DIVISION S-10—WETLAND SOILS

Structure and Function of Peatland-Forest Ecotones in Southeastern Alaska

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ABSTRACT

High-latitude warming could cause northern peatlands to become C sources. Where peatlands border boreal forests, strong differences in ecosystem C balances reflect drainage differences. Because local drainage conditions could be influenced by alterations in temperature and precipitation regimes, peatland-forest ecotones represent useful locations for monitoring potential impacts of global warming. We characterized the soils, hydrology, and forest structure along transects bracketing a peatland-forest ecotone in southeastern Alaska. We expected to find soil properties and processes at the peatland-forest edge that were intermediate between those from peatland and forest. Instead, we found that above- and belowground features of the ecotone did not coincide. Conifers grew on mineral soils, but also grew on Cryofibrists and Cryohemists, soils with high soil organic C (SOC) contents to 100 cm (57 kg m^{-2}) that are significantly greater than the SOC contents of adjacent forested, non-Histosol pedons. Soil respiration rates (SRR) at peatland-forest edges (0.08 g CO_2–C m^{-2} h^{-1}), by contrast, were threefold lower than forest rates and did not differ significantly from peatland rates. Respiration rates were strongly influenced by water table height. Peatland and edge water tables were both significantly shallower than forest water tables. Our conceptual model suggests that if additional forest expansion and warmer summers enhance drainage of these edge soils and stimulate SRR to forest-like levels, 23 kg C m^{-2} could ultimately be mineralized from these extensive peatland-forest boundaries. Afforestation of peatland margins under this scenario could represent a transient positive feedback to rising atmospheric CO_2 levels.

A clear understanding of boundary or ecotone dynamics is critical to gaining insight into landscape-level patterns and processes (Wiens et al., 1985). How ecotones respond to altered precipitation and temperature regimes may presage landscape-level responses to climate change (Allen and Breshears, 1998; Peteet, 2000). The ecotone between boreal forests and northern peatlands may be the locus of strong feedbacks to climate change because general circulation models predict disproportionately large temperature and precipitation increases at northern latitudes (Houghton et al., 2001). For western North America in particular, model estimates include winter and summer air temperature increases as well as winter precipitation increases in excess of the corresponding global means. Carbon balance in high-latitude ecosystems is very sensitive to drainage conditions (Oechel et al., 1993; Alm et al., 1999). Globally, northern peatlands and boreal forests contain more C than the atmosphere; warming of these C reservoirs could generate positive feedbacks to rising atmospheric CO_2 levels (Gorham, 1991).

These cold organic soils may show less respiratory acclimation to increasing temperatures than warmer mineral soils (Luo et al., 2001). Improved drainage conditions at these peatland-forest ecotones could accelerate SOC mineralization (Freeman et al., 2001a). If warming and elevated CO_2 levels stimulate forest productivity at peatland margins, however, C sequestration by forests could offset C losses from peatlands. Peatland-forest ecotones thus represent ideal study sites for monitoring effects of climate change and drainage on landscape-scale SOC dynamics.

In southeastern Alaska, forests occupy 53% of the 11 million ha archipelago (Mead, 1998) and occur in a mosaic with peatlands. Peatlands have expanded and contracted in response to past climate change in southeastern Alaska (Heusser, 1952; Klinger et al., 1990; Hansen and Engstrom, 1996); Neiland (1971) noted that this peatland-forest tension zone could be influenced by climatic and hydrologic changes. In an exploratory survey that included southeastern Alaska, peatland soils were classified as Histosols and forested soils as Spodosols (Rieger et al., 1979). To our knowledge, no other studies have characterized ecotone soils or SRR for this area.

Our objectives were to characterize the soils, hydrology, and vegetation at the peatland-forest ecotone, and to determine the degree of correspondence between above- and belowground components of this ecotone. Because Histosols contain more organic C than any other soil order (Eswaran et al., 1993), we focused on soil properties relevant to C storage and to C loss.

MATERIALS AND METHODS

Site Description

We studied a subset of peatlands referred to as bogs. Across southeastern Alaska, bogs commonly support stunted mixed-conifer forests dominated by shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) and are dominated by peat-forming mosses, ericaceous shrubs, forbs, and sedges. Well-drained forests are dominated by tall western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Sitka spruce [*Picea sitchensis* (Bong.) Carr.], but also include Alaska yellow-cedar [*Chamaecyparis nootkatensis* (ex Don) Spach] and western red cedar (*Thuja plicata* Donn ex D. Don). Riparian forests occupy some of

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Abbreviations: D_b, bulk density; DBH, diameters at breast height; DOC, dissolved organic C; MAP, mean annual precipitation; PVC, polyvinyl chloride; SOC_{30}, soil organic C in upper 30 cm; SOC_{100}, SOC in upper 100 cm; SRR, soil respiration rates; θ_g, gravimetric water content.

the lowest elevations on the landscape, often lying meters below upslope peatlands. At our Common Snipe site, the forested landscape segment was 1.2 m lower than the adjacent bog.

We characterized bog-forest ecotones on Mitkof Island (500 km^2, Fig. 1), which has one of the greatest fractions of bogs of any large island in southeastern Alaska (Dachnowski-Stokes, 1941; USDA, 1997). Mean annual precipitation (MAP) generally increases from Petersburg (MAP 2690 mm, mean annual snowfall 2580 mm; Hogan, 1995) to Crystal Lake Hatchery (MAP 3660 mm) at the base of Crystal Mountain (1015 m). In Petersburg, air temperatures average −1.2°C in winter and 12.6°C in summer. Most soils in southeastern Alaska developed over glacio-marine deposits uplifted approximately 11 000 yr before present (Ives et al., 1967). Southern Mitkof Island is underlain by Cretaceous and Jurassic sedimentary rocks with outcroppings of Cretaceous greenschist, granodiorite, and volcanic rock (Brew et al., 1984; USDA, 2001).

