Ecological Responses to the 1980 Eruption of Mount St. Helens

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Editors

Ecological Responses to the 1980 Eruption of Mount St. Helens

With 115 Illustrations

With a Foreword by Jerry F. Franklin



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Foreword

Reconfiguring Disturbance, Succession, and Forest Management: The Science of Mount St. Helens

When Mount St. Helens erupted on May 18, 1980, it did more than just reconfigure a large piece of Cascadian landscape. It also led to dramatic revisions in our perspectives on disturbances, secondary succession, and forestry practices. The Mount St. Helens landscape turned out to be a far more complex place than the "moonscape" that it initially appeared to be. Granted, a large area was literally scoured and sterilized, and that vast expanse of newly formed rock, mudflows, and avalanche debris up and down the mountain made the Mount St. Helens landscape unique. But I still remember my surprise when, as I stepped out of the helicopter on first landing within the extensive "devastated zone," I saw hundreds of plants pushing their way up through the mantel of tephra.

Surviving organisms were stunning in their diversity, abundance, and the mechanisms by which they survived. They persisted as whole organisms living below ground, encased within late-persisting snowbanks, and buried in lake and stream sediments. They survived as rhizomes transported along with the massive landslide that accompanied the eruption and as stems that suffered the abrasion of mudflows. Mudflows floated nurse logs covered with tree seedlings and then redeposited them on the floor of a forested river terrace. Millions, perhaps billions, of plants survived as rootstocks and rhizomes that pushed their way up through the tephra, and others survived on the bases of uprooted trees.

Wood (snags, entire boles, and other woody debris) was evident many places in the devastated zone, beginning the fulfillment of its incredibly diverse functional role as habitat, protective cover, sediment trap, energy and nutrient source, and debris jam, among other aspects.

The multiplicity of disturbances, both individual and combined, resulted in an immense diversity of posteruptive conditions and potential study sites, including both terrestrial and aquatic sites ranging from minimally impacted to heavily disturbed. Almost every locale within the devastated zone was affected by two or three contrasting disturbances. Some impacts extended far beyond the devastated zone, particularly the aerial deposits of volcanic materials (tephra) that extended over hundreds of thousands of square kilometers.

The concept of *biological legacies* emerged from this very diverse collection of surviving biota and organically derived structures. Biological legacies encompass the array of organisms and organically derived structures and patterns that persisted from the predisturbance landscape to populate and influence recovery. Great insight was unnecessary: the noses of the ecologists investigating the devastated zone were daily rubbed in the concept of legacies and their importance.

Mount St. Helens was the catalyst for the biological legacy concept and many other important additions and modifications to our basic understanding of ecological recovery following disturbance, or "secondary succession," as old hands might have described it. Why should this have been so when the concepts are so obvious in retrospect? Perhaps it is because of the magnitude of the event, which led to the early and very incorrect perception of a moonscape at all locations. Or, it may be because many early studies of secondary succession focused on old fields with their limited legacies of organisms and near absence of structural legacies. Handy as the old fields may have been to early centers of ecological science, they were not representative of conditions and processes following natural disturbances.

Whatever the explanation, the importance of biological legacies, which include the "residuals" of Frederic Clements, is evident to disturbance ecologists everywhere, whether their focus is fundamental or applied. Indeed, *one might propose that the most important variables influencing postdisturbance recovery processes are the types and levels of biological legacies that are present*, not the type, intensity, size, or any other attribute of the disturbance. The legacies are at least among the most important predictors of what will happen during the initial recovery process.

The concept of biological legacies has had a similar effect on applied ecology, specifically forestry practices or silviculture. The dominant forest-harvest technique of clear-cutting proves to have little similarity to such natural disturbances as fire, wind, and even volcanic eruption. Clear-cutting leaves little in the way of biological legacies. Natural disturbances provide the appropriate models for silviculture, where maintenance of biological diversity and natural ecosystem functions is a primary or collateral goal of forest management, such as on U.S. federal timberlands. From research at Mount St. Helens has emerged the concept of variable-retention harvesting, a silvicultural system in which varying types, amounts, and patterns of living trees, snags, and logs as well as small forest islands are left to "lifeboat organisms" and structurally enrich the regenerating forest.

Mount St. Helens is providing us with other important conceptual or "big-picture" perspectives on large disturbances, such as patterns of recolonization and the role of large, slowly regenerating disturbed areas. Authors in this volume describe many spatial aspects of the recolonization process, including "hotspots" or focal points of community recovery that resulted from both survivors and from particularly favorable environmental conditions for organisms to establish, such as margins of ponds and wetlands. They also talk about "coldspots," such as sites where posteruption erosional deposits buried surviving plants and slowed recolonization.

Recolonization of the Mount St. Helens devastated zone has emerged from multiple centers and not primarily by incremental advances of invading organisms from the margins, as many predicted. The recovery process began with innumerable hotspots of surviving organisms, some as small as individuals and others as large patches of intact communities, such as those surviving in snowbeds. I have applied the term "metastasizing" to describe the recovery process within the devastated zone; according to Webster, metastasis is a pathological term, but it does convey the sense of multiple centers of colonization ("infection") that grow, spread, and eventually converge. This pattern of colonization provides an alternative to the "wave-front" model often favored in successional studies.

Mount St. Helens is also informing us about the important role that large, slowly reforesting disturbed areas may contribute to the maintenance of regional biodiversity. Large and diverse populations of major faunistic groups (such as songbirds, amphibians, and mesopredators) characterize the naturally developing (and unplanted) portions of the devastated zone. Who would have predicted western meadowlarks colonizing an area on the western slopes of the Cascade Range? Hardwood trees and shrubs, not conifers, dominate significant portions of this landscape.

We can expect that this structurally and environmentally diverse landscape is going to dominate the unsalvaged, unplanted portions of the Mount St. Helens devastated zone for many decades to come. The reestablishment of extensive tracts of closed coniferous forest so characteristic of this region is going to be a long time in coming!

The biological richness of the Mount St. Helens landscape has direct relevance to debates that are currently emerging regarding appropriate restoration policies following major

wildfires and other disturbances. Timber salvage and rapid reforestation with conifers have been accepted policies that are aggressively pursued. As a consequence, naturally disturbed, unsalvaged, and unplanted early-successional habitat is the scarcest of the natural forestland states in the Pacific Northwest, much rarer than that of old-growth forest.

Research at Mount St. Helens is demonstrating the potential value of such naturally regenerating, early-successional landscapes as regional hotspots of biodiversity as well as demonstrating that such habitat is not to be confused with planted clear-cuts or even salvaged burns.

In this book, we have the first significant summary of this paradigm-busting science based on 25 years of research on one of the largest and most complex disturbance events accessible for intense study. The chapters provide both the details and idiosyncrasies of individual organisms as well as broad general lessons regarding the physical and biological processes associated with recovery.

The chapters of this book show the relevance of the Mount St. Helens eruption to fundamental ecological theory and not the "special case" that some scientific critiques once suggested. Ecologists should study it carefully because general ecological theory of disturbances and recovery processes must encompass the lessons from Mount St. Helens.

Similarly, applied ecologists (the foresters, wildlife managers, fisheries biologists, and other resource managers) will find much that they can incorporate into management regimes that are more closely based on natural disturbances and provide better for maintenance of biodiversity and ecosystem processes.

Finally, stakeholders and policy makers will find much in the Mount St. Helens science that should cause them to reflect on the role of natural, early-successional habitat as a part of our regional forest landscapes. When one reassesses resource management in the 20th century, the commodity-based perspective of "timber salvage and reforest" should be a major part of that reflection, and we can hope that it will be informed by a continuing flow of knowledge from the Mount St. Helens landscape.

This extraordinary volume provides an opening to the future. We owe major thanks to the hundreds of scientists, students, and technicians who have participated in this research and to the authors of these chapters for providing us with this stimulating synthesis. But the opportunities for further study are infinite and important. We hope that, among you readers, will be some who will assume the challenge of carrying the research on Mount St. Helens forward for the next 25 years.

JERRY F. FRANKLIN

Preface

The May 18, 1980 eruption of Mount St. Helens abruptly altered the geological and ecological systems of southwestern Washington State. The eruption was so well documented by the media that it was viewed around the world and it changed people's perception of volcanoes. The eruption created new landscapes that were subsequently studied by dozens of ecologists. This book integrates and analyzes much of the information learned from those studies and adds recent insights and findings by the contributors and their colleagues.

