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Fertility of the early post-eruptive surfaces of Kasatochi Island volcano

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ABSTRACT

In the four years after the 2008 eruption and burial of Kasatochi Island volcano, erosion and the return of bird activity have resulted in new and altered land surfaces and initiation of ecosystem recovery. We examined fertility characteristics of the recently deposited pyroclastic surfaces, patches of legacy pre-eruptive surface soil (LS), and a post-eruptive surface with recent bird roosting activity. Pyroclastic materials were found lacking in N, but P, K, and other macronutrients were in sufficient supply for plants. Erosion and leaching are moving mobile P and Fe downslope to deposition fan areas. Legacy soil patches that currently support plants have available-N at levels (10-22 mg N kg⁻¹) similar to those added by birds in a recent bird roosting area. Roosting increased surface available N from <1 mg N kg⁻¹ in the new pyroclastic surfaces to up to 42 mg N kg⁻¹ and increased soil biological respiration of CO₂ from essentially zero to a level about 40% that of the LS surface. Laboratory plant growth trials using Lupinus nootkatensis and Leymus mollis indicated that the influence of eroded and redeposited LS in amounts as little as 10% by volume mixed with new pyroclastic materials could aid plant recovery by supplying vital N and soil biota to plants as propagules are introduced to the new surface. Erosion-exposure of fertile pre-eruptive soils and erosion-mixing of pre-eruptive soils with newly erupted materials, along with inputs of nutrients from bird activities, each will exert significant influences on the surface fertility and recovery pattern of the new post-eruptive Kasatochi volcano. For this environment, these influences could help to speed recovery of a more diverse plant community by providing N (LS and bird inputs) as alternatives to relying most heavily on N-fixing plants to build soil fertility.

Introduction

Kasatochi Island is one of nine seabird monitoring sites in the Alaska Maritime National Wildlife Refuge located in the central chain of Alaska's Aleutian Islands (Fig. 1). The island is also important to sea lion and other maritime ecological studies, with data collections spanning several decades (Bucheit and Ford, 2008; Williams et al., 2010). Pre-eruption, there was a general description and a map of island vegetation (Scharf et al., 1996; Talbot et al., 2010) but not much was known of the island's soils or volcanic history (Wang et al., 2010; Waythomas et al., 2010).

The 7–8 August 2008 eruption was the first in recorded history, and the entire island was buried in meters to tens of meters of pyroclastic flow (Scott et al., 2010). Within a few years after the eruption, erosion removed or thinned significantly the new pyroclastic deposits, especially in isolated northern parts of the island that are dominated by steeper talus slopes and rock outcroppings that extend from the crater rim to the shoreline (Fig. 1; Waythomas et al., 2010). On this more rugged northern terrain, limited areas of pre-eruptive vegetation have been exposed (Talbot et al., 2010). On the southern half of the island where slopes are gentle and longer, plant refugia have been observed grow-

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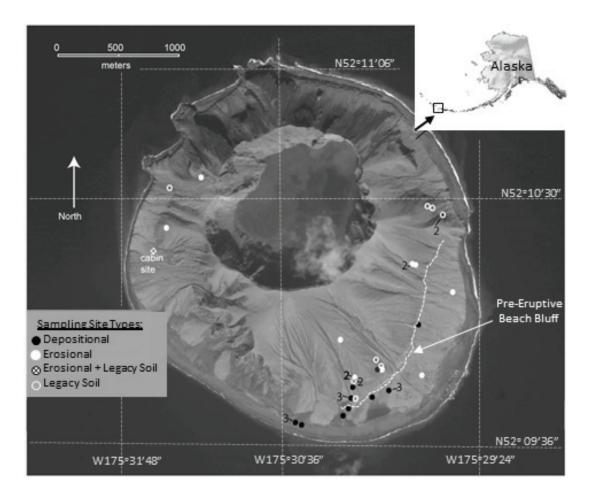


FIGURE 1. Kasatochi Island sampling sites and types, post-2008 eruption (geology after Scott et al., 2010). Numbers near site markers indicate multiple sampling sites with markers overlapping.

ing along the steeper crest of the island's pre-eruptive beach bluff. This bluff extends across part of the island's southeast quadrant, and following the recent eruption, the bluff is now some 400 m inland. Refugia were also observed with plants growing in isolated bands along deeply incised gullies that have eroded down the long slopes and cut deeply through the 2008 pyroclastic deposit, breaching the pre-eruptive surface and exposing it in a thin band along steep gully walls.

Early post-eruptive studies that characterized the pyroclastics and buried soils (Wang et al., 2010; Waythomas, 2010) reported that the thickness of new deposits varied widely over the island up to 10s of meters. The buried pre-eruptive soils were found to be relatively thinly developed (<0.5 m) and organic pre-eruptive surface layers were a <5-cm-thick accumulation. These studies reported that exposed patches of the pre-eruptive surface contribute almost exclusively to support surviving plants and that those patches were es-

sentially providing all plant rooting media and all plant propagules observed post-eruption. Wang et al. (2010) and Waythomas et al. (2010) along with others reported that island ecosystem recovery had begun, assisted by the strong-continual erosive action of runoff waters that are uncovering preeruptive surface soils that contain organic matter and plant propagules. Insects, birds, and sea lions are also re-establishing on the island (Sikes and Slowik, 2010; Williams et al., 2010). Many studies have linked bird activities, especially in rookery areas, with their guano derived N- and P-inputs to soil fertility (Bird et al., 2008; Mizota, 2009; Mulder et al., 2011; Callaham et al., 2012). Bird nutrient inputs have also been linked to broaderarea soil fertility of the Aleutian Islands (Maron et al., 2006), but little is known of their impacts on ecosystem recovery. Considering the relative isolation of Kasatochi Island from any large land masses, and the strong and continual erosive action present, along with the island's link to abundant seabird populations, the island could offer a different and interesting perspective with regard to recovery of this severely disrupted ecosystem (Walker et al., 2013). The relative interactions of the surface pyroclastic material along with the nutrient and biota inputs from legacy soils and returning birds will certainly be crucial to plant reestablishment and development of new soils and restoration of a fertile surface for vegetation. These circumstances for post-eruptive Kasatochi Island offer an opportunity to identify input pathways to the recovering system beginning at a point very early in the process. Currently, little is known about the fertility of either the legacy soils or the new pyroclastic surfaces (DeGange et al., 2010).

This study was conducted to characterize nutrient status of the newly forming post-2008 eruptive surfaces of Kasatochi Island volcano, and to compare the new surface pyroclastic deposits to the legacy (preeruptive) soils that are being exposed in isolated areas of the island. In anticipation of newly forming soils and plant communities, we attempt to determine some of the potential plant-nutrient and fertility effects that pyroclastics, legacy soils, and bird inputs could have on plant growth and the reestablishment of plant community cover. Specifically, we examine the fertility or nutrient influences that the exposed legacy soils could have as they are eroded and mixed with the new pyroclastic surface along with the nutrient effects of new localized bird roosting sites.

