Bayesian Criterion; Littell et al. 1996). Analyses were run on ranked data, creating distribution-free tests, as our data, in general, did not meet parametric model assumptions (Conover 1980).

If an overall treatment effect was found, we analyzed years separately in PROC MIXED, using the same blocked design. We looked at three pre-planned contrasts, comparing each treatment (AT, E, and NT) to the undisturbed or control (U) plot. We used a Bonferroni correction (0.05/3) to arrive at a per-comparison error rate of 0.017 (von Ende 1993), which controls the experiment-wise error rate at $\alpha = 0.05$ (Day and Quinn 1989). In our results, we also noted comparisons that were significant at the 0.05 level.

Live and dead root data from 2004 and individual *Carex* species shoot data from 2005 were analyzed with the same blocked design in PROC MIXED. We again ran analyses on ranked data to create nonparametric tests, and analyzed the three pre-planned comparisons, comparing each treatment to the undisturbed plot. All statistical calculations were done in SAS v. 9.1 (SAS Institute lnc., Cary, North Carolina, USA).

RESULTS

We found a significant overall treatment effect for total live shoot biomass over the four years of the study (Table 1). This is due to the consistent and substantially lower biomass in all years on active trails compared to the undisturbed plots (Figure 2A and B, Figure 3A, Table 2).

Treatment effects on total aboveground live biomass changed over the four years of the study on new trail and exclosed plots as indicated by a significant year*treatment effect (Table 1). When plots were established in the spring of 2002, airboats were forced onto areas of undisturbed mat, forming the new trail areas. **In** 2002 and 2003 the total biomass on the new trail plots was very similar to total biomass on undisturbed plots (Figure 3A, Table 2). However, in 2004 and 2005, as airboats continued to use the new trails, total biomass dropped to significantly lower levels than in undisturbed areas (Figure 2A and D, Figure 3A, Table 2). When we established tripods in the spring of 2002, exclosed plots had similar total biomass to active trails and had far less total biomass than undisturbed plots (Figure 3A, Table 2). However by 2005, after four years of re-growth, the total live

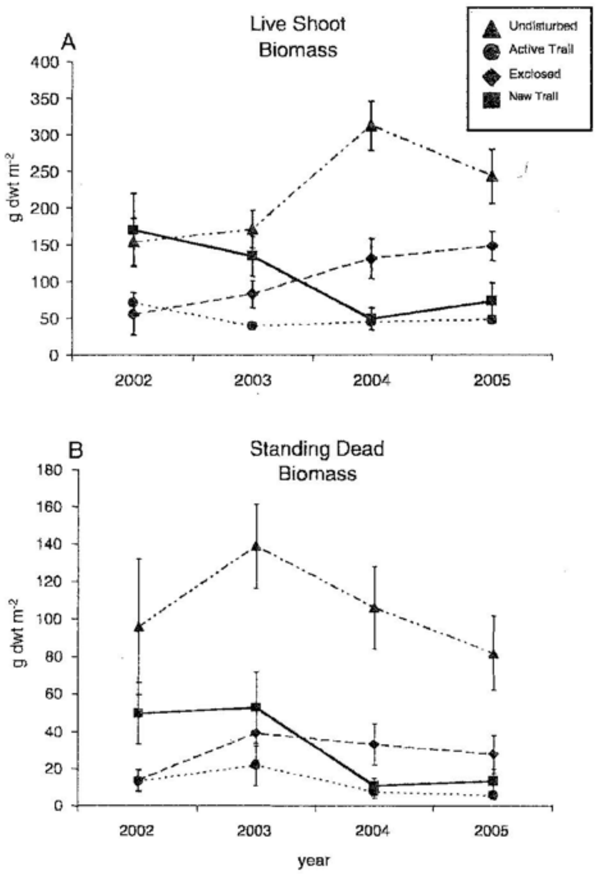

Figure 3. Response of shoot biomass to airboat traffic, 2002 through 2005, Tanana Flats fens, Alaska. Comparison between undisturbed, active trail, exclosed, and new trail plots for A) total live shoot biomass and B) total standing dead biomass.

shoot biomass on exclosed plots was not significantly different from that in undisturbed areas (Figure 3A, Table 2).