Many of the authors of this book have been studying ecological responses to the 1980 eruption since the early days. Several of us were on the first team of ecologists to enter the volcanic disturbance zones shortly after May 18. We were awed at the dramatic changes to the landscape and have returned for field studies in subsequent years. Others have joined the team over the ensuing years, and the loose-knit research group has met as a whole several times. Researchers working on the ecological recovery at Mount St. Helens gathered during the summer of 2000 when the USDA Forest Service's Pacific Northwest Research Station sponsored a week-long field camp, termed a "pulse." They visited each other's field sites and collected data on the 20-year status of ecosystems. The idea for this volume grew out of that pulse.

Over time, the physical and biological environment at Mount St. Helens has changed dramatically, yet the compelling character of the landscape remains. The eruption destroyed and buried much of the system of logging roads that had laced the landscape outside the remote, foot-access-only areas of Mount St. Helens and the Mount Margaret backcountry to the north. Thus, access was extremely limited in the first months and even years. Helicopters proved essential for many studies. As salvage logging proceeded outside the designated National Volcanic Monument and visitor access developed from 1981 to 1986, some of the preeruption road system was reestablished, and new roads were constructed, providing access to areas peripheral to the core of the volcanically disturbed area. With completion of salvage logging and closure of many roads by design and storm damage, access again became restricted in many areas. Yet scientists continued to return to find a fascinating, changing landscape.

Funding for ecological studies at Mount St. Helens has had a varied history. The Forest Service and National Science Foundation funded initial access and two 2-week-long field pulses in the summers of 1980 and 1981, which greatly facilitated cross-disciplinary interactions. Several National Science Foundation grants and Forest Service funding supported a series of studies from the 1980s to the present. Individual projects were funded by small grants from the National Geographic Society, Earthwatch, Washington Department of Fish and Wildlife, and several foundations. A great deal of work has been accomplished by personal initiative and by building upon related projects. The Forest Service has provided continuous support for work by Crisafulli, Swanson, and others at Mount St. Helens and for collecting, documenting, and archiving datasets from long-term ecological studies in the area.

This book is the direct result of the contributions of many people in addition to the authors. Frederick O'Hara did an excellent job as technical editor for the book. A special thanks is owed to the numerous scientists who reviewed drafts of the chapters. For this important work, we wish to thank Steve Acker, Wendy M. Adams, Joe Ammirati, Matt Ayers, Lee Benda, Edmund Brodie, Tom Christ, Warren Cohen, Kermit Cromack, Dan Druckenbrod, John S. Edwards, Roland Emetaz, Jerry F. Franklin, Scott Gende, Peter Groffman, Charlie Halpern, Miles Hemstrom, Jan Henderson, Sherri Johnson, R. Kaufmann, Jon Lichter, James A. MacMahon, Jon J. Major, Frank Messina, Randy Molina, Aaron Peacock, Daniel Schindler, Dave Skelly, Don Swanson, Lars Walker, Peter White, Amy Wolfe, Jingle Wu, and Wayne Wurtzbaugh. Theresa Valentine and Kathryn Ronnenberg (USDA Forest Service, Pacific Northwest Research Station) helped greatly with the preparation of maps and figures. Suzanne Remillard (USDA Forest Service, Pacific Northwest Research Station) assisted with information management. Jordon Smith assisted with editorial and compilation tasks. We also thank many colleagues at the U.S. Geological Survey, Cascades Volcano Observatory, for providing information and interpreting the events that occurred during the 1980 and other eruptions, particularly Jon J. Major, Dan Miller, Don Swanson, Richard Waitt, and Ed Wolf.

The editors' institutional homes provided essential support for their work at Mount St. Helens, including the writing and editing this book. Charlie and Fred gratefully acknowledge support of the Pacific Northwest Research Station and especially John Laurence, Peter A. Bisson, Tami Lowry, and Debby McKee. Virginia appreciates the support from the Environmental Sciences Division at Oak Ridge National Laboratory and specifically Linda Armstrong and Anne Wallace. The editors thank the Gifford Pinchot National Forest and Mount St. Helens National Volcanic Monument and their staffs for logistic support and access to records, maps, and research sites.

On a personal note, during the past 24 years we have spent much time in the volcanic landscape learning a great deal about disturbance ecology and Cascadian natural history and becoming quite familiar with the area. Perhaps most important have been the friends, colleagues, and family members with whom we have interacted and shared this fascinating landscape. Virginia especially thanks her family, who enjoyed assisting in the fieldwork and relinquished weekends and early mornings of her time. Fred gratefully acknowledges his family's tolerance of his Mount St. Helens fixation and the support of David Foster for the opportunity to work on the book while in residence at Harvard Forest. Charlie thanks James A. MacMahon, mentor and friend, for introducing him to Mount St. Helens and Charles P. Hawkins, Robert R. Parmenter, and Michael F. Allen for years of collaboration. Charlie thanks Hans Purdom, Josh Kling, Eric Lund, Aimee McIntyre, and Louise S. Trippe for their unwavering interest and collaboration at the volcano. Finally, Charlie thanks his daughters Erica and Teal Crisafulli, for their youthful wonder, and his parents, Helen and Carmelo Crisafulli, for tolerating his childish habitats of catching frogs and salamanders into adulthood. Collectively, the editors and authors owe special gratitude to Jerry F. Franklin, James A. MacMahon, and Jim Sedell for their personal commitments to science at Mount St. Helens and their colleagues who work there.

After 18 years of quiescence, Mount St. Helens broke her silence and entered an eruptive state on September 23, 2004. As we go to press, the volcano has been erupting for 18 continuous weeks; primarily building a new dome in the 1980 crater. Numerous small tephra falls have also been deposited near the mountain, and a few small mudflows have emanated from the crater and traveled down streams. Although it is not known how long this current eruption will last or if it will increase its activity, it is a testimony to the dynamic nature of Mount St. Helens.

As we reach the quarter-century anniversary of the major eruption, it is also timely for scientists who worked in the first posteruption period to begin passing the science baton to the next generation of scientists who will work at Mount St. Helens. This book describes observations, interpretations, and speculations from the first 25 years of ecosystem response and complements our efforts to leave well-documented, publicly accessible descriptions of long-term field plots and associated data. We hope to continue our research for years into

VIRGINIA H. DALE FREDERICK J. SWANSON CHARLES M. CRISAFULLI February 2005

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Note: A Web site has been established at http://www.fsl.orst.edu/msh/ containing background details (pictures, data details, graphs, etc.) to supplement the information included in this book.

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Part I Introduction

1 Disturbance, Survival, and Succession: Understanding Ecological Responses to the 1980 Eruption of Mount St. Helens

Virginia H. Dale, Frederick J. Swanson, and Charles M. Crisafulli

1.1 Introduction

The ecological and geological responses following the May 18, 1980, eruption of Mount St. Helens are all about change: the abrupt changes instigated by geophysical disturbance processes and the rapid and gradual changes of ecological response. The explosive eruption involved an impressive variety of volcanic and hydrologic processes: a massive debris avalanche, a laterally directed blast, mudflows, pyroclastic flows, and extensive tephra deposition (Lipman and Mullineaux 1981; Swanson and Major, Chapter 3, this volume). Subsequent, minor eruptions triggered additional mudflows, pyroclastic flows, tephra-fall events, and growth of a lava dome in the newly formed volcanic crater. These geological processes profoundly affected forests, ranging from recent clear-cuts to well-established tree plantations to natural stands, as well as meadows, streams, and lakes. This book focuses on responses of these ecological systems to the cataclysmic eruption on May 18, 1980.

Initial ecological response to the 1980 eruption was dramatic both in the appearance of devastation (Figure 1.1) and in subsequent findings that life actually survived by several mechanisms in many locations (del Moral 1983; Halpern and Harmon 1983; Andersen and MacMahon 1985a and 1985b; Franklin et al. 1985; Crawford 1986; Adams et al. 1987; Zobel and Antos 1986, 1992). Ecological change occurred as a result of survival, immigration, growth of organisms, and community development. The pace of these biological responses ranged from slow to remarkably rapid. In addition, subsequent physical changes to the environment influenced biological response through weathering of substrates and by secondary disturbances, such as erosion, that either retarded or accelerated plant establishment and growth, depending on local circumstances. The net result of secondary physical disturbances was increased heterogeneity of developing biological communities and landscapes.

