Chapter 5. P. 137-160, in Ecosystems of Disturbed Ground, L. R. Walker, editor.

Volcanic Disturbances and Ecosystem Recovery

Roger del Moral [1] and Sergei Yu. Grishin [2]
[1]University of Washington, Department of Botany, Box 355325, Seattle, WA 98195-5325;
[2]Institute of Biology and Pedology, Russian Academy of Sciences, Vladivostok 690022 Russia

INTRODUCTION

Volcanic eruptions are major natural disturbances with varied and complex consequences. Recent studies of how plants colonize newly created volcanic surfaces already have begun to clarify our understanding of succession. Because volcanoes create disturbance mosaics, it is imperative that we more fully understand the biotic responses. The 1883 eruption of Krakatau captured the world's imagination and initiated widespread and intensive studies of succession following volcanic events (Docters van Leeuwen, 1929). In this chapter, we review the state of our knowledge of succession after volcanic events and attempt to develop a general understanding of the mechanisms that affect the development of volcanic landscapes.

Volcanic eruptions punctuate the geological record and human history. The Santorini, Greece, eruption (ca. BC 1470) probably destroyed Minoan civilization, and the collapse of the Maya is attributed to climatic impacts caused by eruptions of El Chichón in AD 900 and AD 1250 (Anonymous, 1993). Indirect volcanic effects also destroy. When Iceland's Laki fissure spawned the largest volcanic episode in recorded history (AD 1783), Icelanders starved, summer failed, and European markets crashed (Gratten and Braysay, 1995). Despite monitoring warnings, ash and mud flows from the Mount Pinatubo, Philippines eruption in 1991 that killed 700 people, displaced 500 000 villagers, closed a U. S. air base, and eliminated 40 000 jobs. Ash veiled the planet and sulfuric acid reduced the ozone layer thickness. Altered weather patterns led to extreme floods of the Mississippi River Valley in central U. S. A. (Tizon, 1996).

Volcanoes occur along tectonic plate margins and within plates (Francis, 1993). There are currently about 550 active land volcanoes. Volcanoes associated with ocean plates occur in the Maldives and Réunion in the Indian Ocean, the Azores in the Atlantic, and Hawaii in the Pacific. Continental plates once produced floods of lava from fissures (e.g., the Indian Deccan plateau), but today most active volcanoes are along plate margins. Diverging plates spawn open-ocean volcanoes such as Surtsey, Iceland, or rifts, as in East Africa. Converging plates spawn huge earthquakes and volcanism, such as routinely occur along the Pacific Basin Ring of Fire.

This chapter describes typical volcanic disturbance regimes and their ecological consequences. How does the biota respond to these impacts? We will emphasize disturbance regimes, recovery mechanisms, and recovery rates.

VOLCANIC IMPACTS

New volcanic surfaces are created by lava, pyroclastic flows and air-borne deposits (tephra), debris flows, lahars, and avalanches (See Table 1 for definitions). Primary succession is associated with lavas, pyroclastic flows, and most lahars, but may occur on any material. Secondary succession occurs most frequently on thin tephra and some lahars because some biota or soil may survive (Halpern et al., 1990; Grishin et al., 1996). Volcanic gases create strong, but local, impacts. Once the gases subside, primary succession usually results, modified by the nature of the substrate in question (Fig. 1). Climate, substrate type, and landscape factors all affect the recovery rate.

Volcanism is associated with earthquake zones, being produced by the same fundamental forces. Tsunamis are a consequence of both. These sea waves are usually spawned by coastal earthquakes, but a devastating tsunami resulted from the collapse of the Rakata cone of Krakatau (1883) and killed more humans than the eruption itself (Francis, 1993). The effects of earthquakes and tsunamis on an ecosystem may be ephemeral or persistent. Space does not permit a review of these effects here, but the consequences share much with the principles developed in this chapter.

Lava

Lavas cover much of the earth, but recent large flows are rare. Lavas are viscous and flow slowly—thus they are the least dangerous volcanic event. Molten lavas may ooze from fissures, vents, hot spots (e.g., Réunion and Hawaii), and rifts (e.g., East Africa) to form new land. For ecological purposes, lavas can be divided into those forming a mass of small, loose, irregularly shaped blocks (known by the Hawaiian term *a'a*), smooth, ropy lavas (known by the Hawaiian term *pahoehoe*), large angular blocks, and domes found within craters.

Pyroclastic Rocks

Any solid material forcibly ejected from a volcano is spawned amid great heat and pressure. These pyroclastic (Greek = fire-broken) events are variously classified (cf., Chester, 1993; Francis, 1993). Forms leading to distinct ecological results are noted below.

Pyroclastic Flows

Pyroclastic flows include any incandescent mixture of gas and solids produced by explosive eruptions (Francis, 1993).They move rapidly along the ground (>100 km hr^{-1}). Pumice flows, the most common, leave behind deposits called ignimbrites. *Nuées ardentes* are less common and include a wide variety of solid materials, dominated by pulverized rocks. Scoria (Greek = refuse) may also be found in deposits from such flows.

Air-borne Pyroclastics (Tephra)

Air-borne pyroclastic materials are the most widespread volcanic disturbances. Upon falling to earth, they are called tephra (Greek = ashes). Tephra deposits are size-sorted and, at any distance from a volcanic source, are homogeneous. Size categories vary, but fine material is called ash, intermediate stones are termed *lapilli*, and large blocks are called breccia, blocks or bombs. Larger tephra fragments are composed of scoria or pumice. Scoria is coarse, fragmented, and dense. It forms slopes near the angle of repose. Pumice is a low density, frothy rock that floats in water.

Lahars & Debris Flows

Lahars (Indonesian = mud-flow) are cool, unsorted, slurries of rocks, mud, and vegetation with > 50% water when emplaced. Debris flows are less fluid (< 50% water) and usually more heterogeneous. Both can be spawned by volcanoes (cf., Gecy and Wilson, 1990). Normally, they result from rapidly melting ice and snow during an eruption. Lahars and debris flows can include heterogeneous material from many elevations and ages, so it is difficult to generalize about their composition. Avalanches, which are primarily solid, are even more heterogeneous.

DISTURBANCE REGIMES.

Disturbance regimes profoundly affect vegetation and have been discussed thoroughly by Pickett, et al. (1987), Walker and Chapin (1987) and Chapin et al. (1994) . Volcanic impacts normally are either so intense that ecosystem development starts on an abiotic substrate, or so infrequent that the term “regime” is inappropriate. Volcanoes are not associated with any vegetation type (as is fire), climate (as is drought), biotic interaction (herbivory), or chronic event (hurricanes). Active volcanoes occur from the arctic to Antarctica. Together, geographic diversity, variations in magnitude, and the variety of responses blur global patterns. Individual eruptions do, however, vary in scale, frequency, magnitude, and severity and volcanic landscapes display community-level patterns related to these variations. Below we review how some aspects of disturbance regimes affect ecosystem recovery and structure.

Scale

Volcanic events vary widely in scale. Lava flows are usually quite localized, usually flowing less than 10 km (Wadge, 1983). Pyroclastic flows cover hundreds of km^2, tephra covers thousands of km^2, and lahars may descend for many kilometers from the volcano. Scale affects the type of colonists and the rate of recovery indirectly. Isolated recovering vegetation is dramatically different from comparable vegetation near intact vegetation. Isolation led to the dominance of wind-dispersed species on Mount St. Helens (del Moral and Bliss, 1993).

Table 1. Definitions of major types of volcanic materials mentioned in text. Materials which have little direct impact on succession are not listed. Definitions follow Francis (1993).

Term	Definition
Lava	molten rock (magma) formed of basalt, andesite, dacite, or rhyolite, rocks (in order of increasing silicate content).
a’a	basalt forming a jumble of irregular cindery blocks; low in silicates
pahoehoe	basalt forming smooth, glossy surfaces; low in silicates
block lava	formed of large, smooth-sided blocks; may form domes; usually andesitic
domes	viscous intrusions found in craters, commonly of dacite or rhyolite.
Pyroclastic rocks	material ejected in solid fragments
Pyroclastic flows	an eruption cloud consisting of gas and very hot solids driven by gravity and hugging the ground; include surges and *nuées ardentes* (incandescent mix of ash and large materials); form deposits called *ignimbrites*
Pyroclastic falls	any solid material returning to earth after eruption into the air, called *tephra*
Ash	tephra less than 4 mm in size
Lapilli (little stones)	tephra between 4 and 32 mm in size
Blocks (bombs)	tephra greater than 32 mm in size
Scoria	fragmented, cindery textured pyroclastic material, whether from falls or flows of any sort
Pumice	frothy, low density pyroclastic rock deposited by flows or falls
Lahar (mud-flow)	all water-transported debris flows, regardless of origin, with > 50% water
Debris flow	a large, wet mass of material falling under the force of gravity, with <50% water
Avalanche	a mass of nearly dry material falling under the force of gravity

Scale effects are attenuated in secondary succession. For example, tephra impacts are widespread, but shallow deposits do not eliminate all vegetation. Destroyed habitats recover more quickly if the impact is small, while areas with large-scale damage can recover quickly if there are survivors. For example, the recovery rate of the Kautz Creek lahar on Mount Rainier (Frenzen et al., 1988), a long, narrow deposit surrounded by intact vegetation, was much more rapid than that of the broad Muddy River lahar.

Frequency

Volcanoes normally have long intervals between major eruptions, though some, like Sakurajima, Japan (Tagawa, 1964) and Tolbachik, Kamchatka (Grishin, 1992), erupt frequently. Return intervals of 200-300 yr reduced species diversity and endemism on Mount St. Helens, which lacks endemics (del Moral and Wood, 1988). Mt. Vesuvius, Italy, has 18 endemics in a flora of over 300 species (Mazzoleni and Richardi, 1993), and has had only localized impacts since AD 79.

Magnitude and Severity

The magnitude of a volcanic event can be described by volume or intensity, while severity describes its biotic impact. Lavas are of such magnitude and pyroclastic flows of such severity that survival is rare. Lahars and debris flows rarely permit survival, but along their margins and, serendipitously, in isolated pockets, some organisms survive. Distance attenuates the magnitude of pyroclastic flow events and tephra deposits become thinner, so that there is differential survival of the biota.

Lahar deposits are heterogeneous. Experience on Mount St. Helens (del Moral, 1983; Franklin et al., 1985) suggests that rhizomatous species are more likely to survive. However, a variety of species survive on root wads and soil blocks, so survival on lahars is capricious. Recovery rate should be proportional to the ratio of topsoil to total volume which serves as an indicator of the potential for residual species and debris to end up near the deposit surface.

Whereas blast effects favor plants such as hemicryptophytes and geophytes that grow at or below ground level, tephra impacts can be particularly harmful to mat formers, mosses, lichens, low herbs, and species lacking rhizomatous growth or incapable of growing through thick deposits (Antos and Zobel, 1985a, 1991, 1992; Grishin et al., 1996). Lateral eruptions in which directed pyroclastic blasts are followed by a deep tephra rain devastate the biota.

