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THESIS APPROVAL

The abstract and thesis of Jennifer Michelle Karps for the Master of Science in Geography were presented February 16, 2006, and accepted by the thesis committee and the department.

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ABSTRACT

An abstract of the thesis of Jennifer Michelle Karps for the Master of Science in Geography presented February 16, 2006.

Title: Regeneration Patterns and Facilitation Following Blowdown in a Self-Replacing Lodgepole Pine (*Pinus contorta*) Stand in Central Oregon

Nurse plant and object facilitation is an important factor mitigating abiotic stress, improving seedling recruitment, and shaping the fine-scale spatial patterns of many plant communities. I investigate the role of facilitation on lodgepole pine regeneration following blowdown in central Oregon. My objective is to examine the importance of nurse objects on seedling recruitment under varying stand conditions. I base my analysis on 1) the mapped locations and attributes of seedlings, saplings, trees, shrubs, snags, stumps, and sound and decomposed logs in each of five, 500 m² circular plots, 2) water holding capacity estimates of woody and leafy litter and pumice soil, and 3) growing-season air temperatures. My analysis identifies seedling patterns at multiple spatial scales (~0-8 m) using nearest neighbor and Ripley's K statistics and identifies differences in canopy structure, seedling development, and temperature using non-parametric rank-sum tests.

My results show blowdown severity varies with pre-disturbance stand structure, resulting in a multi-modal stand structure with a wide range of canopy and

seedling microhabitat conditions. Stand-wide, post-blowdown regeneration patterns reveal >80% of seedlings grow near nurse shrubs, logs, and woody litter, suggesting preferential germination and survival in these microhabitats. High seedling densities correspond with median shrub diameters, and up to 38% of seedlings grow near recently downed logs, indicating both shrubs and logs serve as important nurse objects. The role of nurse objects in mitigating moisture stress is implicated by the potentially high evaporative stress under extreme growing season temperatures in areas of severe blowdown and by the high moisture-holding capacity of woody litter relative to the pumice soil. Stand-wide, 91% of all seedlings and 87% of all shrubs grow on woody litter, and seedlings growing on woody litter show the greatest development.

The positive spatial correlation of seedlings and shrubs with nurse plants and woody litter supports the assertion that both are important facilitators for seedling regeneration and emerging spatial patterns of stand recovery. These results have important management implications, suggesting that the removal of nurse plants and objects through salvage logging or prescribed burning may have negative long-term impacts on local and regional forest regeneration.

REGENERATION PATTERNS AND FACILITATION
FOLLOWING BLOWDOWN IN A SELF-REPLACING
LODGEPOLE PINE (*PINUS CONTORTA*) STAND IN
CENTRAL OREGON

by

JENNIFER MICHELLE KARPS

A thesis submitted in partial fulfillment of the
requirements for the degree of

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Chapter 1

INTRODUCTION

Understanding the dynamic and heterogeneous nature of forest landscapes requires knowledge of local disturbance regimes and succession (*e.g.*, Whittaker 1951, Sousa 1984, Pickett and White 1985). Post-disturbance regeneration is influenced by several factors, including community composition, community structure, and the type, severity, frequency, and extent of the disturbance (Connell and Slatyer 1977, Denslow 1980). In addition, climate, topography, and edaphic characteristics influence which species successfully establish after a disturbance event, the subsequent interactions of individual plants with their neighbors, and community development (*e.g.*, Grime 1977, Callaway *et al.* 1996, Walker and del Moral 2003). Ultimately, the regeneration patterns for a given population are determined by the autecological traits – fecundity, shade and drought tolerance, and growth rate – that enable each member to take advantage of disturbance-freed resources (Noble and Slatyer 1980) in concert with positive and negative plant-plant interactions (Gosz 1993).

Recent research suggests the effects of positive ecological interactions (facilitation) on community structure have been underemphasized as compared to competitive interactions (Callaway and Pugnaire 1999). These findings have led to controversy (Shouse 2003) among plant and animal ecologists regarding the roles of competition and facilitation, and they challenge a well-ingrained paradigm in ecology.

Incorporating facilitation into ecological models will alter our understanding of community ecology (Bruno *et al.* 2003). Because efficient and effective management of natural systems depends on our understanding of how these systems function, it is critical that our methods of management evolve as our knowledge base increases. My work will provide further insight into the role of facilitation in population dynamics by examining self-replacing lodgepole pine stands in the pumice area of central Oregon where facilitation may play an as yet unrecognized role in stand structure.

Approximately 70% of eastern Oregon's forested land is managed at the federal level, primarily by the U.S. Forest Service and the Bureau of Land Management (Campbell *et al.* 2003). From 1987 to 1999, eastern Oregon's forests lost more timber to extraction, roughly 0.01% per annum (8.8 million m³), and mortality than gains compensated by growth (Campbell *et al.* 2003). For more than a decade, post-fire salvage logging has provided additional timber resources in spite of ecological concerns about the prudence of removing coarse woody material from burned sites (Donato *et al.* 2006). In some areas, especially in more marginal environments where climate, soil, slope, aspect, or a combination of these factors interact to limit regeneration, the removal of woody vegetation from the system may inhibit its regeneration potential and long-term vitality. In such extreme habitats, facilitation by existing plants or structures may be vital to the continuance of the plant community.

Questions of why and where phenomena occur are inherently geographic and are not limited by spatial scale. Investigation of forest regeneration patterns, then,

falls within geography's purview and is well suited to a geographer's approach (*e.g.*, Veblen 1992, Parker *et al.* 1997). This work relies on a scale-based approach to reveal the complexities and subtleties of lodgepole pine community dynamics in a stressful environment. While this research has theoretical implications, it also provides sound science on which to base forest management policy and contributes to the education and management goals of the Newberry National Volcanic Monument in central Oregon.

Objectives

My goal is to investigate how resource patchiness and environmental stress affect local and stand scale regeneration patterns and persistence of lodgepole pine on the High Pumice Plateau in central Oregon. Specifically, I seek to demonstrate the likelihood that lodgepole pine seedlings are facilitated by moisture retained in old (~85 years), rotten logs and by shade provided by trees, shrubs and recently (~20 years) blown down logs. I hypothesize that positive spatial correlations exist between seedlings and facilitating nurse objects within the community. I test this hypothesis by examining the spatial association of lodgepole pine seedlings relative to trees, saplings, shrubs, and logs in a self-replacing lodgepole pine stand that has experienced a recent blowdown.

This thesis comprises the research conducted to test my hypothesis. I begin with a review of pertinent literature (Chapter 2), providing the ecological context for

my study, followed by a description of the physiography, biogeography, and land use of my study area (Chapter 3). I then describe my field, lab, and analytical methods (Chapter 4). The results of this investigation, a discussion of those findings, and concluding remarks, Chapters 5-7, complete this document.

Chapter 2

LITERATURE REVIEW

Positive Plant Interactions

A major goal of ecologists and biogeographers over the past century has been to understand the mechanisms of plant community dynamics (Tilman 1988, Young *et al.* 2003). While climate is the major factor controlling large-scale plant community composition, soil heterogeneity and biotic interactions affect plant community pattern and structure at the local scale (Gosz 1993). Individual plants can interfere with or facilitate the viability of other plants. Competitive interactions have received considerable attention as agents affecting plant abundance and distribution (Grime 1977, Connell 1983, Huston and Smith 1987, Tilman 1987). Although less thoroughly examined, positive interactions among plants can also affect the distribution and composition of some plant communities (*e.g.*, Niering *et al.* 1963, Callaway 1995, Kitzberger *et al.* 2000). Established plants can ameliorate environmental stressors, thereby facilitating conditions suitable for germination and viability of other plants. In extreme or variable environments, regeneration can be limited by environmental factors such as temperature and moisture availability; nurse plants and objects provide microhabitat conditions that allow some species to persist and others to expand their realized niche (Went 1942, Franco and Nobel 1988, Callaway and Pugnaire 1999,

Bruno *et al.* 2003). Further, competition may become less important as abiotic stress increases (Grime 1977, Bertness and Yeh 1994, Callaway *et al.* 1996).

In stressful environments, fluctuations in the availability of moisture or nutrients, as well as temperature extremes, limit plant germination, growth, and fitness. Established plants improve local conditions by providing shade and protection from herbivores (McAuliffe 1984, Callaway 1992, Haase *et al.* 1997), and by increasing local soil fertility and moisture availability (Figure 1, Table 1). Shading decreases daytime surface and soil temperatures and slows evaporative moisture loss and, in some cases, decreases salinization (Parker 1987, Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991, Bertness and Yeh 1994). Litterfall from nurse plant canopy and root exudates increase local soil fertility and oxygenation (Callaway *et al.* 1991, del Moral and Bliss 1993, Chapin *et al.* 1994, Hacker and Bertness 1995). Nurse plant structure provides protection from wind desiccation and herbivory and may indirectly benefit other plants by trapping wind or water borne materials, or by providing structural support in crowded systems (Callaway 1992, Harley and Bertness 1996). Flores and Jurado (2003) inventoried papers concerning nurse plant interactions and found that researchers have studied 147 nurse species and 429 facilitated species. Of the 296 papers surveyed, just over 50% describe facilitative relationships in arid environments (Flores and Jurado 2003).

Figure 1. Conceptual model of the strength of relationships among facilitation, abiotic stress, and the availability of nurse objects (from Walker and Callaway 1997). The importance of facilitation tends to increase with increasing abiotic stress. When facilitative strength is relatively low, smaller, less dense nurse plants increase facilitative effectiveness. As facilitative strength increases, larger, denser nurse plants provide greater effectiveness.

Table 1. Examples of nurse plant facilitation in a variety of environments.

Mitigated Factor	Environment	References
Temperature and water availability	Sonoran Desert	Parker 1987
	Sonoran Desert	Franco and Nobel 1988, 1989
	Tehuacan Valley, Mexico	Valiente-Banuet and Ezcurra 1991
	Patagonian Desert	Kitzberger <i>et al.</i> 2000
Soil fertility	California Oak Woodland	Callaway <i>et al.</i> 1991
	Alaskan Interior Floodplain	Chapin <i>et al.</i> 1994
	Mount St. Helens	del Moral and Bliss 1993
Herbivory	California Oak Woodland	Callaway 1992
Structural support	S. New England Salt Marsh	Harley and Bertness 1996
Soil salinity	S. New England Salt Marsh	Bertness and Shumway 1993
		Bertness and Yeh 1994
Available soil oxygen	S. New England Salt Marsh	Hacker and Bertness 1995

Net facilitation reflects the cumulative effects of positive and negative interactions among neighboring plants (Callaway and Walker 1997). The reliance of species on nurse plants increases with increasing abiotic stress (Callaway *et al.* 1996). Conversely, as environmental conditions become more moderate, negative interactions dominate. Interplant relationships respond to abiotic gradients in both time and space (Greenlee and Callaway 1996, Kitzberger *et al.* 2000). In this way, microhabitat conditions and interannual climate variation interact to affect the dominant mechanisms directing plant community structure and demographics. Gomez-Aparicio and colleagues (2004) illustrated this interaction by comparing the fates of seedlings planted under shrub canopy with those planted in an open environment in the Sierra Nevada Mountains in southeastern Spain. They found greater survivorship and growth in seedlings sited under shrubs, with the magnitude of the trend attenuated on north-facing slopes and during years of greater moisture.

Additional evidence supporting the importance of variable facilitative relationships to plant community structure comes from montane woodland-shrub steppe ecotone in northern Patagonia (Kitzberger *et al.* 2000). In this system, the conifer *Austrocedrus chilensis* grows in the woodland community and can invade the ecotone under certain conditions. Recruitment of *A. chilensis* into the ecotone can be enhanced by nurse shrub facilitation. No recruitment occurs during extremely dry years or during mesic conditions that favor competitive interactions. When environmental conditions are suboptimal but sufficiently wet for seed germination, facilitation strongly affects the distribution of *A. chilensis* seedlings in the ecotone. In

this way, nurse shrubs mitigate interannual climate variability in the ecotone. Field studies examining the interaction of biotic and abiotic factors in both time and space enable one to parse the underlying mechanisms affecting plant community dynamics under natural conditions at ever-finer scales (Bertness and Shumway 1993). In this way, the relative importance of facilitative and competitive interactions, and how those factors vary with interannual and larger-scale climate variation, community structure, and plant life stage, is learned.

Stuart *et al.* (1989) work on stand structure and development in self-replacing lodgepole pine in central Oregon revealed that competition under severe microclimates led to preferential seedling success in areas with more available soil moisture. While the moisture-limited status of the pumice area in central Oregon is well established (Franklin and Dyrness 1988, Stuart *et al.* 1989), there is a lack of research into nurse plant and object facilitation in self-replacing lodgepole pine stands. Such a mechanism might contribute directly to fine-scale stand structure and indirectly to disturbance and regeneration regimes (Castro *et al.* 2004, Armas and Pugnaire 2005). Global climate change may result in increased aridity and higher growing-season temperatures in central Oregon (Pohl *et al.* 2002), increasing the importance of nurse plants and objects to the long-term viability of lodgepole pine forests.

Lodgepole Pine Life History

Lodgepole pine (*Pinus contorta*) ranges widely in elevation from sea level to over 3,050 m and latitudinally from the Yukon Territory to Baja California. The U.S. Forest Service currently recognizes four geographic varieties of *P. contorta* based on differences in growth form, needle, and cone characteristics (Sudworth 1908, Critchfield 1980). Shore pine (var. *contorta*) and Mendocino County White Plains (var. *bolanderi*) are coastal forms; Rocky Mountain (var. *latifolia*) and Sierran (var. *murrayana*) are mountain forms found in upper montane and sub alpine zones. Populations of *P. contorta* var. *latifolia* persist in the Rocky Mountains and the Washington state portion of the Cascade Mountains. The variety investigated in this research, *P. contorta* var. *murrayana*, is found in the central and south Cascade, Klamath, Sierra Nevada, and Sierra de Juarez Mountains. Lodgepole pine-dominated stands exist where environmental conditions exclude local climax species (*i.e.* ponderosa pine) and where the local disturbance regime maintains the system at a pre-climax sere (Franklin and Dyrness 1988).

