ABSTRACT

Title of Document:	THE ATTACK DYNAMICS AND ECOSYSTEM CONSEQUENCES OF STEM BORER HERBIVORY ON SITKA WILLOW AT MOUNT ST. HELENS
	Christian Che-Castaldo, Doctor of Philosophy, 2014
Directed By:	Dr. William Fagan, Department of Biology

Variation in plant quality across space and time is considered a driving force behind the heterogeneous distribution of herbivorous insects on their host plants. At the same time, herbivory itself can mediate ecosystem processes that can cause feedbacks directly affecting plant quality. Here I examine both of these processes in a primary successional system to ask how insect herbivory can shape successional outcomes. I performed a three year observational study to determine which host plant factors - stress, vigor, and sex - were associated with insect herbivory by the poplar willow weevil (*Cryptorynchus lapathi*) on Sitka willow (*Salix sitchensis*), a dioecious pioneer shrub recolonizing Mount St. Helens after the 1980 eruption. I found that weevils prefer or perform best on vigorously growing willows that are seasonally water stressed. This result highlights the need to integrate hypotheses regarding insect response to stress and vigor into a single phenologically based framework focusing on nutrient mobilization to early insect herbivore life stages. I performed a field experiment involving leaf litter from stems attacked and not by weevils to determine whether weevils mediate nutrient cycling by altering willow leaf litter quality or resources available in its root environment. I found that although weevils do not consume leaves directly, stem herbivory is associated with a large reduction in leaf phosphorus, which in turn decelerates phosphorus cycling on Mount St. Helens. Lastly, I performed observational and experimental studies to show that the large female bias seen in willow on Mount St. Helens is not caused by weevil herbivory or other late acting ecological factors, but likely result from biased seed sex ratios. Taken together, these results suggest that weevil herbivory is retarding willow colonization in upland areas on Mount St. Helens, possibly allowing for alternative successional trajectories.

THE ATTACK DYNAMICS AND ECOSYSTEM CONSEQUENCES OF STEM BORER HERBIVORY ON SITKA WILLOW AT MOUNT ST. HELENS

CHRISTIAN CHE-CASTALDO

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2014

Advisory Committee:
Dr. William Fagan, Chair
Dr. John Bishop
Dr. Bahram Momen
Dr. Daniel Gruner, Dean's Representative
Dr. Irwin Forseth

PREFACE

All research was conducted in accordance with permits issued by the U.S. Forest Service.

This dissertation was created using the `classicthesis` template developed by André Miede and inspired by Robert Bringhurst's *"The Elements of Typographic Style"*. `classicthesis` is available for both LaTeX and LyX:

`http://code.google.com/p/classicthesis/`

Dedicated to my wife, Judy, and my son, Asa.

ACKNOWLEDGEMENTS

I cannot thank Bill Fagan, John Bishop, and Charlie Crisafulli enough for giving me the chance to learn and grow as a scientist under their watchful eyes. It is very difficult to do many years of intensive fieldwork 2,322 miles from your advisor's lab, and this dissertation would simply not be possible without their continuous support. The other members of my committee, Dan Gruner, Bahram Momen and Irv Forseth, also provided advice that improved the quality of my work.

In the field, I was fortunate to work with a large number of outstanding assistants: Katlyn Williard, Ian Barrows, Anna Wallis, Jessica Nelson, Chris Burgess, Emily Peterson, Melissa Boyd and Matt Warman. Here in Maryland, John Parker at the Smithsonian Environmental Research Center was extremely generous with letting me use his lab to grind things up and figure out how much phosphorus was inside them. At the Patuxent Research Center, Evan Grant, Elise Zipkin, Richard Chandler, Andy Royle, and Jim Nichols fielded endless questions on occupancy models over many years, as did Marc Kéry at the Swiss Ornithological Institute. Thanks to all for your generous assistance.

Special thanks to Greta Park in the Fagan Lab, for cheerfully helping with so much data entry, proofing, and other assorted miscellaneous drudgery.

I owe a huge debt of gratitude to Jim Gawel at the University of Tacoma, Washington, and Jay Halvorson, at the U.S. Dept. of Agriculture's Northern

Great Plains Research Laboratory, for analyzing my resin and soil samples *gratis*. Thank you for your generosity to a graduate student in need.

This work was generously supported by the BEES graduate program and the National Science Foundation LTREB and REU programs.

Throughout this project, I have continuously benefited from the friendship, support, and advice provided by members of the Fagan lab, Bishop lab, and Crisafulli field crews. There are too many people to mention everyone by name, but your friendship, advice, and help kept me sane during those long wet summers.

I would also like to thank my parents, Allan and Stephanie, and my friends, Ray and Starr Yurkewycz, for making making Portland a second home to my wife, Judy, and myself.