Airboats were highly effective in trampling standing dead shoot biomass (Tables 1 and 2, Figure 38). In the initial year of the study, new trail and undisturbed plots had similar amounts of standing dead biomass (Figure 38, Table 2). However, after one year of airboat traffic on new trails, levels of standing dead biomass were significantly less than on undisturbed plots, (Figure 3B, Table 2) and after two years, standing dead biomass on new trails dropped to levels similar to active trails (Figure 38). Exclosed areas did not develop standing dead biomass to levels found on undisturbed plots, even after four years without airboat traffic (Figure 38, Table 2).

Of the functional groups studied, forbs showed the least response to airboat traffic, with no overall treatment effect (Table 1). However, a year by year analysis showed less forb biomass in 2004 and 2005 on active and new trails compared to undisturbed areas (Figure 4A, Table 2). Although there were small amounts of many forbs in our study site, including *E. fluviatile, Epilobium palustre,* and *Pedicularis macrodonta, M. trifoliata* constituted the vast majority of forb biomass (86% averaged across all years and treatments). A repeated measures analysis on *M. trifoliata* biomass found no overall treatment effect for the four years of the study ($F_{3,28}$ = 0.60, p = 0.62), but less biomass in 2004 on active trails ($F_{1,21}$ = 7.71, p = 0.01) and on new trails ($F_{1,21}$ = 10.39, p = 0.004) compared to

Table 2. Results of pre-planned single degree of freedom contrasts for the years 2002–2005 for total live shoots, standing dead shoots, forbs, woody, sedges, and the Shannon-Weaver diversity index. The $F_{1,21}$ values are presented, with levels of significance indicated. U=Undisturbed, AT=Active Trail, E=Exclosed, NT=New Trail.

	Year	Total live shoots	Standing dead	Forbs	Woody	Sedges	Diversity
U vs. AT	2002	5.23§	12.41*	0.08	27.21***	7.23*	21.81***
	2003	20.83***	21.94***	0.08	38.42***	15.06**	53.50***
	2004	32.76***	41.31***	10.67*	18.42**	11.75*	37.69***
	2005	34.09***	43.84***	5.86*	28.81***	8.94*	17.63**
U vs. E	2002	12.10*	13.92*	0.02	26.69***	19.29**	43.66***
	2003	8.42*	13.18*	0.00	31.96***	2.02	12.86*
	2004	10.17*	15.80**	0.04	17.19**	4.88§	10.78*
	2005	3.84	11.75*	0.03	15.97**	0.16	0.31
U vs. NT	2002	0.53	0.88	0.02	1.83	0.91	0.42
	2003	1.36	7.94*	0.02	0.20	3.58	4.42§
	2004	33.70***	35.40***	12.03*	6.86*	6.51*	9.07*
	2005	21.89***	32.82***	4.58§	9.41*	6.40*	9.97*

§ P<0.05; *P<0.017; ** P<0.001; *** P<0.0001.