Lodgepole pine grow to ~30 m in height with diameters up to ~60 cm at 1.4 m above ground. Lodgepole pine have short needles (2.5-7.5 cm), two per fascicle, and thin bark. Shallow root structure allows colonization in thin soils, but, combined with thin bark, makes lodgepole pine susceptible to scorch and fire-related mortality (Minore 1979). Although individual trees can live for more than 350 years (Stuart *et al.* 1989), in most systems fire and other disturbance agents maintain younger stands

(Agee 1993). Plentiful annual to biannual seeding and the ability to produce serotinous cones allow lodgepole pine to persist in fire-prone environments (Tackle 1961, Critchfield 1980). Lodgepole pine germinate best on mineral soil, with fire enabling greater densities and distributions of seedling recruitment by removing or reducing the litter layer (Tackle 1961, Minore 1979).

Shade intolerance limits lodgepole pine regeneration to open environments where it pioneers aggressively (Moir 1969, Brown 1975). Light levels in tree-fall gaps support small-scale regeneration events in harsh environments where interspecific competition is not a confounding factor (Parker 1986, Stuart *et al.* 1989). Lodgepole pine persist at the extremes of other coniferous species' tolerances in shallow, rocky, nutrient-poor, acidic soils in areas with limiting diurnal soil temperature fluctuations or growing season (Lotan and Perry 1983). Although seral throughout much of its range, both Rocky Mountain (Moir 1969, La Roi and Hnatiuk 1980, Despain 1983) and Sierran varieties (Stephens 1966, Ziegler 1978, Parker 1986, Franklin and Dyrness 1988) also occur as climax dominants in parts of their respective ranges.

Lodgepole Pine Fire Ecology

Fire acts as a major disturbance agent in lodgepole pine systems (Brown 1975, Agee 1993). Patterns in post-fire regeneration in lodgepole pine communities depend on the severity and extent of the disturbance as well as seasonal environmental variation. Large-scale disturbances such as stand-replacing fire destroy most of the

aboveground vegetation and provide optimal conditions for pioneer species. Since lodgepole pine colonizes vigorously on mineral soil, large-scale disturbance in lodgepole pine systems results in landscape-scale regeneration. Typically, this even-aged, post-fire cohort self-thins via suppression mortality, freeing resources for potential climax species and contributing to fuel load (Oliver and Larson 1990). Extensive stands of seral lodgepole pine persist where episodic crown fires eliminate potential climax species. These stands typically display a unimodal age structure.

Rocky Mountain lodgepole pine produce up to 75% serotinous cones, allowing rapid colonization after catastrophic fire (Brown 1975, Muir and Lotan 1985). Conversely, Sierran lodgepole pine express almost no serotiny and rely on regeneration from live seed (Mowat 1960). Periodic, small-scale disturbance events, such as tree-fall, increase local access to light and nutrient resources, promoting patch-scale recruitment and resulting in multi-aged stands (Parker 1986, Stuart *et al.* 1989). Self-replacing lodgepole pine systems normally experience less frequent, less intense fires than seral systems. Relatively sparse, disconnected fuels limit fire spread as well as fire intensity; however, extreme environmental conditions, such as hot, dry wind, can introduce fire from neighboring stands (Agee 1993). Slow-moving, low-intensity, log-to-log burns typify climax lodgepole pine systems (Stuart *et al.* 1989).

Disturbance in self-replacing lodgepole pine stands results from the interaction of fire with mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe (*Arceuthobium americanum*) (Figure 2) (Ziegler 1978, Stuart *et al.* 1989, Godfree *et al.* 2002). Dwarf mistletoe, an obligate parasite on *Pinus*, reduces host tree vigor and

growth rates and may increase fuel load and mortality (Hawksworth and Wiens 1996). Mistletoe increases vertical complexity in the canopy, creating fuel ladders that can escalate fire severity. So-called witches' brooms, dense localized growth in response to mistletoe infection, may shed material, increasing fine fuels and contributing to increased stand flammability (Brown 1975).

Figure 2. Disturbance and regeneration in self-replacing lodgepole pine on the High Pumice Plateau (derived from Geiszler *et al.* 1980 and Gara *et al.* 1985).

Fungal and mountain pine beetle disturbance agents also influence the fire regime. The pathogenic fungus *Phaeolus schweinitzii*, associated with fire-scarred

trees, accesses the host tree via fire-damaged tissue. The fungus not only weakens the host tree's resistance to mountain pine beetle attack, it may also release a chemical whose breakdown product acts as a mountain pine beetle-aggregating pheromone (Geiszler *et al.* 1980). Mountain pine beetles preferentially infect fire-scarred and large-diameter trees (Geiszler *et al.* 1980). Adults excavate egg galleries in host tree cambium. When larvae hatch, they feed on cambial tissue and can girdle the host tree if beetle densities are sufficiently large (Stuart *et al.* 1989). Beetle-induced tree mortality introduces coarse fuels into the system. Subsequent fire scars a subset of remaining trees, resetting the fungus-beetle-fire cycle (Geiszler *et al.* 1980).

The Lodgepole Pine Zone in Central Oregon

Forest communities in the pumice area tolerate wide diurnal temperature fluctuations, limited and sporadic soil moisture availability, and infertile soil conditions. Pedogenically young pumice soils support forest vegetation dominated by ponderosa pine (*Pinus ponderosa*) with local topo- and topoedaphic-climax stands of hybrid fir (*Abies grandis*-*Abies concolor*) and lodgepole pine (*Pinus contorta*), respectively (Franklin and Dyrness 1988, Arabas *et al.* in press). In the flats and depressions where nighttime growing-season temperatures are low and/or soils are nutrient poor, the locally dominant ponderosa pine do not compete well, and are supplanted by self-replacing lodgepole pine stands (Berntsen 1967, Franklin and Dyrness 1988). Local variations in soil fertility, soil texture, and soil depth of

Mazama pumice deposits likely support the persistence of these self-replacing lodgepole pine stands (Hansen 1942, Youngberg and Dyrness 1965, Cochran *et al.* 1967). Self-replacing lodgepole pine stands correspond with patches of extreme microhabitat in the High Pumice Plateau. Low productivity, sparse understory and bare ground between vegetation patches characterize these communities. Where more mesic conditions are found, such as on north-facing slopes, true fir are a dominant or co-dominant species.

Low productivity and sparse (<50%) understory cover characterize climax lodgepole pine stands on the most environmentally extreme sites, and biomass and litter accumulate more slowly than in adjacent ponderosa pine stands (Agee 1993). Fire frequency in High Pumice Plateau climax lodgepole pine is not well-studied. No single fire severity regime dominates; low, medium, and high severity fires occur (Hadley 2005). Agee (1993) approximates fire frequency at 60 to 80 years, with more frequent fires in areas bordering more productive stand types. However, some stands with discontinuous vertical and horizontal fuels have been without fire for 350 years (Stuart *et al.* 1989). Because of the sparse, patchy structure of the community, climax lodgepole pine stands act as natural fire breaks under typical environmental conditions (Agee 1993).

Moisture availability limits recruitment in High Pumice Plateau forest communities (Ziegler 1978, Franklin and Dyrness 1988, Stuart *et al.* 1989). Ponderosa pine are limited by temperature extremes and moisture availability; lodgepole pine and true fir are likewise limited by desiccation mortality and frost

heaving (Minore 1979). Recruitment in self-replacing lodgepole pine stands occurs during climatically favorable years and where downed, coarse woody debris and snags provide favorable microhabitat, mitigating temperature extremes and desiccation mortality (Cochran 1985, Stuart *et al.* 1989). Daytime shade reduces direct heat and evapotranspiration; nighttime longwave radiation emission reduces frost heaving mortality. Rapid post-fire regeneration occurs in these patches of favorable microhabitat (Agee 1993).

Disturbance severity, seasonality, and environmental factors determine the density, extent, and species diversity of these seedling regeneration pulses. In addition to increasing access to light and recycling nutrient resources, disturbance increases structural heterogeneity in the stand, providing the redundancy necessary to protect the system from catastrophic events. Between disturbance events, large, old trees act as resource sinks and inhibit recruitment (Godfree 2000).

Chapter 3

STUDY AREA

My research site is located in the High Pumice Plateau of Newberry National Volcanic Monument in the Deschutes National Forest in central Oregon (Figure 3). Situated east of the Cascades crest, Newberry Crater sits 1,100 m above the surrounding plateau. My research was conducted at the Lava Cast Forest Geological Area (hereafter, Lava Cast Forest) (1,500 m elevation; 43.69° N, 121.25° W) on the north slope of Newberry Crater shield volcano, roughly 8 km northwest of the caldera, in the western High Lava Plains Province (Franklin and Dyrness 1988).

High Pumice Plateau elevations range from 1200-1525 m where frosts punctuate the short growing season. Strongly seasonal precipitation, 35-70 cm annually, falls mostly as snow in the winter months (Franklin and Dyrness 1988), and moisture availability limits seedling recruitment (Ziegler 1978, Franklin and Dyrness 1988, Stuart *et al.* 1989, Chappell and Agee 1996). Shallow depressions and volcanic cones comprise the rolling terrain. Cold air drainage into the depressions, coupled with the low thermal conductivity of the pumice soil, makes the depressions an extremely cold microenvironment (Cochran *et al.* 1967).

Figure 3. Lava Cast Forest (1,500 m) is located in Newberry National Volcanic Monument (NNVM), ~30 km south of Bend, OR (NAIP 2005).

Physiography

Landforms and substrate in the Newberry Crater area are of volcanic origin. The Brothers fault zone, a system of northwest-southeast trending wrench faults, underlies the High Lava Plains Province and intersects the Sisters Fault from the north and Walker Rim Fault from the south near Newberry Crater (Figure 4) (Orr *et al.* 1992). The darker basaltic and lighter rhyolitic lavas associated with the Brothers wrench-fault system are from 4.3 to 0.8 mya and decrease in age from southeast to northwest (Orr *et al.* 1992). Newberry Crater is itself a 0.5 mya shield volcano, covering over 1,300 km² (MacLeod *et al.* 1981).

Newberry National Volcanic Monument contains a series of Holocene-age lava flows along the Northwest Rift Zone. Two major concurrent surface flows of basaltic andesite (54% SiO₂), the Lava Cast Forest flow and the Lava Cascade flow, covered ~800 ha of what is now Lava Cast Forest ~6,600 years ago (Figure 4) (Peterson and Groh 1969, Jensen 1995). These flows created a ~65 ha area of naturally fragmented forest isolates (kipukas). The 12 isolates vary in size from 0.4 to 113 ha.

Figure 4. (a) Three fault systems, the Sisters Fault, the Walker Rim Fault Zone, and the Brothers Fault Zone converge at Newberry Volcano (from Orr *et al.* 1992). (b) Select Northwest Rift Zone flows at Lava Cast Forest (from Jensen 1995 after Peterson and Groh 1969).

Soils

The eruption of Mount Mazama $6,845 \pm 50$ years ago ($7,640 \pm 50$ calibrated calendar age) deposited a plume of pumice and ash over more than $6,000 \text{ km}^2$ to the north and east of the former peak (Figure 5) along the east flank of the south-central Oregon Cascades, including my study area (Bacon 1983, Jensen 1995, Geitgey 1992). Pumice, a highly vesicular volcanic glass ($\sim 65\% \text{ SiO}_2$), solidifies from gas-infused magma ejected during explosive volcanic activity. Pumice has low bulk density, unusually large particle size to surface area ratio, and if vesicles are not too large, high water holding capacity (Youngberg and Dyrness 1965, Geitgey 1992).

Mount Mazama pumice, a hydrous rhyodacitic pumice containing roughly $70\% \text{ SiO}_2$ by weight (Bacon and Druitt 1988), develops into soils with low thermal conductivity and low heat capacity; these soils experience wide diurnal temperature fluctuations and are nutrient-limited (Youngberg and Dyrness 1965, Cochran *et al.* 1967). While there is a general trend toward shallower deposits with distance from Mount Mazama (Figure 5), actual pumice depths can vary with respect to pre-eruption topography (Geitgey 1992).

Soils in Lava Cast Forest have been characterized in the USFS *Soil Resource Inventory* for Deschutes National Forest (Larsen 1976). Mapping unit 15 describes soils in lodgepole pine basins as pumiceous loamy sands and sands evolved from sandy volcanic ash and pumice lapilli parent material. These soft, loose, single grain soils are nonsticky, nonplastic and skeletal. Susceptibility to frost heaving, low

Figure 5. Isopach map showing the extent and depth (m) of the Mazama pumice plume, originating from Crater Lake (née Mount Mazama) (from Geitgey 1992).

fertility, and wide diurnal and seasonal temperature extremes in lodgepole basins make these systems relatively unproductive with low regeneration potential (Franklin and Dyrness 1988).

Past Climate, Vegetation, and Land Use

Climate and vegetation in central Oregon have varied since the Cascades-Coast Range rainshadow reached operative heights in the upper Miocene, creating a more continental eastside climate (Detling 1968). Warmer, drier conditions in the Miocene and Pliocene supported grassland and modified Arcto-Tertiary geoflora, respectively (Table 2). The modern yellow pine (*i.e.*, ponderosa pine) and fir flora established by mid-Pliocene, but was supplanted by steppe vegetation during the Pleistocene. Regional proximity to the Cordilleran ice sheet resulted in a colder, drier climate in the

Table 2. Past climate and vegetation in central Oregon. Adapted from Detling 1968 and Whitlock 1992.