Study Design

Using 1:24 000 aerial photographs, we identified >100 suitable ecotone study sites using roads, creeks, and the coastline as reference elements. We randomly selected one site (Common Snipe [CS], 15 m elevation) for intensive characterization and an additional five extensive sites. We described bog and forest pedons at all six sites. At CS, we established transects perpendicular to the bog-forest edge and stratified sampling locations: bog interior, bog edge, edge, forest edge, and forest interior (Fig. 1). Because our design was intended to bracket the ecotone, we defined edge stations based on visible characteristics (tree height, diameter, and density) and referenced the remaining stations to this edge (i.e., bog interior −10 m, bog edge −1 m, forest edge +1 m, forest interior +10 m).

When comparing soil properties (four stations: bog interior, bog edge, forest edge, and forest interior) to hydrology and tree structure (three stations: bog interior, edge, forest interior), we averaged bog edge and forest edge results to obtain a single edge value. In our synthesis of property changes across the bog-forest ecotone, we averaged data from multiple depths to obtain a single station-specific value. We present data from the Year 2000 in our synthesis because there were no qualitative differences in water level and soil respiration data between years.

Field Methods

To calculate surface slopes across ecotones, we surveyed all six approximately 0.5-ha sites at a 5-m grid interval (Topcon AT-F2 level, Paramus, NJ; Harrelson et al., 1994) referenced to differentially corrected GPS elevations (Trimble GeoExplorer II, Sunnyvale, CA) at permanent spike monuments. At each grid point at CS, we estimated the depth to mineral soil using a 1.2-cm diam. steel rod.

Pedons

To avoid disrupting the local vegetation and hydrology along transects at CS, we dug 16 soil pits (mean depth 108 ± 5 (SE) cm) at representative locations offset from the transects (Fig. 1, Table 1). At all sites, soils were classified to the subgroup assuming a cryic soil temperature regime (Soil Survey Staff, 1999; Alexander, 1991). Pedons were described using standard methods (Soil Survey Staff, 1993). We also measured the sodium pyrophosphate extract color (Soil Survey Staff, 1996) using a 1:2 (v/v) moist soil/saturated solution, and we estimated fiber content in the field by breaking open a 30 cm^3 clod and determining the fraction of each clod face occupied by non-living fibers, before and after rubbing (McKinzie, 1974). Pyrophosphate extract color and rubbed fiber content were used to categorize horizons as fibric, hemic, or sapric. To compare depth-specific data between pedons with differing horizon depths, we calculated average horizon depths for the uppermost five horizons and averaged soils data for these horizon depths.

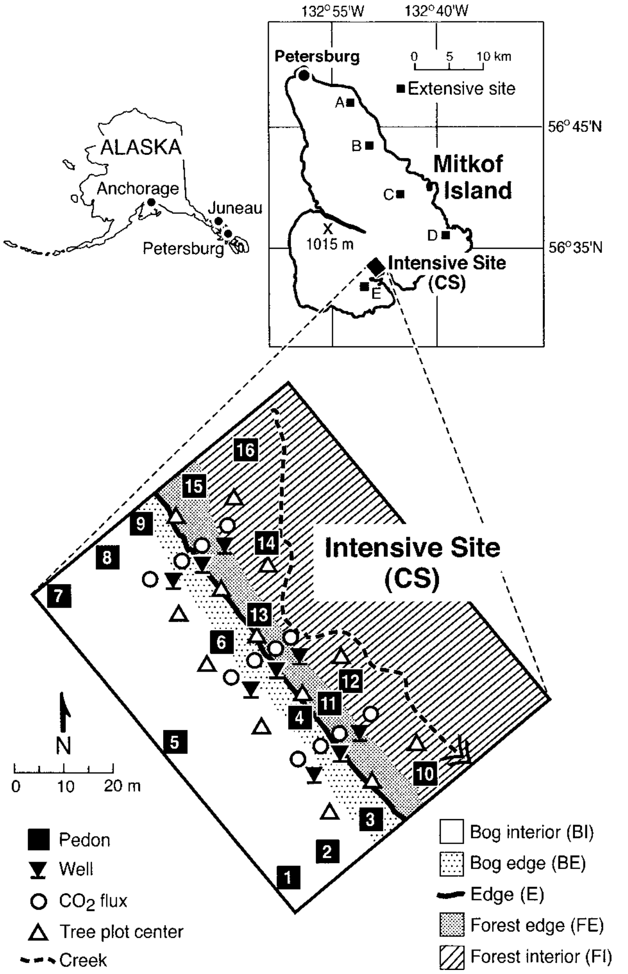

Fig. 1. Location of pedons, wells, tree plots, and soil respiration rings at Common Snipe (CS). Insets show locations of CS and five extensive sites on Mitkof Island as well as the location of Mitkof Island in southeastern Alaska.

Common Snipe Measurements

Hydrologic properties were measured along three transects at CS (Fig. 1). We used a water-activated alarm to measure summer water tables one to five times per week (1999 to 2001) at pairs of shallow and deep piezometers at bog, edge, and forest stations. Piezometers consisted of 2.5-cm i.d., 35- or 105-cm lengths of polyvinyl chloride (PVC) pipe coupled to 8-cm lengths of 0.25-mm-slotted PVC. Pump tests (Hvorslev, 1951; Freeze and Cherry, 1979) were performed on a subset of piezometers once in 1999 and twice in 2000. We removed water from the piezometers using multiple 60 cc syringes and recorded water levels over time. Hydraulic conductivities were calculated after graphically measuring the basic time lag and assuming shape factor "C" (Hvorslev, 1951). Because there were no differences between water table elevations obtained from pairs of shallow piezometers and wells slotted along their

Table 1. Soil properties (mean ± 1 SE) by station and by soil depth interval at Common Snipe. Different lowercase letters designate significant ($P < 0.05$) differences between depth intervals for a given station. Different uppercase letters designate significant ($P < 0.05$) differences between stations for a given depth interval.

