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Succession following the catastrophic eruption of Ksudach volcano (Kamchatka, 1907)

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Abstract

Ksudach Volcano, southern Kamchatka Peninsula, erupted in 1907 and impacted over 2000 km^2 of forests with air-fall pumice deposits. We identified three impact zones. In Zone I, deposits deeper than 100 cm destroyed all vegetation. Two early successional stages occur, a lichen-dominated desert and isolated patches of a pioneer herb stage. Zone II is defined by pumice deposits 30 to 100 cm deep. Deposits of 70 to 100 cm destroyed all vegetation, but left scattered snags. Here primary succession dominates recovery, but its rate varies. Isolated trees survived in deposits of 30 to 70 cm and primary and secondary successional stages form a complex mosaic termed an intermediate succession. In Zone II, the primary stages found in Zone I are joined by a dwarf shrub-herb stage and a secondary birch forest stage. Zone III occurs where thinner deposits permitted some vegetation to survive in all locations. Secondary succession dominates in deposits of 10 to 30 cm. Trees suffered damage, but survived deposits of 20 to 30 cm, while other vegetation layers were eliminated. Deposits of 10 to 20 cm eliminated mosses and lichens and but only reduced the number of dwarf shrubs and herbs. Deposits of less than 10 cm damaged herb, moss and lichen layers but did not eliminate any species. All sampled vegetation remains in a pre-climax state, having yet to recover fully from earlier eruptions. Reconstructed vegetation maps for before 1907 and for ca. 1925 are compared to the map of vegetation in 1994. Based on degree of soil formation, vegetation recovery and colonization rates at different pumice depths, and the current vegetation, we estimate that full recovery of the soil-vegetation system will take more than 2000 years.

Introduction

On March 28, 1907, the Shtyubel' Cone within the caldera of Ksudach Volcano in Southern Kamchatka erupted violently. About 1.5 to 2 km^3 of tephra were ejected. Tephra is composed of any pyroclastic deposit ejected as solid fragmented material. Ash is fine tephra ($<$ 4 mm), while lapilli range between 4 and 32 mm in size (Francis 1993). Dacite (silica-rich) pumice, a porous volcanic rock, composed most deposits outside the caldera. Most pumice was deposited near the caldera as lapilli or 'bombs' (Bursik et al. 1993), but Petropavlovsk-Kamchatsky, over 160 km to the north, received 2–3 cm of tephra (Figure 1). Tephra fell throughout Kamchatka and on the coast of the Sea of Okhotsk (Komarov 1912, 1940; Dubik & Meniailov 1971; Melekestsev & Sulerzhitskii 1987; Bursik et al. 1993).

In 1922, Hultèn (1924, 1974) described impacts of the eruption on vegetation north of Ksudach volcano. The caldera was visited by geologists in 1910 (Konradee & Kell' 1925) and by volcanologists starting in 1937 (Morozov 1948; Vlodavets & Piyp 1957). Grishin et al. (1995) made the first modern survey of vegetation in this area in August 1991.

We conducted detailed studies of lichen deserts that dominate thicker deposits and recovering forests north of the caldera in August 1994. This paper reconstructs the effects of the 1907 eruption on vegetation, analyzes vegetation responses, and discusses the interactions between primary and secondary succession and mere recovery from perturbation. Recovery involves

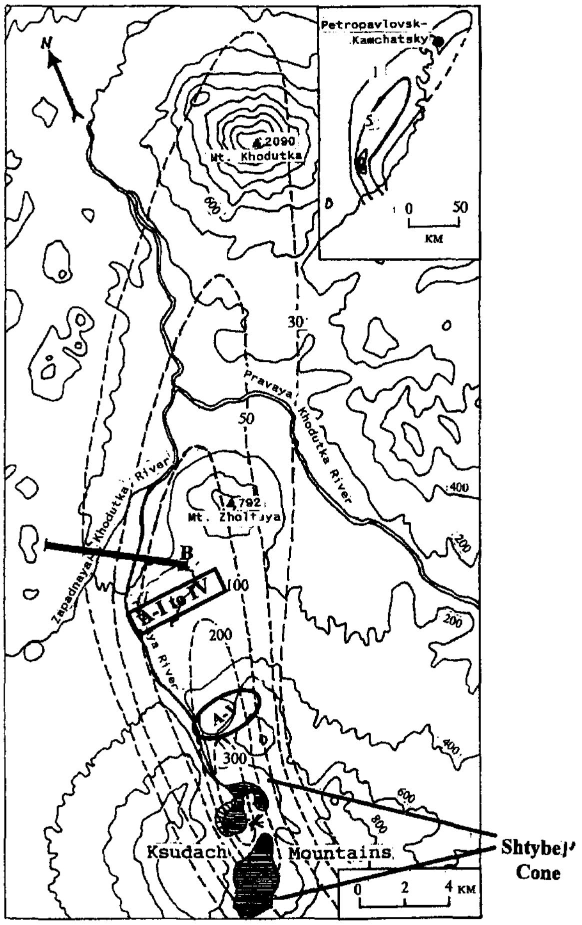

Figure 1. Study area. Pumice depths shown by isopachytes for 30-, 50-,100-, 200- and 300-cm thicknesses. Region of Transects A - I to IV is outlined near Transect B. Transect A-V is shown further south. Location of Transect B is shown by the bold line. Inset map shows 1 and 5 cm deposits (from Melekestsev & Sulerzhitskii 1987; Bursik, *et al.* 1993).

development of biomass and structure, but since no species are eliminated, does not involve colonization. This study is part of a larger one describing how volcanism has molded the Kamchatka landscape.

Methods

Study area

Natural History

Ksudach volcano is 160 km south-southwest of Petropavlovsk-Kamchatsky, Russia (Figure 1) at Latitude 51°45′ N, Longitude 158°00′ E. This active shield volcano has a diameter of 35 km, enclosing a caldera and two lakes. The most recent caldera formed ca. 300 AD, and is enclosed by the Shtyubel' Cone from which all recent eruptions originated. This event ejected a volume comparable to that of Krakatau (1883) and was 5 to 10 times larger than the 1907 eruption (Bursik et al. 1993). Smaller eruptions occurred ca. 750 AD and ca. 1640 AD (Melekestsev & Sulerzhitskii 1987), but we focus on the most recent one that destroyed much of the vegetation damaged by these earlier eruptions. There are 29 active volcanoes on Kamchatka and the 1907 Ksudach eruption was among the four largest on Kamchatka this century.

Physiography

The modern caldera is nearly closed. The rim, at a height of 900 to 1000 m a.s.l., has a diameter of about 8 km. Two lakes at 411 m a.s.l. are drained by a river through a breach in the rim. North of the caldera, deposits exceed 4 m in depth and over 14 km north, maximum depth remains over 1 m. The region of deep tephra extends from 900 m a.s.l. to below 200 m a.s.l., and covers over 100 km^2. At any distance, depths diminish perpendicular to the deposition axis.

Climate

The climate of Southern Kamchatka is maritime northern boreal with short, cool summers, and moderately cold long winters (Walter et al. 1975; Walter & Breckle 1986). Weather records near Mt. Khodutka (Figure 1) provide precipitation and temperature. Mean annual precipitation was moderate (1430 mm) for the ten years between 1955 and 1964. Precipitation occurs throughout the year, and is variable. Growing season temperatures are mild (10 to 12 °C), but winters are extreme. A characteristic feature of the peninsula is a deep snow cover (over 2 m) that frequently persists into July, particularly in gullies.

Soils

These soils display complex profiles formed by thick pumice tephra horizons alternating with buried soils formed between eruptions. An 8-meter profile on a river terrace revealed the history of the last few millennia. This profile shows three thick Ksudach pumice layers, two buried soil horizons, and a modern incipient soil horizon with traces of primitive soil forming over the 1907 pumice. This profile is typical of the gentle slopes of Ksudach volcano and is similar to those in other volcanically active regions (Foxworthy & Hill 1982).

General vegetation

Hultèn (1974) described the vegetation of Southern Kamchatka. The forest zone in our study area is dominated by *Betula ermanii* extending to 300 to 400 m a.s.l. Above this zone, there is a subalpine alder (*Alnus kamtschatica*) krummholz up to 800 m a.s.l. True alpine vegetation dominates above the krummholz, as well as at lower elevations on immature surfaces. These zones occur at low elevations at this latitude due to strong marine influences, short growing seasons, and heavy snow pack (Grishin 1995).

River valleys from which tephra was eroded support poplar-willow forests and willow scrub often enriched with white birch (*Betula kamtschatica*). Alluvial terraces and local depressions support diverse meadows with scattered shrubs. Swamps and marshes occur where drainage is impeded. All of this vegetation was severely altered by the eruption of 1907.

Nomenclature

Vascular plant nomenclature is from the seven volume publication entitled: Vascular Plants of the Soviet Far East (1985 to 1995). Czerepanov (1995) was not used. Mosses were identified using Ignatov & Afonina (1992). Lichens were identified using Mikulin (1990).

Vegetation sampling

Two complementary studies were undertaken. The first emphasized vegetation on deeper deposits where primary succession dominates succession. Five transects (prefixed by 'A') were sampled. Their location is shown in Figure 1. The second study describes a geobotanical transect (prefaced by 'B') that includes devastated sites that have been subsequently colonized by trees to sites within forests where there was substantial survival (Figure 1).

Sampling on deeper deposits (A)

Four transects were established 9 to 10 km north of the caldera between 200 and 250 m a.s.l., on pumice up to 2 m deep. Exact plot locations were chosen subjectively to represent the immediate area and, if possible, be distinct from a previously sampled plot. A-I had tephra over 80 cm deep at 240 m a.s.l. Six plots were established at 200 m intervals in a westerly direction, forming a 1 km long transect. A-II was 300 m south of A-I at 260 m a.s.l. This 2 km-long transect had ten plots, between 100 and 300 m apart, that were established subjectively in varied terrain. A-III commenced south of A-II at 245 to 260 m a.s.l., and was on thicker deposits. Four plots, on both exposed and protected sites, were sampled at 200 m intervals on a 600 m transect oriented to the west. A-IV started 300 m south of A-III. It extended west for 2 km and included seven plots. The general location of these transects is shown in Figure 1, but their exact location was not determined. A-V was established on pumice generally over 3 m deep at 500 m a.s.l. located 4 km north of the caldera. The site was 500 m west of the deep valley that drains the crater. The five plots were within 200 m of one another, and were not linearly arrayed.

Dominance by different strata dictated different sampling methods. Lichen-dominated plots were sampled with ten 1 m^2 quadrats at 10 m intervals along a 100 m transect, and percent cover estimated. This intensity is recommended for ground layer vegetation (Mueller-Dombois & Ellenberg 1974). Additional species within ten 10 by 10 m quadrats (0.1 ha) were listed, their cover estimated, and values converted to the Braun-Blanquet cover scale (r = solitary, very small cover; + = scattered, cover $< 1\%$; 1 = scattered, but numerous, cover 1% to $< 5\%$; 2 = cover 5 to 25%; 3 = cover 26 to 50%; 4 = cover 51 to 75%; and 5 = cover $> 75\%$). Transects A-I, A-II 1 to 7 and 9, A-III 2 to 4, and A-V were sampled in this way.