Plant responses to a given impact depend on their size and growth form. At a sufficient distance from the cone, directed blasts, and pyroclastic events will most severely impact taller vegetation. Ground layer and juveniles may be protected by topography, while buried structures are protected by soil. Dormant plants will be more likely to survive, and a snow pack will enhance survival. Species with seed banks are more likely to dominate recovering vegetation.

Stress

Each volcanic habitat imparts different degrees of stress. Lavas break down slowly and present huge colonization challenges, so that microsites that collect moisture, trap debris and offer refuge are crucial (Lohse, 1995). In the tropics, ferns often form a major group of colonists (Tagawa, et al., 1985), while flowering plants initially colonize dry tropical habitats. Lichens colonize exposed surfaces over a wide range of temperatures. Early succession in cold climates is dominated by cryptogams, especially N_2-fixing cyanobacteria (Griggs, 1933). Mosses dominate wetter climates, lichens drier ones. Vascular plants may pioneer in cracks, or invade following physical amelioration.

Pumice and scoria are drought-prone and nutrient-poor. They weather to provide better growth conditions, but they dry quickly and may be unstable. Steep slopes remain bare where drought and chronic erosion prevail (Day and Wright, 1989). Fig. 2 shows scoria habitats at least 2000 yrs since their formation in Idaho. Very cold, windy winters and summer drought combine to prevent rapid succession on these substrates (Day & Wright, 1989).

Tephra is the most widespread volcanic deposit and under ideal conditions can be colonized quickly. Deep tephra will be colonized at rates related to the local climate. Wet habitats on Katmai, Alaska, required 3 yr for colonization (Griggs, 1919), while moist uplands were colonized more slowly by liverworts, then mosses and finally willows, grasses and shrubs (Griggs, 1933). In contrast, dry tephra on Ksudach, Kamchatka, floristically comparable to Katmai, was colonized by lichens that were still dominant after 90 yr (Grishin et al., 1996).

On any substrate, the overall climate will ameliorate or accentuate stress. In temperate and tropical regions, available moisture is most likely to control the rate of succession. Along an elevation gradient of the same substrate, for example lava or lahars, the succession rate normally increases with increasing moisture, until decreasing temperatures curtail the growing season (Chevennement, 1990; Tagawa et al., 1994). Aplet and Vitousek (1994) demonstrated that the biomass accumulation rate on Hawaiian lavas was correlated to precipitation. In cold regions and at high elevations, temperature is more likely to be correlated with the rate of succession.

Patchiness

Habitats may be heterogeneous on either a local or a landscape scale. New deposits rarely result in a patchy landscape, though they may skip over or partially damage vegetation. Differential protection by snow, topographic irregularities, rock walls, and deep canyons may all shelter the biota from tephra deposits, lava flows, lateral blasts, and pyroclastic flows. Even when surviving species cannot colonize surrounding barren landscapes, birds that do introduce suitable plants may be attracted to such residual sites.

Tephra can extinguish habitat heterogeneity by filling in cracks to form smooth surfaces. Subsequent erosion can create new opportunities for colonists (Collins et al., 1983; Kadomura et al., 1983; Suwa and Okuda, 1983; Tsuyuzaki, 1994). Local heterogeneity is enhanced by differential physical amelioration and by the establishment of early pioneers that facilitate subsequent establishment by other species (cf., Blundon et al., 1993). Inhibition of colonists by the initial invaders also can increase the variability of habitat conditions (Clarkson and Clarkson, 1983; Wood and Morris, 1990). As a few dominant species create homogeneous canopy cover, site patchiness is significantly reduced, leading to lower diversity and to successional changes (del Moral, pers. observ. on Mount St. Helens, Mt. Fuji, and Ksudach volcano.)

RATES OF SUCCESSION

The rate of succession varies with the type of the impact, climate, and geographic factors. First we will discuss the effects of substrates, then the effects of climate on a given substrate.

Substrate Effects

Table 2 lists representative papers that address primary succession on volcanoes.

Lavas

Succession on lavas is usually slow, but the type of colonizers vary greatly. Typically there are two juxtaposed successions. On flat surfaces lichens (Eggler, 1941; Cooper and Randolph, 1953) establish and slowly form soil. In cracks, dust and organic matter accumulate and moisture collects. In warm, moist climates, vascular plants can establish more quickly. Tagawa (1964, 1965) described juxtaposed successions on lavas on Sakurajima, Kyushu, Japan, dating from 1476, 1779, 1914 and 1946. Seed plants rapidly colonized crevices and dominated the 1914 flow, and cryptogams dominated the smooth surfaces. Sakurajima continues to eject tephra that covers the lava, the climate is warm and rainfall well-distributed, so soil formation is relatively rapid and succession relatively quick. Fig. 3 shows young *Pinus thunbergii*, *Alnus firma*, and *Ficus erecta* invading the 1914 flow of Sakurajima.

Local biological effects modify colonization rates. The density of safe-sites (microsites favorable for seedling establishment) is crucial for establishment but safe-sites are subject to competition. For example, lava domes on Mt. Tarawera, New Zealand (erupted in 1886) were first colonized in a limited number of cracks by mosses and the mat-forming *Muehlenbeckia axillaris*, thus limiting the invasion by other species (Clarkson and Clarkson, 1983). In contrast, nitrogen fixers can facilitate colonization and accelerate biomass production, thus promoting succession (Hirose and Tateno, 1984; Clarkson, 1990; Halvorson et al., 1991). Microsite availability and dispersal distance are two major factors that affect the rate of succession on lava.

Pyroclastic Flows

There are few studies of succession on pure pyroclastic deposits. On Mount St. Helens, U. S. A., erosion of surges and *nuées ardentes* created heterogeneity and resulted in recovery rates similar to those of pumice. Vascular plants dispersed by wind dominated the early colonists. In contrast, Beard (1976) found that early colonists of *nuées ardentes* on Mt. Pelée, a warmer, wetter site, were dominated by mosses and lichens, but that vascular plants had returned within 60 yr. *Pitcairnia sulphurea*, a rock outcrop pioneer species, dominated these communities, while shrubs occurred only in protected locations. Seed plants with succulent fruits dispersed by birds and bats had also returned within 60 yr (Sastre and Fiard, 1986).

Pyroclastic Falls

Air-fall deposits are usually size-sorted. Lapilli fall near the source. Ash can travel hundreds of km. Ash and sulfuric acid may be injected high into the atmosphere and thus affect climate or ecosystems hundreds of kilometers away (Inbar et al., 1995).

Coarse tephra is inhospitable because it has little water-holding capacity, is extremely nutrient poor, and is unstable. Coarse basaltic tephra formed Surtsey, Iceland, (erupted in 1963; Fridriksson and Magnusson, 1992). In addition to the hostile substrate, Surtsey is so isolated that few disseminules arrive. The limited flora is dominated by bird- and water-dispersed species. Isolation accentuates stress to affect succession on most volcanoes, whether or not they occur on islands.

Climatic stress further affects succession on air-fall deposits. At timberlines with scoria, succession proceeds slowly. On Mt. Fuji, Japan, normal timberline is at 2600 m. Fig. 4 shows an advancing timberline at 2500 m, below the Hoei crater that erupted in 1707. The forest slowly continues its advance, limited by low nitrogen levels, lack of organic matter, instability, lack of germination sites, deep snow, and dispersal (Masuzawa, 1985; Maruta, 1994). Where disturbance has been frequent, timberline successions may lack regionally common species that have limited dispersal (Ohsawa, 1984; Kruckeberg, 1987; del Moral and Wood, 1988a).

Climatic stress also affects the succession rate on pumice deserts that are dominated by lapilli-sized rocks, and are nutrient stressed. One such desert near Crater Lake that is over 6500 yr old (Horn, 1968), has half the species richness and cover comparable to the Abraham Plain pumice desert on Mount St. Helens (del Moral and Wood, 1993a) that is 17 yr old. Less intense drought, thinner pumice, and less isolation contribute to the rapid recovery on Abraham Plain.

Succession on scoria cones is slower than on fine-textured pyroclastic materials, but can be accelerated by erosion. Eggler (1948) noted that erosion of the cone of El Parícutin (erupted in 1943) in Mexico facilitated seedling establishment by creating safe-sites and by removing tephra (cf., Riviere, 1982). However, for the buried seed bank to emerge, nearly complete erosion was required. Eggler (1959, 1963) later determined that removal of tephra by water and wind had permitted recovery to be dominated by surviving seeds and plants. By 1977, there

Table 2. Summary of major papers dealing with common substrates on different volcanoes. Note: Ash is fine tephra, lapilli is coarse tephra.

Volcano or Area	Impact Type	Authors (Year)
Galápagos Islands	Lava	Hendrix (1981)
Hawaii	Lava	Atkinson (1970); Eggler (1971); Drake and Mueller-Dombois (1993); Aplet and Vitousek (1994); Karpa and Vitousek (1995); Kitayama et al. (1995)
Kekla, Iceland	Lava	Bjärnason (1991)
Krakatau, Indonesia	Lava	Tagawa et al. (1985); Whittaker et al. (1989); Tagawa (1992); Partomihardjo et al. (1992).
La Réunion, Mascarene Islands	Lava	Chevennement (1990)
Papua New Guinea	Lava	Taylor (1957)
Sakurajima, Japan	Lava	Tagawa (1964, 1965)
Mt. Tarawera, New Zealand	Lava, Scoria	Clarkson and Clarkson (1983); Timmins (1983)
Mt. Tolbachik, Russian Far East	Lava; Tephra	Grishin (1992, 1994)
Mt. Kula, Turkey	Lava	Oner and Oflas (1977)
Vesuvius, Italy	Lava	Mazzoleni and Ricciardi (1993)
Mount St. Helens, U. S. A.	Lateral Blast	Franklin et al. (1985); Halpern et al. (1990)
Mt. Lassen, U. S. A.	Lahar	Heath (1967)
Mt. Ontake, Turkey	Lahar	Nakashizuka et al. (1993)
Mt. Rainier, U. S. A.	Lahar	Frenzen et al. (1988)
Mount St. Helens U. S. A.	Lahar	Halpern and Harmon (1983); Dale (1989, 1991)
Mt. Taranaki, New Zealand	Lahar	Clarkson (1990)
Mt. Fuji, Japan	Pumice, Scoria	Ohsawa (1984); Masuzawa (1985); Nakamura (1985)
Mount St. Helens U. S. A.	Pumice, Pyroclastic flows, Lahars	Wood and del Moral (1987); del Moral (1993); del Moral and Bliss (1993); del Moral et al. (1995)
El Chichón, Mexico	Pyroclastic flows, Tephra	Burnham (1993)
Mt. Pelée, Martinique	Pyroclastic flow; Lahar	Beard (1976); Sastre and Fiard (1986)
Motmot, Papua New Guinea	Scoria	Ball and Glucksman (1975)
Crater Lake, Oregon U. S. A.	Scoria, Lapilli	Jackson and Faller (1973); Horn (1968)
El Parícutin, Mexico	Scoria, Lapilli, Ash	Eggler (1948, 1963); Rejmanek et al. (1987)
Surtsey, Iceland	Scoria	Fridriksson and Magnusson (1992)
Mount St. Helens, U.S.A.	Ash	Antos and Zobel (1985a, c, 1986); del Moral (1983; 1993); del Moral and Bliss (1993); Zobel and Antos (1986)
Kyushu, Japan	Ash	Tagawa et al. (1994)

were 39 vascular plant species and 20% vegetation cover, mostly due to residual species (Rejmanek et al., 1987).

