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Arthropods as Pioneers in the Regeneration of Life on the Pyroclastic-Flow Deposits of Mount St. Helens

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Dedication

We dedicate this chapter to the memory of a great and intrepid volcano ecologist, Ian Thornton, 1928–2002.

9.1 Introduction

The eruption of Mount St. Helens, on May 18, 1980, affected an area of 600 km² within which communities of animals and plants sustained a wide range of impacts, depending on proximity to the volcano and local topography. The most extreme destruction occurred in the area immediately north of the crater, now known as the Pumice Plain (see map, Figure 9.1), where the eruption apparently destroyed the entire biota over tens of square kilometers. Our interest concerned the response of arthropods to the eruption and changed landscape, particularly in the most intensively disturbed area and one remote site. Early questions to address included the following:

- What was the pattern of survival across the area impacted by the blast and subsequent eruption?
- In particular, was the Pumice Plain truly devoid of eruption survivors and thus, with the biological calendar reset to zero, a classic landscape for the study of primary succession?
- What was the pattern of initial colonization?

Given the extraordinary (but largely underappreciated) capacity of arthropods for aerial dispersal and bearing in mind their ubiquity in the summer airstream, the eruption of Mount St. Helens gave us the perfect opportunity to test the hypothesis that, microorganisms aside, arthropods would be the true pioneers of the barren pyroclastic surfaces and the initiators of biological succession. Answers to these questions bear on the broader issue of spatiotemporal dynamics, recently described as the “final frontier for ecological theory” (Kareiva 1994).

The secret of the evolutionary success of the insects and spiders is, in large part, their capacity for widespread dispersal.

Insects on their wings and spiders passively on silk threads become airborne on flights that may range from a few meters to hundreds of kilometers and on landing may become colonists in a landscape that is ever changing. On a summer’s day, at least half the insect biomass may be airborne, a fact well known to swallows and swifts but little appreciated by earthbound humans.

One problem in studying the dispersal capacity of arthropods is the difficulty of differentiating immigrant dispersers from local residents. The eruption of Mount St. Helens provided an opportunity to study immigration because the Pumice Plain offered a large area devoid of local residents except those undertaking primary colonization. A wide variety of immigrant arthropods was expected at Mount St. Helens, but we surmised that few would be adapted for survival in barren and physiologically challenging sites like the Pumice Plain. Wide-ranging summer temperatures, abrasive mineral dust, which can abrade the superficial waxes on which water retention depends, and intermittent drought are hazards for all arthropods, especially small ones that have high surface-to-volume ratios. Those unable to survive in the radically changed landscape would nonetheless have ecological significance as an import of organic matter to the new pyroclastic surfaces. Hence, it was important to ask what the biomass of this arthropod fallout was and what it represented in terms of important nutrients, such as nitrogen and phosphorus.

Few studies have addressed the roles of arthropods in the context of primary succession. Primary succession is, by definition, initiated in an area devoid of plant life, but an absence of plants does not necessarily mean an absence of resident animal populations. Based on his studies following the catastrophic eruption of Krakatau in 1883, Dammerman (1948) showed that the primary successional sequence began there with scavengers feeding on organic material brought to the island by wind and ocean currents. But what held for a tropical island was not necessarily the case in the north temperate zone, because Lindroth et al. (1973) concluded from studies

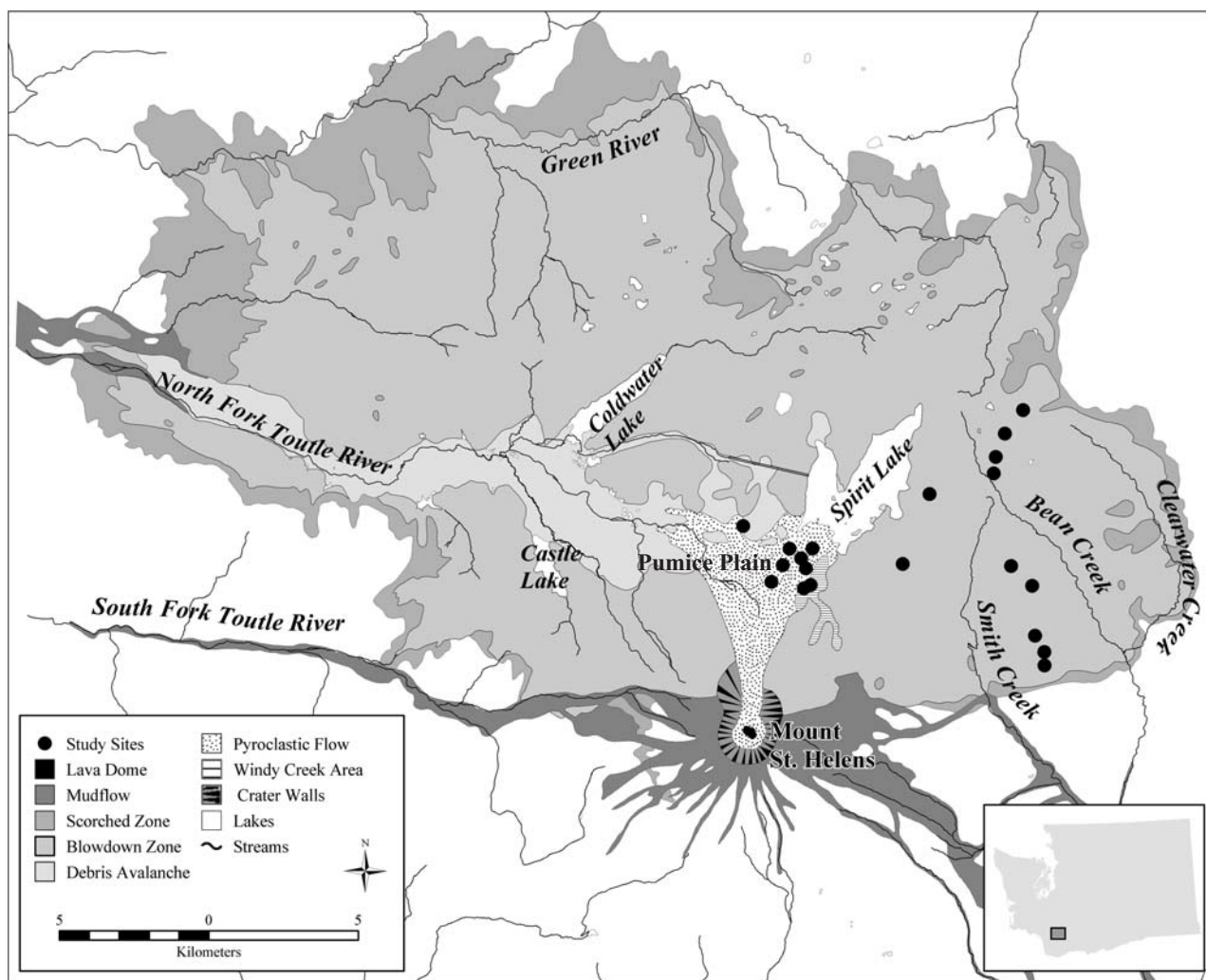


FIGURE 9.1. The area north of the crater, showing the distribution of pyroclastic-flow deposits, surrounding blowdown, and standing-dead zones. Circles denote arthropod sampling sites. [From Sugg and Edwards (1998); used with permission.]

