5 · *Life histories of early colonists*

5.1 Introduction

Primary succession begins with the input of seeds, spores, animals and organic matter or by vegetative expansion from adjacent habitats. Distance alone plays a major role in determining what reaches a new site, so the landscape context of a new surface is crucial. Most species fail to disperse beyond some short distance and the total propagule density is low, so chance plays a large role in governing which species reach isolated surfaces. Thus the initial vegetation of isolated sites can be highly variable. Early species composition is governed by a complex suite of interacting forces, often leading to a chaotic mosaic of early species association (see sections 5.3.4 on predictability and 5.4.1 on stability).

In this chapter, we explore colonization and establishment phenomena and their consequences for primary succession. We focus first on pre-dispersal effects such as pollination and seed set, then on dispersal mechanisms. Finally, we explore the factors that affect establishment and the repeatability of the first species assemblages. Most primary seres are colonized by propagules dispersed by wind, water or animals. We ask, 'How do different degrees and types of isolation and substrate types affect colonization?' We then examine the factors that permit establishment and the consequences of differential longevity.

5.2 Pre-dispersal considerations

Primary succession lets us evaluate community assembly without the confounding influences of residual vegetation. We can search for patterns among sites of similar origin and between sites created by different processes. In this way, critical factors can be highlighted. As succession unfolds, controlling processes such as competition become increasingly similar to those of secondary succession.

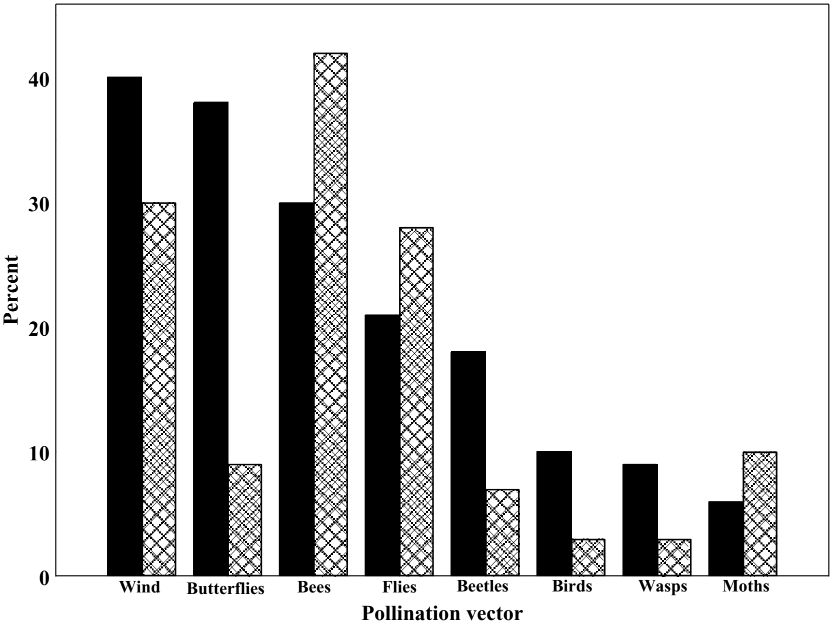

Fig. 5.1. Proportion of plant cover pollinated by different vectors in forests of the western (hatched bars) and eastern (solid bars) Cascades. From del Moral & Standley (1979). Totals exceed 100% because several taxa have more than one pollination mechanism.

5.2.1 Pollination and seed set

Pollination biology has rarely been studied in a successional context. Major pollination vectors that augment self-pollination include wind, insects, birds and bats. Climatic features and the successional stages of surrounding landscapes influence the pool of potential pollinators. The pollination mechanisms of most plant species can be inferred from flower morphology, and direct observations normally confirm these inferences. For example, del Moral & Standley (1979) compared the probable pollination vectors in open, dry conifer forests (East Cascades) to moist conifer forests with closed canopies (West Cascades). They demonstrated that dry coniferous forests had more beetle-, bird-, butterfly- and wind-pollinated species than did the moist coniferous forests, which were dominated by species pollinated by bees, flies and moths (Fig. 5.1). These differences often lead to a flora with different dispersal type spectra.

Off-site pollination

The successional status of the surrounding landscape affects colonization rates and types of pollinator. For most primary seres that start within landscapes experiencing early secondary succession, pollination rarely limits the availability of suitable colonizers because pollinators of such species are common. However, if vegetation adjacent to the new site is mature and contrasts sharply with the new primary surface, it may have few pollinators that can service typical colonizing species. Off-site pollen and pollinator limitations may slow early primary succession, although we know of no studies of this phenomenon.

On-site pollination

Recently formed sites normally lack a diverse fauna so the absence of pollinators could limit the expansion of non-autogamous flowering colonists. Perhaps for this reason, successful pioneers are usually dominated by wind- and self-pollinated (autogamous) species. Rydin & Borgegård (1991) showed that most pioneers of recently formed islands in Sweden were self-pollinated. On Mount St. Helens, 18 of 21 invading species were either wind-pollinated or potentially self-pollinated (del Moral & Wood, 1993a). The seed set of the widespread nitrogen-fixing pioneer shrub *Dryas*, found on glacial moraines throughout subarctic and arctic habitats, was unaffected by pollinator limitations (Wada, 1999). Such findings suggest that pollinator limitations rarely affect the rate or trajectory of early succession in temperate or arctic settings (cf. Prach *et al.*, 1997). This is partly due to the frequency of species that are self-compatible (Rydin & Borgegård, 1991) and to the usual general nature of pollinator requirements of pioneers (Larson & Barrett, 2000). However, pollinator limitations may be important for some animal-pollinated, obligate out-crossing tropical species or in some specialized habitats such as mangroves. For example, seed set of two tropical *Ficus* tree species found on Anak Krakatau (a recently formed volcanic island in Indonesia) was reduced significantly by pollinator shortages (Compton *et al.*, 1994). They did not suggest successional consequences, but did emphasize consequences for frugivorous birds and bats. The absence of pollinators must alter vegetation structure in mature tropical forests. Vertebrate and invertebrate pollinators on tropical islands are among the most threatened species (Cox & Elmquist, 2000). The loss of these pollinators strongly suggests that tropical primary succession in the future will not resemble that of the past. Partial self-compatibility of the widespread colonizing tree *Metrosideros* on volcanic surfaces in Hawaii led to adequate levels of seed production (Carpenter, 1976). However, higher levels of seed production were obtained when endemic birds were permitted access to flowers. In contrast, the almost complete self-incompatibility of the giant perennial forb *Argyroxiphium* on the upper slopes of Hawaiian volcanoes has led to sharp declines in plant populations as the native insect pollinators have declined (Carr *et al.*, 1986; Powell, 1992). The absence of suitable pollinators in the recovery of isolated tropical sites should be considered when rehabilitation of tropical sites is being planned (Walker & Powell, 1999a) (see section 8.3.1 on dispersal).

On-site seed production

Stressful habitat factors can limit the seed production of invading species. A plant may become established, but be prevented from flowering or producing mature seeds owing to soil infertility or drought. This pattern was observed repeatedly on Mount St. Helens (del Moral, 1993b) where the forb *Epilobium* is common, but is rarely observed to mature on barren pumice (Fig. 5.2A). In contrast, this and other pioneer species thrive on residual soils (Fig. 5.2B). Restoration ecologists recognize that stress retards recovery, but their rationale has involved biomass production, not reproductive failure. The success of rehabilitation projects may be improved if more attention is paid to reproductive success, not just survival and vegetative expansion.

5.2.2 Seed banks

Seed banks are crucial to secondary succession, because they influence initial community composition. The numbers of species and seedlings produced from seed banks decay with time (Thompson, 1978; Roberts & Vankat, 1991) unless they are replenished by the same species. During primary succession, the opposite occurs: seed density and species richness of the seed bank increase as new species invade and the populations of each species increase and reach maturity (Houle & Phillips, 1988; Looney & Gibson, 1995; Duncan & Duncan, 2000), although the seed bank initially may not resemble the developing vegetation (Titus, 1991). Grandin & Rydin (1998) described the seed bank on islands that formed in Lake Hjälmaren in 1882. The seed banks in the most deeply buried soils were pioneer species (annuals with good dispersal), whereas surface seed banks at each vegetation analysis from 1886 to 1995 were similar to the vegetation at the time of analysis. The similarity between the vegetation

Fig. 5.2. Epilobium angustifolium plants. (A) Plants that established readily on deep pumice failed to flower for many years. (B) Plants growing on shallow pumice where roots could reach the old soil flowered and set seed profusely.

in 1995 and the seed bank declined with soil depth, and several seed bank species no longer occurred in the vegetation. Clearly, the soil retains a memory of previously occurring species, but where conditions change rapidly, recruitment must come from outside the system.

No seed bank may develop in dynamic seres where surfaces are eroded or deposition is rapid (Walker *et al.*, 1986). Tekle & Bekele (2000) found little similarity between compositions of the seed bank and the vegetation on eroded Ethiopian hills. They suggested that this was because disturbance affects vegetation and seed banks differentially. In Hawaiian forests, a similar lack of congruence occurs. Most plant cover and seed rain was from native species but most of the seeds in the seed bank were from alien species (Drake, 1998), which suggested that future disturbances would favor establishment of these aliens. Parker *et al.* (1989) support the proposition that disturbance integrates many variables that can explain disparities between vegetation and seed bank composition. One quite unusual disparity occurs on cliff faces in Ontario, Canada. Here, seeds are transported from the undisturbed forest above the cliff by wind and gravity and accumulate on these exposed cliffs to produce higher species richness for the seed banks (Larson *et al.*, 2000).

Severe disturbances remove the seed bank, eliminating any signal to the new sere. However, seed banks from pre-existing vegetation sometimes can be important in primary succession. Propagules can be transported with the disturbance (e.g. landslides, glaciers, lahars or dunes) or remain in place until they are exposed by erosion. Soils with viable seeds, or viable spores of moss, ferns and microbes, are often associated with melting ice and can have an impact on primary succession on Antarctic fell fields (Smith, 1993) or glacial moraines (Matthews, 1992). Seeds in the lower deposition zone of landslides can accelerate primary succession (Guariguata, 1990; Walker *et al.*, 1996) and lahars may incorporate seeds that start primary succession (Nakashizuka *et al.*, 1993). Shifting dunes are an unlikely place to find seed banks (Ehrenfeld, 1990), but buried seeds do persist in some dune systems (Zhang & Maun, 1994). As a sere develops, its seed bank changes and can influence later stages and trajectories.

Seed banks that remain *in situ* can be exposed when water levels fall. This occurred when Spirit Lake (Mount St. Helens) was lowered to expose sediments that rapidly developed wetland vegetation (Titus *et al.*, 1999). *Juncus* and *Scirpus* graminoids, which presumably existed as seed banks, dominated succession. A Norwegian lake lowered in 1987 revealed barren sediments that contained a large seed and spore bank of species incapable of germinating before the draw-down (Odland, 1997). Similarly, the removal of sod in dune slack vegetation in The Netherlands revealed a dynamic seed bank in the soil layer containing both viable early successional species and accumulating late successional species (Bekker *et al.*, 1999).

A special type of seed bank is the short-term persistence of seeds in the canopy (Noble & Slatyer, 1980). For example, some *Pinus* trees retain closed cones for several years. Many tree species retain mature seeds within protective fruits for long periods prior to dispersal. Should a major destructive event occur that either sterilizes the soil or deposits a new substrate without killing these arboreal seeds, they may be shed on to a receptive surface. Lahars and tephra deposits may kill trees while leaving them relatively intact with a viable seed crop in the canopy. A lahar on Mount Rainier (Washington, U.S.A.) smothered the roots of existing trees without uprooting them. Because the riparian *Alnus* trees retained mature fruit, viable seeds subsequently were shed upon a virgin surface, leading to rapid recolonization (Frenzen *et al.*, 1988). Similar events occurred on Mount Ksudach (Kamchatka, Russia) where tephra 1–3 m deep killed *Betula* and *Alnus* trees, yet seeds persisted in the canopy. Because the substrate was deep and infertile, few of these seeds germinated successfully, but on the margins of this deposit many stems were new seedlings, not regenerating adults (Grishin *et al.*, 1996).

5.2.3 Vegetative reproduction

Vegetative expansion along margins can accelerate primary succession in small sites such as rock faces, landslides and animal feces. This diffusion has strong spatial constraints. Diffusion can also be important where the disturbance affects a narrow corridor (e.g. a riparian zone). For example, vegetative reproduction by such herbs as *Phragmites*, *Iris* and several *Carex* sedges permitted rapid recolonization along the banks of the Rhône River (France; Henry *et al.*, 1996). Yet vegetative expansion was limited by inundation and physical damage near a Canadian river channel and by silt burial and perhaps decreased soil aeration at further distances from the channel (Douglas, 1987).

After the initial establishment from seed, vegetative expansion permits a species to expand and thrive in a harsh habitat where further seedling establishment would be rare. On pumice and lahars of Mount St. Helens, *Penstemon* and *Luetkea* (Fig. 5.3) are two common species of subshrub that have increased disproportionately by clonal expansion after their initial

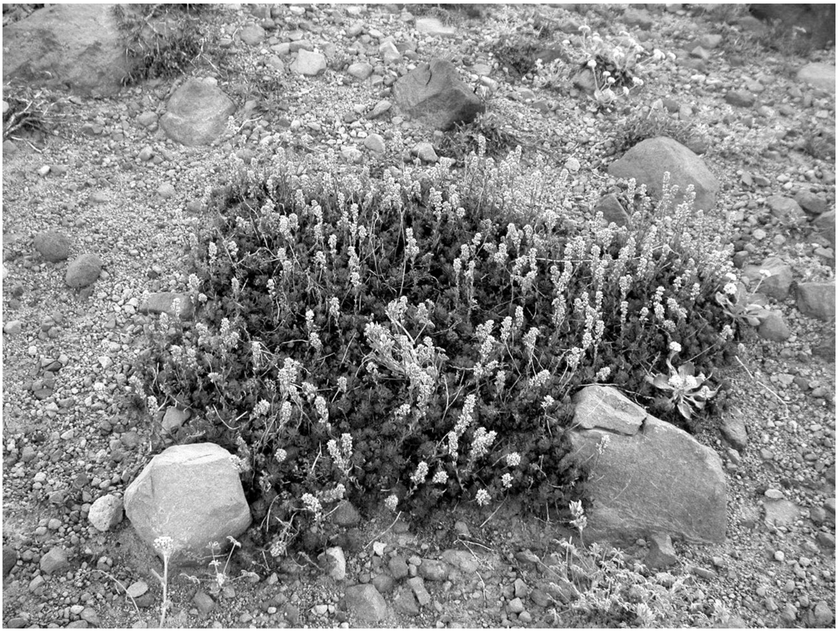

Fig. 5.3. Luetkea pectinata on pumice at Mount St. Helens. This species is typical of those that have expanded greatly by vegetative means.

establishment (del Moral, 1999a; del Moral & Jones, 2002). Vegetative expansion is very common on young volcanic landscapes, with small shrubs in the Ericaceae particularly common in temperate and boreal regions.

