SECTION II

Mechanisms of Succession

Upper Pumice Plain, with building dome and Loowit Falls; this complex landscape made it hard to recognize any one, particular succession sequence because each site offered its unique combination of processes.

The classic perspective

The traditional view of primary succession is that it is predictable and repeatable, determined by a few key rules. Each time you re-run the experiment (for example when a volcano clears the landscape), you should get the same vegetation on the new landscape. Frederick Clements, the most influential American plant ecologist until the 1970s, studied succession for decades. He coined most of the terms that still burden us (e.g., pioneer). He believed resolutely that *post hoc, ergo Procter hoc* (after this, therefore because of this). He always observed that a consistent group of species (pioneers) invaded after disturbance and these species were followed inevitably by another suite of species that he called seral species. He inferred that because seral species followed pioneers, the pioneers must have acted in some way to create conditions required by the seral species. The consistent composition of pioneer species may have been true in the broad plains of Nebraska, where environmental conditions much change over long distances. Pioneers facilitated the invasion of seral species, which in their turn, prepared the site for climax species capable of sustaining themselves indefinitely. This idea began to fall apart in the 1970s when numerous ecologists conducted experiments to determine if seral species indeed required facilitation.

The classic idea of succession also mandates that communities occur in discrete successional stages, with temporal transitions occurring quickly, followed by relatively stable periods. During the last 30 years, many workers have determined that development is a gradual process and that stages are convenient, but arbitrary, designations.

Clements further declared that in any given environment, successional trajectories converged to form a single vegetation type (the climax). Over time, vegetation in different parts of one habitat must become increasingly similar. There is some support for this idea, but, as we shall see, it is neither simple nor universal.

Overview of Section II

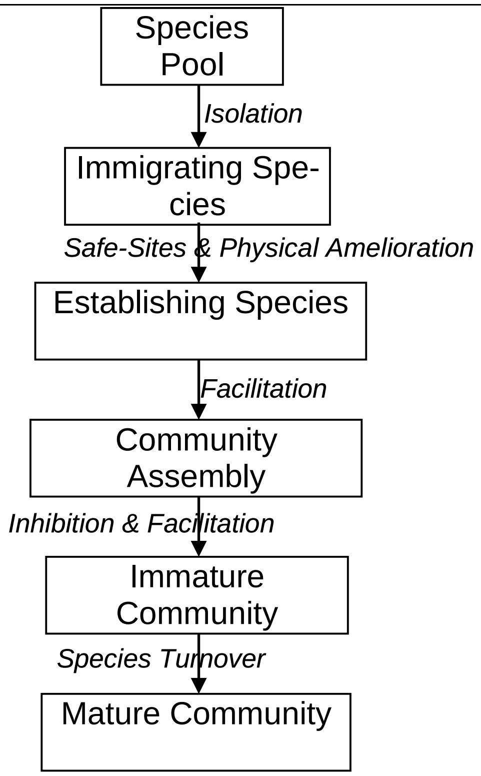

Fig. II.1. *Mechanisms of primary succession. Isolation restricts species immigration; immigrants that land in a safe-site may establish; improving site conditions enhances seedling success and improves productivity; facilitation results from biotic modification and the creation of more, diverse safe-sites and a community of species slowly assembles. During assembly, plants may inhibit others through competition or they may facilitate the success of other plants, thus leading to a changing community. Species turnover leads to a mature community that may differ completely from the initial vegetation on the site. Different mature communities may develop from similar initial conditions.*

Plant succession on surfaces surrounding the cone of Mount St. Helens was initiated by disturbances whose intensity and severity varied profoundly in space (Section I). The chapters in this section describe the ecological mechanisms that characterize primary succession on these landscapes, with examples from my research to help clarify the concepts. The paper by del Moral et al. (2005) provides an overview of the concepts described here. These results differ from some of the concepts proposed by Clements; particularly that succession was readily predictable. However, Clements did provide a logical framework for the steps in succession that I use to organize this discussion. **Fig. II.1** will help to understand how each chapter fits into the scheme of successional mechanisms. This figure has evolved from early studies on Mount St. Helens (del Moral 1993) and based on concepts developed by Walker and myself (2003).

In this section, I describe how plants reclaimed primary surfaces on Mount St. Helens and how vegetation developed and interacted to produce comprehensible patterns. I will describe these four stages of primary succession in the following chapters: dispersal, establishment, community assembly and maturation. At the conclusion of these chapters is a chapter that summarizes the main points developed, with an emphasis on how the collective Mount St. Helens experience has altered general concepts about succession. Data are based on permanent plots described in **Table II.1**.

CHAPTER 6 (Dispersal and the Effects of the Landscape) describes dispersal mechanisms and early species assembly. Distance and the landscape context of a site are significant filters of the species pool so that the seed rain is determined in part by distance to sources of potential colonists. Until some form of reproductive material wafts on to a newly created or recently exposed surface, no succession can occur. Most species cannot disperse consistently beyond tens of meters and the total propagule density even next to intact vegetation is surprisingly low. Chance therefore plays a large role in determining WHICH species arrive at isolated surfaces. Early plant communities may be quite variable, but their effects may be felt for decades. Therefore, successional pathways may not be very predictable. However, both pioneers and late arrivals each display distinct sets of ecological traits. Good dispersers are generally intolerant of conditions in newly formed substrates and although they may arrive, they rarely establish (e.g., Wood and Del Moral 1987). Early random dispersal effects can alter rates and direction of succession (i.e. trajectories). This chapter focuses on what limits the species pool.