of the volcanic island Surtsey, which rose above the surface of the Atlantic Ocean in 1963 about 30 km southeast of Iceland, that plants were needed as a primary resource before animal colonization could occur. This view of the primacy of plant establishment before colonization of viable animal populations was also supported by the observations of Delong (1966) from areas newly exposed by a receding Alaskan glacier. Yet even at Surtsey, Lindroth et al. (1973) reported transient populations of blowflies supported on allochthonous inputs, namely carcasses of seals and sea birds washed up on the shore. A more recent and detailed monograph on the ecology of recently deglaciated terrain, based largely on Scandinavian sites (Matthews 1992), makes no mention of arthropods as pioneers. It is, however, well established that areas with no significant vegetation, such as alpine zones, periglacial landscapes (Kaufmann 2001), and deserts (Koch 1960; Louw and Seely 1982) where little or no primary productivity occurs, can nonetheless support resident arthropod populations. Indeed, Swan (1963) coined the term

aeolian zone for the habitat of such communities supported by allochthonous inputs of nutrients carried by winds; aeolian communities have been documented on several Cascade volcanoes (Mann et al. 1980; Edwards 1987). The importance of allochthonous inputs has long been appreciated for aquatic systems (Teal 1957), and studies of Polis and others (Polis et al. 1997; Polis and Hurd 1996) have more recently demonstrated its importance, as well, for terrestrial communities other than alpine zones.

Arthropod dispersal thus plays a dual role in the initial stages of succession, providing a source of primary colonists of new sites and nutrients in the bodies of immigrants that die upon reaching the site. Our working hypothesis for the study of primary colonization on Mount St. Helens was that an assemblage of arthropod predators and scavengers comparable to those found in other barren habitats would be the primary colonizers of the severely disturbed surfaces, where no residual biota remained.

9.2 Methods of Sampling in the Posteruption Landscape

In the area of the Pumice Plain, all biota was cooked, buried, blown away, or scoured clear. The inundation of the Pumice Plain by the debris avalanche, its subjection to the lateral blast, and then its coverage by extremely hot pyroclastic-flow deposits are described in Chapter 3 (this volume). Beyond this core area, the force of the lateral blast left a fan-shaped area of blown-down forest (blowdown zone; Figure 9.1) bordered by a narrow zone of standing trees singed and killed by the heat of the blast. Finally, the plineal phase of the eruption deposited tephra over a vast area immediately surrounding the volcano with the deepest deposits to the east-northeast.

We established sample sites in 1981 through 1986 at locations covering a range of disturbance intensities, from the pyroclastic-flow surfaces of the Pumice Plain to the tephra deposited in the plineal phase of the eruption in the eastern portion of the blowdown zone, where tephra depths at sample sites ranged from less than 10 cm to more than 0.5 m. Most of the blowdown sites were situated in preeruption clear-cuts because they provided a greater diversity of preeruption arthropod populations, especially ants, from which an index of destruction could be determined. Ant colonies are common in clear-cuts and aspects of their biology (e.g., being generalist predators and nesting below ground surface or in dead wood) enhanced their chances of survival. For comparison, sites were also established in clear-cuts and old-growth forest about 90 km north-northeast of the volcano. Clear-cuts in lightly dusted areas with less than 2 cm of tephra depth from the May 18 eruption were used as “control” sites, which ranged in age from 1 to 22 years, and samples from these sites provided a picture of secondary succession following clear-cutting. This pattern allowed an estimation of the community diversity and composition of clear-cuts near the volcano before the eruption.

We sampled arthropod activity using pitfall traps constructed from plastic tumblers set level with the ground surface in sleeves of polyvinyl chloride plastic pipe. The cups were partially filled with a 50% aqueous solution of ethylene glycol and were protected from rain and disturbance by a plywood cover supported about 2 cm above the soil surface by a tripod of nails. Pitfalls were sampled at about 2-week intervals, generally from May through October. Most results are based on linear arrays of 10 to 20 pitfall traps at each site, with pitfalls within a site placed at 10-m intervals. Comparisons between vegetated patches and the surrounding barren tephra were made at three sites with paired sets of five pitfalls each in vegetated and adjacent nonvegetated areas. Daily activity of colonizing arthropods, which were abundant in the Pumice Plain, was measured by captures in a grid of dry pitfalls in 1986. Forty-nine pitfalls were set at 10-m intervals in a 7×7 grid. The traps were sampled at 1- to 4-hour intervals for about 40 hours on three occasions. All captured individuals were identified and then released at least 2 m from the trap.

We sampled the flux of organic material from aerial fallout of arthropods and plant fragments at the ground surface in the Pumice Plain using linear arrays of 10 fallout collectors spaced 10 m apart. The collectors were composed of 0.1-m² wooden frames containing a monolayer of close-packed golf balls that simulated the desert pavement-like surface and provided dead space where material could accumulate (Edwards 1986b; Edwards and Sugg 1993). The frames were backed with fine nylon mesh to allow drainage but to retain the fallout. The accumulated contents of the collector, comprising fine mineral material and organic fragments, were removed at about 2-week intervals. Arthropod and other organic fragments were separated in the laboratory. Measures of the contribution of elemental nutrients over time by arthropod fallout were made by use of dried fruit fly samples set in situ as a fallout surrogate, as discussed later in this chapter.

9.3 Survival Patterns

One of the keys to the ubiquity of terrestrial arthropods is their capacity for dispersal. As an obligate phase of their life histories, the majority of insects and spiders exploit wind patterns either actively by flight or passively by ballooning on silk threads. It is a wasteful process to the extent that many dispersers end their lives in hostile places, but it ensures that some find their niche in diverse landscapes that are changing in space and time. Thus, the dispersal behavior patterns of arthropods ensured that transient populations of insects and arachnids were arriving on the Pumice Plain and other impacted areas shortly after the eruption. Indeed, search and rescue helicopter pilots reported seeing numerous insects on the tephra in the first days after the eruption. The problem lay in knowing whether individual arthropods present at a site were recent arrivals or from a surviving local population. Any species capable of aerial dispersal could conceivably have colonized a site since the eruption occurred. Only species limited to a pedestrian mode of dispersal (hereafter referred to as pedestrians), and hence limited to relatively small annual increments of population spread, could be used as unequivocal evidence of local survival.

The question of local survival in refugia in the posteruption landscape is a classic issue that has been argued since the eruption of Krakatau (Thornton 1996). Dammerman (1948) first raised the critical question: Given survival, what is the possibility of persisting when food resources are gone from the posteruption landscape? Ants at Mount St. Helens provide a good example of initial survival and subsequent death. Large numbers of carpenter ants (*Camponotus*) were found foraging on barren tephra at the border of the blast area 1 month after the eruption. These ants must have emerged from a nest in dead wood that was presumably sheltered in the lee of a ridge and covered by deep snow. Windborne insects and localized blooms of fungal growth around seepages appeared to be the only source of nutrients. The disappearance of ants from this location in subsequent years is presumed to have been caused

by the absence of sufficient food. Kuwayama (1929) found a comparable pattern after the June 1929 eruption of Mount Komagatake in Japan, where ants were active 9 days after the eruption, but all colonies were dead 11 days later.

Because of their small size and cryptic habits, it was expected that, in contrast to the Pumice Plain, many arthropods initially survived the eruption in the blowdown zone. The possibility of survival was enhanced by the timing of the eruption in early spring, when many resident species were still dormant at the elevations immediately surrounding the volcano. Even further protection was provided in some locations by snowbanks in protected areas on north slopes or shaded by the forest canopy. Thus, there may have been widespread survival of the immediate impact of the eruption, but survivors in the blowdown zone would also find the local habitat drastically changed; long-term survival would depend on the ability of individuals to find adequate resources.