Last but not least, I thank Judy for demonstrating extreme patience with this dissertation. Your love and support humbles me.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

1

SEASONAL VARIATION IN THE ROLE OF STRESS AND VIGOR ON STEM-BORER HERBIVORY: RECONCILING CONFLICTING EVIDENCE

ABSTRACT

The plant stress and plant vigor hypotheses are widely used to explain the distribution and abundance of insect herbivore response on their host plants. Although it is recognized that these hypotheses are not strict alternatives, some studies have found simultaneous support for both hypotheses for the same plant-herbivore interaction. In this study, I address the question of how such simultaneous support is possible using dynamic site-occupancy models in Bayesian framework. I quantify the oviposition and larval feeding preferences of the poplar-willow weevil (*Cryptorynchus lapathi* L.) (Curculionidae: Coleoptera) on its dioecious host plant, Sitka willow (*Salix sitchensis* Bong.) (Salicaceae: Malpighiales), on Mount St. Helens, in relation to host plant habitat, sex, and vigor. I determined that weevil larvae respond positively to water stress associated with a seasonal dry-down in upland habitat, which supports the plant stress or pulsed stress hypotheses, and disproportionately to large upland stems in relation to stem surface area available for attack, supporting the plant vigor hypothesis. Weevils also preferred to attack reproductive riparian stems, revealing that weevil herbivory imposes an ecological costs on willow reproduction. Weevils did not respond to host plant sex in a consistent way that could explain the

large female bias in willow populations on Mount St. Helens, although I find evidence of higher inducible defenses in female, as compared to male plants, but only in upland habitat. The metapopulation dynamics of weevil attack shows that colonization of new stems drives herbivory dynamics. Disproportionate attack of large upland stems causes juvenilization of willow plants, and possibly delays establishment of willow dominated upland sere. I propose that the two oviposition windows that occur per generation allow stem-borers to "double-dip", as early larvae feed both as flush and senescent feeders on willow depending on time of year. These results highlight the overlapping nature of the plant stress and plant vigor hypotheses and the need for a single integrative hypothesis that focuses on how stress changes the quality of plant resources available to early instars.

1.1 INTRODUCTION

Variation in plant quality across space and time is considered a driving force behind the heterogeneous distribution of herbivorous insects on their host plant(s) (Louda and Collinge, 1992; Crawley and Akhteruzzaman, 1988; Raupp and Denno, 1983; Schultz, 1983; Whitham and Slobodchikoff, 1981). Plant quality is determined in part by how host plants acquire and allocate resources while under stress (Herms and Mattson, 1992; Bazzaz et al., 1987; Chapin III et al., 1987; Mooney, 1972). Consequently, insect ecologists have largely relied on two hypotheses, the plant stress hypothesis (White, 1993, 1984, 1974, 1969) and plant vigor hypothesis (Price, 1991), to predict how herbivorous insects respond to stress-induced differences in plant quality. The plant vigor and stress hypotheses are considered endpoints on a continuum of herbivore responses to plant stress, but this interpretation is problematic as these hypotheses overlap conceptually. One commonality that is often overlooked is that the plant stress and plant vigor hypotheses are inherently phenology-based explanations for insect outbreaks. Both make phenologically explicit assumptions about the age of the food resource available to the herbivore and the age of the tissue the herbivore normally feeds on. In addition, stress must coincide with the herbivore's most vulnerable life-stages in order to impact herbivore distribution and abundance.

Herbivory in response to host plant vigor and stress

The plant stress hypothesis predicts that herbivorous insect outbreaks should be more likely on stressed plants (White, 1993, 1984, 1974, 1969). This is because herbivorous insects are usually nutrient-limited (Mattson, 1980), and stressed plants exhibit elevated concentrations of nitrogenous compounds, such as amino acids and osmoprotectants, in their leaf and vascular tissues (Brodbeck and Strong, 1987; White, 1984; Aspinall and Paleg, 1981; Kozlowski, 1979; Hsiao, 1973; Levitt, 1972). In this case, stress is defined as a transitory state, different from the norm of what a plant experiences, and fundamentally different from chronic stress associated with persistent resource scarcity (Larsson, 1989). White (2009; 1993; 1984) has repeatedly emphasized that an herbivore's performance on stressed plants depends on the insect's developmental stage and the type of tissue on which it feeds. Both White (2009; 1993; 1984) and Price (1991) distinguish between flush-feeding herbivores, that feed on growing tissues that are resource sinks for nutrients translocated within plants during active plant growth, from senescent-feeding herbivores, that consume senescing tissues that are resource sources for nutrients remobilized within plants at the end of the growing season. White (2009) argues that plant stress would benefit mainly the earliest developmental stages of herbivores that normally feed on senescing plant material, but not flush-feeding herbivores that consume new growth. For many insect species, survivorship for the earliest developmental stage is often the lowest of all life stages, and the inverse relationship between an insect's relative growth rate and ontogeny observed for many species is likely to be an evolved response to minimize time spent in these early vulnerable stages (Zalucki et al., 2002; Scriber and Slansky, 1981). Plant stress, which can prematurely initiate the host's normal physiological program of senescence and temporarily elevates its tissue nitrogen content, facilitates a fast growth strategy for young senescent feeders to escape stage-based mortality (White, 2009, 1993).