The sensational volcanic eruption of Mount St. Helens initially dwarfed the ecological story in the eyes of the public and the science community; but as the volcanic processes quieted, ecological change gained attention. The variety of disturbance effects and numerous interactions between ecological and geological processes make Mount St. Helens an extremely rich environment for learning about the ecology of volcanic areas and, more generally, about ecological and geophysical responses to major disturbances. More than two decades after the primary eruption, geophysical and ecological changes to the Mount St. Helens landscape have become so intertwined that understanding of one cannot be achieved without considering the other.

The 1980 eruption of Mount St. Helens and its ecological aftermath are the most studied case of volcanic impacts on ecological systems in history (Table 1.1). Ecological research at other volcanoes has often considered ecological responses based on observations made several years, decades, or even centuries after the eruption. In contrast to eruptions of some other volcanoes, lava surfaced only in the crater of Mount St. Helens; and most of the disturbance processes left deposits of fragmented volcanic rocks through which plants can easily root and animals can readily burrow. Furthermore, studies at other volcanoes typically investigated only one group of organisms (e.g., plants) and one type of volcanic process or deposit, which contrasts to the diversity of terrestrial and aquatic life and volcanic processes and deposits considered in this book.

Since the 1980 eruption of Mount St. Helens, analyses of ecological response to eruptions of other volcanoes and to ecological disturbance, in general, have made important advances. Ecological responses to other volcanic eruptions have been the subject of retrospective investigations of historic eruptions [e.g., Krakatau in Indonesia (Thornton 1996)] and analyses of responses to recent eruptive activity [e.g., Hudson volcano in Argentina (Inbar et al. 1995)]. More broadly, the field of disturbance ecology has blossomed through development of theory (Pickett and White 1985; White and Jentsch 2001; Franklin et al. 2002); intensive study of recent events, such as the Yellowstone fires of 1988 (Turner et al. 1998) and Hurricane Hugo (Covich and Crowl 1990; Covich et al. 1991; Covich and McDowell 1996); and consideration of effects of climate change on disturbance regimes (Dale et al. 2001). Lessons

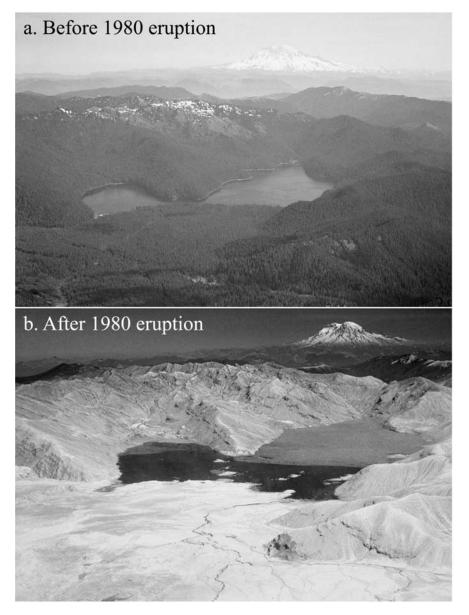


FIGURE 1.1. Before and after photographs of the Mount St. Helens landscape: (a) view north from top of Mount St. Helens toward Mount Rainier across Spirit Lake before 1980; (b) same view in summer 1980. (*Source:* USDA Forest Service photos.)

about ecological response at Mount St. Helens are shaping understanding of succession (Turner et al. 1998; Walker and del Moral 2003), disturbance ecology (Turner et al. 1997; Turner and Dale 1998; del Moral and Grishin 1999), ecosystem management (Swanson and Franklin 1992; Dale et al. 1998, 2000; Franklin et al. 2002), evolution and the origin of life (Baross and Hoffman 1985), trophic interactions (Fagan and Bishop 2000; Bishop 2002), and landscape ecology (Foster et al. 1998; Lawrence and Ripple 2000).

In the context of this progress in disturbance ecology in general and ecological studies at Mount St. Helens more specifically, it is timely to synthesize knowledge of ecological response to the 1980 eruption of Mount St. Helens. In the first 7 years after the eruption, several compilations documented the numerous, intensive studies of ecological response (Keller 1982, 1986; Bilderback 1987); however, since 1987, the scientific community has not prepared a book-length synthesis of the scores of ecological studies under way in the area. Yet, more than half of the world's published studies on plant and animal responses to volcanic eruptions have taken place at Mount St. Helens (see Table 1.1) (Dale et al. 2005; Edwards 2005). The 25-year synthesis presented in this volume makes it possible to more thoroughly analyze the initial stages of response, to assess the validity of early interpretations, to examine the duration of early phenomena in a broader temporal context, and to consider landscape processes and patterns that were not evident in the early years. These studies provide an understanding of ecological change in a complex, continually changing environment. Hence, the Mount St. Helens volcano has come to hold a special place in the study of volcanic eruptions not only in the Pacific Northwest of the United States but also throughout the world.