As expected, samples from the Pumice Plain indicated that local survival was nil. The extreme heat and great thickness of the deposits killed and buried any potential survivors. Virtually all arthropods taken in our sampling on the Pumice Plain from 1981 to 1983 were capable of aerial dispersal (the few individual exceptions are addressed below), whereas pedestrian species as well as aerial dispersers were common at all sites sampled in the blowdown zone (Table 9.1).

Arthropods in the blowdown zone had a range of food resources available. In clear-cuts especially, by midsummer 1980

there was emergent herbaceous vegetation dominated by fireweed (*Chamerion angustifolium*) that supported herbivores such as aphids, moths, and leaf beetles. Predators [e.g., carabid (Carabidae), staphylinid (Staphylinidae), and ladybird beetles (Coccinellidae)] had local herbivore populations available as well as the fallout of dispersing arthropods. Generalists, such as ants, were able to subsist on local arthropod survivors and new immigrants as well as on honeydew from aphids that colonized emergent vegetation. Dead wood provided habitat and food for a variety of arthropods [e.g., longhorn beetles (Cerambycidae), throscid beetles (Throscidae), and robberflies (Asilidae)]. Furthermore, wood-rotting fungi using the abundant resource of newly dead trees provided a resource for a variety of fungivores, such as the tenebrionid beetle *Iphthimus serratus*.

Although arthropod survival was apparent at all sites sampled across the blowdown zone, it was not uniform. Sampling of clear-cuts 90 km to the north-northeast of the volcano in 1983 revealed 9 to 13 ant species in all clear-cuts more than 5 years old, whereas sampling sites established in 12-year-old clear-cuts across the eastern portion of the blowdown zone revealed only 1 to 9 ant species. The number of surviving ant species in the blowdown was related to the depth of tephra deposited in the plineal phase of the eruption (Figure 9.2); where tephra depths were less than 20 cm, species number was similar to that of control sites.

Among pedestrians found at blowdown sites, and thus assumed to have survived the eruption in various refugia, were predators such as flightless carabids [e.g., *Pterostichus (Hypherpes)* spp. (including *P. neobrunneus*, *P. castaneus*, and *P. herculeanus*) and *Scaphinotus* spp. (*S. angusticollis* and *S. marginatus*)]. Other pedestrian predators included centipedes and nonballooning spiders, such as agelenids (*Cybaeus* sp.), hahniids (*Neoantistea* sp.), and antrodiaetids (*Antrodiaetus* sp.). Pedestrian scavenger/predators included

TABLE 9.1. Summary of presence or absence of select taxa from samples taken at 17 blowdown sites and 3 sites in the Pumice Plain from 1981 to 1983.

	Blowdown	Pumice Plain
<i>Aerial dispersers:</i>		
Formicidae (alates)	X	X
Carabidae (e.g., <i>Bembidion</i> , <i>Harpalus</i> , <i>Amara</i>)	X	X
Araneida (e.g., Lynphiidae, Lycosidae, Thomisidae)	X	X
Orthoptera (Acrididae)	X	X
<i>Pedestrian taxa:</i>		
Formicidae (workers)	X	(x) ^a
Carabidae (e.g., <i>Scaphinotus</i> and <i>Pterostichus (Hypherpes)</i>)	X	(x) ^a
Araneida (e.g., Agelenidae, Antrodiaetidae)	X	
Phalangida	X	
Chilopoda	X	
Diplopoda	X	
Orthoptera (e.g., Gryllacrididae, Prophalangopsidae)	X	
Notoptera (Grylloblattidae)	X	

Pedestrian taxa are those incapable of aerial dispersal and so indicate probable local survival of populations following the eruption.

^aPedestrian taxa in the Pumice Plain are considered aberrant cases (see text).

Source: From Sugg and Edwards (1998); used with permission.

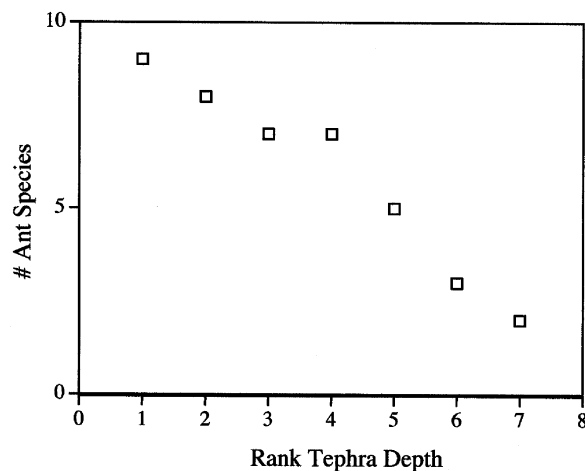


FIGURE 9.2. Numbers of ant species found at sites in the blowdown affected by different depths of tephra. Sites are rank ordered from least (1; 12 cm) to greatest (7; 52 cm) in tephra depth.

camel crickets (*Pristoceutophilus* spp.) and phalangids (e.g., *Leptobunus* sp.).

One dramatic die-off among pedestrian taxa was noted in the vicinity of Ryan Lake in September 1980, when innumerable dead millipedes (*Harpaghe* sp.) were found in the blowdown zone. These millipedes are important litter consumers and died with guts packed with ash ingested as they attempted to feed on ash-covered litter.

The diverse microarthropods that are characteristic members of the soil microfauna (e.g., mites and springtails) were present in low numbers in the Pumice Plain but were more abundant in the blowdown zone in the early years following the eruption. They are susceptible to wind transport because of their small size, and so their later presence in the Pumice Plain could not be taken as evidence of local survival. Sminthurid Collembola were the most numerous microarthropods taken in pitfall traps on the barren surface of the pyroclastic-flow deposits near Spirit Lake. These springtails live not only in soil but also on the foliage of conifers, where they are often abundant, and their presence in pitfall captures likely reflects their propensity for passive wind carriage from the distant forest canopy. The minimal presence of mites, springtails, and other soil microarthropods on the barren surfaces of the Pumice Plain is probably because of the dearth of organic material in the posteruption surface deposits.

9.4 Diversity of Arthropod Immigrants to the Pumice Plain

The capacity of arthropods for aerial dispersal is profound but little understood because of the difficulty of differentiating dispersers from local residents in most habitats. Mount St. Helens provided an opportunity to study this phenomenon. A wide variety of immigrants was expected to arrive on the denuded or new mineral surfaces, but few of those were adapted for survival in barren sites such as the Pumice Plain.

A sense of the diversity of arthropod immigrants to the Pumice Plain comes from analysis at the family level of pitfall samples, amounting to more than 20,000 specimens. From 1981 to 1983, when all materials taken in pitfall trap collections other than the few known pioneer residents (see following) were certainly of allochthonous origin, 150 families representing 18 orders were identified. Taxonomic identifications in this chapter are based on the Integrated Taxonomic Information System (<http://www.itis.usda.gov>).