Although insect herbivore outbreaks associated with water stress have been observed in natural systems, quantitative analyses and qualitative reviews of experiments testing the plant stress hypothesis have provided inconclusive support (Huberty and Denno, 2004; Koricheva et al., 1998; Watt, 1994; Larsson, 1989; Brodbeck and Strong, 1987; Mattson and Haack, 1987; Waring and Pitman, 1985; White, 1969). This disconnect has led to criticism and refinements of this hypothesis based on the recognition that (1) for any given stressor, plants have multiple physiological responses, (2) these responses vary by stress type, intensity, and duration, and (3) how and when herbivores use stressed host plants dictate the cumulative effect this suite of responses has on herbivore fitness (White, 2009; Huberty and Denno, 2004; Inbar et al., 2001; Koricheva et al., 1998; Herms and Mattson, 1992; Mopper and Whitham, 1992; Price, 1991; Larsson, 1989; Gershenzon, 1984; Larsson and Tenow, 1984; Mattson, 1980; Hsiao, 1973). The pulse-stress hypothesis (Huberty and Denno, 2004) incorporates some of these complexities to predict the response of sub-guilds to intermittent or continuous water stress, depending on whether their members feed on leaf or vascular tissue and whether they possess or lack specific adaptations to overcome plant defenses, leaf toughness, and reduced tissue water content. Experimental evidence for the pulse-stress hypothesis has been inconclusive (Bauerfeind and Fischer, 2013; Grinnan et al., 2013; Simpson et al., 2012; Tariq et al., 2012; Walter et al., 2012; Gutbrodt et al., 2011; Paine and Hanlon, 2010; Krugner et al., 2009; Mody et al., 2009). One difficulty in reaching a consensus here is that these studies often differ with respect to both the amount of and interval between waterings, and whether herbivore utilization of the experimental plants occurs simultaneously with the pulse stress treatments or after plant have been allowed to recover.

The plant vigor hypothesis posits that herbivores prefer and perform better on vigorous plant or plant parts due to a variety of mechanisms, such as higher nutritional content, increased water content, and reduced abscission risk (Price, 1991; Price et al., 1987a,b). A vigorous plant or plant part is defined as one with an above-average growth rate or size relative to the population mean (Price, 1991). In this framework, a stressed plant or plant part is one that has not achieved optimal size at maturity (Price, 1991), which is a very different definition of stress from that in the plant stress hypothesis. In contrast to senescent-feeders, flush-feeders should not respond positively to transitory plant stress as defined under the plant stress hypothesis (White, 2009). These insects are unlikely to be nutrient-limited while feeding on vigorous plant tissues, and plant stress of this kind limits the benefits these tissues provide herbivores by reducing plant growth rates (White, 2009; Cobb et al., 1997; White, 1993).

The linkage between herbivore preference and performance is strongly emphasized under the plant vigor hypothesis because the majority of herbivores feeding on vigorous tissues are either sessile or endophytic (Williams and Cronin, 2004; Price, 1991), making a positive preference-performance correlation necessary for these insects to have higher fitness on vigorous tissues (Thompson and Pellmyr, 1991). However, in a recent meta-analysis, Cornelissen (2008) shows that while experimental evidence largely supports the preference component of the plant vigor hypothesis for certain guilds, increased herbivore performance on vigorous plant or plant part is less frequently tested and the results are equivocal. Many studies have demonstrated that vigor is not the most important bottom-up factor determining herbivore performance (Nyman et al., 2011; Williams and Cronin, 2004; Fritz et al., 2003; Rehill and Schultz, 2001; Fritz et al., 2000; Roininen et al., 1997; De Bruyn, 1995; Kolehmainen et al., 1994; Roininen et al., 1993; Tscharntke, 1988; Craig et al., 1986). In addition, the loose definition of vigor itself makes evaluating this hypothesis difficult for a variety of methodological and conceptual reasons (Faria and Fernandes, 2001). The sink-competition hypothesis (Larson and Whitham, 1997) addresses some of these issues by adding a mechanistic basis to the plant vigor hypothesis. In addition to the size of a plant part (resource sink) where galls are located, this hypothesis incorporates the nature by which vascular feeders acquire nutrients to make galls, competition between sinks for resources, and their interconnectedness in terms of vascular architecture. These last two factors need not be restricted to phloem parasites; in this study I adopt their framework for an herbivore that intercepts resources along the vascular connections between sinks and sources.