Property	Depth	Bog interior		Bog edge		Forest edge		Forest interior	
	cm								
D_b, Mg m^{-3}	0–6	0.03 ± 0.01	a A	0.03 ± 0.01	a AB	0.06 ± 0.06	a AB	0.10 ± 0.02	a B
	6–14	0.05 ± 0.01	a A	0.08 ± 0.00	a AB	0.10 ± 0.02	a AB	0.18 ± 0.03	a B
	14–25	0.06 ± 0.01	a A	0.08 ± 0.01	a A	0.15 ± 0.02	ab A	0.74 ± 0.15	b B
	25–37	0.08 ± 0.00	a A	0.11 ± 0.01	a A	0.49 ± 0.21	b B	0.62 ± 0.13	b B
	37–51	0.08 ± 0.00	a A	0.11 ± 0.00	a AB	0.52 ± 0.25	b BC	0.98 ± 0.18	b C
C, %	0–6	41.0 ± 0.3	a A	43.9 ± 0.2	a A	44.8 ± 0.6	a A	39.7 ± 2.0	a A
	6–14	40.6 ± 1.0	a A	42.3 ± 0.5	a A	42.9 ± 2.6	ab A	34.8 ± 3.2	ab A
	14–25	42.8 ± 0.7	a A	43.5 ± 0.9	a A	42.4 ± 1.8	ab AB	5.0 ± 1.8	b B
	25–37	45.3 ± 0.5	a A	42.4 ± 1.9	a AB	26.5 ± 11.5	bc BC	13.4 ± 8.4	b C
	37–51	44.6 ± 0.6	a A	48.4 ± 1.0	a A	20.2 ± 12.3	c B	5.0 ± 1.2	b B
N, %	0–6	0.8 ± 0.2	a A	0.7 ± 0.1	a A	0.9 ± 0.0	ab A	1.2 ± 0.1	ab A
	6–14	1.1 ± 0.2	ab A	1.1 ± 0.1	ab A	1.6 ± 0.2	ab A	1.4 ± 0.2	b A
	14–25	1.4 ± 0.1	ab A	1.8 ± 0.2	b A	1.9 ± 0.2	a AB	0.2 ± 0.1	c B
	25–37	1.9 ± 0.1	b A	1.8 ± 0.1	b AB	0.8 ± 0.4	b BC	0.4 ± 0.2	ac C
	37–51	1.7 ± 0.0	ab A	1.8 ± 0.0	ab A	0.6 ± 0.3	b AB	0.2 ± 0.0	c B
C/N ratio	0–6	63 ± 11	a A	62 ± 5	a A	48 ± 1	a A	34 ± 4	a A
	6–14	44 ± 8	a A	40 ± 3	ab A	28 ± 5	a A	27 ± 5	a A
	14–25	32 ± 3	ab A	25 ± 4	ab A	23 ± 2	a A	22 ± 3	a A
	25–37	24 ± 2	b A	24 ± 1	b A	33 ± 2	a A	27 ± 3	a A
	37–51	26 ± 0	ab A	27 ± 0	ab A	33 ± 3	a A	32 ± 2	a A
θ_g, kg kg^{-1}	0–6	14.4 ± 2.4	a A	12.3 ± 3.7	a AB	7.6 ± 1.0	a AB	5.6 ± 0.8	a BC
	6–14	15.8 ± 2.6	a A	10.9 ± 0.5	a AB	7.8 ± 0.9	a AB	3.8 ± 0.2	ab BC
	14–25	14.0 ± 1.2	a A	10.8 ± 1.0	a A	7.2 ± 0.3	a A	0.8 ± 0.2	bc B
	25–37	10.6 ± 0.3	a A	8.1 ± 1.0	a AB	3.0 ± 1.2	a BC	1.3 ± 0.6	bc C
	37–51	11.6 ± 0.6	a A	8.5 ± 0.2	a AB	1.9 ± 1.2	a BC	0.5 ± 0.2	c C

entire length, we report the shallow piezometer readings as water tables.

We measured daytime SRR at four stations on 3 to 14 d each summer (1998 to 2001, Fig. 1). All living vegetation inside PVC rings (4-cm tall, 21-cm diam.) was clipped at least 1 h before SRR measurements with a portable infrared gas analyzer (EGM-1, PP Systems, Haverhill, MA). The gas analyzer was referenced to ambient CO_2 immediately before each reading; coefficients of variation for the 12 stations typically averaged <25%. At the same time, we measured soil temperatures at depths of 2 and 12 cm adjacent to the PVC collar.

We measured tree diameters at breast height (DBH, 1.4 m) and tree heights (Opti-Logic 400LH hypsometer, Tullahoma, TN) for five trees (>2 m tall and >5 cm DBH) in variable area plots (Fig. 1). One core from each tree was collected and rings were counted. Two plots were not included in the analyses because there were no trees >0.5 m tall within 5 m of the plot centers. We estimated whole tree, oven-dry biomass using allometric equations compiled by Stanek and State (1978: 51) and assumed C was 47% of oven dry biomass (Barnes et al., 1998).

Laboratory Methods

At CS, we measured bulk density (D_b; clod results presented on a field-moist volume basis; Blake and Hartge, 1986; Klemetti and Keys, 1983) of horizon-specific soil samples from 14 pedons. We also measured the percentage of C (%C) and percentage of N (%N) (Integra-CN system, Europa Scientific, UK), gravimetric water content (θ_g; expressed on a dry weight basis), and soil pH (0.01 M $CaCl_2$; Soil Survey Staff, 1996) for samples of the fine earth (<2 mm) fraction. Coefficients of variation were <10%. Soil organic C pool sizes were calculated by summing volumetric C values for horizons ($N = 58$) that had both D_b and %C data to 30 cm (SOC_{30}). We also estimated SOC pool sizes to 100 cm (SOC_{100}) for all pedons by estimating D_b, %C, and gravel content values for deep horizons ($N = 27$) that could not be sampled because of shallow water tables or poorly consolidated material. For organic horizons, gravel content was assumed to be 0% and D_b and %C were estimated with horizon midpoint depths (z) as an independent variable ($D_b = 0.0016\ z + 0.0359$, $R^2 = 0.60$, $P < 0.001$; %C $= 0.0013\ z + 0.4084$, $R^2 = 0.52$, $P < 0.001$). For mineral horizons, we used D_b, %C, and gravel content values from comparable depths in neighboring pedons.