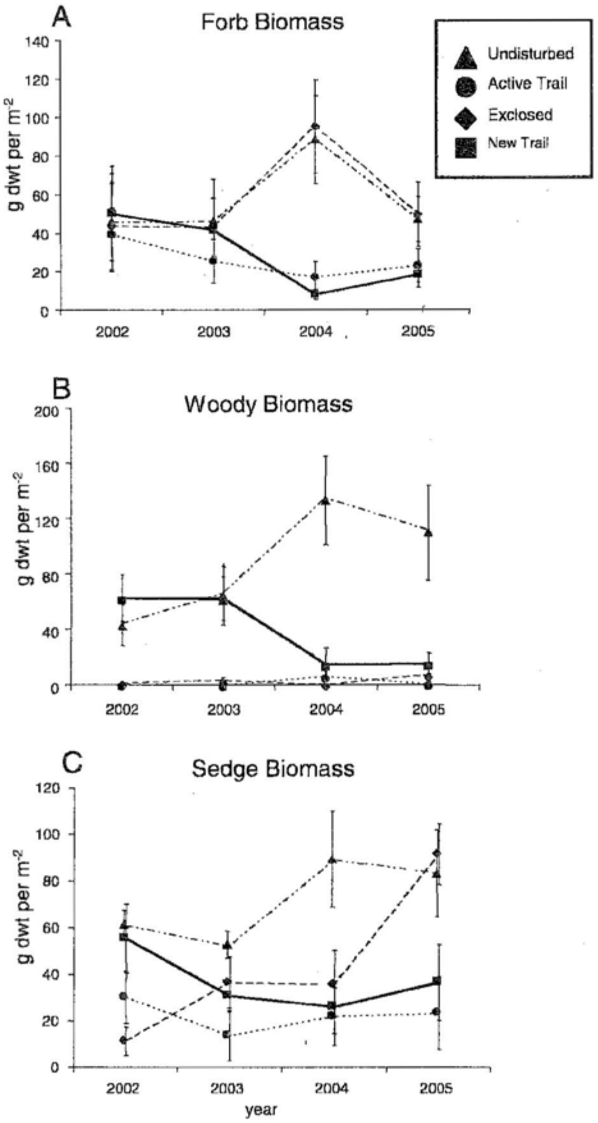

Figure 4. Response of shoot biomass to airboat traffic, 2002 through 2005, Tanana Flats fens, Alaska. Comparison between undisturbed, active trail, exclosed, and new trail plots for A) total forb biomass, B) total woody biomass, and C) total sedge biomass.

control areas. In other years, there were no differences in biomass in *M. trifoliata* between undisturbed and treatment plots.

Woody plants showed a strong overall treatment effect (Table 1). Active trails had little or no woody biomass, and woody biomass did not re-grow in exclosed areas even after four years without traffic (Figure 48, Table 2). There was also a year*treatment interaction (Table 1). New trails and undisturbed plots had similar levels of woody biomass in the first two years of the study, but by the third year of traffic woody growth was significantly reduced in new trails (Figure 48, Table 2). Although undisturbed areas contained small amounts of woody plants such as *Myrica gale*, *Chamaedaphne calyculata*, and *Salix* spp., 93% of all woody biomass (averaged over all years and all treatments) consisted of *Potentilla palustris*. A repeated measures analysis on *P. palustris* biomass found similar results to that of woody biomass. That is, active trails and exclosed plots had significantly less biomass than control plots in all years (active trails: in 2002, $F_{1,21} = 7.42$, $p = 0.013$; in 2003, $F_{1,21} = 12.33$, $p = 0.002$; in 2004, $F_{1,21} = 25.54$, $p < 0.0001$; in 2005, $F_{1,21} = 31.51$, $p < 0.0001$; exclosed areas: in 2002, $F_{1,21} = 6.90$, $p = 0.016$; in 2003, $F_{1,21} = 11.07$, $p = 0.003$; in 2004, $F_{1,21} = 28.17$, $p < 0.0001$; in 2005, $F_{1,21} = 26.72$, $p < 0.0001$). *Potentilla palustris* biomass on new trails in the first two vears of the study did not differ from that on control plots (in 2002, $F_{1,21} = 1.46$, $p = 0.24$; in 2003, $F_{1,21} = 0.00$, $p = 0.97$). In the third year of

control levels (in 2004, $F_{1,21} = 21.85$, $p = 0.0001$; in 2005, $F_{1,21} = 22.42$, $p = 0.0001$).

The sedge functional group showed an overall treatment effect (Table 1), mainly because active trail plots had less sedge biomass than undisturbed plots for all years of the study (Figure 4C, Table 2). The year*treatment interaction (Table 1) is due to the more complex response of sedges in the new trail and exclosed plots. Sedge biomass in the new trails did not differ significantly from undisturbed areas in 2002 and 2003, but was less in the following two years of the study (Figure 4C, Table 2). In 2002, sedge biomass under exclosures was significantly less than in undisturbed areas (Figure 4C, Table 2). In 2003, sedge biomass under exclosures had increased markedly to levels comparable to that in control areas (Figure 4C, Table 2). In 2004, exclosed sedges did not have the high levels of biomass exhibited in undisturbed areas (Figure 4C). However, by the final year of the study, exclosed and undisturbed sedges were at similar levels, much greater than biomass in plots with airboat traffic (Figure 4C, Table 2).