impact and volcano	Location	Dates of eruption	Reference
Lava Mount Wellington	New Zealand	9000 years before present (YBP)	Newnham and Lowe 1991
Mt. Fuji	Japan	1000	Hirose and Tateno 1984; Ohsawa 1984; Masuzawa 1985; Nakamura 1985
Rangitoto	New Zealand	1300, 1500, 1800	Clarkson 1990
Mt. Ngauruhoe and Mt. Tongariro	New Zealand	1550+	Clarkson 1990
Snake River Plains	Idaho, USA	~ 1720	Eggler 1971
Jorullo	Mexico	1759	Eggler 1959
Ksudach	Kamchatka, Russia	1907	Grishin et al. 1996
Waiowa	New Guinea	1943	Taylor 1957
Kilauea Iki and Mauna Loa	Hawaii, USA	1959	Fosberg 1959; Smathers and Mueller-Dombois 1974; Matson 1990; Kitayama et al. 1995; Aplet et al. 1998 Baruch and Goldstein 1999; Huebert et al. 1999
Surtsey	Iceland	1963	Fridriksson and Magnusson 1992; Fridriksson 1987
Isla Fernandina	Galapagos, Ecuador	1968	Hendrix 1981
Hudson	Argentina	1991	Inbar et al. 1995
Krakatau	Indonesia	1883, 1927	Whittaker et al. 1989, 1992, 1998, 1999; Partomihardjo et al. 1992; Thornton 1996
Pyroclastic flow			
Vesuvius	Italy	79	Mazzoleni and Ricciardi 1993
Kilauea Iki	Hawaii, USA	1750, 1840, 1955	Atkinson 1970
Miyake-Jima	Japan	1874, 1962, 1983	Kamijo et al. 2002
El Paracutin	Mexico	1943	Eggler 1948, 1959, 1963; Rejmanek et al. 1982
Mount St. Helens	Washington, USA	1980	 Wood and del Moral 1988; Morris and Wood 1989; Wood and Morris 1990; Halvorson et al. 1991b, 1992; del Moral and Wood 1988a,b, 1993a,b; del Moral et al. 1995; Chapin 1995; Halvorson and Smith 1995; Tsuyuzaki and Titus 1996; Tsuyuzaki et al. 1997; Titus and del Moral 1998a,b,c; Bishop and Schemske 1998; Tu et al. 1998; del Moral 1998, 1999a; Fagan and Bishop 2000; Bishop 2002; del Moral and Jones 2002; Fuller and del Moral 2003
Avalanche Mt. Tarapaki	Now Zooland	1550	Clarkeen 1000
Mt. Taranaki	New Zealand Kamebatka, Puscia	1550	Clarkson 1990 Grishin 1004: Grishin et al. 1006
Mt. Taranaki Ksudach	Kamchatka, Russia	1907	Grishin 1994; Grishin et al. 1996
Mt. Taranaki Ksudach Mt. Katmai	Kamchatka, Russia Alaska, USA	1907 1912	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933
Mt. Taranaki Ksudach Mt. Katmai	Kamchatka, Russia	1907	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale
Mt. Taranaki Ksudach	Kamchatka, Russia Alaska, USA	1907 1912	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i>	Kamchatka, Russia Alaska, USA Washington, USA Japan	1907 1912 1980 1984	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia	1907 1912 1980 1984 1883	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA	1907 1912 1980 1984 1883 1914–1915	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA	1907 1912 1980 1984 1883 1914–1915 1947	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea	1907 1912 1980 1984 1883 1914–1915 1947 1951	 Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA	1907 1912 1980 1984 1883 1914–1915 1947	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980	 Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002;
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980	 Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002;
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991	 Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus Krakatau	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus Krakatau Laacher Volcano	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines New Zealand Indonesia	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991 ~9,500 YBP ~1880	 Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991 Whittaker et al. 1998
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus Krakatau Laacher Volcano Laguna Miranda	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines New Zealand Indonesia Germany	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991 ~9,500 YBP ~1880 ~12,900 YBP	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991 Whittaker et al. 1998 Schmincke et al. 1999 Haberle et al. 2000 Tsuyuzaki 1991, 1995; Tsuyuzaki and del Moral 1995;
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus Krakatau Laacher Volcano Laguna Miranda Mount Usu	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines New Zealand Indonesia Germany Chile	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991 ~9,500 YBP ~1880 ~12,900 YBP ~4,800 YBP	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991 Whittaker et al. 1998 Schmincke et al. 1999 Haberle et al. 2000 Tsuyuzaki 1991, 1995; Tsuyuzaki and del Moral 1995; Tsuyuzaki 1997; Tsuyuzaki and Haruki 1996; Haruki
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo <i>Tephra and ash deposition</i> Auckland Isthmus Krakatau Laacher Volcano Laguna Miranda Mount Usu Lascar Volcano	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines New Zealand Indonesia Germany Chile Japan	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991 ~9,500 YBP ~1880 ~12,900 YBP ~4,800 YBP 1977–1978	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991 Whittaker et al. 1998 Schmincke et al. 1999 Haberle et al. 2000 Tsuyuzaki 1991, 1995; Tsuyuzaki and del Moral 1995; Tsuyuzaki 1997; Tsuyuzaki and Haruki 1996; Haruki and Tsuyuzaki 2001
Mt. Taranaki Ksudach Mt. Katmai Mount St. Helens Ontake <i>Mudflow</i> Krakatau Mt. Lassen Mount Rainier Mount Lamington Mount St. Helens Mount Pinatubo	Kamchatka, Russia Alaska, USA Washington, USA Japan Indonesia California, USA Washington, USA New Guinea Washington, USA Philippines New Zealand Indonesia Germany Chile Japan	1907 1912 1980 1984 1883 1914–1915 1947 1951 1980 1991 ~9,500 YBP ~1880 ~12,900 YBP ~4,800 YBP 1977–1978	Grishin 1994; Grishin et al. 1996 Griggs 1918a,b,c, 1919, 1933 Russell 1986; Adams et al. 1987; Adams and Dale 1987; Dale 1989, 1991; Dale and Adams 2003 Nakashizuka et al. 1993 Tagawa et al. 1985 Heath 1967; Kroh et al. 2000 Frehner 1957; Frenzen et al. 1988 Taylor 1957 Halpern and Harmon 1983 Mizuno and Kimura 1996; Lucht et al. 2002; Gu et al. 2003 Newnham and Lowe 1991 Whittaker et al. 1998 Schmincke et al. 1999 Haberle et al. 2000 Tsuyuzaki 1991, 1995; Tsuyuzaki and del Moral 1995; Tsuyuzaki 1997; Tsuyuzaki and Haruki 1996; Haruki and Tsuyuzaki 2001 Risacher and Alonso 2001

TABLE 1.1. Summary of				

5

Type of physical			
impact and volcano	Location	Dates of eruption	Reference
Mt. Taranaki	New Zealand	1655	Clarkson 1990
Jorullo	Mexico	1759	Eggler 1959
Mt. Victory	New Guinea	1870	Taylor 1957
Krakatau	Indonesia	1883	Bush et al. 1992; Thornton 1996
Mt. Tarawera	New Zealand	1886	Clarkson and Clarkson 1983; Clarkson 1990; Clarkson et al. 2002; Walker et al. 2003
Soufriere	St. Vincent, BWI	1902	Beard 1976
Katmai	Alaska, USA	1912	Griggs 1917
Popocatapetl	Mexico	1920	Beaman 1962
Mount Lamington	New Guinea	1951	Taylor 1957
Kilauea Iki	Hawaii, USA	1959	Smathers and Mueller-Dombois 1974; Winner and Mooney 1980
Isla Fumandina	Galapagos, Ecuador	1968	Hendrix 1981
Usu	Japan	1977–1978	Riviere 1982, Tsuyuzaki 1987, 1989, 1991, 1994, 1995, 1996; Lambert et al. 1992; Tsuyuzaki and del Moral 1994
Mount St. Helens	Washington, USA	1980	 Mack 1981; Cook et al. 1981; Antos and Zobel 1982, 1984, 1985a,b,c, 1986; del Moral 1983, 1993; Seymour et al. 1983; Cochran et al. 1983; Hinckley et al. 1984; del Moral and Clampitt 1985; Frenzen and Franklin 1985; Zobel and Antos 1986, 1987a, 1991a, 1992, 1997; Adams et al. 1987; Harris et al. 1987; Wood and del Moral 1987; Pfitsch and Bliss 1988; Chapin and Bliss 1988, 1989; del Moral and Bliss 1993; Tsuyuzaki and del Moral 1995; Foster et al. 1998
El Chichòn	Mexico	1982	Burnham 1994
Hudson	Argentina	1991	Inbar et al. 1994
Mount Koma	Hokkaido, Japan	1929	Tsuyuzaki 2002; Titus and Tsuyuzaki 2003a,b; Nishi and Tsuyuzaki 2004
Santorini	Greece	~9,000 YBP	Bottema and Sarpaki 2003
Mijake-Jima	Japan	~9,000 YBP	Kamijo et al. 2002
Kula	Turkey	~9,000 YBP	Oner and Oflas 1977
Blowdown			
Mount Lamington	New Guinea	1951	Taylor 1957
Mount St. Helens	Washington, USA	1980	Franklin et al. 1985, 1988; Frenzen and Crisafulli 1990; Halpern et al.

1990

TABLE 1.1. (continued

Source: Updated from Dale et al. (2005).

This chapter provides background on concepts of disturbance, succession, and the integration of ecological and geophysical perspectives that are explored further in this book. First, it defines disturbance, survival, and succession, and then briefly examines the major components of ecological response: survival, immigration, site amelioration, and community development. Next, the chapter addresses linkages among biotic and physical factors influencing succession. Finally, it considers the relation of events at Mount St. Helens to succession and disturbance ecology concepts. The chapter closes with an overview of what follows in subsequent chapters.

1.2 Ecological Change: Definitions and Descriptions of Disturbance, Survival, and Succession

1.2.1 Disturbance

Ecological disturbance has been defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Rather than being catastrophic agents of destruction, many disturbances are normal, even integral, parts of long-term ecological dynamics. The composition, structure, and function of ecological systems are partially products of disturbances. In fact, some species and ecosystems are well adapted to frequent disturbances, so in some cases the absence of disturbance constitutes a disruption that can lead to changes in species, structures, or processes (White and Jentsch 2001; Dodds et al. 2004). To better understand any particular disturbance event, it should be considered in the context of the typical disturbance regime of the area.

Important characteristics of disturbance include their intensity (i.e., force exerted, such as heat release per unit length of fire front), severity (i.e., ecological effect, such as change in live plant cover), frequency, predictability, size, and spatial distribution (White and Pickett 1985). Severity and intensity are related but commonly differ because of differential species response to disturbance. Disturbance regimes span a broad range of frequency and predictability of occurrence. Disturbance size may be simply delineated when the area affected is uniform or may be quite complex where disturbance-impacted areas are patchy or the disturbance is variable in intensity and severity. Small, more frequent disturbances include individual tree falls; small fires; and small, patchy insect outbreaks. Large, infrequent disturbances include volcanic eruptions, crown fires, and hurricanes. Areas affected by large disturbance events commonly encompass complex patterns of disturbance intensity and severity, reflecting heterogeneity in the predisturbance landscape as well as complexity of the disturbance process itself (Turner et al. 1997). Timing of a disturbance can influence its effect on an ecological system. For example, ice storms can have more severe consequences in a deciduous forest if they are late enough in the spring that trees have leafed out (Irland 1998).