Statistical Methods

To examine spatial patterns in soil properties across the bog-forest ecotone, we used two-way ANOVA to test for differences in soil properties between stations and between depths. To evaluate patterns of other ecosystem properties, including SOC and SRR, we used one-way ANOVA to test for differences between stations. Data were transformed as needed to meet ANOVA assumptions, but all results are presented untransformed. Where significant ($P < 0.05$) ANOVA results were obtained, Bonferroni-adjusted pairwise comparisons were performed. All analyses were performed with Systat 7.0 (SPSS Inc., 1997).

RESULTS

Soil Properties

There were significant differences in soil properties across the CS bog-forest ecotone, and some of these differences were depth-specific. For the uppermost depth interval (0–6 cm), D_b was lower and θ_g was higher at bog interior pedons than forest interior pedons (Table 1). Profile characteristics for four representative pedons are shown in Table 2. For 54 horizons from 15 pedons, pH values ranged from 2.8 to 3.6.

By the third depth interval (14–25 cm), all properties except C/N differed significantly between the bog and the forest (Table 1). In this depth interval, average %C, %N, and θ_g for bog interior, bog edge, and forest edge pedons were nearly an order of magnitude greater than corresponding values for forest interior pedons. Differences were less pronounced between forest edge and

Table 2. Description, classification, and selected properties of representative bog interior, bog edge, forest edge, and forest interior pedons at Common Snipe.

Horizon	Lower horizon depth	Moist color†	SPEC‡	RFC§	UFC¶	D_b	Texture#	C	N	pH ($CaCl_2$)
	cm					Mg m^{-3}		—— % ——		
				Pedon 8. Typic Cryohemist (Bog interior)						
Oi1	5	7.5YR 2/2	8/1	0.65	0.85	0.05	p	42	1.5	3.2
Oi2	18	5YR 3/3	8/1	0.50	0.80	0.07	p	44	1.7	3.2
Oi3	25	5YR 3/3	8/1	0.50	0.75	0.07	p	45	1.8	3.3
Oe1	41	5YR 3/2	8/1	0.30	0.75	0.08	mp	45	1.6	3.3
Oe2	63	5YR 3/2	8/2	0.30	0.75	*0.12*††	mp	*48*	–‡‡	–
Oe3	110	7.5YR 3/2	7/3	0.30	0.66	*0.14*	mp	*52*	–	–
				Pedon 9. Typic Cryohemist (Bog edge)						
Oi1	5	0.5 7.5YR 3/4, 0.5 10YR 5/6	8/1	1.00	1.00	0.04	p	44	0.6	3.3
Oi2	11	7.5YR 3/2	8/2	0.75	0.95	0.08	p	42	1.0	3.1
Oi3	18	7.5YR 3/3	8/2	0.66	0.80	0.08	p	44	1.3	3.2
Oi4	23	7.5YR 3/2	7/3	0.50	0.95	0.06	p	43	1.4	3.2
Oi5	38	5YR 3/3	8/1	0.40	0.75	0.09	p	42	1.6	3.1
Oe	47	7.5YR 2/2	7/2	0.30	0.60	*0.11*	mp	*46*	–	–
Oi’	68	5YR 3/2	8/2	0.45	0.75	*0.12*	p	*46*	–	–
Oe’	90	7.5YR 2/2	8/2	0.20	0.66	*0.14*	mp	*51*	–	–
				Pedon 15. Terric Cryohemist (Forest edge)						
Oi1	6	10YR 4/3	8/1	1.00	1.00	0.03	p	44	0.9	3.3
Oi2	12	10YR 2/2	8/1	0.60	0.85	0.06	p	44	1.2	3.1
Oe1	23	7.5YR 2/2	8/1	0.20	0.60	0.12	p	44	2.2	3.1
Oe2	35	10YR 2/1	7/2	0.05	0.20	0.19	m	34	1.0	3.2
Oa	52	10YR 2/2	4/4	0.10	0.50	0.27	m	32	0.9	3.2
C	86	0.5 2.5Y 3/2, 0.5 10YR 2/2, fff 2.5YR 2.5/4 mottles	–	–	–	0.85	gr s l	6	0.2	–
				Pedon 16. Oxyaquic Haplocryod (Forest interior)						
Oi	6	10YR 4/3	8/1	1.00	1.00	0.05	p	43	0.9	3.2
Oe	18	7.5YR 2/2	8/1	0.33	0.50	0.09	mp	44	1.0	2.9
E	29	N 3/0	–	–	–	0.61	gr s l	8	0.3	3.2
Bh	36	10YR 2/2	–	–	–	0.64	gr s l	5	0.2	–
Bsm	48	0.5 10YR 4/3, 0.3 5YR 4/6, 0.2 7.5YR 3/2	–	–	–	1.40	gr l co s	3	0.1	–
C1	63	0.7 5Y 4/2, 0.3 5Y 7/2 (m.g.)	–	–	–	1.12	gr s	1	0.0	–
C2	120	0.7 5Y 4/1, 0.3 5Y 7/2 (m.g.)	–	–	–	*1.12*	gr s	*0.5*	–	–

† Fff, few fine faint; m.g., mineral grains.
‡ Sodium pyrophosphate extract color.
§ Rubbed fiber content.
¶ Unrubbed fiber content.
# Gr, gravel(ly); l, loam(y); m, muck(y); p, peat; s, sand(y); co, coarse.
†† Estimated (italicized).
‡‡ Not determined.

forest interior pedons with increasing depth, although forest edge %C was four times greater in the deepest depth interval (37–51 cm). Although C/N ratios did not differ significantly across the ecotone at any depth, C/N ratios decreased monotonically from the bog interior to the forest interior at all depths.

The O horizon thicknesses decreased significantly from bog to forest at CS (Tables 3 and 4). The SOC_{30} and slope showed the opposite pattern, nearly doubling from bog to forest pedons. The SOC_{100}, by contrast, was significantly higher at edge pedons (56.5 kg m^{-2}) than at forest pedons (32.8 kg m^{-2}). The fraction of SOC_{100} in the upper 30 cm was greatest for forest pedons (0.49), more than double that of edge pedons and triple that of bog pedons. SOC contents of forest O horizons varied dramatically, ranging from 6 to 33 kg m^{-2} (mean 16 kg m^{-2}); horizon-specific C densities also ranged widely (4–165 kg m^{-3}), exceeding 72 kg m^{-3} in 12 horizons.