Among classic studies of succession on ash is that of Griggs (1933), who followed recovery from the Katmai, Alaska (1912), eruption. Previous papers by Griggs described hot lahars (1918a), recovery of buried vegetation (1919), and recovery on thinner deposits (1918b). Griggs demonstrated that deep deposits precluded emergence of survivors, so only long-distance dispersal could initiate succession. The cool, wet climate permitted pioneering leafy liverworts to form turf, and these turfs facilitated the colonization of mosses, willows, grasses, and forbs.

The season of deposition contributes to determining the degree of damage and survival (Antos and Zobel, 1982). Where snow protected vegetation during the May 1980, eruption of Mount St. Helens, damage to the understory from ash fall was significantly less and recovery significantly more rapid than where vegetation was exposed (Halpern et al., 1990).

Tephra buries and can kill components of existing vegetation, initiating succession. Deep burial precludes survival and primary succession ensues. However, tephra can increase succession rates on lava by providing a rooting material (Tagawa et al., 1994). Thin deposits also may have ephemeral mulching effects that enhance biomass production for some species (Harris et al., 1987; Chapin and Bliss, 1988). Between these extremes, ecosystem recovery patterns are complex. Recovery will be affected by differential survival, erosion and concentration of tephra deposits, proximity to potential colonists, and many other factors.

Lahars & Debris Flows

Lahars can wreak havoc over huge areas (Mizuno and Kimura, 1996). Stabilized, narrow lahars and debris flows can be colonized rapidly from adjacent vegetation (Dale, 1989). Fig. 5 shows the lower Toutle River lahar, Mount St. Helens, after 16 yr. The stabilized margins are densely vegetated by *Salix* spp. and *Alnus rubra*, while erosion continues to scour the banks. The mixture of soil types and rocks provides heterogeneity and potential safe-sites. However, large, high elevation lahars, such as that near Mt. Taranaki, New Zealand (Clarkson, 1990) and on Mount St. Helens (del Moral, 1993), develop slowly due to isolation and climatic stress.

Trees often colonize lahars, provided seed sources are adjacent (Heath, 1967; Frenzen et al., 1988). Fig. 6 shows invasion 28 yr after Kautz Creek lahar occurred. However, on the Muddy River lahar, Mount St. Helens, Halpern and Harmon (1983) found that species richness clearly decreased away from the forest edge. Local diversity was enhanced by stumps, soil clumps and root wads providing seeds, organic matter and safe-sites. By 1995, dense *Alnus rubra* stands had developed at 800 m a.s.l., where conditions were mild and dispersal did not limit invasion. At 1000 m a.s.l., the vegetation remained open and diverse. Unexpected species from higher elevations dominated (del Moral, pers. observ.). Nutrient limitations inhibited conifer growth rates, but *Pseudotsuga menziesii* had become more common. Mosses such as *Racomitrium canescens* did not occur until several years after significant colonization by vascular plants. They are pioneer species only in that they establish on barren microsites.

The importance of residual soil or plant fragments has been observed repeatedly on lahars. Nakashizuka et al. (1993) found that the debris avalanche from Ontake volcano, Honshu, Japan, was colonized by wind-dispersed species, but that residual soil and root fragments accelerated succession. The early dominance of lupines on Mount St. Helens lahars resulted in part from surviving seeds and root fragments (del Moral, pers. observ.).

Tropical lahars and debris flows can recover quickly, but often are colonized by only a few species (cf., Eggler, 1959; Whittaker et al., 1989). Burnham (1993) described hot debris flows spawned by El Chichón in Mexico (1982). Vascular plant diversity was low because vines inhibited the colonization by other vascular plants. Biomass on lahars in temperate climates develops slowly, but diversity recovers quickly (Frenzen et al., 1988; Dale, 1991). This anomaly may occur because on temperate or higher elevation lahars, where physiological stresses often limit productivity, many species still can establish in the relative absence of competition.

Rates

Succession on lava is always slow, but its rate can be affected by surface heterogeneity, subsequent tephra deposits, distance, and by climatic stress. Coarse air-fall deposits permit more rapid development, but the details are affected by site instability and low nutrient status. Succession on ash and ignimbrites may develop rapidly if erosion ameliorates initial conditions. Lahars are composed of older, more mature substrates, so dispersal limitations strongly influence development. The degree of environmental stress can modify the rate of succession on each substrate.

Environmental Stress

Factors that facilitate biomass accumulation during succession will accelerate succession. This rule is apparent on volcanoes since they occur under most combinations of environmental stress. The recovery on two identical volcanic substrates will vary with temperature and moisture conditions. Recovery is rapid in the tropics and slow at high latitude and high elevations. Succession is more rapid in moist climates than in semi-arid ones of the same latitude.

Substrate microtopography will alter local succession rates by affecting environmental stress. Grishin (1992, 1994) described succession on lavas of two Kamchatka volcanoes. Primary succession and soil development are slow on *a'a* lava in this cool, temperate forest region. Initially, herbs such as *Chamerion angustifolium*, *Leymus interior*, *Poa platyantha*, and *Lerchenfeldia flexuosa* colonized fractures, while lichens (*Stereocaulon* spp.) and mosses

(*Polytricum juniperinum*) dominated exposed surfaces. Woody species (e.g., *Populus suaveolens, Salix caprea*, and *Betula ermanii*) were rare during the first 50 yr and remained stunted on 500 yr old surfaces. On 1000 yr old lavas, shallow soil occurs, supporting dense forests of stunted *Pinus pumila*. Gradually, forest communities of *Betula*, *Larix cajanderi*, and *Alnus kamtschatica* develop, and after 2500 yr, the vegetation begins to resemble mature surrounding communities. This succession is at least four times longer than succession described in warm temperate southern Japan (Tagawa, 1964, 1965).

In any given region, on any substrate, moisture availability is crucial. Tagawa et al. (1994) showed that succession on lavas on subtropical islands was more advanced in the cloud layer at 800 m a.s.l. than at the drier 500 m a.s.l. Fernández-Palacios and de Nicolás (1995) found that zonation on Tenerife, Canary Islands, was related to both temperature and moisture along an altitudinal gradient. On Mount St. Helens (del Moral et al., 1995), stable streams and small oases found on pumice developed much more rapidly than in the surrounding uplands. Aplet and Vitousek (1994) found that on Mauna Loa, Hawaii, biomass decreased with decreasing precipitation and temperature. In contrast, Velázquez (1994) determined that temperature was more important than moisture gradients in controlling succession in central Mexican volcanoes, but his study occurred over a small moisture range and a large elevational range.

TYPICAL VEGETATION RESPONSE

Habitats spawned by volcanic eruptions are as varied as any on earth. The nature of colonists, rates of succession, degree of predictability, and similarity to adjacent vegetation all vary widely. Below we discuss some vegetation patterns common to many volcanoes.

Landscape Effects

Timberline Depression

Brown (1994) predicted that any disturbance lowers timberlines from levels predicted by geomorphic and climatic factors. Timberline depression on volcanoes is widespread (Beamon, 1962, near Mexico City; Fosberg, 1959, on Mauna Loa, Hawaii). Clarkson (1990) determined that upper limits of *Weinmania racemosa* forests on Mt. Taranaki, New Zealand, were suppressed and that species diversity was reduced by chronic tephra deposits. Veblen et al. (1977) reported that catastrophic volcanism depressed *Nothofagus betuloides* timberline 100 to 300 m in south-central Chile. Ohsawa (1984) and Masuzawa (1985) both noted that the timberline on Mt. Fuji, Japan, was suppressed. Both indicated that the upward colonization recapitulates succession. These studies also showed that alpine climax species can pioneer lower sites. Reasons for the slow upward forest migration generally include nutrient limitations, poor soil development, substrate instability (Jackson and Faller, 1973), poor upward seed dispersal, wind, snow effects, and inability of tree seedlings to establish in most years.

Reduced Diversity and Turnover

Initial turnover rates on volcanoes appear to be lower than might be expected and gradual accumulation of species is more usual. Their floras are rarely at equilibrium. The best evidence that species richness is reduced on volcanoes comes from studies showing continual species richness increases through time. The accumulation of species and, where data are available, the species turnover are discussed below. Table 3 summarizes representative studies of richness during early succession.

Tagawa (1964, 1965) listed vascular plants found on lavas of four distinctive ages. The youngest was dominated by lichens and mosses, and five vascular species. The 47 yr old flow had 54 vascular species, dominated by herbs, with non-vascular plants at high cover. The 475 yr-old flow supported a late seral forest with 76 species.

Whittaker et al. (1992) summarized changes in the flora of Rakata, Indonesia, during 100 yr. By 1989, there were 397 species, with richness continuing to increase. The warm tropical habitat, habitat complexity, proximity to sources of propagules and Rakata's escape from subsequent eruptions has permitted the flora to develop rapidly and richness continues to increase. Anak Krakatau emerged from the sea in 1930. Bush et al. (1992) recorded 138 species in 1989-91, though a combined total of 157 species have been noted. This relatively low turnover rate (19 species once found, not present in latest survey) occurs despite subsequent disturbances that set back succession. Each restart, has led to different colonization patterns. Turnover here is directly related to volcanic events, not to extinction.

Fridriksson (1987) summarized his work on Surtsey, formed in 1963. Initially, there were two species. By 1986, 24 vascular plant species had been recorded (Table 3), most of them rare. By 1990, 28 species had been recorded, of which 24 occurred in that year (Fridriksson and Magnusson, 1992). Some species had several colonization and extinction events. Surtsey combines elements that ensure high rates of turnover: it is small, climatically harsh, isolated by sea water, unstable, and composed of substrates very low in nutrients and organic matter. Therefore, colonization rates and population densities are low, and stochastic variation is high.

Mt. Tarawera, in New Zealand, erupted massively in 1886 (Clarkson and Clarkson, 1983; Clarkson, 1990). Between 1964 and 1979, species richness increased from 63 to 74, representing 28 colonization events and 17 local extinctions. The richness increase was modest, but there was a substantial increase in cover, primarily from shrubs that expanded as resources accrue. This succession is in a phase of slow species accumulation with modest turnover and gradual expansion of plant cover.