Unlike species within the forb and woody functional groups, sedge biomass was distributed somewhat uniformly among five dominant sedges: C. *gynocrates* (approximately 25% in August 2005), C. *utriculata* (23%), C. *aquatilis* (19%), *C diandra* (15%), and C. *magellanica* (17%). Even though sedges were treated as a functional group in our analysis, different responses to airboat traffic by different *Carex* species caused more overall variability in the group sedge response. For example, *C. aquatilis* biomass in active trails equalled that in

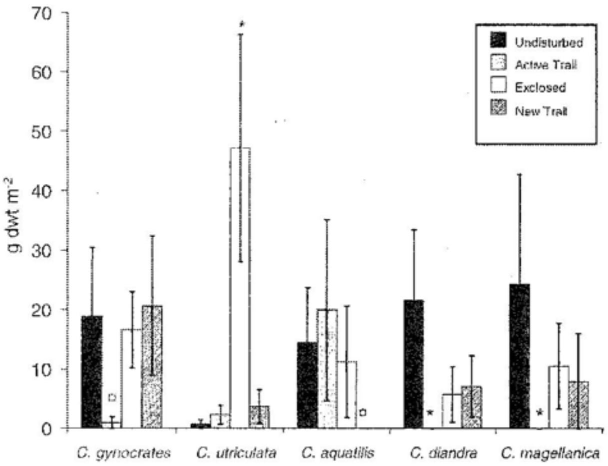

Figure 5. Response of *Carex* biomass to airboat traffic, August 2005, Tanana Flats fens, Alaska. Biomass of *C. gynocrates*, *C. utriculata*, *C. aquatilis*, *C. diandra*, and *C. magellanica* on undisturbed, active trail, exclosed, and new trail plots. Significant differences between undisturbed plots and other treatments are indicated by: *P < 0.05; *P < 0.017.

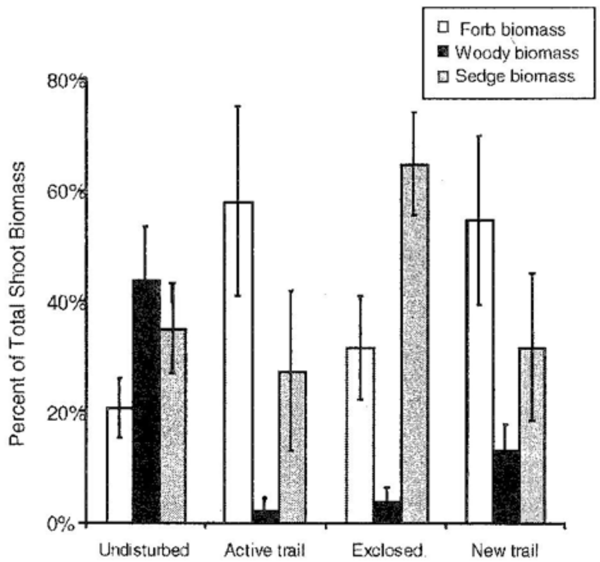

Figure 6. Response of shoot biomass to airboat traffic, August 2005, Tanana Flats fens, Alaska. Percent of total shoot biomass of sedges, forbs, and woody growth for undisturbed, active trail, exclosed, and new trail plots.

undisturbed plots. while the other major *Carex* species had little or no biomass in active trails (Figure 5). Although all major *Carex* species re-grew in excIosed plots, C. *utriculata* increased to dramatically greater levels than in undisturbed areas (Figure 5).

Functional groups showed substantially different responses to and recovery from airboat traffic, resulting in different distributions of functional groups within treatments by the fourth year of the study. In 2005. sedges and woody plants on undisturbed plots comprised roughly 40% each of total biomass. while forbs only constituted 20% (Figure 6). Compared to undisturbed areas at that time. active trails and new trails had a much lower proportion of woody biomass (10%), approximately the same proportion of sedge biomass (30%), and a far greater proportion (60%) of forb biomass (Figure 6). Re-growth in exclosed plots deviated from both undisturbed and active trail patterns, as sedges comprised a much larger proportion of biomass (65%) than in other treatments (Figure 6).