METHODS

The study consisted of two parts. The first was the sampling and analysis of island surface materials, including the newly deposited surface pyroclastics, pre-eruptive legacy soils, and new surface pyroclastics that are being influenced by nutrient inputs associated with recent bird roosting. The second part of the study was a laboratory plant-growth study using the newly deposited surface pyroclastics and the exposed pre-eruptive legacy surface soils to assess the initial effects that each may have on plant re-establishment and growth.

Sampling and Analysis

The study area is located in the central Aleutian Islands chain (52.17°N, 175.51°W) of Alaska about

80 km northeast of Adak, Alaska. During the summers of 2009-2012, surface layer pyroclastics (PY) and surface horizons of pre-eruptive legacy soils (LS) were sampled at locations across the approximately 3 km diameter island of Kasatochi volcano (Fig. 1). The PY samples were from 30 sites, with 14 from eroding surfaces (ES) and 16 from depositional surfaces (DS). The LS were sampled at 11 sites. All of the PY layers formed a 0.5–2.0-cm-thick surface crust that hardened and cracked with the periodic drying of the surface causing the hardening of the layer with precipitated salts, mainly impure gypsum (Wang et al., 2010). This surface crust was sampled separately and the remaining thickness of the surface layer was sampled in two additional incremental thicknesses determined by differences in layer morphology observed at each location (Fig. 2, part B). The surface horizons of buried LS profiles were described and collected according to soil horizon development or morphology (Schoeneberger et al., 2012). Surface pyroclastics under a current roosting site (Fig. 2, part D) were sampled in triplicate for both on the roost and immediately adjacent to or off the roost from areas with no apparent roosting or biotic activity. Each sampling was by dimensional block-excavation at three incremental depths 0-0.5 cm (crust), 0.5-2 cm, and 2-5 cm (Michaelson et al., 2012). Four 3 cm diameter cores from a 0-5 cm depth were taken for measuring soil respiration, one set in the on-roost and one set in the off-roost microsites, along with four cores from an exposure of the LS upslope from the roosting fan site. Cores were kept in sealed respiration jars and refrigerated until they were attached to a Columbus Instruments Oxymax soil respirometer, they were incubated at 25 °C for 140 hours, and headspace CO₂ measurements were taken every hour.

The bulk density (Db) of samples was determined using dimensional samples that were taken as either fixed volume cores for both PY and LS, or dimensionally measured blocks excavated for PY crusts and the roosting site. Field moist materials were sealed in plastic bags, transported to the laboratory, and then air-dried for analysis. Subsamples of the air-dried samples were dried to 105°C for calculation of Db on an oven-dried basis. Air-dried samples were analyzed for total C and N by high temperature ignition on a LECO TCN analyzer and total S by perchloric acid digestion followed by inductively coupled plasma atomic emission spectroscopy (ICP-AES) analysis.

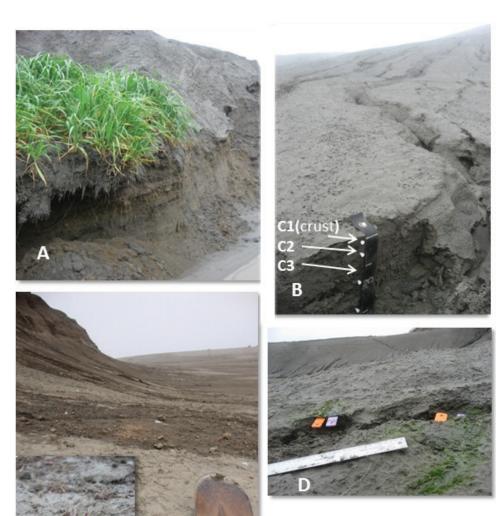


FIGURE 2. Examples of areas with various surface types: (A) exposed legacy soils (LS) surface with Leymus sprouting, (B) new (post-2008) pyroclastic surface (PY) with layers indicated, (C) mixed legacy soil/pyroclastic (LS/PY) and insert view of Lupinus sprouting from the mix, and (D) current bird roosting site.

Exchangeable cations and cation exchange capacity (CEC) were determined by neutral ammonium acetate cation extraction followed by measurement of adsorbed ammonium by distillation into an alkaline boric acid indicator solution and HCl titration for CEC. The extracted cations were determined by ICP-AES (Soil Survey Staff, 1996). Soil particle size distribution was determined by the hydrometer method. The pH and electro-conductivity were determined on a saturated paste and paste extract using a pH electrode and conductivity meter, respectively. Extractable ammonium and nitrate-N was determined using a 2M KCl extraction followed by autoanalyzer-colorimetry and plant-available P, K, Cu, Zn, Mn, and Fe determined

by Mehlich-3 extraction followed by ICP-AES analysis (Michaelson and Ping, 1986; Walworth et al., 1992). Organic C and total N accumulation in LS profiles were calculated using total C and N analysis, soil Db, coarse fragment content and horizon thicknesses as described by Michaelson et al., (2013). Averages of the data from above analyses are given in Table 1.

Laboratory Plant Growth Study

To confirm the potential for propagation of live plants from legacy propagules 3 years after burial, preeruptive surface legacy soils (LS) were collected for incubation-confirmation of viable propagules. We col-

TABLE 1

(A) Average chemical and (B) physical and exchange properties for morphologically different surface layers at post-eruptive surface sites (ES-eroding slope surfaces and DS depositional fan surfaces) compared to that of the pre-eruptive legacy surface soil profiles (LS). Single-factor ANOVA indicates mean values are significantly (* at $P \le 0.05$) different for comparisons between the post-eruptive ES or DS surface C-horizons for number of sites (n).