<u>Epoch</u>	<u>Climate</u>	<u>Vegetation</u>
Holocene (present)	Xeric to dry	Ponderosa pine, lodgepole pine, hybrid fir forest (est. ~ 5 ka)
Pleistocene	Cooler and drier than Present	Steppe vegetation
Pliocene (Upper)	Cooling into Pleistocene ice ages	Biomes forced downslope by cooling conditions
(Mid)	Drier summers than Previous	Yellow pine and fir on Cascades east slope
(Lower)		Modified Arcto-Tertiary geoflora
Miocene (Mid)	Semi-arid (warmer than present)	Grasslands

Pacific Northwest during the last glacial period (Whitlock 1992). Following the last glacial maximum roughly 10,000 years ago, lodgepole pine was likely the first conifer to establish, followed by ponderosa pine, fir, and western white pine until present vegetation established (Detling 1968).

The eruption of Mount Mazama (~7,700 yBP) and concomitant pumice deposition radically altered growing conditions and reset the system, shifting the competitive advantage to lodgepole pine (Hansen 1942). Conditions improved for other species as vegetation, precipitation, and gravity reworked pumice soils. Munger (1914) posits that prolonged, repetitive burning by native peoples may have supplanted ponderosa pine with the more aggressive post-disturbance pioneer, lodgepole pine. Although lodgepole pine can dominate, the anthropogenic alteration of the fire regime enabled lodgepole pine to encroach in areas suited to ponderosa pine dominance, especially in the High Pumice Plateau (Munger 1914).

Archeological evidence supports use of Newberry Crater from 11,000-7,600 BP and 4,000-1,300 BP by sparse, transitory family and work groups of Klamath-Modoc and Wadadika Northern Paiute for obsidian mining, hunting, and trading (Connolly 1999). The pumice and ash plume from the eruption of Mount Mazama, coupled with increasing aridity over the past 10,000 years, created a pumice desert, dramatically decreasing the productivity of the landscape and discouraging use by native peoples for roughly 3,600 years (Connolly 1999).

Anthropogenic alteration of the natural fire regime, introduction of grazing animals, and logging have all changed the landscape of central Oregon. Robbins

(1994) asserts that native tribes used fire on the east slopes of the Cascade Range to encourage production of food plants and to attract browsing ungulates. The combination of anthropogenic burning and lightning-strike fires resulted in a landscape of open, park-like forests. With European Americans in the 1800s came roads and railroads, horses and other grazing animals, and land-clearing activities: logging and fire. Surface fires improved conditions for grazers, and logging provided raw materials for fledgling economies.

The Deschutes National Forest, including the future Lava Cast Forest Geological Area, was established in 1908. Newberry National Volcanic Monument, created in 1990 and managed by the U.S. Forest Service, protects over 20,000 hectares, including the Lava Lands area which contains Lava Cast Forest Geological Area (Deschutes National Forest 2005). With the exception of Hoffman Island which was logged as recently as the 1960s (USFS 2002), the kipukas' separation from the surrounding contiguous forest protected them from commercial exploitation. Access to the relatively remote study area includes ~18 km by gravel road and a ~200 m traverse across uneven terrain (*i.e.*, craggy, difficult to traverse lava). As a result, the kipukas offer a relatively pristine version of High Pumice Plateau forests.

Chapter 4

METHODS

Field and Lab

Nurse plant or object facilitation is reliant on the relative proximity of the facilitated individual to its associate. The facilitated individual must be close enough to the associate to benefit from the shade, radiant heat, increased moisture and nutrient availability, or structural support the associate has to offer. Mapping the positions of all the members of a plant community within study plots, and establishing that the environment is extreme, enables the demonstration and quantification of facilitative relationships. In this study, I investigate facilitation by mapping the spatial distribution of lodgepole pine seedlings in a self-replacing lodgepole pine stand characterized by soils with low moisture retention. The stand is located on nearly level terrain at the base of a cinder cone and covers roughly 20 ha in the northeast portion of the largest pristine kipuka (113 ha) at Lava Cast Forest (Figure 6). Tree densities and canopy cover vary throughout the stand, as does the density and diversity of understory species. A recent blowdown event removed a large number of dominant trees from the canopy. The severity of this disturbance and the magnitude of the concomitant regeneration pulse vary throughout the stand.

Figure 6. The study site is a self-replacing lodgepole pine stand on the northeast portion of the largest kipuka (USFS 2001).

I quantified the spatial pattern of seedlings relative to the other woody vegetative components of the stand by mapping seedlings, saplings, trees, shrubs, snags, stumps, and sound and decomposed logs in each of five, 500 m² circular plots. The coordinates of the center of each plot were determined with a Garmin Magellan GPS unit (accuracy ± 15 m); then, distance (± 0.1 m) and azimuth ($\pm 1^\circ$) to all components of the stand were measured from this known position (Figure 7).

Figure 7. Mapping and understory sampling protocol. I measured distance and azimuth from the center of the plot to each woody plant, log, and stump in the stand (*e.g.*, NE quadrant). For understory percent cover characterization, I sited twelve, 1 m² plots using randomly derived distance and azimuth values, stratified so that each cardinal quadrant contains three plots (*e.g.*, NW quadrant).

I sited the five plots subjectively with the intent of capturing the range of post-blowdown canopy conditions (Figure 6). Two plots (B and E) are at the base of the cinder cone slope, two are at the edge of the lava (A and D), and Plot C is at the stand boundary with a denser lodgepole pine stand. All plots have slopes of $<1^\circ$.

I collected attribute data in each plot, detailing species, dimensions, and age or relative development of each vegetation type (Table 3). I aged 250 trees from the five sample plots. For each tree (>4 cm DBH, diameter at breast height, 1.4 m), I measured height, canopy height (*i.e.*, the horizontal extent of the live vegetation), and canopy diameter and collected one increment core using standard dendrochronological practices for age determination (Stokes and Smiley 1996). I harvested nine, 40 cm lodgepole pine seedlings from the adjacent, non-kipuka forest to determine age at coring height and to determine if branch node corresponds with one year's growth in lodgepole pine. Tree age equals the ring count from each increment core plus the median age at coring height as determined by the harvested seedlings.

I measured seedling and sapling heights and counted branch nodes to estimate age. A *post-hoc* comparison of branch node counts and ring counts from harvested seedlings revealed a x year difference in mean age estimates, invalidating the use of node counts for age estimates. In lieu of absolute age, I substituted the product of seedling height and number of branch nodes as an indicator of seedling development. This metric assumes that taller seedlings with more branch nodes are better competitors and have a greater likelihood of succeeding to the sub-canopy and canopy

Table 3. Attribute data collected for woody vegetation, logs, and understory. Diameter of decayed logs measured at 1.4 m from an end, and stump diameter measured at stump height.

	Spp	Dimensions				Age		Associated Seedlings
		Height/ Length	Canopy Height	Canopy Diameter	DBH	% Cover	Ring Count	
Trees	X	X	X	X	X		X	
Saplings	X	X					X	
Seedlings	X	X					X	
Snags	X	X			X			
Stumps	X	X			X			X
Shrubs	X	X		X				X
Logs, decayed	X	X			X			X
Logs, sound	X	X			X			X
Understory	X					X		

levels and that relative seedling development varies with seedling position vis-à-vis the nurse plant or object.

I also measured shrub height, maximum canopy diameter, and perpendicular canopy diameter to characterize possible nurse object dimensions. I noted length, DBH, azimuth of orientation, and decay class for all logs. Logs were assigned one of two decay classes, sound and decomposed, respectively. Although stochastic tree-fall does occur, I assumed that all decomposed logs were emplaced following the last stand-replacing fire in 1918 (Arabas *et al.* in press) and that all sound logs resulted from the blowdown. I defined decomposed logs as woody litter on the forest floor still in the shape of a log. Sound logs retained stem integrity, branches or branch stubs, and, in some cases, cones. I noted the number of seedlings associated with stumps, logs, and shrubs. Associated seedlings included those on, located under, or adjacent to stumps or logs and within the dripline of shrubs. Where applicable, I noted the distance from each seedling to the nearest associate. I relied on the mapping to determine the position of seedlings growing under tree canopy.

I determined the relative timing of the blowdown event using the tree-ring records of the standing trees in each plot. Growth releases may be the result of increased resource availability for surviving trees. I used $\geq 200\%$ growth increase (*cf.* Veblen *et al.* 1989) over a five year period relative to the preceding five years to define a growth release.

I quantified blowdown severity by reconstructing pre-blowdown basal area and canopy cover values for those logs that had been growing inside each plot. I used the

DBH of each log to reconstruct basal area for the log constituent, and I used the relationship between DBH and canopy diameter of standing trees to approximate canopy diameter for the blown down logs. Based on these data, I calculated three indicators of blowdown severity: basal area (BA) lost, percent canopy cover lost, and percent BA lost. I then constructed a metric, the blowdown severity index (BSI), as a function of all three indicators to represent total blowdown severity. The BSI is the average of the three indicator values normalized by the largest value achieved in each category then multiplied by 100 so that values range from 0-100. *Post-hoc* plot labels, A-E, reflect increasing blowdown severity.

Understory composition was characterized using a stratified random sampling protocol and modified Daubenmire percent cover classes (Daubenmire 1959). Percent cover of all understory plants, litter, and debris was recorded in twelve, 1m² quadrats per plot, with three quadrats sited in each of the plot's four cardinal quadrants (Figure 7).

To quantify affinity for growing in an organic-rich substrate, I catalogued whether 30 randomly selected shrubs in each of the five plots grow on woody litter versus mineral soil. I also noted how many seedlings occur within the dripline of each of the randomly selected shrubs. I determined water-holding capacity for pumice soil, leaf litter, and woody litter at each plot using the gravimetric method (Puustjarvi 1973) to demonstrate increased moisture retention capacity by woody litter.

I captured the physical characteristics of the pumice soil at seven soil profiles using standard soil description procedures (Birkeland 1999). Two profiles each were

sited under a lodgepole pine tree, a wax current shrub, and a decomposed log adjacent to Plots B and D; the remaining profile was sited under the relatively woody vegetation- and litter-free mineral pumice “barren” adjacent to Plot B.

Temperature probes (Spectrum Technologies, Inc. Model 100 WatchDog data loggers) collected hourly temperature values during the summers of 2003 and 2004, roughly June through September. In 2003, I sited three probes each at Plots B and D in the following places: at ~1m above the center of the plot to capture ambient temperature, at ~35 cm aboveground within the canopy of a randomly selected wax currant shrub, and at ground level underneath the same wax currant shrub. A fourth probe collected temperatures 2 cm belowground, also under the wax currant shrub at Plot D. In 2004, five temperature probes collected hourly ambient temperature data ~75 cm above the center of each of the five plots.

Data Analyses

I quantified seedling patterns relative to community structure by digitizing my vegetation data into a geodatabase using ArcGIS 9.1 (ESRI 2005), ArcView 3.3 (ESRI 2002), and Distance/Azimuth tools v. 1.5 (Jenness Enterprises 2004). Age structure and diameter class structure diagrams were created for each plot to characterize the range of size and age structures in the stand and develop a *post-hoc* assessment of disturbance among my plots. I quantified the magnitude of the blowdown in each plot using my blowdown severity index (BSI). These values were then compared with the

number of seedlings to determine the relationship between the magnitude of the blowdown and the number of seedlings in each plot.

I compared distribution patterns of trees, saplings, shrubs, and seedlings using the ‘Average Nearest Neighbor’ analysis (ESRI 2005) following field observations suggesting nurse plants and objects result in a clumped seedling distribution. Nearest neighbor techniques reveal distribution patterns within a population by summing the distances from each individual to its nearest neighbor for a sample or population within a discrete parcel then calculating the mean nearest neighbor distance (Greig-Smith 1983). The resulting test statistic (Z score) reveals whether the population is clustered (<0), random (0), or dispersed (>0) as well as the magnitude of the pattern with $\geq 95\%$ confidence.

I quantified scale-dependent patterns in seedling distribution using the Ripley’s K method in CrimeStat III (Ripley 1976, Haase 1995, Levine 2004). Ripley’s K, a second-order analysis, quantifies the variance in nearest neighbor distances for multiple spatial scales up to the size of the sample parcel itself (Haase 1995). The pattern of seedling distribution is compared with complete spatial randomness for the plot and for multiple subordinate spatial scales. This allows the assessment of seedling distribution patterns at multiple spatial scales (0–8 m). To foster ease of interpretability, the exponential K distribution is transformed to the linear square root function, L, such that $L(d) = 0$ = complete spatial randomness. Values of L(d) less than zero indicate a dispersed distribution, and values of L(d) greater than zero indicate clustering. The absolute value of L(d) indicates the magnitude of the pattern.

I conducted 199 Monte Carlo simulations to determine whether sample $L(d)$ values vary from those of a random distribution. The Monte Carlo procedure randomly reorients the sample point data within the sample parcel then runs the Ripley's K protocol on the reoriented data. By running multiple Monte Carlo trials, one creates an envelope bound by the maximum and minimum Monte Carlo (random) distributions. Where the sample $L(d)$ distribution lies outside the envelope, one can be 95% confident that the distribution at that spatial scale is significantly different from a distribution arranged by chance. This method highlights the spatial scales at which seedling distributions vary significantly from a chance distribution.

I modeled open forest floor in each plot (*i.e.*, ground surface not areally covered by tree canopy, shrub canopy, sound logs or stumps) to assess the contiguity of unshaded areas and the proportion of seedlings growing there. I then created a raster surface using Spatial Analyst (ESRI 2005) for each plot that shows distance from sources of cover (*i.e.*, tree and shrub canopy, sound logs, and stumps) and seedlings to visually assess areas of positive and negative spatial association with cover and open forest floor. Because the cover of canopy trees may be too distant for these trees to act as nurse plants, I quantified seedling-nurse object associations by mapping seedling locations relative to shrub canopies, logs and stumps, and woody litter. This involved a two-step procedure: 1) mapping seedling locations relative to shrub canopies and 2) generating a list in the field of seedlings growing on decomposed logs or woody litter, under or adjacent (≤ 15 cm) to sound logs or stumps, or without a discernable nurse object association. I modeled logs and stumps with a

diameter-based buffer. I modeled shrub canopies with a circle overlay derived from two orthogonal canopy diameter measurements and positioned on the center of each shrub stem. All seedlings falling within the diameter of the derived shrub canopies I counted as shrub associates. Lastly, I explored seedling-associate relationships with differences in seedling development, based on the seedlings' heights and branch node counts.

