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Abstract

We studied the vegetation of Kasatochi Island, central Aleutian Islands, to provide a general field assessment regarding the survival of plants, lichens, and fungi following a destructive volcanic eruption that occurred in 2008. Plant community data were analyzed using multivariate methods to explore the relationship between pre- and post-eruption plant cover; 5 major vegetation types were identified: *Honckenya peploides* beach, *Festuca rubra* cliff shelf, *Lupinus nootkatensis–Festuca rubra* meadow, *Leymus mollis* bluff ridge (and beach), and *Aleuria aurantia* lower slope barrens. Our study provided a very unusual glimpse into the early stages of plant primary succession on a remote island where most of the vegetation was destroyed. Plants that apparently survived the eruption dominated early plant communities. Not surprisingly, the most diverse post-eruption community most closely resembled a widespread pre-eruption type. Microhabitats where early plant communities were found were distinct and apparently crucial in determining plant survival. Comparison with volcanic events in related boreal regions indicated some post-eruption pattern similarities.

Introduction

Volcanic eruptions are among the most destructive natural disturbances on earth. They can destroy all life and leave barren surfaces that only gradually regain a living component (del Moral and Grishin, 1999). However, over time, plants and animals do colonize and soils do develop on most volcanic surfaces via a process called primary succession (Walker and del Moral, 2003). Recolonization generally occurs from adjacent, undamaged biota, but newly formed volcanic islands such as Surtsey in the North Atlantic (Magnússon et al., 2009) and Bogoslof in the North Pacific (Byrd et al., 1980) depend on long-distance dispersal of organisms. When volcanic eruptions do not destroy all life, surviving plants and animals may contribute to the recolonization process, thereby providing a legacy effect. The contribution of such legacies is difficult to determine because of the unpredictable timing and damage of volcanoes. An ideal situation is when investigators have pre-eruption data and can follow post-eruption processes over time. Such an opportunity can help clarify our understanding of the role of residual species on changes in biodiversity and rates of successional change and potentially improve our ability to restore severely damaged ecosystems (Walker and del Moral, 2009; Svavarsdóttir and Walker, 2009). The eruption of Kasatochi Island provides such an opportunity.

When Kasatochi Island, a remote volcanic island located in the Andreanof Islands in the central Aleutian Islands in the North Pacific, erupted on 7–8 August 2008 (after ca. 180 years without erupting), the island was covered with a dense carpet of vegetation. Our initial observations from offshore, only two weeks after the eruption, suggested that the explosion had produced such extensive pyroclastic flows, and so altered the shape and size of the island that no plants could have survived. The island was covered with deep layers of volcanic ash and rock, fumaroles still emitted steam, and the dominant colors were shades of gray. However, during subsequent visits by an interdisciplinary team in 2009, some plants

were found that had apparently survived the eruption, while other plants may have already begun to colonize from neighboring islands.

We do not expect rapid changes in the flora, as suggested from other studies of volcanic succession in the boreal zone including Iceland (Surtsey: Fridriksson, 2005), Japan (Hokkaido: Tsuyuzaki, 2009), Russian Federation (Kamchatka: Dirksen and Dirksen, 2007; Grishin et al., 1996; Grishin et al., 2000), and North America (Kodiak and Katmai: Griggs, 1933). However, with time we expect that Kasatochi Island will once again be covered with a verdant layer of hardy plants. Pre-eruption plant community data are available in the form of seven relevés, providing a partial description of the original composition of the island's vegetation (S. S. Talbot, unpublished data), as well as a vegetation map (Scharf et al., 1996) and a list of vascular plants accumulated over time by biologists collecting data during long-term monitoring of seabirds (Drummond, 2006, 2007). Thus, observations involving descriptions of vegetation in years subsequent to the eruption can help to clarify the relative importance of revegetation from extant plants, or from colonization, in a devastated landscape.

In this paper, we present the first results of investigations of succession on Kasatochi Island. The objectives of our study were to: (1) provide a general field assessment regarding the survival of plant, lichen, and fungal species; (2) describe the plant assemblages or communities and their possible origins and microhabitats; (3) compare the plant cover of pre- and post-eruption Kasatochi vegetation with those from other boreal regions; and (4) provide recommendations for future studies, based on models of survival and colonization emerging from our initial observations.

STUDY AREA

Kasatochi Island occurs in the "Aleutian Islands Ecoregion," characterized as a naturally treeless region where dwarf shrub communities predominate at higher elevations and on sites

exposed to the wind, and where herbaceous communities occur on more protected sites (Gallant et al., 1995). Species comprising the vegetation of the Aleutian Islands are characteristically perennial. Küchler (1966) classified the former dwarf shrub communities as "Aleutian heath and barren (*Empetrum-Vaccinium*)," and the latter herbaceous communities as "Aleutian meadows (*Calamagrostis-Anemone*)." A vegetation map of Kasatochi Island (Fig. 1) shows five map units; these are listed in descending order of areal extent: (A) "short grass meadow" community, occurring on lower and middle slopes; (B) "bare rock" around the crater rim and on the marine shoreline; (C) "vegetated talus" on lower and middle slopes ; (D) "lichen/moss community" at upper elevations adjacent to the crater rim; and (E) "dense *Leymus*" at lower elevations with some isolated patches on middle slopes.

Kasatochi Island is an emergent summit of a predominantly submarine volcano that last erupted in 1828 (Miller et al., 1998). Prior to the 2008 eruption, the island consisted of a single, undissected cone with a central lake-filled crater about 0.75 km in diameter and steep flanks (18–45°) rising to a maximum elevation of 314 m. The pre-eruption soils of Kasatochi were mapped as rough mountainous land composed of steep rocky slopes with thin soils occurring on lower slopes and valleys (Rieger et al., 1979); data from surrounding islands suggest that Typic Cryandepts were likely well-represented on Kasatochi. A characterization of the pyroclastic deposits and pre-eruptive soil following the 2008 eruption of Kasatochi Island is given by Wang et al. (2010 [this issue]). Pollen studies of Aleutian soil profiles show a repeated pattern of volcanic ashfalls followed by vegetation recovery (Anderson and Bank, 1952; Heusser, 1978).

Climatically, Kasatochi Island is within the northern boreal subzone described by Tuhkanen (1984) in the hyperoceanic (O_2) sector and humid (h) province. Based on available records (1971–2000) from Adak Island, the nearest climatic station (51.88°N, 176.65°W), 80 km southwest of Kasatochi, the mean annual temperature and precipitation recorded are 4.6 °C and 1372 mm, respectively (WRCC, 2009); August is the warmest month with a mean temperature of 10.5 °C (Fig. 2). Multivariate analysis of climate along the southern coast of Alaska indicates that the Aleutian Islands form a distinct climatic group with moderately cool temperatures in the fall, winter, and spring and much colder summers than other coastal stations (Farr and Hard, 1987).

Materials and Methods

VEGETATION AND ENVIRONMENTAL SAMPLING

We sampled vegetation in twenty-one 25 m^2 relevés (Westhoff and van der Maarel, 1973) during three periods: the pre-eruption periods 13 August 2001 (relevés 1–4) and 20 August 2003 (relevés 5–7), and the post-eruption period from 10 to 12 August 2009 (relevés 8–21). The pre-eruption relevé sites were selected to represent a spectrum of structural and compositional variation in the landscape from lower to upper mountain sites, but excluded beaches. The post-eruption sites were selected by searching for plants from beaches to within 100 m of the crater rim and recording a relevé wherever plants occurred. Safety concerns precluded sampling near the post-eruption rim. Cover abundance was estimated for all vascular plants, bryophytes, and macro-lichens according to the nine-point ordinal scale of Westhoff and van der Maarel (1973). Although not part of our study, fallout collectors for sampling insects (Sikes and Slowik, 2010 [this issue]) were utilized to collect samples for wind-dispersed plants (Edwards and Sugg, 2005). Ten 0.1 m^2 collectors were placed 10 m apart along a 100 m transect oriented from NW to SE on the westernmost coast of the island on 14 June 2009 and recovered on 10 August 2009. Plant nomenclature follows USDA, NRCS (2009). Voucher specimens were deposited at several herbaria: University of Alaska Museum (ALA), fungus; State University of New York, Binghamton (BING), *Sphagnum*; Canadian Museum of Nature (CAN), Poaceae and *Salix*; Iowa State University (ISC), *Botrychium*; Missouri Botanical Garden (MO), *Epilobium*; New York State Museum (NYS), *Platanthera*; University of Waterloo (WAT), *Stellaria and Cerastium*; University of British Columbia (UBC), bryophytes and lichens (2003 vouchers); U.S. National Herbarium (US), *Poa*; and University of Wisconsin (WIS), lichens (2001 vouchers).