	mical Prope	rties												_		
		Ave.		E.C.	Ex	tractable			Mel	hlich-3	Extrac	table		_		
		depth		(dS	NH ₄ ⁺	NO ₃	$N_{_{Total}}$	Р	K	Cu	Zn	Mn	Fe	_ C	N	S
	Layer	(cm)	pН	m ⁻¹)	,				ig kg ⁻¹					(%)	(%)	(%)
				POS	T-ERU	PTION	PYRO	CLAS	STIC S	SURFA	CE					
ES-Erod	ing Surface	s (Slopes))													
	C1(crust)	0–2	7.1*	2.0*	<1	<1	<1	4	173*	21	7	102	702	0.10	<.01	0.58
(n = 14)	C2	2-14	7.1*	2.4*	<1	<1	<1	3	204*	22	7	97	694	0.09	<.01	0.81
	C3	14–25	6.6	2.7*	<1	<1	<1	4	230*	17	4	76	606	0.10	<.01	0.82
DS-Dep	ositional Su	rfaces (U	pland	and C	oastal fa	ns)										
	C1(crust)	0-2	6.5	1.9	<1	<1	<1	18*	133	33*	11*	92	811*	0.07	<.01	1.46*
(n = 16)	C2	2-5	6.5	1.7	<1	<1	<1	18*	123	34*	12*	96	806*	0.06	<.01	1.46*
` ,	C3	5–9	7.0	2.0	<1	<1	<1	13*	146	34*	13*	101	804*	0.10	<.01	1.72*
					DD E	ERUPT	ION SO)II S	I ID E	ACE						
LS-Lega	cy Surface S	Soils			1 IXL-	LICOII	101436	J1L 3		1CL						
	O	0-3	5.0	5.7	11	9	20	61	210	46	11	79	400	11.4	0.60	0.38
(n=11)	A	3-12	4.9	3.5	16	6	22	41	150	39	4	34	359	6.27	0.37	0.28
	Bw	12-24	4.8	3.6	8	2	10	17	111	11	1	16	247	0.97	0.04	0.15
(B) Phys	ical & Exch	Dronert	ies													
		i. i toperi		we.										Extract	able	
	2001 00 22101	i. i ioperi	A	ve.	Db	>2.mm	Sand	Sil	lr (Clav	CEC		τ	Extract		Na
			Ar de _j	pth		>2mm (%)	Sand (%)	Sil		Clay _ (%)	CEC		ζ [cmol	Ca	Mg	Na
		yer	Ar de _j	pth m) (s	g cm ⁻³)	>2mm (%) PTION	(%)	(%	ó)	(%)]			Mg	Na
ES-Erod		yer	Ar dej (cr	pth m) (s	g cm ⁻³)	(%)	(%)	(%	ó)	(%)]		Ca	Mg	Na
ES-Erod	La	yer s (Slopes)	Ar dej (cr	pth m) (g POS	g cm ⁻³)	(%)	(%)	(%	STIC S	(%)		0.4	[cmol	Ca	Mg	Na 0.4
ES-Erod $(n = 15)$	La ling Surface C1(c	yer s (Slopes)	Ar dej (cr	pth m) (g POS	g cm ⁻³) T-ERUI	(%) PTION	(%) PYRO	(% CLAS	6) STIC S	(%) Surfa	CE		[cmol	Ca (+) kg ⁻	Mg ¹]	
	La ling Surface C1(c	yer s (Slopes)	Ar dej (cr	pth m) (g POS 2	g cm ⁻³) T-ERUI 1.17	(%) PTION 0.2	(%) PYRO	(% CLAS	STIC S	(%) SURFA	ACE 8.9*	0.4	[cmol	Ca (+) kg ⁻	Mg 1 0.8	0.4
(n = 15)	La ling Surface C1(c C2	yer s (Slopes) rust)	A dej (cr	pth m) (g POS 2 14 25	g cm ⁻³) T-ERUI 1.17 1.52 1.44	(%) PTION 0.2 0.1 0.9	(%) PYRO0 50 57	(% CLAS 33 35	STIC S	(%) SURFA 17 7	8.9* 8.2	0.4	[cmol	Ca (+) kg ⁻ 16.5 28.6	Mg 1] 0.8 0.6	0.4
(n = 15)	La ling Surface C1(c C2 C3	yer s (Slopes) rust) urfaces (U	A dej (cr	pth m) (g POS 2 14 -25 and C	g cm ⁻³) T-ERUI 1.17 1.52 1.44	(%) PTION 0.2 0.1 0.9	(%) PYRO0 50 57	(% CLAS 33 35	STIC S STIC S S S	(%) SURFA 17 7	8.9* 8.2	0.4	[cmol	Ca (+) kg ⁻ 16.5 28.6	Mg 1] 0.8 0.6	0.4
(n = 15)	La ling Surface C1(c C2 C3 cositional Su C1(c	yer s (Slopes) rust) urfaces (U	A de	pth (s) (s) POS 2 14 -25 and C 2	g cm ⁻³) T-ERU 1.17 1.52 1.44 Coastal fa	(%) PTION 0.2 0.1 0.9	(%) PYRO0 50 57 70	(% CLAS 33 35 25	5) STIC S 3 5 5	(%) SURFA 17 7 5	8.9* 8.2 7.2	0.4	[cmol 4* 5 6 6 3	Ca (+) kg ⁻ 16.5 28.6 27.7	Mg 0.8 0.6 0.8	0.4 0.3 0.3
(n = 15)DS-Dep	La ling Surface C1(c C2 C3 cositional Su C1(c	yer s (Slopes) rust) urfaces (U	A dej (cr.) 0-2-1 14- Jpland 0-2	pth m) (g POS 2 1425 and C 2	g cm ⁻³) T-ERUI 1.17 1.52 1.44 Coastal fa	(%) PTION 0.2 0.1 0.9 ans) 0.7	(%) PYRO0 50 57 70	(% CLAS 33 35 25	5) 33 55 55 22	(%) 5URFA 17 7 5	8.9* 8.2 7.2	0.0	[cmol 4* 5 6 6 3 3 3	Ca (+) kg ⁻ 16.5 28.6 27.7	Mg 0.8 0.6 0.8 0.8	0.4 0.3 0.3
(n = 15)DS-Dep	La ling Surface C1(c C2 C3 cositional Su C1(c C2	yer s (Slopes) rust) urfaces (U	A dep (cr	pth m) (g POS 2 1425 and C 2	1.17 1.52 1.44 Coastal fa 1.16 1.43 1.23	(%) PTION 0.2 0.1 0.9 ons) 0.7 0.2 1.2	(%) PYRO0 50 57 70 52 55 52	33 35 25 32 33	5) 3 5 5 5 2 3 6	(%) SURFA 17 7 5 15 13 12	8.9* 8.2 7.2	0.4 0.0 0.0	[cmol 4* 5 6 6 3 3 3	Ca (+) kg ⁻ 16.5 28.6 27.7	Mg 0.8 0.6 0.8 0.8 0.6	0.4 0.3 0.3 0.3
(n = 15) DS-Dep $(n = 16)$	La ling Surface C1(c C2 C3 cositional Su C1(c C2	yer s (Slopes) rust) urfaces (U	A dep (cr	pth m) (g POS 2 1425 and C 2	1.17 1.52 1.44 Coastal fa 1.16 1.43 1.23	(%) PTION 0.2 0.1 0.9 ons) 0.7 0.2	(%) PYRO0 50 57 70 52 55 52	33 35 25 32 33	5) 3 5 5 5 2 3 6	(%) SURFA 17 7 5 15 13 12	8.9* 8.2 7.2	0.4 0.0 0.0	[cmol 4* 5 6 6 3 3 3	Ca (+) kg ⁻ 16.5 28.6 27.7	Mg 0.8 0.6 0.8 0.8 0.6	0.4 0.3 0.3 0.3
(n = 15) DS-Dep $(n = 16)$	La ling Surface C1(c C2 C3 Positional Su C1(c C2 C3	yer s (Slopes) rust) urfaces (U	A dep (cr	pth m) (g POS 2 14 -25 and C 2 5	1.17 1.52 1.44 Coastal fa 1.16 1.43 1.23	(%) PTION 0.2 0.1 0.9 ons) 0.7 0.2 1.2	(%) PYRO0 50 57 70 52 55 52	33 35 25 32 33	5) 3 5 5 2 3 6 5 CURFA	(%) SURFA 17 7 5 15 13 12	8.9* 8.2 7.2	0.4 0.0 0.0	[cmol 4* 5 6 3 3 4 4	Ca (+) kg ⁻ 16.5 28.6 27.7	Mg 0.8 0.6 0.8 0.8 0.6	0.4 0.3 0.3 0.3
(n = 15) DS-Dep $(n = 16)$	La ling Surface C1(c C2 C3 Positional Su C1(c C2 C3 cy Surface S	yer s (Slopes) rust) urfaces (U	A dej (cr.) 0-2-1 14- Jpland 0-2 2-5	pth (m) (graph POS) 2 1425 and C 2 5 5 5	1.17 1.52 1.44 Coastal fa 1.16 1.43 1.23	(%) PTION 0.2 0.1 0.9 0.7 1.2 ERUPT	(%) PYRO0 50 57 70 52 55 52 TION SO	(%) (%) (%) (%) (%) (%) (%) (%) (%) (%)	5) 3 5 5 5 6 CURFA	(%) SURFA 17 7 5 15 13 12 ACE	8.9* 8.2 7.2 7.4 7.0 7.8	0.4 0.6 0.6 0.2	[cmol 4* 5 6 3 3 4 4 5 5	Ca (+) kg ⁻ 16.5 28.6 27.7 14.1 15.2 23.5	Mg 0.8 0.6 0.8 0.6 0.5	0.4 0.3 0.3 0.3 0.2 0.3