Soil properties varied by depth differently in the bog and the forest, reflecting the different depths at which the transition from organic to mineral horizons occurred. At forest edge and forest interior pedons, the significant increases in D_b with depth were matched by significant decreases in %C (Table 1). Bog D_b and %C changed little with depth because this organic-to-mineral transition occurred at greater depths for bog interior and bog edge pedons (95–253 cm, Tables 2 and 3). Unlike %C, %N increased with depth in bog pedons and decreased with depth in forest pedons. Ratios of C/N decreased with depth for all pedons, but the only significant decreases were at bog interior and bog edge pedons. At these pedons, surface C/N ratios (approximately 62) were >2.5 times greater than C/N ratios for the 25- to 37-cm depth interval. Only %C and %N yielded significant depth-by-station interactions, attributable to the abrupt and shallow transitions from organic to mineral soil in forest interior pedons.

Table 3. Pedon classifications and organic horizon thicknesses for six sites on Mitkof Island. Pedon locations at Common Snipe (CS) are mapped in Fig. 1.

Station	Site	Pedon	Classification	Organic horizon thickness
				cm
Bog interior	CS	1	Typic Cryohemist	236
		2	Sphagnic Cryofibrist	226
		5	Typic Cryohemist	228
		7	Typic Cryohemist	253
		8	Typic Cryohemist	218
Bog edge	CS	3	Typic Cryofibrist	146
		4	Terric Cryohemist	95
		6	Typic Cryohemist	140
		9	Typic Cryohemist	153
	A	17	Typic Cryofibrist	> 135
	B	18	Typic Cryohemist	> 165
	C	19	Typic Cryohemist	> 250
	D	20	Sphagnic Cryofibrist	99
	E	21	Typic Cryofibrist	> 145
Forest edge	CS	11	Terric Cryohemist	50
		13	Typic Cryaquod	29
		15	Terric Cryohemist	52
	A	22	Fluvaquentic Cryofibrist†	> 135
	B	23	Typic Cryofibrist	> 140
	C	24	Terric Cryohemist	81
	D	25	Terric Cryohemist	100
	E	26	Typic Cryohemist	> 145
Forest interior	CS	10	Terric Cryohemist	56
		12	Oxyaquic Haplocryod	8
		14	Histic Cryaquept	20
		16	Oxyaquic Haplocryod	18

† Cg from 23–49 cm.

Pedon Classifications

Across all six sites, pedon classifications reflected O horizon thickness differences between and within stations (Table 3). The thick O horizons of bog interior, bog edge, and forest edge stations resulted in all but one of 22 pedons being classified as Histosols. Of these 21 Histosols, the most common subgroups were Typic Cryohemists (9) and Terric Cryohemists (5). All Histosols were in dysic families. The only forest edge pedon not classified as a Histosol (CS Pedon 13: Typic Cryaquod; Fig. 1) shared qualities of the two forest interior Haplocryods: slopes >5%, shallow E-Bh-Bsm horizon sequences, and thixotropic material. At CS, forest interior pedons showed large differences in O horizon thicknesses and encompassed three soil orders: Histosols, Spodosols, and Inceptisols.

Soil Respiration, Hydrologic, and Forest Patterns

Interannual variability in SRR was low (Fig. 2). Over a 4-yr period, average forest interior SRR were more than double rates at bog interior, bog edge, and forest edge stations (<0.12 g CO_2–C m^{-2} h^{-1}). Forest interior water tables were consistently and significantly deeper than bog interior or edge water tables (Table 4) because the nearby creek created a sharp hydraulic gradient (Fig. 1). Edge hydraulic conductivities at 25 cm (1.3×10^{-7} m s^{-1}) were an order of magnitude lower than bog or forest conductivities. Hydraulic conductivities decreased with depth and were approximately two orders of magnitude lower at 75 cm than at 25 cm. Tree heights and basal areas in the bog interior were significantly lower than corresponding measures of edge or forest interior trees (Table 4). Although there were no

Table 4. Comparison of soil, hydrologic, and forest characteristics for bog interior, edge, and forest interior stations at Common Snipe. For soil data, bog edge and forest edge pedon data were averaged to obtain a single edge value. Values (mean ± 1 SE) in rows followed by different lowercase letters are significantly different ($P < 0.05$).

Data type	Characteristic	Bog interior		Edge		Forest interior	
Soil	Organic soil thickness, m	1.60 ± 0.45	a	1.06 ± 0.13	ab	0.46 ± 0.14	b
	SOC_{30}, kg C m^{-2} (30 cm)$^{-1}$	7.7 ± 0.5	a	13.6 ± 2.5	a	14.2 ± 2.8	a
	SOC_{100}, kg C m^{-2} (100 cm)$^{-1}$	54.3 ± 1.1	ab	56.5 ± 4.9	a	32.8 ± 9.1	b
	SOC_{30}/SOC_{100}	0.14 ± 0.01	a	0.24 ± 0.04	a	0.49 ± 0.07	b
Hydrology	1999 water table depth, cm	−3.0 ± 0.5	a	−3.4 ± 0.4	a	−13.7 ± 0.5	b
	2000 water table depth, cm	−2.4 ± 0.6	a	−3.0 ± 0.6	a	−20.8 ± 0.5	b
	2001 water table depth, cm	−7.6 ± 1.5	a	−8.6 ± 1.6	a	−16.3 ± 1.5	b
	k† at 25 cm (10^{-7} m s^{-1})	19.6 ± 8.3	a	1.3 ± 0.7	a	51.2 ± 17.5	a
	k† at 75 cm (10^{-9} m s^{-1})	3.0 ± 0.0	a	5.2 ± 2.3	a	2.6‡	
	Slope, %	10.1 ± 3.8	ab	6.1 ± 1.2	a	20.1 ± 8.8	b
Forest	Height, m	4.4 ± 0.7	a	7.6 ± 0.7	b	8.4 ± 1.6	b
	Basal area, m^2 ha^{-1}	5.5 ± 2.4	a	28.6 ± 8.3	b	37.2 ± 4.4	b
	Age, yr	100 ± 22	a	127 ± 21	a	140 ± 15	a
	Mean maximum age, yr	194 ± 63	a	213 ± 40	a	246 ± 13	a

† k, hydraulic conductivity.