Transects A-II 8 and 10, A-III 1, and A-IV had substantial tree cover and were sampled with 20 by 100 m plots (0.2 ha). These plots were twice the size of a Whittaker plot, with similar sampling intensity for ground layer vegetation (Stohlgren et al. 1995). Stem diameters, tree height and tree canopy cover in each 10 by 10 m plot were determined. Percent cover of the ground layer was determined in 20×1 m^2 quadrats sampled along the long axis in one corner of each of twenty 10 by 10 m plot. Braun-Blanquet scores were determined for each species in each subplot of the A transects to provide a concise summary. Where trees were common, their density, diameter and height were determined.

We sampled 32 plots as described above. For this study, plots that were similar to others, not deemed to be primary succession, or otherwise atypical (e.g., flood plains and deeply dissected canyons) are not reported. Pumice deposits on all reported plots exceeded 80 cm, and vegetation on these plots is assumed to have developed on new substrates with no survivors.

Sampling on thinner deposits (B)

The basic data used to describe the transition from primary to secondary succession were acquired from Transect B, perpendicular to the pumice depth gradient. This transect was 10 km north of the caldera at 200 m a.s.l. Eight plots, each 20 by 100 m in size, were established. Each plot consisted of 20 contiguous 10 by 10 m quadrats, arrayed in two rows. We determined tree density on each subplot. The height of typical and of the tallest individuals of each species was measured. The age of representative trees, shrubs and saplings was determined from rings of cut stems. The presence and abundance of each species in the shrub and ground layers were determined using the Braun-Blanquet scale on thirty 1 by 1 m quadrats spaced regularly along the central axis of the plot. Profile diagrams and horizontal pattern diagrams were constructed to provide detailed visual characterizations. Soil profiles were described in each plot. The soil profiles were 1 m deep, except for No. 3, which was 8 m on the exposed slopes near the Teplaya River.

Mapping

Large-scale vegetation maps were produced from interpretations of aerial photographs (1:25 000), from additional transects (Grishin et al.1995), and from the transect data. The photos were made and provided by the Russian State Department of Geodesy and Cartography. Size of each identified unit was determined by placing a fine transparent grid over the map and counting the number of squares covered by each unit. Additional information based on descriptions by Hultèn (1974) and Komarov (1940) were incorporated for earlier dates.

Results

Impact zones

There is a complex interaction between impact and recovery. We define three impact zones. Within each, succession is affected by a different combination of processes (cf. Pickett et al. 1987) and proceeds differently. We also recognize five stages of succession that may lead to climax forests, though only four were sampled in this study.

Zone I received pumice deposits deeper than 100 cm. No vegetation survived. Sub-shrubs, herbs, mosses and lichens were buried deeply while trees were killed immediately, or shortly after impact. Trees have not re-established in this zone, which remains a lichen desert, with only sporadic herbs and shrubs. Only primary succession occurs in this zone. Factors that have restricted vegetation transition to more developed stages include isolation (which limits colonization), stressful substrates and microclimate, and inhibition of seedlings by lichens.

Zone II occurs where pumice is 30 to 100 cm deep. Primary and secondary succession interdigitate on shallower deposits. The vegetation is represented by birch stands, including individuals that survived the eruption, intermixed with lichen-dwarf shrub glades. Succession is affected by the presence of snags that attracted birds and facilitated dispersal, plentiful dead wood that created favorable microsites, sporadic survival of trees and tall shrubs, proximity to surviving vegetation, and thinner pumice that permitted colonizing species to reach buried soils. These factors combined to permit primary succession to proceed more rapidly than in Zone I, and for secondary succession to occur in places. Where primary and secondary successional stages are intermixed, the succession may be termed 'intermediate.' In more stressful sites, lichen deserts like that of Zone I remain dominant.

Zone III received less than 30 cm of pumice, which permitted substantial survival. Secondary succession has resulted in well-developed forests similar to nearby less disturbed forests. Where deposits were thin and no species was eliminated, it is proper to speak of vegetation recovery rather than secondary succession.

Habitat heterogeneity

Any succession study risks errors by making space-for-time substitutions. Succession has proceeded at different rates along the depth gradient, but transects do not directly reflect succession. Flood plains suffered chronic erosion and had tephra removed soon after deposition and canyons now harbor distinctly different vegetation. These plots were excluded from the A transects and B#4 (alluvial valley) was not central to the interpretations. Tephra depth is a good predictor of the relative rate of succession. Tephra depth is directly related to the degree of damage, degree of survival, and the possibility that snags remain standing. However, wind redistributes pumice so that thick and thin deposits may be adjacent. Protected microsites therefore have finer texture and greater water-holding capacity. Substrate heterogeneity increased as deposit depths decreased. Plots with thinner deposits were

Table 1. Mean monthly air temperature and precipitation at meteorlogical station Khodutka (see Figure 1 for location), southern Kamchatka. Data for 10 years from 1955 to 1964.

Parameter	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	Total
Temperature (°C)	−8.1	−8.2	−5.8	−1.5	−2.3	−7.3	−11.2	12.0	9.0	4.3	−1.5	−5.8	1.3
Precipitation (mm)	123	83	144	123	104	63	119	79	122	154	165	151	1430

closer to well-developed forest and hence more likely to have received diaspores. The combination of greater heterogeneity and proximity to potential colonists resulted in plots on thinner deposits having more complex and diverse vegetation than those on deeper deposits. All sites were created simultaneously, but succession has proceeded at different rates due to local and landscape factors. Currently barren sites on deep pumice eventually may come to resemble sites on shallower deposits, but this process could require several centuries (cf. Mazusawa 1985). Of course, the details on each site will vary in response to contingent factors and local topographic effects, but the patterns should be sufficiently consistent to recognize successional stages.

Succession on thicker deposit

We did not observe Stage 1 (*pioneer herb stage*) at lower elevations, though Hultèn (1974) reported this stage in 1922. He described sparse cover by wind-dispersed plant species such as *Chamerion angustifolium, Lerchenfeldia flexuosa* and *Pennelianthus frutescens* after 15 years.

Table 2 summarizes species composition in A transects. Stage 2 (*lichen stage*) is a pioneer stage that now covers most deep deposits. It differs from Stage 1 in that ground cover is nearly complete and vascular plant richness is greater. Stage 2 sites were exposed, with low species diversity (Table 2). *Stereocaulon grande*, common to all sites on deeper pumice, was the dominant lichen. The mosses *Polytrichum juniperinum* and *Racomitrium fasciculare* were common in more favorable sites. A total of 39 lichen species was identified by A. G. Mikulin.

Pioneer herbs rarely occurred near other species and therefore are not involved in nucleation (Yarrington & Morrison 1974), nor have they facilitated invasion (Franco & Nobel 1989). In this landscape, facilitation appears to have been almost exclusively physical (cf. del Moral & Bliss 1993), and nitrogen fixing species are rare. Woody species first appeared in Stage 2, where adults of *Empetrum sibiricum* and seedlings of *Betula kamtschatica, Alnus kamtschatica* and *Spiraea beauverdiana* were common. The latter species occurred sparsely in favorable microsites. It is dispersed by birds, tolerant of nutrient-poor conditions, and is evergreen. Only two other vascular species were common. The wind-dispersed grass *Lerchenfeldia flexuosa* occurred with *Empetrum*, more often in shallow pumice deposits. *Pennellianthus frutescens* was widespread, suggesting that Hultèn's (1924, 1974) observations of this species as an early pioneer were correct. It persists by means of strong lateral vegetative growth (cf. Tsuyuzaki & del Moral 1995). *Chamerion angustifolium* also was scattered throughout this stage.

Succession on deeper deposits progressed faster where favorable topography and proximity to later vegetation stages were combined. Stage 3 (*woody colonization*) is characterized by clumps of dwarf shrubs and bunch grasses. This stage retains most species that colonized during earlier stages. These species now occur as mature plants or as expanded clones. Vascular plant species diversity remains low, and lichens and mosses continue to dominate these sites. However, an accumulation of species has become evident. As on El Paricutín (Eggler 1963; Rejmanek et al. 1982), succession has been marked more by accumulation than by turnover.

Saplings of birches up to 2 m in height occurred in Stage 3, but the pumice remained acid and low in water and nutrients. These birches have dense root systems extending over 500 m^2, yet they are unstable. Many uprooted and physically abraded roots were found, along with a few alders and stunted pine. All this suggests that while seeds are available and some of these individuals may survive, these sites will not soon develop into the fourth stage.

We recognized Stage 3 at higher elevations (Table 2). Erosion produced substantial topographic variation, so that vascular plants colonized protected swales. There were several willows, other woody species, and herbs and mosses. Wind erosion had reduced lichens dominance in exposed sites, and much of the surface was bare. The presence of mature alder, birch

Table 2. Primary succession plots (Transect A). Rare and low frequency species are excluded. Nomenclature in Table 5.

Species	Barrens Stage 2 (250 m)					Barrens stage 3 (500 m)		Shrubs patches Stage 3 (250 m)			Forest patches stage 4 (250 m)						
	AI-4	AI-5	AII-3	AII-5	AII-9	AV-1	AV-2	AI-6	AIII-2	AIII-3	AII-8	AII-10	AIII-1	AIV-1	AIV-3	AIV-5	AIV-7
Alnus kamtschatica						1											
Betula ermanii	+		+	+	+		+	+		+	2	2	2	2	4	4	5
Pinus pumila														+	+	+	+
Empetrum sibiricum	1	+	1	+	1	r	r	2	2	2	2	+	2	2	2	1	2
Ledum decumbens			+					+									
Lonicera coerulea															r	r	+
Lonicera chamissoi														r	1	+	+
Rhododendron aureum			+		+			+				+		r	1		+
Rubus sachalinensis						r					r				r		
Salix arctica					+	r	+				r						
Salix caprea	r		+			r		+	+			+	r	+	+	+	+
Salix pulchra		r			+						+			r			r
Sorbus sambucifolia							r								+	+	r
Spiraea beauverdiana					+				+			+	r	+	1	+	
Vaccinium ugilinosum	r			r		r	r		+				r	+	+		+
Anaphalis margaritaceae						r	r										
Calamagrostis purpurea														r	r		r
Cardamine bellidifolia			r					r									r
Carex koraginensis			r			r		1									r
Chamerion angustifolium		+	+		+	r		+	r	r	r	+		1	+	+	+
Lerchenfeldia flexuosa	1	1	1	2	2	2	+	1	1	1	1	1	1	1	2	2	2
Moehringia lateriflora						r	r									+	+
Penellianthus fructescens	+	+	1	+	+	+	r	1	+		+	1	+	+	+		+
Poa platyantha															r		+
Pyrola media																+	+
Pyrola minor				1		r						+	+	+	+		+
Saxifraga merkii						r	r										
Stellaria fenzlii																+	+
Trientalis europaea															r	+	+

Table 2 continued.