lected the 0–5 cm layer, including the O and A horizons, of buried LS surface. Two collections were made each from an area about 0.25 m^2 (0–5 cm depth in LS). One sample was from a recent upland gulley LS exposure, and the other from the southeastern pre-eruptive beach bluff, just back from the current exposure and only shallowly buried (Fig. 1). The LS was spread out to a 5 cm deep layer in greenhouse flats. An 8-week, moist and lighted laboratory incubation (26°C) of these flats yielded an average of 154 ± 23 grass or herbaceous propagules sprouting per m² pre-eruptive surface.

To investigate the influences of LS and added nitrogen on fertility of the surface, bulk samples of the preeruptive legacy surface soil (LS) and the surface layer pyroclastics (PY) were collected in August 2011 from sites at the midslope position of the southeast island transect (Fig. 1). The LS material collected included the 0-10 cm depth of the pre-eruptive LS profile as it was exposed by the eroded gully wall as shown in Figure 2, part A. Bulk PY material was collected at about the same midslope position, but from the 0-10 cm depth of a smaller rill adjacent to the LS gully collection site. Materials collected were kept sealed, moist, and cool during transport to and storage at the UAF-Palmer Research Center Plant and Soils laboratory. Laboratory growth trials were initiated 17 October 2011. Five different growth mediums were prepared for use in the trial using the bulk field-moist LS and PY materials as collected: LS only, LS/PY 50%/50% volume, LS/PY 10%/90% volume, PY only, and PY+25 mg N kg⁻¹as ammonium nitrate solution. For each of these five media preparations there were 15 individual pots that contained 160 cm⁻³ media. Three different plant/propagule types were planted in five pots (replicates) from each of the five media preparations (above). The three plantpropagule types grown in each treatment were as follows: seeded lupine (Lupinus nootkatensis collected from Hatcher Pass, Talkeetna Mountains, Alaska), beach wild ryegrass seeded, and beach wild ryegrass sprigs (both Leymus mollis, var. Benson obtained from the Alaska Department of Natural Resources Plant Materials Center, Palmer, Alaska). All seeds were pregerminated in distilled water, and sprigs were washed in distilled water and selected for uniform overall size with green leaves removed so only root and stem-base material was present at planting. The five replications of each of the three plant-propagule types were grown in each of the five media mixes for 14 weeks under lights. At 14 weeks, the aboveground plant material from each pot was cut,

dried (65°C), and weighed (Fig. 3). The belowground plant material was removed, washed in distilled water, dried (65°C), and weighed. Laboratory treatment media mixes were analyzed at the initiation of the growth trial period for total C, total N, pH, and available P and K (Table 2), each by the methods given above.

RESULTS

Pre- and Post-Eruptive Surfaces

Selected fertility-related parameters of the surface pyroclastic layers were averaged across two general site condition types: (1) eroding surfaces or slopes (ES: n =14) and (2) depositional surfaces (DS: n = 16) including upland and coastal fans (Table 1, part A). The same fertility-related parameters are averaged for the preeruptive legacy surface soils sites (LS: n = 11) sampled. The surface layers for the ES and DS and the surface soil horizons for the LS sites were sampled according to morphology of the profiles observed at each site. Post-eruptive surface crusts (C1 layers), were similar in average thickness (0-2 cm) for both ES and DS sites. However, the next two C2 and C3 layers averaged thicker on the ES compared to the DS sites at 12 and 11 cm thick for the ES sites compared with only 3 and 4 cm thick for the DS sites. In comparison, the surface soil horizon of the LS consisted of an organic (O) horizon followed by an organic enriched mineral (A) horizon and then a weakly weathered mineral (B) horizon with average depths of 3, 9, and 12 cm, respectively. Average pH and the soluble salt levels as indicated by electro-conductivity (EC) were slightly higher for the ES compared to the DS sites. The pH of ES sites was in the range of 6.6-7.1 compared to 6.5–7.0 for the DS sites, and EC was in the range of 2.0-2.7 dS m⁻¹ for the ES sites compared to 1.7-2.0 dS m⁻¹ for the DS sites. The LS sites, having soil development and organic matter and nutrient accumulation, had lower average pH (4.8-5.0) and higher EC (3.5–5.7 dS m⁻¹) compared to the ES and DS sites. Total-extractable plant-available nitrogen (nitrate plus ammonium-N) was generally very low at <1 mg kg⁻¹ soil for both the ES and DS sites compared to the LS where total-extractable N ranged from 10–22 mg kg⁻¹. Similarly total C and N were also very low for both the ES and DS sites averaging ≤0.10% C and <0.01% N across sites. The average total C and N for the LS sites ranged from 0.97% to 11.4% and 0.04%

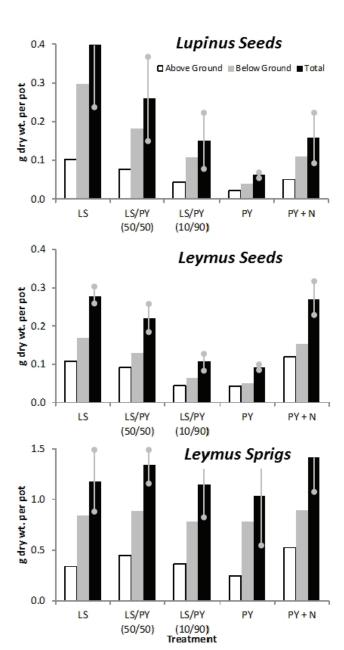


FIGURE 3. Average (five replicates each) laboratory 14-week dry-weight production (g pot⁻¹) for *Lupinus* and *Leymus* seeds and *Leymus* sprigs grown in five growth media mixes made from bulk collections of legacy pre-eruptive soil surface and bulk pyroclastic surface (media mixes: LS = legacy soil consisting of surface O and A horizons only; LS/PY 50/50 = legacy surface soil mixed with pyroclastic surface 50/50v; LS/PY 10/90 = legacy surface soil mixed with surface pyroclastics 10/90v; PY = pyroclastic surface only; and PY+N = pyroclastic surface plus 25 mg N kg⁻¹ as ammonium nitrate). Bars are one standard deviation unit above and below the mean.