There is a gradation between primary and secondary succession and many disturbances can create a mosaic within which the two form a matrix. Residuals may survive immediately adjacent to barren sites, but seeds of residual species may not be adapted to establishment on primary surfaces (Fuller, 1999). However, vegetative expansion of residuals along the edges of lahars or landslides, or in erosion features (Fig. 5.4) initiates succession sooner than otherwise possible. In 1980, buried roots of the forb *Lupinus* sprouted on lahars on Mount St. Helens to form 'nascent foci' for subsequent expansion. In Puerto Rico, the fern *Dicranopteris* invades landslides (Walker *et al.*, 1996), while on Mauna Loa, Hawaii, *Dicranopteris* dominates the understory during primary succession because of its strong rhizomatous growth (Russell *et al.*, 1999) (Fig. 5.5). The balance between sexual and vegetative reproduction therefore depends on residual plant parts, life forms and physical conditions. On an Alaskan

Fig. 5.4. Erosion removed silt and permitted the recovery of plants, which subsequently expanded into the barren regions (Pine Creek, Mount St. Helens, 1980).

floodplain, Krasny *et al.*(1988) found vegetative reproduction dominated in unstable (erosive or frequently flooded) and dry sites. Seedlings were only important on mesic and stable surfaces.

5.3 Dispersal

Dispersal is an essential adaptation because the worst place for most seeds to fall is beneath a parent (Rey & Alcántara, 2000). Most plant species have dispersal abilities that permit only local expansion (diffusion) because short-distance dispersal confers sufficient advantage for success. Few species are adapted for routine long-distance dispersal. After a catastrophe, however, dispersal from a distant point must occur before ecosystem development can proceed. Therefore, early seres are 'donor controlled' (Wood & del Moral, 1987). As the surface is colonized, it comes under local control: the first colonists produce the great preponderance of new seedlings in the immediate vicinity. In general, poor dispersal ability means that relatively few species can spearhead an invasion. However, because these few mobile species have difficulty dominating barren primary successional sites, the early trajectory still may be determined by species that are less able to disperse but that arrive before their establishment

Fig. 5.5. Dicranopteris ferns invade (A) landslides in Puerto Rico and (B) forest understories in Hawaii.

can be inhibited. In this section, we explore landscape factors that affect dispersal into newly formed habitats.

5.3.1 Dispersal parameters

Distance alone can affect species that will colonize. Therefore dispersal affects all aspects of primary succession. We summarize model approaches to dispersal and investigate the effects of distance on the kinds of species reaching a site. We then summarize the experimental work documenting seed shadows and ask how models help to explain colonization.

Dispersal models

Empirical studies suggest that most species have limited dispersal distances (Malanson & Cairns, 1997). These studies imply that primary succession should be slow and constrained by dispersal limitations. Although this may be true for dispersal into stressful habitats in a short time frame, pollen records indicate that tree species migrated much faster after the last glacial retreat than experimental data suggest. For example, Fastie (1995) observed that *Picea* trees migrated 400 m yr^{-1}. This rate is consistent with the rate needed to explain post-glacial northward migration rates of

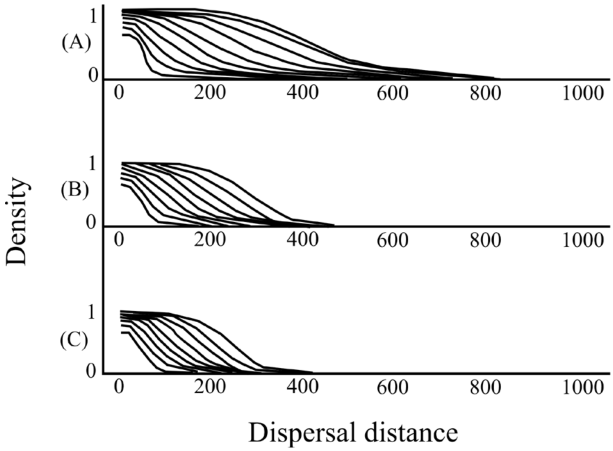

Fig. 5.6. Models of population spread under different assumptions. The average dispersal distance is the same for each case, but in the top panel the maximum distance is greater; this gives rise to a population with an accelerating rate of spread. From Clark *et al.* (1998). Density and distance units are arbitrary.

temperate forests based on the pollen record. Reid's paradox (Clark *et al.*, 1998) describes the conflict between usually observed migration rates and dispersal rates calculated in experimental studies. Clark *et al.* (1999) advanced a solution to this paradox, although we note that the presence of relict sites is not precluded by this solution. They proposed a mixed dispersal model that fits short distance dispersal patterns well, but which also has a 'fat' tail, meaning that a measurable fraction of the seeds falls at long distances (Fig. 5.6) and are capable of establishing populations that are disjunct from the main population. Species are characterized by their dispersal efficiency. The '2Dt' model of Clark *et al.* (1999) combines local with long-distance dispersal models and assumes that the Gaussian distance factor varies randomly. It predicted seed rain more accurately across a range of species from several biomes than did the classical model. The model predicts that many species can migrate long distances in the absence of barriers. It also predicts that migration is characterized by long jumps followed by expansion from the locus of establishment. These 'nucleation' processes are common in primary succession (Clarkson & Clarkson, 1983). Bullock & Clarke (2000) suggested another way around Reid's paradox. They measured seed dispersal in several low heath species and found that seeds were trapped up to 80 m from the shrubs. These authors suggested that better sampling protocols and better models would indicate that most species can disperse over greater distances than often assumed.

Augspurger (1986) modeled the effects of seed morphology on dispersal ability based on aerodynamic qualities and mass. For 34 tree species, she determined mean dispersal distances of 22 to 194 m, assuming release from the canopy in a modest wind. Although the tails of typical curves with means in this range would be substantial, this study did not account for the presence of adjacent plants that would further reduce dispersal distances. Indirectly, this study suggests that invasion of primary sites in the moist tropics will be dominated by species in the immediately adjacent vegetation and therefore will be highly variable. Parrotta & Knowles (1999) confirmed this expectation on mined surfaces in Brazil. These conclusions based on trees apply more strongly to low shrubs and herbs because these growth forms normally disperse seeds from lower heights within a dense canopy.

Empirical studies

Whereas models help to explain enigmas about dispersal, empirical studies of seed dispersal permit direct comparisons among species and estimates of seed rain. Most wind-dispersed species disperse only for short distances. Distance–dispersal curves rapidly approach zero. The tails of such curves are imprecisely known, but tails determine the rate of migration and the chance of an occasional single jump. Seed shadows vary spatially and temporally and are difficult to predict. The large variability found in seed trap studies (Rabinowitz & Rapp, 1980; Wood & del Moral, 2000) implies that seed arrival early in succession is stochastic. Fort & Richards (1998) found that sandy flats (playas) received a substantial seed rain (over 50 seeds m^{-2} d^{-1}) at distances over 700 m from the source. However, this unusual seed rain involved high winds, smooth surfaces and few barriers. Platt & Weis (1977) found that the mean dispersal distance could be predicted according to seed appendages. Species without plumes were restricted to less than 3 m; those with large plumes averaged about 20 m. All these dispersal curves had fat tails, suggesting that jump dispersal over long distances is probable.

Studies by Nathan *et al.* (2001) developed a detailed wind-dispersal model and tested it empirically using *Pinus halepensis*. They found that the model accurately predicted dispersal patterns determined by seed traps. Wind velocity was more important than such biological factors as the height of seed release, terminal fall velocity and number of seeds released. These authors suggested that synchronization of seed release with strong winds is the most effective biological mechanism to increase dispersal distance.

Table 5.1. *Summary of types of seed dispersal*

Dispersal mechanism	Variants	Examples	Relative distance
Passive mechanisms			
Gravity (*barochory*)		*Malus*, *Juglans*	Very short
Wind (*anemochory*)	Minuscule	Orchidaceae, Ferns	Very long
	Parachute	Asteraceae, Salicaceae	Long
	Parasail	Aceraceae, Pinaceae, Betulaceae	Moderate
	Tumbler	*Polygonum*, *Salsola*	Short to moderate
Water (sea = *thalassochory*)		*Cocos*, *Rhizophora*, *Cakile*	Very long
Active mechanisms			
Ballistic (*ballochory*)	Dehiscent	Brassicaceae	Short
	Explosive	*Eschscholtzia*, Fabaceae, *Arceuthobium*, *Impatiens*	Short
Ants (*myrmecochory*)		Fabaceae	Short
Vertebrates (*zoochory*)			
Birds	Internal (*endochory*)	*Juniperus*, *Solanum*	Moderate to long
	External (*epichory*)	*Quercus*, *Lemna*, *Juncus*	Moderate
Mammals	Internal (*endochory*)	Lauraceae, *Cistanthe*	Short to moderate
	External (*epichory*)	*Bidens*, *Ambrosia*, *Plumbago*, *Castanea*	Moderate to long
Humans (*anthrochory*)		Weeds	Moderate to extremely long

5.3.2 Dispersal mechanisms and their consequences

The nature of dispersal provides the first hint about how a sere will unfold. Here, we will discuss both passive and active dispersal mechanisms. We summarize these dispersal mechanisms in Table 5.1. Relative distances in the table are typical of local dispersal, but any species may achieve extremely long dispersal distances by a variety of contingent factors (e.g. hurricanes and airplanes).

Passive dispersal

Passive dispersal agents are those powered by external, non-biological forces such as wind, water and gravity. Willson *et al.* (1990) summarized the distribution of dispersal adaptations in 35 studies of temperate zone plant communities to produce dispersal spectra (percentages of a flora) for each category. They categorized very small seeds, scatter-hoarded seeds and censer plants (wind-shaken seeds from pods) as having no particular mechanism because they could not categorize the mechanism based on morphology alone, but most of these would be dispersed passively. They found unaided and wind-dispersed species to be the most common, whereas ballistic mechanisms and transport by animals were rare. They found that frugivore dispersal varied from 10% of the flora in most studies to 60% in New Zealand. Primary succession near glaciers had almost no frugivore-dispersed species, perhaps because moraines rarely attract birds. Animal dispersal increased during succession in this study as dispersal mechanisms became more specialized. In contrast, early primary succession is dominated by wind-dispersed species (cf. Nakamura, 1984; Chapin, 1993).

The spores of lower plants are effectively wind-dispersed because they are minuscule and buoyant, so mosses or ferns often start primary succession in mesic habitats (Griggs, 1933; Brock, 1973; Lewis Smith, 1993; L. Walker, 1994). In some seres, such as on glacial moraines (Worley, 1973; Matthews, 1992) and in disturbed arid lands, cryptogamic crusts form and stabilize the exposed surfaces (see section 4.3.1 on soil texture). Although the stabilizing effect of crusts is important, crusts are not usually required for succession. Vascular plants routinely colonize barren substrates without indirect facilitation (Winterringer & Vestal, 1956; Veblen & Ashton, 1978).

Wings or other buoyancy mechanisms facilitate long-distance dispersal, particularly during intense storms (e.g. hurricanes). Often overlooked are species whose fruits (or the entire plant) tumble across the ground, sometimes for long distances or across formidable barriers. *Polygonum* forbs produce many small fruits and then the entire shoot dries and breaks from the rootstock. In this mode, seeds can travel several kilometers in a strong wind. The widespread annual forb *Salsola* has a similar tumble dispersal method and is an effective colonist of newly exposed surfaces such as mined lands or road embankments in arid climates (Vanier & Walker, 1999). Some taxa have prodigious dispersal abilities. The Orchidaceae possess tiny seeds that form a major component of the aeolian seed pool, along with ferns, some mosses and a few animals. Empirical (Kalliola *et al.*, 1991; Kadmon & Pulliam, 1995) and theoretical (Clark *et al.*, 1999) studies agree that wind dispersal can provide longer jumps than animal-mediated dispersal (but see below).

Rivers and ocean currents effectively move propagules, but usually only to the shore. Seeds and flotsam arrive at the beach, but usually do not advance inland. Andersen (1993) reported that water-dispersed species dominated the Danish coast, but were restricted to the strand. Only 23 species reached the new volcanic island of Surtsey (1963), 30 km south of Iceland, by 1992. Six were sea-borne (Fridriksson & Magnusson, 1992) and the remainder wind- and bird-dispersed. On Rakata (Indonesia), sea-dispersed species dominated immigration during the first 40 yr. Thereafter there were few water-dispersed species that had not yet arrived and there were few open habitats that could readily be colonized (Whittaker & Jones, 1994a).

Freshwater dispersal typically dominates newly formed islands. In a Swedish lake formed in 1882, 42% (47 species) were transported by water (Rydin & Borgegård, 1991). For many riparian species, there is no alternative to water transport. Johansson *et al.* (1996) found that species with the best floating mechanisms were most frequent along rivers (Sweden). They also found that terrestrial barriers could have profound effects on early communities. Floods and streams normally disperse riparian species to initiate succession, maintain gene flow and replace species losses. When passive water dispersal was disrupted by dams (Sweden), mean richness in each impoundment was lower and the between-impoundment variation higher than on a free-flowing river (Jansson *et al.*, 2000). Water also can move seeds over ice and snow, to cross otherwise unbridgeable barriers and deposit seeds in unlikely places (Ryvarden, 1971, 1975).

Some taxa disperse actively. Dehiscent species produce seeds within fruits that split. Examples include mustards and some geraniums. The latter produce achenes that can bury themselves. More dramatic are species that explode with little provocation to disperse their seeds up to 2 m from the parent (e.g. *Cytisus* shrubs and *Eschscholtzia*, *Euphorbia* and *Lupinus* forbs).

Active dispersal by animals

Although primary succession is usually initiated by wind-dispersed species, birds and small mammals often transport large seeds (e.g. *Pinus* and *Fagus* trees) that colonize bare substrates (Grubb, 1987). Animal dispersers are especially important in the tropics. Birds transport seeds moderate distances and have even transported seeds between hemispheres. Many birds are tireless frugivores, resulting in endozoochory. Inedible seeds pass through the gut to emerge primed to germinate in a nutritious spot. Wetland species are transported in mud clinging to wading birds (epizoochory). This directs dispersal from one wetland to the next. Other plants produce large seeds that are transported and cached by species of woodpeckers and related birds. *Quercus*, *Nothofagus* and *Castanea* trees benefit from seed burial by birds. Wilkinson (1997) suggested that many plants that are considered wind-dispersed might be dispersed over longer distances by birds. Travel by exploring naïve birds, carrying seeds in odd directions, may be more important than migrations and could explain how species with limited dispersal ability migrate rapidly after glacial retreats (Clark, 1998).