	AI-4	AI-5	AII-3	AII-5	AII-9	AV-1	AV-2	AI-6	AIII-2	AIII-3	AII-8	AII-10	AIII-1	AIV-1	AIV-3	AIV-5	AIV-7
Athyrium filix-femina				+			r								+		+
Dryopteris expansa							r		r				+		+	r	r
Diphasiastrum alpinum											r			r	+		r
Diphasiastrum complanatum							+							r	+	r	+
Lycopodium clavatum		+											r	r		+	+
Dicranum bergeri	r		r				+			*			+	+	+	+	+
Polytricum juniperinum	1	2	1	1	+	1	+	1	1	+	1	1	1	2	2	1	1
Ptilium sp.							+								r	r	r
Rhacomitrium canescens			+			r	+					+		+	+	+	+
Rhacomitrium fasciculare	+		2	1	1	1	2	+	+	1	1	2	2	1	1	1	+
Alectoria nigricans							r								r		+
Cetraria laevigata	+	+	+		+			+	+	+	+	+	1				r
Cladina portentosa	+	+	+	+	+	r	+	+	1	+	1	1	2	1	1	1	+
Cladina rangiferina	+						+	+		+	+	+	2	1	1	1	1
Cladina stellaris														+	+	r	r
Cladonia favillicola	+	+		+	+		r	+	+	1	+	+	1	+	+	+	+
Cladonia macrocerus	+	+		+	+		+	+	+	+	+	1	1	1	1	1	1
Cladonia multiformis														r	+	+	
Cladonia sp.							r					+	+	+	1	+	+
Sterecaulon grande	5	5	4	4	4	3	2	5	5	3	4	4	3	4	3	2	1
Stereocaulon vesuviaum			+	+	+		r				+	+	+	+	2	+	+
RICHNESS-Woody	4	2	5	3	6	5	5	5	4	5	5	5	5	9	9	7	10
Herbs	2	3	5	4	4	10	6	5	3	2	3	4	3	6	10	8	21
Lower Plants	0	1	0	1	0	1	4	0	1	0	1	0	3	3	4	3	5
Mosses	3	1	4	2	2	3	4	2	2	3	2	3	3	4	5	5	6
Lichens	6	5	5	6	6	3	9	6	6	6	8	8	10	10	12	9	10
TOTAL	15	12	19	16	18	22	28	18	16	16	19	20	24	32	40	32	52

r = solitary; + = scattered; 1 = cover 1 to < 5%; 2 = cover 5 to 25%; 3 = 26 to 50%; 4 = 51 to 75%; 5 = over 75%.

and willow suggests that there is a significant seed rain of wind-dispersed species.

Stage 4 (*forest consolidation*) of primary succession was sampled in the western portion of A-II and all of A-IV (Zone II). Consolidation of the vegetation was demonstrated by increased *Betula* cover, *Pinus pumila* colonization, increased importance of woody species such as *Salix caprea*, increased cover of *Lerchenfeldia*, increased diversity of herbs, ferns and lycopods, and reduced lichen dominance (Table 2). Richness increased from 19 to 52 species across Zone II, primarily among herbs and lower plants.

Stage 4 also progressed differentially in response to local conditions, proximity to colonizing sources, and pumice depth. Table 3 shows increased mean percent cover and mean density in diameter classes of *Betula ermanii* ranging from < 2 cm to over 23 cm as a function of inferred decreasing pumice depth along transect A-IV. *Betula* cover increased from about 12%, where it occurred in scattered patches, to 75% in a nearly closed dwarf forest. The height of the largest individuals increased from 7 to 11 m. This reflects their increasing age and time since establishment. The increasing size and number of stems confirm this interpretation. Trees larger than 20 cm are confined to the last two plots, located on relatively thin deposits.

Vegetation development on thinner deposits

Developmental pattern

The geobotanical transect (B) revealed the critical pumice depth that separates obliterated vegetation from that in which some species survived (Table 4). Along this transect, pumice thickness declined from 95 cm to 19 cm. The transect started where the lichen desert is intermixed with an open, young birch forest and scattered *Lerchenfeldia flexulosa*. There was no evidence that plants survived the eruption (B#1; Table 5). On shallower deposits, herbs became more abundant, mosses were common and some lichens persisted. On the thinnest deposits, lichens were absent, mosses rare, and the understory was dominated by forest herbs (Table 5). Tree stem density was high (Table 4).

Transect B, #1 to 6 was dominated by young birch stands and demonstrated the transition into Stage 5 (*sub-climax forest*). B#1 to 3 were in thicker volcanic deposits, with very rare, if any, surviving trees. B#4 was in the river valley, where erosion and alluvium mitigated pumice effects. Vegetation in the valley reflects microrelief: on slightly elevated (0.5 m), more stable sites, young birch stands with forest understory species have developed. On depressed microsites, willows (*Salix udensis, S. caprea, S. arctica, S. pulchra*) and white birch with an open layer of *Empetrum sibiricum*, *Lerchenfeldia flexuosa* and *Chamerion* prevail.

B#5 was on the edge of an old (about 1500 years) lava flow, and B#6 was on the slope with lava covered alluvium. Up to 30% of B#6 includes pumice outcrops. We estimated that surviving tree density in plots B#5 and B#6 was much less than 1 tree per ha. B#7 and #8 represent older, less impacted forests with trees rooted in old soil. These plots represent Stage 5 vegetation, where at least some trees survived the 1907 eruption.

Effect of soils

Plant communities on pumice of different thicknesses differ significantly. Specific changes in soil development at five locations are shown on a gradient from lichen desert and open young birch forests to climax stone birch forests with tall herbs (Figure 2). A pumice layer of 95 cm under open birch forests shows primitive soil formation: the surface with fragments of litter is replaced by an alluvial horizon with small mixtures of brown fine grained soil in spaces between larger pumice particles. Below the friable pumice layer, no soil formation was noted. Nevertheless, the roots of white and stone birches are able to pierce all deposits in these severe habitats to reach the rich, buried humus horizon. A similar description applies to other profiles with thinner pumice deposits.

Qualitative changes of morphological attributes in the soil profile appeared about 5 km west of the axis of the deposits, where the deposits were only 30 cm deep. Here, vegetation is characterized by the presence of old birches that survived the eruption and by a marked increase in herb layer species diversity. The soil profile shows a 2 cm thick litter layer and a 3 cm thick humus horizon. The illuvial horizon (A1B) is immature and includes a layer of friable pumice little tinged by humus, but already connected by roots.

The first trees that certainly survived the eruption appear in Zone II where the pumice thickness is less than 70 cm (B#2). Young birch stands gradually increase their canopy, average stem diameters, average heights and stem densities (Table 4). Figure 3 shows that B#7 and B#8 birches were more vigorous than climax birch stands. They were dominated by smaller trees, but included several larger ones that appear to be survivors of the eruption. Figure 4 describes the density and size distributions of *Betula ermanii*

Table 3. Structural features of *Betula ermanii* along a transect of decreasing pumice depth. Density is mean number of stems in twenty 10 by 10 m plots.

TRANSECT A–IV	#1	#2	#3	#4	#5	#6	#7
Cover (%)	12.6	40.7	46.1	66.1	60.6	61.8	74.8
Frequency (%)	95	100	100	100	95	100	100
Mean density in each diameter class:							
< 2 cm	4.7	3.5	3.3	4.4	5.4	5.7	6.1
2–6 cm	5.2	7.3	12.1	9.0	7.6	8.0	6.6
7–10 cm	1.2	2.1	1.9	4.4	3.8	3.6	1.5
11–14 cm	0.1	0.2	0.4	2.0	1.7	2.0	1.0
15–18 cm	0.1	0.1	0.1	0.9	1	0.7	0.5
19–22 cm						0.2	0.4
23 +						0.1	0.2
Maximum height (m)	7	7	9	10	10	11	11
Typical height (m)	3	4	4	5	6	7	8

Table 4. Structural characteristics of dominant trees along Transect B and pumice deposit depths in soil pit.

Plot	RELIEF	Pumice Thickness (cm)	Canopy Height (m)	Stem Density (#/ha)		Basal Area (m^2/ha)			Mean DBH (cm)		Sapling density (#/ha)	
No.				B_k	B_e	B_k	B_e	SUM	B_k	B_e	B_k	B_e
1	Volcanic plain, covered pumice pyroclastics	95	6–7	635	1720	3.1	4.9	8.0	7.8	6.0	170	520
2	Same as above	70	8	–	–	–	–	–	–	–	–	–
3	High river terrace	58	8	5	4360	–	18.3	18.3	–	7.3	5	6215
4	Alluvial valley	33	10	–	–	–	–	–	–	–	–	–
5	Terrace covered by old lava flow	37	8	1705	705	10.4	3.7	14.1	8.8	8.1	995	1615
6	Lava flow covered by deluvium	31	9	825	1075	10.0	5.9	15.9	12.4	8.3	630	4260
7	Same as above	24	15	–	3480	–	25.3	25.3	–	9.6	–	3960
8	Same as above, covered by thick deluvium	19	15	–	940	–	30.8	30.8	–	20.4	–	40

B_k = *Betula kamtshatica*; B_e = *Betula ermanii*

and *B. kamtschatica* in plots B#1, B#3, and B#5 to #8. Through B#6, mean *B. ermanii* size distribution became larger. *B. kamtschatica* invaded these plots, but appears to be loosing ground in more mature vegetation. Only small dead *B. kamtschatica* occur in B#7 and B#8.

Stand dyamics

As the canopy closed and stems die, the first generation of white birch is replaced by stone birch. Figure 5 shows the development of stand structure across Transect B. The canopy has become progressively taller and denser, and the understory becomes more complex.