We characterized the local environment at each relevé by recording aspect (°), elevation (m), litter cover (%), slope inclination (°), latitude and longitude (with a GPS using WGS84 datum). Three to five samples of the top 15–20 cm of post-eruption material (henceforth called soil) from the center of each relevé were collected, pooled, and placed in plastic zip-lock bags; these were kept cool until analysis. Where present ($n = 7$ relevés), pre-eruption soil horizons were also sampled in the same manner, but up to 30 cm depth. Soils were not collected during the 2001 and 2003 season, although soil texture was estimated (Burt, 2004).

VEGETATION CLASSIFICATION

Our data set of 21 relevés and 91 species was entered in TURBOVEG (Hennekens and Schaminée 2001). We used the method OPTIMCLASS in JUICE 6.5 (Tichý, 2002; Tichý et al., 2010) to determine the optimal number of relevé groups. Numerical analysis was performed with the classification and ordination methods of the MULVA-5 program (Wildi 1989; Wildi and Orlóci, 1996), following Talbot et al. (2010). In brief, relevés were first clustered into relevé groups using the similarity ratio and complete linkage, and species were clustered into species groups using a similar procedure. Next, analysis of concentration (Feoli and Orlóci, 1979) ordered dense species-relevé groups along the diagonal (the main floristic gradient) according to the first axis in correspondence analysis (Hill, 1974). A set of highly discriminating species was then determined using Jancey's (1979) ranking.

An ordination was performed using CANOCO 4.5 (ter Braak and Šmilauer, 2002) with the WinKyst1.0 Add-On (Šmilauer, 2003) to provide non-metric multidimensional scaling (NMDS). The species data were transformed using a square-root transformation and a distance matrix calculated using Bray-Curtis distance. The file of 91 species was treated in CANOCO 4.5 and CANODRAW 4.1 as suggested by Šmilauer (2003) with environmental data related to the sample scores in an unconstrained analysis.

SOIL ANALYSIS

Soils were analyzed by the Kuo Testing Labs, Inc. (KTL), Othello, Washington. All methods followed Burt (2004). Organic matter was analyzed by the Walkley-Black method; orthophosphate by Olsen's extraction; cations by inductively coupled plasma spectrophotometry; nitrate-N and ammonium-N by colorimetric analysis of a KCl extract; SO$_4$-S, Boron, Zn, Mn, Cu, and Fe by extraction with a DPTA-Sorbitol solution; texture by the hydrometer method; and organic matter by ashing in a muffle furnace.

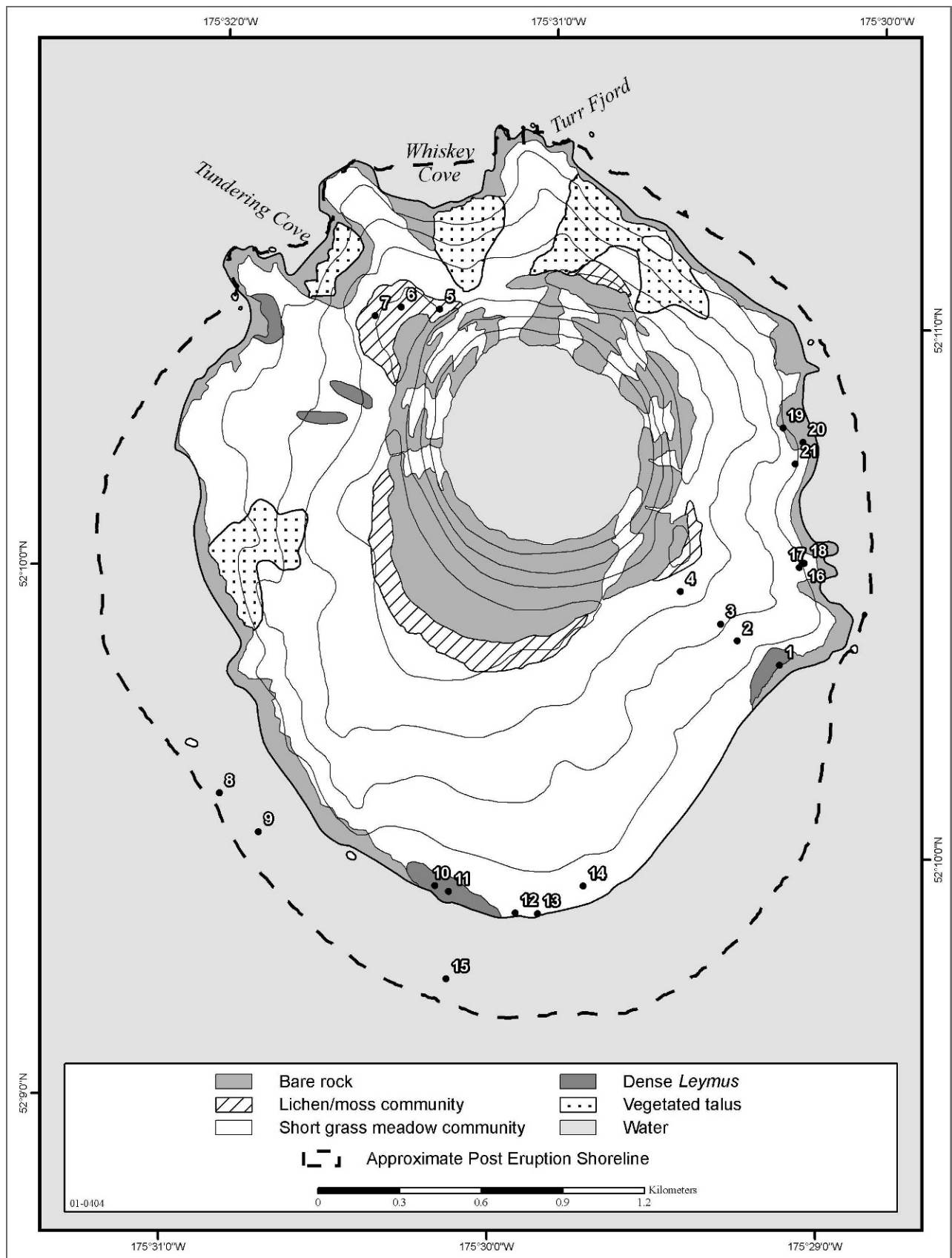**FIGURE 1.** Pre-eruption vegetation of Kasatochi Island, Alaska, in 1996 (modified slightly from Scharf et al., 1996). Numbers on the map indicate relevé locations; these relevés were sampled during three periods: the pre-eruption periods 13 August 2001 (relevés 1–4) and 20 August 2003 (relevés 5–7), and the post-eruption period from 10 to 12 August 2009 (relevés 8–21).
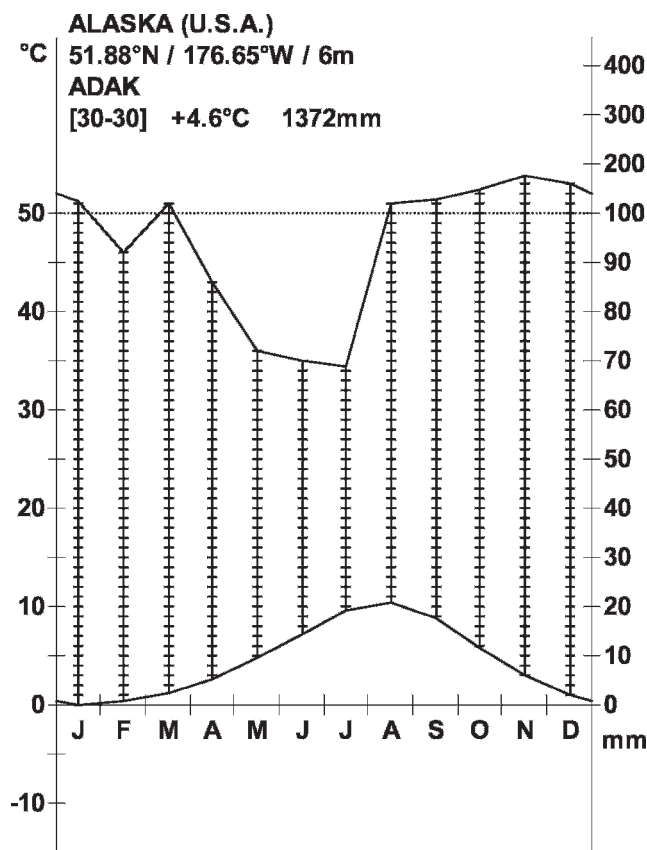
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FIGURE 2

ALASKA (U.S.A.)
°C | 51.88°N / 176.65°W / 6m
ADAK
[30-30]   +4.6°C   1372mm

FIGURE 2. Climate diagram for Adak Island, Alaska. Abscissa shows the months January to December. Ordinate: the first dash-mark upwards represents 10 °C and 20 mm, respectively. Name of station given in upper left-hand corner with latitude/longitude and elevation given below. Number of years data were collected for temperature and precipitation given in brackets, followed by mean annual temperature and mean annual precipitation. Top curve is mean monthly precipitation and lower curve is mean monthly temperature. The diagram was prepared following Lieth et al. (1999).