The plant stress and plant vigor hypotheses differ in their definitions of stress, implying that plants can simultaneously experience both transitory and chronic stress (White, 2009; Cobb et al., 1997; Mopper and Whitham, 1992; Price, 1991). For example, plants growing in a nutrient-limited environment may become drought stressed during summer, raising the possibility of additive or interactive effects between nutrient limitation and water stress on herbivore attack. Furthermore, both hypotheses make the identical predictions that flush-feeders should perform better on vigorously growing plants not experiencing transitory stress whereas senescent-feeders should prefer and perform better on mature plants that grew vigorously prior to senescence (White, 2009, 1993; Price, 1991).

Sex-biased herbivory in terms of host plant vigor and stress

For dioecious host plants, the plant stress and plant vigor hypotheses can also explicitly connect herbivore feeding preferences to sexual dimorphism in traits related to plant quality, stress susceptibility, and reproduction. Female plants typically allocate more resources to reproduction than males (Delph, 1999; Ågren, 1988; Allen and Antos, 1988; Lloyd and Webb, 1977; Putwain and Harper, 1972), often incurring greater reproductive costs in the form of tradeoffs between reproduction and other plant functions (see review by Obeso, 2002), although these costs can sometimes be mitigated (Delph et al., 1993; Ågren, 1988; Tuomi et al., 1983; Cox, 1981; Lloyd and Webb, 1977). These tradeoffs result in sexual dimorphism where females often exhibit reduced vegetative growth rates, fewer and smaller leaves, reduced shoot lengths, and lower nitrogen concentrations in vegetative tissues (Cornelissen and Stiling, 2005) At the same time, females are usually better defended than males, either as a physiological consequence of having lower vegetative growth rates or because of selection pressure by herbivores themselves (Cornelissen and Stiling, 2005; Herms and Mattson, 1992; Jing and Coley, 1990; Coley et al., 1985). The commonly observed pattern of male-biased herbivory in dioecious plants is usually attributed to these sex-based differences in growth and defense (Cornelissen and Stiling, 2005; Ågren et al., 1999). Although the rationale for linking sex-biased herbivory to these dimorphic traits is identical to that behind the plant vigor hypothesis (Price, 1991), this hypothesis is rarely directly invoked in these studies (but see Boecklen et al., 1990).

Reproduction itself is a form of vigor from the herbivore's perspective, as reproductive structures increase the sink strength of plant parts on which they are located (Dawson and Ehleringer, 1993a,b; Kozlowski, 1992). Herbivores that feed on these parts during plant reproduction, for example directly below inflorescences, should be more abundant or perform better due to the shunting of assimilates towards or reduced defenses in reproductive structures (Elmqvist et al., 1991). However, to truly understand this it is essential to compare herbivore preference or performance on vegetative to reproductive plant parts, where the reproductive structures themselves are not consumed.

Females have also been shown to be more sensitive to environmental stress than males (Dawson and Geber, 1999; Houssard et al., 1992; Dawson and Bliss, 1989a,b; Zimmerman and Lechowicz, 1982) This has led to spatial segregation of the sexes in some species, with females usually prevalent in resource-rich habitat, as well as divergence between the sexes in life history strategies for tolerating or avoiding stress (Dawson and Geber, 1999; Bierzychudek and Eckhart, 1988). Despite this, the degree to which sex-differences in sensitivity to environmental stress and habitat preference affect sex-biased herbivory has not been well explored. These sexual dimorphisms can be evaluated in the context of the plant stress hypothesis, to test whether herbivore abundance is affected by a sex × environment interaction (Boecklen and Hoffman, 1993), or if the relationship between stress intensity and herbivore response (sensu Larsson, 1989) depends on host plant sex (Inbar and Kark, 2007).