Because my tree, seedling, and temperature data distributions violate the assumptions of normality or homogeneity of variance necessary to use parametric statistics, I used non-parametric Kruskal-Wallis and Mann-Whitney (Sokal and Rohlf 1995) tests to investigate differences in canopy structure, tree age, seedling development, and temperature between the five plots. The Kruskal-Wallis test compares the distributions of three or more independent samples, returning a test statistic that identifies the existence of significantly different median values. The Mann-Whitney test does the same rank sum operation for two independent samples. For each test, all the values in all the sample distributions are ordered from smallest to largest and ranked; then, the ranks are summed for each distribution. The statistic tests the likelihood that the differences in rank sums between the distributions are insufficient to determine that the sample medians are different. Although non-parametric tests are less powerful than their parametric counterparts, they function under fewer assumptions about the nature of the sample distributions, so they are appropriate tools for the analysis of ecological data.

Chapter 5

RESULTS

Stand Structure

Lodgepole pine dominate all study plots, comprising 75 to 100% of the canopy trees, 45 to 100% of saplings, and 76 to 97% of seedlings. Tree densities among plots vary from 260 stems/ha to 2680 stems/ha (Table 4). These values correspond to differences in canopy cover ranging from 8-50%, representing open, gap-patch, and closed canopy conditions (Table 5). Snag (*i.e.*, standing coarse woody debris >1.4 m in height) densities range from 0-40 snags/ha in all but one study plot (C) where 640 snags/ha remain. Wind-snapped stumps vary from 80-380/ha among the sample plots. Roughly 65% of blown-down logs snapped off at ground level, with rootthrow accounting for the remaining 35%.

Tree height ($p < 0.02$) and tree canopy height ($p < 0.001$) vary significantly among the five plots (Appendices A and B). The tallest trees grow in Plot B with Plot C maintaining the greatest median tree height (Figure 8a). The distribution of tree heights varies significantly between plot pairs A/B, B/C, and C/D (Appendix A). Plot A has the greatest range of tree canopy height values (Figure 8b). Plot D has the smallest range and amount of canopy cover. No significant variance in tree basal area exists among the five plots (Appendix C).

Table 4. Density of trees, saplings, seedlings, snags, and shrubs by sample plot at Lava Cast Forest. Densities listed are for all species except “PICO only” includes *P. contorta* only.

Plot #	Density (Stems/ha)					
	All Trees	PICO only	Saplings	Seedlings	Snags	Shrubs
A	1060	1060	960	2800	40	1940
B	680	620	240	4200	20	1480
C	2680	2680	760	1360	640	2020
D	320	240	220	17300	0	4800
E	260	240	20	10960	40	1460

Table 5. Stand characteristics of sample plots at Lava Cast Forest.

Plot #	Location	Blowdown Severity	Canopy Type	Basal Area (m ² /ha)				Canopy Cover (%)		
				Standing Trees	PICO only	Pre-Blowdown	Snags	Standing Trees	Pre-Blowdown	Shrubs
A	Lava edge	None	Gap-patch	18.33	18.33	18.8	0.90	50	51	4
B	Slope base	Moderate	Gap-patch	12.94	11.75	20.2	0.57	28	38	13
C	Slope (<1°)	Moderate	Closed	29.90	29.90	42.2	5.34	42	56	9
D	Lava edge	Severe	Mostly open	4.87	3.37	19.4	0	12	33	19
E	Slope base	Severe	Open	5.63	5.56	21.2	1.67	8	33	5

Figure 8. Range and median values of (a) tree height and (b) tree canopy height. Plots A-E contain the following numbers of trees: 53, 34, 134, 16, and 13. In panel (a), grey boxplots with dashed whiskers and white median lines represent pre-blowdown tree heights; boxplots outlined in black with heavy whiskers and median lines represent current tree heights. The box encloses the interquartile range (25th-75th percentile); the whiskers define the minimum and maximum values within 1.5 box lengths of the box. Outliers (circles) and extremes (asterisks) are from 1.5 to 3 and >3 box lengths above the 75th percentile.

Age structures reveal a multi-modal, 107-year-old stand with the youngest tree-sized stems establishing around 1960 (Figure 9). Age distributions vary significantly among all plots ($p \leq 0.04$) except between Plots D and E (Appendix D). All trees in Plots A, C, and E are lodgepole pine, with Plots B and D having <11% and 25% ponderosa pine in the 61-100 year age range. Stems by age class vary among the plots. The majority of trees in Plot A occur in the 41-60 year age group, while Plots B and D and Plots C and E have the greatest number of trees in the 61-80 and 81-100 year age groups. The oldest trees grow in Plot C, and the youngest tree-sized stems grow in Plot E. Seedling and sapling densities are dissimilar in Plots A-C (low) relative to Plots D and E (high).

Stand structure reconstructions reveal similar pre-blowdown basal area and percent canopy cover for all but Plot C (Figure 10, Table 5). Diameter-class distributions, including a reconstruction of blown-down stems, show that the blowdown removed trees with a wide range of stem diameters (5-35 cm), with the exception of those in Plot C where losses included stems in the 5-10 cm range (Figure 11). The majority of the stems lost during the blowdown were >15 cm DBH.

Tree densities in Plots A, B, D, and E before the blowdown were $\sim 20 \text{ m}^2/\text{ha}$; Plot C had twice that value. Post-blowdown stand structures exhibit a range of conditions as measured by DBH, basal area, and canopy cover (Tables 5 and 6). Plot A lost only 1% canopy cover and <1% tree basal area. By comparison, Plots D and E lost 21% and 25% of their canopy cover and 75% and 73% tree basal area.

Figure 9. Age structure diagrams for all trees, saplings, and seedlings in five study plots at Lava Cast Forest. Trees are shown in 20-year age classes by species for each plot; seedlings and sapling are grouped separately in the final panel.

Figure 10. Total basal area (m²/ha) by plot for standing and blown-down trees.

Figure 11. Diameter class reconstructions for five sample plots. N_{ST} and N_{BD} represent the number of standing and blown down trees in the plot. Saplings (SAP) have diameters <4 m.

These differences are reflected in the wide range of blowdown severity index values (2 to 99 on a scale of 0-100) (Table 6). Plot A (BSI = 2) experienced almost no blowdown, Plots B and C (BSI = 45 and 58) experienced intermediate blowdown, and Plots D and E (BSI = 92 and 99) experienced severe blowdown.

Table 6. Reconstruction of pre-blowdown stand structures and blowdown severity. Blowdown severity index (BSI) is the change in basal area (BA), % canopy cover, and % BA between pre- and post-blowdown conditions, i.e. current stand conditions minus the BA and cover estimated from sound logs.

Plot #	BA Lost (m ² /ha)	% Canopy Cover Lost	% BA Lost	BSI (0-100)
A	0.47	1	0.025	2
B	7.26	10	36	45
C	12.3	14	29	58
D	14.53	21	75	92
E	15.57	25	73	99

The blowdown significantly altered the structure of the canopy by reducing the size ranges of tree diameters and tree heights. Before the blowdown, no significant differences in diameter existed (Appendix E). Following blowdown, tree diameter distributions vary significantly ($p < 0.001$) in six (60%) interplot comparisons (Appendix C). The greatest number of downed stems occurs in Plot C where stem densities remain highest. The blown-down trees in Plot C were among the shortest trees in the stand (Figure 8a). Conversely, the areas of greatest blowdown severity (Plots D and E) had fewer stems before the blowdown and lost their tallest trees. Plots

D and E had the greatest median tree heights before the disturbance and currently have the first and third lowest tree heights.

The number of seedlings growing at each plot varies with blowdown severity (Figure 12). Plots A, B, and C experienced essentially no (BSI=2) to moderate (BSI=45 and 53) blowdown and have 1,360, 2,800, and 4,200 seedlings/ha. By contrast, Plots D and E experienced severe blowdown (BSI=92 and 99) and have thirteen times more seedlings than Plot A (17,300 and 10,960 seedlings/ha). In Plots B and D, 43% and 30% of seedlings grow in groupings of two to thirty-eight stems. By contrast, only two and seven seedlings occurred in groups in Plots A and C; all seedlings in Plot E grow individually (*i.e.*, not in groupings).

Trees that survived the blowdown may record the relative timing of the disturbance by showing increased growth enabled by freed resources after the event. Growth releases in trees begin in 1983 and end in 1998 with bimodal peaks corresponding to 1986 and 1997 (Figure 13). Trees from Plots C, D, and E recorded all but one growth release, Plot B recorded one, and Plot A recorded no growth releases. Plot C includes ~80% of the trees recording releases in the 1990s.

Figure 12. The number of seedlings found in each plot varies with local blowdown severity.

Figure 13. Growth releases recorded in live, standing trees in Plots B-E following a blowdown disturbance. A growth release represents $\geq 200\%$ growth for a five year period relative to the previous five years' growth. The arrows indicate the likely timing of the blowdown events.

Understory

The understory is characterized by patches of woody and herbaceous plants within a matrix of woody and leafy litter and bare pumice soil (Figure 14). Wax currant (*Ribes cereum*) is the dominant understory plant in all sample plots (Figure 15, Appendix F). Green manzanita (*Arctostaphylos patula*) and bitterbrush (*Purshia tridentata*) are the second and third most populous shrub species. Shrub density and diversity are greatest at Plot D with more than twice as many stems/ha as any other plot (Figure 15). Plots A and C have the most organic material, Plots B and D have the greatest amount of bare mineral soil, and Plot E has the least understory vegetation (Figure 14).

The forest floor is a mosaic of patches consisting of bare pumice soil within a matrix of organic materials derived from decomposed logs, other woody material, and leaf and needle litter. All five plots contain decomposed logs, ranging from 8-72 cm in width and averaging from 26-36 cm in width among the five plots (Figure 16). Most decomposed logs have not been directly colonized by seedlings and shrubs but appear to be the source of the redistributed woody litter supporting the growth of the majority of shrubs (68-90%) in each plot. These results are consistent with the broad distribution of disaggregated woody material found in the litter layer at all five plots and the rare presence of seedlings and shrubs on bare mineral soil.

Figure 14. Percent cover of organic material (litter and sound and decomposed logs), bare mineral soil, and woody and herbaceous vegetation under self-replacing lodgepole pine at Lava Cast Forest. Totals >100% reflect the use of % cover class midpoint values in data summarization.

Figure 15. Shrub density and dominance in sample plots at Lava Cast Forest. The 'other' designation comprises up to six additional species (Appendix F).

Figure 16. Photograph and GIS recreation of woody vegetation, snags, stumps, and logs

Figure 16 (cont.). Photograph and GIS recreation of woody vegetation, snags, stumps, and logs.

Plot C

Figure 16 (cont.). Photograph and GIS recreation of woody vegetation, snags, stumps, and logs

Plot D

Figure 16 (cont.). Photograph and GIS recreation of woody vegetation, snags, stumps, and logs

Plot E

Figure 16 (cont.). Photograph and GIS recreation of woody vegetation, snags, stumps, and logs

Regeneration Patterns

The spatial distribution of woody vegetation ranges from highly clustered (seedlings and shrubs) to mostly clustered (saplings) and dispersed (trees) (Figures 16 and 17 and Appendix G). Saplings are clustered in Plots A, B, and C and dispersed in Plot D. Plot E contains only one sapling. Plots A (N=48) and C (N=38) have four and three times more saplings than do Plots B (N=12) and D (N=11).

Seedling clustering varies from local to plot-wide scales (Figure 18). In all but Plot A, significant clustering ($p < 0.05$) occurs from roughly 0-8 m; in Plot A, significant clustering occurs up to 4 m. In Plot B, clustering is greatest at ~0.5 m and generally decreases with increasing interplant distance. Seedling aggregation peaks at roughly 2 m in Plot C. Plot A has two maxima at roughly 0.5 and 2 m. The magnitude of clustering in Plots D and E does not change appreciably with spatial scale. Median shrub diameters vary from 0.22 to 0.67 m among the five plots.

Plot A contains the largest trees and, at 50% tree canopy cover, has the least open forest floor of the five plots (Figures 11 and 16, Table 5). The majority of the seedlings, saplings, and shrubs occur in the southeast quadrant of the plot where tree canopy structure is the most complex (Figure 16). Few seedlings occur under large-canopy trees, especially in the west one-half of the plot where the canopies of several large trees overlap. Plot B possesses a range of tree sizes with most in the 5-25 cm diameter range (Figures 11 and 16). Tree canopies cover 28% of the plot area, leaving relatively large, contiguous areas of open forest floor. Most seedlings occur in small

Figure 17. Strength of clustering and dispersion in seedlings, saplings, trees, and shrubs derived from average nearest neighbor analyses. Each bar represents the population at a sample plot in ascending order (A-E). *Only one sapling present at Plot E.

groups with a few large clusters and a few lone individuals. Plot C has the highest density of smaller trees (5-20 cm) and discontinuous canopy conditions (Table 4, Figures 11 and 16). A cluster of seedlings occurs under a shrub/tree complex in the southwest quadrant of the plot; the remainder of the seedlings occur individually or as pairs or triplets throughout the plot.

Plots D and E have low canopy cover (12% and 8%) and considerably more seedlings (17,300/ha and 10,960/ha) than the other three plots (Tables 4 and 5). Plot D has 16 trees, the majority of which fall into the 5-15 cm range (Figure 11). The 13 trees in Plot E fall into three size classes: 5-10 cm, 15-20 cm, and 25-30 cm. Seedlings are found under tree and shrub canopy, adjacent to blown down logs, and in canopy gaps (Figure 16). Although Plots D and E have similar tree canopy cover, Plot D has considerably more shrub cover and less area with canopy openings.