The Kautz Creek lahar described by Frenzen et al. (1988) on Mt. Rainier demonstrated a gradual accumulation of species as well as spread of vegetative cover. Previously encountered species absent in 1980

Table 3. Number of vascular plant species during early development, middle years and the last measurement in a particular study; n.d. = no data available.

Volcano	Reference	Eruption Date	Type of Surface	Age (yr)	Young Surface	Intermediate Surface	Oldest Surface
					Number of Species		
Sakurajima, Japan	Tagawa 1964	1476	Lava	475	5	54	76
Rakata, Krakatau, Indonesia	Whittaker et al. 1992	1883	Mixed	106	24	253	397
Anak Krakatau, Indonesia	Bush et al. 1992	1930	Scoria	60	17-20	45	138
Mt. Tarawera, New Zealand	Clarkson 1990	1886	Lava	93	n. d.	63	74
El Parícutin, Mexico	Rejmanek et al. 1982	1943	Pumice	34	2	17	39
Mt. Rainier, U. S. A.	Frenzen et al. 1988	1947	Lahar	33	17	21	32
Surtsey, Iceland	Fridrickson 1992	1963	Lava/Tephra	27	2	15	24
Mount St. Helens, U. S. A.	del Moral and Wood 1993	1980	Pumice	16	n. d.	21	44
Mount St. Helens, U. S. A.	del Moral, unpubl.	1980	Blasted	16	3	16	27
Mount St. Helens, U. S. A.	del Moral and Wood 1988b.	1980	Lahar	16	5	31	46

were weeds that had been excluded by developing forest cover. Here, turnover is due neither to disturbance nor to biogeographic effects, but to competition among plants, probably for light as well as soil resources.

The record or vegetation recovery for Mount St. Helens includes time series studies in several habitats. The lahar sample is near intact vegetation, so that rapid recovery was expected. Colonists were first encountered in 1982 and by 1994 richness was comparable to that of the adjoining meadow, but cover was much lower (del Moral and Bliss, 1993). Studebaker Ridge was sampled in ten permanent plots starting in 1984. It is within 1 km of potential colonists. Total richness in 1995 and cover were very low. There has been no turnover, only accumulation of species. Sampling on the isolated Abraham Plain started in 1988 on a barren grid (del Moral and Wood, 1993a). There were then 23 species, most of them rare. Only one species had disappeared, while an additional 23 species had colonized by 1996. Cover remained sparse; the mean number of species in 400 plots continues to increase annually. These results suggested that in stressful sites, turnover is concentrated on rare species. Extinctions may become more frequent after canopy closure and trees or shrub become dominant.

Disharmony

Floristic disharmony occurs when isolation leads to a species composition distinct from the regional flora. An immature or isolated flora is drawn from a subset of the surrounding flora, producing vegetation that is markedly distinct from the donor vegetation. Disharmony can be reflected in life-form spectra, dispersal types, or dominance hierarchies. The degree and nature of the disharmony depends on the type and degree of isolation from sources and the age of the developing vegetation. Surtsey provides ample evidence of disharmony. Of the few species that have arrived, only 9% are wind-dispersed and 27% sea-borne. The remaining 64% are bird-dispersed, in sharp contrast to Iceland (Fridriksson and Magnusson, 1992), where most species are wind-dispersed and few are sea-borne. Chronic minor disturbances also differentially reduce the flora (Antos and Zobel, 1984, 1985a,c; Zobel and Antos, 1986;

Grishin et al., 1996) to accentuate floristic growth-form disharmony. For example, mosses, lichens, and non-rhizomatous perennials are most susceptible to tephra impacts than are trees or shrubs.

Whittaker et al. (1992) described several interesting aspects of disharmony. On Krakatau’s remnant, Rakata, sea birds and bats distributed 30.0% of the species Structural disharmony was studied on Mount St. Helens lahars (del Moral and Bliss, 1993). A lahar adjacent to intact forest has been invaded by conifers, and is more similar to the forest (Percent Similarity = 0.59) than the meadows (PS = 0.41). A more isolated lahar is equally similar to the woodland (PS= 0.47) and meadow (PS =

0.48). The comparison flora was already reduced due to frequent large-scale volcanic activity and the youth of Mount St. Helens (del Moral and Wood, 1988b), so differences were less than they might have been. The cone of Mount St. Helens had only 72 native species in 1987, compared to at least 95 before the eruption. Three nearby volcanoes had from 185 to 276 subalpine and alpine species. Kruckeberg (1987) listed 70 expected species missing from Mount St. Helens prior to 1980. Most of the missing species disperse poorly.

Chance and Contingency

Isolation and differential dispersal permit singular events or historical accidents (contingent factors) to affect community development, even as abiotic processes lead predictably to habitat amelioration. Novel assemblages may develop in which the relationship between vegetation and environmental factors is weak (cf., McCune and Allen, 1985).

Bush et al. (1992) stated that successional pathways may be extrapolated somewhat, but that too many stochastic biotic forces act to make valid long-term predictions on Krakatau. Each island of the group was developing differently as a result of unique colonization events and subsequent disturbance. Whittaker et al. (1992) noted that the lack of larger mammals confined many species to the coast. Such hierarchical links, highly subject to stochastic effects between plants, animals, and fungi are important determinants of succession on these islands.

Tagawa (1992) emphasized that stochastic dispersal events that determine initial colonizers force succession for centuries and create novel communities (Tagawa et al., 1994). *Ardisia* forms a stable pioneer scrub community in southwest Japan that resists invasion indefinitely. One stochastic element that affects succession is unusual climatic events. Lohse et al. (1995) suggested that drought could alter primary succession on *pahoehoe* lavas on Hawaii.

Stochastic effects weaken environmental relationships. Del Moral et al. (1995) applied canonical correspondence analysis (ter Braak, 1987) to communities on Mount St. Helens. The analysis of the primary succession sites accounted for only 14% of the variance, which was associated with geographic position. In the early stages, it appears that chance plays the dominant role in determining which species occur where and at what abundance.

Differential Effects

An interesting aspect of tephra is its differential impact on vegetation. The gradual nature of tephra deposition over space blurs the distinction between primary and secondary succession. Grishin et al. (1996) described recovery from tephra from the Ksudach volcano, Kamchatka (erupted in 1907). They mapped three vegetation zones depending on the depth of tephra. In deposits deeper than 100 cm, all vegetation was killed, trees were crushed and after 90 yr, primary succession was only in a second stage, dominated by lichen mats, with only scattered herbs. Deposits between 30 and 100 cm deep defined a complex zone. Deposits over 70 cm destroyed all vegetation, but left snags, and the rate of primary succession that dominated recovery was variable. Lichen stages were joined by a dwarf shrub-herb mosaic and a secondary birch forest stage. Isolated trees survived in deposits less than 70 cm and primary and secondary stages formed a mosaic. Deposits less than 30 cm permitted trees to survive, while deposits of 10 to 20 cm eliminated mosses and lichens but only damaged dwarf shrubs and herbs. Deposits under 10 cm damaged herb, moss, and lichen layers but did not eliminate any species, so recovery, not succession, has been the predominant process. The succession rate was related to survival. Without survivors, the primary succession rate related to deposit depth, distance to survivors, and presence of standing dead trees. Snags provided perches for birds that import fleshy fruits (cf., McDonnell and Stiles, 1983) and subsequently dropped leaves to enrich the pumice beneath (Fig. 7). These oases have been colonized by a haphazard assortment of bird-dispersed species intermingled among common wind-dispersed species.

Effects on Animals

While volcanoes occasionally kill many humans (e.g., 20 000 in the lahar spawned by Nevado del Ruiz, Columbia), animal populations are usually devastated. Tephra fallout decimates insects since ash abrasion causes swift desiccation (Edwards, 1986). Ant colonies survived on Mount St. Helens (del Moral, 1981), but survivors lacked resources and most colonies failed. Wildlife losses during the Mount St. Helens eruption included 5000 deer, 1500 elk, 200 black bear, and 15 mountain goats, in addition to uncounted rodents, birds, and fish. Fifty-seven humans were killed. Small animals have recovered from pools of survivors (e.g., gophers) and by invasion (e.g., mice).

Wildlife can recover quickly after volcanic events. Many species thrive in post-eruption ecosystems when forage recovers quickly. Most animal species have at least moderate dispersal powers, so populations of insects, birds, and mammals follow vegetation recovery. Fish recovery may be much slower in new or sterilized systems. For example, Spirit Lake adjacent to Mount St. Helens was boiled and displaced. Only in 1994 was the first fish found, and populations remain very low.

RECOVERY MECHANISMS

Recovery from devastation on volcanic landscapes has several common features. The importance of these features varies, and is conditioned by several factors. An understanding of recovery mechanisms is of both practical and theoretical importance. On the practical side, we can learn how to design more efficacious remediation of devastated landscapes and how to better alleviate potential volcanic destruction. Aspects of succession theory will be improved if abiotic amelioration, dispersal, survivors, biotic interactions, and factors affecting predictability are better understood.

Abiotic Amelioration

Invasion of new volcanic landscapes cannot occur without physical amelioration (del Moral and Bliss, 1993). Chemical weathering is one crucial ameliorating factor (Ugolini et al., 1992), but physical weathering (del Moral, 1983; 1993), organic fallout (Edwards and Sugg, 1993), and erosion (Franklin et al., 1985; Tsuyuzaki and Titus, 1996) all play important roles. These abiotic processes create safe-sites suitable for seedling establishment (cf., Fridriksson, 1987; Tsuyuzaki and del Moral, 1994). Fig. 8 shows a rill formed by minor erosion, with invaders concentrated on the rill edge.

Physical processes form microsites that are extremely important for nucleation in early succession (Yarrington and Morrison, 1974). All studies of lavas demonstrate that cracks are where vascular plant establishment occurs early in succession. Surface manipulations on Mount St. Helens demonstrated the crucial role of physical amelioration (del Moral and Wood, 1988a, 1993b; Titus, 1995). Safe-sites are the sites of first establishment in many studies (e.g., del Moral and Bliss, 1993), but this pattern becomes more diffuse as mature plants survive and expand on gradually ameliorating surfaces. As a rule, seedling establishment and survival on barren volcanic substrates is enhanced by any factor that promotes seed capture, reduces drought stress, concentrates organic matter, or increases nutrient uptake ability.

The physical destruction of a site through erosion can promote succession. Tephra buries vegetation, but if erosion soon occurs, most plants survive (cf., del Moral, 1981; Riviere, 1982; Kadomura et al., 1983). Recovery on Mt. Usu, Japan, was greater in gullies from which tephra had been eroded than in adjacent sites. The seed bank and surviving buried organs contributed greatly to initial recovery. Tephra-covered sites recovered more slowly, and colonizers were dominated by wind-dispersed taxa such as *Salix hultenii*, *Betula maaximowcziana*, and Asteraceae such as *Petasites japonicus*, *Anaphalis margaritacea*, and *Picris hieracioides* (Tsuyuzaki, 1987, 1989, 1991, 1995; Tsuyuzaki and del Moral, 1995).