Focus of study

If both the plant stress and vigor hypotheses can act in concert, then instead of determining where an herbivore falls on the traditional stress-vigor spectrum, the more relevant question to ask is how transitory and chronic stresses change the quality of resources available by a host plant to the most vulnerable life stages of its herbivores? Likewise, the close connection between sex-biased herbivory and the plant vigor and stress hypotheses raises the question of whether herbivore responses to transitory and chronic stress depends on plant sex. In this study, I address these two broad questions by examining the herbivory dynamics of the invasive poplar-willow weevil (*Cryptorynchus lapathi* L.) (Curculionidae: Coleoptera) on Sitka willow (*Salix sitchensis* Bong.) (Salicaceae: Malpighiales) on the Mount St. Helens Pumice Plain, a 15 km^2 primary successional landscape of rock and ash formed and sterilized by pyroclastic flows during the 1980 eruption. Mount St. Helens provides an excellent system in which to examine the interplay between insect herbivory and host plant vigor, stress, and sex. Resource scarcity and stress can play large roles in structuring early successional plant communities (Bishop, 2002; Halvorson and Smith, 1995; Del Moral and Wood, 1993; Wood and Del Moral, 1987). Previous work has shown that plant quality drives consumer-resource dynamics between *Lupinus lepidus* var. *lobbii*, a native nitrogen-fixing legume colonizing Mount St. Helens, and its suite of Lepidopteran herbivores (Bishop et al., 2010; Apple et al., 2009; Fagan et al., 2005, 2004; Fagan and Bishop, 2000).

On the Pumice Plain, the poplar-willow weevil (hereafter weevil) produces two temporally distinct cohorts of larvae each generation, whose youngest members differ in the type of tissue on which they feed: young fall larvae are senescent-feeders whereas young spring larvae are flush-feeders. Sitka willow (hereafter willow) is found in both riparian zones and dry upland areas, where plants experience transitory water-stress throughout the summer. This species is dioecious and the Pumice Plain population is strongly female-biased in both riparian and upland habitats, but not spatially segregated by sex. Weevils oviposit in willow stems each season, either colonizing new stems, or re-attacking stems that survived attack from the previous generation. I tracked weevil larval herbivory in willow stems on sexed plants in riparian and upland habitat over three successive seasons on the Pumice Plain. I used dynamic site-occupancy models (Royle and Kéry, 2007; MacKenzie et al., 2003) to investigate how weevils responded to chronic and transitory stress and whether these responses varied by habitat and sex. By treating stems as sites available for weevil attack each season, dynamic site occupancy models provided a flexible modeling framework that allowed an examination of both the metapopulation dynamics of this plant-insect interaction as well as the covariates that affected colonization and re-attack. I asked the following specific questions:

1. Were rates of weevil colonization and re-attack of willow stems associated with stem vigor? I investigated whether these rates differed for reproductive as opposed to vegetative stems, how weevil colonization scaled with respect to stem size and stem aboveground biomass (as a metric of sink strength), and whether higher rates of weevil attack was negatively associated with stem growth rates.

2. Were rates of weevil colonization and re-attack of willow stems associated with seasonal water stress and plant sex? I investigated whether these rates differed for male and female plants growing in upland areas as opposed to riparian zones, and the degree to which weevil responses to stem-vigor depended on plant habitat and sex.

3. How were annual differences in the vigor of stems available for colonization and re-attack associated with the metapopulation dynamics underlying weevil attack? I investigated how annual differences in stem size and reproductive status, combined with their effects on

colonization and re-attack, could explain the seasonally-observed herbivory patterns for stems of both sexes in upland areas and riparian zones.

4. How did weevil larva abundance differ by habitat and time of oviposition? I investigated whether counts of weevil eggs and early instars oviposited in the fall and spring cohorts differed between riparian zones and upland areas.

1.2 METHODS

Study System

Sitka willow is the dominant shrub species recolonizing the Mount St. Helens Pumice Plain (Figure 1). Willow grows frequently in hydric habitats near springs, perennial seeps, and watercourses while also occurring less frequently in upland habitats (Figure 2A). Field observations on the Pumice Plain from 2004 – 2011 demonstrated that weevils were present at very high densities and were the primary willow herbivores. Willow stem mortality due to weevil herbivory was extremely high, ranging from 50 – 90% annually. Weevils were introduced to North America from Europe in the 1880's and are a common pest in poplar and willow plantations (Matheson, 1917). Populations of *C. lapathi* worldwide have variable life histories that depends on their geographic location, and can be either univoltine or semivoltine, with overlapping generations and a life cycle lasting up to three years (Harris and Coppel, 1967; Smith and Stott, 1964; Matheson, 1917).

On the Pumice Plain, semi-voltinism enables adults to undergo two discrete bouts of oviposition, once in later summer or early fall after adults eclose, and the second in the following spring, after these same adults overwinter. This results in two temporally distinct cohorts of larvae feeding within willow stems each generation. Adults feed on leaves and stems but do minimal damage. The first three weevil instars (hereafter, 'early instars') girdle directly underneath the bark, feeding on the cambium and phloem tissues. In contrast, larger 'late instars' excavate galleys that penetrate the sapwood and heartwood (Figure 3B) (Harris and Coppel, 1967; Matheson, 1917). I defined early instars as those that girdle in the cambium or phloem and late instars as those that feed in xylem's heartwood and sapwood. Early instars from the summer larval cohort can be classified as senescent-feeders (intercepting nutrients moving from senescing leaves towards the roots), whereas those in the spring cohort are flush feeders (intercepting nutrients moving from the roots to vegetative and reproductive buds). Gut dissection of late instars taken from galleries revealed that larvae feed directly on wood. Larvae kill the stems directly via girdling or indirectly by providing access to fungal pathogens (Broberg et al., 2001; Abebe et al., 1990; Harris and Coppel, 1967; Primm, 1918; Matheson, 1917).