Nurse Plant and Object Associations

The proportion of seedlings growing in canopy openings correlates positively with blowdown severity (Figures 19 and 20). In plots with fewer seedlings (A, B, and C), the minority (29-35%) grow in the open. By contrast, where more seedlings are growing (Plots D and E), the majority (64% and 79%) grow in the open. When those seedlings growing within the shade of a log or stump are removed from these totals, the results are less disparate. Plots A and B have ~25% seedlings growing in canopy

Figure 19. The percent of total seedlings at each sample plot growing in canopy openings relative to blowdown severity. (a) shows the proportion of seedlings growing outside the areal cover of tree and shrub canopy; (b) shows the proportion of seedlings growing outside areas of tree and shrub canopy and >15 cm from sound logs. Blowdown severity corresponds, in increasing order with plot letter, A-E.

Figure 20. The distance from tree, shrub, log, and stump cover (black) in 0.5 m increments (white areas >2 m) at the five study plots, A-E. White dots are seedlings growing under cover; black dots are seedlings growing without cover.

openings without log shading, Plots C and D have 31%, and Plot E has 41%.

Seedlings occupy one or more of the following microhabitats: on woody material (*i.e.*, on log-derived material that is sufficiently decomposed to host seedlings), under shrub canopy, under/adjacent to a log, and with no obvious associate. In Plots A and E the majority of seedlings (77% and 91%) grow on woody litter (Figure 21). The proportion of seedlings growing under shrub canopy varies from 25% in Plot E to >50% in Plot B. In all but Plot A, > 50% of seedlings grow in the shade of shrubs and/or logs. Among the five plots, 3-32% of seedlings have no obvious associate.

Seedling development, measured as the product of height and the number of branch nodes, varies significantly ($p < 0.001$) among the five plots (Figure 22 and Appendix H). Plot A has the greatest range of development values and has significantly greater median seedling development than that of all other plots ($p < 0.001$). Median seedling development at Plot E is significantly ($p < 0.001$) less than in Plot A, but significantly greater than in Plots B, C, and D ($p < 0.01$). Plot B has the lowest median seedling development, and median development values do not vary significantly among Plots B, C, and D.

Relative seedling development varies significantly ($p < 0.001$) with association type (Appendix I). Of the four association possibilities for seedlings – on woody material, under shrub canopy, under/adjacent to log, and no associate – only those seedlings growing under shrub canopy and under/adjacent to logs did not differ

Total number of seedlings and number of seedlings per microhabitat by plot.

Plot	N	on woody material	under shrub canopy	under/adj. to log	no associate
A	140	80	40	0	20
B	210	5	108	44	53
C	72	5	32	4	31
D	865	210	258	100	302
E	548	404	92	104	26

Figure 21. The number and proportion of seedlings in association with shrubs and logs among sample plots. Values may total more than 100% because of multiple associations.

Figure 22. Distributions of seedling development at five study plots at Lava Cast Forest. Seedling development is the product of seedling height and number of branch nodes. The y axis shows log transformed seedling development values. The box encloses the interquartile range (25th-75th percentile); the whiskers define the minimum and maximum values within 1.5 box lengths of the box. The outlier above Plot D has a value >1.5 but <3 plot lengths above the 75th percentile.

significantly ($p < 0.003$) in development values. Seedlings growing on woody material show the most development, the greatest range of development values, and the highest mean development (Figure 23).

Abiotic Characteristics

Temperature

Ambient growing season temperatures for 2004 ranged from -3°C to 42°C , with daily mean temperatures from 13°C to 14°C . Ambient temperatures in Plots A, B, and C vary significantly ($p < 0.005$) from the generally higher temperatures in the high severity blowdown plots (D and E) (Figure 24 and Appendix J). Buried and ground level daily high temperatures recorded at Plots B and D vary significantly from each other and from ambient and shrub canopy high temperatures ($p < 0.001$) (Figure 25 and Appendix K). Belowground high temperatures are generally lower than above ground high temperatures, especially after August 5 (JD 218). Ground level high temperatures are generally greater than all others throughout the growing season. At Plot D, ground level and shrub canopy temperatures vary significantly ($p = 0.02$), with ground level temperatures higher until mid-September ($\sim$ JD 259) after which shrub canopy temperatures are higher. Ambient daily high temperatures varied between the 2003 and 2004 growing seasons (Figure 26). Daily high temperatures from the

Figure 23. Relative seedling development by microhabitat type (on woody litter, under shrubs, under or adjacent to a sound log, or with no obvious associate) in self-replacing lodgepole pine at Lava Cast Forest. Seedling development is the log transformed product of seedling height and branch node count. The box encloses the interquartile range (25th-75th percentile); the whiskers define the minimum and maximum values within 1.5 box lengths of the box. Outliers (circles) have values >1.5 but <3 plot lengths above the 75th percentile.

Figure 24. Daily high ambient temperatures during the growing season at the five study plots.

Figure 25. Daily high temperatures in microhabitats during the growing season at one low blowdown (B) and one high blowdown (D) plot.

Figure 26. Daily high ambient temperatures during the 2003 and 2004 growing seasons at one low blowdown (B) and one high blowdown (D) plot. Tree canopy cover is 28% and 12% at Plots B and D.

beginning of July (~JD 180) to mid-August (~JD 225) at Plots B and D range from 20-42°C in 2003 and from 16-41°C in 2004, with more frequent high temperatures in 2003.

Soils

Dacite pumice soils at Lava Cast Forest show limited development (Table 7), exhibiting an A/C profile with an emerging AB horizon. These soils classify as Vitrandic Cryorthents based on their limited development, pyroclastic parent material, and the cryic soil temperature regime. A horizon depths vary from 5-13 cm with abrupt to gradual wavy boundaries, and moist colors range from grayish brown (10YR 5/2) to dark brown (10YR 3/3). Particle structure is single grain to weak, granular, and varies in size from very fine (< 1 mm diameter) to very coarse (> 10 mm diameter). Gravel content is less than ten percent, and consistence is nonsticky, nonplastic, and loose in all profiles. Textures vary from sand to loamy sand. Those profiles (1-4) with single grain structure have sand texture, and those profiles with weak structure (5-7) have loamy sand texture.

C horizon characteristics are less heterogeneous. Moist colors range from very pale brown-yellow (10YR 7/5) to yellow (10YR 8/8) with individual grains exhibiting a wider range of colors from dark gray (10YR 4/1) to light yellowish brown (10YR 6/4) to white (10YR 8/1). Single grain, granular structure particles represent all sizes

Table 7. Range of physical properties of Mazama dacite pumice soil at Lava Cast Forest.

Site/ Profile ^a	Horizon	Depth (cm)	Color (moist) (dry)		Structure ^b	Gravel (%)	Consistence ^c (Wet Moist Dry)	Texture ^d	Boundary ^e	
Plot 1 B	A	0-8	10YR4/2	10YR5/2	sg.vf.gr	< 10	so.po.lo.lo	S	c	w
	C	8-58+	10YR8/5	10YR8/4	sg.f, m.gr	10	so.po.lo.lo	S		
	2	A	0-11	10YR4.5/2	10YR5.5/2	sg.vf-m.gr	< 10	so.po.lo.lo	S	c w
	C	11-70+	10YR7/5	10YR6/5	sg.vf-vc.gr	10	so.po.lo.lo	S		
	3	A	0-9	10YR4.5/2	10YR4.5/2	sg.vf-m.gr	< 10	so.po.lo.lo	S	c w
	C	9-60+	10YR8/7	10YR7/5	sg.vf-m.gr	10	so.po.lo.lo	S		
	4	A	0-13	10YR5/1	10YR5/2	sg.vf-f.gr	< 10	so.po.lo.lo	S	g w
	C	13-50+	10YR7/5	10YR6/4	sg.vf-vc.gr	10	so.po.lo.lo	S		
Plot 5 D	A	0-11	10YR5/2	10YR5/3	1.vf-m.gr	< 10	so.po.lo.lo	S-LS	a	w
	C	11-50+	10YR7/6	10YR5/4	sg.vf-vc.gr	10	so.po.lo.lo	S		
	6	A	0-6	10YR3/3	10YR4/2	sg.vf-vc.gr	< 10	so.po.lo.lo	S-LS	c w
	C	6-50+	10YR7/6	10YR8/5	sg.vf-vc.gr	10-25	so.po.lo.lo	S		
	7	A	0-5	10YR5/1	10YR5/2	1.vf-f.gr	< 10	so.po.lo.lo	S-LS	c w
	C	5-60+	10YR8/8	10YR8/5	sg.vf-m.gr	10	so.po.lo.lo	S		

^aProfile: 1 = lupine barren, 2 & 5 = under wax currant, 3 & 6 = under lodgepole pine, 4 & 7 = under rotten log^bStructure: sg = single grain, 1 = weak;

vf = very fine, f = fine, m = medium, c = coarse, vc = very coarse; gr = granular

^cConsistence: so = nonsticky, po = nonplastic;

lo = loose

^dTexture: S = sand, LS = loamy sand^eBoundary: a = abrupt, c = clear, g = gradual; w = wavy

from very fine to very coarse. These sand-texture horizons are nonsticky, nonplastic, and loose in consistence and contain roughly ten percent gravel-sized particles.

Water Holding Capacity

The water holding capacity (WHC) of pumice soil varies from that of leafy and woody debris (Figure 27). The pumice soil treatments yielded 38-77% (0.4-0.8 g water/g soil) of their weight in water three hours after saturation. By contrast, leaf litter and woody litter retain 87-188% (0.9-1.9 g water/g litter) and 185-315% (1.9-3.1 g water/g litter) of their weight in water. Pumice soils are sands and loamy sands with ~10% gravel (Table 7). Leaf litter consisted primarily of pine needles and wax currant leaves. Proportion of leaf type (needle or broadleaf) varied from >75% needles in three samples to >75% broadleaves in two samples (Figure 27). Woody litter varied from dust-sized to ~2 cm diameter, with the majority of pieces <1 cm diameter.

Figure 27. The water holding capacity (WHC) of pumice soil, leaf litter, and woody litter in a lodgepole pine stand at Lava Cast Forest. For leaf litter, the first three samples (bars) contained >75% needles and the last two samples contained >75% broadleaves.

Chapter 6

DISCUSSION

Stand Structure and Blowdown Severity

A primary objective of this research is to examine post-blowdown regeneration in a self-replacing stand of lodgepole pine following different intensities of canopy disturbance. Earlier research in similar self-replacing lodgepole pine stands in the Rocky Mountains (Whipple and Dix 1979, Peet 1981, Despain 1983) and the Sierra Nevada-Cascade Mountains (Gara *et al.* 1985, Parker 1986, Stuart *et al.* 1989) documents unimodal to multimodal stand structures, depending on the nature of the local disturbance regime. These results show a continuous, gap-phase replacement with similar size and age structure to that of my control plot (no blowdown). By contrast, my four disturbed plots exhibit varying degrees of multimodal structures typical of the self-replacing stands in south central Oregon following mountain pine beetle-related mortality (Gara *et al.* 1985, Stuart *et al.* 1989). This regional similarity suggests the stand conditions at my site may also be related to local topography and weakly structured pumice soils conducive to blowdown.

Disturbance events can increase or decrease landscape and community heterogeneity depending on the characteristics of the disturbance and scale of the system (Turner *et al.* 2001). Similar to studies from New England (*e.g.*, Foster and

Boose 1992) and western Oregon (Hadley and Savage 1996), blowdown severity at my site in central Oregon appears to be a function of topographic position and pre-blowdown stand structure. The location of my study area adjacent to the east and southeast base of a large ($\sim 1 \text{ km}^2$) cinder cone increases stand susceptibility to prevailing SSE-SSW winter winds. This location, along with its abrupt change in slope, alters wind velocities and direction (Schroeder and Buck 1970), creating eddies that may result in localized patches of greater and lesser disturbance severity (*cf.* Rebertus *et al.* 1997). These conditions help explain the location of the more severely disturbed plots (D and E) at the toe of the cinder cone and the low and moderate severity plots further away from the cinder cone (Plots A-C). Arabas *et al.* (in press) suggest that fire patterns are also influenced by topography and the long wind fetch associated with the surrounding lava flows.

Localized differences in stand structure can also influence how a disturbance alters the landscape. For example, resistance to blowdown can be a function of tree size and local structure (Rebertus *et al.* 1997). Although the blowdown at my site removed trees from all size classes, smaller trees were most susceptible to windthrow in dense stands, and taller trees were most susceptible in open portions of the stand. In dense areas, blowdown accelerates thinning during competitive stem exclusion (*sensu* Oliver 1978) common among young lodgepole pine stands. This process increases resource availability, tree growth, and structural heterogeneity. In gap-patch conditions, preferential blowdown of the tallest stems reduces stand structure

complexity, returning it to a size structure more similar to an earlier developmental stage.

Post-windthrow stand conditions may also reflect antecedent mortality during the stem exclusion (thinning) process or weakening of large trees by mountain pine beetle (*Dendroctonus ponderosae*). Beetle galleries are common in the study area on blown-down logs and remaining snags. The timing of beetle infestation is uncertain, but the presence of windsnapped boles (~65% of blowdown) indicates many of the trees were alive at the time of the blowdown. In either case, beetle kill, a common type of disturbance in these forests (Geiszler *et al.* 1980, Gara *et al.* 1985), may have increased wind disturbance susceptibility in the stand by either weakening trees or increasing large-tree susceptibility by decreasing stand densities.

Coarse-textured, weakly-structured soils also play a role in windthrow susceptibility. The coarse-textured pumice soils of south central Oregon impede root growth and abrade root tissue as the bole moves with the wind, resulting in a shallow, weakened root system consisting solely or primarily of lateral roots (Cochran 1985). The lack of a tap root and vertical rooting in general makes lodgepole pine susceptible to windthrow (Minore 1979, Cochran 1985).

Seedling Establishment and Resource Patchiness

The number and spatial pattern of seedlings vary with disturbance severity and post-blowdown stand structure. Greater blowdown severity is positively correlated with seedling regeneration and the proportion of seedlings growing in open conditions (Figure 12). While light availability is necessary for seedling establishment, the *murrayana* variety may require less incident light than the Rocky Mountain variety, allowing it to germinate in the shade of shrub canopy and logs. This finding is consistent with the finding of Stuart *et al.* (1989) that lodgepole pine germination in south central Oregon is primarily limited by moisture rather than shading.