Dispersal

Dispersal barriers clearly affect the recovery of primary volcanic surfaces. Ocean barriers lead to high proportions of water-dispersed species, and wind-dispersed species are usually well represented. Oceanic volcanoes may also have more bird-dispersed species than species with seeds dispersed by ants and mammals. In contrast, continental volcanoes are likely to be colonized primarily by wind-dispersed species (Tsuyuzaki and del Moral, 1995). Where bird-dispersed plant species are common, it is usual that frugivorous birds fly considerable distances over barren terrain to isolated snags.

Colonists are drawn from species that can reach a site, not from a suite of pre-adapted “pioneer” species. Wood and del Moral (1987) demonstrated that late successional species survived better than pioneers on barren surfaces. They concluded that the first colonists were “pioneer” species only where their superior dispersal abilities overcame their inferior establishment ability. Late successional species that somehow reach isolated sites accelerate succession. The mysterious case of isolated patches formed by the late successional species *Lupinus lepidus* (Morris and Wood, 1989) demonstrated that dispersal barriers can be more important than stress in determining the identity of the first colonists.

Dispersal barriers and poor dispersal ability of stress-tolerant species affect high elevation vegetation. On Mount St. Helens, there are steep richness gradients upward along ridges. In one case, richness declined from 18 species per plot to nine species over an elevation increase of 250 m (del Moral, pers. observ.). Species missing at higher elevations have poor to moderate dispersal abilities.

Invasion near the margin of a lahar or lava flow is typically described as a phalanx, where vegetation advances along a gradually advancing front. Phalanx invasions are common where dispersal distances are short and colonization probability high. Smathers and Mueller-Dombois (1974) described such in invasion on a lava flow from Kilaeua, Hawaii, near undisturbed *Metrosideros polymorpha* forests. Beyond 100 m or less the seed rain is typically extremely diffuse and initial populations are confined to safe-sites. Here populations expand from a few isolated colonists, a process termed nucleation (Yarrington and Morrison, 1974). Seemingly trivial events, such as where a spider spins a web (cf., Dale, 1991), can affect establishment. A sparse vegetation with many unoccupied safe-sites results. Once a plant germinates, establishes and matures, it becomes the predominant source of the local seed rain. The capricious nature of dispersal in stressful, isolated sites strongly affects subsequent succession.

Survivors

Residual species have survived the impact of a volcanic disturbance, while relict sites escaped the devastation. The best known relicts are *kipukas*, the Hawaiian term describing vegetation surrounded by, yet spared from, lava. Such relicts retain mature vegetation, but result in few colonists of young lavas. Many colonists appear drawn from among a pool of long distance dispersing ferns, orchids, Asteraceae, etc., capable of tolerating initially stressful conditions (Smathers and Mueller-Dombois, 1974), though *Metrosideros* does colonize from *kipukas*. In such cases, species adapted to mature soils and forests cannot establish.

Del Moral et al. (1995) described residual species patches on the Pumice Plain of Mount St. Helens. These patches retained understory plants, but the canopy disappeared. The hypothesis that these patches would accelerate primary succession was not confirmed. After 15 yr, only seedlings of residual species (e.g., *Rubus spectabilis*) occurred outside a patch. These patches were themselves being invaded by species dominant on barrens and do not accelerate forest development.

Rather, these tattered remnants provide sites where pioneers grow and reproduce vigorously to enhance the seed rain of the surrounding barrens. The cases of Hawaiian relicts and Mount St. Helens residuals imply that there is a limit to the ability of plants from late succession or climax conditions to colonize barren substrates.

Franklin et al. (1985) described residual vegetation within the blast zone of Mount St. Helens. Rhizomes found in lahars, seeds lodging near the surface, and plants protected by snow were common. Succession was accelerated by these survivors, though species composition had been altered substantially. Alteration results from differential survival and from invasion by small or light-seeded taxa such as *Salix* spp., *Alnus rubra,* and *Epilobium angustifolium*.

Biotic Interactions

Facilitation and Inhibition

Facilitation involves any biotic effect that promotes colonization, while inhibition refers to any process, that precludes colonization (Connell and Slatyer, 1977). Inhibition typically includes both resource competition and allelopathy, the chemical inhibition of adjacent plants.

Soil amelioration has been noted for taxa as different as *Polygonum cuspidatum* (Hirose and Tateno, 1984), *Myrica faya* (Vitousek et al., 1987), *Alnus rubra* (Dale, 1989), *Lupinus lepidus* (Wood & del Moral, 1988) and liverworts (Griggs, 1933). Trapping wind-blown soil and seeds (Chambers et al., 1991), nurse-plant effects (Hirose and Tateno, 1984) and delayed facilitation (Eggler, 1963; del Moral and Wood, 1993b) are recognized as important factors in succession.

Very early primary succession on volcanoes seldom yields densities sufficient to inhibit invasion, but inhibition will occur where sufficient cover develops. Clarkson (1990) described how *Coriaria arborea*, a nitrogen-fixing shrub on Mt. Tarawera, formed a dense thicket that reduced species richness from 50 to about 10 species. The balance between facilitation and inhibition is delicate. *Lupinus lepidus* plays a dramatic role on Mount St. Helens (Halvorson et al., 1991, 1992; Halvorson and Smith, 1995). Dense *Lupinus* prevented invasion of wind-blown plants, while scattered *Lupinus* enhanced survival of planted seedlings (Morris and Wood, 1989). Del Moral (1993) showed that while *Lupinus* improved local soil and microclimatic conditions, competition precluded establishment by seedlings of other species. Once the adult died, seedlings of several species become common on the edge but not in the clump.

Mycorrhizae

Mycorrhizae play a major role in community structure and function, but their role in primary succession on volcanoes is poorly understood. Allen (1987) and Allen and MacMahon (1988) suggested that the lack of mycorrhizae limits colonization on Mount St. Helens. However, Titus (1995) demonstrated in field and greenhouse experiments that mycorrhizae had little effect on growth or reproduction of colonizing plants, though they were common in well-vegetated sites. Koske and Gemma (1997) studied sand dune succession involving *Ammophila arenaria* in Massachusetts, U. S. A. Mycorrhizae were not found in barren sites, but only in association with planted grasses. The latter results suggest that mycorrhizae usually follow initial colonizers and that they then can facilitate later colonists.

Animals

Animals obviously disperse seeds and subtly contribute to soil development. Edwards et al. (1986) trapped arthropods on Mount St. Helens from 1980 to 1985 and found that while most soon perished, the organic fallout accelerated recovery of volcanic barrens (Edwards, 1988; Edwards and Sugg, 1993). The organic matter contributed by the victims, seeds and pollen is crucial to plant establishment, improving water holding capacity and soil nutrients that promote seedling survival (Edwards, 1986). Spiders, a major group of colonists in barren sites, spin ground webs that trap seeds in and near safe-sites (Dale, 1991; del Moral, pers. observ.).

Burrowing species often survive to emerge into a landscape devoid of predators with an abundance of below-ground food. Gophers broke up tephra layers and accelerated the recovery of buried vegetation (Anderson and MacMahon, 1985a, b). Soil fertility was improved, as evidenced by yields significantly higher gopher-worked tephra, compared to undisturbed tephra (del Moral and Clampitt, 1985).

Large animals may create safe-sites. Griggs (1919) provided a wonderful photograph of seedlings growing in bear tracks on Kodiak, Alaska, after the Katmai eruption. Though most large mammals avoid devastated landscape until vegetative recovery has provided food, elk herds on Mount St. Helens are an exception. They have routinely traversed barren sites, importing seeds and creating safe-sites where they travel through mud.

Predictability

In addition to intrinsic site qualities, the accumulation of species on volcanoes is determined by chains of low-probability events conditioned by landscape effects that are often historically unique. Differentially isolated identical habitats can develop different vegetation in a seemingly chaotic way (Kazmierczak et al., 1995). Distance alone affects the rate and direction of early succession on many volcanoes. Vegetation is initially sparse and many empty safe-sites occur. Any lucky success contributes disproportionately to recruitment and accentuates the initial colonization effect. Biotic interactions that might structure plant communities remain weak. Such results pose difficulties for those who argue that primary succession is deterministic and vegetation develops predictably. Therefore, reductionist, deterministic approaches to predicting successional pathways may fail (Talling, 1951).

Succession may be explained by traditional mechanisms and be arbitrarily divided into stages (e.g., pioneers, seral species and climax species), but a particular result is not predetermined—it is merely the current lottery draw. Novel species combinations not predictable from the local flora are often observed early in succession. Examples include studies on Krakatau (Tagawa et al., 1985; Tagawa, 1992; Whittaker et al., 1989, 1992; Partomihardjo et al., 1992), Sakurajima (Tagawa, 1964), Surtsey (Fridriksson and Magnusson, 1992), Mount St. Helens (del Moral, 1993), and New Zealand (Clarkson and Clarkson, 1983).

Sale (1977) proposed a lottery model which states that if any of several species might occupy a site and that if colonization rates are low, then identical habitats will support different species (cf., Lavoral and Lebreton, 1992). Establishment patterns on Mount St. Helens agree with this model (del Moral, 1993). The suite of common colonizing species overlap broadly in their microsite distributions, yet they rarely occur in close proximity.

Long-term successional patterns may be described by the "carousel" model (Hanski, 1982; Collins et al., 1993; van der Maarel and Sykes, 1993), that states that communities are dynamic at small scales and that cyclic replacement by any of a guild of species can occur. Colonists win lotteries, and winners are "rewarded" with disproportionate contributions to nearby safe-sites. Then, more stochastic events determine where the next generation establishes. Biotic interactions only gradually become discernible as competition, local dispersal, herbivory, and facilitation dampen stochastic variation and species patterns become more predictable. Despite such predictable abiotic processes as erosion and soil weathering, much stochastic variation remains and may contribute to the large unexplained variance found in most vegetation studies. As long-lived perennials begin to dominate, the carousel slows.

MANAGEMENT

Alien Species

Weeds are increasingly common on volcanoes. Most 20th Century eruptions have occurred in the new biological context provided by the "Columbian Exchange" (Crosby, 1972), that massive redistribution of the biota that followed the European encounter with the Americas. Alien species may have ephemeral effects, but some successional paths have been altered completely by exotic species.

Northern Hemisphere conifers were introduced to New Zealand, altering normal succession. Exotics such as *Pinus* spp., *Lupinus arboreus*, *Holcus lanatus*, *Cirsium vulgare*, *Hypochaeris radicata*, *Senecio jacobaea*, and *Trifolium* spp. now dominate many successional sites (Clarkson and Clarkson, 1983). The 49 introduced species encountered on Mt. Tarawera were more abundant than the 116 native vascular species.