‡ This term not included in ANOVA because $N = 1$.

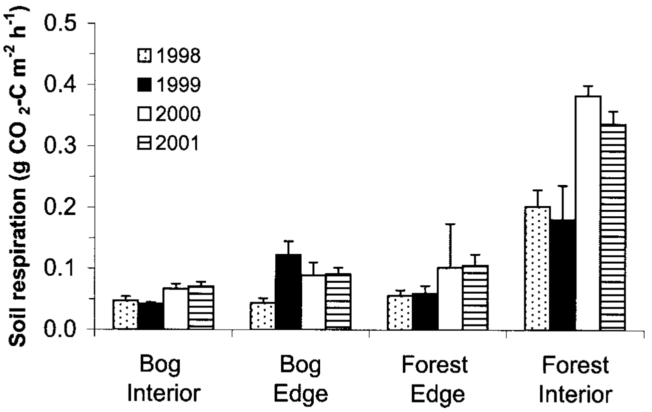

Fig. 2. Mean (+ 1 SE) soil respiration rates (1998 to 2001) for four Common Snipe stations. For each year, forest interior rates were significantly greater ($P < 0.05$) than bog interior, bog edge, or forest edge rates.

significant differences in the average or maximum ages across the ecotone, ages consistently increased from the bog to the forest.

Changes across the Ecotone

We categorized patterns of change across the ecotone. If edge values fell outside the range of corresponding bog and forest values, this reflected an anomalous change. If edge values were intermediate between those of the bog and forest, we examined whether the differences between edge and non-edge values were significant (abrupt) or not (gradual).

The aboveground ecotone, which we quantified using both tree basal area and height, changed abruptly, as both edge basal area and height were significantly greater than corresponding bog values (Table 4). In Fig. 3, 15 edge properties are plotted on normalized scales defined by bog interior (−1) and forest interior (+1) values to facilitate comparison between properties. The two properties used to define the aboveground ecotone (basal area and tree height) are plotted at the top, to highlight the lack of correspondence with belowground properties. Other than basal area and tree height, only edge tree age and SOC$_{30}$ plotted closer to the forest interior value than the bog interior value. Of the remaining 11 edge properties, five changed anomalously or abruptly. Edge hydraulic conductivities, slopes, and SOC$_{100}$ were outside the ranges defined by bog and forest values (anomalous). Water table and SRR (both from summer 2000) changed abruptly.

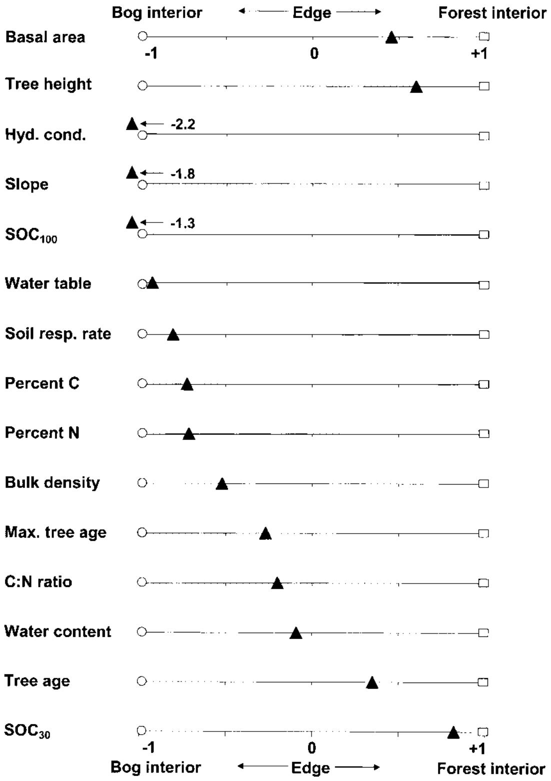

Fig. 3. Mean Common Snipe edge values (solid triangles) for 15 properties normalized to the ranges defined by mean bog interior (left side; open circles; −1) and forest interior (right side; open squares; +1) values. If an edge value were the average of the corresponding bog and forest interior values for a particular property, it would plot in the center of the graph with a value of 0. Hyd. cond. (hydraulic conductivity at 25 cm); original units as in Tables 1 and 4 and Fig. 2.

DISCUSSION

Lack of Correspondence between Above- and Belowground Properties

Belowground differences across the bog-forest ecotone did not coincide with the abrupt changes we observed in aboveground properties: at edge stations, belowground properties were more bog-like, while aboveground properties were more forest-like. Soil C stocks to 100 cm, water tables, and SRR differed significantly between edge and forest stations, but there were no significant differences between edge and forest basal areas or tree heights. Thus, belowground structural elements such as water tables and SOC$_{100}$ appeared to influence ecosystem functions such as soil respiration more strongly than did aboveground structural elements. Soils and vegetation may have distinct response thresholds to changing temperature and precipitation regimes, with pedogenetic changes lagging vegetative changes (Camill and Clark, 2000; Hansen and Engstrom, 1996). If vegetation responds more quickly to climate change than soils, vegetation and soils at ecotones could become decoupled (Stohlgren and Bachand, 1997). Any decoupling would be amplified by positive feedbacks. Once pine seedlings exceed 2 cm in diameter, for example, they are capable of slowing or stopping peat growth, a common agent of pine mortality (Ohlson et al., 2001). Wiens et al. (1985) have argued that edaphic patterns determine the locations of boundaries between vegetative communities, but our results show that vegetation patterns need not precisely reflect belowground soil properties and processes (Swanson and Grigal, 1989; Stohlgren and Bachand, 1997).