Species diversity, measured by the Shannon-Weaver index, showed highly significant treatment and year*treatment effects (Table 1). In all years, active trail plots had significantly lower diversity than undisturbed plots (Figure 7, Table 2). After one year of airboat traffic on new trails, diversity was lower than in undisturbed areas (Figure 7, Table 2). Differences between new trail and undis-turbed plots continued to increase throughout the study (Figure 7, Table 2). Although a reduction in diversity occurred quickly on new trail plots, it took four years for diversity in excIosed areas to approach that in undisturbed areas (Figure 7, Table 2).

There was significantly less total live root biomass in active and excIosed areas compared to control plots in August 2004 (Figure 8A). This indicates that neither aboveground biomass (Figure 3A) nor root biomass (Figure 8A) had recovered to undis-turbed levels after three years of protection from

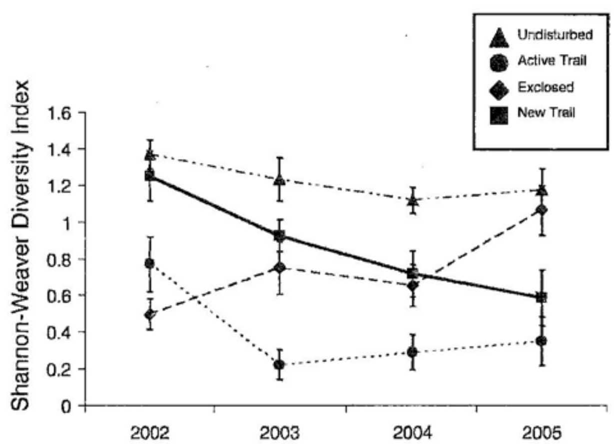

Figure 7. Response of plant species diversity to airboat traffic, 2002 through 2005, Tanana Flats fens, Alaska. Comparison between undisturbed, active trail, exclosed, and new trail plots for the Shannon-Weaver diversity index. The Shannon-Weaver diversity index is calculated as ($H' = -\Sigma \ln P_i(P_i)$) where P_i is the proportional biomass of an individual species within a plot.

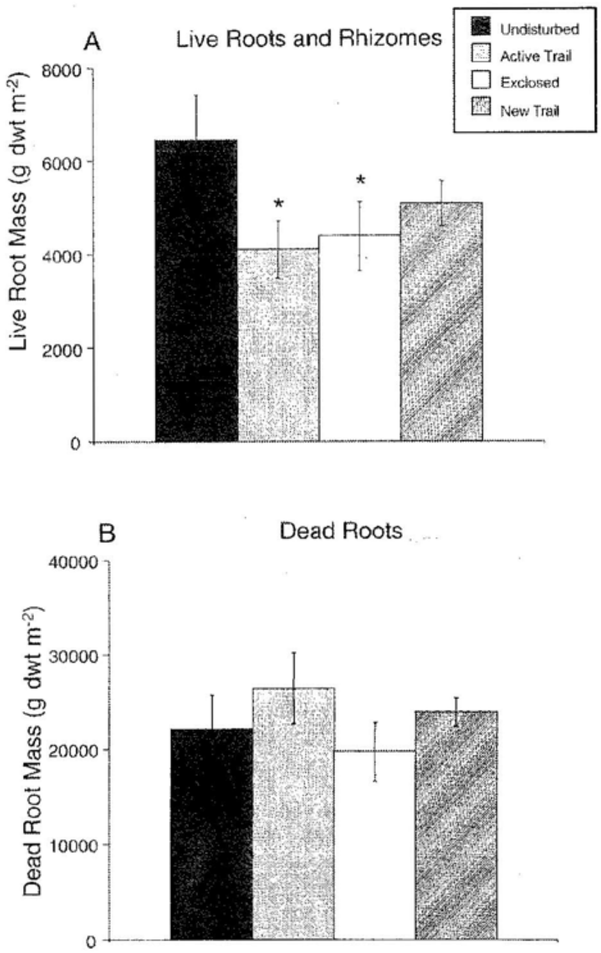

Figure 8. Response of root and rhizome biomass to airboat traffic, August 2004, Tanana Flats fens, Alaska. Comparison between undisturbed, active trail, exclosed, and new trail plots for A) live and B) dead biomass between 0 and 60 cm depth. Significant differences between undisturbed plots and other treatments are indicated by: $*P < 0.017$.