It is useful to distinguish between disturbance type and mechanism. Disturbance type refers to the geophysical or ecological phenomenon that has a disturbance effect, such as windstorm, fire, glacier advance or retreat, volcanic eruption, flood, wave action, insect or pathogen outbreak, or human activity. Mechanisms of disturbance are the specific stressors sensed by organisms, such as heat, impact force, and erosion or deposition. Both volcanic and nonvolcanic disturbance processes involve combinations of disturbance mechanisms. Intense forest fires, for example, can include high temperature and strong wind; and mudflows of volcanic or nonvolcanic origin involve impact force, scour, and deposition. Different disturbance types may have similar mechanisms of disturbance, such as occurs with both wildfire and volcanic processes that involve mechanisms of heating. Initial biological response to disturbance is reaction to the *mechanism* rather than the *type* of disturbance. Hence, understanding both the mechanisms involved in a particular disturbance process and the biotic response to individual mechanisms is critical to interpreting and predicting disturbance effects. There are several implications of this perspective. First, if the mechanism and intensity of disturbance by two different processes are similar, similar biological response would be expected, despite the difference in disturbance type (e.g., spores of some fungal species germinate when exposed to heat of wildfire or of volcanic eruption). Thus, some species may be adapted to mechanisms imposed by rare disturbance types (e.g., volcanic blast) because of adaptations to a more common disturbance type (e.g., fire). Second, where several mechanisms are involved in a particular disturbance type, the mechanism with the greatest severity overrides effects of the others.

1.2.2 Survival

Survival is a critical ecological process involving the interaction of organisms and disturbance processes, and survivors potentially play important roles in succession. Ecological effects of disturbances are determined, in part, by both living entities and nonliving biological and physical structures from the predisturbance system that remain after the disturbance (North and Franklin 1990; Foster et al. 1998; White and Jentsch 2001). The potential importance of residual plants and animals was noted by Clements (1916) and Griggs (1918a) but did not gain much prominence in early work on succession because of a focus on primary succession and oldfield succession, where agricultural practices had erased any vestiges of previous forest. More recently, the term *biological legacy* has been defined as the types, quantities, and patterns of biotic structures that persist from the predisturbance ecological system. Living legacies can include surviving individuals, vegetative tissue that can regenerate, seeds, organisms in resting stages (particularly important for zooplankton), and spores. Dead biological legacies include standing dead trees, wood on the ground, litter, and animal carcasses. *Physical legacies* can strongly influence plant and animal survival, colonization, and growth. Important physical legacies after many disturbances are remnant soil, talus, rock outcrops, and aquatic habitats (e.g., seeps and springs).

1.2.3 Succession

The interplay of disturbance and response is an essential part of ecological change in landscapes. The process of gradual ecological change after disturbance, termed succession by Thoreau (1993), refers to changes that occur over time in biological and physical conditions after a site has been disturbed (Figure 1.2). Succession is the suite of progressive changes that occur to an ecological system and not the regular, seasonal, or interannual change in biological systems. In forests, succession can proceed over decades or centuries; whereas in microbial systems, succession occurs over days or months. Succession has intrigued ecologists since the first studies of ecology (McIntosh 1999). Early views of gradual ecological change were drawn, in part, from observations of sets of sites thought to represent different stages along a sequence of biotic development following some common initiating event, such as abandonment of farm fields, sand-dune formation, or deposits left by retreating glaciers (Cowles 1899; Clements 1916; Gleason 1917; Olson 1958). After a long period of debate about the processes and consequences of succession (Whittaker 1953; Odum 1969; Drury and Nisbet 1973; Bazzaz 1979; Odum 1983; McIntosh 1999), in recent decades ecologists have increasingly turned their attention to the study of disturbances and their ecological effects (Pickett and White 1985; White and Jentsch 2001).

Historically, ecologists distinguished *primary succession*, which follows formation of entirely new substrates and areas cleansed of biota, from *secondary succession*, which follows disturbances that leave substantial legacies of earlier ecological systems. Primary succession was thought to take place on entirely denuded sites, such as in the aftermath of a lava flow or glacier retreat, and in newly created habitats, such as lakes and streams on fresh landslide deposits. Primary succession is now commonly considered an endpoint along a continuum of abundance of residual organisms and biological structures left by a disturbance.

Following disturbance, succession does not follow an orderly path to a single endpoint. Instead, succession is commonly complex, having different beginning points, stages

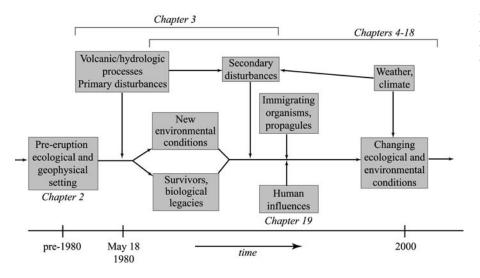


FIGURE 1.2. Sequential interactions of disturbance and succession processes over time and the relation of these topics to chapters in this book.

with different mixes of species and dominance patterns, and interruptions of successional trajectories by subsequent disturbances or other factors. Consequently, multiple pathways of succession may occur (Baker and Walford 1995). Ecosystems may undergo succession toward prior ecological conditions if the prevailing climate, species pools, and substrates have not been altered significantly. Yet, when one or more of these or other factors change, such as preemption of a site by a particular species or a profound change in soil conditions, a new stable state may be achieved (Paine et al. 1998).

1.3 Response to Disturbance: Processes of Change

Succession includes influences of biological and physical legacies, if any are present; immigration of organisms; establishment of some of these migrants; accrual of species and biomass; replacement of some species by others; and amelioration of site physical conditions. The replacement concept can be extended to include (1) replacement of one kind of community by another and (2) progressive changes in microbes, fungi, plants, and animal life, which may culminate in a community that changes little until the next disturbance.

1.3.1 Processes Affecting Survival

Survival depends on interactions between properties of the disturbance events and traits of organisms that allow them to avoid, resist, or respond neutrally or positively to disturbance impacts. Organisms may withstand disturbance by being in a protected location within the disturbed area (e.g., subterranean or under cover of lake ice) (Andersen and MacMahon 1985a) or being well adapted to withstand disturbance (Gignoux et al. 1997). Organism size can also foster survival; small macroalgae, for example, can better withstand the thrashing of intense wave action than can large algae (Blanchette 1997).

Some species may persist in a disturbed landscape by having either all or part of their populations away at the time of disturbance. For example, migratory birds and anadromous fish may be away from sites during disturbance and, upon their return, reoccupy the area if suitable habitat and food are present.

Despite apparently tight coupling of species–disturbance interactions, survival of individual organisms and populations is frequently a matter of chance. Nuances of site conditions, organism vigor, disturbance intensity at the site, timing of disturbance relative to the life history of the organism, and other factors can tip the balance of life versus death in ways that are difficult to anticipate.

1.3.2 Immigration, Establishment, and Site Amelioration

The early stages of succession are strongly influenced by persistence and growth of survivors; immigration, establishment, and growth of colonists; and interactions among these colonists. Mobility of organisms and propagules, as well as the conditions of the environment through which they move, affect dispersal patterns. Highly vagile organisms, such as those capable of flight and passive movement by wind, typically are first to reach disturbed areas distant from source populations. In contrast, low-mobility organisms, such as seed plants that lack structures for wind dispersal and animals which travel through soil, would be expected to slowly reach distant, disturbed sites. Many species with poor dispersal mechanisms can be transported great distances by hitchhiking in or on animals, moving in flowing water, or capitalizing on the influence of gravity. Dispersal is commonly thought to be determined by the distance to source populations, but complexities of disturbance processes and patterns and the state of the affected ecological system make such simplistic, distance-related interpretations unrealistic.

Once an organism disperses to a new location, its ability to establish, grow, and reproduce is determined by prevailing climate, site conditions, previously established organisms, and the organism's own requirements and tolerances. For animals, the requirements for successful establishment are often expressed as adequate cover and food. Cover provides protection from physical stresses as well as a place to hide from potential predators. Plant establishment requires appropriate light, moisture, and nutrient levels for germination and growth.