Mammals transport seeds and fruits both internally and externally. Primates (Chapman & Onderdonk, 1998) and bats frequently disperse tropical fruits after eating them. Fruit bats can transport seeds up to a few hundred kilometers (Shilton *et al.*, 1999) and the absence of bats can slow or alter succession (Whittaker *et al.*, 1997). Ungulates transport seeds and defecate them far from the source in fertile clumps (Wood & del Moral, 2000). The loss of many large herbivores from the Americas at the end of the Pleistocene has surely altered vegetation patterns and successional pathways. In addition, the reintroduction of livestock has resulted in significant changes in plant dispersal patterns. Weedy plants are now routinely distributed along trails in pristine areas via the dung of horses (Campbell & Gibson, 2001). Animals also transport seeds externally with barbs, spines or sticky glands, as dog owners and cattle herders know. Among other oddities is the transport of seeds across long oceanic distances by tortoises (Fenner, 1985) and the dispersal of cactus by cattle.

Ants move seeds that have elaiosomes (attached lipid bodies) for short distances. More than 70 plant families include elaiosome-bearing (myrmecochorous) species, with many in Australia and South Africa. Hughes & Westoby (1992a,b) demonstrated that these seeds were normally transported less than 4 m and that seed predation by ants was high. Ants play only a small role early in most primary seres.

Humans are the most adept – if often unconscious – seed dispersers and merit special mention. We have reshaped the biological landscape by the global transport of biota. Plants that humans introduce either intentionally or inadvertently are often wind-dispersed, although there are many examples of animal-dispersed introductions in both temperate (e.g. *Rubus* shrubs and *Crataegus* trees) and tropical (e.g. *Lantana* shrubs) habitats. However, species that successfully invade new habitats usually do not have exceptional dispersal abilities. Newly formed surfaces will receive immigrants from the immediate surroundings regardless of where the colonists originated. Therefore, previous dispersal of plants to the surrounding landscapes by humans will strongly affect early primary succession because the colonists will be drawn largely from the immediate surroundings.

Humans also create dispersal corridors of many types, most of which facilitate species well adapted to disturbed or open habitats. Transportation corridors such as railway and highway edges offer abundant opportunities for ruderal species (Tikka *et al.*, 2001). Power transmission corridors often traverse undisturbed habitats, permitting species otherwise barred from undisturbed landscapes to invade natural plant associations.

Dispersal of animals

Animals are important vectors for plants, but of course they also must disperse into new habitats if complete ecosystems are to develop. Wind is a powerful force for dispersal that molds early ecosystem development (Howarth, 1987; Edwards, 1988; Ashmole *et al.*, 1992; Edwards & Sugg, 1993; Antor, 1994; Sugg & Edwards, 1998). Jet streams and storms transport aerial plankton that may fortuitously find a barren site (Greenslade, 1999); such waif dispersal also occurs in water (Cheng & Birch, 1987). Both the adult and reproductive stages of animals (eggs or larvae) are routinely transported. Animals often reach a site before seeds germinate and establish pre-vegetation communities (Howarth, 1979; New & Thornton, 1988; Thornton *et al.*, 1988). Spiders invaded pumice barrens on Mount St. Helens in massive numbers, although only six of 125 observed spider species established viable populations (Crawford *et al.*, 1995). Initially, without plants or prey, spiders ate one another. Along with pollen, dust and arthropods, spiders contributed significantly to early soil development. Spiller *et al.* (1998) found that spiders recolonized small islands in the Bahamas immediately after destruction by a storm surge. They also suggested that the lack of lizards was due to their poor dispersal ability. L. R. Walker (pers. obs.) found spiders landing on still warm lava in Hawaii, an example of precocious 'neogeoaeolian' invasion.

Extremely isolated islands such as New Zealand, Hawaii and the Galápagos lacked terrestrial mammals before human colonization. Less isolated new islands such as Anak Krakatau still lack monkeys, but they could be expected to reach there eventually by rafting. Many islands contain terrestrial animals that established by swimming narrow water barriers, but most populations are relicts that have persisted on land bridge islands. For example, foxes on Santa Cruz Island (California), a subspecies of the mainland population, are believed to be relicts cut off from the mainland by the rising post-Pleistocene seas.

Although flightless land vertebrates have difficulty in crossing larger water barriers, they sometimes manage impressive feats. Deer and bears, for example, can swim several kilometers to reach islands. Normal movements or seasonal migrations may introduce large animals to barren sites, but most flightless terrestrial animals require assistance to colonize isolated barren sites. Rafting on mats, trees or other flotsam provides an avenue for animals to reach developing sites (Fig. 5.7). Rafting is a lottery whose winners may include rodents, lizards and monkeys. Small mammals will explore primary surfaces, but establishment cannot occur until plants develop or there are relict sites that offer refuge.

Many animals disperse actively as part of their normal movements and migrations or to seek new habitats. The migrations of birds (e.g. golden plover, ruby-throated hummingbird and many swallow, sparrow and finch species), bats (e.g. *Lasiurus*, a species of which occurs in Hawaii) and some insects (e.g. the monarch butterfly) cover remarkably long distances. These and many other insects, birds and bats colonize new habitats and may be important vectors for plants colonizing new surfaces on islands. Insects may reach barren sites before plant development, hastening soil development by introducing carbon and nitrogen. Birds are attracted to oases or refugia and contribute to early ecosystem development by importing nutrients and seeds. The endangered Hawaiian goose (nene) is an important disperser of the native *Vaccinium* shrub on new volcanic surfaces (Mueller-Dombois, 2000). In the tropics, the absence of a bat species can limit pollination or seed dispersal in figs, thus altering the succession (Thornton, 1996). Bats can cross narrow water barriers, but they are normally absent until the vegetation matures. Accidental bird and bat dispersal can have cascading effects on succession by introducing unlikely plants early in the colonization process. Early introduction may lead to unusual trajectories by the priority effect (see section 7.1 on types of trajectory). Other vertebrates may cross short distances to reach refugia. These animals must navigate unsuitable habitats to reach even marginal ones. Deer mice (*Peromyscus*) crossed wide barren areas to recolonize relicts and wetlands on Mount St. Helens (C. Crisafulli, pers. comm.). Elk traverse these barrens, pausing at springs and thickets, but spend most of their time in nearby lush vegetation.

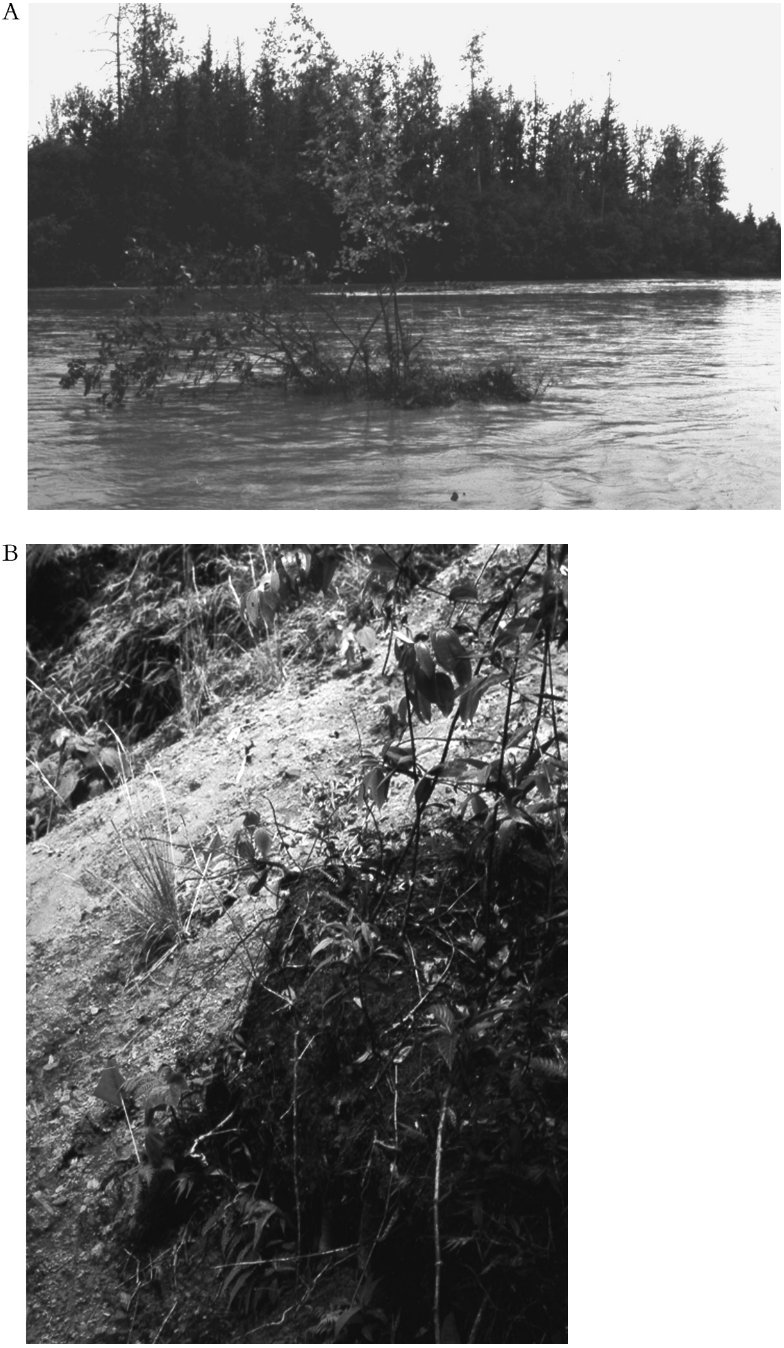

Fig. 5.7. Rafted vegetation may aid in dispersal of plants and animals on (A) the Tanana River in Alaska; (B) a landslide in Puerto Rico.

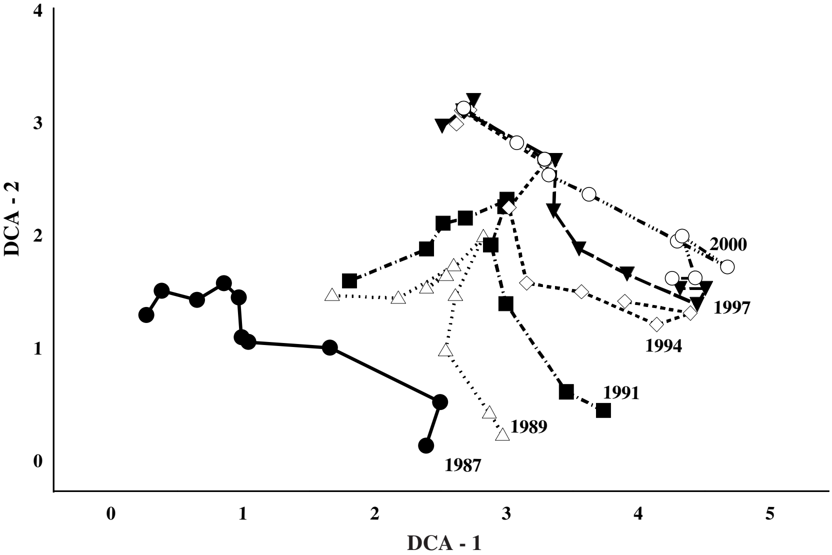

Fig. 5.8. Vegetation dynamics between 1987 and 2000 after the draw-down of a Norwegian lake. Each vector is the detrended correspondence analysis (DCA) score of the transect in successive years between 1987 and 2000, as shown. The position of the transects moves to the right on DCA-1 through the years and moves generally down DCA-2 with transect elevation. Modified from Odland & del Moral (2002).

Diffusion

Gradual dispersal along a front from an edge is a common mode for vegetative expansion onto stressful environments. On a small scale, diffusion occurs by centripetal invasion on rock outcrops (Ware, 1991; Meirelles *et al.*, 1999). On a larger scale, invasions along lake margins are also centripetal invasions (van Noordwijk-Puijk *et al.*, 1979). Phase transition, for example lake eutrophication, is a good example of pure diffusion. Populations expand slowly into lakes by vegetative means. However, when the environment changes suddenly, vegetative expansion is swift. Odland & del Moral (2002) determined that *Equisetum* horsetails invaded a former lakebed at a rate of 1.8 m yr^{-1} (Fig. 5.8).

Most examples of diffusion come from broad-scale expansions across landscapes. At large scales, gaps are irrelevant, but diffusion on a small scale is a result solely of distance. Any transect from intact vegetation onto newly formed sites is characterized by declining richness, density and size – distance by itself alters the seed rain. Evidence for this effect is common (Robertson & Augspurger, 1999).

Animal species with well-documented patterns of diffusion across a landscape include the muskrat (*Ondatra zibethicus*) in Europe, starlings (*Sturnus vulgaris*) in North America, fire ants (*Solenopsis geminata*) in the southern U.S.A., and house finches (*Carpodcus mexicanus*) and the opossum (*Didelphis virginiana*) in the western U.S.A. *Bromus* (a grass) and *Senecio* (a forb) are plants with well-described expansion patterns. Both spread by local diffusion after large jumps that were assisted by human activities. Late successional species may have a difficult time crossing fragmented landscapes because they depend primarily on local diffusion. Hiroki & Ichino (1993) showed that *Castanopsis* trees only advanced from mature trees along the margins of a lava flow 40 yr old. This slow diffusion was in sharp contrast to the jump dispersal of *Machilus* trees, which established only under the crown of the wind-dispersed pioneer shrub *Alnus*.

Tagawa (1964) showed that wind dispersal resulted in differential effects. A lava surface 48 yr old (Sakurajima, Japan) had high diversity downwind of an old surface, but low diversity upwind from the same surface. There was also a strong asymmetric pattern of density that corresponded to wind direction and force. Lahars on Mount St. Helens differed only in their proximity to intact vegetation. After eight growing seasons, mean cover was significantly lower on the isolated lahar. Dispersal limited density of two conifer species that dominated the adjacent woodland. *Abies* tree cover was initially 0.7%, whereas on the isolated lahar it was less than 0.08%; by 1998, cover had increased to 14% on the adjacent lahar but only 0.6% on the isolated one. *Pinus* cover increased from 0.2% to 9% on the adjacent lahar, but only from 0.01 to 0.4% on the isolated lahar. Plant species dispersion strongly depends on proximity to the woodland. On the adjacent lahar, *Abies* density declined sharply with distance, but *Pinus* was scattered and demonstrated no density gradients (Fig. 5.9). On the isolated lahar, there were no gradients because distances to sources were effectively the same for all points in the sample.