Observational studies examining the relationship between insect outbreaks and plant stress have been criticized for their inability to eliminate confounding factors, mainly the direct effects of the environment on herbivore development and their natural enemies (Koricheva et al., 1998). Likewise, experimental studies have been criticized for their difficulty in calibrating experimentally imposed plant stress to match the natural stress herbivores experience (White, 2009; Koricheva et al., 1998; Larsson, 1989). I believe the

Mount St. Helens willow-weevil system overcomes these drawbacks while offering several distinct advantages. Top-down effects on weevils were unlikely here; I observed no parasitoids known to utilize *C. lapathi* as a host (Broberg et al., 2002) and I found no evidence of parasitism on weevil larvae sampled during the three year course of this study. The willow population on the Pumice Plain undergoes an annual dry-down that conveniently serves as a natural water stress experiment. During the course of this study, the months of May and June were typically cool and wet, with abundant and consistent precipitation, while July and August, were hot and dry with little overall rainfall and long stretches of no precipitation (Figures A1,A2). Each year, the upland willows experienced a dry-down during the summer months, as reduced precipitation lowered soil water potential below field capacity, resulting in repeated episodes of transitory water stress (Figure A2). Riparian willows experienced higher temperatures and reduced relative humidity in the summer months, but these effects were less severe (Figure A1). In addition, continuous watering by perennial streams ensured that soils remained saturated throughout the summer months. During the summer dry-down, weevil larvae fed internally in galleries located at the base of willow stems, where they remained largely insulated from the direct effect of increased temperature and reduced relative humidity. By monitoring weevil attack of naturally grown willow, I was able to evaluate how weevils responded to natural stress on mature woody host plants, something that would have been extremely difficult to reproduce experimentally.

Willow-weevil database

I tagged 277 Pumice Plain *S. sitchensis* plants early in 2009 and tracked their stems for three growing seasons (2009 – 2011). For upland habitat, I selected plants along 1 km subsets of five 2.5 km permanent transects. These transects form a grid overlaid on the Pumice Plain, with points along each transect separated by 100 m and the distance between transects is 500 m (Figure 1). In 2009, I sexed, if possible, and marked the five willow plants nearest to each transect point that had at least one stem $\geq$ 15 mm in basal diameter. The minimum stem size requirement was to insure that I only tagged willow plants with stems large enough to be targeted by weevils. I tracked marked non-reproductive plants in my study even though I could not determine their sex initially, because flowering in future years would allow us to later sex a subset of these plants. Individual upland plants could usually be distinguished visually, but when plants were located very close to one another, or when I was unable to see an obvious caudex due to burial of stems by sediment, I traced shallow roots from each plant to group stems by genet. For riparian habitat, I established paired riparian transects 100 – 140 m in length along both sides of three permanent streams dominated by dense *Salix* and *Alnus* thickets (Figure 1). Visual separation of stems by genets was not possible due to the high density of *Salix* in riparian zones. To ensure that marked plants represented different individuals, I searched for plants at 5 m intervals, and sexed and marked only plants that had at least one stem $\geq$ 15 mm in basal diameter and whose stems all could be clearly traced back to its caudex.

I tagged all stems $\geq$ 12 mm in basal diameter on each tagged plant that originated from the ground or caudex (defined as 1st order stems) and tracked these stems until their death or the conclusion of the study. Weevils generally oviposit near the base of 1st order stems and near the branching points of large side branches on these stems (defined as 2nd order stems). Consequently, I tagged 2nd order stems above 12 mm (upland) and 15 mm (riparian) in basal diameter to ensure consistent survey effort for weevil larval presence across a gradient of stem architectural complexity. Each spring, newly recruited 1st and 2nd order stems that met the size criteria were tagged and added to my study. Stems were removed from the study a year after their death, which was either due to stem-borer attack or, in a few cases, undetermined. New plants were added to my study during the second year of sampling to offset the high mortality caused by weevil herbivory. Appendix B details my method for quantifying willow stem topologies.