Smathers and Mueller-Dombois (1974) indicated that exotics on Hawaii were rare pioneers on lava, but did invade tephra sites. However, *Myrica faya*, a nitrogen-fixing Canary Islands native, has displaced the native Hawaiian *Metrosideros polymorpha* on more recent tephra (Vitousek *et al*., 1987; Walker and Vitousek, 1991). *Myrica* can grow rapidly under stressful conditions and is at a competitive advantage over any Hawaiian woody species. The invasion of Myrica makes it plain how a single invasion can have a major effect on successional development to transform a landscape. Herbaceous seed plants, poorly represented in Hawaii, also are becoming dominant. Smathers and Mueller-Dombois (1974) asserted that "herbaceous exotics fill a practically vacant niche" that will not interfere with successional development. We are not so sanguine. Hawaiian volcanic grasslands are also affected by exotics such as *Anthoxanthum odoratum* (Karpa and Vitousek, 1994). MacDonald et al. (1991) showed that exotics have severely altered the remaining native vegetation of La Réunion lavas, and it is likely that a detailed survey of insular volcanoes would echo this pattern.

On Mt. Usu, Hokkaido, erosion control efforts seeded exotics such as *Festuca rubra*, *Poa compressa* and *Trifolium repens* (Riviere, 1982). Dale (1991) reported that misguided attempts to stabilize the slopes of Mount St. Helens through hydroseeding introduced many European weeds, reduced tree density, and inhibited native species development on the debris avalanche.

The presence of weeds in new volcanic landscapes is inevitable and again reminds us that plant communities are assembled from the available components. While plant communities result from many factors, the vegetation of any habitat is dependent on its historical and landscape context.

Management of Volcanic Hazards

Active management of volcanic landscapes is uncommon (see *Aliens* section). Erosion control through hydroseeding and tree planting has been attempted in Japan (Fig. 9) and the U. S. A. On Mt. Usu and on Mount St. Helens, native tree seedlings were planted widely in sites with surviving soil. These actions appear to have had few unexpected effects, and are analogous to replanting after clear cut logging. Forest composition will not return to some pre-eruption condition, but will be conditioned by reforestation efforts. Engineering approaches to erosion control are common in Japan and they were applied to Mount St. Helens. On Sakurajima, Japan, where ash fall is chronic (several kg m^{-2} $yr^{-1)}$, inhabitants of the volcano build small concrete shelters for protection against the ash falls (see Fig. 10).

The U. S. Army Corps of Engineers built a check dam on the Toutle River, flowing from Mount St. Helens, that effectively trapped sediment for a few years. The outflow of the new Spirit Lake was dammed by the debris avalanche. A tunnel was drilled to lower the lake level several meters, ensuring that towns on the lower Toutle would not suffer a catastrophic flood.

Many volcanoes with a history of recent eruptions are monitored to provide early warnings. Mt. Rainier may be the most dangerous volcano in the United States—lahars spawned by earthquakes or an eruption easily could kill over 100 000 people and cause uncountable damage (S. Malone, pers. commun., 1996). Few have left the drainages, depending instead on a civil alert system that would provide up to 30 minutes warning.

Lahars may revegetate quickly, if dispersal and fertility limitations are overcome. The 1991 Mt. Pinatubo lahars destroyed over 30 000 ha (Mizuno and Kimura, 1996). Experimental studies showed that with nitrogen fertilization, rice grew moderately well, and agriculture may return to this lahar in record time.

Minor volcanism may be manageable, but in most cases, escape is the only rational response to imminent volcanic hazard. Chester (1993) reviewed hazard mapping from various data. He found that recent work has assessed hazard potential well, but the magnitude of impacts may be, as at Mount St. Helens, underestimated. Dobran et al. (1994) modeled the AD 79 Vesuvius event (see Sigurdsson et al., 1985) and determined that pyroclastic flows could destroy all life within 7 km. Hazard maps are the basis for evacuation and development planning. Many volcanoes are monitored for such tell-tales as earthquake swarms, tilts and bulging, and increasingly this monitoring employs geographical positioning systems and satellite systems. Armed with such information, planners are better prepared to meet challenges posed by active and currently dormant volcanoes.

CONCLUSIONS

Volcanoes impact all ecosystems and represent the most intense of nature's forces. Francis (1993) notes historic examples of eruptions with demonstrable global climatic effects (e.g., Thera, ca. 1500 BC; Mt. Katmai, 1912; and Mt. Pinatubo, 1991). The large-scale global climatic effects of such eruptions are only now beginning to be understood.

Ecosystem responses to volcanism vary with the type, scale, frequency and severity of the event, the nature of impacted vegetation, and contingent factors. Lavas destroy all biota and recovery rates on lavas are slow, but their texture helps determine the rate and nature of colonists. Lava succession rates appear to be more responsive to moisture than to temperature. Summer-dry lavas 2000 yr old on Mount St. Helens remain moss and lichen dominated, with vascular plants in the cracks. Kamchatka lavas are well-forested within 1500 to 2000 yr.

The effects of pyroclastic events and air-borne tephra depend on intensity, scale, and the impacted biota. Forests are more resilient after tephra events than are shrub or grassland vegetation since trees often survive impacts that kill other growth-forms. Forests are also resilient to pyroclastic events since growth form diversity enhances the possibility that some individuals survive.

Biogeographic factors strongly condition community development on volcanoes because volcanism either creates large impacts or the volcano is isolated. Because dispersal plays a central role and dispersal is highly subject to stochastic processes, disharmony and novel species combinations abound on volcanoes. One implication is that restoration can be accelerated by overcoming dispersal barriers and planting species from more mature vegetation. A second, major and general implication is that one should not be concerned if the resulting species composition is composed of a different mixture of native species than was present prior to the eruption. Natural processes would also produce different results.

Understanding how volcanic landscapes recover informs us about fundamental ecological processes. Biogeographic effects strongly condition species richness and composition, but abiotic factors such as weathering, erosion and nutrient inputs control rates. Because the landscape context affects many factors in a stochastic way, while amelioration effects are more deterministic, the *rate* of succession may be more predictable than the *course* of succession after major volcanic eruptions.

ACKNOWLEDGMENTS

We thank V. Dale, R. Fuller, S. Harpole, J. Matthews, D. Riege, L. Walker, and an anonymous reviewer for their instructive comments on the paper. This paper is dedicated to the memory of Professor C. H. Muller.

REFERENCES

Allen, M.F., 1987. Re-establishment of mycorrhizae on Mount St. Helens: migration vectors. *Transactions of the British Mycological Society*, 88: 413-417.

Allen, M.F. and MacMahon, J.A., 1988. Direct VA mycorrhizal inoculation of colonizing plants by pocket gophers (*Thomomys talpoides*) on Mount St. Helens. *Mycologia*, 80: 754-756.

Anderson, D.C. and MacMahon, J.A., 1985a. Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. *American Midland Naturalist*, 114: 62-69.

Andersen, D.C. and MacMahon, J.A., 1985b. The effects of catastrophic ecosystem disturbance: the residual mammals at Mount St. Helens. *Journal of Mammology*, 66: 581-589.

Anonymous, 1993. El Chichón and the Maya. *Discover*, 14: 12-13.

Antos, J.A. and Zobel, D.B., 1982. Snow pack modification of volcanic tephra effects on forest understory plants near Mount St. Helens. *Ecology*, 63: 1969-1972.

Antos, J.A. and Zobel, D.B., 1984. Ecological implications of belowground morphology on nine coniferous forest herbs. *Botanical Gazette*, 145: 508-517.

Antos, J.A. and Zobel, D.B., 1985a. Plant form, developmental plasticity and survival following burial by volcanic tephra. *Canadian Journal of Botany,* 63: 2083-2090.

Antos, J.A. and Zobel, D.B., 1985b. Upward movement of underground plant parts into deposits of tephra from Mount St. Helens. *Canadian Journal of Botany,* 63: 2091-2096.

Antos, J.A. and Zobel, D.B. 1985c. Recovery of forest understories buried by tephra from Mount St. Helens. *Vegetatio,* 64: 105-114.

Antos, A.J. and Zobel, D.B., 1986. Seedling establishment in forests affected by tephra from Mount St. Helens. *American Journal of Botany,* 73: 495-499.

Aplet, G.H., and Vitousek, P.M., 1994. An age-altitude matrix analysis of Hawaiian rain-forest succession. *Journal of Ecology,* 82: 137-147

Atkinson, I.A.E., 1970. Successional trends in the coastal and lowland forest of Mauna Loa and Kilauea volcanoes, Hawaii. *Pacific Science,* 24: 387-400.

Ball, E. and Glucksman, J., 1975. Biological colonization of Motmot, a recently-created tropical island. *Proceedings of the Royal Society, London,* 190: 421-442.

Beamon, J.H., 1962. The timberlines of Lstaccihuatl and Popocatapetl, Mexico. *Ecology,* 43: 377-385.

Beard, J.S., 1976. The progress of plant succession on the Soufriére of St. Vincent: Observations in 1972. *Vegetatio,* 31: 69-77.

Bjärnason, A.H., 1991. Vegetation on lava fields in the Kekla area, Iceland. *Acta Phytogeographica Suecica* No. 77, 84 pp.

Blundon, D.J., MacIsaac, D.A. and Dale, M.R.T., 1993. Nucleation during primary succession in the Canadian Rockies. *Canadian Journal of Botany,* 71: 1093-1096.

Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science,* 5: 641-656.

Burnham, R. 1994. Plant deposition in modern volcanic environments. *Transactions of the Royal Society Edinburgh: Earth Sciences,* 84: 275-281.

Bush, M.B., Whittaker, R.J. and Partomihardjo, T., 1992. Forest development on Rakata, Panjang and Sertung: contemporary dynamics (1979-1989). *GeoJournal,* 28: 185-199.

Chambers, A.C., MacMahon, J.A. and. Haefner, J.H., 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology,* 72: 1668-1684.

Chapin, D.M. and Bliss, L.C., 1988. Soil-plant water relations of two subalpine herbs from Mount St. Helens. *Canadian Journal of Botany,* 66: 809-818.

Chapin, III, F.S., Walker, L.R., Fastie, L.R. and Sherman, L.R., 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64: 149-173.

Chester, D., 1993. *Volcanoes and society*. Edward Arnold, London, 351 pp.

Chevennement, R., 1990. La colonisation végetale d'un champ de lave de La Réunion. *Compes Rondus Societé Biogeographie,* 66: 47-63.

Clarkson, B.D., 1990. A review of vegetation development following recent (<450 years) volcanic disturbance in North Island, New Zealand. *New Zealand Journal of Ecology,* 14: 59-71.

Clarkson, B.R. and Clarkson, B.D., 1983. Mt. Tarawera: 2. Rates of change in the vegetation and flora of the high domes. *New Zealand Journal of Ecology,* 6: 107-119.