Although edge basal areas were intermediate between those of bog and forest stations, edge hydraulic conductivities, SOC$_{100}$, and slope were not bracketed by the corresponding bog and forest values. Carbon storage at peatland-forest edges could be more strongly influ-

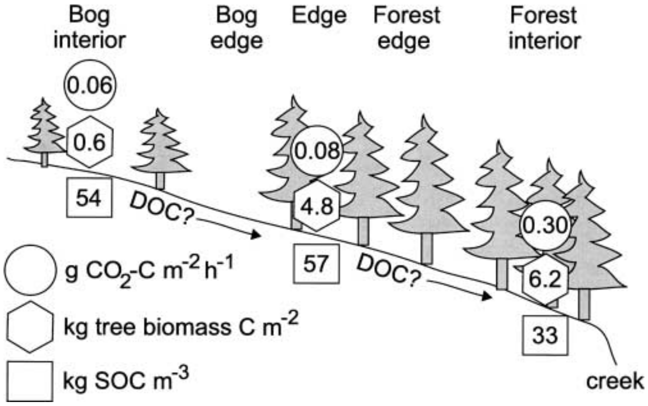

Fig. 4. Conceptual model based on soil respiration rates, tree biomass carbon estimates, and soil organic carbon pool sizes for the bog-forest ecotone at Common Snipe. Dissolved organic carbon (DOC) could link different parts of the catena.

enced by factors governing C losses (i.e., respiration, leaching) than by factors responsible for C inputs (i.e., run-on, litter) (Schuur et al., 2001; Schlesinger and Andrews, 2000). Soil respiration rates in northern peatlands and boreal forests are controlled by drainage (Oechel et al., 1993) or by the seasonal allocation of photosynthates belowground (Hogberg et al., 2001). For both temperate (A.S. Hartshorn, 2003) and tropical (Davidson et al., 2000) rainforests, soil water content was a better predictor than soil temperature of SRR. Although summer soil temperatures were not significantly different between stations at CS, soil temperatures were commonly lowest at shaded forest interior stations where SRR were highest (A.S. Hartshorn, 2003). Although we did not measure SRR outside of the growing season, we expect that cooler temperatures would further amplify the importance of water table differences and minimize the importance of soil temperature differences.

Soil respiration rates were consistent between years and across stations. Bog SRR were not significantly different from edge SRR (Fig. 2 and 4) and fell within the range of values reported for other northern peatlands (Silvola et al., 1996). The low SRR we recorded at bog edge and forest edge stations may be one reason for the large SOC stocks at the bog-forest edges (Valentini et al., 2000). Forest SRR, by contrast, were greater than rates reported for European boreal forests dominated by pine or spruce (Hogberg et al., 2001; Buchmann, 2000; Widen and Majdi, 2001) and were associated with the lowest SOC_{100}. Additional characterization of C inputs (e.g., run-on, litter) would clarify the role of C losses via respiration in defining the pattern of C stocks across this ecotone.

Variability in Forest Properties

Forest properties were highly variable. We were able to detect significant edge-forest differences despite this variability. For example, average forest SOC_{100} was significantly lower than edge SOC_{100} (Table 4, Fig. 4) although forest SOC_{100} ranged from 17 to 54 kg m^{-2}, comparable with the variability in SOC_{100} reported for four forest pedons in Alaska (Ping et al., 1997). The average forest SOC in O horizons at CS is nearly double that reported for southeastern Alaska (Alexander et al., 1989) and nearly sevenfold greater than that reported for the western Oregon (Homann et al., 1995). These discrepancies likely resulted because the Alaska pedons did not include forested peatland margins and because the Oregon pedons were subjected to prescribed fire. The threefold greater D_b of forest surface horizons (Table 1) may result from greater decomposition rates or root compaction (Chappell et al., 1996). Although we measured SRR at stations offset from pedon locations, the high SRR we recorded at forest interior stations indicate high decomposition rates that could lead to the accumulation of recalcitrant and dense SOC in the surface horizons of the forest.

Across the bog-forest ecotone, SOC_{100} was greatest in poorly drained settings with lesser slopes (bog interior-forest edge) and lowest in well-drained settings with greater slopes (forest interior). The high variability we observed in forest SOC_{100} also reflected variability in slopes, which could influence local drainage patterns. Local drainage appears to affect O horizon thickness and development of Histosols, Spodosols, and Inceptisols. Drainage of forest pedons is a function of steep hydraulic gradients resulting from channel incision, sharp texture contrasts between O and E horizons, and higher transpiration rates. Forest interior SOC_{100} peaked in the most poorly drained setting (Pedon 14), 2 m from the creek channel (Fig. 1). Intermediate SOC_{100} was found for the only forest pedon classified as a Histosol (42 kg m^{-2}; Pedon 10; Table 3), which was located on a nearly level bench >10 m from the creek channel. Forest SOC_{100} was lowest in steeply sloping settings where deep water tables facilitated the development of Haplocryods. Thus, forests contained well-drained sites despite lying downslope of bogs. In forests, pedogenetic processes in general, and C storage in particular, appear to be strongly influenced by drainage conditions. Drainage varies spatially because run-on is concentrated into discrete flowpaths and because creeks define the hydraulic gradients for the immediate area. Just as drainage conditions strongly influence vegetation patterns in southeastern Alaska (Neiland, 1971; Hanley and Brady, 1997), soil properties and classifications reflect the spatial variability in drainage conditions, both across the peatland-forest ecotone and within the forest.

Suárez et al. (1999) used mean maximum tree ages to argue that forests were expanding into adjacent tundra in northwest Alaska, a pattern also reported for northern Alaska (Sturm et al., 2001; Serreze et al., 2000). Afforestation of peatlands may also be occurring in southeastern Alaska. Although we found no significant differences in mean maximum tree ages across the bog-forest ecotone at CS, the trend in ages was consistent with these recent findings from northern Alaska.

Catena Patterns and Processes

Catenas represent sequences of linked soils across topographic gradients (Milne, 1935) and have been regarded as consisting of upslope eluvial, midslope colluvial, and downslope illuvial landscape complexes (Morison, 1948). In southeastern Alaska, dissolved organic C (DOC) fluxes could link upslope peatlands to downslope forests (Fig. 4). Although we did not measure DOC, stream water color clearly indicates that DOC is mobile in this environment. Exceptionally high DOC river export (approximately 9 kg DOC-C ha^{-1} yr^{-1}; Sugai and Burrell, 1984) and average concentrations in overland flow (20 mg L^{-1}; Engstrom et al., 2000) have been documented for southeastern Alaska. Fluxes of DOC might function in the same way that element transfers across a landscape have been proposed to represent lateral podzolization (Sommer et al., 2000).