Light availability varies across my study site corresponding to both plot and adjacent forest differences in canopy cover, canopy structure, and canopy height. My least and moderately disturbed plots (A and B) consist of small to large (<~6 m diameter) treefall gaps or are bordered by dense forest in all but the SW quadrant (Plot C). Fifty-eight percent of Plot C lacks direct canopy cover, but has only a small area of contiguous, open seedling habitat because of shading by neighboring trees. Only thirteen trees covering 8% of my highly disturbed plot (E) survived the blowdown, resulting in high light availability. Plots A (closed canopy) and D (open canopy) are less influenced by adjacent canopy conditions. The orientation of the blown-down logs in Plots C, D, and E also affects light and microhabitat availability at the forest floor, with low light penetration occurring in the stacked and crossed logs of Plot C

and higher light penetration associated with the orderly, near parallel log pattern in Plot E (Figure 16).

Moisture is the limiting resource in High Pumice Plateau forests (Franklin and Dyrness 1988) and, as in other arid and semi-arid environments, may be offset by the shading and moisture retention provided by nurse plants and objects. This also appears to be true at Lava Cast Forest where >80% of seedlings are associated with a nurse plant or object. The highly clustered seedling patterns at my site suggest preferential seedling germination, survival, and persistence under the influence of nurse objects (*cf.* Lampainen *et al.* 2004).

Both shrub cover and a woody substrate appear to be important factors influencing post-blowdown regeneration. Median shrub diameter is an important factor contributing to seedling germination and survival in all but the most heavily disturbed plot (E). Shrub clustering further increases the functional shrub diameters for facilitation and may explain seedling clustering beyond median shrub diameter values suggested by Callaway and Walker (1997) (Figure 1). These results are consistent with the negative correlation between seedlings and open conditions in the absence of woody litter. Woody litter alone (*i.e.*, in the absence of other nurse objects) also appears to be an important factor contributing to seedling success. Even though lodgepole pine is regarded as a shade-intolerant species that prefers to germinate on mineral soil, my results show that more seedlings grow on woody litter and under shrub and log shade than in the open.

Rescaling Callaway and Walkers' (1997) theoretical facilitation model by substituting percent of total seedlings facilitated for facilitation strength, the degree of multiple associations for canopy size and aggregation of nurse plants, and blowdown severity for disturbance severity reveals similar results between my observations and their theoretical model (Figure 28). With a few notable exceptions, increasing abiotic stress (blowdown severity) corresponds with a greater percentage of facilitated seedlings and a greater degree of multiple associations. Differences in observed versus expected outcomes include the higher number of facilitated seedlings and multiple associations in the least disturbed plot (A) based on its low BSI value. This discrepancy may be explained, in part, by the canopy gap clustering of seedlings where abiotic stress may be greater than expected for a stand maintaining a high (50%) canopy cover (Figure 16 and Table 5). Conversely, the intermediately disturbed plots (C and D) have fewer facilitated seedlings than expected. These results are likely the result of the small number of seedlings (72) present in Plot C where in-plot and neighboring tree shading, and a high log density has resulted in fewer favorable seedling germination sites. The comparatively high density and diversity of shrubs in Plot D may indicate increased soil moisture holding capacities resulting from a slightly more developed A horizon (Table 7) which may compensate for facilitation during years without exceptional moisture stress (*cf.* Youngberg and Dahms 1970). Where the blowdown was most severe (Plot E), the greatest proportion (97%) of seedlings are facilitated and the degree of multiple associations (65%) is more than six times greater than in less-disturbed parts of the stand, supporting the

Figure 28. The relationships between BSI (x axis), the degree of multiple associations (y axis), and the percent of total seedlings facilitated in the five study plots. Seedling totals are shown in parentheses. *denotes the “neutral model” where no facilitation occurs.

assertion that facilitative strength increases with increasing abiotic stress (Callaway and Walker 1997).

My results are similar to those reported in other extreme environments. Recent work with Scots pine (*Pinus sylvestris*) in semi-arid southern Spain shows germination success and seedling survival beyond the first growing season are higher under nurse shrubs (Castro *et al.* 2004). In a related study in the same region, experimental reforestation of eleven species of seedlings under sixteen species of nurse shrubs shows that, while the strength of the facilitative relationship varies with species, aspect and elevation, and interannual climate variability, facilitation improved seedling survival in 75% of all experimental treatments (Gomez-Aparicio *et al.* 2004).

Kitzberger *et al.* (2000) found interannual climate variation in Patagonia alters the need for nurse plant and object facilitators and increases the importance of nurse plant-facilitated germination under more stressful environmental conditions. The presence of seedlings both with and without nurse associates at Lava Cast Forest may also implicate the role of annual to decadal climate variability. Lacking seedling germination and mortality data for multiple years, including a variety of growing-season conditions from mesic to dry, the relative reliance on nurse plants and objects cannot be quantified. Nonetheless, my results suggest that disturbance-induced changes in forest canopy can elicit facilitative roles similar to the temperature and soil moisture conditions evoked by interannual climate variation.

The increased ambient temperatures in the severe blowdown plots indicate higher levels of incident radiation and higher albedo that can create extreme

environmental conditions that may jeopardize seedling survival. Although these conditions are mitigated by nurse object shading, ground-level temperatures at Lava Cast Forest exceeded ambient, within shrub canopy, and belowground temperatures. These high temperatures in shaded areas suggest increased moisture availability is more important than temperature amelioration for seedlings growing under nurse objects. Consequently, woody litter and leaf litter accumulation under nurse object canopies appears to provide an effectively more moist environment than the surrounding mineral soil.

The water holding capacity of woody litter at Lava Cast Forest is as much as eight times that of pumice soil. This fact appears to explain first, why >68% of shrubs and up to ~90% of all seedlings encountered in my five sample plots grow on woody litter and second, the linear patterns of trees, saplings, seedlings, and shrubs underlain by decomposed logs (Figure 29). This positive spatial correlation supports the assertion that woody litter is a primary facilitator for all woody vegetation in the stand (Figure 30) and may play a role in the emerging spatial pattern of stand recovery.

A shortcoming of the GIS maps is the exclusion of woody litter not associated with a distinct log shape, possibly accounting for the apparent discrepancy between the positions of the decomposed logs and the woody vegetation. Nonetheless, if lodgepole pine is a topo-edaphic climax at Lava Cast Forest as the literature suggests (Franklin and Dyrness 1988), then initial environmental conditions appear too severe for other species (*i.e.*, ponderosa pine) to dominate. Under such limiting conditions, increased facilitation is predicted. Preferential seedling survival and persistence near

Figure 29. Shrubs and seedlings growing on decomposed logs in Lava Cast Forest. Linear patterns of trees may be the result of establishment along decomposed logs (arrows).

Figure 30. Disturbance and regeneration in self-replacing lodgepole pine on the High Pumice Plateau revised to include nurse plant and object facilitation (dashed circles and lines) (derived from Geiszler *et al.* 1980 and Gara *et al.* 1985).

nurse plants and objects may also affect stand structure by reinforcing linear patterns and open stand conditions (Figure 29).

Shrubs may offer more than structural benefits. Because leaf litter collects under shrub canopy, soil fertility is likely improved in this microhabitat. Wei and Kimmins (1998) work in a sub-boreal lodgepole pine forest in central interior British Columbia found that the greatest rates of asymbiotic nitrogen fixation occur in belowground decomposing organic material, followed in decreasing order by woody litter, leaf litter, and mineral soil, with rates in belowground organics over two hundred times greater than in mineral soil. Fungal associates may provide additional benefits. Carrillo-Garcia and colleagues (1999) found that “islands” of organic material under plants in the Sonoran Desert host mycorrhizal fungi. If shrubs at Lava Cast Forest host species of mycorrhizal fungi that form associations with lodgepole pine, then seedlings sited under shrub canopy may have the benefit of earlier inoculation and thereby greater access to moisture and nutrients.

Researchers have found that competition for resources between the nursed individual and its associate may result in reduced growth relative to seedlings grown without the aid of a nurse plant (Callaway *et al.* 1991, Castro *et al.* 2004), depending on the position of the seedling relative to the nurse plant canopy (Moro *et al.* 1997). The pattern at Lava Cast Forest is not straightforward. In two of the low to moderate blowdown plots, the independent-growing seedlings, those with no association with a nurse plant or object, show greater development. In the two severe blowdown plots, seedlings growing on woody litter are the most developed. The final moderate-

blowdown plot has the most developed seedlings growing under shrub and log shade. These results suggest seedlings growing on woody litter have the benefit of increased moisture availability, without sharing rhizospheres with a nurse plant, but they have an increased risk of desiccation from exposure. Belowground competition for resources, however, may affect even those seedlings not growing under shrub canopy. Seedlings growing under shrubs have the benefit of reduced ambient temperature and exposure during the day and protection from frost heaving at night. Although the spatial patterns identified here are strongly suggestive, determining the specific role of these factors will require controlled, *in situ* growth experiments.

Seedling Regeneration and Succession

Succession is the process by which the structural complexity of a stand increases with time, often involving stand-altering disturbances and shifts in species dominance. Heterogeneity of stand structure varies with the interplay of resource availability, interplant interactions, and disturbance stochasticity. Multiple successional pathways may be theoretically possible for a given stand (Cattellino *et al.* 1979), with the current structural incarnation a result of past disturbance-mediated succession (*e.g.*, Weber *et al.* 2006). The composition of the seedling and sapling cohorts indicates the future successional direction of the stand.

Disturbance in general and blowdown in particular can lead to immediate changes in the successional trajectory of lodgepole pine forests. Veblen *et al.* (1989),

for example, found that blowdown accelerates succession in the Colorado Front Range by enabling the release of shade-tolerant, sub-canopy fir and spruce trees more than the establishment of new shade-intolerant lodgepole pine seedlings. In the self-replacing lodgepole pine at Lava Cast Forest, blowdown initiated new seedling establishment rather than triggering sub-canopy tree release. Only 33 trees recorded growth releases after 1982, 19 in the 1980s and 14 in the 1990s. More than 90% of the 1990s releases occurred in a single plot (C), suggesting a response to a localized, high-severity disturbance. With the exception of this plot which is densely treed and surrounded by dense structure, the majority of the stand has a gap-patch structure, and light availability is not limiting. In the absence of increased moisture availability during the growing season, the additional light resources freed by the blowdown may not significantly alter growth rates. Unlike *P. contorta* var. *latifolia* whose serotinous cones require fire to release their seeds, the *murrayana* variety have >90% non-serotinous cones and produce ample seed annually to biannually, so seed availability does not hamper new seedling establishment (Sudworth 1908, Minore 1979).

The lodgepole pine forests of south central Oregon are generally considered a topo-edaphic climax (Franklin and Dyrness 1988) that developed following the regional deposition of Mount Mazama pumice and ash. Munger (1914), however, postulated that anthropogenic alteration to natural disturbance regimes, primarily increased frequency of burning, caused encroachment of lodgepole pine into historically ponderosa pine-dominated landscapes. Evidence in the form of post-fire biological legacies such as decomposed logs may support the mechanism of Munger's

assertion. Fire-scarred trees and snags on the kipukas and surrounding landscape at Lava Cast Forest recorded the most recent high-severity fires at the study site in 1883 and 1918 (Arabas *et al.* in press). Some of the decomposed logs in the stand have charred bases, supporting the assertion that they are relics of the last local stand-replacing fire. Many of these decomposed logs are larger (*i.e.*, wider) than expected for lodgepole pine, suggesting that the study area may have supported many more ponderosa pine before the last stand-replacing fire, a condition consistent with Munger's historical description (1914) of local forests. The replacement of ponderosa pine by lodgepole pine would suggest a fundamental, long-term shift in forest conditions following Euro-American settlement coinciding with the end of the Little Ice Age climate period and a shift in local fire regimes (Arabas *et al.* in press).

The 1918 stand-replacing fire at Lava Cast Forest represented a major departure from the native disturbance regime in both severity and magnitude (Arabas *et al.* in press). Evidence in the width of post-fire decomposed logs suggests that the self-replacing lodgepole pine area may have contained more ponderosa pine before the 1918 fire. These ponderosa pine would have established during the more mesic Little Ice Age, and, once established, produced taproots to access moisture and resources in buried soils under the pumice, enabling their continued persistence in the increasingly xeric climate. After the 1918 fire removed the majority of the stand, however, environmental conditions may have prevented ponderosa pine germination. Currently, the vast majority of stems in the canopy, sub-canopy and sapling/seedling layers of the stand are lodgepole pine. With the trend toward a warmer, drier central Oregon as

global climates change (Pohl *et al.* 2002), the question of whether ponderosa pine can return to the stand remains in doubt.

Chapter 7

CONCLUSIONS

Facilitation in Extreme Environments

This study reveals a range of seedling regeneration patterns following blowdown in a self-replacing stand of lodgepole pine in central Oregon. These patterns generally correspond to local differences in blowdown severity and post-blowdown stand structure. Where the disturbance was most severe, removing one quarter of the canopy, the smallest percentage of seedlings (3%) grow without the assistance of nurse plants or objects. Woody debris derived from decomposed logs and shade provided by shrubs and sound logs appear to mitigate the droughty nature of the pumice soils by increasing the amount and persistence of moisture available for seedling germination and survival.

This research highlights the importance of scale-dependent processes. Major disturbance agents such as fire and blowdown can alter stand structure at a variety of spatial scales. Post-disturbance recovery in the form of seedling establishment, however, happens at the microscale with the microhabitat provided by nurse shrubs, logs, and woody litter. In this way, the fate of the landscape relies on how local biotic and abiotic conditions interact to make safe sites for seedling germination. This result has important management implications, suggesting that post-fire salvage logging may

have a negative impact on the long-term regeneration potential of this and other environmentally stressed systems.