I visited all living tagged stems twice each season for up to three years and recorded annual survivorship, basal diameter, reproductive status and allocation, and the presence or absence of weevil larval herbivory. Reproductive data were collected each spring during flowering. During the season's second visit in late summer, I measured each stem's basal diameter with calipers and recorded its fate, scoring the stem as "alive" if it possessed any living foliage and "dead" if all foliage had senesced prematurely or if the stem was broken. During the season's second visit, two observers independently surveyed weevil larval herbivory on each stem by searching for exit holes at the base of borer galleries. These herbivory surveys were timed to occur as larvae were pupating and exit holes were easier to find because of exuded frass (Figure 2B). Larvae detected in stems during a survey were oviposited one of two time periods: 1) in the late summer or early fall of the previous year, after adults from the previous generation eclosed, or 2) the current year's spring, after these same adults had overwintered. While the herbivory surveys were non-destructive, allowing us monitor stems over multiple seasons, they precluded the counting of larvae within each stem. Instead, I scored herbivory as a binary state: 1 if any evidence of weevil larval herbivory was detected and 0 otherwise. I assessed the efficacy of my herbivory surveys by destructively harvesting sacrificial stems after surveying them to determine whether weevil larvae were truly present. Although my false positive rate became negligible after minimal observer training, the false negative rate (i.e., failure to detect larvae within the stems) remained a persistent issue. Below, I detail the statistical methods used accommodate this imperfect detection, allowing us to separate lack of detection from true absence of weevil larvae within a stem.

True basal stem diameters cannot be directly observed due to routine measurement error associated with positioning the calipers correctly on the stem. These errors have been shown to increase in size as basal diameter increases (Rüger and Condit, 2012) and resulted in either negative or positive-but-unusually large annual growth rates for some stems. To correct for this, I used a Bayesian model with informed priors for both the annual stem growth increments and measurement error. Appendix C details my method for imputing unobserved and adjusting observed basal diameters. In summary, I monitored and included in my database 1998 stems on 277 plants for up to three years. For each plant, I recorded its habitat and sex as the plant–level stress and sex covariates. For each stem, I recorded its annual size (BD) as the stem-level vegetative vigor covariate, fate (S), as well as two independent surveys for weevil larvae presence or absence (w). In 2010 and 2011, I recorded the annual reproductive status (RA), as the stem-level reproductive vigor covariate, and relative growth rate (RGR), to capture the potential negative effect of weevil herbivory on stem growth. Appendix D illustrates my method for pooling stems to calculate the stem-level covariates.

Weevil phenology database

I harvested 291 stems from untagged *S. sitchensis* plants in both riparian zones and upland areas on the Pumice Plain over two successive growing seasons. Harvesting occurred at weekly or biweekly intervals from June through October 2008 and then again from June through August 2009. In this way, I captured three discrete cohorts of weevil larvae. The first larval cohort was oviposited in the spring of 2008 by the generation of weevils whose adults eclosed in summer of 2007. This was followed by two additional larval cohorts that were oviposited in the fall of 2008 and the spring of 2009 by the generation of weevils whose adults had eclosed in the summer of 2008. I haphazardly selected plants, randomly choosing a single stem per plant that was roughly 15 – 20 mm in basal diameter. I processed stems within 1 – 2 days of their collection, first by carefully removing their bark and inspecting its underside for weevil eggs and early instars. I then split stems longitudinally from basal to distal end with a chisel and hammer. Once a stem was split, I carefully searched it for late instars, pupae, and adults. I counted individuals in each of these life stages in all stems.

Effects of plant and stem factors on weevil herbivory

I conducted three analyses to address my four study questions. For my first two questions, I used the willow-weevil database to estimate the effects of stem-level and plant-level covariates on weevil larval herbivory, given imperfect detection of weevil larvae within stems. At the stem–level, I focused on vigor covariates and relative growth rate, whereas at plant–level, I focused on stress and sex covariates. Willow stems could have been in one of three 'states' during an herbivory survey: 1) the stem may be occupied by weevil larvae that were detected by the observer, 2) the stem may be free of weevil larvae, or 3) the stem may be occupied by weevil larvae, that were undetected. Failure to account for imperfect detection biases estimates of the stem– and plant–level covariates hypothesized to affect weevil herbivory towards zero, and covariates that affect both detection and occupancy become confounded. Not only did my herbivory surveys suffer from imperfect detection, but the detection rate likely depended on stem size (it was easy to miss exit holes on large stems, as these tended to have many side branches) and plant habitat (it was often physically impossible to visually inspect all sides of a stem in the densely thicketed riparian zones) (Figure 2A), two covariates I hypothesized to affect weevil herbivory.