to 0.60%, respectively, with Bw horizons lowest and O horizons highest. The DS sites averaged higher plant-

available indices (Mehlich-3) for P, Cu, Zn, and Fe as compared to the ES sites with P ranging from 13 to 18 mg kg⁻¹ compared to 3–4 mg kg⁻¹, Cu 33–34 mg kg⁻¹ compared to 17–22 mg kg⁻¹, Zn 11–13 mg kg⁻¹ compared to 4–7 mg kg⁻¹, and Fe 804–811 mg kg⁻¹ compared to 702–694 mg kg⁻¹ each for the DS and ES sites, respectively. Total sulfur also averaged higher in the DS sites compared to the ES, ranging 1.46%–1.72% compared to 0.58%–0.82%, respectively. There was little difference in extractable Mn between the two pyroclastic site types, but extractable K averaged higher for the ES than DS sites at 173–230 mg kg⁻¹ compared to 123–146 mg kg⁻¹ for the DS sites.

Selected physical and exchange properties of the surface layers were similar for the ES and DS sites (Table 1, part B). Surface bulk densities (Db) ranged from 1.16 to 1.52 g cm⁻³. Both ES and DS surface materials were sandy-loam according to U.S. Department of Agriculture (USDA) texture classification (Soil Survey Division Staff, 1993) with few (0.1%-1.2%) coarse fragments of >2 mm. Particle size distributions ranged from 50%–70% sand, 25%–36% silt, and 5%–17% clay. The LS tended to have more coarse fragments in the B horizon, averaging 9.7% compared to the post-eruptive surfaces that ranged from 0.1% to 1.2%, similar to the O and A horizons of LS. Legacy soils were more coarse-textured (loamy sands) having higher sand content (80%–82%) than post-eruptive surfaces (50%-69% sand). As observed for the physical properties, the cation exchange capacity (CEC) and exchangeable cations were similar in the ES and DS sites. The CEC ranged from 7.0 to 8.9 cmol(+) kg⁻¹ with Ca dominating the exchange. Concentrations of exchangeable cations for ES and DS samples were in the range of 0.3-0.6 cmol K(+) kg⁻¹, 14.1-28.6cmol Ca(+) kg⁻¹, 0.5-0.8 cmol Mg(+) kg⁻¹, and 0.2-0.4 cmol Na(+) kg⁻¹. The LS reflected their higher soil organic levels in the O and A horizons with lower bulk densities (Db = 0.56 and 0.81 g cm⁻³) compared to the ES and DS surfaces (1.16– 1.48 g cm⁻³) along with higher CEC (25.7 and 12.9 cmol(+) kg⁻¹) compared to the ES and DS surfaces (6.9–8.9 cmol(+) kg⁻¹). In the mineral B horizons of the LS, both the Db and CEC were similar to and in the same range as found for the ES and DS post-eruptive surfaces. The exchangeable cations for the LS surface were similar to the

TABLE 2

Selected chemical properties of growth media prepared from bulk collections of legacy soil and post-eruptive pyroclastic surface, and then used in the laboratory *Lupinus* and *Leymus* growth study (Growth Media: pre-eruptive legacy soil = LS, surface pyroclastics = PY and the media with mixed materials: LS/PY 50/50 = legacy soil mixed to 50% with surface pyroclastics, and LS/PY 10/90 = legacy soil mixed to 90% with surface pyroclastics, PY + N = surface pyroclastics with 25 mg N kg⁻¹ added as ammonium nitrate).

			E	extractable-	N	Meh	lich-3	To	tal
			NH ₄ ⁺	NO ₃	$N_{_{Total}}$	P	K	С	N
Growth Media	n	рН			(mg kg ⁻¹)			(%	6)
LS	1	6.2	3	2	5	43	60	3.97	0.26
LS/PY 50/50	1	7.2	1	<1	1	14	140	0.95	0.02
LS/PY 10/90	1	7.1	<1	<1	<1	11	143	0.23	<.01
PY	1	7.3	<1	<1	<1	11	154	0.09	<.01
PY+N	1	7.2	11	4	15	11	156	0.08	<.01

ES and DS in that Ca dominated CEC, but unlike the post-eruptive surfaces Ca did not exceed the CEC in the LS. There were increased levels of K, Ca, Mg, and Na in the profiles of LS associated with the higher CEC of the surface O and A horizons relative to the underlying mineral B horizons. Potassium levels in the LS were similar to those of the post-eruptive surface, as were the Ca levels in the O horizon. Sodium was elevated throughout the LS surface (0.7–2.7 cmol(+) kg⁻¹) compared to the new post-eruptive surface (0.2–0.4 cmol(+) kg⁻¹).

Laboratory Growth Trials Comparing Pre- and Post-Eruptive Surfaces

The 14-week averages for dry-weight production of Lupinus and Leymus seeds and Leymus sprigs grown in five growth-media mixes are presented in Figure 3. The two seeded plant species were equally well suited for growth across media types. The overall dry weight production per pot for Lupinus and Leymus seeds was nearly the same at 0.21 ± 0.10 and 0.19 ± 0.05 g per pot, respectively, with greater variation in growth overall and within media-mix for Lupinus. The pattern for average yield across the different media mixes was similar for both of the seeded plant types, with the legacy surface soil (LS) averaging the highest at 0.14 ± 0.17 and 0.28± 0.03 g per pot for seeded Lupinus and Leymus, respectively. Yields were reduced for pots as the proportion of pyroclastic surface (PY) increased in the media-mix up to the pure PY treatment where

the lowest yields that were observed at 0.06 ± 0.01 and 0.09 ± 0.01 g per pot for seeded *Lupinus* and *Leymus*, respectively. Nitrogen addition to the PY increased average yields of seeded *Lupinus* by 250% and seeded *Leymus* by 290%. *Leymus* sprig plantings had less variation in yield across the range of media mixes with higher deviation within each mix. Thus, the effects of varying media were less clear for sprigs, although the PY pots yield average was lowest at 1.03 ± 0.53 g per pot and the PY pots with nitrogen added averaged the highest yield at 1.41 ± 0.43 g per pot.