Site amelioration is an important process that can involve changes to soil conditions, microclimate, and microtopography. Soil development is often an essential factor in succession, especially in the case of primary succession, where soil is initially of poor quality. Soil formation involves physical and chemical weathering of rocks and minerals, accumulation and decay of biotic material, establishment of a microbial fauna, and marshalling of any legacies of earlier soil on the site. The death or stress of biota in response to the disturbance may deliver a pulse of litter to the soil surface or within the soil via root death. As a site ameliorates, plants establish and spread, species interact, and a community develops. Animals are tightly coupled to plant composition or physiognomy, so their colonization frequently tracks the development of vegetation.

Humans can profoundly influence the course of succession in many ways, both intentionally and unintentionally. A common influence is the introduction of invasive, nonnative species, which can have far-reaching ecological and management repercussions. Disturbance commonly favors establishment of invasive species, but predicting the vulnerability of a system to invasion is still a challenge (Mack et al. 2000). Planting of native trees and stocking with native fish can profoundly alter community structure and function.

1.3.3 Concepts of Change in Ecological and Environmental Factors During Succession

Changes in ecological and environmental conditions are both consequences and determinants of the path of succession. Today, concepts of succession and disturbance ecology have reached the point where they are examined and modified through experimental and modeling approaches as well as by studies of ecological change imposed by major disturbance events.

1.3.3.1 Community Development Through Succession

Species richness, biomass, and structural complexity of communities increase during succession. Various types of interactions among species drive community development, and these processes may change in their relative importance over the course of succession. In some cases, one species is replaced by another over time in what is called the process of relay succession. In these cases, the change in species is as abrupt as the handing over of a baton from one runner to another (building In an attempt to advance understanding of succession, Connell and Slatyer (1977) proposed three models of mechanisms of succession, termed: facilitation, tolerance, and inhibition. These models describe the way in which species interact with their environment and with later-arriving species to either promote, hinder, or have minimal effects on the establishment and/or growth of some species and thus to shorten or lengthen the time to dominance by another species (Connell and Slatyer 1977). However, succession is highly variable; and in most cases, these three mechanisms, plus others, occur simultaneously during a successional sequence (McIntosh 1999). In addition to these models of succession, numerous speciesspecies interactions, such as mutualism, predation, parasitism, and herbivory, help shape the pace and direction of succession.

Facilitation was first interpreted as the process of early successional species altering conditions or the availability of resources in a habitat in a way that benefits later successional species (Clements 1916; Connell and Slatyer 1977). For example, the first species to become established create shade, alter soil moisture, and ameliorate soil texture and nutrient conditions via decomposition of their parts and other processes. Commonly, nitrogen is a limiting factor in early successional stages, and the presence of plants with the ability to infuse the soil with nitrogen through association with nitrogen-fixing bacteria enhances soil development. Facilitation is now more broadly interpreted as positive interactions between species (Bruno et al. 2003) and as processes that improve a site's physical conditions (e.g., soil development) (Pugnaire et al. 2004). These beneficial interactions appear to be common under stressful environmental conditions (Callaway and Walker 1997).

In contrast to facilitation, the process of *inhibition* may slow or temporally arrest successional development (Grime 1977; Connell and Slatyer 1977). This process occurs when a resource, such as space, water, or nutrients, is so intensely used by one or more species that it is not available in life-sustaining quantities to other species. For example, following a mudslide along Kautz Creek on the flanks of Mount Rainier in Washington State, the depositional area was quickly colonized by an almost continuous mat of mosses and lichens. Germinating tree seedlings could not penetrate the mat and reach mineral soil, and thus tree establishment was inhibited for decades (Frehner 1957; Frenzen et al. 1988).

Tolerance refers to the situation where organisms best able to tolerate prevailing conditions are favored, but recognizes that prevailing conditions change with time. Under this model, later successional species are unable to become established without site amelioration by pioneer species that do not inhibit the later colonists (Connell and Slatyer 1977). A primary premise of the tolerance model is that later successional species can grow with lower resource levels than can earlier species and are better at exploiting limited resources. As later successional species grow and produce progeny, they replace the earlier, less-tolerant species and become dominant. Thus, life-history characteristics are critical in determining the sequence of species replacements.

1.3.3.2 Biotic and Geophysical Forces of Succession

Drivers of disturbance and succession can be viewed as falling on a continuum of relative influence of geophysical forces (*allogeneic* succession) versus biological factors (*autogenic* succession) (White and Pickett 1985). Where allogeneic succession dominates, physical forces (such as chronic, secondary geophysical disturbances) override biological causes of succession. Autogenic succession is driven by intrinsic properties of a community and the ability of organisms to affect their environment, such as when certain species preempt sites, create shade, and alter soil structure and chemistry.

Patterns of water runoff, sediment transport, and other geophysical processes can change dramatically after severe landscape disturbance. Some processes alter site conditions in ways that prepare a site to experience other processes. Analyses of drainage basin evolution (Koss et al. 1994) and sediment routing following wildfire and forest cutting (Swanson 1981; Swanson et al. 1982b; Benda and Dunne 1997), for example, reveal sequential interactions among geomorphic processes in ways that are akin to facilitation in biotic succession.

Often, biotic and geophysical patterns of succession occur in parallel following severe disturbance and involve both positive and negative feedbacks:

- Episodic disturbances, such as landslides, can erase a decade or more of ecological response following the primary disturbance event.
- Development of vegetation and its associated litter layers and root systems can suppress erosion processes.
- In some instances, erosion of new deposits exposes buried plant parts in the predisturbance soil, thus favoring plant and animal survival and development of ecological interactions.

Recognition of the succession of ecological and geophysical processes in severely disturbed landscapes can be useful in interpreting the direction, rate, and cause of ecological responses to disturbance. Ecological response to severe disturbance is, in part, a function of the pace at which the landscape stabilizes geophysically to a point where biological response can proceed with vigor. For example, fish reproduction may not occur in a disturbed site because of physical instability that degrades spawning habitat or conditions required for egg development.

Secondary disturbance processes (i.e., those that are influenced by a primary disturbance) often play important roles in ecological change. Examples of secondary disturbances include the increased pace of lateral channel migration as a result of increased sediment load and precipitation runoff. This chronic disturbance repeatedly removes developing riparian vegetation.

1.4 Linking General Concepts and the Mount St. Helens Experience

The wealth of knowledge about disturbance, survival, and succession briefly summarized above and elsewhere (Pickett and White 1985; McIntosh 1999; White and Jentsch 2001; Walker and del Moral 2003) provides useful concepts for examining the initial effects and subsequent ecological and geophysical change at Mount St. Helens during and following the 1980 eruption. These science concepts are in continuing states of development and searches for generality (McIntosh 1999; White and Jentsch 2001). No single concept or theory is adequate to structure the scientific analysis or the telling of the highly multifaceted Mount St. Helens story. On the other hand, lessons from studies at Mount St. Helens have influenced the development of these topics.

The Mount St. Helens landscape and the lessons drawn from research conducted there have changed substantially during the quarter of a century since the 1980 eruption. Initial observations emphasized the nearly desolate character of the landscape, the importance of surviving organisms, factors influencing patterns of species dispersal and colonization, and community development. Some of these initial ecological responses have had lasting effects, but others of them proved to be transient. After 25 years, much of the landscape has filled with plants, and the once stark gray area has been transformed to mostly green. Extensive tracts of the most severely disturbed areas remain in early seral stages dominated by herbs and shrubs and will require several more decades before becoming closed-canopy forest, if they ever do. Numerous conifer saplings are present in all disturbance zones, and the development of forest cover is accelerating in many locations. By 2005, the ash-choked lakes and streams of 1980 glisten with clear, cold, well-oxygenated water and support biota typical of the region. The growth and spread of surviving and colonizing species during the first 25 years after the 1980 eruption have provided many new opportunities to address questions about succession, patterns of landscape response, and consequences of secondary geophysical processes. Even so, many questions regarding ecological responses to the 1980 eruption remain unanswered. Continuing change of the Mount St. Helens landscape may bring new answers and certainly will bring new questions about ecological responses to major disturbances.