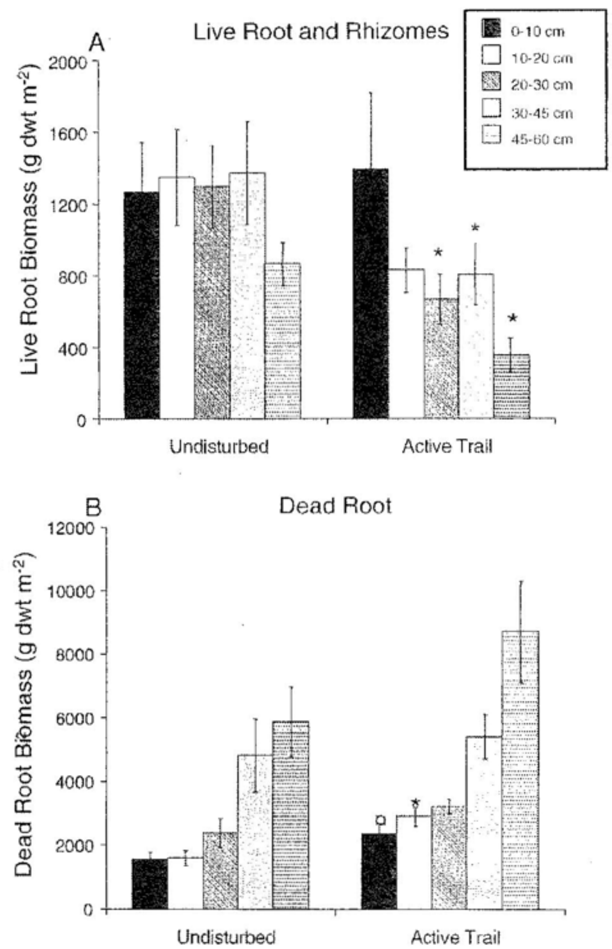

Figure 9. Response of root and rhizome biomass to airboat traffic, August 2004, Tanana Flats fens, Alaska. Comparison between undisturbed and active trail plots at different depths below the mat surface for A) live and B) dead biomass. Significant differences between undisturbed areas and active trails at each depth are indicated by: $*P < 0.05$; $*P < 0.017$.

airboats. There was a trend towards lower live root biomass in new trails relative to control plots in 2004 (- 25%, Figure 8A), contrasting the near 87% reduction in aboveground biomass in new trails in that year (Figure 3A).

In addition to differences in total live root biomass between active trails and undisturbed areas, there were differences in the distribution of live roots with depth. Undisturbed plots had a relatively uniform distribution of live biomass from the surface to 45 cm depth (Figure 9A). In contrast, live roots in active trails were concentrated at the surface. Active trails had live biomass comparable to undisturbed trails from the surface to 20 cm depth, but significantly lower biomass between 20 and 60 cm (Figure 9A).

There were no differences in the overall amount of dead belowground biomass between treatments (Figure 8B). The amount of dead biomass in the root mat increased with depth, with somewhat more dead biomass near the surface in active trail plots (Figure 9B).

DISCUSSION

Our experimental design allowed us to evaluate the resistance of the Tanana Flats fens to airboat disturbance by measuring the time it took for disturbance to have an effect, as shown in the comparison of new trail plots and undisturbed plots. Although airboat damage was apparent after a single season, it required three years of airboat traffic to reduce total live aboveground biomass and species diversity in previously un-trampled vegetation to levels below control levels. There was no difference in resistance between the three functional groups in the fens (woody, forbs, and sedges), each requiring three years of traffic to be degraded below control levels. However. some individual sedge species were more resistant to disturbance than others. *Cares gynocrates,* C. *diandra,* and C. *magellanica* in new trails had biomass comparable to that in controls after four years of traffic, although other sedge species did not. In general, vegetation in the Tanana fens was relatively resistant compared to wet fens in Alaska (Ahlstrand and Racine 1993) and wet tundra in Canada and Russia (Forbes 1993, Forbes et al. 2001), which, in some cases. showed observable changes in species composition after a single vehicle pass. Diversity decreased in new trails with the elimination of virtually all forbs, grasses and woody plants. The only speeies that persisted were the forbs *M. trifoliata* and *E. fluviatile*.