Seed availability can limit diffusion in isolated habitats that contrast sharply with their matrix. Small isolated rock outcrops may lack suitable species to invade as soils develop so that seres remain arrested until suitable species eventually colonize.

Other stresses may limit diffusion. Houle (1996) showed that seed germination sites for *Elymus* grasses were limited and it expanded on dunes only by clonal growth (cf. Poulson & McClung, 1999). Maun (1994) explored mechanisms of plant establishment on dunes and emphasized the importance of physiological tolerance mechanisms and, in contrast to Houle (1996), the importance of nurse plants. Conditions can be so

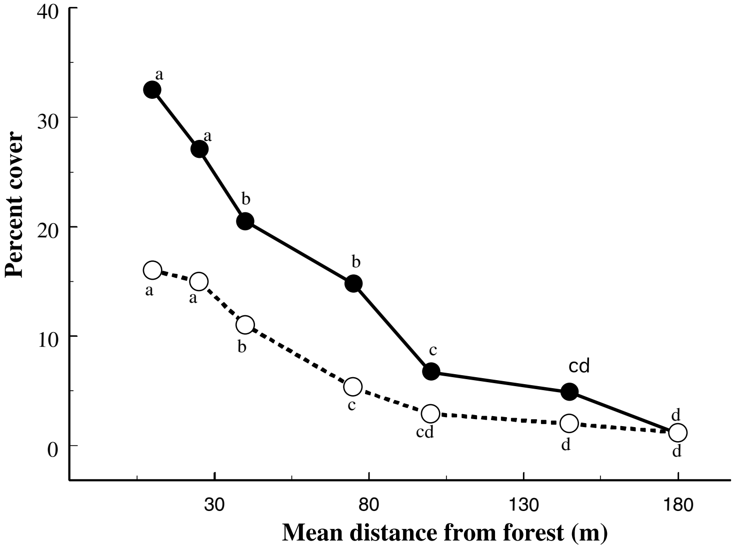

Fig. 5.9. Effect of distance from an intact forest on cover of *Abies lasiocarpa* (filled) and *Pinus contorta* (open) in 1998 on a lahar created in 1980.

severe that diffusion even by rhizomes is restricted. Ishikawa *et al.* (1995) showed that rhizomatous species were confined to less stressful shoreline environments and could not invade sites occupied by more stress tolerant species even though the growth rate was maximal at their leading edge (Ishikawa & Kachi, 1998). The parent plant can transfer resources and support diffusion into a hostile habitat. *Polygonum* herbs on scoria on Mount Fuji expanded vegetatively to provide a major stabilization force (Adachi *et al.*, 1996a). This study demonstrated that N accumulated by older parts of a clone was transported to the margins to support expansion.

Diffusion from established plants by vegetative means or from intact vegetation by propagule dispersal is effective, but spatially limited. It is insufficient to explain migration rates. It is also insufficient to explain the rates of early succession.

Jump dispersal

Many primary surfaces are neither infertile nor very stressful. They may be isolated from sources of colonization or they may be next to intact vegetation, but inhospitable only to the species found there. Rapid diffusion is precluded, but long-distance seed dispersal can lead to local colonization points. Because establishment conditions are not restrictive, expansion

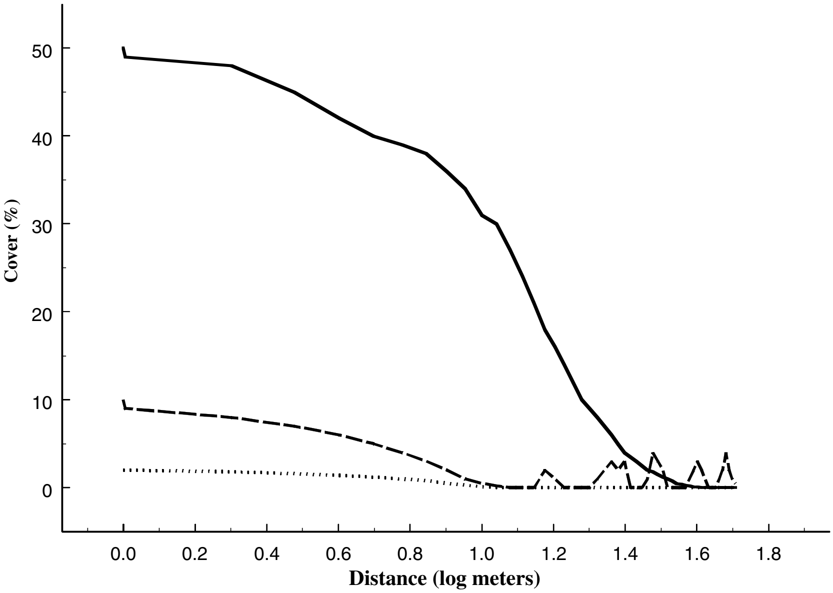

Fig. 5.10. Dispersal as a function of stress: theory. Solid line, normal dispersal by diffusion from a proximate source; dashed line, limited diffusion, with infrequent establishment by jump dispersal into a moderately stressful habitat; dotted line, rare establishment under stressful conditions.

from these initial colonizers is rapid. It seems likely that colonists that combine effective seed dispersal with strong vegetative expansion will dominate early stages of many seres (Bazzaz, 1979).

Diffusion occurs when proximal species can invade the primary surface. Alternatively, if there are no suitable species nearby and conditions are not very stressful, initial cover will be low and distributions will be characterized by spikes at random distances (Fig. 5.10). These spikes result from the infrequent establishment of lucky colonists followed by local diffusion. If suitable colonists are distant and the site is stressful, diffusion will contribute little and there will be only small cover changes with distance. Stressful conditions will limit the rate of secondary spread from the few colonists. In contrast, if the surroundings remain diverse, it is likely that many species will be able to invade and that densities will build more quickly than in systems of low biodiversity (cf. Grime, 1998).

Combined dispersal

Invasion from a distant source is the rule in primary succession simply because no propagules survive and adjacent species are unsuited to colonization. Only a few propagules reach an isolated site and most of these are wind-dispersed species. This reality suggests that an effective colonization mechanism is to establish, then expand by local seed dispersal. Of course, this requires maturation. Many species are diplochorous, with two principal forms of dispersal (Ohkawara & Higashi, 1994). They may hitchhike across barriers with vertebrates, then diffuse from founder individuals. Although the winged fruits of the forb *Cistanthe* are adapted for buoyancy, their mass and prostrate plant morphology suggest only local wind dispersal. However, elk eat these fruits and transport the seeds endogenously over several kilometers before defecating. Primates also form an important dispersal vector (Andersen, 1999). As tropical tree species usually have poor dispersal, directed dispersal by primates can transport seeds among forest fragments or to sites recovering from degradation (cf. Whittaker *et al.*, 1997).

Combined dispersal was true for 16 of 18 species tested on pumice at Mount St. Helens (del Moral & Jones, 2002). A simulation study demonstrated that emerging spatial patterns were consistent with rare colonization from distant sources, followed by diffusion from nascent foci. Plants expand from founders as ripples in a pond expand from a thrown rock (see, for example, Game *et al.*, 1982). This pattern is common when the invaded habitat is isolated and the barren habitat is inhospitable.

5.3.3 Barriers

In order to understand fully the assembly of communities on newly barren surfaces, characteristics of the landscape and the surrounding biota must be known. Landscapes form a mosaic of challenges for dispersal. Schmitt & Whittaker (1998), after Pickett *et al.* (1987), presented a hierarchy of causes and mechanisms of succession. Their analysis showed that the size and severity of disturbances, the propagule pool, dispersal abilities, climatic factors and disturbance timing all influence dispersal. White & Jentsch (2001) reviewed how disturbance regimes control ecosystem change, including primary succession. They proposed that in addition to disturbance size and severity (or magnitude), the duration and abruptness of the impact dominate the future of the system. On any landscape, disturbances are common. They include small-scale, low-impact disturbances that have no successional consequences, and moderate impacts that create gaps best understood through patch dynamics approaches that may include secondary successional systems. Only intense, high-magnitude disturbances remove

Table 5.2. *Relative percent cover in each of five dispersal categories on four grids at Mount St. Helens showing how isolation affected dispersal to a site*

Isolated sites were initially dominated only by species with good to excellent dispersal.

Dispersal category	Adjacent lahar	Isolated lahar	Isolated pumice	Very isolated pumice
Poor	6.8	6.8	5.1	8.8
Modest	58.5	27.2	19.5	20.7
Moderate	7.4	18.0	14.8	6.7
Good	16.0	32.1	23.9	13.8
Excellent	11.5	16.6	33.7	50.0

From del Moral (1998).

all biomass to initiate primary succession. These disturbances can so profoundly alter a site that the recovering trajectory never approaches conditions found in undisturbed sites. The floristic context, sometimes ignored, is significant because it restricts the species that can invade. Fastie (1995) noted that seed sources on a glacial moraine included refugia of undamaged trees and successional stands that represented post-glacial invaders.

Barriers to colonization accentuate isolation caused by mere distance (Table 5.2). They create differential filters, so knowledge of potential and actual barriers assists in predicting the first colonists. Physical barriers include water, mountains and inhospitable habitats. Newly formed, isolated wetlands on Mount St. Helens were dominated by wind-dispersed species and were highly variable. This suggested a stochastic effect mediated by the upland barriers surrounding each wetland (Titus *et al.*, 1999; del Moral, 1999b). Less obvious barriers that affect dispersal include the direction of wind and currents.

Oceans bar most species from colonizing new habitats. Island floras can be dominated by wind and bird dispersal or by water dispersal, depending on distances and currents. Currents around Krakatau often convey unlikely passengers such as monkeys (Thornton, 1996). Because Indonesian currents are seasonal, another variable is the direction of currents or winds when seeds are released. Sea-water toxicity also filters the pool of colonists.

Subsequent dispersal of water-dispersed species into suitable upland is often thwarted by the absence of mammals. Andersen (1993) studied shore communities along the Danish coast and found different dispersal

Table 5.3. *Fraction of the vascular flora dispersed by birds in a variety of successional habitats*

Habitat	Percent bird dispersed	Examples	Reference
Hawaiian Islands	75%	*Bidens*	Carlquist, 1974
Surtsey	64%	*Cardaminopsis*	Fridriksson, 1987
Krakatau	34%	*Ficus*, *Solanum*, *Pandanus*	Whittaker & Jones, 1994a; Thornton, 1996
Peruvian Amazonia	16%	*Inga*, *Phytolacca*	Kalliola *et al.*, 1991
Lake Hjälmaren (Sweden)	12%	*Rubus*, *Solanum*	Rydin & Borgegård, 1991
Wetlands, Mount St. Helens	0%	None	Tu *et al.*, 1998

types along a gradient from the sea. Water dispersal dominated the shore, with wind dispersal becoming more common inland. Where vegetation was developed, animal dispersal, especially by ants and external transport, became more common. Wind-dispersed species can cross moderate ocean barriers and ocean currents can help to distribute species among island groups.

New oceanic volcanoes demonstrate the effects of isolation on seed dispersal. Birds routinely reach less isolated islands, dispersing most of the plant species that reach them early in succession. Table 5.3 shows examples of the percentage of the bird-dispersed flora in selected islands. The Hawaiian Islands are extremely isolated so that wind and sea routes are problematic. Even some normally wind-dispersed species may actually have arrived as passengers on a muddy bird (Carlquist, 1994). In contrast, Anak Krakatau is bracketed by Java and Sumatra, large islands that provide ready sources of seeds.

A new caldera with a fresh-water lake formed on Long Island (Vitiaz Strait, 55 km north of New Guinea) in about 1645. In 1968 a new island called Motmot formed in this lake. Motmot is young, with very unstable, porous and infertile soil in a low rainfall region (Harrison *et al.*, 2001). It is isolated by sea, land and fresh water. As a result, its flora of 45 species is about 12% that of Long Island and very different from comparable young, nearby island volcanoes (e.g. Anak Krakatau) that have access to sea-borne biota (Thornton *et al.*, 2001).

Lake Hjälmaren in Sweden surrounds many small islands that have undergone more than 100 yr of primary succession (Rydin &

Borgegård, 1988b). Bird-dispersed species were rare in early successional sites, but increased slightly on islands that developed woody plant dominance. Harsh establishment conditions may be a more stringent barrier than a lack of effective dispersal. For example, Surtsey, a young, harsh and isolated volcanic island, has a limited seed input. Ocean currents provide one vector, but the vegetation appears confined to the strand. Much of the island was barren in 2001, and upland vegetation was confined to bird colonies and a few other ameliorated habitats. River bars along the Peruvian Amazon are not isolated and birds form only a small component of the migrants (Kalliola *et al.*, 1991). Here the vegetation is dominated by wind- and water-dispersed species. The proportion of wind-dispersed species remained constant, confirming that wind is the more effective agent for crossing moderate barriers. Young wetlands forming on pumice and pyroclastic deposits of Mount St. Helens are isolated from intact and relict vegetation and had no bird-dispersed species in 1995 (Tu *et al.*, 1998). This wetland vegetation lacked bird-dispersed species through 2000. In an anthropogenic disturbance (logged islands), Kadmon & Pulliam (1995) found that the number of bird-dispersed woody plant species decreased by 50% as isolation increased from 100 to 500 m.

Studies of terrestrial invasions across barriers all suggest that maximum colonization rates occur when diffusion and jump dispersal combine. Most species have multiple dispersal mechanisms, although one may predominate. This allows plants to hitchhike with animals or effective seed buoyancy mechanisms to be combined with local spread by vegetative expansion, wind, gravity or water. Combined dispersal often produces heterogeneous vegetation initially dominated by species with efficient dispersal, but soon shifting to those that expand vegetatively. Clark's (1998) model explained rapid migration of temperate zone woody plants after glaciation by combining nucleation resulting from jump dispersal with diffusion. The expansion of invading species on primary substrates agrees with this model (cf. Clarkson & Clarkson, 1983). Barriers filter the available flora by restricting those species with poor dispersal abilities from crossing.