Results

GENERAL FEATURES

Typically, the plants we found on post-eruption Kasatochi during 2009 were relatively isolated and localized, and particularly occurred on lower mountain slopes and beaches; no plants were found growing on middle and upper mountain slopes. The soils from the 2008 eruption were undergoing rapid erosion, and occurred on upper mountain slopes (rills to 30 cm deep), increasing in depth on lower slopes (gullies to several meters deep). Such active erosion resulted in low substrate stability. Plant diversity was highest in the southern and southeastern corner of the island and was associated with the presence of antecedent soil horizons particularly at the top of a bluff ridge and on lower mountain slopes where rill erosion exposed the pre-eruption soil.

The number of taxa recorded in the relevés totaled 91 (51 vascular plants, 23 lichens, 16 bryophytes, and 1 fungus; Table 1); of these, 86 species were recorded in the pre-eruption landscape, 18 in the post-eruption, 13 occurred in both the pre- and post-eruption, and 5 were only recorded in the post-eruption landscape.

CLASSIFICATION AND ENVIRONMENTAL CHARACTERISTICS OF VEGETATION TYPES

Numerical-phytosociological analysis of all relevés (pre- and post-eruption) identified 5 vegetation or community types, hereafter called relevé groups (RGs), and 8 species groups. The 5 (relevé groups) × 8 (species groups) contingency table, ordered in Table 1 along the main floristic gradient (= the ordering of the species and relevés along the first axis of the correspondence analysis), showed block structure that deviated from random expectation. A mean square contingency coefficient of 0.442 indicated that group structure was relatively strong (Wildi and Orlóci, 1996). A quantitative display of relationships among the 5 RGs is presented in Figure 3.

The 5 RGs showed differences in species composition and dominance (Table 1), vegetation structure (Table 2), and site and soil characteristics (Tables 2 and 3). A summary of each type follows (ordered as in Table 1, along the floristic gradient). Percent cover, elevation (m), and slope (°) are expressed as mean values:

Honckenya peploides *Beach (RG3)*

This species-poor, post-eruption type occurred on the back slope of sandy beaches above mean high tide. It was composed of a single species, *Honckenya peploides*, with only 1–3 individual plants in a post-eruption habitat, and had the sandiest soil, the lowest organic matter content, and generally the lowest nutrient values of all types (Table 3).

Festuca rubra *Cliff Shelf (RG1)*

This species-poor, post-eruption type was associated with very steep rock cliffs, where it occurred on cliff shelves at moderately low elevation. Soil was a sandy loam with relatively high organic matter content. Cover of bare rock cliffs predominated. A single species, *Festuca rubra*, was recorded in this post-eruption habitat.

Lupinus nootkatensis–Festuca rubra *Meadow (RG2)*

This mesic meadow type was the characteristic original, pre-eruption vegetation (Stephen Talbot, personal observation) that occurred from lower to upper mountain slopes; elevation ranged from 12 to 311 m. Field estimation of soil texture varied from sand to sandy loams. Of all vegetation types these meadows had the highest cover of herbs, mosses, and lichens and the highest species diversity. Species of high presence (that is, found in >80% of the relevés) included the herbs: *Achillea millefolium* v. *borealis*, *Angelica lucida*, *Conioselinum gmelinii*, *Festuca rubra*, *Lupinus nootkatensis*, *Phleum alpinum*, *Platanthera huronensis*, *Ranunculus occidentalis*; mosses: *Rhytidiadelphus squarrosus*, *Sanionia orthothecioides*; and the lichen: *Peltigera membranacea*.

Leymus mollis *Bluff Ridge (and Beach) (RG4)*

This species-poor, post-eruption type occurred primarily on bluff ridges that were wave-cut cliffs prior to the eruption. Although this type is species-poor, mean species diversity was generally higher that in the other post-eruption types. Ridge slopes were steep and at low elevations. Most of the soil was from the eruption, but, significantly, pre-eruption soil horizons were present. In Table 3, values for pre-eruption soils (subgroup 4B) were distinctly different from the post-eruption material (subgroup 4A). Higher values were measured for all nutrients in the pre-eruption soils. In addition, pH was lower in these soils and

electrical conductivity and organic matter content higher than in the post-eruption soils.

Aleuria aurantia *Lower Slope Barrens (RG5)*

This post-eruption type was characterized by the presence of the bright-orange ascomycete fungus *Aleuria aurantia* and the moss *Ceratodon purpureus*. The type occurs at low elevations on low to middle eroding slopes of moderate steepness. Individual species comprise only a few plants. For soils, a pattern similar to that of RG4 occurred (Table 3); as in RG4, pre-eruption soils were visible in RG5, and the soils were analyzed similarly by separating analyses of pre-eruption (subgroup B) and post-eruption (subgroup A) soils. Accordingly a very similar pattern emerged with higher values for all nutrients in the pre-eruption soils, lower pH, and higher electrical conductivity and organic matter content than in the post-eruption soils.

ORDINATION OF RELEVÉS

Nonmetric multidimensional scaling ordination (Fig. 4) showed 21 relevés in 5 relevé groups. The primary NMDS solution for two dimensions was found with 41 iterations out of 100, stress = 0.12133 indicating a good fit. The eigenvalues of the first two axes of PCA, applied to NMDS configuration to rotate it so that the spread of relevés was maximized along the two axes, showed that the resulting first axis had pronounced explanatory value, compared with the second one (0.663 vs. 0.337).

The 5 relevé groups were relatively distinct on the ordination biplot (Fig. 4) and were delineated by slope and elevation. The pre-eruption community (RG2) occupied a central position in the ordination and most closely resembled one relevé in post-eruption community RG4 (relevé no. 14) because of several shared species.

SPECIES OCCURRING OUTSIDE THE RELEVÉS

Several species were found that were not sampled in the relevés, including two crustose lichens, two mosses, and two vascular plants. The lichens included *Caloplaca* sp. and *Verrucaria* sp. growing on rock outcrops in the salt-spray zone. The mosses were *Eurhynchium praelongum*, found growing around a small volcanic vent, and *Funaria hygrometrica* that included old capsules and new gametophytes (O. Lee, UBC Herbarium, personal observation). The vascular species included: a fern, *Cystopteris fragilis*, found in a rock crevice; *Ligusticum scoticum*, a plant typical of seashores that occurred on a bluff ridge; and *Senecio pseudoarnica*, a species characteristic of Aleutian beaches, which was associated with antecedent soil (J. Williams, personal observation).

Discussion

The vegetation of the Aleutian Islands is subjected to an array of natural disturbances, including volcanic lava or ash, wind erosion, and heavy rains (Bank, 1953). Nonetheless, most of the islands are normally covered with a lush green carpet of vegetation comprised of species adapted to such unstable conditions. Human impacts on the evolution of plant communities have been minimal; although Aleuts occupied the islands for over 3000 years and may have transported some plant species, such as stinging nettle (*Urtica*) among islands, they did not establish permanent

habitations on Kasatochi (D. Corbett, USFWS, personal communication). During the past century, however, human impacts on the Aleutian Islands have increased, becoming extreme in localized areas due to activities by the military during and subsequent to World War II, but also due to the introduction of exotic mammalian species such as foxes, rats, and ungulates (Ebbert and Byrd, 2002). Kasatochi, however, was not heavily impacted by most of these activities, and, after the removal of foxes in the 1980s (Deines and Willging, 1985), remained relatively pristine except for the seasonal presence of seabird biologists and possibly fishing activity.

Vegetation on pre-eruption Kasatochi comprised a high number of species common throughout the Aleutian Islands (Hultén, 1968). Approximately 530 species make up the Aleutian vascular flora (Hultén, 1960); the flora of the central Aleutian Islands (the Rat Islands and the Andreanof Islands) numbers about 244 vascular species (Tatewaki, 1963).

Thus, 16% of the total vascular flora of the Aleutian Islands, and 35% of the central Aleutian vascular flora occur on the relatively small island of Kasatochi, given 85 vascular species described from pre-eruption Kasatochi. However, it should be noted that the 2001 or 2003 efforts were not intended to fully represent the vegetation of Kasatochi, as the sampling was performed opportunistically while we were present on the island for a short period of a few hours. Similarly, the lists of plant species accumulated by sea bird researchers over many years (Table 4) were made opportunistically but without voucher specimens. Thus, a greater proportion of the vascular flora of the Aleutians than reported here is likely to have been present on pre-eruption Kasatochi.