1.5 Overview of Book

This book presents much of the existing research that explores succession, disturbance ecology, and the interface between geophysical and ecological systems at Mount St. Helens (see Figure 1.2). Chapters 2 and 3 review the geological and ecological setting before the 1980 eruption and the geophysical environments created by the May 18, 1980, eruption. Chapters 4 to 8 focus on the survival and establishment of plant communities across diverse volcanic disturbance zones. Chapters 9

to 14 consider responses of animal communities, in particular, arthropods, fish, amphibians, and small mammals. Chapters 15 to 18 discuss responses of four sets of ecosystem processes: the symbiotic relationship between mycorrhizal fungi and plants in soils, animal decomposition in terrestrial environments, effects of a nitrogen-fixing plant on soil quality and function, and the complex biophysical processes of lake responses. Chapters 19 and 20 synthesize changes that have occurred across land-management issues, species, ecological systems, and disturbance zones during the first quarter century after the 1980 eruption.

Together, these chapters provide an in-depth analysis of ecological patterns of response after the 1980 eruption of Mount St. Helens. Conventional terminology is used throughout the book (see the Glossary at the end of the volume), and throughout the book locations of the various research studies are shown on a common reference map. A single bibliography for all chapters is at the end of the book. The major taxonomic source for species mentioned in the book is the Integrated Taxonomic Information System (*http://www.itis.usda.gov*). Additional information about the area and the research results is available at *http://www.fsl.orst.edu/msh/*.

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2 Geological and Ecological Settings of Mount St. Helens Before May 18, 1980

Frederick J. Swanson, Charles M. Crisafulli, and David K. Yamaguchi

2.1 Introduction

Volcanoes and volcanic eruptions are dramatic players on the global stage. They are prominent landscape features and powerful forces of landform, ecological, and social change. Vesuvius, Krakatau, Pompeii, and, in recent decades, Mount St. Helens hold an important place in our perceptions of how the Earth works and the incredible, destructive effects of violent eruptions. Perhaps less appreciated is the great diversity of interactions between volcanoes and the ecological systems in their proximity.

Volcanic activity and ecological change at Mount St. Helens have been particularly dynamic and instructive. Frequent eruptions of diverse types have interacted with terrestrial and aquatic ecological systems to display a broad range of responses (Franklin and Dyrness 1973; Mullineaux and Crandell 1981; Foxworthy and Hill 1982). Leading up to the 1980 eruption of Mount St. Helens, Cascade Range volcanoes of the Pacific Northwest of the United States were the subject of a good deal of study for objectives that were both academic and applied, such as assessing volcanic hazards and prospecting for geothermal resources. The fauna and flora of forests, meadows, lakes, and streams of the region were generally well known and described. The 1980 eruption put a spotlight on Mount St. Helens, as the world watched volcanic and ecological events unfold in real time. These events also stimulated an interest to better understand the volcanic and ecological conditions that existed before 1980. The geological, ecological, and historical settings provide context for interpreting the physical and ecological responses following the 1980 eruption. [Here we use the term history in the broad sense to include geological time as well as recorded human history.]

Study of any ecological system should start with consideration of its context in space and time and in geographical, geological, and ecological dimensions. From a geographical perspective, the position of Mount St. Helens in a north–south chain of volcanoes along a continental margin sets up strong east–west geophysical and biotic gradients between the sea and mountain top and along a north–south climate gradient (Figure 2.1). Understanding of these broad gradients is useful in interpreting similarities and differences among different parts of a region. These gradients also organize fluxes of materials, organisms, and energy across broad areas. Marine air masses, for example, deliver water to the continental edge, and this abundant moisture flows back to the sea, forming a regional hydrologic cycling system. A well-connected marine– freshwater system fostered development of numerous stocks of anadromous fish. Similarly, the north–south climatic gradient and topographic features of mountain ranges and chains of coastal and inland wetlands form travel corridors for migratory birds. Movement of such wide-ranging terrestrial and aquatic species results in a flow of nutrients, propagules, genes, and organisms in and out of local landscapes within the region and even more widely.

Past activity of a volcano influences its surroundings and affects biophysical responses to new disturbance events. Legacies of earlier eruptive activity may be expressed in landforms, soils, lakes, streams, animal communities, and vegetation patterns. This pattern is especially true at Mount St. Helens, which has erupted about 20 times in the past 4000 years (Table 2.1 on page 16). Vestiges of both the preeruption ecological systems and recent eruptive activity can strongly influence the posteruption landscape and patterns of change in ecological systems. Across the region and over evolutionary time scales, climate and biota interact with disturbance regimes of fire, wind, floods, volcanism, and other agents. Thus, the ecological history of the local area and its regional context determine the pool of species available to colonize a disturbed area, the capabilities of those species to respond to disturbance, and the array of types and configurations of habitats available for postdisturbance ecological development.

Given the importance of spatial and temporal context, this chapter begins the analysis of ecological responses to the 1980 eruption of Mount St. Helens by describing the area before 1980. Our objective in this chapter is to set the stage for subsequent chapters, which detail the geological events and ecological responses unfolding on May 18, 1980, and during the subsequent quarter century. We characterize the Mount

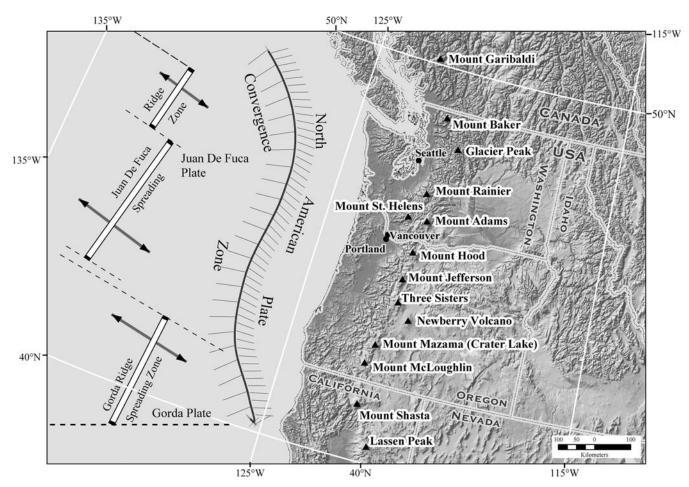


FIGURE 2.1. Regional context of Mount St. Helens, including major volcanic peaks and plate-tectonic setting in terms of spreading and convergence zones. [Adapted from Foxworthy and Hill (1982).]

St. Helens area in terms of its physiography, climate, geology, geomorphology, plant and animal assemblages, and ecological processes and its broader setting. Our geographical focus is the area affected by the 1980 event, generally within 30 km of the cone (Figure 2.2; see also Swanson and Major, Chapter 3, this volume).

Terminology in these discussions is summarized in the Glossary section of this book, generally following Lipman and Mullineaux (1981), Foxworthy and Hill (1982), and Fisher and Schmincke (1984). Plant-association and species nomenclature follows Franklin and Dyrness (1973) and the Integrated Taxonomic Information system (http://www.itis.usda.gov).

2.2 Geophysical Setting

2.2.1 Geological, Physiographic, and Geomorphic Setting

Mount St. Helens is part of the Cascade Range of volcanoes that extends from Canada to northern California (see Figure 2.1). The present and earlier alignments of Cascade volcanoes result from pieces of Pacific oceanic crust plunging beneath the North American continental plate (Figure 2.1). This geological setting has persisted for millions of years, thus shaping the broad outline of the region's physiography and the geophysical dynamics of chronic and catastrophic volcano growth and decay. These conditions are broadly representative of the circum-Pacific "ring of fire," where chains of volcanoes grow in response to geological forces operating within the Earth's mantle and crustal plates.