We defined resilience as the time required for a community to return to its original biomass, diversity, and species composition when disturbance was removed. and measured the resilience of the fen community by comparing exclosed and undisturbed plots over four years. While total aboveground biomass and species diversity in exclosed plots were the same as undisturbed controls after four years, fen vegetation had not returned to its original species composition by the end of the study. Specifically. woody plants, with the exception of small amounts of *P. palustris;* did not re-grow. We also found that even though forbs and sedges, as groups, achieved live biomass levels similar to undisturbed sites. the distribution of species within these groups also changed. Among the forbs, *M. trifoliata, E. fluviatile,* and *Lemna minor* re-grew, but many of the less numerous forbs did not. Among the sedges. C. *gynocrates,* C. *aquatilis,* C. *diandra* and C. *magellanica* re-grew, but the biomass of C. *utriculata* greatly increased (Figure 5). Using Sorensen's Quotient of Similarity to compare species composition ($Q/S = 2j/(a+b) \times 100$ where a = number species in sample 1, b = number species in sample 2, and j=number of species common to both; Wallwork 1976) there was only a 75% similarity between exclosed and control plots in 2005. We therefore conclude that the fens were not resilient after four years respite from disturbance.

A long-term loss of woody plants frequently occurs in anthropogenically disturbed arctic and sub-arctic sites (Chapin and Shaver 1981, Forbes 1992, Forbes 1996, Forbes et al. 2001). Also common is the proliferation of graminoids, particularly sedges, in disturbed areas (Chapin and Shaver 1981, Forbes 1992, Forbes and Jefferies 1999, Forbes et al. 2001). Rhizomatous graminoids are apparently able to quickly grow into space left by the loss of woody species because of their ability to propagate from subsurface meristems. Re-growth along airboat trails in the Tanana fens follows these common trends, although it is unknown whether these changes are long-term.

Dwarf shrubs provide three-dimensional structure in the arctic tundra, and in the Tanana fens, keeping snow from drifting and sublimating (Sturm et al. 2001). Shrubs thus encourage the accumulation of a thicker, better insulating snow pack (Sturm et al. 2001). This layer has been found in other studies to decrease the thickness of surface ice on ponds in the boreal forest (Jeffries and Morris 2006). The lack of woody vegetation on current and recovered trails could increase the depth of ice development in trails over the winter. This in turn, may retard ice melt in the spring, slowing initial root and shoot growth, and possibly slowing litter decay and nutrient cycling (Sturm et al. 2001, 2005).

Certain morphological and life history characteristics are common in plant species that re-grew well under exclosures in the floating mats. These include a high investment in below ground biomass, basal meristems located at or near the mat surface (Cole 1995), and robust rhizome development. Forbs with minimal belowground investment, such as *S. (Tassifolia* and *E. palustre* did not re-grow, while sedges and *M. trifoliata* with extensive root and rhizome development, re-grew quickly (Bernard and Fiala 1986, Haraguchi 1996, Tande and Lipkin 2003). *Menyanthes trifoliata* grows from a basal meristem at the mat surface (Grime et al. 1988), as do sedges. Sedges robustly re-growing under the exclosure were clonal plants that may have spread over several square meters, with only a portion of the plant in the degraded trails (Forbes 1996, Forbes and Jefferies 1999, Tande and Lipkin 2003). Live shoots adjacent to the trail could provide photosynthate (Pennings and Callaway 2000) and oxygen (Armstrong et al. 2006) to facilitate new shoot growth under exclosures, In contrast, woody plants maintain their perennating buds well above the mat surface. decreasing their ability to recover from trampling (Cole 1995).