Post-eruption additions to the flora of Kasatochi Island comprised one fungus, four bryophytes, and two lichens; no new vascular plants were added in the first year following the 2008 eruption. All these non-vascular taxa are known to occur throughout the Aleutian Islands and most fare well in recently disturbed habitats. *Aleuria aurantia* is a saprophytic fungus that lives on decaying material, especially humus, and on bare soil and disturbed ground of landslides (Evenson, 1997; Seaver, 1914). The soils data indicated the presence of organic matter associated with antecedent soils and the presence of this fungus supported this observation. The bryophytes seen in the post-eruption habitats are all cosmopolitan species; *Ceratodon purpureus*, *Funaria hygrometrica*, and *Marchantia polymorpha* often occur on bare, disturbed soil (Schofield, 1992, 2002). *Eurhynchium praelongum* is characteristic of damp, swampy forest sites but also occurs on maritime rocks (Schofield, 1992). It is likely most, if not all, of these species were present during some period on pre-eruption Kasatochi, but not previously recorded. The lichens *Caloplaca* sp. and *Verrucaria* sp. growing on rock outcrops in the salt-spray zone apparently survived the eruption *in situ*. It has not escaped our notice that both *Ceratodon purpureus* and *Marchantia polymorpha* are known or suspected to fix nitrogen via associated cyanobacteria (Adams, 2002; Okitsu et al., 2003). These species may play an important role on Kasatochi, as may another nitrogen fixer observed on post-eruption vegetation, the vascular plant, *Lupinus nootkatensis* (Magnússon et al., 2004).

COMPARISON WITH OTHER BOREAL REGIONS

The long-term knowledge gained from the study of the eruption of the Icelandic island of Surtsey provides useful comparative data (Jakobsson et al., 2009). Kasatochi and Surtsey differ in their origins; Kasatochi is of Late Tertiary and

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TABLE 1

Vegetation of Kasatochi Island, Alaska, including pre-eruption type (RG2) and post-eruption types (RG1, RG3, RG4, RG5). Key to types: RG1—*Festuca rubra* cliff shelf; RG2—*Lupinus nootkatensis–Festuca rubra* meadow; RG3—*Honckenya peploides* beach meadow; RG4—*Leymus mollis* bluff ridge (and beach); RG5—*Aleuria aurantia* lower slope barrens. The order of relevé and species groups is based on analysis of concentration (Feoli and Orlóci, 1996) along the main floristic gradient according to the first axis in correspondence analysis (Hill, 1974). Table 1 continues on next page.

Relevé group (RG) no.	3		1			2							4					5			
Relevé no.	9	8	19	20	21	2	1	4	3	7	6	5	8	11	5	1	6	3	4	5	3
Number of species	1	1	1	1	1	21	28	34	23	27	33	51	10	14	11	15	12	18	17	16	13
Characteristic species of relevé groups																					
Honckenya peploides	1	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Trisetum spicatum	.	.	.	.	.	.	.	1	1	.	2	2	.	.	.	.	.	.	.	.	.
Cerastium beeringianum	.	.	.	.	.	.	.	1	.	1	2	1	.	.	.	.	.	.	.	.	.
Luzula multiflora s. *multiflora* v. *kobayasii*	.	.	.	.	.	2	2	.	2	2	.	.	.	.	.	.	.	.	.	.	.
Cardamine oligosperma v. *kamtschatica*	.	.	.	.	.	2	1	.	2	1	.	.	.	.	.	.	.	.	.	.	.
Rhinanthus minor	.	.	.	.	.	2	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.
Anaphalis margaritacea	.	.	.	.	.	5	2	.	2	2	.	.	.	1	.	.	.	.	.	.	.
Agrostis exarata	.	.	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.
Lobaria linita	.	.	.	.	.	.	1	1	1	.	.	2	.	.	.	.	.	.	.	.	.
Poa arctica	.	.	.	.	.	1	.	2	2	.	2	1	.	.	.	.	.	.	.	.	.
Phleum alpinum	.	.	.	.	.	.	1	1	1	1	2	1	.	.	.	.	.	.	.	.	.
Hylocomium splendens	.	.	.	.	.	5	.	8	4	.	5	1	.	.	.	.	.	.	.	.	.
Sanionia orthothecioides	.	.	.	.	.	2	5	4	2	2	1	3	.	.	.	.	.	.	.	.	.
Rhytidiadelphus triquetrus	.	.	.	.	.	1	.	3	2	.	4	.	.	.	.	.	.	.	.	.	.
Rhytidiadelphus squarrosus	.	.	.	.	.	2	3	2	2	5	6	1	.	.	.	.	.	.	.	.	.
Achillea millefolium v. *borealis*	.	.	.	.	.	2	1	4	2	2	2	3	.	1	.	.	.	.	.	.	.
Festuca rubra	.	.	1	1	1	3	7	3	2	5	5	2	.	1	.	.	.	.	.	1	.
Peltigera membranacea	.	.	.	.	.	2	5	3	4	2	2	.	.	.	.	.	.	.	.	.	.
Platanthera huronensis	.	.	.	.	.	2	2	1	1	3	2	.	.	.	.	.	.	.	.	.	.
Angelica lucida	.	.	.	.	.	1	6	6	2	2	6	.	.	1	.	.	1	.	.	.	.
Anemone narcissiflora v. *villosissima*	.	.	.	.	.	4	4	.	3	7	.	.	.	1	.	.	.	.	.	.	.
Conioselinum gmelinii	.	.	.	.	.	2	4	4	1	4	2	1	1	3	1	.	2	.	.	.	1
Epilobium hornemannii s. *behringianum*	.	.	.	.	.	.	2	1	1	2	1	.	1	1	1	.	.	.	.	.	.
Ranunculus occidentalis	.	.	.	.	.	1	2	5	1	1	2	.	1	1	.	.	1	.	.	1	1
Lupinus nootkatensis	.	.	.	.	.	1	1	2	2	6	1	4	1	1	2	.	1	.	1	.	.
Leymus mollis	.	.	.	.	.	3	1	.	.	1	.	.	2	3	1	1	2	.	.	.	.
Cardamine oligosperma v. *kamtschatica*	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.
Aleuria aurantia	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	1	1
Ceratodon purpureus	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	1	1	.
Marchantia polymorpha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.
Other species																					
Luzula kjelmanniana	.	.	.	.	.	.	.	3	1	.	.	2	1	.	.	.	.	.	.	.	.
Cerastium fischerianum	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.
Cladonia gracilis	.	.	.	.	.	.	1	.	.	.	2	2	.	.	.	.	.	.	.	.	.
Platanthera dilatata	.	.	.	.	.	.	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	1	1	.	.	.	3	.	.	.	.	.	.	.	.	.
Polytrichastrum alpinum	.	.	.	.	.	1	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.
Cladina mitis	.	.	.	.	.	.	.	1	.	.	4	3	.	.	.	.	.	.	.	.	.
Viola langsdorffii	.	.	.	.	.	.	.	6	.	.	1	1	.	.	.	.	.	.	.	.	.

Quaternary origin, whereas Surtsey first emerged in 1963. Nevertheless, there are strong similarities in climate and flora. For example, the mean annual temperature and precipitation of Surtsey is 4.8 °C and 1589 mm (Fridriksson, 2005), respectively (Fig. 2), while corresponding values on Adak are 4.6 °C and 1372 mm, respectively. The floristic similarity between the Surtsey and the Aleutian Islands is high with 58% (36 species) of the total vascular plant flora of Surtsey (62 species; Fridriksson, 2005) occurring in the Aleutian Islands (cf. Hultén, 1968). Two of the first pioneer species on Surtsey, *Honkenya peploides* and *Leymus mollis*, were common pre- and post-eruption species on Kasatochi Island. Throughout the Aleutians these species are abundant and form the basis of the main community type at the leading edge of the vegetation along the shoreline (Viereck et al., 1992; Talbot and Talbot, 1994; Talbot et al., 2010).

Although not closely monitored over time, Bogoslof Island in the eastern Aleutian Islands may serve as a useful baseline for the speed of vegetation origin, via colonization (but not survival of pre-eruption plants), in the Aleutian Islands, and subsequent succession. Byrd et al. (1980) summarized the changes in the island's flora, which are abstracted here. On Bogoslof, which emerged as a new island due to volcanic activity, the vegetation began to appear in 1817, twenty-one years after its origin in 1796. Over many years, periodic reports of the vegetation alternated between records that vegetation was present or that it was absent, but in 1916, patches of vegetation (primarily "coarse grass") began to take hold, and by 1946 the island's plateau was covered with "tundra vegetation." By 1973, the plateau was completely vegetated. Volcanic activity continued periodically in the vicinity of Bogoslof with the most recent eruption in 1992. A total of 12 vascular plants are reported (Byrd et al. 1980), notably *Honckenya peploides*, *Leymus mollis*, *Ranunculus occidentalis*, and *Senecio pseudoarnica*, which are on post-eruption Kasatochi. Colonization and establishment of mature plant communities typical of other naturally treeless Aleutian islands appear to have proceeded quite rapidly on Bogoslof, over ca. 180 years. This is quite different from other boreal areas; Grishin et al. (1996) estimated vegetation recovery on Ksudach Volcano in Kamchatka will take more than 2000 years, where the climate supports forest vegetation on zonal sites. It must be reiterated that there are differences between these areas in terms of climate and plant communities. On Kamchatka, forests of *Betula ermanii* reach their mature stage (not the final stage of succession) at an age of 120–150 years in favorable conditions with good soils. In addition, soil formation on

TABLE 1 (cont.)