Barriers cause the initial vegetation to be an unrepresentative sample of the flora. Compared with mature vegetation, there will be too many species with excellent dispersal mechanisms (usually by wind) and too few with large seeds or specialized dispersal mechanisms. Dispersal by birds onto barren sites is uncommon because such directed dispersal requires some attraction (resources or perches). However, when early successional trees or shrubs do attract birds, the seed rain (e.g. on landslides in Puerto

Rico; A. Shiels, pers. comm.) becomes dominated by bird-dispersed species (Walker & Neris, 1993). Many common functional types will be excluded simply because they cannot reach a site. The absence of certain plant species can result in missing animals. Disharmony on oceanic islands is well known, but less appreciated is that disharmony is apparent in most early seres and can persist. Recovering ecosystems can sustain more species and more rapid development than is usually apparent. This suggests opportunities for rehabilitation that will be explored in Chapter 8.

5.3.4 Predictability

Prediction is the goal of any science. Early studies of succession assumed directionality that was combined with determinism (see section 3.3 on holism). Although primary seres sometimes develop in predictable ways, both natural and human-created vegetation often develop in surprising ways. Here we investigate the factors that may lead a sere to develop contrary to the conventional wisdom.

Chance and prediction

The distance a bird might disperse a seed is less predictable than distances achieved by passive transport by wind. If we consider that most typical early pioneer species will be drawn from a suite of species with good wind dispersal, then on a large scale, the composition of early successional stages is predictable. By contrast, dispersal to isolated sites via birds is less predictable; the pool of potential colonists is large, the number of seeds being introduced is small and the vectors are few (Ward & Thornton, 2000).

In addition to normal dispersal methods, lottery events are so rare as to be unpredictable. Amphitropical distributions of taxa in the southwestern U.S.A. and in Chile and Argentina imply a few extremely rare long-distance dispersal events (Morrell *et al.*, 2000). Migrating birds sometimes are blown off course (e.g. geese in Hawaii); should they carry a seed, a new introduction might occur. On a smaller scale, no one who has studied *Lupinus* on Mount St. Helens (e.g. Wood & Morris, 1990; Halvorson *et al.*, 1992; Bishop & Schemske, 1998) can offer a better explanation for its appearance on barren pyroclastic material within one year of the eruption than this: capsules were blown onto snow and then transported with the snow melt. Seeds started a few scattered populations that expanded into 'patches.'

Both stochastic and deterministic processes operate during primary succession. Environmental factors gradually assert control over the distribution and growth of individual species, forging tighter links between the vegetation and light, moisture and nutrient availability. However, even as the environment begins to exert control on the vegetation, the composition of the subsequent wave of colonizers may be *less* predictable. This suite of later colonists will include those with a low probability of invasion, so the identity of successful species in any given case can be uncertain. McCune & Allen (1985) found that chance led to a series of different dominants in similar valleys after severe fires in Montana. Forces that affect the degree of determinism appear to be operating in most seres, leading to a variety of trajectories.

However, predictability may also be affected by the degree to which a relationship develops between species composition and the environment. Initially, the environment of a site is poorly related to species composition. Lack of competition permits species to occupy a broad range of environments. Bowers *et al.* (1997) found that vegetation on young debris flows in the Grand Canyon was highly variable, but that each could be explained in terms of seed dispersal and local climate factors. del Moral (1999b) found that the predictability of wetland vegetation after 18 yr increased dramatically compared with the same sites sampled six years earlier (Titus *et al.*, 1999). Similarly, del Moral (1999a) found that initial composition of small isolated communities on pumice was highly variable. Later studies revealed that there was an increasing, although still tenuous, relationship between composition and the environment.

The biological legacy, nearby species that survived the disturbance, can reduce stochastic effects because the seed rain will be denser, species invading will be more consistent and more species will be represented. The presence of legacies (Franklin & MacMahon, 2000) may accelerate early primary succession. However, while residual plants, animals and diaspores are important to secondary succession, their effects in barren primary landscapes are constrained. Fuller (1999), working on Mount St. Helens, found that the effects of refugia within which forest understory species survived were limited to a distance of less than 50 m from the refugia. Surviving species did not invade barren pumice, but the margins of refugia had soil that provided an ideal habitat for invading species. Whereas pioneers on the barrens produced few seeds, those that established on refugia were robust and reproduced copiously. Their progeny were well placed to colonize the surroundings. The refugia not only contributed a greater seed rain of barren zone species, but also attracted birds and rodents and exported organic matter to the adjacent plots. In Hawaii, similar processes occur when fresh lava flows are recolonized from kipukas (islands of forest that survive). However, only a small subset of the forest species can colonize the lava.

The importance of safe-sites, regeneration niches (Grubb, 1977) and amelioration is related to the degree of stress (e.g. infertility, drought, salinity or toxicity). As a result, trajectories on initially stressful sites are less predictable than those on more benign sites situated in similar landscapes, even though the initial colonists may be predictable. Turner *et al.* (1998) developed a qualitative model of the predictability of succession. Predictability is reduced as disturbance size, intensity and frequency increase. All of these factors act against a shifting background of landscape factors, a changing biota and other stochastic elements. Savage *et al.* (2000) modeled forest dynamics as a function of disturbance. They concluded that in regimes with moderately frequent disturbance, many alternative communities developed, reflecting closely balanced competitive properties.

Habitat size

The vegetation of large habitats will be less predictable than small sites because the interior composition of large sites will be constrained by dispersal and subject to stochastic processes. A small suite of species with good dispersal and rapid reproduction can invade large newly created habitats rapidly and expand quickly, but which members of the suite are successful often has a large stochastic component. In terrestrial habitats, wind-dispersed species predominate because there is little to attract animals. The seed rain and initial population densities will be low. Therefore, although the predictability of the first wave of colonists will be good, spatial heterogeneity and dispersal gradients will be high. As colonization progresses, heterogeneity may decline as the initial colonists expand from their initial loci and colonization continues. However, subsequent colonists may be unexpected and a generally rare species may become dominant in a given sere. This potential paradox of decreasing long-term predictability even as the vegetation becomes more homogeneous needs to be examined carefully by permanent plot methods.

Habitat stress

Stress restricts successful colonization strategies and may lead to improved predictability, at least with respect to functional types. Díaz *et al.* (1998) found that there are consistent relationships between the species pool and environmental factors for most traits in all 13 Argentine habitats investigated. García-Mora *et al.* (1999) found that unstable dunes were colonized primarily by species with spreading root systems. We conclude that stressful habitats (e.g. salt pans, sand dunes and mined lands) will be invaded by a small subset of the species pool and initially will be more predictable than less extreme habitats. In general, predictability will be high if the pool is small and if the stress is extreme. However, subsequent development from the small pool of species may be less predictable.

Habitat isolation

Early dispersal may be more deterministic in some isolated sites because only a few species can become established; however, it is locally stochastic. Later, it may become more stochastic because many factors influence which seral species may arrive. The availability of dispersal agents in tropical habitats is a crucial bottleneck (Ward & Thornton, 2000). The presence or absence of birds for dispersal will profoundly alter the initial and ultimate composition of the vegetation. Islands with different degrees of isolation may differ profoundly simply because bird dispersal agents may, or may not, reach them (Table 5.3). Priority effects may alter the nature of subsequent colonization. In temperate regions, habitat fragmentation leads to colonization by different sets of species, alternative trajectories and ultimately to multiple stable states (cf. Jacquemyn *et al.*, 2001).

5.3.5 Dispersal conclusions

Primary succession normally requires propagule dispersal because seed bank survival is rare. Dispersal is the first major filter that governs primary succession. Suitable species may be precluded from participation because they are initially incapable of reaching the site. Distance alone is an important isolating factor because typical dispersal distances are limited. Jump dispersal occurs for most species, but is stochastic for less able dispersers because so few propagules reach a site. Predicting early and mid-course succession requires knowledge of the locations of the available species pool. Physical barriers differ in their ability to filter species, so knowledge of the landscape is also required to predict the immigrant pool. Aquatic barriers are more difficult than inhospitable terrain because there are no opportunities for refugia or stepping-stones for terrestrial species.

Ultimately, the rate of species change declines because no additional species can reach the site and the dominants can successfully reproduce. Islands retain their unbalanced biotic composition, but it is unclear to what extent disharmony is reflected in mature mainland primary seres. Migration by diffusion occurs if barriers are minimal and new surfaces are not significant barriers to establishment. Jump dispersal appears to be a common feature of invasion whether or not diffusion occurs. Isolated or extreme sites are characterized by limited jump dispersal. However, dispersal from these initial colonists then follows a diffusion mode. Most primary succession sites have a limited ability to sustain biomass because they are stressful (*sensu* Grime, 1979). Many more species can be pioneers than actually are. These species are often stress-tolerant, but owing to their poor dispersal, they rarely reach sites early in succession. In contrast, species that do form the first wave of immigrants are usually poorly adapted to the site and readily displaced by subsequent invaders. The degree to which the initial species composition of a site may be predictable is a function of the scale of observation, the degree of isolation and the diversity of the available flora.

5.4 Establishment

Propagules that reach a barren site have passed one filter, but they are immediately confronted with others. While dispersal characteristics and isolation will dictate the number and types of species that arrive, site characteristics determine which of these can establish. Many species are limited by both dispersal and microsite availability (Eriksson & Ehrlen, 1992), but other factors such as seed predation and competition from established plants often regulate subsequent seedling density. A breeding population may develop immediately, but is more likely to be delayed by harsh environments. We will explore early life history traits to assess their effects on establishment.

5.4.1 Germination

Amelioration

Walton (1990) suggested that dispersal occurs without regard for the suitability of the habitat. Despite a large seed rain, immediate establishment may be impossible until after the development of the new substrate. However, the act of dispersal itself is a major and early form of site amelioration, leading to higher probability of success for subsequent immigrants. Ashmole & Ashmole (1987) showed that the biological fallout on very young lava flows in the Canary Islands supported rich arthropod communities and Edwards & Sugg (1993) demonstrated that similar fallouts are a major form of physical amelioration. Aeolian fallout leading to significant populations of invertebrate predators, parasites or detritivores have been shown in communities as diverse as glacial moraines (Hodkinson *et al.*, 2002), volcanoes (Wurmli, 1974), dunes

(Goralczyk, 1998), landfills (Judd & Mason, 1995) and coal spoils (Mrzljak & Wiegleb, 2000). Dissolved nutrients, whose origins may be very distant from the site (Chadwick *et al.*, 1999), are also added through rain. All such inputs significantly affect soil development. Many other forms of organic matter, including leaves, pollen, spores and feces, can reach a site and contribute to its amelioration.

Safe-sites

Seeds of *Salix* shrubs waft over barren sites on Mount St. Helens (Wood & del Moral, 2000), but establish only near springs and seeps. Seeds of *Anaphalis* forbs fall into a wetland and perish. Each invading species will respond differently to the same environment and germinate under different conditions. There has been little research conducted on the fraction of the incoming seed rain that contains species able to germinate under the conditions of a barren surface. On most substrates, conditions remain inhospitable for many years, so that successful germination can only occur on a small fraction of the habitat. Germination success can be enhanced by manipulating the site, thus demonstrating that the lack of microsites restricts germination (Greipsson & Davy, 1997; Titus & del Moral, 1998a). However, even in the presence of suitable microsites, propagules will not germinate unless all other physical requirements are met (Smyth, 1997).

As physical amelioration proceeds, the initial homogeneity of surfaces such as desert playas, smooth lavas (pahoehoe), rocks, pumice and mud flats breaks down. Particularly well-favored microsites eventually develop that can sustain establishment. The forces that create initial heterogeneity are physical. Although erosion is often a destabilizing and destructive force, it can also expose residual soil. On Mount St. Helens, erosion created small rills in featureless barren pumice that became foci for early seedling establishment (del Moral, 1983). Even though most plants had been killed, this old material was more readily invaded, and the erosion released survivors before they died. Freeze–thaw cycles fracture rocks to create microsites where seeds, moisture and dust may accumulate. Wet–dry cycles perform a similar function on fine-textured surfaces, creating cracks between smooth surfaces. These cracks trap seeds and provide protection from drying that permits seedlings to establish. *Umbilicus* forbs on Mount Etna pioneer cracks in weathered lavas very early in the sere and can persist for centuries (Fig. 5.11).

Sites such as talus, scoria and sand dunes are intrinsically unstable by the nature of their formation (see section 4.2.4 on erosion). Here, succession is routinely reset by erosion. Colonizing plants are buried, killed by

Fig. 5.11. Umbilicus rupestris grew well in crevices in lava on Mount Etna (Sicily). Note that lava surfaces sustain lichens in exposed microsites, mosses in more protected sites and various herbs in areas that have accumulated soil since the deposition of this lava in 1636.

exposure or torn from the surface by wind. However, wind also can stabilize a surface. It removes fine-textured particles and leaves behind a stable surface that traps seeds (Tsuyuzaki *et al.*, 1997). This 'desert pavement' conserves moisture and enhances seedling survival. Water erosion sometimes removes unstable surface materials to reveal a stable substrate ready for colonization (del Moral & Bliss, 1993). Species with vigorous rhizomatous growth such as the grasses *Leymus* and *Ammophila* often stabilize dunes and other loose materials to initiate succession. These various amelioration effects act in concert, gradually or rapidly preparing a site for successful colonization. It is rare that large sites develop homogeneously or simultaneously. In nearly every case, some microsites are more favored, and these are destined to harbor the first colonists.

John Harper coined the term 'safe-site' and described its significance in a comprehensive series of papers culminating in his classic book (Harper, 1977). Safe-sites often contrast sharply with the background surface and can harbor seedlings. They gradually become favorable to more species and can support greater productivity. As the sere develops, they comprise an increasing fraction of the landscape. These physical sites provide relief from drought, moderate temperature, reduce wind, collect nutrients, trap seeds and otherwise satisfy the regeneration requirements for at least some species that reach the site (cf. Grubb, 1977). A few propagules eventually lodge where they might germinate, usually in such physical features as small rills, fracturing rocks or eroding unstable material. Eventually, the microsite offers a chance of success to a germinating seed. Gradually, seedlings establish.

Stability

Microsites differ in their stability. Stable sites offer a long window of establishment opportunity. Bishop & Chapin (1989a) showed that rehabilitation of gravel pads was relatively easy because established plants responded to fertilization and were not subject to erosion. Such sites filled in quickly as the planted species set seed. In contrast, Frenot *et al.* (1998) found that glacial outwash plains supported low densities of plants that only expanded slowly. The sites lost fine material through wind erosion, so scant germination could occur on the eroded surfaces. Houle (1996) found that dune stability was required for germination and that only germination determined establishment patterns.