The Interplay of Disturbance and Succession

Local blowdown severity is a function of stand structure, removing the smallest trees in denser areas and the largest trees where densities are low. Removal of smaller stems in high-density areas hastens competitive thinning and accelerates stand development; where the largest trees are removed, structural complexity and mountain pine beetle habitat are reduced. In this way, blowdown can alter stand development bi-directionally.

A disturbance event changes the availability of resources, affects stand development and succession, and can increase landscape heterogeneity as it propagates with mixed severity across the landscape. Integral to the effective management of a forest is the knowledge of its natural history of succession and disturbance. We must understand the successional pathways that determine what species dominate the system and how stochastic processes can influence those pathways at a variety of scales. The native disturbance regime under which a plant community evolves tends to reinforce community structure. A significant stochastic or anthropogenic departure from the background disturbance regime may cause the system to cross a threshold from which a return to previous community composition and structure may not be possible.

Methodological Considerations

The interpretation of process from pattern plays a fundamental role in the development of biogeography (*e.g.*, Wallace 1911), ecological principles (*e.g.*, Cowles 1899), and landscape ecology (*e.g.*, Turner *et al.* 2001). It is also fraught with the challenges inherent in spatial autocorrelation and the correct interpretation of complex processes (*e.g.*, Schumm 1991). While these challenges do not invalidate robust and statistically significant results, they do justify additional explanation and suggestions for future research. These are often derived from field observations that provide great insight into processes, but cannot necessarily be included in the results of a study because they lack methodological rigor. Below I address several of these considerations as part of my conclusions to this study. The topics include seed dispersal, sampling artifact, and seedling dating.

The proportion of seedlings growing under shrubs and near logs at Lava Cast Forest may be affected by seed rafting. During thunderstorms, precipitation inputs can exceed infiltration rates, causing overland flow to redistribute organic material (Karps, personal observation). Herbaceous and woody stems and coarse woody debris (*i.e.*, snags and logs) reduce water velocity, intercepting and collecting rafted litter, and potentially redistributing seeds.

The large number of seedlings growing in tight groupings (*i.e.*, apparently multiple seeds from the same cone germinated) in some plots artificially inflates predictions of seedling recruitment into larger size classes in those locations. The

likelihood of more than one seedling surviving at one location is low, and the increased pressure on grouped seedlings from competitive interactions may decrease the likelihood that any of the stems will survive. The exclusion of these grouped seedlings from the total number of seedlings at each plot does not alter the correlation between blowdown severity and number of seedlings, but it does change the proportion of seedlings growing in particular microhabitats. Under less-disturbed conditions at Plot B, the proportions of seedlings growing with no associate and growing on woody litter were inflated by 5% and 8%, and the number of seedlings under shrubs was under-reported by 14%. Seedlings growing with no associate were also inflated (10%) at the highly disturbed Plot D, while seedlings on woody litter (7%) and under shrubs (1%) were under-reported. The number of seedlings growing with no associate changes from 29% to 19%.

The inability to age seedlings and shrubs may result in artificial inflation of the number of seedlings facilitated by shrubs. The assumption that all seedlings under shrub canopy are facilitated by that shrub is based on relative shrub and seedling sizes; however, the shrub must be older than the seedlings it facilitates to function as a nurse plant. My field notes suggest <1% of seedlings may be older than their shrub associates based on large size differences. Demonstration of this requires an accurate, non-destructive assessment of seedling and shrub ages.

Future studies of this nature should address the aforementioned methodological concerns. The application of controlled field experiments within a research strategy can reduce or remove bias, providing important, albeit limited, insights. Experimental

planting (*e.g.* Gomez-Aparicio *et al.* 2004) treatments that eliminate errors of seed accumulation, sampling artifact, and seedling dating, and should be employed.

Although methodological concerns limit the scope of these findings, they raise important questions about the lodgepole pine zone in central Oregon. In light of global climate change, increasing aridity may alter community dynamics in many systems, especially those, like the High Pumice Plateau, where abiotic stress is already a limiting factor. Understanding how facilitation mitigates environmental extremes may aid efforts to preserve ecosystem types in a warming world.

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APPENDIX A

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for tree height.

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	53	102.07
B	34	135.46
C	134	136.56
D	16	97.03
E	13	116.08
χ^2	d.f.	p
12.043	4	0.017

Mann-Whitney (M-W) U Tests for tree height.

Plot	N	Mean Rank	Σ Ranks
A	53	39.68	2103
B	34	50.74	1725
M-W U	Z	p (2 tailed)	
672	-1.992	0.046	

Plot	N	Mean Rank	Σ Ranks
A	53	74.71	3959.5
C	134	101.63	13618.5
M-W U	Z	p (2 tailed)	
2528.5	-3.065	0.002	

Plot	N	Mean Rank	Σ Ranks
A	53	35.34	1873
D	16	33.88	542
M-W U	Z	p (2 tailed)	
406	-0.256	0.798	

Plot	N	Mean Rank	Σ Ranks
A	53	33.34	1767
E	13	34.15	444
M-W U	Z	p (2 tailed)	
336	-0.137	0.891	

Plot	N	Mean Rank	Σ Ranks
B	34	84.09	2859
C	134	84.6	11337
M-W U	Z	p (2 tailed)	
2264	-0.055	0.956	

Plot	N	Mean Rank	Σ Ranks
B	34	28.01	952.5
D	16	20.16	322.5
M-W U	Z	p (2 tailed)	
186.5	-1.778	0.075	

Plot	N	Mean Rank	Σ Ranks
B	34	25.12	854
E	13	21.08	274
M-W U	Z	p (2 tailed)	
183	-0.904	0.336	

Plot	N	Mean Rank	Σ Ranks
C	134	78.04	10458
D	16	54.19	867
M-W U	Z	p (2 tailed)	
731	-2.076	0.038	

Plot	N	Mean Rank	Σ Ranks
C	134	74.78	10021
E	13	66	858
M-W U	Z	p (2 tailed)	
767	-0.710	0.478	

Plot	N	Mean Rank	Σ Ranks
D	16	14.31	229
E	13	15.85	206
M-W U	Z	p (2 tailed)	
93	-0.482	0.630	

APPENDIX B

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for tree canopy height.

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	53	157.85
B	34	45.56
C	134	140.52
D	16	38.38
E	13	155.08
χ^2	d.f.	p
83.343	4	<0.001

Mann-Whitney (M-W) U Tests for tree canopy height.

Plot	N	Mean Rank	Σ Ranks
A	53	58.42	3096
B	34	21.53	732
M-W U Z p (2 tailed)			
137	-6.646	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	53	104.49	5538
C	134	89.85	12040
M-W U Z p (2 tailed)			
2995	-1.667	0.096	

Plot	N	Mean Rank	Σ Ranks
A	53	42.25	2239
D	16	11	176
M-W U Z p (2 tailed)			
40	-5.46	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	52	33.7	1786
E	13	32.69	425
M-W U Z p (2 tailed)			
334	-0.169	0.866	

Plot	N	Mean Rank	Σ Ranks
B	34	32.51	1105.5
C	134	97.69	13090.5
M-W U Z p (2 tailed)			
510.5	-6.978	<0.001	

Plot	N	Mean Rank	Σ Ranks
B	34	25.57	869.5
D	16	25.34	405.5
M-W U Z p (2 tailed)			
269.5	-0.052	0.959	

Plot	N	Mean Rank	Σ Ranks
B	34	18.44	627
E	13	38.54	501
M-W U Z p (2 tailed)			
32	-4.495	<0.001	

Plot	N	Mean Rank	Σ Ranks
C	134	82.32	11031.5
D	16	18.34	293.5
M-W U Z p (2 tailed)			
157.5	-5.568	<0.001	

Plot	N	Mean Rank	Σ Ranks
C	134	73.16	9803
E	13	82.69	1075
M-W U Z p (2 tailed)			
758	-0.771	0.441	

Plot	N	Mean Rank	Σ Ranks
D	16	9.19	147
E	13	22.15	288
M-W U Z p (2 tailed)			
11	-4.078	<0.001	

APPENDIX C

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for tree basal area (*i.e.*, diameter).

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	53	116.74
B	34	151.76
C	134	120.76
D	16	125.03
E	13	141.96
<hr/>		
χ^2	d.f.	p
6.526	4	0.163

Mann-Whitney (M-W) U Tests for tree basal area (*i.e.*, diameter).

Plot	N	Mean Rank	Σ Ranks
A	53	40.31	2136.5
B	34	49.75	1691.5
M-W U	Z	p (2 tailed)	
705.5	-1.701	0.089	

Plot	N	Mean Rank	Σ Ranks
A	53	90.49	4796
C	134	95.39	12782
M-W U	Z	p (2 tailed)	
3365	-0.558	0.557	

Plot	N	Mean Rank	Σ Ranks
A	53	34.55	1831
D	16	36.5	584
M-W U	Z	p (2 tailed)	
400	-0.341	0.733	

Plot	N	Mean Rank	Σ Ranks
A	53	32.39	1716.5
E	13	38.04	494.5
M-W U	Z	p (2 tailed)	
285.5	-0.951	0.341	

Plot	N	Mean Rank	Σ Ranks
B	34	103.21	3509
C	134	79.75	10687
M-W U	Z	p (2 tailed)	
1642	-2.516	0.012	

Plot	N	Mean Rank	Σ Ranks
B	34	27.19	924.5
D	16	21.91	350.5
M-W U	Z	p (2 tailed)	
214.5	-1.199	0.231	

Plot	N	Mean Rank	Σ Ranks
B	34	24.12	820
E	13	23.69	308
M-W U	Z	p (2 tailed)	
217	-0.095	0.924	

Plot	N	Mean Rank	Σ Ranks
C	134	75.26	10085
D	16	77.5	1240
M-W U	Z	p (2 tailed)	
1040	-0.195	0.845	

Plot	N	Mean Rank	Σ Ranks
C	134	72.86	9763
E	13	85.77	1115
M-W U	Z	p (2 tailed)	
718	-1.046	0.295	

Plot	N	Mean Rank	Σ Ranks
D	16	14.63	234
E	13	15.46	201
M-W U	Z	p (2 tailed)	
98	-0.263	0.792	

APPENDIX D

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for tree age.

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	53	53.2
B	34	71.09
C	134	172.88
D	16	96.66
E	13	109.69
χ^2	d.f.	p
133.036	4	<0.001

Mann-Whitney (M-W) U Tests for tree age.

Plot	N	Mean Rank	Σ Ranks
A	53	38.69	2050.5
B	34	52.28	1777.5
M-W U Z p (2 tailed)			
619.5	-2.451	0.014	

Plot	N	Mean Rank	Σ Ranks
A	53	34.84	1846.5
C	134	117.4	15731.5
M-W U Z p (2 tailed)			
415.5	-9.407	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	53	30.57	1620
D	16	49.69	795
M-W U Z p (2 tailed)			
189	-3.345	0.001	

Plot	N	Mean Rank	Σ Ranks
A	53	30.1	1595.5
E	13	47.35	615.5
M-W U Z p (2 tailed)			
164.5	-2.905	0.004	

Plot	N	Mean Rank	Σ Ranks
B	34	28	952
C	134	98.84	13244
M-W U Z p (2 tailed)			
357	-7.591	<0.001	

Plot	N	Mean Rank	Σ Ranks
B	34	22.57	767.5
D	16	31.72	507.5
M-W U Z p (2 tailed)			
172.5	-2.072	0.038	

Plot	N	Mean Rank	Σ Ranks
B	34	20.74	705
E	13	32.54	423
M-W U Z p (2 tailed)			
110	-2.644	0.008	

Plot	N	Mean Rank	Σ Ranks
C	134	81.26	10889.5
D	16	27.22	435.5
M-W U Z p (2 tailed)			
299.5	-4.709	<0.001	

Plot	N	Mean Rank	Σ Ranks
C	134	77.88	10436
E	13	34	442
M-W U Z p (2 tailed)			
351	-3.553	<0.001	

Plot	N	Mean Rank	Σ Ranks
D	16	13.53	216.5
E	13	16.81	218.5
M-W U Z p (2 tailed)			
80.5	-1.033	0.302	

APPENDIX E

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for pre-blowdown tree basal area (*i.e.*, diameter).

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	54	163.61
B	43	226.94
C	191	156.60
D	41	218.67
E	36	259.01
<hr/>		
χ^2	d.f.	p
44.68	4	<0.001

Mann-Whitney (M-W) U Tests for pre-blowdown tree basal area (*i.e.*, diameter).

Plot	N	Mean Rank	Σ Ranks
A	54	41.63	2302
B	43	57	2451
M-W U Z p (2 tailed)			
817	-2.499	0.012	

Plot	N	Mean Rank	Σ Ranks
A	54	123.49	6668.5
C	191	122.86	23466.5
M-W U Z p (2 tailed)			
5130.5	-0.058	0.954	

Plot	N	Mean Rank	Σ Ranks
A	54	42.43	2291
D	41	55.34	2269
M-W U Z p (2 tailed)			
806	-2.262	0.024	

Plot	N	Mean Rank	Σ Ranks
A	54	37.56	2028.5
E	36	57.4	2066.5
M-W U Z p (2 tailed)			
543.5	-3.53	<0.001	

Plot	N	Mean Rank	Σ Ranks
B	43	156.07	6711
C	191	108.82	20784
M-W U Z p (2 tailed)			
2448	-4.143	<0.001	

Plot	N	Mean Rank	Σ Ranks
B	43	43.41	1866.5
D	41	41.55	1703.5
M-W U Z p (2 tailed)			
842.5	-0.35	0.727	

Plot	N	Mean Rank	Σ Ranks
B	43	36.47	15.68
E	36	44.27	15.92
M-W U Z p (2 tailed)			
622	-1.498	0.134	

Plot	N	Mean Rank	Σ Ranks
C	191	109.43	20900.5
D	41	149.45	6127.5
M-W U Z p (2 tailed)			
2564.5	-3.471	0.001	

Plot	N	Mean Rank	Σ Ranks
C	191	103.5	19768.5
E	36	169.71	6109.5
M-W U Z p (2 tailed)			
1432.5	-5.558	<0.001	

Plot	N	Mean Rank	Σ Ranks
D	41	35.33	1448.5
E	36	43.18	1554.5
M-W U Z p (2 tailed)			
587.5	-1.538	0.124	

APPENDIX F

Plant species encountered in self-replacing lodgepole pine at Lava Cast Forest.