Collins, B.D., Dunne, T.D. and Lehre, A.K., 1983. Erosion of tephra-covered hill slopes north of Mount St. Helens, Washington: May 1980-May 1981. *Zeitschrift für Geomorphologie* 43*:*103-121.

Collins, S.L., Glenn, S.M. and Roberts, D.W., 1993. The hierarchical continuum concept. *Journal of Vegetation Science*, 4*:* 149-156.

Connell, J.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist,* 111: 1119-1144.

Cooper, R. and Rudolph, E.D., 1953. The role of lichens in soil formation and plant succession. *Ecology,* 34: 805-807.

Crosby, A.W., Jr. 1972. *The Columbian exchange: biological and cultural consequences of 1492.* Greenwood Press, Westport, Connecticut, 268 pp.

Dale, V.D., 1989. Wind dispersed seeds and plant recovery on Mount St. Helens debris avalanche. *Canadian Journal of Botany,* 67: 1434-1441.

Dale, V.D., 1991. Revegetation of Mount St. Helens debris avalanche 10 years posteruptive. *National Geographic Research and Exploration,* 7: 328-341.

Day, T.A. and Wright, R.G., 1989. Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones: seed trapping nurse plants. *Vegetatio,* 80: 37-45.

del Moral, R., 1981. Life returns to Mount St. Helens. *Natural History,* 90: 36-49.

del Moral, R., 1983. Initial recovery of subalpine vegetation on Mount St. Helens. *American Midland Naturalist,* 109: 72-80.

del Moral, R., 1993. Mechanisms of primary succession on volcanoes: a view from Mount St. Helens. In: J. Miles and D.H. Walton (Editors), *Primary succession on land*. Blackwell Scientific

Publications, London, pp.79-100.

del Moral, R. and Bliss, L.C., 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. *Advances in Ecological Research,* 24: 1-66.

del Moral, R. and Clampitt C.A., 1985. Growth of native plant species on recent volcanic substrates from Mount St. Helens. *American Midland Naturalist*, 114:374-383.

del Moral, R., Titus, J.H. and Cook, A.M., 1995. Early primary succession on Mount St. Helens, Washington, USA. *Journal of Vegetation Science,* 6: 107-120.

del Moral, R. and Wood, D.M., 1988a. The high elevation flora of Mount St. Helens. *Madroño*, 35: 309-319.

del Moral, R. and Wood, D.M., 1988b. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio,* 74: 11-27.

del Moral, R. and Wood, D.M., 1993a. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *American Journal of Botany,* 80: 981-992.

del Moral, R. and Wood, D.M., 1993b. Early primary succession on the volcano Mount St. Helens. *Journal of Vegetation Science,* 4: 223-234.

Dobran, F., Neri, A. and Todesco, M., 1994. Assessing the pyroclastic flow hazard of Vesuvius. *Nature*, 367: 551-554.

Docters van Leeuwen, W. M., 1929. Krakatau's new flora. Proceedings of the Fourth Pacific Science Congress, Pt. 2, pp. 56-71.

Drake, D.R. and Mueller-Dombois, D., 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. *Ecology* 74, 1012-1019.

Edwards, J.S., 1986. Derelicts of dispersal: arthropod fallout on Pacific Northwest volcanoes. In W. Danthanaraya (Editor) *Insect flight: Dispersal and migration*. Springer Verlag, New York, pp. 196-203.

Edwards, J.S., 1988. Life in the allobiosphere. *Trends in Ecology and Evolution*, 3: 111-114.

Edwards, J.S., Crawford, R., Sugg, P.M. and Peterson, M.A., 1986. Arthropod recolonization in the blast zone of Mount St. Helens. In S.A.C. Keller (Editor), *Mount St. Helens: Five years later*. Eastern Washington State University Press, Cheney, Washington, pp. 329-333.

Edwards, J.S. and Sugg, P., 1993. Arthropod fallout as a resource in the recolonization of Mount St. Helens. *Ecology,* 74: 954-958.

Eggler, W.A., 1941. Primary succession on volcanic deposits in southern Idaho. *Ecological Monographs,* 11: 277-298.

Eggler, W.A., 1948. Plant communities in the vicinity of the volcano El Parícutin, Mexico, after two and a half years of eruption. Ecology, 29: 415-436.

Eggler, W.A., 1959. Manner of invasion of volcanic deposits by plants with further evidence from Parícutin and Jurullo. *Ecological Monographs,* 29: 267-284.

Eggler, W.A., 1963. Plant life of Parícutin volcano, Mexico, eight years after activity ceased. *American Midland Naturalist,* 69: 38-68.

Eggler, W.A., 1971. Quantitative studies of vegetation on sixteen young lava flows on the island of Hawaii. *Tropical Ecology*, 12: 66-100.

Fernández-Palacios, J. M. and de Nicolás, J. P. 1995. Altitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science* 6: 183-190.

Fosberg, R.F., 1959. Upper limits of vegetation on Mauna Loa, Hawaii. *Ecology,* 40: 144-146.

Francis, P., 1993. *Volcanoes: a planetary perspective.* Oxford University Press, Oxford, 443 pp.

Franklin, J.F., MacMahon, J.A., Swanson, F.J., and Sedell, J.R. 1985. Ecosystem responses to the eruption of Mount St. Helens. *National Geographic Research,* 1: 198-216.

Frenzen, P.M., Krasney, M.E. and Rigney, L.P., 1988. Thirty-three years of plant succession on the Kautz Creek mudflow, Mount Rainier National Park, Washington. *Canadian Journal of Botany,* 66: 130-137.

Fridriksson, S., 1987. Plant colonization of a volcanic island, Surtsey, Iceland. *Arctic and Alpine Research*, 19:425-431.

Fridriksson, S. and Magnusson, B., 1992. Development of the ecosystem on Surtsey with reference to Anak Krakatau. *GeoJournal,* 28: 287-291.

Gecy, J.L. and Wilson, M.V., 1990. Initial establishment of riparian vegetation after disturbance by debris flows in Oregon. *American Midland Naturalist*, 123: 282-291.

Gratten, J. and Braysay, M., 1995. An amazing and portentous summer: environmental and social responses in Britain to the 1783 eruption of an Iceland volcano. *Geographical Journal*, 161: 125-134.

Griggs, R.F., 1918a. The great hot mudflow of the Valley of 10,000 Smokes. *Ohio Journal of Science,* 19: 117-142.

Griggs, R.F., 1918b. The recovery of vegetation at Kodiak. *Ohio Journal of Science*, 19: 1-57.

Griggs, R.F., 1919. The beginnings of revegetation in Katmai Valley. *Ohio Journal of Science* 19: 318-

342.

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

Grishin, S. Yu., 1992. Succession of subalpine vegetation on lava flows of the Tolbachik area. *Botanicheskiy Zhurnal*, 77: 92-100 (Russian).

Grishin, S. Yu., 1994. Role of *Pinus pumila* in primary succession on the lava flows of volcanoes of Kamchatka. In: W.C. Schmidt and F.-K. Holtmeier, (Editors). *Proceedings of International workshop on subalpine stone pines and their environment: the status of our knowledge*. U.S.D.A., Forest Service Gen. Tech. Rep. INT-GTR-309.

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

Halpern, C.B., Frenzen, P.M., Means, J.E. and Franklin, J.F. 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *Journal of Vegetation Science,* 1: 181-194.

Halpern, C.B. and Harmon, M.E., 1983. Early plant succession on the Muddy River mudflow, Mount St. Helens. *American Midland Naturalist*, 110: 97-106.

Halvorson, J.J. and Smith, E.H., 1995. Decomposition of lupine biomass by soil microorganisms in developing Mount St. Helens' pyroclastic soils. *Soil Biology and Biochemistry* 27: 983-992.

Halvorson, J.J., Smith, J.L. and Franz, E.H., 1991. Lupine influence on soil carbon, nitrogen and microbial activity in developing ecosystems at Mount St. Helens. *Oecologia (Berlin*) 87: 162-170.

Halvorson, J.J., Franz, E.H., Smith, J.L. and Black, R.A., 1992. Nitrogenase activity, nitrogen fixation and nitrogen inputs by lupines at Mount St. Helens. *Ecology*, 73: 87-98.

Hanski, I., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38: 210-221.

Harris, E., Mack, R.N. and Ku, M.S.B., 1987. Death of steppe cryptogams under the ash from Mount St. Helens. *American Journal of Botany*, 74: 1249-1253.

Heath, J.P., 1967. Primary conifer succession, Lassen Volcanic National Park. *Ecology*, 48, 270-275.

Hendrix, L.B., 1981. Post-eruption succession on Isla Fernandina, Galapagos. *Madroño,* 28: 242-254.

Hirose, T. and Tateno, M., 1984. Soil nitrogen patterns induced by colonization of *Polygonum cuspidatum* on Mt. Fuji. *Oecologia (Berlin)*, 61: 218-223.

Horn, E.M., 1968. Ecology of the pumice desert, Crater Lake National Park. *Northwest Science,* 42: 141-149.

Jackson, M.T. and Faller, A., 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. *Ecological Monographs*, 43: 441-461.

Kadomura, H., Imkagawa, T. and Yamamoto, K., 1983. Eruption-induced rapid erosion and mass movements on Usu Volcano, Hokkaido. *Zeitschrift für Geomorphologie*, 46: 123-142.

Karpa, D.M. and Vitousek, P.M., 1994. Successional development of a Hawaiian montane grassland. *Biotropica*, 26: 2-11.

Kazmierczak, E., van der Maarel, E., and Noest, V. 1995. Plant communities in kettle-holes in central Poland: chance occurrence of species? *Journal of Vegetation Science,* 6:863-874.

Kitayama, K., Mueller-Dombois, D. and Vitousek, P.M., 1995. Primary succession of Hawaiian montane rain forest on a chronosequence of eight lava flows. *Journal of Vegetation Science,* 6: 211-222.

Koske, R. E. and Gemma, J. N., 1997. Mycorhizae and succession in plantings of beach grass in sand dunes. *American Journal of Botany*, 84: 118-130.

Kruckeberg, A.R., 1987. Plant life on Mount St. Helens before 1980. In D. Bilderback (Editor), *Mount St. Helens: One Year Later*. U.C. California Press, Berkeley, pp. 2-23.

Lavorel, S. and Lebreton, J.D., 1992. Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science*, 3: 91-100.

Lohse, K.A., Nullet, D. and Vitousek, P.M., 1995. Effects of extreme drought on vegetation of a lava flow on Mauna Loa, Hawai'i. *Pacific Science*, 49: 212-220.

MacDonald, I.A.W., Thebaud, C., Strahmand, W., and Strasberg, D., 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). *Environmental Conservation*, 18: 51-61.

McDonnell, M. J. and Stiles, E.W., 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia*, 56: 109-116.