Data at the species level for diversity of early arrivals are available for 25 of the 150 arthropod families sampled on the Pumice Plain. The total species count for this sample of 9 spider and 16 insect families is 250, giving a mean number of 10 species per family. Although the selection of families for identification to species level was made on the basis of available expertise and thus not in a strictly random fashion, it was not biased toward species-rich groups. An independent set of data concerning arthropod diversity in the

Cascade Range comes from the detailed catalogue of arthropod species recorded at the H.J. Andrews Experimental Forest, a Long-Term Ecological Research site (Parsons et al. 1991). The average number of species per family in this tabulation source is 8.6, a figure close to the value of 10 for our Mount St. Helens material. On the basis of these data, we estimate that at least 1500 arthropod species reached the surface of the Pumice Plain during the first few years following the eruption.

Insect immigrants made up about 80% of the arthropod fallout. At the family level, flies (Diptera) dominated the fallout diversity with 42 families. The flies were followed by beetles (Coleoptera) with 30 families, bugs and close kin (Hemiptera/Homoptera) with 18, butterflies and moths (Lepidoptera) with 15, and wasps and relatives (Hymenoptera) with 10. Minor orders were represented by 1 to 6 families, and spiders contributed 9 families. Lacewings (Neuroptera) may be one example of a group represented in the fallout but unable to establish breeding populations on the barren mineral surfaces. On Mount St. Helens, 250 lacewing specimens from 23 species were collected in traps. The habitat preferences of the majority of the lacewing species captured indicate the prevalence of long-distance dispersal on winds blowing predominantly from forest and farmland southwest of the mountain (Sugg et al. 1994).

Spiders were well represented in the early posteruption fallout; from 1981 to 1986, 14,325 specimens comprising 125 species were taken in pitfalls and fallout collectors, making up 23% of the arthropods that reached the sampling sites. Overall, about half of them were wolf spiders (Lycosidae), with linyphiids contributing 34% of the catch (Crawford et al. 1995). The eruption of Mount St. Helens provided a unique opportunity to examine a little-studied aspect of spider dispersal on wind currents by means of ballooning on threads of silk. Although that behavior has been known for centuries, the issue of its ecological importance has been subject to debate, for there have been few opportunities to measure rates of landing at sites known to be otherwise devoid of spiders. This deficiency of data has led to underestimates of the importance of ballooning in dispersal (e.g., by Decae 1987 and by Wise 1993). During the 125-day field season in 1983, the average rate of spider arrival, as measured by occurrence in fallout collectors, amounted to 0.84 spiders $m^{-2} day^{-1}$. These observations bear on the issue of metapopulation dynamics (Hanski 1999), for which there are few data concerning spiders. Although standard pitfall sampling of spiders in the Pumice Plain during the first few years after the eruption revealed the presence of significant numbers, the apparent absence of reproduction indicates that these spiders represented sink populations of ballooners from distant sources, in some cases demonstrably more than 50 km distant (Crawford et al. 1995). They were unable to survive, presumably because of the rigors of the physical environment, for example, high summer temperatures, insolation, and desiccation. By 1986, six species of spider, comprising two lycosids and four linyphiids, had established reproducing populations on the Pumice Plain, but only

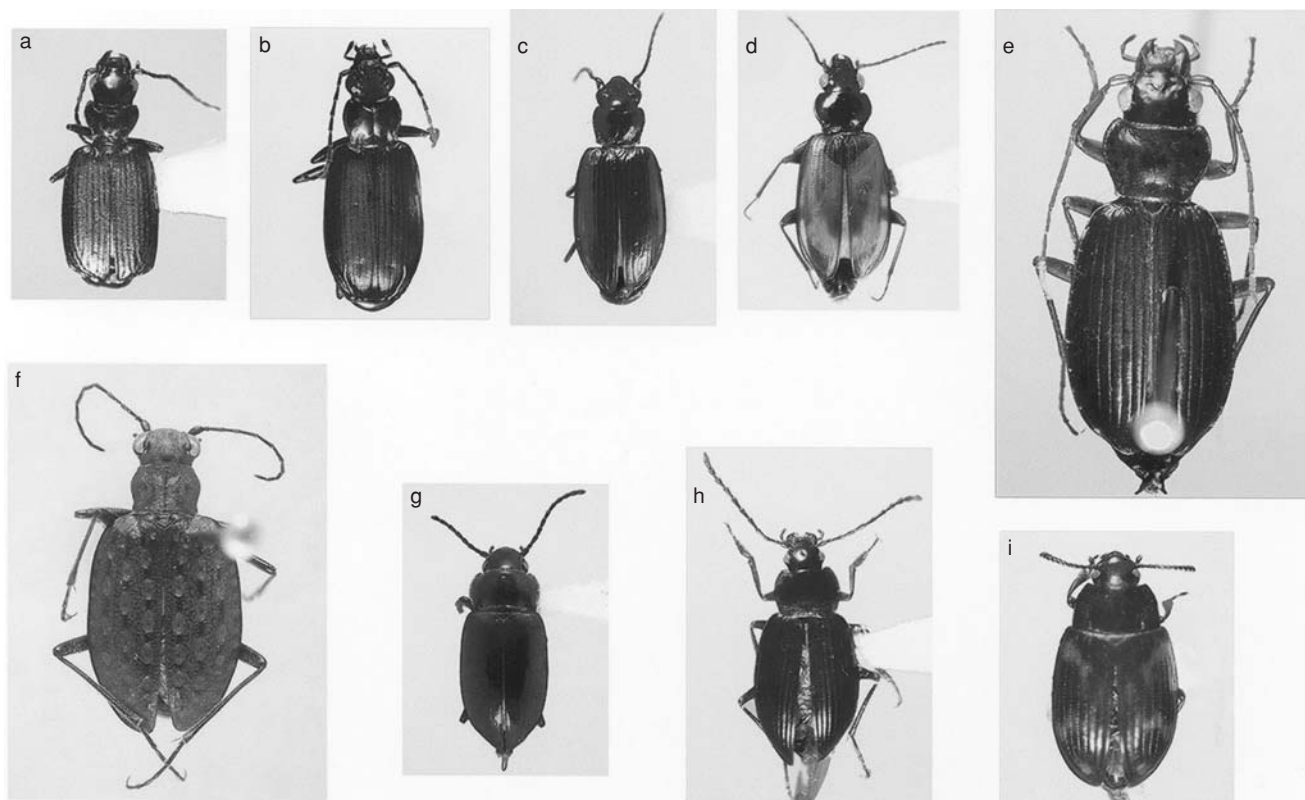


FIGURE 9.3. Primary colonist beetles from the Pumice Plain at Mount St. Helens. Carabidae: a, *Apristus constrictus*; b, *Bembidion planatum*; c, *B. improvidens*; d, *B. obscurellum*; e, *Nebria escholtzii*; f, *Opisthius richardsoni*. Trachypachidae: g, *Trachypachus holmbergii*. Agyrtidae: h, *Apteroloma caraboides*. Tenebrionidae: i, *Scaphidema pictum*.

at sites where sparse pioneer vegetation had already become established.

9.5 Primary Arthropod Colonists of the Pumice Plain

The main criterion for recognition of primary colonists on barren tephra surfaces in the Pumice Plain was firm evidence for successful breeding populations, such as juvenile stages (beetle larvae or hemipteran nymphs) or egg sacs (lycosid spiders). On this basis, we found four beetle families (Carabidae, Trachypachidae, Agyrtidae, and Tenebrionidae; Figure 9.3) and two families of true bugs (Lygaeidae and Saldidae) that established breeding populations on the Pumice Plain within 3 years of the eruption. Carabid species dominated in numbers of species and of individuals. Although it was not possible to match adults with larvae for all carabid and trachypachid species, we were able to assign larvae to five genera: *Apristus*, *Bembidion*, *Nebria*, and *Opisthius* for carabids and *Trachypachus* (Thompson 1979). Larval tiger beetles (*Cicindela* spp.) are sedentary tunnel dwellers and thus not susceptible to pitfall capture but were observed in moist streamside tephra from 1984 on. The single species of agyrtid

and tenebrionid beetles common in the samples had larvae that could be unequivocally recognized.