Species of low presence and diagnostic value usually occurring three times or less. Each species name is followed by relevé group number (RG), releve number, and cover-abundance value.

Species		Species	
Poa macrocalyx	RG2, 1, 2; 7, 2	*Empetrum nigrum*	RG2, 2, 9; 3, 9
Listera cordata	RG2, 2, 1; 4, 1	*Plagiomnium insigne*	RG2, 2, 1; 7, 3
Cladonia amaurocraea	RG2, 4, 3, 1	*Psoroma hypnorum*	RG2, 3, 1; 5, 1
Stereocaulon alpinum	RG2, 4, 1; 5, 2	*Carex macrochaeta*	RG2, 5, 1; RG5, 16, 1
Cetraria islandica	RG2, 6, 1; 5, 1	*Poa* species	RG2, 6, 1; 5, 1
Thamnolia vermicularis	RG2, 6, 2; 5, 3	*Draba borealis*	RG2, 7, 1; 6, 2
Botrychium lunaria	RG2, 1, 1	*Carex gmelinii*	RG2, 1, 3
Gentianella amarella	RG2, 1, 2	*Ligusticum scoticum*	RG2, 1, 1
Cladonia ecmocyna	RG2, 4, 1	*Racomitrium canescens*	RG2, 4, 1
Cladonia gracilis s. *chordalis*	RG2, 4, 1	*Alectoria nigricans*	RG2, 5, 3
Bryocaulon divergens	RG2, 5, 1	*Bryoria nitidula*	RG2, 5, 1
Cetraria aculeata	RG2, 5, 2	*Cladonia borealis*	RG2, 5, 2
Cladonia gracilis s. *turbinata*	RG2, 5, 1	*Epilobium anagallidifolium*	RG2, 5, 2
Festuca brachyphylla	RG2, 5, 1	*Hippuris montana*	RG2, 5, 1
Hieracium triste	RG2, 5, 2	*Huperzia selago*	RG2, 5, 1
Lasallia pensylvanica	RG2, 5, 1	*Lophozia* species	RG2, 5, 1
Peltigera leucophlebia	RG2, 5, 1	*Peltigera malacea*	RG2, 5, 1
Potentilla villosa	RG2, 5, 2	*Ranunculus eschscholtzii*	RG2, 5, 2
Racomitrium fasciculare	RG2, 5, 2	*Racomitrium lanuginosum*	RG2, 5, 8
Solorina crocea	RG2, 5, 2	*Sphaerophorus globosus*	RG2, 5
Stellaria borealis	RG2, 5, 1	*Stellaria ruscifolia*	RG2, 5, 1
Taraxacum species	RG2, 5, 2	*Veronica wormskjoldii*	RG2, 5, 1
Gymnomitrion corallioides	RG2, 5, 1	*Botrychium minganense*	RG2, 6, 1
Cladonia fimbriata	RG2, 6, 1	*Dicranum scoparium*	RG2, 6, 1
Aconitum maximum	RG2, 7, 1	*Brachythecium frigidum*	RG2, 7, 1
Bryhnia hultenii	RG2, 7, 2	*Taraxacum officinale* s. *ceratophorum*	RG2, 7, 1
Platanthera species	RG4, 12, 1		

Kamchatka occurred on unstable, acidic (pumice) substrates over 1 m thick in climatic conditions with temperature minimums below −20 °C (Grishin et al., 1996, 2000). Accordingly, mature plant communities on Bogoslof are not quite the same as "final stage of succession," a term equal to climatic climax that Grishin et al. (1996) meant in their study for estimating the term of succession.

The coastal plant communities of the Aleutians are typically disturbed by surf and wind erosion and their species selected for quick successional response, and observations from Bogoslof suggest that colonization, in addition to recovery via extant vegetation, will likely play a role in the revegetation and succession on Kasatochi as on Bogoslof.

In post-eruption colonization studies of the boreal zone—Hokkaido (Tsuyuzaki, 2009), Kamchatka (Dirksen and Dirksen, 2007), and southwestern Alaska (Griggs, 1933)—several factors were common to all in the reconstruction of natural communities. These included spatial and temporal heterogeneity (particularly ash depth) that played a major role in influencing whether preexisting plants were able to survive an eruption. Generally, the greater the distance from a volcano, the greater the decrease in the depth of the deposit; this allowed plants to come up through deposits less than about 30 cm deep. This factor, combined with the existence of buried soils with surviving underground vegetative structures such as rhizomes, permitted local survival; the plants persisted underground. Rain erosion typically cut down through the ash, exposing the antecedent soil to sunlight and warmer temperatures and facilitating recovery of buried plants. These buried soils provide a less hostile substrate for plants than ash (in sense of stability of ecological regimes). Antecedent soils are important for providing a substrate both for surviving plants, and for the roots of seedlings or spores that have been deposited and germinate on thin layers of surface ash. The presence of refugial microhabitats also played an important role in a legacy effect in all these cases, permitting plants to spread from survival foci. The lee offered by obstacles sheltered habitats or organisms from the effects of ash fall or pyroclastic flows. Each of these factors applies as well to Kasatochi Island.
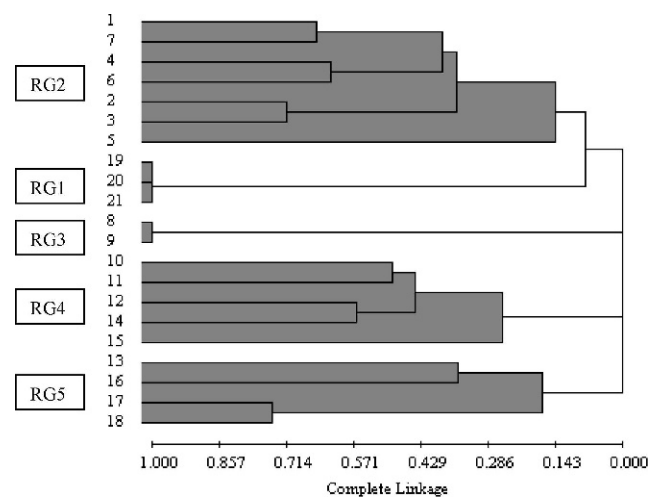

FIGURE 3. Classification dendrogram of five relevé groups (community types) from Kasatochi Island, Alaska, obtained using the van der Maarel coefficient and complete linkage (farthest neighbor) clustering (Wildi and Orloci, 1996) of 21 relevés. The dendrogram was prepared using ClustanGraphics7 (Wishart, 2003).

TABLE 2

Vegetation structure and environmental variables of five community types from Kasatochi Island, Alaska.

Relevé group (RG) no.	3		1		2		4		5	
No. of relevés	2		3		7		5		4	
Statistic	Mean	SE[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Vegetation structure										
Cover total (%)	1	1	1		98	1.6	2.6	1	1	.
Cover herb layer (%)	1	1	1		66	15	2.6	1	1	.
Cover moss layer (%)					29	11	0.2	0.2	0.8	0.3
Cover lichen layer (%)					7	1.9			.	.
Environmental variables										
Elevation (m)	7.8	1.7	60	2.2	165	38	26	5.4	56	29
Aspect (degrees)	50		88	8.3	187	28	142	35	84	32
Slope (degrees)	2		73	4.4	29	3.5	40	12	23	3.1
Cover litter layer (%)	1		0.3	0.3	8.1	5.7			1	0.4
Cover bare rock (%)	1	1	73	8.8	0.1	0.1	0.2	0.2	8.5	4.3

SE[a] = standard error of the mean

ORIGIN OF THE POST-ERUPTION FLORA ON KASATOCHI

Plant propagules are expected to reach Kasatochi using different dispersal mechanisms. Cody (2006) proposed three major means of interisland transportation of propagules: anemochory, zoochory, and hydrochory. Anemochores travel on the wind. Examples of post-eruption species found on Kasatochi that might use anemochory include plants with plumed seeds such as *Achillea millefolium* var. *borealis*, *Anaphalis margaritacea*, *Senecio pseudoarnica*, and *Epilobium hornemannii* ssp. *behringianum*, and the spores of *Cystoperis fragilis* and *Ceratodon purpureus*. Fern and moss spores are light—many have longevity ranging from several weeks to over 100 years—and thus have great dispersal potential by wind (Cody, 2006), as do bryophyte diaspores (Schofield,

1985). However, the *Cystopteris fragilis* observed in the protected rock crevice is unlikely to have derived from spores, given there has been no time to pass through the gametophyte stage. The vegetative parts of mosses, although heavier than spores, can also be wind dispersed (Fridriksson, 2005). *Marchantia polymorpha* is widespread and common in the Aleutian Islands (Davison, 1993). Young and Klay (1971) provided evidence of its apparent long-distance dispersal to a crater of Deception Island, Antarctica, and it may have arrived on Kasatochi via the same mechanism. Alternatively, the spores of *Marchantia* may have survived the eruption in a soil bank. Thus, some doubt exists as to its presence either from long-distance dispersal or spore bank.