Synusia

Table ɔ summarizes species composition in each plot, while Figure 6 illustrates major ground layer changes that occur as birch forests develop. Among the more prominent trends are that bare ground is eliminated, ground lichens become rare, tall or smaller herbs and shrubs become dominant, and graminoids become common during Stage 4. In B#1 (pumice thickness = 95 cm), the lichen synusia cover up to 80% of the

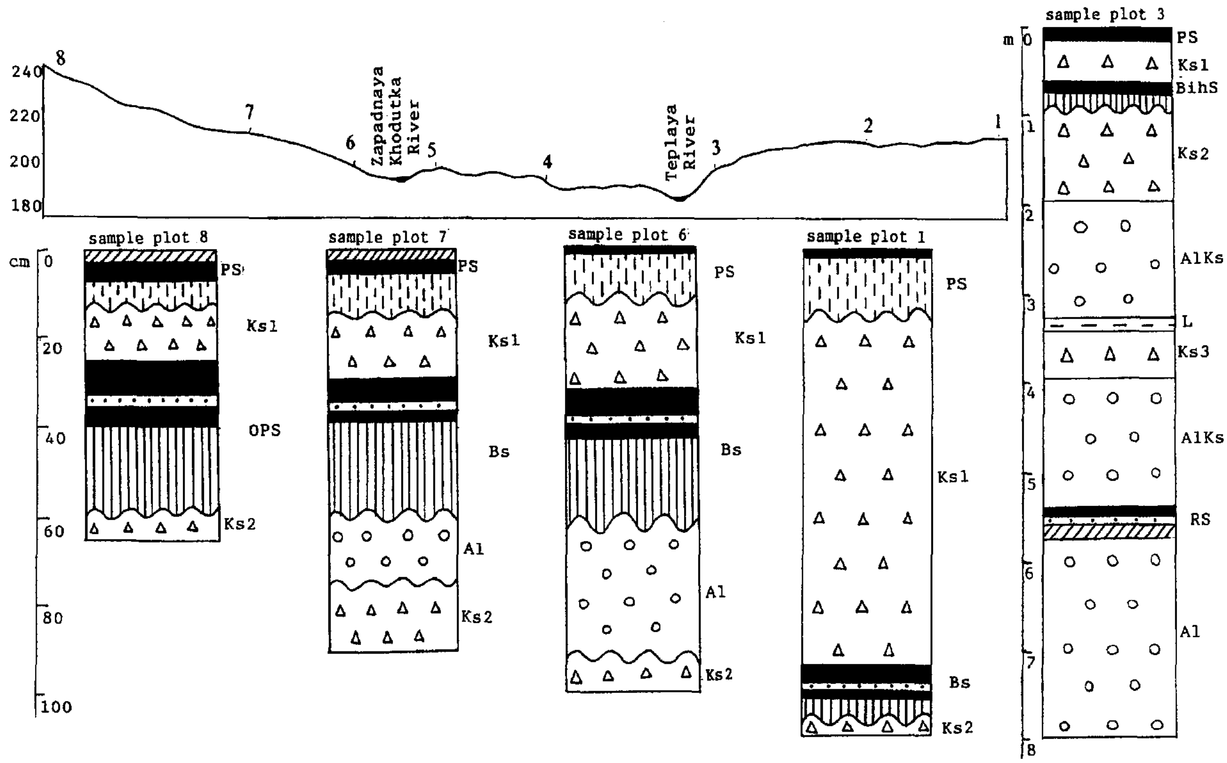

Figure 2. The geobotanical transect (B) and soil profiles. Abbreviations: PS, primitive soil; BS, buried soil; OPS, ocherous-podzolic soil; RS, relict soil; Ksl, pumice of 1907 eruption; Ks2, pumice of AD 300 eruption; Ks3, pumice of 2400 BP eruption; Al, alluvial deposits; AlKs, alluvium, intermixed with pumice; BihS, buried illuvial-humus soil; L, loam

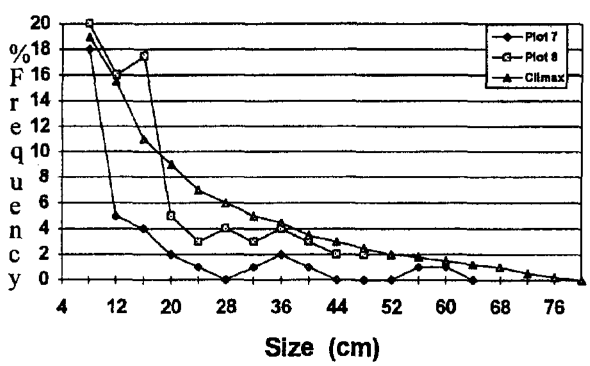

Figure 3. Frequency (%) of *Betula ermanii* stem diameter classes (dbh, cm) on B-#7 and B-#8 and in a typical climax stand.

pumice in a young birch forest (Table 6). Synusia of *Stereocaulon grande* occur in canopy gaps. Species of *Cladina* (*C. portentosa, C. ecmocina, C. digitata, C. stellaris*) form synusia under the birch canopy and the shrubs. Synusia of *Empetrum sibiricum* and *Lerchenfeldia flexuosa* occur around the birch stems in concentric circles. Litter accumulates in the dense stands of young birches. With canopy closure (B#3, #4, pumice depth between 30 and 60 cm), the role of the lichen synusia is significantly reduced. The cover of *Stereocaulon grande* is decreased sharply. Patches of green mosses (*Polytrichum juniperinum, Sanionia uncinata*) become more apparent, but their cover remains low. Monodominant synusia of *Empetrum sibiricum* and *Lerchenfeldia flexuosa* have become extensive. All synusia are becoming more densely populated, their species composition is becoming more saturated by colonization of small herb species (e.g., *Moehringia lateriflora, Stellaria fenzlii, Trientalis europaea,* and *Pyrola minor*) and club mosses (*Lycopodium clavatum, L. annotinum + Diphasiastrum complanatum*), (B#3, #4). Patch sizes are small (from 0.2–0.5 to 1–3 m in diameter). As they expand, they often merge to form polydominant small herb synusia (B#3, #6). During the early stages of herb layer formation the synusia are spatially delimited. However, as the canopy closes, it becomes difficult to mark the boundaries of these synusia. The horizontal structure of the

Table 5. Species composition in the understory of the *Betula ermanii* phytocoenose along Transect B. Nomenclature: 'The vascular plants of the Soviet Far East (1985–1995).

Species, authority	Braun-Blanquet Score/Frequency (%) in sample plots							
Shrub Layer	#1	#2	#3	#4	#5	#6	#7	#8
Alnus kamtschatica (Regel) Kom.				2/				4/50
Lonicera chamissoi Bunge ex P. Kir.	+/3	+/	+/40		+/17	+/27	+/17	+/
Lonicera caerulea L.			+/7		+/17	+/23	r/3	+/
Pinus pumila (Pall.) Regel	+/7	+/	+/7		+/3	+/7		
Rhododendron aureum Georgi			+/3					
Rosa amblyotis C.A.Mey.				+/			+/	+/
Salix arctica Pall.					+/3			
Salix udensis Trautv. et Mey.	r/3	r/						
Sorbus sambucifolia (Cham. et Schlecht.) M. Roem.			+/3		+/3		+/3	
Spiraea beauverdiana Schneid.		+/	+/7	+/	+/20		+/3	
Herb Layer	#1	#2	#3	#4	#5	#6	#7	#8
Anaphalis margaritaceae (L.) A. Gray			+/10					
Anemonoides debilis (Turcz.) Holub					r/3			
Artemisia opulenta Pamp.				+/			+/	1/43
Athyrium filix-femina (L.) Roth s.l.								r/3
Calamagrostis purpurea (Trin.) Link. s.l.				1/	+/23	1/80	2/97	2/100
Cardaminopsis lyrata (L.) Hiit.						+/13		
Carex longirostrata C.A. Mey.		+/		+/			r/	
Chamerion angustifolium (L.) Holub	+/10		+/33	1/	+/37	1/70	2/87	+/37
Cimicifuga simplex (Wormsk.exDC.)							+/	3/37
Cirsium kamtschaticum Ledeb.								r/3
Corallorhiza trifida Chtel.						r/3		
Diphasiastrum complanatum (L.) Holub		+/	1/27		+/3	+/10	+/10	
Dryopteris expansa (C.Presl.) Fraser-Jenkins et Jermy			r/3			r/3		
Empetrum sibiricum L.	+/17	+/	1/23	2/	1/43	r/3		
Filipendula camtschatica (Pall.) Maxim.								+/10
Galium kamtschaticum Stell. ex Schult.						+/20	1/63	1/47
Gymnocarpium dryopteris (L.) Newm.		+/		+/	+/10			+/13
Lerchenfeldia flexuosa (L.) Schur	1/43	2/	2/100	+/	2/100	1/80	+/37	
Listera cordata (L.) R. Br.			+/7			+/7		
Lycopodium annotinum L.			+/37		+/3	+/13	+/20	
Lycopodium clavatum L.		+/	+/23		+/30	+/17	1/60	
Luzula parviflora (Ehrh.) Desv.			1/40					
Luzula plumosa E. Mey.							r/	
Maianthemum dilatatum (Wood) Nels.		1/		2/			1/27	
Moehringia lateriflora (L.) Fenzl.		+/	+/20	+/		+/50	+/50	+/7
Neottia asiatica Ohwi			r/3					

Table 5 continued.

Herbs, continued	#1	#2	#3	#4	#5	#6	#7	#8
Pedicularis resupinata L.						+/3		
Picris kamtschatica Ledeb.							r/	
Poa platyantha Kom.			+/10					
Pyrola minor L.	+/13	+/	+/7	+/		+/13		
Rubus arcticus L.			+/13				+/	
Sanguisorba tenuifolia Fisch. ex Link				+/		+/7	+/27	
Senecio cannabifolius Less.							+/	2/67
Solidago spiraeifolia Fisch. ex Herd.			+/3	+/	+/13			
Stellaria fenzlii Regel		+/	+/3	+/	r/3	+/10	+/7	
Streptopus amplexifolius (L.) DC							r/	r/3
Thalictrum minus L.							+/	1/43
Trientalis eurupaea L.		+/	+/3	1/	+/13	1/67	3/100	1/80
Trillium camschatcense Ker-Gawl.								+/17
Trisetum sibiricum Rupr. s.l.						+/10	+/20	
Vaccinium uliginosum L.	+/7				+/23	+/3		
Veratrum oxysepalum Turcz.							r/	+/20
Viola biflora L.							r/	

Moss and lichen layer	#1	#2	#3	#4	#5	#6	#7	#8
Cetraria islandica (L.) Ach.	+/7							
Cladina portentosa (Duf.) Follm.	+/10	+/				+/23		
Cladina rangiferina (L.) Nyl.	1/63	1/		1/		+/17		
Cladina stellaris (Opiz.) Brodo	2/73	+/	1/73					
Cladonia cepvicornis (Ach.) Flot.	1/53							
Cladonia digitata (L.) Hoffm.	+/10	1/			+/27	+/17		
Cladonia ecmocyna Leight.	+/20		+/50		+/30	+/30		
Cladonia gracilliformis Zahlbr.	+/7					r/3		
Dicranum bergeri Blant. in Starke			+/27		+/27	+/13		
Peltigera canina (L.) Willd.						+/3		
Polytrichum juniperinum Hedw.	1/57		+/47		+/57	+/50	+/10	
Sanionia uncinata (Hedw.) Loeske			+/3		1/67	+/27	r/3	

Table 6. Percent Cover of the principal synusia in each plot on Transect B.