Physical features can be used to identify safe-sites in barren habitats. Jumpponen *et al.* (1999) characterized safe-sites in front of retreating glaciers. They could predict the unique combination of physical traits that constituted the safe-site for each species. Stocklin & Baumler (1996) showed that safe-sites became less common along a chronosequence associated with a retreating glacier as the surface developed. Lavas develop different microsite heterogeneity patterns. A'a (Figs. 2.4B, 5.12) is fractured and contains many apparent safe-sites, whereas pahoehoe (Fig. 2.4A) is smooth. On Hawaii, Aplet *et al.* (1998) showed that under moist conditions, succession was more rapid on a'a, but pahoehoe supported more

Fig. 5.12. Broken a'a lava field on Mount St. Helens (400 yr old). Rock surfaces are dominated by lichens and mosses; cracks support the invasion of conifers and other woody species.

rapid development in dry conditions. Thus the quality of a safe-site is conditional and safe-sites differ in their quality, general suitability and size (Kroh *et al.*, 2000).

Safe-sites are not immutable. Continuing physical amelioration increases their abundance and quality, but they may also erode, desiccate, become wetter, be buried (del Moral 1993b; Tsuyuzaki & Titus, 1996; Tsuyuzaki *et al.*, 1997) or be claimed by an adult plant (Walker & Powell, 1999a). Safe-sites often disappear under dominance by pioneer species and they may not be replaced by safe-sites suitable to other species. Stocklin & Baumler (1996) demonstrated that what constituted a safe-site differed on a glacier moraine transect and that older habitats were drier and contained few safe-sites for pioneers. Del Moral (1993a) described microsite relationships in suites of pioneers on pumice at Mount St. Helens. As the terrain matured and initial species spread vegetatively, sites suitable for germination became scarce (del Moral & Jones, 2002). Walker (1989) demonstrated that N and organic litter accumulation on developing Alaskan floodplains restricted the number of species that could establish and this led to succession. Early floodplain colonists typically depend on seed dispersal during an ephemeral period of receding water that provides a moist yet well-drained seed-bed (Nechaev, 1967; Walker *et al.*, 1986). Immediate germination and rapid growth assure that seedlings will not wash away or become desiccated. When safe-sites become scarce, succession slows.

The nature of safe-sites in early succession is usually obvious and based on physical attributes. Many species may be capable of establishment in a particular safe-site. Thus, early primary succession is a lottery in which arrival is the prime determinant of the early course of events. In mature vegetation, safe-sites and regeneration niches may depend on subtle biological interactions as well as physical conditions and therefore are difficult to recognize and quantify. Similarly, replacement of individuals in a safe-site may be driven only by chance, such that turnover is common, but not directional. The broad tolerance of pioneers and their lack of safe-site specificity are characteristics of the carousel model (see section 3.9 on models). This view of early stochastic development in primary succession implies that primary succession is not predictable on a species level, although it may be on a functional level. The early trajectory will be conditioned by what might be termed stochastic priority effects.

Dormancy mechanisms often prevent inappropriate germination and permit germination only during a favorable season. Environmental cues permit seeds to germinate when they are more likely to establish successfully. Environmental factors that can break dormancy include light, high and low temperatures, moisture and some combinations of these factors. In cool, temperate habitats, many species require stratification (long periods under cold, moist and dark conditions). In dry habitats, saturating rains frequently break dormancy, or seeds may be abraded as they are blown along grainy surfaces. Many ruderal species remain dormant in soil until some soil disturbance exposes them to a brief flash of light. This triggers a sequence of events that breaks dormancy and initiates germination. Baskin & Baskin (1998) provide an excellent compendium of the dormancy and germination ecology of seeds. Seed germination depends on several internal and external factors.

Niederfringiger-Schlag & Erschbamer (2000) found that seedling establishment on moraines in the Austrian Alps was enhanced where there was existing vegetation and that safe-sites including microsites modified by adult plants or stones each enhanced success. Established plants on older moraines inhibited establishment. Late successional species could germinate on young moraines, suggesting that dispersal limits and not germination failures slowed succession.

5.4.2 Growth

Once a seed has reached a safe-site, it must survive and grow in order to succeed. On most barren primary surfaces, it is initially only the most favorable sites that permit seedlings to mature, and the nature, distribution and abundance of safe-sites is therefore important not only to germination but to establishment. For example, Kochy & Rydin (1997) demonstrated that species diversity on new islands was related to the degree of habitat heterogeneity, not to any area or distance effects, thus emphasizing the importance of safe-sites for growth as well as germination. Safe-sites are also crucial in exposed habitats such as cliffs (Houle & Phillips, 1989) where wind and erosion preclude seed capture. Hilton & Boyd (1996) showed how slow growth constrained the development of species on dunes.

The extent to which chance effects persist is unclear, but it is likely that they are never fully erased. For such effects to be eliminated would require that there be a very close connection between each species and the physical environment, strong competitive interactions such that the superior species predictably predominates, and relatively homogeneous habitats to provide few refuges for inferior species. These conditions are uncommon.

Abiotic conditions

Most primary successional surfaces are stressful (see Chapters 4 and 8). Plants of infertile surfaces such as sand dunes (Olff *et al.*, 1993), floodplains (Walker *et al.*, 1986), glacial moraines (Chapin *et al.*, 1994), tephra (Hirose & Tateno, 1984), pyroclastic materials and mined lands (Game *et al.*, 1982; Marrs & Bradshaw, 1993) are all characterized by slow growth. Nutrient deficiency retards seedling development. Slow growth usually translates into a failure to develop a sufficient root system and seedlings succumb to drought (cf. Morris & Wood, 1989).

Drought is a feature common to many primary seres. Obvious examples include coastal and inland sand dunes, rock outcrops, scoria and lava. Less obviously, drought effects can occur on river gravel bars, near bogs and on wetland margins. Algae colonizing gaps in vegetation in rocky intertidal zones can even experience desiccation in the larger gaps (Kim & DeWreede, 1996). García-Fayos *et al.* (2000) demonstrated differential seed germination on eroded ‘badlands’ in Alicante and Murcia, Spain, where the summers are dry and winter rains are intermittent and scant. Seven of eight species tested suffered reduced germination at 0.34 MPa, and none germinated at 0.99 MPa. Bog expansion can be limited by a lack of sufficient water (Grosvernier *et al.*, 1997). Excessive water rarely affects primary succession, although *Sphagnum* moss may expand as water tables rise (van Breemen, 1995). 'Hydrarch' succession may be impeded by seasonal drought or alterations of the water table. A drop of 15 cm in the water table led to an invasion of raised *Sphagnum* bogs by *Pinus* trees and *Calluna* shrubs in Germany (Frankl & Schmeidl, 2000). Wetlands such as those in Azraq, Jordan, face an accelerating danger of desiccation due to draw-down of ground water for irrigation and drinking (Sampat, 2000).

Chronically extreme temperatures can limit establishment and biomass accumulation. Low temperatures retard the accumulation of organic matter on moraines, and hence slow succession (Frenot *et al.*, 1998). Thawing permafrost in Manitoba led to rapid succession from *Sphagnum* bogs to hummocks invaded by *Picea* trees (Camill, 1999). Low temperatures, unusually short seasons or persistent snows retard upward migration of timberline species, but high temperatures limit growth more frequently than low temperatures. Seedling death on tephra is usually due to heat, not drought (D. Chapin, 1995). Eggler (1963) noted that soils on Parícutin Volcano, Mexico, were hot during much of the growing season, thus intensifying drought and slowing recovery. Similarly, mined lands suffer temperature extremes during the growing season that can interact with drought or nutrient stresses.

Acidity often limits plant growth in both natural and human-created systems. Extreme pH levels immobilize P and other minerals (see section 4.3.4 on pH). Volcanic tephra is often acidic (pH 4–4.5; Wagner & Walker, 1986). Many industrial wastes are either very acid (pH 3.5 or less for coal mine tailings) or very alkaline (pH 9 or higher for Leblanc waste; Ash *et al.*, 1994). A goal of rehabilitation (Chapter 8) is often to accelerate amelioration of extreme pH levels, for example by adding lime or slag to very acid wastes or compost, manure or sewage sludge where pH is high.

Some natural sites suffer from excessive salinity. Invasion or growth in inland playas is limited to extreme halophytes, and growth on coastal dunes may be limited by salt. As lakes retreat within isolated basins, soil salinity increases. West & Young (2000) describe the transition from typical upland *Artemisia* shrubs through *Atriplex* shrubs to *Sporobolus* grasses and finally *Salicornia* forbs in the western U.S.A. Desert wetland systems may contain normal hydrophytes (e.g. *Typha* and *Scirpus* graminoids) but their margins are often saline (e.g. dominated by *Distichlis* or *Puccinellia* grasses) and terminate in a barren hypersaline playa (Hamilton & Auble, 1993). Studies of the salinity of coastal dunes have produced conflicting results. Dune plants are often moderately salt tolerant, with the most tolerant plants found nearest the shore (Barbour *et al.*, 1985). Salt spray and saline soils may or may not (Van der Valk, 1974) play an important role in controlling coastal dune succession.

Anthropogenic substrates often contain heavy metals that retard succession. Mining wastes or soil near smelters often contain copper, arsenic, lead, zinc, chromium or other heavy metals at levels too extreme for plant growth. Shrubs and trees are rarely adapted to these materials. However, Bradshaw (1952; see Bradshaw *et al.*, 1978) developed lead-tolerant strains of herbs to reclaim lead mine tailings. In the absence of remediation, derelict sites remain dominated by a few species and undergo succession very slowly. Humans may accelerate primary succession through many amelioration methods (cf. Salonen *et al.*, 1992), but the practical problem is often which forms of amelioration are appropriate (see Chapter 8).

Pre-reproductive growth

Germination does not assure success, and seedling death is common. Chapin & Bliss (1989) demonstrated that seedling survival of two tolerant perennials growing on tephra varied substantially, between 10 and 40% for two cohorts of *Eriogonum* and *Polygonum* herbs over three years. That these species are among the most tolerant in this habitat suggests that survival of most species is much lower. Annuals, to be successful, must reproduce immediately. Most do not. Perennials risk mortality for several years prior to reproduction, but survivors can accumulate resources and eventually be assured of successful reproduction. Even if the individual establishes, it remains at risk for many years. Conifer seedlings occur on the Pumice Plains of Mount St. Helens, but have not achieved reproductive success. Successful seedling establishment near mature plants is constrained by any of several factors. Plants may flower, but fail to set seed due to a lack of pollinators. Fruits may be produced, but not dispersed. Fruits may be dispersed, but not into an appropriate habitat. The individual persists in an effectively vegetative state, gradually spreading out over the terrain, but never producing seeds.

Growth to maturity

The growth phase continues with the development of a reproductively mature plant. This phase continues in ways that vary with the life history of the species in question. For annual plants, the growth phase merges into a reproductive phase. For herbaceous perennials, it may be several years before the individual accumulates sufficient reserves to flower. For any species, this phase depends on local stresses outlined above. For shrubs, this phase also can last from several to many years. For most trees, there may be a long growth phase. Tree species that reproduce quickly may be at an advantage over those that mature slowly. For example, *Pinus contorta* produced their first cones on high-elevation lahars on Mount St. Helens within 18 yr (del Moral, 1998); no other conifer there has yet reproduced on new substrates. The consequences are not yet evident, but small *Pinus* seedlings have become more abundant than *Abies* seedlings on lahars more than 100 m from the intact forest.

Growth forms

Growth form spectra change through succession and differ among succession types. Under severe nutrient stress, early succession is dominated by clonal species with good wind dispersal (Prach & Pyšek, 1999). A few examples follow which will contrast growth forms in very early succession with growth forms from later stages in several primary seres.

Turnover in early succession may be a result of simple death of short-lived pioneers, autogenic changes in the environment, competition from later-arriving species, grazing or other factors. Turnover results in growth form changes, which implies that under most circumstances, biotic interactions drive change (see Chapter 6).

On glacial moraines, species that dominate older sites are more persistent and deep-rooted. On the sub-Antarctic Kerguelen Island, a few shallow-rooted, short-lived herbs occupy the youngest terrain (Frenot *et al.*, 1998). A more robust perennial grass with deeper roots replaces them. Finally, a prostrate herb with deep, widely spreading roots achieves dominance. Only seven species occurred during the estimated 200 yr sequence, and only the annual did not persist. Rebounding coastal Arctic plains also show a shift in dominant growth forms. Small grasses and sedges are replaced along a toposequence by a robust perennial grass with low herbs and finally by mat-forming willows, rhizomatous grasses and prostrate perennial herbs (Bliss & Gold, 1994). In severe environments species accumulate, there is a preference for persistent, spreading species, and successional states are marked more by dominance shifts than by complete turnover.

Growth forms also change as dunes develop. In a simple coastal dune system on the Gulf of Cadiz, García-Mora *et al.* (1999) found that unstable dunes were dominated by perennials with deep, spreading root systems and by species capable of withstanding frequent burial. Winter

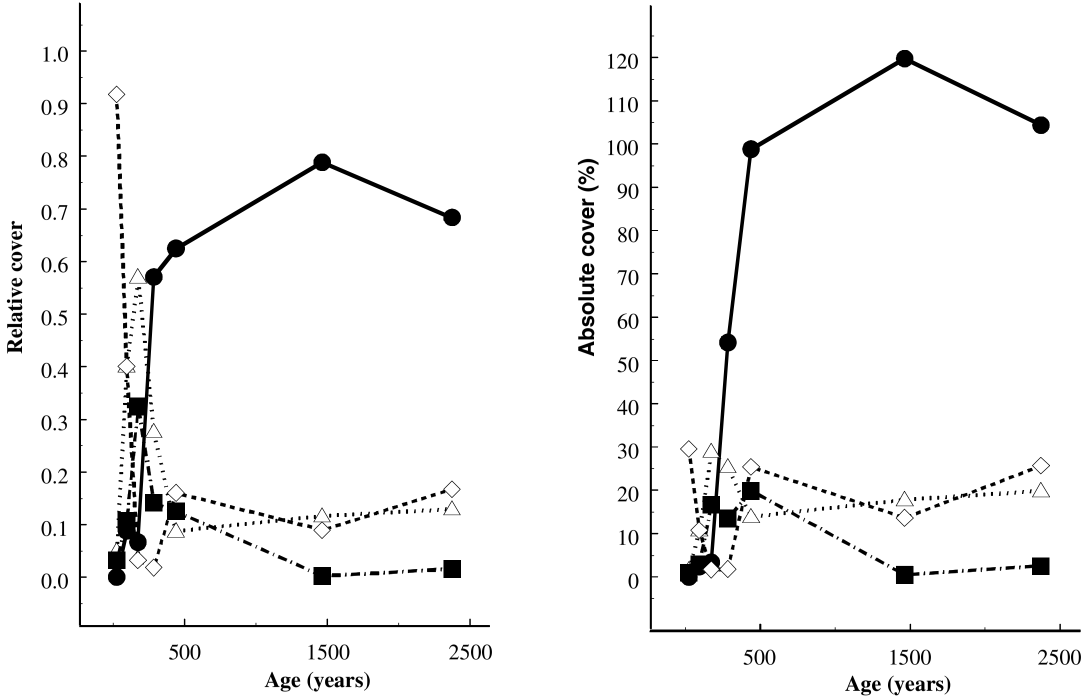

Fig. 5.13. Changes in relative and absolute cover of various growth forms along a chronosequence on Lake Michigan (U.S.A.). Filled circles, phanerophytes; open triangles, chamaephytes; filled squares, hemicryptophytes; open diamonds, geophytes. Modified from Lichter (1998). See text for more explanation.

annuals similar to inland vegetation dominated stabilized dunes, a reversal of typical progressions from annuals to persistent perennials.