Trees	
<i>Abies grandis/Abies concolor hybrid</i>	grand fir-white fir hybrid
<i>Pinus contorta</i>	lodgepole pine
<i>Pinus ponderosa</i>	ponderosa pine

Shrubs	
<i>Arctostaphylos patula</i>	green manzanita
<i>Ceanothus velutinus</i>	snowbrush
<i>Chimaphila umbellata</i>	prince's pine
<i>Chrysothamnus viscidiflorus</i>	green rabbitbrush
<i>Holodiscus microphyllis</i>	oceanspray
<i>Pachistima myrsinites</i>	Oregon boxwood
<i>Purshia tridentata</i>	bitterbrush
<i>Ribes cereum</i>	wax currant
<i>Ribes viscosissimum</i>	sticky currant
<i>Symphoricarpos mollis</i>	snowberry

Forbs and Grasses	
<i>Epilobium angustifolium</i>	fireweed
<i>Fragaria virginiana</i>	strawberry
<i>Lupinus aridis</i>	desert lupine
Poaceae	grasses

APPENDIX G

Results of Average Nearest Neighbor tests for seedlings, saplings, trees, and shrubs.

	Plot	N	Observed	Expected	O:E	Z score	p value
Seedlings	A	140	0.52	0.99	0.52	-10.76	0.01
	B	210	0.24	0.81	0.29	-19.61	0.01
	C	72	0.90	1.40	0.64	-5.67	0.01
	D	865	0.20	0.42	0.49	-28.92	0.01
	E	548	0.32	0.52	0.62	-17.10	0.01
Saplings	A	48	1.33	1.47	0.91	-1.20	>0.05
	B	10	1.81	2.13	0.85	-0.99	>0.05
	C	38	1.36	1.74	0.78	-2.57	0.05
	D	9	2.93	2.38	1.23	1.49	>0.05
	E	1					
Trees	A	53	1.63	1.46	1.11	1.56	>0.05
	B	34	1.78	1.76	1.01	0.13	>0.05
	C	134	0.79	1.00	0.79	-4.61	0.01
	D	16	3.24	2.17	1.49	3.76	0.01
	E	13	2.66	2.00	1.33	2.29	0.05
Shrubs	A	97	0.84	1.13	0.74	-4.84	0.01
	B	74	1.13	1.37	0.83	-2.86	0.01
	C	101	0.95	1.11	0.86	-2.71	0.01
	D	242	0.60	0.77	0.78	-6.66	0.01
	E	73	1.17	1.35	0.87	-2.13	0.05

APPENDIX H

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for log-transformed seedling development by plot.

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	140	1188.9
B	210	791.29
C	72	851.57
D	865	834.43
E	548	1037.99
<hr/>		
χ^2	d.f.	p
99.625	4	<0.001

Mann-Whitney (M-W) U Tests for log-transformed seedling development by plot.

Plot	N	Mean Rank	Σ Ranks
A	140	214.86	30081
B	210	149.26	31344
M-W U Z p (2 tailed)			
9189	-5.958	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	140	117.74	16483
C	72	84.65	6095
M-W U Z p (2 tailed)			
3467	-3.721	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	140	663.76	92926
D	865	476.98	412589
M-W U Z p (2 tailed)			
38044	-7.080	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	140	404.05	56566.5
E	548	329.29	180449.5
M-W U Z p (2 tailed)			
30023.5	-3.973	<0.001	

Plot	N	Mean Rank	Σ Ranks
B	210	140.09	29418.5
C	72	145.62	10484.5
M-W U Z p (2 tailed)			
7263.5	-0.499	0.618	

Plot	N	Mean Rank	Σ Ranks
B	210	508.11	106702.5
D	865	545.26	47647.48
M-W U Z p (2 tailed)			
84547.5	-1.562	0.118	

Plot	N	Mean Rank	Σ Ranks
B	210	310.34	65171.5
E	548	406	222489.51
M-W U Z p (2 tailed)			
43016.5	-5.387	<0.001	

Plot	N	Mean Rank	Σ Ranks
C	72	467.23	33640.5
D	865	469.15	405812.5
M-W U Z p (2 tailed)			
31012.5	-0.058	0.954	

Plot	N	Mean Rank	Σ Ranks
C	72	263.57	18977
E	548	316.67	173532.99
M-W U Z p (2 tailed)			
16349	-2.366	0.018	

Plot	N	Mean Rank	Σ Ranks
D	865	642.04	555364.48
E	548	809.54	443626.5
M-W U Z p (2 tailed)			
180819.5	-7.528	<0.001	

APPENDIX I

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for log-transformed seedling development by microhabitat type.

Kruskal-Wallis Test		
MH Type	N	Mean Rank
on woody material	967	1311.7
under shrub	601	1203.37
under/adj. to log	456	1206.54
no associate	360	836.37
χ^2	d.f.	p
125.936	3	<0.001

Mann-Whitney (M-W) U Tests for log-transformed seedling development by microhabitat (MH) type (WM=on woody material, SH=under shrub, LOG=under/adjacent to log, and NA=no associate).

MH	N	Mean Rank	Σ Ranks
WM	967	811.56	784781.53
SH	601	740.96	445314.52
M-W U	Z	p (2 tailed)	
264413.5	-3.004	0.003	

MH	N	Mean Rank	Σ Ranks
WM	967	735.36	711097
LOG	456	662.45	302078.99
M-W U	Z	p (2 tailed)	
197883	-3.125	0.002	

MH	N	Mean Rank	Σ Ranks
WM	967	732.77	708592.98
NA	360	479.26	172535
M-W U	Z	p (2 tailed)	
107555	-10.732	<0.001	

MH	N	Mean Rank	Σ Ranks
SH	601	527.14	316813.5
LOG	456	531.45	242339.51
M-W U	Z	p (2 tailed)	
135912.5	-0.227	0.820	

MH	N	Mean Rank	Σ Ranks
SH	601	537.27	322901.48
NA	360	387.05	139339.5
M-W U	Z	p (2 tailed)	
74359.5	-8.145	<0.001	

MH	N	Mean Rank	Σ Ranks
LOG	456	469.64	214156.5
NA	360	331.05	119179.5
M-W U	Z	p (2 tailed)	
54199.5	-8.363	<0.001	

APPENDIX J

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for ambient growing season temperatures by plot.

Kruskal-Wallis Test		
Plot	N	Mean Rank
A	2042	4885.35
B	2042	4994.25
C	2042	5030.41
D	2042	5329.17
E	2042	5288.27
χ^2	d.f.	p
35.246	4	<0.001

Mann-Whitney (M-W) U Tests for ambient growing season temperatures by plot.

Plot	N	Mean Rank	Σ Ranks
A	2042	2020.5	4125853
B	2042	2064.5	4215717
M-W U	Z	p (2 tailed)	
2039950	-1.193	0.233	

Plot	N	Mean Rank	Σ Ranks
A	2042	2013.48	4111523
C	2042	2071.52	4230046
M-W U	Z	p (2 tailed)	
202562	-1.573	0.116	
1			

Plot	N	Mean Rank	Σ Ranks
A	2042	1953.81	3989684
D	2042	2131.19	4351885
M-W U	Z	p (2 tailed)	
1903782	-4.808	<0.001	

Plot	N	Mean Rank	Σ Ranks
A	2042	1962.07	4006541
E	2042	2122.93	4335029
M-W U	Z	p (2 tailed)	
192063	-4.36	<0.001	
8			

Plot	N	Mean Rank	Σ Ranks
B	2042	2035.09	4155660
C	2042	2049.91	4185910
M-W U	Z	p (2 tailed)	
2069758	-0.401	0.688	

Plot	N	Mean Rank	Σ Ranks
B	2042	1975.38	4033723
D	2042	2109.62	4307847
M-W U	Z	p (2 tailed)	
194782	-3.638	<0.001	
0			

Plot	N	Mean Rank	Σ Ranks
B	2042	1983.78	4050889
E	2042	2101.22	4290682
M-W U	Z	p (2 tailed)	
1964986	-3.183	0.001	

Plot	N	Mean Rank	Σ Ranks
C	2042	1982.21	4047683
D	2042	2102.78	4293887
M-W U	Z	p (2 tailed)	
196178	-3.268	0.001	
0			

Plot	N	Mean Rank	Σ Ranks
C	2042	1991.28	4066195
E	2042	2093.72	4275376
M-W U	Z	p (2 tailed)	
1980292	-2.775	0.005	

Plot	N	Mean Rank	Σ Ranks
D	2042	2050.08	4186269
E	2042	2034.92	4155302
M-W U	Z	p (2 tailed)	
206939	-0.411	0.681	
9			

APPENDIX K

Results of Kruskal-Wallis and Mann-Whitney rank-sum tests for daily high growing season temperatures by microhabitat at one moderate blowdown (B) and one extreme blowdown (D) plot.

Kruskal-Wallis Test		
Microhabitat	N	Mean Rank
Ambient (Plot B)	111	347.51
Ambient (Plot D)	111	358.22
Shrub (Plot B)	58	365.38
Shrub (Plot D)	111	322.82
Ground (Plot B)	111	511.21
Ground (Plot D)	111	383.48
Buried (Plot D)	111	250.25
χ^2	d.f.	p
93.871	6	<0.001

Mann-Whitney (M-W) U Tests for daily high growing season temperatures by microhabitat at one moderate blowdown (B) and one extreme blowdown (D) plot. Microhabitat and plot abbreviations follow: Ambient=AM, Shrub=SH, Ground=GR, Buried=BU, Plot B=1, and Plot D=2.

Plot	N	Mean Rank	Σ Ranks
AM1	111	109.83	12191
AM2	111	113.17	12562
M-W U	Z	p (2 tailed)	
5975	-0.388	0.698	

Plot	N	Mean Rank	Σ Ranks
AM1	111	83.61	9281
SH1	58	87.66	5084
M-W U	Z	p (2 tailed)	
3065	-0.51	0.61	

Plot	N	Mean Rank	Σ Ranks
AM1	111	115.43	12813
SH2	111	107.57	11940
M-W U	Z	p (2 tailed)	
5724	-0.913	0.361	

Plot	N	Mean Rank	Σ Ranks
AM1	111	85.93	9538
GR1	111	137.07	15215
M-W U	Z	p (2 tailed)	
3322	-5.933	<0.001	

Plot	N	Mean Rank	Σ Ranks
AM1	111	105.93	11758.5
GR2	111	117.07	12994.5
M-W U	Z	p (2 tailed)	
5542.5	-1.292	0.196	

Plot	N	Mean Rank	Σ Ranks
AM1	111	126.78	14072.5
BU2	111	96.22	10680.5
M-W U	Z	p (2 tailed)	
4464.5	-3.545	<0.001	

Plot	N	Mean Rank	Σ Ranks
AM2	111	84.72	9403.5
SH1	58	85.54	4961.5
M-W U	Z	p (2 tailed)	
3187.5	-0.104	0.917	

Plot	N	Mean Rank	Σ Ranks
AM2	111	117.81	13077
SH2	111	105.19	11676
M-W U	Z	p (2 tailed)	
5460	-1.465	0.143	

Plot	N	Mean Rank	Σ Ranks
AM2	111	86.33	9582.5
GR1	111	136.67	15170.5
M-W U	Z	p (2 tailed)	
3366.5	-5.84	<0.001	

Plot	N	Mean Rank	Σ Ranks
AM2	111	106.79	11854
GR2	111	116.21	12899
M-W U	Z	p (2 tailed)	
5638	-1.092	0.275	

Plot	N	Mean Rank	Σ Ranks
AM2	111	129.4	14363.5
BU2	111	93.6	10389.5
M-W U Z p (2 tailed)			
4173.5	-4.154	<0.001	

Plot	N	Mean Rank	Σ Ranks
SH1	58	92.37	5357.5
SH2	111	81.15	9007.5
M-W U Z p (2 tailed)			
2791.5	-1.416	0.157	

Plot	N	Mean Rank	Σ Ranks
SH1	58	59.56	3454.5
GR1	111	98.29	10910.5
M-W U Z p (2 tailed)			
1743.5	-4.887	<0.001	

Plot	N	Mean Rank	Σ Ranks
SH1	58	80.75	4683.5
GR2	111	87.22	9681.5
M-W U Z p (2 tailed)			
2972.5	-0.817	0.414	

Plot	N	Mean Rank	Σ Ranks
SH1	58	107	6206
BU1	111	73.5	8159
M-W U Z p (2 tailed)			
1943	-4.227	<0.001	

Plot	N	Mean Rank	Σ Ranks
SH2	111	82.57	9165
GR1	111	140.43	15588
M-W U Z p (2 tailed)			
2949	-6.713	<0.001	

Plot	N	Mean Rank	Σ Ranks
SH2	111	101.33	11248
GR2	111	121.67	13505
M-W U Z p (2 tailed)			
5032	-2.359	0.018	

Plot	N	Mean Rank	Σ Ranks
SH2	111	125.01	13876
BU2	111	97.99	10877
M-W U Z p (2 tailed)			
4661	-3.135	0.002	

Plot	N	Mean Rank	Σ Ranks
GR1	111	133.27	14793.5
GR2	111	89.73	9959.5
M-W U Z p (2 tailed)			
3743.5	-5.052	<0.001	

Plot	N	Mean Rank	Σ Ranks
GR1	111	145.47	16147
BU2	111	77.53	8606
M-W U Z p (2 tailed)			
2390	-7.881	<0.001	

Plot	N	Mean Rank	Σ Ranks
GR2	111	131.59	14607
BU2	111	91.41	10146
M-W U Z p (2 tailed)			
3930	-4.662	<0.001	