Synusium	#1	#2	#3	#4	#5	#6	#7	#8
Cladina stellaris + *Cladina rangiferina* + *Cladonia cepvicornis*	80	50	10	30	–	10	1	–
Emptrum sibiricum	18	1	10	–	10	–	–	–
Lerchenfeldia flexuosa	2	41	54	25	–	50	1	–
Lycopodium annotinum	–	1	25	4	–	–	5	–
Maianthemum dilatatum + *Trientalis europaea* + *Rubus articus*	–	1	–	–	30	30	18	–
Chamerion angustifolium + *Calamagrostis purpurea*	–	–	–	2	60	10	70	20
Senecio cannabifolius + *Filipendula camtschatica* + *Calamagrostis purpurea*	–	–	–	–	–	–	–	80

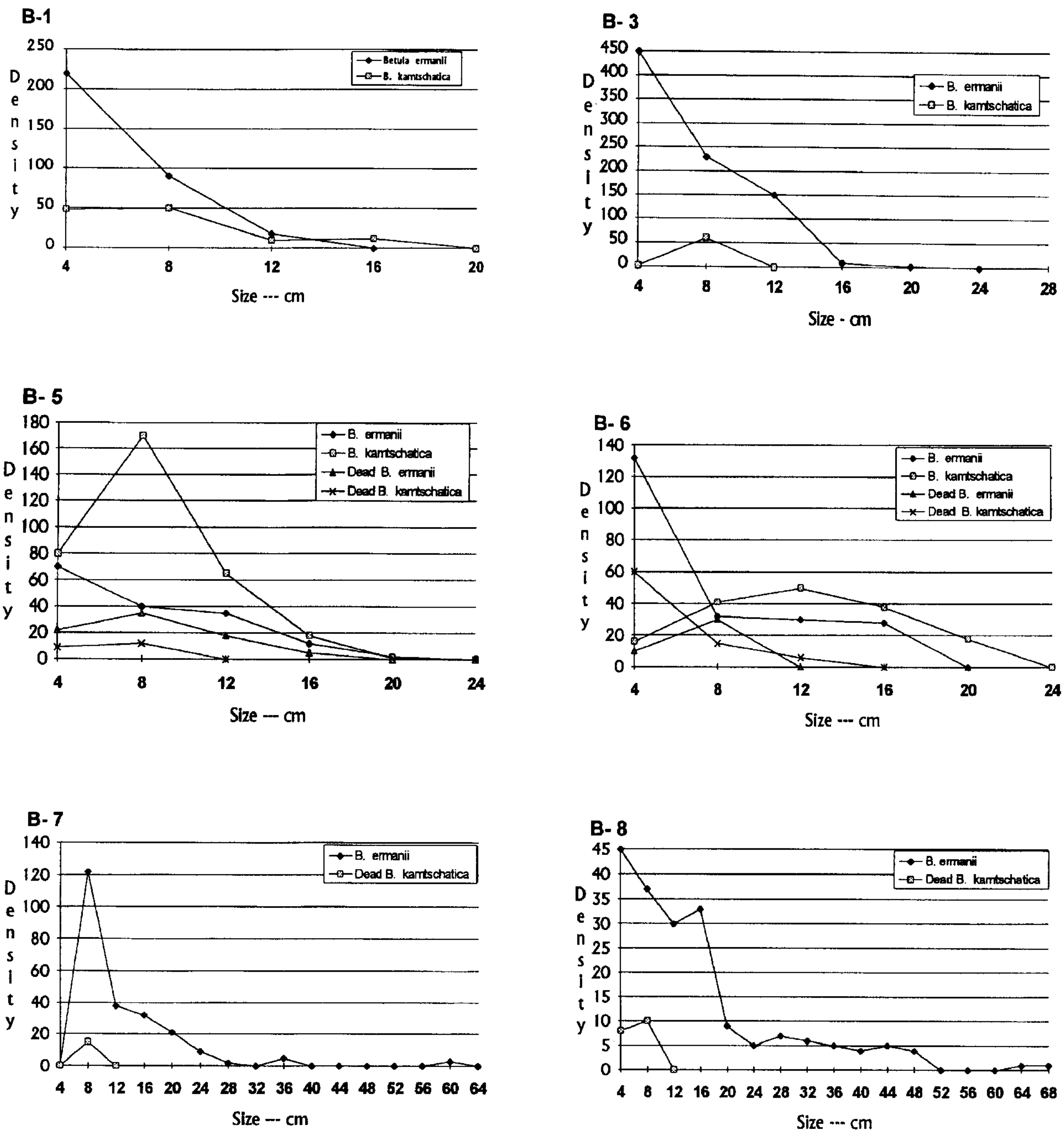

Figure 4. Frequency distribution (per 0.2 hectare) of stems by d.b.h. (cm) on plots of Transect B: *Betula ermanii*, *B. kamtschatica*, dead stems of *B. ermanii* and dead stems of *B. kamtschatica*.

ground layers at these stages of birch stand formation is complex, while its vertical organization is simplified.

Herb species richness and cover increase across the transect as moss and lichen species richness and cover decrease (Figure 7). Patch sizes appear to be determined primarily by the sizes of tree crowns, which creates shade and deposit litter, and by microrelief, which provides establishment opportunities. B#6 (on lava, with 31 cm pumice) is the best developed heavily impacted forest. The herb layer consists of these synusia: *Maianthemum dilatatum* + *Stellaria fenzlii*; *Lycopodium annotinum*; *Pyrola*

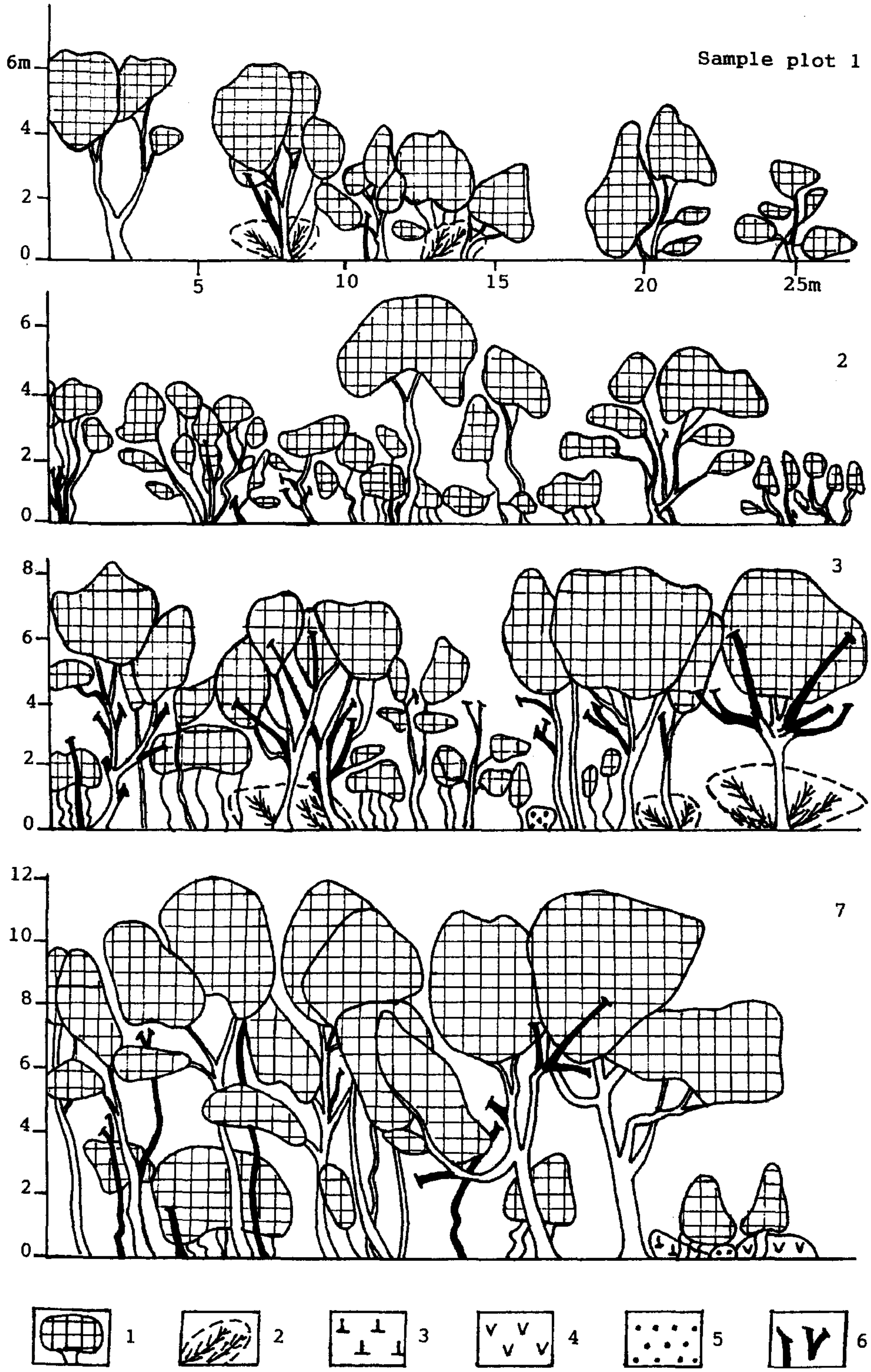

Figure 5. Profile diagrams of *Betula ermanii* forest in different stages of succession. 1, *Betula ermanii*; 2. *Pinus pumila*; 3, *Rosa amblyotis;* 4, *Sorbus sambucifolia*; 5, *Lonicera chamissoi*; 6,= dead branches and trunks.