Maruta, E., 1994. Seedling establishment of *Polygonum cuspidatum* and *Polygonum weyrichii* var. *alpinum* at high altitudes of Mt. Fuji. *Ecological Research*, 9:205-213.

Masuzawa, T. 1985. Ecological studies on the timberline of Mount Fuji. I. Structure of plant community and soil development on the timberline. *Botanical Magazine Tokyo*, 98: 15-28.

McCune, B. and Allen, T.F.H., 1985. Will similar forests develop on similar sites? *Canadian Journal of Botany,* 63: 367-376.

Mazzoleni, S. and Ricciardi, M., 1993. Primary succession on the cone of Vesuvius. In J. Miles and D. W. H. Walton, (Editors) *Primary succession on land*. Blackwell Scientific Publishers, London, pp. 101-112.

Mizuno, N. and Kimura, K., 1996. Vegetational recovery in the mud flow (lahar) area. In M. Nanjo, (Editor), *Restoration of agriculture in Pinatubo lahar areas*. Research Report (Project 07 044174) International Research of the Faculty of Agriculture, Tohoku University.

Morris, W.F. and Wood, D.M., 1989. The role of *Lupinus lepidus* in succession on Mount St. Helens: Facilitation or inhibition? *Ecology,* 70: 697-703

Nakamura, T., 1985. Forest succession in the subalpine region of Mt. Fuji, Japan. *Vegetatio,* 64: 15-27.

Nakashizuka, T., Iida, S., Suzuki, W. and Tanimoto, T., 1993. Seed dispersal and vegetation development on a debris avalanche on the Ontake volcano, Central Japan. *Journal of Vegetation Science,* 4: 537-542.

Ohsawa, M., 1984. Differentiation of vegetation zones and species strategies in the subalpine region of Mt. Fuji. *Vegetatio,* 57: 15-52.

Oner, M. and Oflas, S., 1977. Plant succession on the Kula volcano in Turkey. *Vegetatio,* 34: 55-62.

Partomihardjo, T., Mirmanto, E. and Whittaker, R.J., 1992. Anak Krakatau's vegetation and flora circa 1991, with observations on a decade of development and change. *GeoJournal*, 28: 233-248.

Pickett, S. T. A., Collins, S. L. and Armesto, J. J., 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio,* 69: 109-114.

Rejmanek, M., Haagerova, R. and Haager, J., 1982. Progress of plant succession on the Parícutin Volcano: 25 years after activity ceased. *American Midland Naturalist*, 108: 194-198.

Riviere, A., 1982. Plant recovery and seed invasion on a volcanic desert, the crater basin of USU-san, Hokkaido. Ecological Congress, Sapporo, *Seed Ecology*, 13: 11-18.

Sale, P.F., 1977. Maintenance of a high diversity in coral reef fish communities. *American Naturalist,* 111: 337-359.

Sastre, C. and Fiard, J.P., 1986. Evolution de la flore terrestre de la Montagne Pelée (Martinique) après les eruptions du XXeme sèecle. Mise en évidence de bio-indicateurs volcaniques. *Compes Rondus Societé Biogeographie,* 62: 19-42.

Sigurdsson, H., Carey, S., Cornell, W. and Pescatore, T., 1985. The eruption of Vesuvius in AD 79. *National Geographic Research,* 1: 332-387.

Smathers, G.A. and Mueller-Dombois, D., 1974. *Invasion and recovery of vegetation after a volcanic eruption in Hawaii.* National Park Service Science Monograph Series, No. 5, Government Printing Office, Washington, D.C., 128 pp.

Suwa, H. and Okuda, S., 1983. Deposition of debris flows on a fan surface, Mt. Yakedake, Japan. *Zeitschrift für Geomorphologie,* 46: 79-101.

Tagawa, H., 1964. A study of the volcanic vegetation in Sakurajima, South-west Japan. I. Dynamics of vegetation. *Memoirs of the Faculty of Science Kyushu University, Series E*. 3: 165-228.

Tagawa, H., 1965. A study of volcanic vegetation in Sakurajima, southwest Japan. II. Distributional pattern and succession. *Japan Journal of Botany,* 19: 127-148.

Tagawa, H., 1992. Primary succession and the effect of first arrivals on subsequent development of forest types. *GeoJournal*, 28: 175-183.

Tagawa, H., Suzuki, E., Partomihardjo, T. and Suriadarma, A., 1985. Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio,* 60: 131-145.

Tagawa, H., Kobayashi, M. and Ngakan, P.O., 1994. Dynamic of vegetation in the Tokara Islands. *WWF Japan Science Report,* 2: 117-143.

Talling, J.F., 1951. The element of chance in pond populations. *The Naturalist*, 839: 157-170.

Taylor, B.W., 1957. Plant succession on recent volcanoes in Papua. *Journal of Ecology,* 45: 233-243.

ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio,* 69: 69-77.

Timmins, S., 1983. Mt. Tarawera: 1. Vegetation types and successional trends. *New Zealand Journal of Ecology*, 6: 99-105.

Titus, J.H., 1995. The role of mycorrhizae and microsites in primary succession on Mount St. Helens. Ph. D. Dissertation, Dept. Botany, University of Washington, Seattle, 245 pp.

Tizon, A. 1996. Pinatubo: the unpredictable fire. Seattle Times, February 18, 1996.

Tsuyuzaki, S., 1987. Origin of plants recovering on the volcano Usu, Northern Japan, since the eruptions of 1977 and 1978. *Vegetatio,* 73: 53-58.

Tsuyuzaki, S., 1989. Analysis of revegetation dynamics on the volcano Usu, northern Japan, deforested by 1977-1978 eruptions. *American Journal of Botany,* 68: 1468-1477.

Tsuyuzaki, S., 1991. Species turnover and diversity during early stages of vegetation recovery on the volcano Usu, northern Japan. *Journal of Vegetation Science,* 2: 301-306.

Tsuyuzaki, S., 1994. Fate of plants from buried seeds on Volcano Usu, Japan, after the 1977-1978 eruptions. *American Journal of Botany,* 81: 395-399.

Tsuyuzaki, S., 1995. Vegetation recovery patterns in early volcanic succession. *Journal of Plant Research*, 108: 241-248.

Tsuyuzaki, S. and del Moral, R., 1994. Canonical correspondence analysis of early volcanic succession on Mt. Usu, Japan. *Ecological Research*, 9: 143-150.

Tsuyuzaki, S. and del Moral, R., 1995. Species attributes in early primary succession. *Journal of Vegetation Science*, 6: 517-522.

Tsuyuzaki, S. and Titus, J.T., 1996. Vegetation development patterns in erosive areas on the Pumice Plains of Mount St. Helens. *American Midland Naturalist*, 135: 172-177.

Ugolini, F.C., Dahlgren, R., LaManna, J., Nuhn, W.W., and Zachara, J., 1992. Mineralogy and weathering processes in recent and Holocene tephra deposits of the Pacific Northwest, U.S.A. *Geoderma*, 51: 277-299.

van der Maarel, E. and Sykes, M.T., 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science,* 4: 179-188.

Veblen, T.T., Ashton, D.H., Schlegel, F.M. and Veblen, A.T., 1977. Plant succession in a timberline depressed by volcanism in south-central Chile. *Journal of Biogeography*, 4:275-294.

Velázquez, A. 1994. Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico. *Journal of Vegetation Science,* 5: 263-272.

Vitousek, P.M., Walker, L.R., Whittaker, L.D., Mueller-Dombois, D., and Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science,* 238: 802-804.

Wadge, G., 1983. The magma budget of Volcan Arenal, Costa Rica. *Journal of Volcanology and Geothermal Research*, 19: 281-302.

Walker, L. R. and Chapin, F. S. III, 1987. Interactions among processes controlling successional change. *Oikos*, 50: 131-136.

Walker, L.R. and Vitousek, P.M., 1991. An invader alters germination and growth of a native dominant tree in Hawaii. *Ecology,* 72: 1449-1455.

Whittaker, R.J., Bush, M.B. and, Richards, K., 1989. Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs*, 59: 59-123.

Whittaker, R.J., Bush, M.B., Partomihardjo, T., and Asquith, N.M., 1992. Ecological aspects of plant colonization of the Krakatau Islands. *GeoJournal*, 28: 201-210.

Wood, D.M. and del Moral, R., 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology*, 68: 780-790.

Wood, D.M. and del Moral, R., 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. *American Journal of Botany*, 75: 1228-1237.

Wood, D.M. and Morris, W.F., 1990. Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, Washington. *American Journal of Botany*, 77: 1411-1418.

Yarrington, G.A. and Morrison, R.G., 1974. Spatial dynamics of a primary succession: nucleation. *Journal of Ecology*, 62: 417-428.

Zobel, D.B. and Antos, J.A., 1986. Survival of prolonged burial by subalpine forest understory plants. *American Midland Naturalist,* 115: 282-287.

Zobel, D.B., and Antos, J.A., 1991. 1980 tephra from Mount St. Helens: spatial and temporal variation beneath forest canopies. *Biology and Fertility of Soils*, 12: 60-66.

Zobel, D.B., and Antos, J.A., 1992. Survival of plants buried for eight growing seasons by volcanic tephra. *Ecology,* 73: 698-701.

LIST OF FIGURES (not provided with this draft)

Fig. 1. Steam and sulfur vent in crater of Mt. Takumbe, Japan. Adjacent rocks lack vegetation.

Fig. 2. 2000 year old scoria, Craters of the Moon, Idaho: *Chrysothamnus nauseosus* in gully and scattered *Agropyron spicatum*.

Fig. 3. The 1914 lava flow of Sakurajima, Japan: a wide variety of woody species, e.g. *Pinus thunbergii*, *Alnus firma*, *Rhus ambigua*, *Rosa polyantha*, and *Ficus erecta*, with *Polygonum japonicum* and *Miscanthus sinensis*.

Fig. 4. Advancing timberline on scoria, 2500 m a.s.l. on Mt. Fuji. Trees in distance are *Larix* sp., common herbs include *Polygonum weyrichii* and *Calamogrostis* sp.

Fig. 5. Toutle River lahar, Mount St. Helens, U.S.A., with fringes of rapidly developing *Salix* spp., and *Alnus rubra*, shown after 16 years.

Fig. 6. Kautz Creek, Mt. Rainier, U.S.A., lahar of 1947, photo from 1975, showing coniferous snags that accelerated succession.

Fig. 7. Remnant of old *Betula ermanii* snag on volcano Ksudach, Kamchatka Peninsula, Russia, invaded by *Rubus sachalinensis* and *Epilobium (Chamerion) angustifolium.*

Fig. 8. Rill edge on Mount St. Helens, U.S.A.: invading *Anaphalis margaritacea, Hieracium albiflorum*, and other species, confined to edges where seeds are trapped, protection is offered against the wind, and water erosion is minimal.

Fig. 9. Mt. Usu, Japan: installing mixed forest species for erosion control.

Fig. 10. Ash protection huts on Sakurajima, Japan.