Our list of species assumed to have colonized in the first 5 years (Table 9.2) is based on presence of juvenile stages and, in most cases, clear evidence of increasing numbers of adults. This list is probably conservative. We have excluded taxa (e.g., the carabid *Trechus obtusus*) for which there was evidence of increasing numbers but no capture of larvae assignable to that genus. We also limited our account to those taxa apparently successful in breeding on the barren mineral surfaces. Small patches of vegetation that established in the Pumice Plain in the first few years could support a more standard food web of producers, herbivores, and predators, but these sites amounted to an insignificant fraction of the area of the Pumice Plain in the years immediately following the eruption. Nonetheless, vegetated patches had a significant, albeit localized, effect.

The first colonists of the Pumice Plain with apparent reproductive success were species of the carabid beetle *Bembidion*, a genus characteristic of disturbed habitats, such as the barren margins of braided rivers, gravel pits, open periglacial ground, and alpine snowfield fringes (Lindroth 1963; Anderson 1983; Mann et al. 1980). Three species, *Bembidion planatum*, *B. improvidens*, and *B. obscurellum*, were present in 1981, and these were the first to show a population increase during

TABLE 9.2. Species successfully colonizing barren pyroclastic-flow surfaces in the Pumice Plain at Mount St. Helens by 1985.

Aerial dispersers:	
Coleoptera	
Carabidae	
<i>Apristus constrictus</i>	
<i>Bembidion breve</i> (= <i>incertum</i>)	
<i>B. improvidens</i>	
<i>B. obscurellum</i>	
<i>B. planatum</i>	
<i>B. quadrijoveolatum</i>	
<i>B. recticolle</i>	
<i>B. transversale</i>	
<i>Cicindela oregona</i>	
<i>Nebria escholtzii</i>	
<i>N. mannerheimii</i>	
<i>N. sahlbergii</i>	
<i>Opisthius richardsoni</i>	
Trachypachidae	
<i>Trachypachus holmbergi</i>	
<i>T. slevini</i>	
Agyrtidae	
<i>Apteroloma caraboides</i>	
Tenebrionidae	
<i>Scaphidema pictum</i>	
Hemiptera	
Saldidae	
<i>Saldula</i> sp.	
Lygaeidae	
<i>Geocoris</i> sp.	
Pedestrian dispersers:	
Orthoptera	
Gryllacrididae	
<i>Pristoceutophilus</i> spp.	
Notoptera	
Grylloblattidae	
<i>Grylloblatta</i> sp.	

subsequent years (Sugg and Edwards 1998). Two of these species, *B. planatum* and *B. improvidens*, are generally found in moist locations, such as the margin of streams or melting snowfields, whereas *B. obscurellum* is relatively independent of moist habitats (Lindroth 1963) and is found even in arid regions throughout the West. In the Pumice Plain, however, even reputedly hygrophilous species, such as *B. planatum*, colonized places distant from streams. It seems that the tephra deposits of the Pumice Plain had sufficient water-holding capacity to provide a suitable habitat for developing carabid larvae. For many *Bembidion* species, the nature of the substratum, especially grain size, may be more important than proximity to water (Anderson 1983). The *Trachypachus* spp. and *Apristus constrictus* are also associated with riparian habitats but are not restricted to the water's edge (Lindroth 1961, 1968). *Trachypachus holmbergi* was the most abundant caraboid at clear-cut sites in the blowdown and outside the impacted area, and these sites were probably the source of the immigrants to the Pumice Plain. Of all species, the most successful in terms of numbers of adults trapped was the carabid *Bembidion planatum*, which was abundant at all sites sampled. By 1985,

the success of *B. planatum* was matched by the agyrtid *Apteroloma caraboides*, although it did not colonize as rapidly as did the *Bembidion* species. Before this study, little was known of the biology of *Apteroloma caraboides*. It was thought to feed on rotting vegetation (Van Dyke 1928), but from its success on the Pumice Plain, where there was no significant vegetation during its period of establishment, it is clear that *A. caraboides* is a generalist that can also subsist on organic fallout.

Carabid beetles were the most diverse of the primary colonists and the most successful, as evidenced by increasing numbers of adults and larvae. Carabids also manifested the greatest increases in species number and abundance from 1981 to 1985 (Sugg and Edwards 1998). The carabid genus *Bembidion*, in particular *B. planatum* and several of the *incertum* species group (*sensu* Lindroth 1963), mostly *B. improvidens*, showed the greatest reproductive success, with yearly increases in both adults and larvae in the years 1983 to 1985 (Figure 9.4). The greatest species diversity was found along stream margins, which is the characteristic habitat for most of the taxa showing evidence of reproductive success (Lindroth 1963).

In contrast to the carabids already discussed, the tenebrionid beetle *Scaphidema pictum* showed only limited population growth. A common inhabitant of river bars (Hatch 1965), the scavenging habit of this species was confirmed by our observation of several adults feeding within the body of a dead grasshopper on the Pumice Plain.

The two pioneer true bugs differed markedly in habitat preference. The saldid bug *Saldula* was found almost exclusively along stream edges, but the lygaeid *Geocoris* occurred far from open water. Lygaeids are usually thought to be seed feeders, but *Geocoris* is known to be a predator, as are other lygaeids that utilize arthropod fallout (Ashlock and Gagne 1983). While spiders were an abundant element of the immigrant fauna, they did not establish breeding populations until several years after the pioneer beetles and, for reasons that are not yet clear, only after the appearance of pioneer vegetation.

9.6 Colonization of the Pumice Plain by Pedestrians

The presence of two cricket-like insects, gryllacridids (*Pristoceutophilus* spp.) and grylloblattids (an undescribed species of *Grylloblatta*; R.L. Crawford, personal communication), at Willow Spring (WS) on the Pumice Plain late in October 1984 is notable as the first indication of colonization of the Pumice Plain by pedestrian species. Both occur in the surrounding forestland and were collected in the blowdown zone. Although these insects may seem out of place on open tephra surfaces, the presence of similar insects in other volcanic landscapes is well documented (Howarth 1979; Thornton 2000). A year later, in 1985, yet another pedestrian, the spider-relative harvestmen (phalangids), also reached the Pumice Plain on