The pH; plant-available N, P, and K; and total C and N levels for the five media mixes used in the laboratory growth experiment are in Table 2. The pH was lowest in the legacy surface soil (LS) at 6.2 with the other mixes ranging only from pH 7.1 to 7.3. Extractable N levels were highest in the PY+N mix at 15 mg N kg⁻¹ with the LS next highest at 5 mg N kg⁻¹. Extractable N levels of the other mixes were minimal at <1 mg N kg⁻¹ except for a minimal 1 mg N kg⁻¹ in the LS/PY (50:50v) mix. Plant-available P levels as indexed by Mehlich-3 extraction were highest in the LS mix at 43 mg P kg⁻¹ and ranged from 14 mg P kg⁻¹ in the LS/PY 50:50v to 11 mg P kg⁻¹ for all other mixes. Extractable K levels were lowest in the LS at 60 mg K kg⁻¹ and in a similar range (140–156 mg K kg⁻¹) for all other mixes. Total C and N content followed the LS content of the mix with the highest (3.97% C and 0.26% N) in the LS and lowest in the PY and PY+N mixes (0.08%–0.09% C and <0.01% N).

Bird-Affected Post-Eruptive Surface

Bird roosting areas showed evidence of added nutrients due to guano addition and surface algae growth. Table 3 contains data for selected chemical properties of a post-eruptive coastal fan surface as influenced by contemporary bird roosting activity compared with adjacent nonaffected surfaces. Roosting activity had little effect on the pH or EC of the surface pyroclastics down to the 5 cm depth, with the pH ranging from 6.9 to 7.1 and 6.8 to 7.0 for the off-roost compared to the onroost sites. There was little effect on EC that ranged from 2.0-2.4 dS m⁻¹ and 2.1-2.8 dS m⁻¹ for the off-roost and on-roost sites, respectively. Similarly, no changes in the extractable micronutrients Cu or Zn were detectable as a result of roosting. Extractable Fe was slightly depressed in roosting surface but not beyond 0.5 cm. Extractable plant-available N, both in the ammonium and nitrate forms, averaged higher throughout the 5 cm depth of the on-roost surface relative to off-roost. Total available N levels of the on-roost surface were highest at the 0-0.5 cm surface at 42 mg N kg⁻¹ decreasing to 12 mg N kg⁻¹ at the 5 cm depth compared to <1 mg N kg-1 levels found for all depths in the adjacent off-roost surface. Elevated C levels were only detected at the surface 0-0.5 cm depth of the onroost sites at 0.24% C compared to minimal levels

of 0.06%–0.09% C for all other depths and for the off-roost sites. Total S was variable and not significantly different with roosting activity and ranged 1.53%–1.92% S and 1.55%–1.98% S for off-roost and on-roost surfaces, respectively.

As an indicator of general levels of surface biological activity, average respiration of carbon dioxide from incubated cores (0–5 cm) taken from both the onroost and off-roost surfaces were compared with that from cores of the legacy pre-eruptive surfaces (Fig. 4). Over the 140 hr incubation, pre-eruptive legacy soils (4.24% C; 0.24% N) averaged the highest respiration with an average rate of 3.3 \pm 0.3 mg CO $_2$ cm $^{-3}$ hr $^{-1}$, while on-roost surfaces (0.13% C; <0.01% N) were next highest at 1.4 \pm 0.6 mg CO $_2$ cm $^{-3}$ hr $^{-1}$ and the off-roost pyroclastic surface (0.07% C; <0.01% N) averaged lowest at 0.4 \pm 0.3 mg CO $_2$ cm $^{-3}$ hr $^{-1}$.

DISCUSSION

General Island Surface Conditions

With relatively high rainfall (estimated 156 cm yr⁻¹) and lack of vegetative cover, the posteruptive island surface is exposed to high rates of erosion (up to 3.5 vertical m yr⁻¹) and strong leaching of soluble materials, together impacting surface conditions (Waythomas et al., 2010). The resulting post-eruptive island surfaces all consist of 2008 pyroclastic deposits from the late-stage

TABLE 3

Selected average chemical properties of bird roosting (on-roost) compared to adjacent non-roosting (off-roost) microsites on the post-eruptive surface of a coastal fan above the current beach and below the pre-eruptive beach bluff (Fig. 1 and Fig. 2, part D). Single-factor ANOVA indicates mean values are significantly (* at P ≤ 0.05) different for comparisons between the depths for Off-roost compared to On-roost microsites.

				Ex	tractable	:-N			Mehl	lich-3	Extra	ctable			
	Depth		E.C.	NH ₄ ⁺	NO_3^-	$N_{_{Total}}$		P	K	Cu	Zn	Mn	Fe	С	S
Microsite	(cm)	pН	$(dS m^{-1})$					(mg	kg^{-1})					(%)	(%)
Off-															
Roost	0-0.5	6.9	2.4	<1	<1	<1		16	162	38	12	88	829	0.09	1.60
(n = 3)	0.5-2.0	7.1	2.0	<1	<1	<1		14	166	38	13	97	836	0.06	1.53
	2.0-5.0	7.1	2.4	<1	<1	<1		13	175	40	15	104	828	0.07	1.92
On-Roost	0-0.5	6.8	2.8	18*	24*	42*	1	65*	212	31	12	92	769*	0.24*	1.79
(n = 3)	0.5-2.0	7.0	2.1	4*	24*	28*		32*	148	37	13	103	827	0.06	1.55
	2.0-5.0	7.0	2.6	2*	10*	12*		13	174	40	15	108	836	0.07	1.98

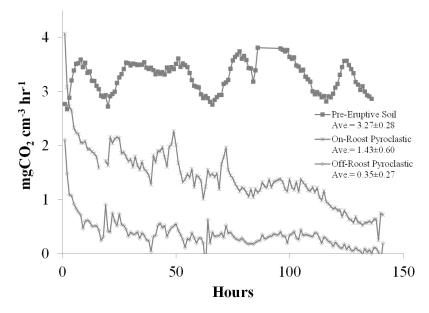


FIGURE 4. Respiration of carbon dioxide from 0 to 5 cm cores (n=4 each) from the pre-eruptive soil surface, and on-roost and off-roost. For selected properties see Table 1 (Pre-Eruptive Soil or LS) and Table 3 (On and Off-Roost pyroclastics).

eruption (Scott et al., 2010) but can be divided into eroding slopes (ES) and depositional surfaces (DS). Results from sampling sites in each surface type are summarized in Table 1. Surface layers are similar and both consist of relatively thin, about 5-10 cm, sandy-loam deposit (C1 horizons of Wang et al., 2010) over a more compacted often slightly more coarse textured, multilayered set of deposits below. Surface pH and soluble salts indicated by EC (Table 1, part A) were very similar between the ES and DS sites. However, the chemical data indicate that runoff and leaching waters have worked to selectively move the more soluble components downslope, most notably extractable P and S. This process, observed by Wang et al. (2010), was noted across the island early after the eruption. Impure sulfate salts were observed as they accumulated on beach bluff abutments of the toe-slopes as they adjoined the beach. These salts also contributed to the crusting of the surface few centimeters that is observed during periodic drying conditions, where they appeared as a white surface precipitate. The higher average extractable P (as phosphate) and total S (as sulfate) of DS sites relative to ES sites indicate that these two important plant macronutrients are moving with water downslope to depositional fan areas. As they have moved, however, extractable levels for all surfaces remain at sufficient or at high levels and are not likely to limit plant growth (Michaelson and Ping,

1989). Some of the plant micronutrients, such as Cu, Zn, and Fe, also show indications of accumulating at higher levels downslope on DS. However at this point in time, all of these plant nutrients remain at levels that appear to be sufficient for plant growth across all sites. They are in the same range of concentration or higher than the average concentrations found for the surface pre-eruptive soils that supported pre-eruptive vegetation (Table 1, part A). Average concentrations for other plant macro-nutrients K, Ca, Mg, and Na showed little difference in concentrations across the ES and DS sites and do not appear to be leaching downslope in great amounts. Although variability was high, there appears to be no large differences in the important physical properties of ES and DS surfaces such as the bulk density (Db) and particle size distribution (Table 1, part B), as both are within a good range for plant available water retention and support of plant life (Brady and Weil, 1999).