CHAPTER 7 (Establishment in the Barrens) offers an exploration of how immigrants meet challenges to their establishment. The concepts of physical amelioration that affects most of the landscape evenly and of safe-sites that represent particularly favorable microhabitats are featured in this discussion. Nurse plants may facilitate the establishment of many species, but established species often impede the success of seedlings germinating beneath their canopy. There is a balance between the positive effects of facilitation and the negative effects of competition.

Once a few species become established, the vegetation can develop and species assemble into communities. CHAPTER 8 (The Development of Communities) builds on the time-course studies described in Section I. It compares rates of succession among the several habitats to infer how habitat stress limits development. Central to species assembly on Mount St. Helens is the prairie lupine, arguably the most studied plant here. It facilitates through nitrogen fixation and competes strongly using its dense, shallow roots, a low canopy and thick persistent leaf layer. It is intricately involved with many plants, herbivores and pathogens.

In CHAPTER 9 (The Maturation of Vegetation), I explore how assemblages of species that are interacting with one another develop closer ties to their environments. Successional trajectories are often complex and the communities through which a sample of vegetation develops are explored here. In this chapter, the relationships between species composition and environmental conditions described in several studies are summarized and an overall conclusion is reached. This chapter also explores alternative possibilities for vegetation within one habitat and the possibility that there are rules that direct the assembly of species into vegetation.

CHAPTER 10 (How Mount St. Helens Changed Our Understanding of Succession) summarizes the major findings presented in the book. Many of these lessons can be applied to attempts to restore and rehabilitate vegetation and to conservation biology.

Table IIA-1. Location of permanent plot transects, dates of monitoring, longitude, latitude, elevation, geographic orientation (aspect), slope, impact type, succession type, number of plots and orientation of transects of plots on the landscape.

Location	Duration	Longitude	Lati-tude	Elevation	Aspect	Slope(°)	Impact	Type	Number of Plots
AP	1995-2010	122.13993	46.21199	1365-1367	E	2-3	Blast; Scour;	Primary	10 plots; grid
BC-A	1980-2009	122.22549	46.17568	1302-1309	SW	2-7	Tephra	Disturbance	3 plots; contour
BC-B	1980-2009	122.21702	46.17926	1550-1555	SSW	3-8	Tephra	Disturbance	6 plots; contour
BC-C	1980-2008	122.21359	46.18169	1626-1630	SW	12-20	Tephra	Disturbance	1 plot
BC-D	1981-2009	122.21452	46.18090	1600-1632	SW	13	Tephra	Disturbance	3 plots; uphill
BC-C	1980-2008	122.21467	46.18114	1630-1640	W	12	Scour-Mild	Secondary	2 plots; uphill
BC-D	1981-2009	122.21238	46.18201	1632-1705	W	18-24	Scour-Mild	Secondary	3 plots; uphill
Lahar I	1982-2009	122.22349	46.17630	1418-1460	W	2	Moderate deposit	Primary	2 plots; uphill
Lahar II	1982-2005	122.22626	46.18289	1430-1470	SW	3-6	Thick deposit	Primary	5 plots; uphill
PC-A	1980-2009	122.15188	46.15335	1425-1435	SE	6-15	Light scour	Secondary	4 plots; contour
PC-B	1980-2009	122.15837	46.15443	1550-1558	ESE	13	Intense score	Secondary	5 plots; contour
PP	1989-2010	122.15966	46.23413	1248-1306	NW	2-6	Blast; pumice	Primary	12 plots, uphill
STR-I	1984-2010	122.19482	46.23291	1218-1341	NW	9-15	Blast	Primary	10 plots; uphill
SR-II	1989-2010	122.19417	46.22807	1354-1467	NW	12-15	Blast	Primary	10 plots; uphill
TR	1981-1997	122.22971	46.21594	1280-1430	WNW	4-18	Blast edge	Secondary	10plots; uphill

Table II-2B. Location of grids, dates of monitoring, longitude, latitude and elevation near mid-grid, impact type, succession type, and number of grid plots.

Location	Duration	Longitude	Latitude	Elevation	Impact	Succession	Number
Abraham Plains	1988-2010	122.14102	46.21167	1360	Blast; scour; pumice	Primary	400
Lahar 1	1987-2008	122.22349	46.17630	1435	Lahar-thick deposit	Primary	175
Lahar 2	1987-2004	122.22757	46.18229	1430	Lahar-thick deposit	Primary	317
Pumice Plain	1989-2010	122.15929	46.23449	1235	Blast; pumice	Primary; relict	200
Willow Spring	1986-2010	122.18237	46.24829	1122	Blast; pyroclastic flow	Primary; wetland	1600