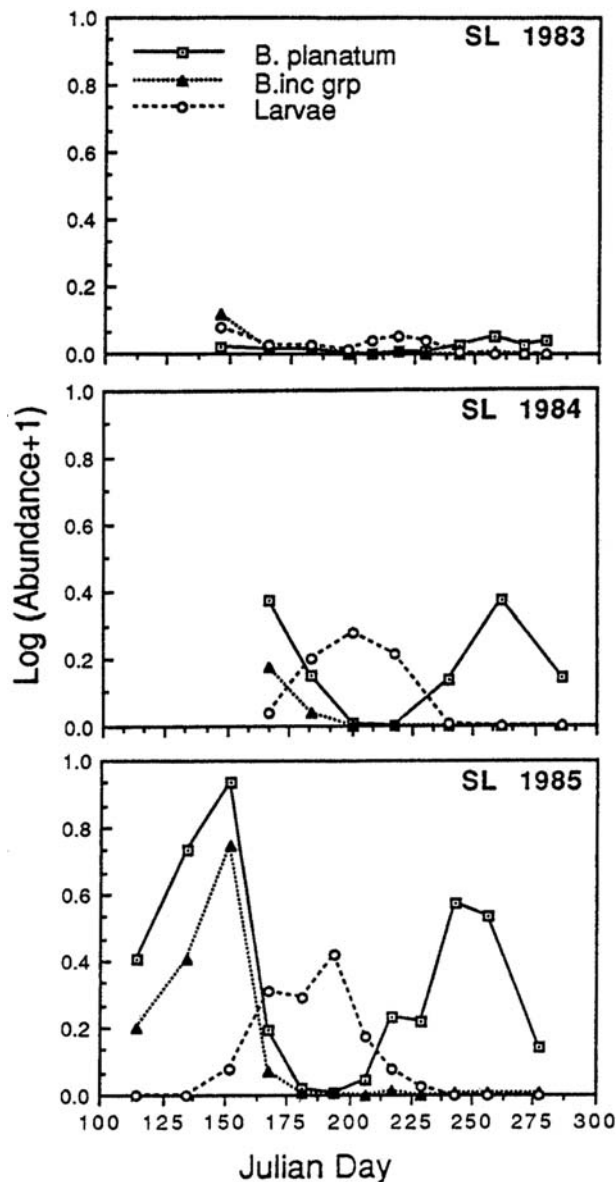


FIGURE 9.4. Relative abundance of *Bembidion planatum* and members of the *Bembidion incertum* species group, referred to as “B.inc grp” (*sensu* Lindroth 1963), mainly *B. improvidens*, and *Bembidion* larvae at sites near Spirit Lake from 1983 to 1985. Abundance is expressed as mean number of captures per pitfall day. [From Sugg and Edwards (1998); used with permission.]

foot. However, their arrival may not have been simply by walking, for harvestmen and grylloblattids are frequently encountered on snow surfaces during winter when the air temperature is above zero. Thus, they could have been blown for considerable distances across the snow surface.

Two exceptional pitfall captures of pedestrian insects warrant comment. The first is the capture of four worker ants (*Formica fusca*) on the Pumice Plain in 1982 at a site immediately below the ridge forming the northern boundary of the Pumice Plain. Ant colonies probably survived under snowpack

on the lee side of this ridge, and, although wingless, workers may have been carried to the Pumice Plain by the frequently high winds that rake the area. The second case is the capture of a single specimen of the carabid beetle *Amerizus* (= *Bembidion*) *oblongulum* on the Pumice Plain near Spirit Lake in 1983. This remarkable species is subterranean in habit, with reduced eyes and nonfunctional wing vestiges (Lindroth 1963). Again, wind dispersal seems to be the most probable source of this single specimen because it was unlikely to have survived the eruption in situ or been transported by a mobile vector, such as an elk.

9.7 Temporal Resource Sharing by Pumice Plain Predators and Scavengers

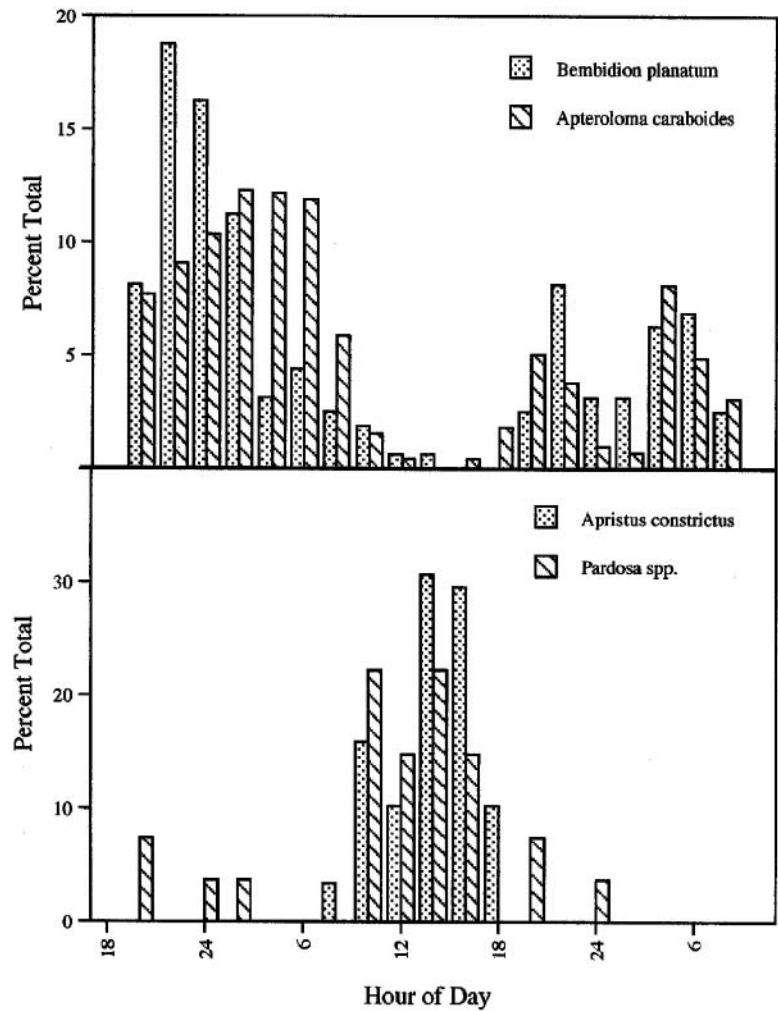
It is at first sight seemingly paradoxical that so many species of predators and scavengers should be exploiting the same fallout resource base in the blast zone. This overlap can be explained, however, at least in part, by temporal differences in activity and life-history patterns. Specific patterns of activity are clear. Some, such as *Bembidion planatum* and *Apteroloma caraboides*, are nocturnal, whereas others, such as *Apristus constrictus* and lycosid spiders, are mainly day active (Figure 9.5). Similarly, there are differences in periods of adult reproductive activity and larval development. For example, the two pioneer species that were most abundant by 1985, the agyrtid beetle *Apteroloma caraboides* and the carabid *Bembidion planatum*, do not overlap in growth and development of larval cohorts. The carabid breeds in the spring and the agyrtid in the fall (Figure 9.6). The day-active species face high temperatures and desiccating conditions during mid- to late summer, but their capacity to thrive under these conditions is, at least in part, a result of their small size, enabling them to remain in the shade of pebbles and stones and to make only brief forays into direct sunlight to capture prey.

9.8 Arthropod Immigration as a Source of Nutrient Enrichment on the Pumice Plain

As already noted, the majority of winged insects enter a dispersive phase at some point during adult life. At that point, they enter the air column and actively migrate or are carried passively on wind currents, sometimes for great distances (Drake and Gatehouse 1995). They may then be deposited by local winds at inappropriate sites from which, because of fatigue, desiccation, or low temperature, they are unable to reenter the air column. These are the arthropods of the fallout fauna, the derelicts of dispersal (Edwards 1986b) that we have observed on the pyroclastic-flow deposits of the Pumice Plain.