Nitrogen is required by plants in relatively high amounts for unrestricted growth. Often new pyroclastic deposits are found to be very low in available N, and vegetation recovery has been observed to be initiated exclusively by pioneering N-fixing plants such as *Lupinus* (Wood and del Moral, 1988) and mainly occurs in microtopographic depression environments where other fertility factors like available moisture are favorable (Tsuyuzaki et al., 1997). Plant-available N levels were very low

in the early years after the Katmai Alaska eruption (Griggs, 1919) and for the most recent Mount St. Helens deposits (Titus, 2009). Low N levels persisted in Katmai deposits for years after deposition. They were measured to be 0.6 mg N kg⁻¹ soil at 13 years later (Griggs, 1933), in a similar low range like Kasatochi pyroclastics (<1 mg N kg⁻¹; Table 1, part A). Available-N levels for Mount St. Helens were also below detection limits for years after deposition (Tsuyuzaki et al., 1997). Katmai pyroclastics were colonized by N-fixers like liverworts and cyanobacteria mats, which after 13 years had only increased available N levels to 0.9 mg N kg⁻¹ and only directly under the mats. The Mount St. Helens deep deposit area known as the pumice plain was so N deficient that very early plant colonization was limited to only the N-fixing Lupinus (Wood and del Moral, 1988) and alder patches under which the N-levels were found to be increased to measureable levels. At this point in time, only a few years after the 2008 Kasatochi eruption, there is little if any colonization of plants on the new deposits but only

on legacy soil-affected patches (Talbot et al., 2010). Soil levels of plant available N are closely tied to the accumulation and cycling of soil organic matter as indicated by soil organic C levels. As mentioned earlier, we have no certain historical record of the previous Kasatochi eruption and thus how long it has taken to reach current state of carbon and nitrogen accumulation. The legacy soils we observed in pre-eruptive surface exposures showed accumulations of an average of 7.0 \pm 3.1 kg C m⁻² and 0.34 ± 0.12 kg N m⁻² (Table 4), resulting in average available N levels of about 20 mg avail-N kg⁻¹ soil (Table 1, part A). Considering the N levels for the depression-areas of Katmai and under alder patches of Mount St. Helens discussed above, these patches of legacy soils contain relatively large pools of N that will likely be very important in sustaining plants and producing propagules while time and biological activity alter the larger areas of new pryroclasic deposits. It has most certainly taken some time for the pre-eruptive, now legacy, soils to build up N-pools to current levels. Time is always an important factor in recovery, and based on average C accumulation rates that have been found for the early years after volcanic deposits across the world's climatic zones (Zehetner, 2010), the approximate age of the Kasatochi pre-eruptive surface can be es-

Organic carbon and nitrogen accumulation and age estimates for the legacy soils (previous to 2008). For the depth of exposure, no soil profiles were observed to be multisequel

				Lo	Location		Pre-erup. soil			Pre-erup. soil
Sample	Elev.		Slope Aspect	Lat.	Long.	Pre-eruptive	$thickness^2$	TOC	Z	est. age³
Location/Id./date sampled	(m)	(%)	(0)	\widehat{Z}_{\circ}	$(^{\circ}W)$	vegetation type ¹	(cm)	(kg	$({\rm kg} \ {\rm m}^{-2})$	(yr.)
S. Old Beach Bluff – 6/13/09	35	30	170	52.16066	175.50542	Grass/herbaceous	80	7.3	0.45	293
W.WST2 - 8/12/09		33		52.17460	175.49533	Moss/woody	41	3.6	0.23	142
S. Terrace gully $-6/18/10$	20	44		52.16142	175.50546	Grass/herbaceous	75	7.9	0.54	315
S.W. Deep Gully2 – 6/16/10		30		52.17630	175.52635	Grass/herbaceous	25	7.3	0.47	291
S.E. Gulley Basin – 8/09/10	64	10	110	52.16281	175.50183	Grass	117	7.2	0.32	287
S.E. Gulley $\exp - 8/9/10$	84	21	140	52.16325	175.50244	Heath	69	13.4	0.40	536
S.W. Cabin Gulley – 8/10/10	32	15	332	52.17188	175.52870	Moss/woody	55	4.1	0.18	163
W. KAS-027 - 8/11/10		35	80	52.17402	175.49542	Moss/woody	37	5.3	0.33	213
$AVERAGE \pm STD$							62 ± 29	7.0 ± 3.1	0.34 ± 0.12	280 ± 122

Dates given as m/dd/yy. Estimated from roots present in upper soil horizons of the buried profile.

age of pre-eruptive soil using an average of 0.025 kg OC accumulation per year using a mid-range value typical for an early post-eruptive period of accumulation: i.e., first 2000 years (Zehetmer, 2010). Thickness of the total surface 'Estimated

timated at about 280 ± 122 years old (Table 4). This approximate time frame would support the speculation of Coats (1950). He asserted that area volcanic activity reported to have been observed in 1760 (about 250 years ago), which Grewingk (1850) had attributed to nearby Koniuji volcano, may actually have been the previous Kasatochi eruption. Any of these legacy soil patches exposed, shallowly buried, mixed, or transported will be good sources of N to maintain plants and other biota capable of tapping these pools of organic and inorganic N as it will likely take tens to hundreds of years to restore legacy soil-like conditions to the new surface.

Fertility of Newly Forming Surfaces

Legacy Effects

The best, most immediately available on-island sources of N, soil biota, and plant propagules is the pre-eruptive surface. Erosion has served to expose isolated patches of pre-eruptive surface on slopes and cliff areas. This process has also detached, moved, and mixed quantities of pre-eruptive surface soils down slopes and gullies to depositional areas (Fig. 2, part C). Moving with the eroding pre-eruptive surface soils are quantities of vital nutrients, especially available-N (Table 1, part A). Available nutrients and soil materials that are moving also contain the organic nutrient pool of the organic C substrates and soil micro and macro biota, including viable plant propagules. Results of the laboratory growth experiment (Fig. 3) indicate that significant quantities of vital available-N can be supplied by this mixing of preeruptive LS with the new pyroclastic deposit (PY). The LS mixed 50% by volume with PY increased total from-seed-growth of Leymus and Lupinus by 139% and 310%, respectively. Smaller amounts (10% by volume) of LS mixed with PY increased growth of Lupinus by 138% but resulted in no significant growth increase for Leymus seed. This is consistent with the potential effects that an inoculation with soil N-fixers from the smaller amount of LS could have provided to boost the Lupinus (legume) growth, whereas this effect would not be expected to affect the Leymus (grass) seed. Also supporting a possible biological effect of added LS (10%) is the low (below detection limits) direct supply of available N observed in the 10% LS media (Table 2). A biological effect would be consistent with the findings of Zeglin et al. (2015), who examined the microbial activity of organic matter from LS at various mixes with pyroclastics in the same area as this study. They found a strong effect of legacy organic matter presence on increased microbial activity not dependent on the quantity of organic matter present.