Zoochores are distributed by animals such as gulls that spread seeds in the process of gathering nest material on Bogoslof

TABLE 3

Ecological data for four relevé groups of Kasatochi Island, Alaska, vegetation. No soils were collected from RG2. Subgroups: A = post-eruption soil material from center of the relevés; B = pooled pre-eruption soil material from within relevés.

Relevé group no.	3			4A		4B		5A		5B	
No. of relevés	1	2		5		3		4		3	
Statistic	1	Mean	SE[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE
OM (%)	3.16	0.2	0.0	0.5	0.2	2.41	0.7	0.7	0.1	4.4	1.4
pH	6.8	7.0	0.2	7.1	0.2	5.8	0.3	7.0	0.2	5.6	0.7
EC (dS m^{-1})	1.5	0.2	0.1	0.6	0.2	2.07	0.4	0.8	0.3	1.3	0.3
NO$_3$ (mg kg^{-1})	4.8	0.6	0.3	1.7	1.4	8.9	4.2	0.5	0.2	6.6	5.7
NH$_4$ (mg kg^{-1})	5.5	0.3	0.0	0.7	0.3	5.4	1.0	0.7	0.1	8.5	2.1
P (mg kg^{-1})	14	4.5	2.5	4.4	1.5	5.7	0.3	3.5	0.5	21.3	11.3
SO$_4$ (mg kg^{-1})	334	36.0	14.0	133.0	40.4	915	169.2	296.5	122.1	385.7	134.7
B (mg kg^{-1})	2.53	0.1	0.0	0.5	0.1	2.41	0.6	0.4	0.1	1.1	0.4
Zn (mg kg^{-1})	4.5	0.2	0.0	0.6	0.2	1.4	0.6	0.9	0.2	1.6	0.6
Mn (mg kg^{-1})	37	4.0	0.0	17.0	6.0	20	12.9	17.5	3.4	13.7	2.3
Cu (mg kg^{-1})	28.6	1.7	0.3	3.0	0.8	4	1.2	4.9	1.3	7.4	3.1
Fe (mg kg^{-1})	29	12.0	0.0	31.0	7.7	39	4.6	39.8	6.0	84.7	14.4
K (cmol kg^{-1})	153	64.0	6.0	139.0	24.7	314	27.7	139.8	19.0	140.7	34.1
Ca (cmol kg^{-1})	8.1	1.8	0.2	4.9	1.5	7.2	1.6	7.6	1.0	9.4	3.4
Mg (cmol kg^{-1})	1.2	0.5	0.0	0.6	0.1	1.1	0.1	0.5	0.0	0.8	0.2
Na (cmol kg^{-1})	0.97	0.4	0.1	0.6	0.2	1.5	0.5	0.2	0.0	0.4	0.0
Total bases (cmol kg^{-1})	10.7	2.8	0.1	6.5	1.5	10.7	1.6	8.6	1.1	10.9	3.6
Soil texture (%)											
Sand	71.2	96.6	0.0	72.4	8.5	75.9	2.4	67.5	6.3	85.3	1.5
Silt	24	2.0	0.0	21.7	6.7	20	3.1	24.8	5.8	13.3	1.3
Clay	4.8	1.4	0.0	5.9	1.9	4.1	0.7	7.8	0.6	1.3	0.3

[a] SE = standard error of the mean
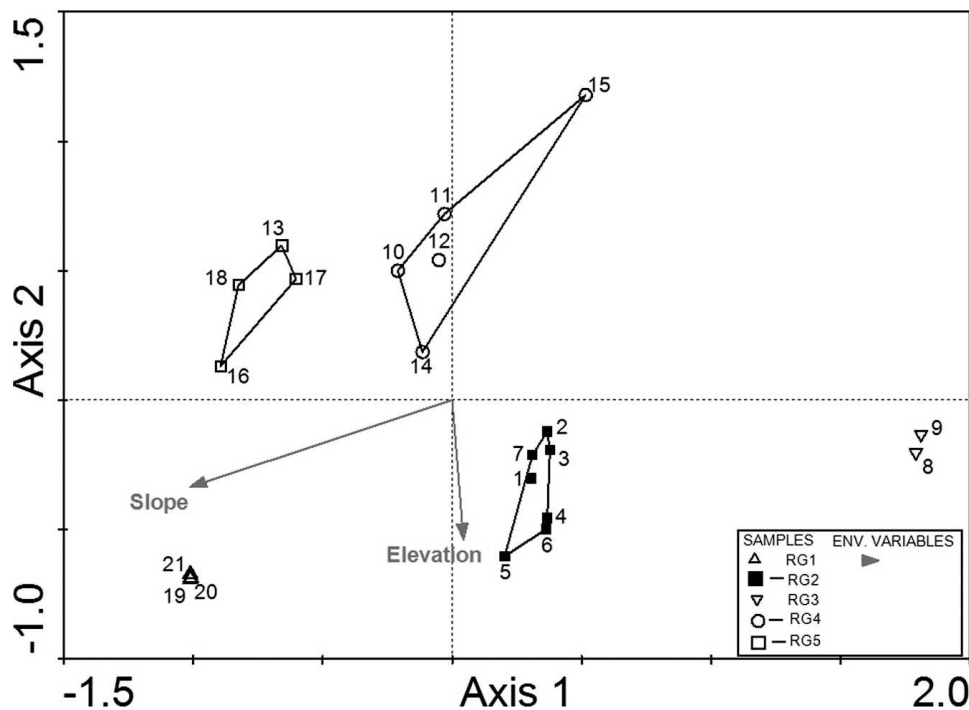
FIGURE 4. Non-metric multi-dimensional scaling ordination (Šmilauer, 2003; ter Braak and Šmilauer, 2002) of 21 relevés with projected environmental variables from Kasatochi Island, Alaska. The scatterplot shows the five cluster models of community types identified in classification dendrogram (Fig. 3). Solid symbols distinguish the pre-eruption group (RG2) and hollow symbols distinguish post-eruption groups (RG1, RG3, RG4, and RG5). Key to types: RG1—*Festuca rubra* cliff shelf; RG2—*Lupinus nootkatensis–Festuca rubra* meadow; RG3—*Honckenya peploides* beach meadow; RG4—*Leymus mollis* bluff ridge (and beach); RG5—*Aleuria aurantia* lower slope barrens.

(Morris, 1937) or snow buntings that distributed seeds on Surtsey (Fridriksson and Sigurdsson, 1968). Notably, we discovered five gull nests with nest material made from plants. The nest material was typically dominated by dead vascular plant litter and brown algae but one nest contained a living culm of *Leymus mollis*. The *Leymus* specimen had not taken root but in the future, plant matter in nests may account for some colonization, as it did on Bogoslof (Morris, 1937; Gabrielson and Lincoln, 1959).

Hydrochores are spread by sea currents; *Honckenya peploides* and *Leymus mollis* are good examples. Cody (2006) pointed out that *Honckenya* has dehiscent capsules and brittle stems that can break easily by wave action; they are often found washed up on beaches throughout the Aleutians, including Bogoslof. We consider hydrochory unlikely as the time period required for establishment via drifting was short, and our reconnaissance of the beaches both in June and August 2009 revealed no vascular plant litter. Furthermore, Kasatochi Island continued to increase in size from the erosion of upper slope ash. To become established any floating plant would have had to overcome this instability.

Individual plants of these two species probably traveled downslope and became established on back beaches some distance from the sea.

On what appeared to be an island smothered in volcanic ash—in some places meters thick, where continuation of plant life seemed improbable—living plants were observed as mature, but mostly vegetative, perennial plants, and seedlings. We consider that the majority of plants observed in post-eruption sampling were survivors of the Kasatochi eruption, rather than colonizers. One relevé (no. 14, RG4) contained an assemblage of several mature plants suggesting a species-poor relict of the previously more widespread pre-eruption RG2 type; this assemblage and similar ones not yet discovered could contribute to legacy effects in the revegetation of Kasatochi.

A number of factors contributed to the survival of at least a fragment of the original vegetation as reported previously for other boreal regions (see above). These included eruption heterogeneity such as thin ash deposits on bluff ridges that exposed the antecedent soils. Similarly, rill erosion cut through the

TABLE 4

List of additional vascular plants from Kasatochi Island assembled over time by biologists collecting data during long-term pre-eruption monitoring of seabirds (Drummond, 2006) but not found in relevés in this study.