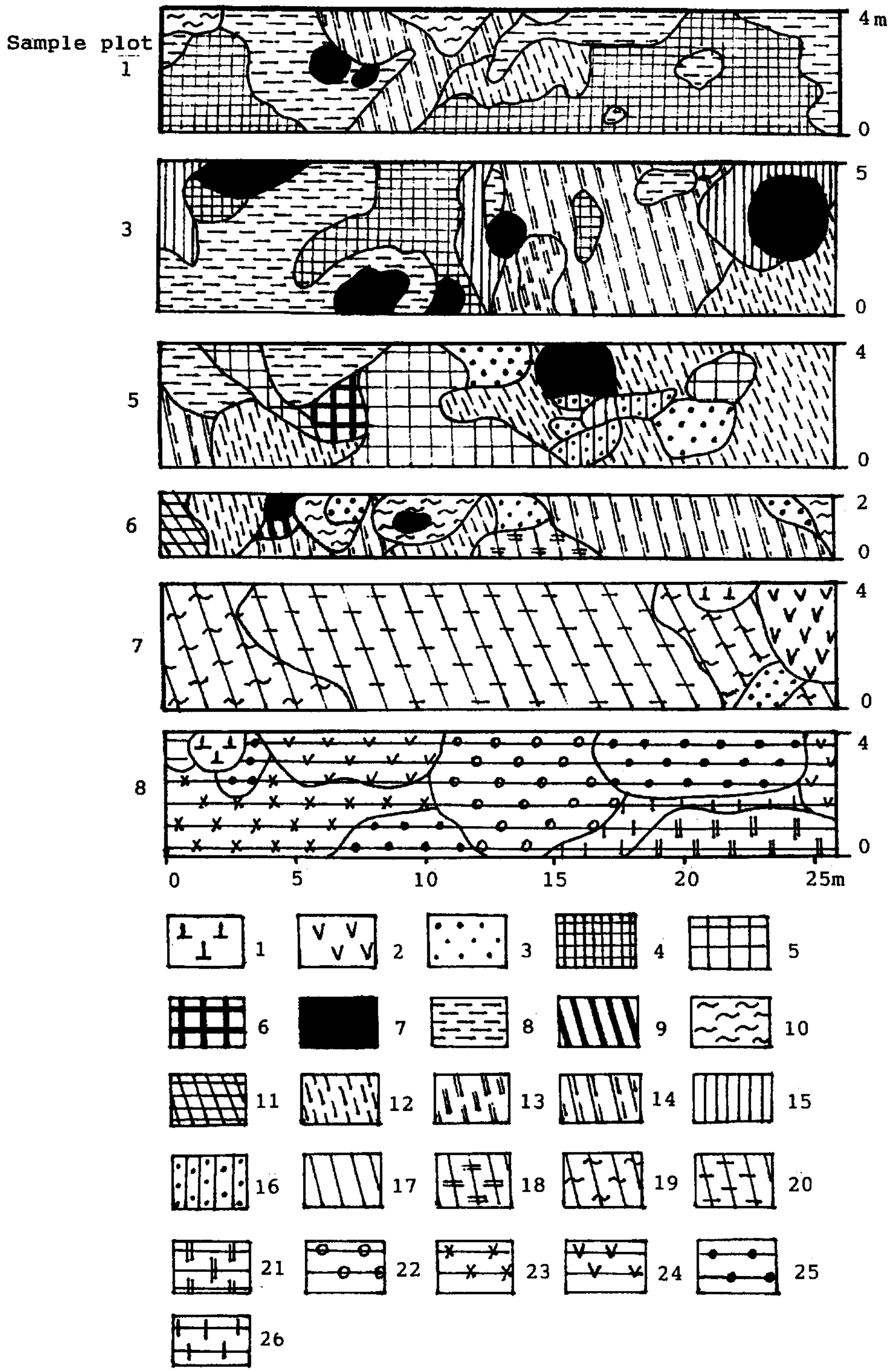

Figure 6. Synusial structure of understory of *Betula ermanii* forest in succession. 1 *Rosa amblyotis;* 2, *Sorbus sambucifolia*; 3, *Lonicera chamissoi-L. caerulea*; 4, lichen synusium; 5, moss-lichen synusium; 6, moss synusium; 7, bare sites; 8, *Empetrum sibiricum;* 9, *Galium kamtschaticum*; 10, *Trientalis europaea*; 11, forest small herbs; 12, *Lerchenfeldia flexuosa*; 13, *Lerchenfeldia flexuosa-Luzula plumosa*; 14, forest small herbs-*Lerchenfeldia flexuosa*; 15, club mosses (*Lycopodium clavatum, L. annotinum, Diphasiastrum complanatum*); 16, *Lerchenfeldia flexuosa*-club mosses; 17, *Calamagrostis purpurascens*; 18, forest small herbs-*Calamagrostis purpurascens*; 19, *Trientalis europaea-Calamagrostis purpurascens*; 20, *Maianthemum dilatatum-Calamagrostis purpurascens.* The tall herbs synusia: 21, *Cimicifuga simplex*; 22, *Filipendula palmata*; 23, *Senecio cannabifolius*, 24, *Veratrum oxysepalum*, 25, *Artemisia opulenta*; 26, *Calamagrostis purpurascens*-tall herbs. Synusia, by definition, do not overlap.

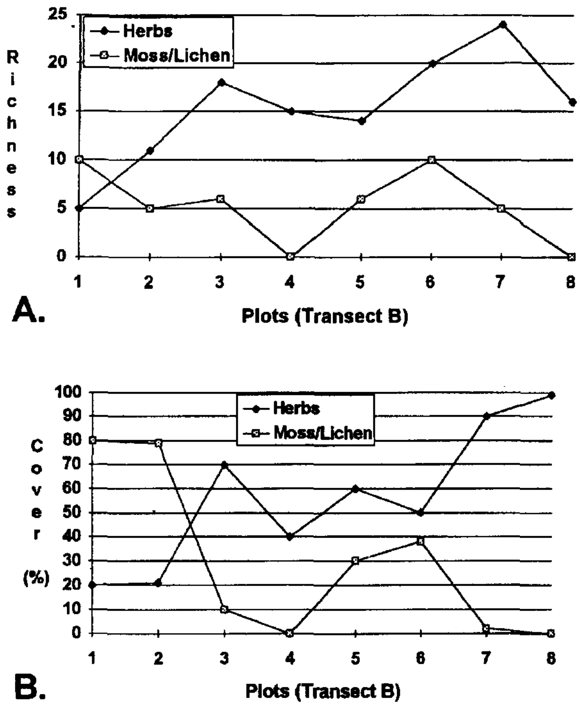

Figure 7. Species richness (A) and cover (B) in herb layer and moss-lichen layer of Transect B.

minor + *Linnaea borealis* and *Lerchenfeldia flexuosa*. *Chamerion angustifolium* and *Calamagrostis purpurea* form synusia located in local concavities.

Recovering vegetation

The transition from Zone II to Zone III is abrupt. Shallower deposits of Zone II support a mosaic of primary successional stands alternating with more mature stands, elements of which survived the 1907 eruption. Topographic heterogeneity and pumice redeposition after the eruption caused variable soil and hydrological conditions and resulted in differential colonization for each life-form. Table 5 summarizes species composition along the transect.

Forests recovering from perturbations were described in plots B#7 and #8. B#7 is on a bench, and B#8 is on a slope covered by alluvium. As a result of partial destruction and loss of some trees and lower strata, compositional changes occurred. These changes are blurred after 87 years, but we can reconstruct them. On B#7, an old stone birch forest, a young birch canopy was formed. Stem diameters of the young trees are 4–16 cm, and there is much regrowth. Large gaps formed in the old canopy. On B#8, some old trees were killed and young trees now form dense clusters in the canopy gaps and have invaded subalpine meadows. Such meadows normally form a mosaic with birch forests near the upper timberline, and would have suffered greater damage.

The age structure of impacted forest stands, based on diameters of trees in B# 7 and #8, differs appreciably from typical climax forests of Kamchatka (Figure 4). There are many more young trees (d.b.h. 4–16 cm) here, and gaps in the frequency profile, indicating lost younger generations. The impact of tephra on trees of different sizes was differential, in that trees between 15 and 35 cm dbh were damaged more intensively than those over 40 cm dbh. The analysis of tree age showed that in many cases the eruption was followed by regrowth. This implies that many young trees survived pumice impacts due to the protection of the overstory and of snow. Their cohort is more common in impacted forests than in typical forests. It is also possible that some of the regrowth if from sprouts using nutrients in buried soil and from decomposing plant remains, as was found on Mount St. Helens (del Moral 1983).

The size structure of trees in stands impacted by about 20 cm of tephra (B#7) differs from typical climax forests of Kamchatka (Shamshin 1974; Grishin 1996). There are more young trees (d.b.h. 4–16 cm) in climax vegetation, and there are size gaps that correspond to the loss of a generation of birches killed in 1907 (the 40 to 52 cm class; Figure 3). This analysis demonstrates that moderate tephra deposites are followed by vigorous regeneration of small birches that were protected by snow and by the canopy of larger trees, and which are released from suppression. In addition, new seedlings may establish on the newly deposited tephra. As a result, impacted stands on Ksudach have a more varied age structure than mature, relatively undisturbed stands.

The mean growth increment of birch is about 3 mm per year. a rate that implies that the time necessary to restore normal uneven-aged climax birch stand is 50 to 70 years. However, changes in understory synusia will require much longer to develop. The evidence suggests that where long-lived species persist and spread, they resist colonization by species better adapted to forest conditions and retard development of a true climax stage.

On B#7, the synusium of small forest herbs (*Maianthemum dilatatum* + *Rubus arcticus* + *Trientalis europaea*) cover about 70% (Figure 6). In gaps, synusium *Calamagrostis purpurea* is clearly expressed, and overlaps synusia of small herbs in light gaps and sometimes under the canopy. On B#8, the herb layer is formed by a tall herb synusium (*Senecio cannabifolius* + *Filipendula camtschatica* + *Calamagrostis purpurea*), and in wet microhabitats by a pure synusium of *Filipendula camtschatica*. Several synusia occur on raised sites. *Senecio cannabifolius* + *Cimicifuga simplex* + *Cirsium kamtschaticum* + *Calamagrostis purpurea* and *Artemisia opulenta* + *Thalictrum minus* + *Chamerion angustifolium* combine to form a tall, closed herb layer that is structurally similar to that which dominates flood plains in this area.

The geographical extent of vegetation damage

Hultèn (1923, 1924, 1974) prepared a small-scale vegetation map of Southern Kamchatka that showed areas with destroyed and damaged vegetation. Heavy damage from the 1907 Ksudach eruption reached the Asacha volcano (50 km to the north).

Logic of the analysis

We can determine the extent and degree of damage to vegetation on a landscape scale by using the distribution of survivors and geobotanical descriptions along Transect B. Pumice deposits less than 30 cm are now characterized by relatively mature forests since most trees, though damaged, survived. Deposits of 30 to 70 cm depth are marked by isolated surviving trees. Pumice deposits greater than 70 cm were characterized by isolated clumps of small shrubs or isolated young trees, established where trees were killed, but remained standing for many years. We found no trees on thicker deposits that were older than 50 years old. Damage and death are attributed to the heat of falling tephra, mechanical damage, effects of subsequent exposure to strong winds and higher air temperatures, and soil burial, causing alterations of soil chemistry, temperature, and aeration.

Impact Size

We estimate the extent of the effects of the 1907 eruption on vegetation by combining our field studies with data from volcanologists on the distribution and depths of deposits (Melekestsev et al. unpubl.; Table 7). The vegetation on the western and much of the eastern and southern external slopes of the caldera was not damaged significantly by the eruption. The exception is the large (about 50 km^2) sector of the southeastern slope that was transformed into a volcanic desert. In 1910, Konradee & Kell' (1925) noted that some vegetation on the southern inner slope of the caldera survived the 1907 eruption. The deep, snow-filled canyons on these slopes provided refugia for *Alnus kamtchatica* thickets.

Based on aerial photography, we estimate that about 1800 km^2 of stone birch forests were impacted. Much of this area was impacted to a minor degree, but an area of 500–600 km^2 (deposits over 30 cm) was substantially impacted. Nearly total destruction occurred on about 124 km^2 (deposits over 70 cm), including sites that remain lichen deserts. About 71 km^2 includes devastated terrain with a few surviving trees. These regions include the caldera, sites along the northern axis and southeast sector of deposits formed when the wind changed during the 1907 eruption. The total area of forest vegetation that was destroyed is about 200 km^2. The remaining territory of nearly complete destruction was covered by subalpine and high-mountain vegetation, alluvial meadows, valley woods and bogs.

How the eruption changed the distribution of vegetation

We reconstructed the vegetation of the devastated area using botanical-geographical data we collected previously on undisturbed territories. From all available data, we compiled maps of potential and actual vegetation (Figure 8). These maps reflect key moments of vegetation change after the eruption.

Figure 8A shows the vegetation reconstructed for about 1900. Vegetation is distributed zonally: stone birch forest, alder thickets, a narrow ecotone between them, alpine tundra and nival zone. Azonal vegetation is represented by willow forests in the river valleys and by herb-shrub vegetation on level sites. Depressions are covered by wet sedges marshes.