The experimental trial indicates that *Leymus* sprigs that are transported and mixed into PY materials will not have a significantly better chance of survival or growth. At least the conditions initially will not be more favorable for establishment even as they probably bring some stored nutrients and biota with them. To date on the island uplands, no Leymus sprigs have been observed rooting exclusively in PY materials; thus far they are only found growing where they are at least partially rooted in shallow-buried LS or transported fragments of LS. This mixing and exposing of LS is interesting in that it could provide crucial support for more diversity earlier in recovery for Kasatochi Island, in contrast to that observed for mostly deeper Mount St. Helens. Moisture is abundant across Kasatochi, not just in depression areas as found for the deepest deposit areas of Mount St. Helens. As a result wherever LS are mixed with PY, nutrients (especially N) and soil biota will be available to support the establishment of a more diverse plant community earlier in recovery. The presence of LS on Kasatochi will encourage more non N-fixing plants and thus potentially support a more diverse plant community earlier in recovery. This is in contrast to the moisture, nutrient, and biota deficient deep deposit areas of Mount St. Helens, where initially pioneer N-fixers established almost exclusively and only in moist areas of the deposits (Tsuyuzaki et al., 1997). The drawback, however, for early establishment of plants across the whole of Kasatochi is the high degree of surface instability due to the very high degree of erosion and deposition that is taking place.

Bird Effects

Pre-eruption Kasatochi was home to a major population of seabirds with large rookeries that are expected to recover and have shown early signs of doing so (Williams et al., 2010). A new roosting site was examined in this study. The site was on the ridge area of a large pyroclastic fan deposit abutting the pre-eruptive beach bluff that is now some 400 m from the shoreline (Fig. 2, part D). Birds are well

known for depositing large quantities of N gathered from oceanic food sources onto the land (Bird et al., 2008). Even with the limited time for roosting activity at this recent site, there were significant increases in available plant macronutrients N, P, K, and total %C (Table 3), and elevated nutrient levels compared to adjacent nonroosting sites. Effects were especially evident in the PY surface crust. Nitrogen that was deposited moved down throughout the depth examined (0–5 cm), P only moved to 2 cm, and both nutrients decreased in concentration with depth while C and K inputs from roosting activity remained near the surface (0-0.5 cm). This roosting activity was only since the 2008 eruption, but there was a thin green presumably algal crust on the surface. With increased C and macronutrient levels, elevated soil respiration was measured in roost sample cores, indicating enhanced biological activity (Fig. 4). Respiration for the on-roost samples was increased over nonroosted pyroclastics, but was still less than that measured for cores of the preeruptive LS surface.

These results agree with the recent findings of Zeglin et al. (2015) where soil and pyroclastic microbial characteristics were examined under similar roosts and LS of the area. They found high microbial indices for numbers and activity in legacy soils and roost affected pyroclastics compared to unaffected pyroclastic sites. We found the C inputs from the roosting activity is minimal relative to amounts found in the LS with the 0-5 cm surface ranging from 0.24% to 0.06% C for the roost compared to 11.4% to 6.37% C for the LS (Tables 3 and 1, part A, respectively). But the weighted average of extractable plant-available N levels for the 0-5 cm surfaces of the on-roost soils are essentially identical to those for the LS at an average of 20 and 21 mg N kg⁻¹, respectively. This level of available N would be sufficient to support establishment of the higher plants as is observed for the LS. In addition, as indicated by the laboratory media growth results, a similar level of 15 mg N kg⁻¹ in the pyroclastic material with added fertilizer-N (Table 2) performed as well in producing plant growth as the LS surface material (Fig. 3). Roost levels for all measured major plant macronutrients compare favorably with the LS surface material. These observations for roosting areas indicate that across the landscape, as plant propagules are introduced, these areas are prepared

to become islands for sustaining the newly establishing plants. Many roosting areas are apparent in the depositional upper beach of the island's south side, with nearby low areas of eroded LS dispersed on fans. These areas will likely see beneficial inputs of soil biota, and nutrients (especially N) from birds and inputs of plant propagules, soil biota, and nutrients from LS redistribution from upslope. Roosting areas could be most important in maintaining stocks of diverse species for later distribution as the landscape stabilizes and soils develop. Mulder et al. (2011) suggested that the same phenomenon happens with bird nutrient inputs, observing that these areas support the faster growing plants that contribute to soil development through acceleration of organic matter accumulation and helping stable plant communities develop.

Conclusions

Available N is the most important nutrient lacking in the post-eruptive pyroclastic surface, with other plant macronutrients in good supply. Legacy soils (LS) can and are providing readily available N as well as an organic C and N pool to support new plant growth. Continuing erosion is causing instability that has resulted in exposure, transportation, mixing, and redeposition of LS, along with their biota, and C and N pools. These processes are likely to play a key role in both the short- and long-term recovery of the island's vegetation, by providing the initial C and N to begin reestablishment of plant communities. The LS, where stable and exposed to the surface, will provide refugia for plants, other biota, and plant propagules. Our results indicate that another important intermediate factor in reestablishment of more complete plant-cover will likely be mixing (with new pyroclastics) and redeposition of the erosion-destabilized LS. As erosion continues, these processes have the potential to speed the establishment of plant cover through this redistribution of C and N substrate and pools along with micro- and macrobiotic inoculum. Bird influences are augmenting the effects of LS on isolated roosting areas by adding much needed N to pyroclastics in amounts that should be sufficient to support good growth of higher plants. Plant propagules from eroded LS upslope are being deposited in the areas of roosts and the combination of propagules, biota, and nutrients from both sources will

likely be very beneficial for establishing plant refugia in depositional areas. It is unclear as to how and when the aerial supply of seed from distant sources will occur in significant amounts for this isolated island. This seed-supply mode has been found to be important for the earliest plant establishment on the pyroclastic surfaces of Mount St. Helens (del Moral and Wood, 1993; del Moral and Eckert, 2005) but could be slower here. Our results indicate that localized areas with LS exposed, transported, and mixed at even low proportions could greatly enhance the survival and growth of plants, especially seeds. This localized LS effect on plant establishment through enhancing available N and providing both micro and macro propagules that sustain biotic activity could compensate for a slower input of seeds from afar. If climate change brings increased intensity and frequency of storm activity to the area, the effect could be to increase both exposure of legacy soil surfaces and erosive mixing of materials downslope and speed recovery of plant cover.

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