Arnica unalaschcensis	*Juncus* sp.	*Primula cuneifolia*
Athyrium filix-femina	*Ligusticum scoticum*	*Ranunculus grandis*
Campanula lasiocarpa	*Listera cordata*	*Sagina saginoides*
Claytonia sibirica	*Lycopodium annotinum*	*Salix arctica*
Cochlearia groenlandica	*Mimulus guttatus*	*Saxifraga bracteata*
Cystopteris fragilis	*Oxyria digyna*	*S. punctata*
Draba aleutica	*Parnassia kotzebuei*	*Senecio pseudoarnica*
D. hyperborea	*Petasites frigidus*	*Taraxacum officinale* ssp. *ceratophorum*
Epilobium ciliatum ssp. *glandulosum*	*Platanthera convallariaefolia*	*Trientalis europaea*
Erigeron peregrinus	*P. dilatata*	*Veronica serpyllifolia*
Geum macrophyllum	*Polypodium glycyrrhiza*	
Heracleum maximum	*Potentilla villosa*	

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ash overburden and exposed the antecedent soil. Volcanic ash can be removed by rain erosion quite rapidly on volcanic slopes (Thornton, 2007). The depth of the rill erosion was an important factor in exposing the antecedent soil but not eroding it away. Some of the pre-eruption soil was eroded; seeds or vegetative propagules were then likely carried downslope by gravity and intermittent streamlets. Given the short growing season in the Aleutians, the size of the plants that developed indicated that they arose from a vegetative portion of plant buried in the antecedent soil.

Seedlings were observed intermixed with mature plants both in June, and in August 2009. We suggest that seedlings arose mostly from seed beds, because (1) no mature plants observed in June or August had seeds; (2) no seeds were collected in insect traps set out on post-eruption Kasatochi, suggesting an absence of diaspores in the early post-eruption environment.; (3) the distance between islands and the short time period elapsing since the eruption suggest colonization via hydrochore seeds is unlikely; (4) no seedlings were found along the beaches, only mature plants; and (5) uncharred organic material in the soil suggested seeds could have survived. Seedlings derived from zoochory were unlikely, as terrestrial avian species typically associated with seed dispersal elsewhere such as Surtsey (Williams et al., 2010 [this issue]), were absent.

The post-eruption landscape provided a number of microhabitats conducive to the survival of plants. The presence of old moss capsules of *Funaria hygrometrica* in the post-eruption environment suggested that mosses survived the eruption intact. Cliff shelves were protected by overhanging portions of the cliff walls from repeated pyroclastic flows that emanated from the volcano caldera and cascaded downslope. These cliff shelves served as refugia where living, loosely caespitose clumps of intact plants survived, because they were not covered for long periods with ash. It is clear that the north and south side of the island differed with regard to provision of these microhabitats. The north side, with steeper slopes and more cliffs than the south side, provided more microhabitats.

We observed buried organic matter in antecedent soils. An extensive bluff ridge on the southern part of the island had a thin layer of ash overburden over the antecedent soils on the ridge top. The pyroclastic flows appeared to have travelled quickly over the ridge top leaving a heavier deposit of ash above and below the bluff top. Many of the plants we observed peaked in their abundance on this ridge top where the thin ash layer left the antecedent soil exposed. Our 25 m^2 relevés at these bluff ridges included both the above and below portions of the ridges, and some ridge plants had been transported down slope by gravity into the lower portion of the bluff.

In future monitoring of plant succession on Kasatochi Island, we will address the relative importance of survivors versus new arrivals in determining change, the dynamic interplay between actively changing topography and microsite availability for colonization, and the establishment and replacement of plant communities. To accomplish this, it will be necessary to identify the source of plants; the application of genetic data can be used for this purpose (Yang et al., 2008). We suggest growth chamber laboratory experiments be initiated on antecedent soils to determine if seedlings will develop from the seeds that might be buried in the soils. In addition, vegetation analysis of a geologically similar nearby island such as Koniuji Island (25 km east of Kasatochi) might shed further light on potential successional pathways on Kasatochi. As recommended by Thornton (2007), investigations should continue with regular and frequent visits and surveys should be done at short intervals,

to identify and monitor stable legacy communities as well as new colonizers. We consider it imperative that the impact of anthropogenic activities be minimized.

Acknowledgments

References Cited

Adams, D. G., 2002: Cyanobacteria in symbiosis with hornworts and liverworts. *In* Rai, A. N., Bergman, B., and Rasmussen, U. (eds.), *Cyanobacteria in Symbiosis*. Dordrecht: Kluwer Academic Publishers, 117–135.

Anderson, S. T., and Bank, T. P. II, 1952: Pollen and radiocarbon studies of Aleutian soil profiles. *Science*, 116: 84–86.

Bank, T. P. II, 1953: Biological succession in the Aleutians. *Pacific Science*, 7: 493–503.

Burt, R. (ed.), 2004: *Soil Survey Laboratory Methods Manual*. Lincoln, Nebraska: U.S. Department of Agriculture, Natural Resources Conservation Service, Soil Survey Investigations Report No. 42, Version 4.0, 700 pp.

Byrd, G. V., Divoky, G. J., and Bailey, E. P., 1980: Changes in marine bird and mammal populations on an active volcano in Alaska. *Murrelet*, 61: 50–62.

Cody, M. L., 2006: *Plants on Islands: Diversity and Dynamics on a Continental Archipelago*. Berkeley: University of California Press, 269 pp.

Davison, P. G., 1993: *Floristic and Phytogeographic Studies of the Hepatic Flora of the Aleutian Islands, Alaska*. PhD dissertation. Knoxville, University of Tennessee, 385 pp.

Deines, F. G., and Willging, B., 1985: *Introduced Arctic Fox Eradication Effort at Kasatochi Island, Aleutian Islands, Alaska, Summer 1984*. Adak, Alaska: U.S. Fish and Wildlife Service, Report AMNWR 85/10, 9 pp.

del Moral, R., and Grishin, S. Yu., 1999: The consequences of volcanic eruptions. *In* Walker, L. R. (ed.), *Ecosystems of Disturbed Ground,* Chapter 5. Goodall, D. W. (ed.-in-chief), Ecosystems of the World Series. Amsterdam: Elsevier Science, 137–160.

Dirksen, V. G., and Dirksen, O. V., 2007: Vegetation dynamics and ecological consequences of the 1996 eruption in Karymsky Volcanic Center, Kamchatka. *Journal of Volcanology and Seismology*, 1: 26–38.

Drummond, B. A., 2006: *Biological Monitoring in the Central Aleutian Islands, Alaska in 2006. Summary Appendices*. Adak,

Alaska: U.S. Fish and Wildlife Service Report, AMNWR 06/06, 125 pp.

Drummond, B. A., 2007: *Breeding Biology and Consequences of Nest Site Use in Fork-Tailed Storm-Petrels (*Oceanodroma furcata*) Recovering from Fox Predation in the Aleutian Islands, Alaska*. MS thesis. Halifax, Nova Scotia, Department of Biology, Dalhousie University, 128 pp.

Ebbert, S. G., and Byrd, G. V., 2002: Eradications of invasive species to restore natural biological diversity on Alaska Maritime National Wildlife Refuge. *In* Veitch, C. R., and Clout, M. N. (eds.), *Turning the Tide: the Eradication of Invasive Species*. Gland, Switzerland: Invasive Species Specialist Group, Species Survival Commission, World Conservation Union, 102–109.

Edwards, J. S., and Sugg, P. M., 2005: Arthropods as pioneers in the regeneration of life on the pyroclastic-flow deposits of Mount St. Helens. *In* Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer-Verlag, 127–138.

Evenson, V. S., 1997: *Mushrooms of Colorado and the Southern Rocky Mountains*. Englewood, Colorado: Westcliffe Publishers, 205 pp.

Farr, W. A., and Hard, J. S., 1987: *Multivariate Analysis of Climate along the Southern Coast of Alaska—Some Forestry Implications*. Portland, Oregon: USDA Forest Service, Pacific Northwest Research Station, Research Paper PNW-RP-372, 38 pp.

Feoli, E., and Orlóci, L., 1979: Analysis of concentration and detection of underlying factors in structured tables. *Vegetatio*, 40: 49–54.

Fridriksson, S., 2005: *Surtsey Ecosystems Formed*. Reykjavik, Iceland: The Surtsey Research Society, 112 pp.

Fridriksson, S., and Sigurdsson, H., 1968: Dispersal of seed by snow buntings to Surtsey in 1967. *Surtsey Research Program Report*, 4: 43–49.

Gabrielson, I. N., and Lincoln, F. C., 1959: *The Birds of Alaska*. Harrisburg, Pennsylvania: The Stackpole Company; and Washington D.C.: Wildlife Management Institute, 922 pp.

Gallant, A. L., Binnian, E. F., Omernik, J. M., and Shasby, M. B., 1995: *Ecoregions of Alaska*. Washington, D.C.: U.S. Geological Survey Professional Paper 1567.

Griggs, R. F., 1933: The colonization of Katmai ash, a new and inorganic "soil." *American Journal of Botany*, 20: 92–111.