The low hydraulic conductivities and low slopes we measured at edge stations indicate that lateral flow can also play a critical pedogenetic role across bog-forest ecotones. Interpedon transfers of materials and energy across the ecotone by lateral flow should increase in importance as bog subsurface horizons humify and as subsoil horizons with lower conductivities develop in forests (Table 2; Ugolini and Mann, 1979). Lateral flow would also intensify nutrient and C cycling by concentrating activity in the upper portion of the profile and by joining upslope and downslope landscape elements. We hypothesize that the strong property contrasts where Typic and Terric Histosols of bogs grade into the forest suite of Histosols, Spodosols, and Inceptisols could further reduce hydraulic conductivities and feed back to poor drainage. Just as vertical textural discontinuities may slow intrapedon water movement (Schaetzl, 1996), horizontal textural discontinuities along a catena could slow interpedon water movement, especially when subsurface properties restrict deep-water movement. Although DOC would be expected to dampen edge SRR in water-gathering locations, DOC could also stimulate forest SRR by acting as a C substrate in better-drained locations. Allochtonous C has been shown to stimulate soil respiration (Gallardo and Schlesinger, 1994; Hogberg and Ekblad, 1996). Since geomorphic redistribution of C can exceed plant C inputs to the soil profile (Yoo et al., 2001), we hypothesize that dissolved fluxes of C may be an important C redistribution mechanism at the landscape scale in southeastern Alaska, linking catena elements and helping explain C storage and C loss patterns.

Implications for Carbon Cycling

Carbon storage in Tongass National Forest soils has been estimated at 1.2 Pg (Alexander et al., 1989), a value that may be conservative since we measured C densities greater than the maximum density used in that study (72 kg m^{-3}). Carbon storage in this region appears to be strongly influenced by drainage conditions. Recent climate modeling work (Houghton et al., 2001) suggests that winter and summer temperatures will both increase in this region as a result of global warming. Estimates of precipitation differences are not as clear, but it is unlikely that increased precipitation would lead to higher water tables and bog expansion since the existing steep hydraulic gradient (Fig. 4) would likely limit additional water storage. Additional precipitation could lead to increased lateral flow. This work helps constrain the scope of soil changes that could result if bog-forest ecotones shift in response to climate change.

Because edge pedons contain significantly more SOC_{100} than adjacent forest pedons, we predict that additional improvements in drainage at edge locations as a result of warming could lead to the mineralization of 23 kg SOC m^{-2}, the difference between edge and forest interior SOC_{100} (24 kg m^{-2}) adjusted for increased C storage in trees (approximately 1 kg m^{-2}; Fig. 4). Warmer temperatures could increase DOC export from peat soils (Freeman et al., 2001b), and if warmer temperatures result in deeper water tables, more aerobic conditions could accelerate SOC mineralization rates (Freeman et al., 2001a) and subsidence (Silins and Rothwell, 1998). We base our prediction on SOC and SRR patterns across the bog-forest ecotone, the forest structure across the ecotone, and paleoecological and modern evidence of forest expansion in Alaska. Our estimate is triple the C losses reported for drained peatlands (Trettin et al., 1995) but only a fraction of the C loss of drained temperate wetlands (156 kg m^{-2}; Zdruli et al., 1995). Although our estimates of SOC_{100} rely in part on estimated D_b and %C values for deep horizons, our average values fall within the range of values reported for six bog and forest pedons in Alaska (17–129 kg m^{-2}; Ping et al., 1997) and the range calculated for 23 forested wetland pedons across southeastern Alaska (33–80 kg m^{-2}; depth range 38 to 213 cm; D'Amore and Lynn, 2002).

Forest expansion at high latitudes might not increase C sequestration (Lal, 2001), just as woody plant expansion into wet grasslands can trigger SOC losses (Jackson et al., 2002). Increased root densities as a result of forest expansion will enhance transpirational dewatering and the temperature sensitivity of the soil profile (Boone et al., 1998). Potential C sequestration by forests is also likely to be offset by decreases in surface albedo as peatlands are replaced by forests (Betts, 2000). These types of complex dynamics will govern the responses of northern peatlands and boreal forests to rising atmospheric CO_2 levels. If these patterns prove to be widespread in southeastern Alaska and across high latitudes, we speculate that initial afforestation of peatlands could represent a significant and transient positive feedback to rising atmospheric CO_2 levels. Such a feedback would be consistent with model simulations (Smith and Shugart, 1993).

CONCLUSIONS

In our study, variations in soils, hydrology, and vegetation across bog-forest ecotones did not coincide. In bogs, Cryohemists supported peat-forming mosses, sedges, and low basal areas. These bogs had very shallow water tables, low hydraulic conductivities, and low SRR. In forests, Cryohemists, Haplocryods, and Cryaquepts supported much higher basal areas, which coincided with the greatest slopes, deepest water tables, highest hydraulic conductivities, and highest SRR. At the bog-forest edge, however, we found evidence of a soil-vegetation uncoupling. Pedons were dominantly Cryohemists, with intermediate O horizon thicknesses but basal areas that were significantly greater than bog basal areas. The O horizon properties and low slopes of edge stations coincided with the lowest hydraulic conductivities across the ecotone, shallow water tables, low SRR, and the highest SOC_{100}.

Soil-vegetation uncoupling provides a preview of how landscapes might respond to climate change. We question the reliability of predicting ecosystem responses to climate change based solely on changes in land cover classes as defined by vegetation patterns without a consideration of soils. The anomalous SOC_{100} at bog-forest edges reinforces the importance of characterizing ecotones in addition to more homogenous landscape elements. The high variability in SOC in forest soils means that forest soil C inventories with much higher spatial resolution will be required to predict how these ecosystems will respond to climate change. Across the ecotone, the largest differences in SRR did not coincide with the largest aboveground differences in tree basal areas, highlighting the importance of characterizing both above- and belowground ecosystem structure. Our conceptual model suggests that forest expansion across these ecotones as a result of continued or accelerated warming in southeastern Alaska could result in the net loss of >20 times as much C from soils as could be assimilated as forest biomass.

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