After tephra deposition, the alpine tundra, herb-shrub vegetation, wet meadows and alder shrubs were appressed by deep snow and completely covered by pumice. Woody vegetation, primarily adult trees damaged by pumice forming deposits less than 1 m, remained viable and continued to grow for 5–10 years (Hultèn 1974). Figure 8B shows the reconstructed vegetation several years after the eruption. Pumice deserts dominate the landscape.

Based on our analysis of existing vegetation on Transects A and B, we delimit the zone of less than 70 cm of deposits, where some adult stone birch survived. It is also possible to define the ecotone between the damaged and destroyed forests. This ecotone corresponds to the line of 30 cm deep deposits. On deep-

Table 7. The relationship between pumice depth and degree of vegetation destruction.

Deposit Thickness (cm)	Deposit Area (km^2)	Nature of Destruction
1–5	8460	Destruction of some moss-lichens, herbs and dwarf shrub; minor damage to taller plants
5–10	1458	Substantial destruction of some species in moss-lichen, herb and dwarf shrub layers; damage to taller plants
10–20	954	Loss of lichen-moss layer; significant destruction to herb and dwarf shrub layer; some trees die slowly by drying
20–30	228	Total destruction of lichen-moss layer, herb layer; most of shrub layer lost; significant die back of trees
30–70	484	Destruction of all layers of vegetation and tree layer; isolated trees survive
70–100	62	Total destruction of all vegetation; reinvasion of vascular plants
Over 100	54	Total destruction of all vegetation; lichen desert persists

Note: Data on deposit thickness, in part, from Melekestsev & Sulerzhitskii (1987) and Melekestsev (unpubl.).

er deposits, both primary and secondary succession intermingle in response to mesotopography, position of surviving trees, and redeposition. On deposits less than 30 cm, there is a mixture of secondary succession (where there was significant loss of species richness) and recovery (where substantial damage reduce cover and density, but did not cause the elimination of strata or species).

Further analysis of modern vegetation patterns (Figure 8C) reveals two additional important borders. These are the ecotones between closed young stands and open stands and the ecotone between open stands and lichen deserts where the development of forests is absent or incipient.

In sites where recovery has been more rapid, only 20–30-year old trees with well-developed open crowns occur. This zone is shown on the map by a shading #13, occupying intermediate sites between open forest stands and desert.

Especially successful recovery has occurred in river valleys, where a complex mosaic of willow forests and lush herb vegetation has recovered nearly completely. Meadow colonization by woody forest vegetation occurs, but is often arrested by repeated flooding. The colonization of forests into higher elevations also is occurring at a slow rate. Both birch and alder forests have not reached their climatically determined elevation limits. Depressed tree lines are a common feature of young volcanoes (Lawrence 1938; Ohsawa 1984).

Discussion

Differential damage

Pumice deposits more than 30 cm severely damaged shrub, herb, and moss-lichen communities. The presence of these growth-forms on Transect B#1 to #6 reflects post-eruption succession. Studies of the moss-lichen layer on 20th Century eruptions of Kamchatka volcanoes (i.e., Kluchevskoy 1932, 1938; Avachinsky 1945; Bezymianny 1956; Shiveluch 1964; and Tolbachik 1975) have confirmed the general pattern that increasing deposit depth impacts successively larger plants. While the tree canopy may survive moderate depositions, broad forest canopy decline is observed as a result of drying out. For example, Grishin (1996) found that 8% of the stand had died with only 3 cm of tephra, while 20% died with 10 to 12 cm of tephra ten years after the Tolbachik eruption. Tephra deposits of over 55 cm, from the February, 1945, eruption of Avachinsky volcano killed saplings and seedlings, but many adults survived (Grishin pers. obs.).

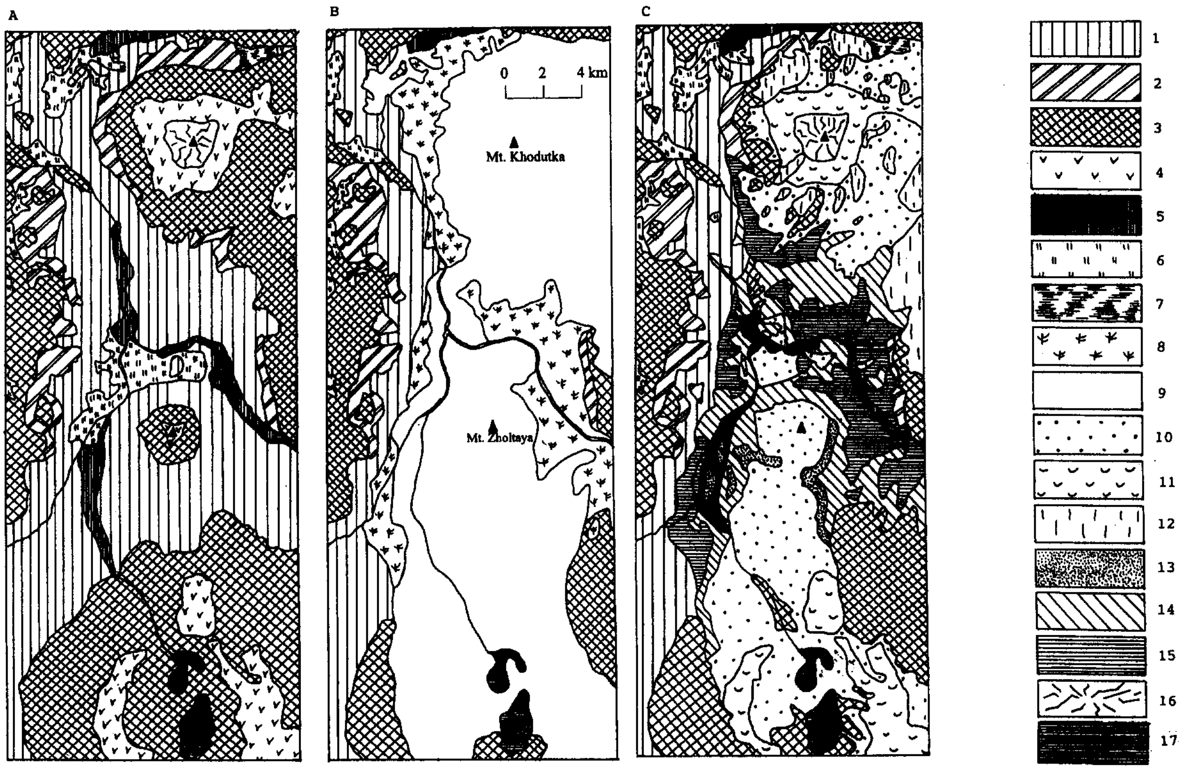

Figure 8. Portions of vegetation maps of the study area. A -potential vegetation (before 1907); B, disturbed vegetation (a few years after eruption); C, modern vegetation. 1, *Betula ermanii* forest; 2, *Betula ermanii-Alnus kamtschatica* subalpine complex; 3, *Alnus kamtschatica* thickets; 4, high-mountain vegetation; 5, river valley forest; 6, meadows with shrubs on level sites in the forest belt; 7, moist *Calamagrostis-Carex* spp. meadow; 8, pumice desert; 9, pumice desert with scattered surviving trees; 10, pumice desert with lichen cover; 11, pumice desert sparse sub-alpine plants; 12, complex of mountain meadows with *Alnus kamtschatica* thickets; 13, pumice desert with lichen cover and isolated birches; 14, open young *Betula ermanii* forest with dwarf shrubs-lichen cover; 15, closed young *Betula ermanii* forest with isolated mature trees that survived the eruption; 16, nival belt; 17, lakes.

Early colonization

Based on observations of more recent eruptions outside Kamchatka (e.g., Griggs 1933; Eggler 1948; Heath 1967; Ball & Glucksman 1975; Riviere 1982; del Moral 1983; Tsuyuzaki 1987; Dale 1989; Burnham 1994), colonization on Ksudach began soon after the eruption and proceeded under diverse conditions. The sterilizing effects of the blast and deep deposits of acid, sterile pumice precluded immediate colonization. Not all taxa began successful colonization simultaneously. Hultèn (1974) reported only isolated herbaceous vascular pioneers, and scattered mosses 15 years after the eruption, but did not report lichen crusts. We assume that there was soon a significant rain of seeds, spores, pollen, and insects that began to ameliorate these nutrient poor habitat (e.g., Edwards 1988). As on other volcanoes (e.g., del Moral & Wood 1993), rain and weathering (e.g., Timmins 1983) improved substrate conditions, increased pH, and helped to facilitate succession and the successful establishment and spread of the lichens that now dominate the pumice desert. Erosion may have limited or inhibited colonization, but it also may have created microsites favorable for establishment (cf. Eggler 1948; Clarkson & Clarkson 1983; del Moral & Bliss 1993). Early colonists may also have facilitated subsequent colonists by altering soil conditions (Hirose & Tateno 1984).

Stages of succession

As defined by Clements (1916), primary succession is initiated in the absence of locally produced organic matter. Examples include tephra deposits, lavas, glacial moraines and sand dunes. In contrast, secondary succession occurs after incomplete destruction of the biota, as after wildfires or the cessation of farming. The transition between these recognized succession types is frequently blurred. Miles (1979) considers some successions to be intermediate, based on the presence of low, but inadequate organic matter. We consider intermediate successions to occur when patches of primary succession stages are intermixed with secondary stages (cf., Vitousek & Walker 1987). In our case, the secondary stages themselves could be considered intermediate, since they are developing on poorly developed soils and since each growth form has differential access to resources.

Disturbances may not eliminate any species, only severely reducing the biomass. After such disturbances as chaparral fire (Christensen & Muller 1975), all species survive and soon begin recovery. Recovery is not succession, though there may be a superficial resemblance. The distinction between secondary succession, which requires the colonization of at least some species, and recovery is also indistinct. In this study, all three types of response to disturbance occur and we have been able to define the transitions in terms of pumice depth and, therefore, to map the distribution of each type.

Within the heavily impacted zone, only disintegrated birch stumps recall the prior forest. Buried soils with a seed bank could not contribute to recolonization, except near streams. There was no biological legacy where pumice deposits exceeded 70 cm, which defines the zone of clear primary succession. These stages are described more fully:

Stage 1

Based on Hultèn's (1974) descriptions, the *Pioneer Herb Stage* was characterized by scattered individuals of wind-dispersed species such as *Chamerion angustifolium, Lerchenfeldia flexuosa,* seedlings of *Betula ermanii, Pennelianthus frutescens,* and *Polytrichum juniperinum.* Less commonly, species such as *Salix* spp., *Anaphalis margaritacea, Minuartia macrocarpa, Pyrola minor, Poa malacantha, Stellaria eschscholtziana,* and *Saxifraga merkii* occur. Stage 1 developed sporadically within the first decade. Based on direct observations by other workers on other volcanoes, we assume that initial colonization was concentrated where some ameliorating factor occurred. A similar stage occurs in the cone (450 to 500 m a.s.l.) where a barren fell-field of these and other species occurs in the absence of a lichen layer.

Stage 2

A *Lichen stage* develops during the second to third decade as lichens colonize. Large areas remain dominated by this stage (Figure 8C). Lichens remain absent in exposed sites due to desiccation and erosive winds. Dominants include *Stereocaulon grande, S. vesuvianum* and *Cladonia macrocerus.* We speculate that these lichens are capable of inhibiting pioneering vascular plants on this particular pumice deposit indefinitely.