The organic fallout not only provides a resource for the resident predators and scavengers but also proved to constitute a significant source of nutrient elements to the site. This

FIGURE 9.5. Diurnal activity patterns as reflected in live pitfall captures of three beetles, on the Pumice Plain. *Bembidion planatum*, *Apteroloma caraboides*, *Apristus constrictus*, and wolf spiders (*Lycosidae*). [From Sugg and Edwards (1998); used with permission.]



source was particularly notable for Mount St. Helens because the newly fallen tephra was nutrient poor, and the input of nutrients from arthropod fallout could play a significant part in generating soil fertility. Of course, the pioneer plants rapidly added organic material, carbon, and nitrogen to the soil, but phosphorus and other mineral nutrients in the siliceous tephra must have come from exogenous sources. Given the low phosphorus content of plant fragments in comparison with animal tissue, we chose to evaluate the contribution of arthropods alone. The quantity and composition of this organic fallout and its significance as a source of nutrients to the initially impoverished tephra was estimated for the early posteruption years. Estimates of fallout biomass were made with fallout collectors designed to simulate the surface of the pyroclastic-flow deposits and thus to give an index of the true flux of organic matter at the surface (Edwards and Sugg 1993). After the first year, known predator and scavenger species that may have been of local origin were removed from the sample before biomass determinations were made. Thus, the data underestimate the fallout flux to the extent that some of the scavengers and predators were new arrivals. Further, large insects, such

as grasshoppers and butterflies that were not enclosed within the fallout collectors, were subject to bird predation and thus lost from our samples. Inputs as high as $18 \text{ mg m}^{-2} \text{ day}^{-1}$ were recorded for dried arthropod bodies and as high as $26 \text{ mg m}^{-2} \text{ day}^{-1}$ for nonarthropod material, consisting mainly of lichen and plant fragments. The overall average for organic fallout was in the range of $5 \text{ to } 15 \text{ mg dry wt m}^{-2} \text{ day}^{-1}$ for 100 days encompassing the summer months. Of this material, 2 to 10 mg comprised bodies of immigrants, such as aphids, flies, and a broad range of other arthropods (Edwards and Sugg 1993). Comparable figures were found by Ashmole and Ashmole (1988) on the lava fields of Tenerife and by Heiniger (1989) in the Bernese Oberland. The main source of the windborne organic fallout carried on prevailing winds to Mount St. Helens is the fertile agricultural and forest lowlands to the west and southwest, while nearer the mountain are areas of blowdown, standing dead trees, mudflows, and riparian habitats with vegetation that supports a diverse arthropod fauna, also contributing to the input of fallout to the Pumice Plain.

Experiments were carried out to determine the rate of release of nutrients from insect bodies. Mesh bags containing weighed

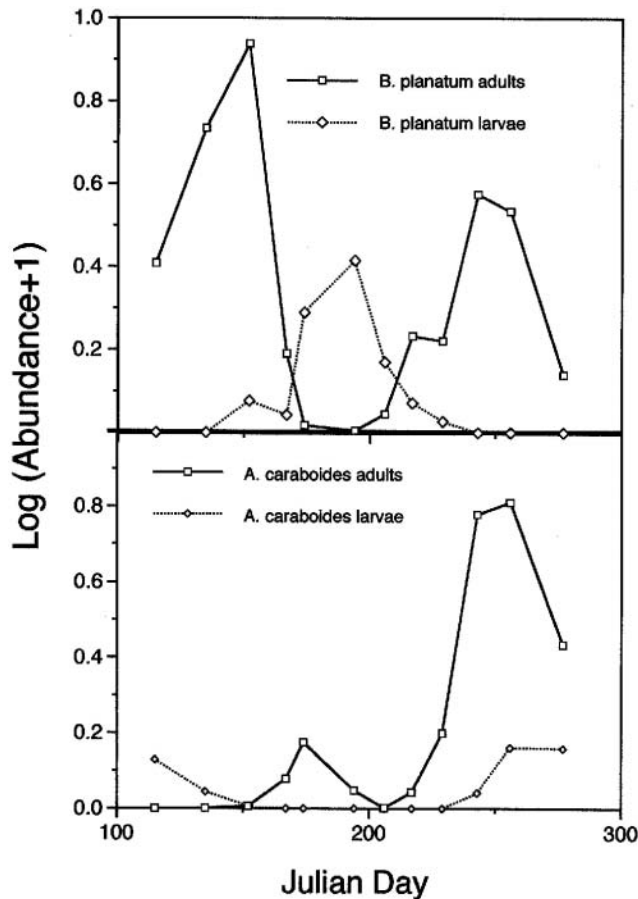


FIGURE 9.6. Annual pattern of abundance of the beetles *Bembidion planatum* and *Apteroloma caraboides*, adults and larvae, based on total numbers taken in pitfall traps on the Pumice Plain. [From Sugg and Edwards (1998); used with permission.]

amounts of dried adult fruit flies (*Drosophila melanogaster*) were placed on the pyroclastic-flow surface and lightly covered with tephra. The bags were subsequently sampled at intervals from 17 to 700 days. The nitrogen content of the insect material from bags from the field declined by 25% during the first 17 days and remained almost constant thereafter, probably because of the stability of the chitin component of the cuticle. The phosphorus content decreased by 73% during the first 17 days and thereafter by a further 10%, giving a total loss of phosphorus of 83%. Using these data, other estimates of the nitrogen and phosphorus content of arthropod fallout, and mean figures for the arthropod fallout on the pyroclastic-flow deposits at Mount St. Helens, we estimate that 80 mg fixed nitrogen and 5.5 mg phosphorus per square meter were added annually to the early posteruption surfaces. We know that these figures are minimal estimates, because data from our fallout collectors certainly underestimate net fallout. Plant and lichen fragments added their contribution, but they were not analyzed in our study.

The original pyroclastic-flow and tephra materials that formed the surface layers of the posteruption landscape

contained very little carbon, nitrogen, and phosphorus. For example, the total organic carbon and total nitrogen content of 1980 samples of pyroclastic-flow materials taken near our arthropod sampling sites were reported as 0 (Engle 1983). By 1985, the levels were still relatively low, with 0.5 to 1 g kg⁻¹ organic material, 10 to 90 mg kg⁻¹ Kjeldahl-extractable nitrogen, and 0.3 to 0.4 g kg⁻¹ phosphorus (Nuhn 1987). The measured increase must have been derived from imported material, of which arthropod fallout was a significant fraction, as revealed by our fallout collectors. The estimated rates of accumulation of total organic carbon (97.7 mg kg⁻¹ year⁻¹) and nitrogen (2.8 mg kg⁻¹ year⁻¹) in plant-free pyroclastic-flow material from Mount St. Helens (Halvorson et al. 1991a) are comparable to estimates for other volcanic areas at latitudes north and south of Mount St. Helens, for example, Mount Katmai (Griggs 1933) and Mount Shasta (Dickson and Crocker 1953). It should be borne in mind that the mean figures given here do not reflect the heterogeneity of the natural surfaces. Even on the superficially monotonous surface in the Pumice Plain area, there were many small cavities and declivities, sometimes covered by the webs of lynphiid spiders, where we found aggregations of both arthropod fragments and seeds. Seeds in these sites were thus germinating in arthropod compost.