Grishin, S. Y., del Moral, R., Krestov, P. V., and Verkholat, V. P., 1996: Succession following the catastrophic eruption of Ksudach volcano (Kamchatka, 1907). *Vegetatio*, 127: 129–153.

Grishin, S., Krestov, P., and Verkholat, V., 2000: Influence of 1996 eruptions in the Karymsky Volcano Group, Kamchatka, on vegetation. *Natural History Research Special Issue*, 7: 39–48.

Hennekens, S. M., and Schaminée, J. H. J., 2001: TURBOVEG, a comprehensive database management system for vegetation data. *Journal of Vegetation Science*, 12: 589–591.

Heusser, C. J., 1978: Postglacial vegetation of Adak Island, Aleutian Islands, Alaska. *Bulletin of Torrey Botanical Club*, 105: 18–23.

Hill, M. O., 1974: Correspondence analysis: a neglected multivariate method. *Applied Statistics*, 23: 340–354.

Hultén, E., 1960: *Flora of the Aleutian Islands and Westernmost Alaska Peninsula with Notes on the Flora of the Commander Islands*. Second edition. New York: Hafner.

Hultén, E., 1968: *Flora of Alaska and Neighboring Territories*. Stanford, California: Stanford University Press, 1008 pp.

Jakobsson, S. P., Magnússon, B., and Gunnarsson, K. (eds.), 2009: *Surtsey Research Volume 12*. Reykjavík, Iceland: The Surtsey Research Society.

Jancey, R. C., 1979: Species ordering on a variance criterion. *Vegetatio*, 39: 59–63.

Küchler, A. W., 1966: *Potential Natural Vegetation of Alaska*. Washington, D.C.: U.S. Geological Survey, National Atlas Series Sheet No. 89.

Lieth, H., Berlekamp, J., Fuest, S., Riediger, S., 1999: *CD1—Climate Diagram. World Atlas. In* , and H. Lieth (ed. in chief), 1999: Climate and Biosphere, CD-Series. First edition. Leiden, Germany: Backhuys.

Magnússon, B., Magnússon, S. H., and Sigurðsson, B. D., 2004: Plant succession in areas colonized by the introduced Nootka lupin in Iceland. *In* van Santen, E., and Hill, G. D. (eds.), *Wild and Cultivated Lupins from the Tropics to the Poles*. Proceedings of the 10th International Lupin Conference, Laugarvatn, Iceland, 19–24 June 2002. Canterbury, New Zealand: International Lupin Association, 170–177.

Magnússon, B., Magnússon, S. H., and Fridriksson, S., 2009: Developments in plant colonization and succession on Surtsey during 1999–2008. *Surtsey Research*, 12: 57–76.

Miller, T. P., McGimsey, R. G., Richter, D. H., Riehle, J. R., Nye, C. J., Yount, M. E., and Dumoulin, J. A., 1998. Catalog of the historically active volcanoes of Alaska: *U.S. Geological Survey Open-File Report*, OF 98-0582, 104 pp.

Morris, G. E., 1937: Bogoslof Island. *Proceedings U.S. Naval Institute*, 63(413): 950–952.

Okitsu, S., Imura, S., and Ayukawa, E., 2003: Structure and dynamics of the *Ceratodon purpureus–Bryum pseudotriquetrum* community in the Yukidori Valley, Langhovde, continental Antarctica. *Polar Bioscience*, 16: 49–60.

Rieger, S., Schoephorster, D. B., and Furbush, C. E., 1979: *Exploratory Soil Survey of Alaska*. Anchorage, Alaska: U.S. Department of Agriculture, Soil Conservation Service, 213, and maps.

Scharf, L., Williams, J. C., and Thomson, G. L., 1996: Biological monitoring in the central Aleutian Islands, Alaska in 1996. Adak, Alaska: *U.S. Fish and Wildlife Service Report*, AMNWR 96/11, 120 pp.

Schofield, W. B., 1985: *Introduction to Bryology*. New York: Macmillan Publishing Co., 431 pp.

Schofield, W. B., 1992: *Some Common Mosses of British Columbia*. Victoria, British Columbia: Royal British Columbia Museum, 394 pp.

Schofield, W. B., 2002: *Field Guide to Liverwort Genera of Pacific North America*. Seattle: University of Washington Press, 228 pp.

Seaver, F. J., 1914: North American species of *Aleuria* and *Aleurina*. *Mycologia*, 6: 273–278.

Sikes, D. S., and Slowik, J., 2010: Terrestrial arthropods of pre- and post-eruption Kasatochi Island, Alaska, 2008–2009: a shift from a plant-based to a necromass-based food web. *Arctic, Antarctic, and Alpine Research*, 42: 297–305.

Šmilauer, P., 2003: WinKyst 1.0 user's guide. České Budjovice, Czech Republic. Available from http://www.canodraw.com (cited 9 September 2004).

Svavarsdóttir, K., and Walker, L. R., 2009: The value of Surtsey for ecological research. *Surtsey Research*, 12: 149–151.

Talbot, S. S., and Talbot, S. L., 1994: Numerical classification of the coastal vegetation of Attu Island, Aleutian Islands, Alaska. *Journal of Vegetation Science*, 5: 867–876.

Talbot, S. S., Schofield, W. B., Talbot, S. L., and Daniëls, F. J. A., 2010: Vegetation of eastern Unalaska Island, Aleutian Islands, Alaska. *Botany*, 88: 366–388.

Tatewaki, M., 1963: Hultenia. *Journal of the Faculty of Agriculture, Hokkaido University*, 53: 131–199.

ter Braak, C. J. F., and Šmilauer, P., 2002: *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Ithaca, New York: Microcomputer Power, 499 pp.

Thornton, I., 2007: *Island Colonization: the Origin and Development of Island Communities*. Cambridge: Cambridge University Press, 287 pp.

Tichý, L., 2002: JUICE, software for vegetation classification. *Journal of Vegetation Science*, 13: 451–453.

Tichý, L., Chytrý, M., Hájek, M., Talbot, S. S., and Botta-Dukát, Z., 2010: OptimClass: using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. *Journal of Vegetation Science*, 21: 1–13.

Tsuyuzaki, S., 2009: Causes of plant community divergence in the early stages of volcanic succession. *Journal of Vegetation Science*, 20: 959–969.

Tuhkanen, S., 1984: A circumboreal system of climatic-phytogeographical regions. *Acta Botanica Fennica*, 127: 1–50 + appendices.

USDA, N. R. C. S., 2009: *The PLANTS Database*. Available from http://plants.usda.gov. Baton Rouge, Louisiana: National Plant Data Center (accessed 19 October 2009).

Viereck, L. A., Dyrness, C. T., Batten, A. R., and Wenzlick, K. J., 1992: *The Alaska Vegetation Classification*. Portland, Oregon: USDA Forest Service, General Technical Report PNW-GTR-286, 278 pp.

Walker, L. R., and del Moral, R., 2003: *Primary Succession and Ecosystem Rehabilitation*. Cambridge: Cambridge University Press, 442 pp.

Walker, L. R., and del Moral, R., 2009: Lessons from primary succession for restoration of severely damaged habitats. *Applied Vegetation Science*, 12: 55–67.

Wang, B., Michaelson, G., Ping, C.-L., Plumlee, G., and Hageman, P., 2010: Characterization of pyroclastic deposits and pre-eruptive soils following the 2008 eruption of Kasatochi Island volcano, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 276–284.

Westhoff, V., and van der Maarel, E., 1973: The Braun-Blanquet approach. *In* Whittaker, R. H. (ed.), *Ordination and Classification of Communities*. The Hague, Netherlands: Junk, 617–726.

Wildi, O., 1989: A new numerical solution to traditional phytosociological tabular classification. *Vegetatio*, 81: 95–106.

Wildi, O., and Orlóci, L., 1996: *Numerical Exploration of Community Patterns: a Guide to the Use of MULVA-5*. New York: SPB Academic Publishing, 171 pp.

Williams, J. C., Drummond, B. A., and Buxton, R. T., 2010: Initial effects of the August 2008 volcanic eruption on breeding birds and marine mammals at Kasatochi Island, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 306–314.

Wishart, D., 2003: *ClustanGraphics Primer, a Guide to Cluster Analysis*. Edinburgh: Clustan Limited, 64 pp.

WRCC, 2009: Historical Climate Information, Western U.S. Historical Summaries, NCDC 1971–2000 Monthly Normals—Adak, Alaska. Available from http://www.wrcc.dri.edu/. Reno, Nevada: Western Regional Climate Center (accessed 5 November 2009).

Yang, S., Bishop, J. G., and Webster, M. S., 2008: Colonization genetics of an animal-dispersed plant (*Vaccinium membranaceum*) at Mount St. Helens, Washington. *Molecular Ecology*, 17: 731–740.

Young, S. B., and Klay, J.-B., 1971: Bryophytes in the 1969 crater of Deception Island, Antarctica: an apparent case of rapid long-distance dispersal. *Ohio Journal of Science*, 71: 358–362.

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