Lichter (1998, 2000) studied a chronosequence of Lake Michigan (U.S.A.) sand dunes in which he sampled dunes ranging in age from 25 to 2375 yr. We categorized Lichter's species on selected dunes into Raunkiaer life forms and determined the cover of each along the chronosequence (Fig. 5.13) expressed in relative terms. Phanerophytes (woody plants taller than 50 cm) became dominant within 300 yr (*Picea*, *Thuja*, *Abies*), and continued to increase in dominance for another 1000 yr (*Tsuga*, *Quercus*, *Acer*). Geophytes (herbs that die back annually to buried perennating organs) such as *Ammophila*, then *Calamovilfa*, both sturdy rhizomatous grasses, stabilized these dunes and dominated the second stage along with chamaephtyes (woody or perennial plants with buds near the ground). A mixture of hemicryptophytes (perennial herbs that die back to the surface) dominated the mid-stage understory, then declined as tall woody species began to dominate and then virtually disappeared. Chamaephtyes (*Arctostaphylos* and *Juniperus*, followed by the ericaceous shrubs *Vaccinium* spp., *Gaultheria* and *Gaylussacia*) dominated middle stages, and then declined in relative terms, though they remained common throughout the chronosequence. This chronosequence demonstrates a typical shift in growth from dominance from geophytes to chamaephtyes and hemicryptophytes to phanerophytes. In this case, therophytes (annuals) were lacking.

Another study of dunes looked only at the first 30 yr (Olff *et al.*, 1993). Immature Dutch dunes demonstrated different life-form patterns according to the geomorphic position. The plains changed little, except that geophytes became increasingly common and hemicryptophytes invaded after 25 years. On the dry slope, phanerophytes and geophytes increased at the expense of therophytes (annuals). On the dune, hemicryptophytes (binding grasses) dominated early stages, but therophytes were virtually absent. Chamaephytes were common in the middle phase, but declined as phanerophytes invaded. The shrubby phanaerophyte *Hippophaë* appeared to exclude grasses and forbs by shading. In this study, geophytes became dominant where soil developed, but they were uncommon on dunes.

Lavas, like dunes, can require millennia for full development, requiring a chronosequence approach to study growth form changes. Poli & Grillo (1975) summarized development on lavas on Mount Etna that were 550 yr old and compared them to younger flows. We combined that work with earlier work by Poli (1965) to assemble a life-form sequence. Young lavas were dominated by therophytes (e.g. *Briza*, *Filago*, *Plantago*) with few phanerophytes or geophytes and a few hemicryptophytes (e.g. *Isatis*, *Rumex*) and chamaephytes (e.g. *Centranthus*, *Senecio*). Stable lavas developed vegetation dominated by hemicryptophytes (e.g. *Daucus*, *Lactuca*, *Crepis*) and chamaephytes (*Micromeria*). As lavas matured, small phanerophytes, notably *Genista* and *Spartium*, began to invade and geophytes (e.g. *Asphodeline*, *Leopoldia*) became common along with many species from exposed sites. Mature lavas at mid-elevations were dominated by phanerophytes (eventually by *Quercus*), with sparse understories of chamaephytes and hemicryptophytes, and few therophytes or geophytes.

Landslides may be productive and are more likely to demonstrate species and life-form turnover due to competition. Introduced herbs initially dominated communities under *Kunzea* (*Leptospermum*) *ericoides* (tea-tree) in New Zealand. As shade intensified, ferns and robust native herbs became dominant. After 50 yr, the rhizomatous graminoid *Microlaena* dominated the understory (Smale *et al.*, 1997). Tropical landslides are more complex. Stable mineral soils are typically colonized by herbs, then overwhelmed by climbing ferns such as *Dicranopteris* (in Puerto Rico), then colonizing trees such as *Cecropia* and *Casearia* and finally by fully mature tree species (Walker *et al.*, 1996). Here there was a distinct turnover of species and growth forms based on competitive replacement.

During early primary succession, there is normally a shift from smaller, more ephemeral species to persistent species with strong vegetative growth, based primarily upon differential success at filling empty space. Subsequent community assembly is characterized by the accumulation of taller species and competitive replacements, based on changing environmental interactions.

Biomass accumulation

Plant growth during early primary succession is limited by local factors such as infertility and drought. Isolation alone may also limit biomass development in the same way that it does species richness. For example, if one were to plant suitable species above the advancing timberline of Mount Fuji (e.g. *Arabis*, *Calamagrostis* or *Polygonum* herbs), biomass accumulation would be accelerated. Distance, not climate, has retarded the upward migration of plants, as evidenced by the gradient of alpine vegetation from tree line to almost no plant cover along an elevational gradient of just 80 m on Mount Fuji (Masuzawa, 1985). Dlugosch & del Moral (1999) demonstrated that successional development of even-aged lahar sites was correlated to elevation. Distance from colonizing sources limited invasion rates while the length of the growing season controlled biomass development.

Biomass will increase during much of a sere, although accumulations may stabilize long before species composition has stabilized. Biomass increased in each of three dune habitats studied by Olff *et al.* (1993) over 28 yr in permanent plots, but then stabilized. Biomass on the dunes increased from 200 to 1400 g m^{-2}. The shrub *Hippophaë* became dominant in dry sites. There was a complex interplay between species dynamics and biomass. Although it is normal for biomass to increase to a stable endpoint, biomass can decrease if, for example, a sod-forming grass replaces a dominant shrub.

Most species reach reproductive maturity through the accumulation of biomass. If conditions remain relatively open, these species are well positioned to dominate the site. Dominance should continue until they no longer produce successful offspring and they succumb to age or competition from later invaders.

Functional groups

Functional groups (or types) consist of species that respond in a particular way to a particular perturbation (Gitay & Noble, 1997). Díaz *et al.* (1998) compared functional traits to environmental factors across a broad region and found a strong filtering effect due to the environment. However, we are unaware of such studies conducted within one region to demonstrate either disturbance effects or more subtle environmental effects. Shao *et al.* (1996) did demonstrate that plant functional groups were correlated with patterns along a coastal barrier island. Three functional groups included (a) foredune grassland vegetation, which is adapted to dry, less stable conditions, (b) woody thickets and forests, adapted to older, stable sites, and (c) marshes dominated by hydrophytes adapted to hydric conditions. Much work remains to evaluate plant functional type changes within successional seres. In particular, this question bears on the degree of predictability in seres and on rehabilitation (Chapter 8). We will consider functional groups in more detail in Chapter 6.

5.5 Persistence and longevity

5.5.1 Persistence

The ability of an individual to persist and expand as soils mature and environmental conditions change has important consequences for primary succession. Diversity of a site can decrease when a few pioneer species persist and expand, while most pioneers die without successful replacement. Later, conditions may be so altered that even initially persistent

Fig. 5.14. A large, solitary *Arctostaphylos nevadensis* spreading on a 20 yr old lahar, Mount St. Helens, Washington (U.S.A.).

species are replaced by larger or more tolerant species. Therefore, the traits of successful invading species change through time. The ideal pioneer disperses ably, grows rapidly and therefore can produce vigorous vegetative growth. Such a species tolerates stress well and can persist indefinitely. Prach & Pyšek (1999) compared pioneers of newly formed mine spoils in the Czech Republic and found the successional dominants to be tall, wind-pollinated, capable of strong lateral spread and responsive to nutrients and moisture. This monopolist syndrome is comparable to Grime's (1977) 'competitor' strategy, not the 'ruderal' strategy common in secondary succession. Annuals were rare in these primary seres, although annual grasses are common in many other seres where conditions are less severe.

Plants will better withstand repeated disturbance if they possess strong vegetative growth. As was described above, vegetative reproduction permits local expansion from intact vegetation (e.g. edges and relicts). Clonal growth also permits individuals to occupy space well before they may be able to produce viable seeds. Long-lived species such as *Arctostaphylos* shrubs (Fig. 5.14) occur sporadically on lahars on the eastern flanks of Mount St. Helens. They flower and bear fruit, but close inspections from 1995 to 2001 have never found young plants. Clones that are disturbed by browsing or erosion usually survive and recoup the damage. Future success of seedlings is also uncertain because dense moss carpets now cover most surfaces. Eventually, even these clones senesce and are invaded by woody species and robust herbs.

Sexual reproduction permits rapid colonization of the immediate surroundings if suitable conditions occur. Because the first colonists may ameliorate the local environment, they may be the center of nucleation – that is, they can facilitate the invasion of other species. To persist, particularly when secondary invaders include species that can grow over the original colonists, these colonists must produce seeds to expand the local population and to inhibit establishment of other species in favorable microsites (see Chapter 6).

5.5.2 Longevity

The ability of a species to persist is limited by its genetic potential and by the nature of the environment. Most primary seres are marked by transitions to longer-lived species. For example, Rydin & Borgegård (1991) noted a strong shift in persistence among species invading newly formed islands. Sixty percent of pioneer species were annuals, but no annuals occurred in later stages. The abundance of biennial species also declined with site age. Changes in life-history dominance imply that replacement by the same species is uncertain and persistence is crucial. A long-lived species that occupies an expanding area will produce many seeds. Paradoxically, the longer the species persists, the less likely it is that its own seedlings will replace it. The local area may be depleted of resources, there may be pathogens that preclude establishment, herbivore densities may increase or site amelioration may change conditions such that the species can no longer establish from seeds.

Longevity is also affected by environmental stresses. Species may live for prolonged periods under chronic nutrient or drought stress, simply occupying the site. This is analogous to stunted saplings, common in dark forests, that persist until some canopy disturbance affords them an opportunity to grow. Once conditions improve, persistent, but not reproductive, plants will have an advantage over those that disperse from a distance. *Metrosideros* forests in Hawaii persist for thousands of years. Individuals change leaf morphology and, under pressure from increased environmental and competitive stress, differ along the chronosequence. This species persists even though there is substantial species turnover in the understory (Kitayama & Mueller-Dombois, 1995a).

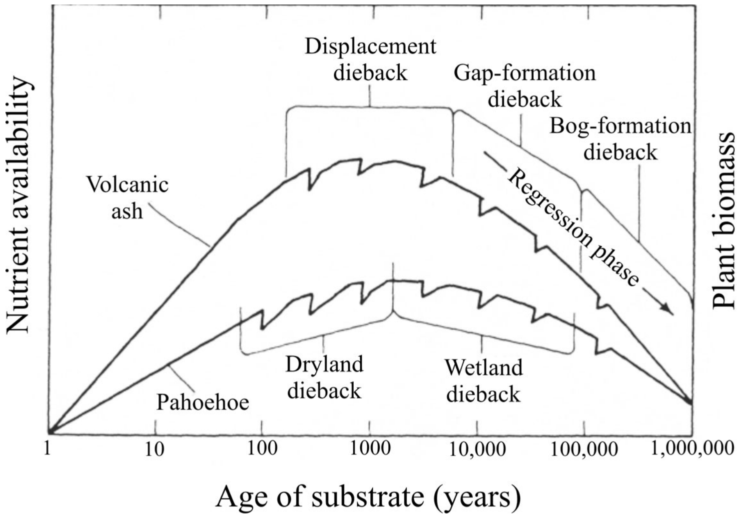

Fig. 5.15. Forest dieback during forest succession in Hawaii. From Mueller-Dombois (1986). With permission, from the *Annual Review of Ecology and Systematics* Volume 17 © 1986 by Annual Reviews. www.AnnualReviews.org

Chronic disturbance may cause the death of individuals and open a system for species not yet established because these conditions are normally less stressful than the initial conditions. Therefore, disturbance is an essential part of any sere. Herbivory can disrupt the system and may, depending on circumstances, arrest, retard or accelerate succession (see Chapter 7).

Cohorts sometimes die simultaneously. *Lupinus lepidus* forbs provide one example. Stem borers and leaf miners periodically devastate this species, which has a short life span. When dense concentrations develop, Fagan & Bishop (2000) demonstrated that herbivory hastened cohort demise and slowed the rate of population expansion. Because this species is pivotal in contributing nitrogen to infertile habitats, herbivory slowed succession. *Metrosideros* is the dominant native tree species on lavas of all ages on the island of Hawaii (Mueller-Dombois, 1987a). It experiences simultaneous cohort death perhaps due to a combination of causes such as extreme weather conditions that cause prolonged flooding or site-specific nutrient limitation (Fig. 5.15) (Balakrishnan & Mueller-Dombois, 1983; Mueller-Dombois, 1985, 2000; Gerrish *et al.*, 1988). Biotic agents (e.g. the fungal pathogen *Phytophthora* and the beetle *Plagithmysus*) may also hasten dieback in some instances. Death of the dominant canopy tree opens up the community for subordinate species such as a climbing fern, *Dicranopteris* or for regeneration of different morphotypes of *Metrosideros* tree (Mueller-Dombois, 1986). Similar mass deaths due to intrinsic causes have been documented for other tree species including the European conifers, *Juniperus*, *Pinus*, *Abies*, *Quercus* and *Betula* in North America, *Abies* in Japan, and *Nothofagus* in New Zealand (Mueller-Dombois, 1987b).

5.6 Successional consequences of dispersal and establishment

5.6.1 Under-saturated early successional communities

Early seres are under-saturated compared with older ones of similar vegetation structure because stressful environments may preclude the growth of many species. Equilibrium conditions are unlikely to develop because the putative equilibrium number of species is increasing as the habitat develops more rapidly than new species can colonize. Many species that could establish simply do not reach the site.