The structure of Mount St. Helens, as viewed before the 1980 eruption, had formed over the preceding 40,000 years on a geological foundation composed of volcanic rocks of Oligocene to early Miocene age (ca. 28 to 23 million years old). However, leading up to 1980, the entire visible cone had been constructed within only the preceding 2,500 years as an accumulation of volcanic domes, lava flows, and volcanic debris emplaced by other processes (Crandell and Mullineaux 1978; Mullineaux and Crandell 1981; Crandell 1987; Yamaguchi and Hoblitt 1995; Mullineaux 1996). The history of the volcano was read from deposits on its surface; from the types and ages of material it shed onto the surrounding countryside (subsequently exposed in the walls of deeply incised stream channels); and, after the 1980 eruption, in the volcano's internal anatomy exposed in the walls of the new crater. Deposits

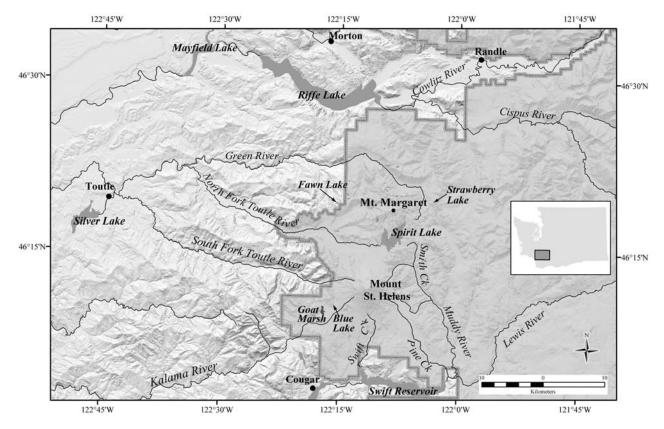


FIGURE 2.2. The Mount St. Helens area.

and events have been dated by analysis of tree rings, which give a record for much of the past millennium, and by radiometric dating of rock and organic material, which can extend much further into the past. The known eruptive history of Mount St. Helens spans periods of dormancy interspersed with periods of activity, which have been grouped into nine eruptive periods (see Table 2.1). Over the past seven eruptive periods, the length of dormant periods ranged from 50 to 600 years and averaged about 330 years.

Eruptive periods involved various combinations of a diverse suite of volcanic processes, which merit some definition. The term tephra refers to ejecta blown through the air by explosive volcanic eruptions. Tephra fall occurs when explosively ejected fine ash to gravel-sized rock debris falls to Earth and forms a deposit on vegetation, soil, or other surfaces. Eruption columns may extend kilometers into the air, and prevailing winds may cause tephra-fall deposits to accumulate in a particular quadrant around a volcano, generally the northeast quadrants of volcanoes in the Pacific Northwest. In contrast, hot (\sim 800°C), pumice-rich eruption columns may collapse, forming pyroclastic flows, which move rapidly (tens of meters per second) down a volcano's flanks and onto the gentler surrounding terrain, accumulating in lobe-shaped deposits up to 10 m or more thick. Toward the other extreme of flow velocity, slow (e.g., millimeters per hour to meters per hour) extrusions of very viscous lava [e.g., with high silica (SiO₂) content] form *lava domes* with a circular or elliptical outline. Less-viscous lava may flow from

vents and cool in lava-flow deposits, forming elongated lobes. Various interactions of water and the weak rocks (e.g., clayrich or highly fractured) composing volcanoes can result in massive landslides, often termed debris avalanches. Volcanic debris avalanches may exceed a cubic kilometer in volume, enveloping a volcano summit and flank and spreading over tens of square kilometers at the base of the volcano. Volcanic mudflows, also termed lahars, may be triggered by many mechanisms, including drainage of debris avalanches, collapse of dams blocking lakes, and the movement of hot, volcanic debris over snow and ice. Mudflows have higher water content than do debris avalanches and, therefore, can flow at higher velocities and over greater distances (tens of kilometers) away from their sources. Less common volcanic processes are lateral blasts, which occur when superheated groundwater develops within a volcano by interaction of magma and infiltrating precipitation and then flashes to steam, producing an explosion. Such steam-driven blasts project large volumes of fragmented mountain-top rock laterally across a landscape. The resulting blast cloud, which can be hundreds of meters thick, topples and entrains vegetation along its path. Lateral blasts leave a blanket of deposits composed of angular sand, gravel, and fragments of organic material.

Some of these processes, such as dome growth and lava flows, contribute to volcanic-cone construction, while other processes contribute to the breakdown of volcanoes and the filling of surrounding valleys with volcanic debris. The Pine

		Processes						
Eruptive period ^a	Approximate age (years) ^b	Tephra fall	Pyroclastic flow	Lava flow	Dome growth	Mudflow	Lateral blast	
Current period	AD 1980–2005	Х	Х		Х	Х	Х	
Dormant interval of 12	23 years:							
Goat Rocks	AD 1800–1857	Х		Х	Х	Х		
Dormant interval of ab Kalama	oout 50 years: AD 1480–mid-1700s	Х	Х	Х	Х			
Dormant interval of ab Sugar Bowl	bout 600 years: 1,080–1,060	Х	Х		Х	Х	Х	
Dormant interval of ab Castle Creek	oout 600 years: Greater than 2,200–1,700	Х	Х		Х	Х		
Dormant interval of ab Pine Creek	bout 300 years: 3,000–2,500	Х	X		Х	Х		
Dormant interval of ab Smith Creek	bout 300 years: 4,000–3,300	Х	Х			Х		
Dormant interval of ab Swift Creek	bout 4,000 years: 13,000–8,000		Х		х			
Dormant interval of ab Cougar	bout 5,000 years: 20,000–18,000		х	Х	х	х		
Dormant interval of ab Ape Canyon	bout 15,000 years: ~40,000(?)–35,000		X			Х		

TABLE 2.1. Summary of the Mount St. Helens eruptive history.

The only lateral blasts interpreted within this record occurred during the Sugar Bowl period and on May 18, 1980.

^a Dormant intervals are periods during which no unequivocal eruptive products from the volcano have been recognized.

^a Ages of Goat Rocks–Kalama eruptive periods are in calendar years; ages of Sugar Bowl to Swift Creek periods, determined by radiocarbon dating, are expressed in years before AD 1950, following the calibrations of Stuiver and Pearson (1993). Ages of older periods are expressed less precisely in uncalibrated radiocarbon years.

Source: Adapted from Mullineaux and Crandell (1981), Mullineaux (1996), and Yamaguchi and Hoblitt (1995).

Creek, Castle Creek, and Kalama eruptive periods of Mount St. Helens (Table 2.1; Figure 2.3) were particularly voluminous, inundating neighboring areas north, southwest, and southeast of the volcano with pyroclastic-flow, mudflow, and lava-flow deposits. Lateral blasts were rare in the pre-1980 eruptive history of Mount St. Helens; only one has been noted in the geological record, and that was in the Sugar Bowl eruptive period (see Table 2.1). The numerous flowage deposits from Mount St. Helens significantly modified parts of all rivers draining the volcano. The deposits filled valleys, smoothing preexisting topography around the cone and disrupting earlier drainage patterns. The buildup of the Pine Creek assemblage diverted the Muddy River, which once followed the valley of Pine Creek, to the valley of Smith Creek. Similarly, accumulation of a broad fan on the north flank of the volcano intermittently dammed the head of the North Fork Toutle River, forming Spirit Lake. Periodically, this dam was partially breached, triggering massive mudflows down the Toutle River, several of which blocked Outlet Creek, forming Silver Lake, 45 km west-northwest of the summit of the volcano. Some streams draining the volcano subsequently cut deep canyons through these deposits, particularly on the south side of the volcano (Crandell and Mullineaux 1978).

Numerous eruptions spewed tephra on various trajectories to the east and northeast of the volcano (Table 2.1; Figure 2.4). The resulting deposits of fine ash to gravel-sized pumice and fragmented lava spread over many thousands of square kilometers, strongly affecting soil properties where their depth exceeded a few centimeters. These deposits have been dated with various tree-ring, radiocarbon, and other techniques, so they can be used as time markers to interpret landscape and vegetation conditions at times in the past (Mullineaux 1996). In some areas, such as 20 km northeast of the cone, tephra deposits of the past 3500 years exceed 5 m in thickness and contain several buried soils, including some trees buried in upright growth position (Franklin 1966; Yamaguchi 1993).

Lava flows during several eruptive periods covered parts of the southern and northern flanks of the volcano and flowed more than 10 km down the Kalama River and south-southeast to the Lewis River (Crandell 1987). Lava flows have been very resistant to erosion and therefore have tended to stabilize the land surfaces and deposits they cover. Hydrology is also strongly affected by lava flows, such as where massive volumes of water flow rapidly through lava tubes and beneath lava-flow deposits before discharging as large springs and streams with stable flow regimes.