Stage 3

The rate of development in the *Woody Colonization stage* is dictated primarily by deposit depth and secondarily by landscape factors. In shallow deposits, this colonization commences within 20 years. The first individuals of wind dispersed woody plants such as *Betula ermanii, B. kamtschatica, Alnus kamtschatica* and *Salix arctica* invade. The presence of plant cover and vertical structure may attract animals. Common in this stage are zoochoric species such as *Pinus pumila* (nutcracker, *Nucifraga caryocatactes*), *Empetrum sibiricum* (many birds and the brown bear, *Ursus arctos*), and several herbs dispersed by hares (*Lepus timidus*), as well as wind dispersed species such as *Lerchenfeldia flexuosa.* All of these species seem to establish within a matrix of closed lichen cover. Colonization is also facilitated by features such as swales and remnants of dead trees. In the early stages of colonization, particularly in Zone I, dwarf shrubs dominate the colonization. The few birch plants are solitary, dwarf saplings of *B. kamtschatica* that suffer from drought, wind abrasion, browsing by hares, acidity and low soil nutrients. Though small, their root systems may be extensive and ultimately contribute to soil development. These small trees are unstable and are frequently toppled by the wind, thus baring the roots, further contributing to soil organic matter.

Stage 4

The *Consolidation stage* develops at different rates, depending on local site quality, and so may be found intermixed with stages 2 and 3. Pumice deposits where we found this phase after 87 years were less than 30 cm. The tree and shrub canopies become dense, and ground heterogeneity and overall ground layer light levels are reduced. White birch declines and lichen patches become reduced in dominance and diversity. True forest understory herbs become more common and subshrub synusia, including *Trientalis europaea,* *Lycopodium annotinum*, and *Maianthemum dilatatum* become common.

Stage 5

The *Sub-climax stage* requires at least 150 years to develop. We observed it only where pumice deposits were thin. We infer that sites now supporting sub-climax vegetation were not substantially impacted in 1907, but are recovering from more intense impacts of the 1640 eruption. This stage is characterized by canopy closure, significant mortality in younger age classes, and development of typical old growth conditions. To reach a normal climax stage in this region may require over 2000 years of undisturbed development, and several generations of stone birches. This would permit normal soil development and time for rarer or poorly dispersed species to colonize.

Probability of stage transition

The five stages form a complex pattern and often occur in close proximity. They are influenced by topographic features, residual organic matter, erosion, differential colonization rates, and differential survival and growth rates. On thinner deposits colonizing birches may reach buried soils to accelerate succession. Primary stages do not form distinct zones where tephra depth is intermediate. Rather, along an east to west transect starting in deposits over one meter, stages do repeat, with later stages gradually increasing in size and frequency, and earlier stages gradually diminishing in size and frequency. Strictly, we sampled a toposequence, not a chronosequence.

Each site of each stage naturally has experienced different histories and it is unlikely that sites we describe in earlier stages will develop to closely resemble later stages. Space-for-time substitutions, particularly in early stages of primary succession (del Moral & Bliss 1993), pose well-known difficulties. We cannot provide a time frame for when lichen deserts will develop forest vegetation. However, since most of Kamchatka has been covered by pumice or lava during the Holocene, and these landscapes are not dominated by pumice deserts, we conclude that eventually physical amelioration and dispersal will lead to vegetation structurally similar to the surroundings. Because the surrounding forests are the most likely source for colonists, the vegetation that may eventually develop on these pumice deserts will probably resemble adjacent forests. The five stages we identified above are *proposed successional* stages. We do not believe that they are Clementsian seres, only that they represent the most probable course of general vegetation development.

A realistic scenario for development in deeper portions Zone II is as follows. Barren pumice is colonized by lichens. Environmentally more favorable sites, for example where there is rich organic matter from decomposing logs, wind-dispersed species of trees and herbs can establish more quickly (cf. Frenzen et al. 1988). This process commences earlier where the pumice thickness is least. The process is self-augmenting. Trees established in buried soil ameliorate the surface microclimate and deposit nutrient-rich litter on the surface Trees attract birds that import seeds of such taxa as *Empetrum*, *Rubus*, *Spiraea* and *Vaccinium*. The development of an understory accelerates the colonization and expansion of herbs and mosses.

Length of succession on pumice

Some of the surrounding landscape not impacted by the 1907 eruption was devastated by the 300 AD eruption. During the intervening 1600 years, only about 12 cm of soil were formed. This is comparable to soil development during 1500 to 2000 years on *a'a*-lava of Tolbachik volcano (Grishin 1992) under stone birch.

Thin soil implies that ecosystem development has not equilibrated and provides insight into the gradual pace of the current primary succession. Lichens continue to dominate large portions of the region. Here, the surface substrate drains rapidly and dries out frequently. The surface is often unstable, poor in nutrients and acidic. Finally, lichens may physically or biologically inhibit colonization by vascular plants for many decades.

Succession during the first century in this region can result in a closed xeromesophyte dwarf shrub-herb vegetation as described by Hultèn (1974), with meadows on alluvial terraces. *Pinus pumila*, forms a continuous cover on Tolbachik (Grishin 1994), but it occupies a subordinate position in the Ksudach region. During this period, drought and poor mineral nutrition preclude establishment of either birch species. This condition can be seen today in Zone II: 50 years-old birches growing on the 1907 pumice are nutrient stressed (despite growth into buried soil) with many dead or dying shoots. During an extended period of development, exceeding 1000 years, this form is gradually changed into a normal growth form and soil profile. The sizes, duration of life and number of trees all increase gradually and the last succession stage begins - the formation of climax forest communities.

Initially, the closing of the stand results in *Betula kamtschatica* being superseded by *B. ermanii*. To form climax forest communities with uneven age tree stand requires advanced vertical and synusial structure, typical floristic composition and an accordingly advanced soil component. This all would required several additional centuries of succession. Thus, the duration of primary succession may extend over 2000 years in this harsh climate.

Survival of vegetation

Antos & Zobel (1985a, b) found that different life forms were differentially affected by similar tephra depths, and that mosses and low herbs were slow to recolonize (Antos & Zobel 1986). Pfitsch & Bliss 1988 determined experimentally on Mount St. Helens that 20 to 30 cm of pumice was sufficient to kill most ground layer vegetation.

These modest thicknesses also result in tree decline, but not elimination. On the southern slopes of Asacha volcano, trees survived over 30 cm of deposits and on Avachinsky volcano we determined that large trees survived after tephra deposits of 55 cm, though younger trees were killed by thinner deposits. A similar differential effect occurred on the Ksudach transect. Very large trees continued growth for several years, even after 1.5 m of deposits, though they eventually died.

Landscape considerations

In many places there is significant heterogeneity on an intermediate scale (tens of meters) that results in sites favorable for tree colonization to be adjacent to unfavorable sites. Unfavorable sites develop through primary succession slowly. Even in Zone II, the lichen stage remains dominant on such sites. Succession on favorable sites has progressed to include young birch stands. In the most favorable sites on Zone II to Zone III transition, self-thinning is beginning. Through it may require several tree generations (and probably, not less than 400–500 years), the uneven aged climax forest will be restored.

Unfavorable sites in Zone II, show few signs of forest development. We predict that succession observed here will eventually occur in Zone I. Alternatively, a treeless xeric vascular plant meadow may develop and be retained in a quasi-stable state for decades. The border between Zones I and II may gradually move towards deeper deposits as newly settled birches survive and reach buried soil. The rate of advance will decline with pumice thickness if it has not already stopped. Further colonization will then require significant amelioration of the substrate, which would occur on a geomorphologic time scale.

Conclusions

Pumice deposits from the 1907 eruption of Ksudach Volcano ranged from over 4 m to less than 30 cm to impact over 1800 km^2 of birch forest. Of this, total destruction occurred on at least 124 km^2. Only a few survivors were found in an additional area of 71 km^2, and so about 200 km^2 were effectively destroyed.

Much of the complexity in succession and recovery patterns results from the different response of different life forms to the same depth of pumice deposit. The moss layer was eliminated by 10 cm deposits, the herb-dwarf shrub layer by deposits of 30 cm, and the tree layer by deposits over 70 cm. Tree survival in deposits between 30 and 70 cm was sporadic, and at greater depths only very rare individuals persisted for several years. Pumice killed all vegetation where deposits exceeded 1 m.

No trees survived within Impact Zone I since deposits exceeded 1 m. Succession has proceeded from the early herbaceous pioneers to Stage 2, the lichen desert stage, where it appears to have ceased. Subalpine fell-field vegetation in the caldera is structurally similar to that described by Hultèn (1974). Very short growing seasons and instability may have prevented further successional development.

Impact Zone II is a complex ecotone between Zones I & III where the distinction between primary and secondary succession blurs. Zone II includes deposits that range from 30 to 100 cm in depth, differentially affecting the survival of growth forms, but other factors further complicate the transition. At least three primary succession stages co-occur, though some examples of Stage 4 may be secondary succession, initiated on a site with some surviving birches. Lichen desert (Stage 2), dwarf shrub/herb (Stage 3) and closed birch forest (Stage 4) interdigitate in response to local topography, pumice depth, and chance survival or persistence of trees after the eruption. Some sites in this zone are undergoing primary succession while adjacent ones are undergoing secondary succession.

Zone III occurs where pumice deposits were thin and only mosses and some of the herb/shrub layer may have been eradicated. Trees and tall shrubs generally survived well. Here secondary succession has dominated recovery. In thinner deposits of Zone III, damage may not have eliminated any species in 1907, so that the observed vegetation is merely recovering from perturbation and the forest (Stage 5) is pre-climax. We infer that a true climax, vegetation in equilibrium with a well-developed soil, will require up to 2000 years.

This study demonstrates that the conventional dichotomy between primary and secondary succession can be arbitrary (cf. Miles 1979), and that the distinction between secondary succession and vegetation recovery can blurr. Vitousek & Walker (1987) adopted the concept of intermediate succession. Their rationale is based on resource availability and is valid. In this study, we demonstrate that intermediate successions may also be based on differential survival and be spatial in nature. Within Zone II, a mosaic of primary and secondary succession occurs that represents a spatially intermediate succession. We also demonstrate that recovery from minor disturbance, not secondary succession, is the antithesis of primary succession.

The succession rate after pumice deposition is affected by several interacting factors. Deposit depth determines the degree of plant survival (if any), whether or not trees remained standing (alive or dead), the ability of plants to colonize, depth to resources in old soil, local meso-topography, the rate of abiotic facilitation, and the distance to sources of colonists. The resulting landscape pattern includes primary succession in several stages, secondary successional stages intermixed with later primary stages, homogeneous secondary stages, and recovering forests. A transect along an axis of declining pumice depth is not strictly a chronosequence. Rather, more developed vegetation exemplifies how immature vegetation may develop structurally. Different degrees of resource availability and contingent factors make it improbable that sites currently in Stage 2 will develop into replicates of later stages.

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