Open habitats on Mount St. Helens were used to test the hypothesis that equilibrium species numbers are related more to dispersal than to habitat values. Four species–area curves for an isolated pumice barren (Abraham Plain) and two for a moderately isolated lahar are shown in Fig. 5.16. Data were obtained in 1999, 20 growing seasons after the sites formed. The curves flatten quickly and after fifty 10 m × 10 m plots were sampled. Thereafter, only a few rare species are added. There are more species on the lahars, which are closer to intact vegetation and are composed of old, reworked substrates. The isolated pumice has low mean cover (< 6%) and there appears to be room for invasion by additional species. However, all suitable species from the immediate area already occur. These data suggest that even 20 yr after their initiation, moderately stressful, moderately isolated sites are not in biogeographic equilibrium. While there are few new species to invade and increase the number of species, there is ample opportunity for existing species to expand so that the curves will be steeper and level off sooner.

5.6.2 Under-saturated late successional communities

Late primary successional sites should also be under-saturated because normal dispersal will not permit a full complement of species to reach a site before it is structurally mature. There will be fewer species present

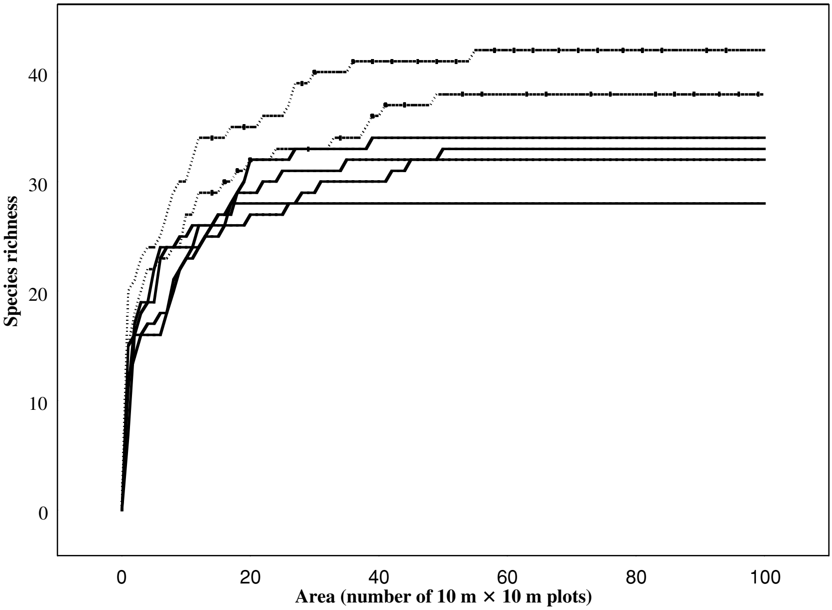

Fig. 5.16. Species – area curves in two sites on Mount St. Helens in 1999: Abraham Plains (solid lines); lahars (dotted lines). Values are cumulative number of species in one hundred 10 m × 10 m plots for each line.

than in similar mature vegetation in the immediate area that has not experienced significant disturbance for several generations of the dominant species. Data for this hypothesis are limited, but Clarkson (1990) reported that volcanic communities are significantly depauperate in species compared to older landscapes. Tussock lands and herb fields on Mount Taranaki lacked many species common in the same vegetation elsewhere. Isolated primary successional sites may not receive all species capable of growth in the developed conditions even after many decades, although species with at least moderate dispersal will arrive within a few years (Peterken & Game, 1984). This view is similar to that of Lawlor (1986), who suggested that very isolated habitats would have a very shallow species–area curve because immigration rates are so low, while extinction rates change little with isolation. In addition, the experience of restoration ecologists suggests that even with active introduction of species, mature restored habitats have fewer species than natural ones. Very old seres often begin to lose species, probably owing to site infertility (Walker *et al.*, 2000). Such ancient landscapes as those on dunes in eastern Australia (Walker *et al.*, 1981) may be analogous to anthropogenic sites that are so degraded that they cannot recover from major disturbance (see Chapter 8).

5.6.3 Novel species assemblages

Because landscape and dispersal effects can be pronounced, particular plant communities developing on new substrates may be new combinations. Plants from different habitats are thrown together and may persist for extensive periods before competitive factors reduce heterogeneity. Added to this is that many species did not occur in a region during previous major disturbances. Clarkson (1990) pointed out that early in New Zealand seres, the limited competition on recent volcanic substrates permits strong overlap among species that rarely co-occur elsewhere in mature vegetation. Tagawa (1992) noted that shrub vegetation dominated by *Ardisia* in southwest Japan formed a stable and nearly monotypic community on the smallest of three islands, but occurred with several species on the larger islands. He suggests that dispersal limited other species, permitting this novel community to persist and to resist invasion.

Early in vegetation assembly on Mount St. Helens, del Moral (1993a) noted that novel species groups had formed. These included the close and unusual association of *Lupinus lepidus* and *L. latifolius* on lahars (Braatne & Bliss, 1999). The European forb *Hypochaeris* continues to persist in association with native forb colonists including *Anaphalis*, *Epilobium* and *Hieracium*. This community has only recently formed, confined to abandoned dirt logging roads. Several wetland communities, dominated by *Salix* shrubs, with *Equisetum* horsetails or with *Juncus* rushes, are also novel (del Moral, 1999b).

5.6.4 Priority effects

If initial colonization has a stochastic component, do subsequent events override chance to produce more predictable vegetation during succession? Another way of stating this is to ask whether assembly order affects the course of succession. Assembly rules are general principles that determine how species combine to form communities (Belyea & Lancaster, 1999). If rules are strong and based on species composition, then convergence during succession should occur. If rules are strong, but based on growth form or other traits, then convergence is not inevitable, yet the sere will be predictable along functional lines. If meaningful rules do not exist, then any findings of pattern result only because there are only a few possible ways for a community to assemble (given, for example, climate or dispersal limitations). Weiher & Keddy (1995) noted that, although the experimental wetland communities they created were different from random and appeared to follow assembly rules, there was still a strong stochastic component. Species rank orders were inconsistent and many species occurred sporadically. In the context of early primary succession, so strongly affected by stochastic factors, any rules may be hidden.

Samuels & J. Drake (1997; see also D. Drake, 1990) suggested that priority effects could retard the development of communities that were predictably structured. They further asserted that assembly rules could only describe species interactions, not environmental controls. Implicit in this view is that chance leads to alternative sets of colonizers that can persist despite any putative assembly rules (see sections 3.8 and 7.1.1 on species assembly).

Tagawa (1992) noted that the chance priority arrival of *Neonauclea* trees strongly conditioned the subsequent development of forests on the three Krakatau islands. Rakata (the youngest) differs strongly from Panjang and Sertung. *Neonauclea* formed a forest on Rakata, but not on the others. These forests have resisted invasion by tree species such as *Timonius*, *Dysoxylum* and *Ficus* and therefore appear to keep assembly rules from being followed. In contrast to exclusionary processes suggested by Tagawa, Eriksson & Eriksson (1998) determined experimentally that species sown after another species had a greater probability of establishment success, suggesting that facilitation could accelerate changes and that there may be sequence rules. However, these rules are dependent on species interactions, not environmental factors. It is clear that in isolated habitats of many types, developing seres will accumulate species depending on landscape and stochastic factors and that the initial colonists may dictate subsequent development for decades. Rules involve biological interactions, that are themselves contingent on so many variables, that consistent prediction based on these rules remains unlikely over the course of primary succession.

5.6.5 Disharmonic communities

Disharmony in a community results when the vegetation is a biased accumulation of species from the surrounding landscape. The bias is the result of isolation, which selects differentially for distinct dispersal modes. However, it may also result from extreme stresses that permit only a few kinds of species to establish.

Surtsey, a small, isolated Icelandic island that formed in 1963, remained so barren in 1990 that Fridriksson (1992) could map each individual of all species except the forb *Honkenya*. The flora was an unrepresentative sample of the nearest large islands and of Iceland. Of the 24 species present in 1990, 72% were from the nearby Westman Islands and 28% from Iceland or beyond. Most (64%) were introduced by sea birds, with 27% carried by ocean currents. The remaining species were wind-dispersed. This study emphasized that geographic location, combining distance across a sea barrier with unfavorable winds, is a main factor that determines the invasion of new habitats.

Several research groups studied the Krakatau Islands extensively where Whittaker *et al.* (1997, 1999) described disharmony. They found that 46 families (represented by 91 species) found on nearby islands were not represented. The lack of suitable dispersal mechanisms was considered the most important factor, but breeding systems might also be important. For example, there may be a lack of specific pollinators (see section 5.2.1 on pollination) or the species may be obligate out-crossers.

Whittaker & Jones (1994a, b) proposed a model of recolonization on Rakata that helps to explain how dispersal leads to disharmony. The first phase was dominated by rapid colonization along the shore by sea-borne dispersal units and colonization of the interior by wind-dispersed ferns, grasses and Composites. During this early phase, animal dispersal to the interior was limited because there was little to attract birds. Sea transport continued to dominate the second phase, but wind dispersal became less important and animal transport became more important. Trees and shrubs developed into woodlands and fern dominance was reduced. Frugivores were increasingly attracted to the woodlands and accelerated the pace of colonization. In the last phase, there was little further invasion along the strand, but some species began to expand inland. These species are diplochorous (sea-borne), but potentially bird- or bat-dispersed; they may have formed an enticement to birds and bats that facilitated the introduction of purely endochorous species. There is now little available shore habitat and most species in the species pool have arrived. Forests have developed nearly continuous canopy and arboreal ferns and orchids have arrived. Woody species introduced by frugivores formed the largest group during this most recent phase. There were also limitations to invasion in this situation that are instructive. Species unlikely to invade the developing vegetation included additional sea-borne species because there was no available habitat, wind-dispersed species with large-winged seeds that were unlikely to cross the water barrier and large-seeded species that

Table 5.4. *Rates of colonization for primary dispersal mechanisms on Rakata Island since 1883*

Phase I, 1883 to 1897; Phase II, 1898–1919; Phase III, 1920–1989. Secondary spread is not considered, but includes at least 24 sea-colonists and 15 human-introduced species. The total was calculated from the number of years in each phase and includes all species that were found in the phase, even if they later disappeared.

	Colonization rate, species per year			
Phase	Sea	Wind, spores	Wind, other	Birds and bats
I (16)	1.64	1.0	1.0	0.14
II (21)	1.18	0.18	0.86	1.32
III (69)	0.29	0.83	0.83	1.26

Data derived from Whittaker & Jones (1994a).

are bat-dispersed or dispersed by land mammals. Table 5.4 summarizes the patterns of invasion in terms of annual rates of species colonization, derived from several sources and summarized by Whittaker & Jones (1994a).

Disharmony has evolutionary consequences. Kitayama (1996b) described the vegetation on Mount Haleakala, a basaltic volcano 800,000 yr old in the Hawaiian group. He found that species richness and turnover in wet forests was much lower than in less isolated comparison sites. Species turnover along landscape gradients was very low on Haleakala, a reflection of the generally broad amplitude of most species and their lack of specialization relative to the comparison flora. Adaptive radiation has been limited on this very isolated volcano.

5.6.6 Biogeographical effects

MacArthur & Wilson (1967) proposed the equilibrium theory of island biogeography (ETIB) that has been applied to primary succession in several ways. Rydin & Borgegård (1988a) studied islands in Lake Hjälmaren, Sweden, that were formed by lowering the lake 1.3 m in 1882. They found that a predictable species log-area curve was the best description of species richness. Interestingly, the distance effect predicted by ETIB disappeared over time. Although area was always the primary determinant, distance effects were important only for the first 20 yr. Thereafter, only area and habitat complexity were important. This suggests that all species able to grow on these islands had reached them within two decades and that thereafter distance was unimportant. The largest islands, over 0.3 ha, appeared to have equilibrated by 1985, with extinctions equal to immigration. Thirty previously recorded species did not occur in 1985, apparently due to competitive interactions. Small islands remained unstable, precluding equilibrium.

In stunning contrast to these Swedish islands is Motmot, a caldera island formed in 1968. It lacks littoral species because it is surrounded by fresh water and has not received many *Ficus* species owing to the lack of dispersal agents (Thornton *et al.*, 2001). The flora remains well below putative saturation levels and it is disharmonic, as would be expected for a young, extremely isolated habitat. As yet, the surrounding Long Island (350 yr old) also remains substantially under-saturated. Owing to its harsh physical environment, it remains in a quasi-stable equilibrium of species richness, well below that of other islands more favorably located in the region. The combined example of Long Island and Motmot cautions us not to expect plant communities undergoing primary succession to rapidly approach equilibrium numbers predicted by ETIB.

5.6.7 Establishment conclusions

All vegetation on this planet results from primary succession, although the initial effects may have long since been erased. Barren sites resulting from massive disturbance or upheavals will be colonized, but how they are colonized is determined by landscape factors and life-history properties of the proximate biota. This phase is strongly stochastic, leading to initially variable species associations. For plants, each life-history stage may have a fatal weakness that prevents success. Proximity to the newly available site is the most important factor, from which much else follows, but proximity alone does not dictate primary succession. A species in the donor pool must produce seeds at an opportune time, be dispersed by effective abiotic (wind, water or gravity) forces or have suitable animal vectors available to it. Distance and barriers to the newly created site restrict the types of initial colonist. The barren landscape must trap seeds and offer opportunities for seedling germination and establishment. The degree of habitat stress governs the initial rate of biomass accumulation and ultimately of species turnover. Once an immature plant is established, it must withstand physical stresses (e.g. drought, low nutrients, high temperatures, instability) and persist. Usually, a viable population is built by successful on-site reproduction. However, the pioneering species may sometimes only serve to ameliorate the site and fail to reproduce successfully. Successful early colonists will expand vegetatively and by seed to rapidly colonize the site.

Communities assembling early in succession are governed largely by chance. This can lead to novel and to disharmonious communities. Disharmony has ecological consequences when a few species continue to dominate a sere, and evolutionary consequences when such taxa undergo adaptive radiation. Most primary seres remain under-saturated for a very long time because colonization cannot keep up with local extinction and because many competent species fail to reach the site.

Arrested succession occurs when better competitor species fail to arrive. Rarely, the population of a potential dominant may not develop due to a lack of pollinators. There also may be priority effects, so that the sere is strongly regulated by the initial colonists. As a system develops, the relationship between species and their environment becomes more predictable in part because competition intensifies to eliminate less adapted species. However, which set of species may occur in later stages of a sere remains less predictable.

The first colonists do not normally persist, although where the pool of immigrants is restricted and conditions are stressful, they may. More typically, ameliorating conditions enhance invasion probabilities of less stress-tolerant species. Species turnover results from the combination of competitive exclusion along a temporal gradient and the elimination of safe-sites for colonist species. After the initial rush of establishment in open habitats, primary succession is driven largely part by biotic interactions. We will explore these in Chapter 6.