The resilience of the fen vegetation in the Tanana Flats was facilitated by a lack of alteration to the water table. the narrow shape of the trail. and the relatively undisturbed root mat. There was no evidence that trails were accelerating movement of water out of the fens to the extent that water levels were lowered, although the rate of water flow in the trails was slightly higher than within the root mat (Racine and Walters 1994). In other peat wetlands, alteration of the water regime increased the damage caused by disturbance and slowed vegetation recovery. For example, in studies of peat mining, wetlands are often drained, resulting in dry conditions that prevent the re-establishment of native species (Lavoie and Rochefort 1996, Girard et al. 2002, Lavoie et al. 2003, Lavoie et al. 2005). In tundra systems, soils in vehicle tracks increased the thaw depth, increased soil moisture, and, in some cases, channelized water flow, resulting in alterations of soil physical and chemical properties and plant community composition (Chapin and Shaver 1981, Chapin et al. 1988, Kevan et al. 1995, Forbes etaI.2001).

The narrowness of the trail (2-5 m wide) also supported the re-growth of sedges and forbs (Forbes and Jefferies 1999, Forbes et al. 2001). Disturbed areas with high edge to interior ratios do not require the introduction of additional genets (seeds or seedlings), as lateral invasion from existing plants is rapid (Forbes 1996; Forbes and Jefferies 1999). In contrast, colonizing large open areas would require extensive seed production. In consistently flooded wetlands, vegetative reproduction is more common than seed propagation (Grace 1993), primarily because of the difficulty of seed growth in aquatic environments. In the Tanana fens, plant species generally rely on vegetative spread (Grime 1988, Haraguchi 1996). Flowering bodies on *Carex* species and on *M. trifoliata* were scarce and although *P. palustris* produced seed, we found few seedlings of any kind,

Roots and rhizomes constitute the vast majority of live biomass (93.6 ± 0.8% on undisturbed plots, August 2004) in the Tanana fens. Therefore, the effects of airboats on belowground biomass are of major importance in this system. Active trails in our study had 44% less total live root biomass than undisturbed plots because of lower live root biomass below 20 cm, It seems likely that the upper layers of the mat would primarily show reduced biomass if airboat traffic was directly destroying the mat. Instead, loss of live mat biomass may be caused by extensive shoot damage, preventing investment in deep roots.

Undisturbed fen vegetation contains a large quantity of standing dead material, which is trampled into the mat by airboat traffic. Incorporation of litter and dead plant material into soil surfaces may accelerate decomposition by fragmenting plant material and moving it into the soil, increasing the surface area of material available to decomposers (Floate 1981, Ruess 1987, McNaughton et al. 1988, Manley et al. 1995). Trampling could thus decrease the amount of carbon and nitrogen sequestered in the slowly decomposing litter and standing dead compartments, and may speed nitrogen cycling though the ecosystem (House et al. 1984, McNaughton et al. 1988, Manley et al. 1995, Zacheis et al. 2002).

Spatially limited disturbance can open up new patches with the potential for increased vegetation heterogeneity (Komarkova 1993). We found no evidence that patches created by airboats increased the incidence of existing rare species. Instead, robust sedge re-growth probably prevented rare species from successfully competing for space or light and made it unlikely that rare species richness will increase in the future. In addition, we did not observe evidence of the establishment of exotic species, although the possibility exists. Recent establishment of non-native invasive species have been noted in boreal fens in Newfoundland (Rose and Hermanutz 2004), and along recreational portage trails in Minnesota (Dickens et al. 2005). Responsible vectors were moose, humans, and boats, all of which are present in the Tanana fens.

The damage caused by airboats is long-term, and may cause permanent changes in the plant community and in the ecosystem. However, the damage is localized, limited to airboat trails that cover a small, but unknown, fraction of the Tanana fens. Closing the fens to airboat traffic is probably not feasible, as there is considerable public pressure for use of airboats in the area, particularly during hunting season. Closing the fens would also not correct the damage, as we have found that original communities will not reestablish, at least not in the short-term. We would recommend, however, that airboats be encouraged to use only existing trails, thus restricting further damage to the small fraction of the fens already damaged. Continuous use of existing trails may cause severe degradation of the mat, and possibly accelerate water movement out of the fens; however, the evidence for this is not strong. Our data clearly show that the initial two years of traffic on a pristine area can cause severe long-term damage with the loss of woody plants; avoiding this type of damage is imperative.

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