As already noted, the source of much of the arthropod fallout must have been distant (i.e., several to many kilometers), but there was also clear evidence of redistribution of organic material within the impacted area. For example, bodies of water, such as Spirit Lake, contained a rich organic soup derived from cooked vegetation. The soup provided the substrate for massive bacterial blooms during the first 2 years after the eruption. In Spirit Lake, those blooms reached the extraordinary figure of nearly a half billion cells per milliliter (Baross et al. 1982). This bloom provided the substrate, in turn, for mosquito larvae, which were able to tolerate the anoxic condition because of their air-breathing siphon that acts as a snorkel. The prolific productivity of mosquitoes in these waters showed up in high captures in 1981 pitfall traps situated several kilometers from the nearest open water and thus provided a striking example of nutrient redistribution at the landscape scale. Although the mosquito pulse was limited to the first year or two, other aquatic insects such as chironomid midges colonized the streams and lakes and maintained more local sources of fallout; seeps acted as nurseries, and the very open landscape permitted much greater wind dispersal than one normally sees in a forested landscape.

9.9 Role of Vegetated Patches

The newly established ecological systems also provided the opportunity to ask what effect plant establishment had on the primary community. Plants certainly are the base for most food webs, providing food for herbivores, which, in turn, are available for predators. Plants also provide physical habitat, with live and dead foliage giving shelter and holding moisture.

TABLE 9.3. Totals of select taxa in 1986 from sets of five pitfall traps at three sites on the Pumice Plain, PE, PL, WS, defined in the text below.

	PE		PL		WS	
	Vegetated	Barren	Vegetated	Barren	Vegetated	Barren
<i>Bembidion planatum</i> ^a	8	143*	87	216*	174	2460*
<i>Bembidion incertum</i> group ^a	—	—	6	28*	96	128
<i>Nebria</i> spp. ^a	145	427*	41	88*	76	415*
<i>Apristus constrictus</i> ^a	1	9*	23	73**	0	127
<i>Apteroloma caraboides</i> ^a	22	245*	120	259*	156	1068*
<i>Scaphidema pictum</i> ^a	7	12	88	77	24	66
<i>Trachypachus</i> spp. ^a	—	—	20**	9	22	39
<i>Bembidion transversale</i> ^a	—	—	—	—	3	33*
<i>Bembidion dyschirinum</i> ^a	—	—	—	—	12*	0
<i>Trechus obtusus</i>	—	—	—	—	50*	2
<i>Amara</i> sp.	12**	5	32*	4	43*	6
<i>Pterostichus adstrictus</i>	32*	5	19*	0	24*	2
Aphididae (nonwinged)	267*	18	2329	4413*	12	13
Other Homoptera	41*	2	35**	9	115*	4

Aphids and other homopterans are juveniles or nonwinged adults. Lack of an entry indicates that the total number of individuals from the paired transects for the taxon was less than 10. WS, Willow Spring; PE, PL.

^aThese taxa had established breeding populations on barren surfaces by 1985.

* $p < 0.05$, t test.

** $p < 0.1$, t test.

All in all, one might assume that vegetation would act as a magnet for predators attracted to the milder microclimate and populations of potential prey. Three vegetated sites were sampled with paired sets of pitfall traps, five traps placed at approximately 10-m intervals in the vegetated surface and another five in adjacent barren tephra set 10 m from the nearest plant. One site (WS) was a stream edge with the vegetation dominated by willows (*Salix* sp.) and pearly everlasting (*Anaphalis margaritacea*). A second site (PL, which was located on the Pumice Plain, 0.8 km south of Spirit Lake) was dominated by prairie lupine (*Lupinus lepidus*) established in well-drained pyroclastic-flow deposits. The third (PE, which was located on the Pumice Plain, 0.4 km south of Spirit Lake) was vegetated with a mix of grasses and forbs.

Vegetated areas supported populations of plant-feeding insects that were potential prey for the primary community of predatory arthropods. Notable were various homopterans, such as aphids and leafhoppers (Table 9.3). Yet, although this prey base was available in the vegetated patches, those taxa initially successful in the expanse of unvegetated tephra were generally still more abundant on the barren tephra surfaces. These are species that specialize in colonization of barren ground; for them, the presence of plants spoils the neighborhood.

Bembidion planatum and *A. caraboides* were most abundant, and both showed strong preference for unvegetated surfaces (see Table 9.3). Among the taxa that were reproductively successful on the barren tephra by 1985, a mixed response was seen only with *Trachypachus* spp. and the tenebrionid *S. pictum*, with higher numbers in the vegetation at the lupine patch site, PL (Table 9.3). Other carabids were more abundant on vegetated surfaces, namely *B. dyschirinum* and *T. obtusus* at the stream-edge site, WS, and *P. adstrictus* and *Amara* sp. at

all sites (Table 9.3). The latter two taxa are of interest because they are characteristic of field habitats (Lindroth 1966, 1968) and were assumed to represent taxa that would become more dominant as vegetation increased, a prediction confirmed by later sampling (see Parmenter et al., Chapter 10, this volume).

The availability of prey by the secondary production of herbivores is not limited to the immediate area with vegetation cover. This pattern is made clear by results from site PL, where senescing lupines resulted in a wave of aphid pedestrian dispersal, moving in great numbers from the dying plants into the unvegetated surroundings and accounting for the greater number of aphids caught in the barren pitfall transect at the site (see Table 9.3). Thus, even if predatory arthropods are disinclined to move into vegetation, islands of plant establishment can provide an available food supply, supplementing arthropod fallout in the surrounding area.

The importance of arthropods in the larger context of primary succession is not limited to the brief time preceding significant vegetation establishment. The course of plant succession itself can be affected by insect populations (Fagan and Bishop 2000; Bishop 2002; Bishop et al., Chapter 11, this volume).

9.10 Conclusions: Primary Succession and Aeolian Communities

We conclude that the first stage of terrestrial primary succession, the colonization of the pyroclastic-flow zone, was initiated at Mount St. Helens by an assemblage of predatory and scavenging arthropods. The influx of unsuccessful immigrants, the “derelicts of dispersal,” provided the resource base. The

sustenance of communities by organic matter from external sources is well known for aquatic communities; leaf fall, for example, can be the major input to streams (Teal 1957). Aeolian communities are the terrestrial analogue and are widespread in alpine and desert areas (Edwards 1986b, 1987). The prevalence of arthropod dispersal and the magnitude of the biomass reflected in trap captures on the pyroclastic-flow deposits of Mount St. Helens (Edwards and Sugg 1993) imply that this pattern is a widespread and perhaps a general one for terrestrial primary successional habitats, such as retreating glaciers, landslide scars, flood-scoured river bars, and post-eruptive volcanic surfaces. These environments dramatically exemplify the importance of spatial dynamics in ecology.

The continuing production of new mineral surfaces by crustal movement, volcanic activity, glacial retreat, isostatic rebound, and floods provides habitat for specialist arthropods, which, along with microorganisms, are the pioneer colonists, often preceding plant colonization by considerable periods. Except for very recent studies, for example, Kaufman (2001), the role of these pioneers has been largely neglected in studies of primary succession, where the emphasis has generally been on plants. We propose that comparable pioneer predatory and scavenging arthropods operate around the entire Pacific Ring

of Fire and other volcanic areas, wherever volcanic activity produces new surfaces. Mount St. Helens has erupted at least 20 times in the past 4500 years (Crandall and Mullineux 1978), and in 1980 it was still recovering from the previous eruption 180 years earlier. With every eruptive cycle, ecosystems are destroyed, or altered and the cycle repeats, with pioneer arthropods playing their part in Act 1, Scene 1, of the succession play as consumers of the ubiquitous fallout of arthropod aerial plankton.

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