I repeated my herbivory surveys within a short period of time, short enough to ensure that the stem did not change state between the repeated samples. This repeatability allowed us to meet my first objective using site-occupancy models. These models separate stem states (2) and (3) by modeling an observation process (which determines whether weevil larvae are observed if present in a stem) that is hierarchically linked to the underlying biological process (which governs whether or not the stem is occupied by weevil larvae). Treating stems as sites, I used a Bayesian implementation of Royle and Kéry's (2007) hierarchical dynamic site-occupancy model,

$$Pr(\boldsymbol{\Omega}, z_{j[i],k} \mid w_{j[i],s,k}) \quad \propto \quad \begin{matrix} \textit{Biological} \\ \textit{Process} \\ \textit{Model} \end{matrix} \quad \times \quad \begin{matrix} \textit{Observational} \\ \textit{Process} \\ \textit{Model} \end{matrix} \quad \times \quad \textit{Priors}, \tag{1}$$

where $\boldsymbol{\Omega}$ is a 44 element vector of coefficients used to parameterize the biological and observational models based on covariates from my willow-weevil database, $\boldsymbol{z}$ is a vector of the true occurrence of weevil larvae in stems, and $\boldsymbol{w}$ is a vector of the observed weevil larvae in stems from my herbivory surveys. The subscript j indexes plants $j = (1...277)$, the subscript i indexes stems $(i = 1...1998)$, the subscript k indexes years $(k = 1...3)$, and the subscript s indexes weevil herbivory surveys $(s = 1...2)$ in the k_{th} year on the i_{th} stem of the j_{th} plant.

Biological process model

The biological process model assumed the true occurrences of weevil larvae in stems $(\boldsymbol{z})$ were independently and identically distributed (i.i.d) Bernoulli random variables, conditional on the probability of weevil larvae attack (ψ), where $z = 1$ when a stem was occupied by weevil larvae and $z = 0$ when it was unoccupied. I amended Royle and Kéry's (2007) biological process model,

$$\prod_{i=1}^{1998} \text{Bern}\left(z_{j[i],k=1} \mid \psi_{j[i]} S_{j[i],k=1}\right) \times$$
$$\prod_{k=2}^{3} \text{Bern}\left(z_{j[i],k} \mid \left[z_{j[i],k-1}\phi_{j[i],k} + (1 - z_{j[i],k-1})\gamma_{j[i],k}\right] S_{j[i],k}\right), \quad (2)$$

by also conditioning (z) on the fate of each stem (S), where $S = 1$ when the stem was alive and tagged $S = 0$ when the stem was dead or not yet recruited to the plant. This binary indicator suppressed the terms in the likelihood where stems did not exist or were too small to be attacked. In year $k = 1$, ψ was estimated directly. In contrast, the dynamics that govern a stem's probability of weevil attack in years $(k = 2...3)$ were represented by a metapopulation model, where ψ was a function of z in year $k - 1$ and two vital rates: the colonization rate (γ), defined as the probability that weevil larvae attacked a stem unattacked the previous year, and the persistence rate (ϕ), defined as the probability that weevils attacked a stem already attacked the year prior by the previous weevil generation and referred to hereafter as re-attack. This Markovian process, in combination with the fate of the stem (S), determined which term, colonization or re-attack, was operative in the model for a given stem in years $(k = 2...3)$. For example, $S = 0$ in year $k - 1$ for a newly recruited stem, forcing $z = 0$ in year $k - 1$

and the occurrence of weevil larvae to depend solely on the colonization rate in year k.

I investigated the association between the stem-occupancy model's state variables (ψ, γ, ϕ) and host plant vigor, relative growth rate, stress, and sex by using generalized linear mixed models with both stem- and plant-level predictors. At the stem-level, I estimated the weevil attack (ψ) or vital rates (γ, ϕ) for the i_{th} stem on the j_{th} plant as,

$$
\begin{aligned}
\operatorname{logit}\left(\psi_{j[i]}\right) &= \alpha_{\psi_j} + \left(\beta_{\psi 1} RM_j + \beta_{\psi 2} RF_j + \beta_{\psi 3} UM_j + \beta_{\psi 4} UF_j\right) BD_{j[i],k=1} && (3)\\
\operatorname{logit}\left(\gamma_{j[i],k}\right) &= \alpha_{\gamma_j} + \left(\beta_{\gamma 1} RM_j + \beta_{\gamma 2} RF_j + \beta_{\gamma 3} UM_j + \beta_{\gamma 4} UF_j\right) RA_{j[i],k} + && (4)\\
&\quad \left(\beta_{\gamma 5} RM_j + \beta_{\gamma 6} RF_j + \beta_{\gamma 7} UM_j + \beta_{\gamma 8} UF_j\right) BD_{j[i],k} + \\
&\quad \left(\beta_{\gamma 9} RM_j + \beta_{\gamma 10} RF_j + \beta_{\gamma 11} UM_j + \beta_{\gamma 12} UF_j\right) RGR_{j[i],k} \\
\operatorname{logit}\left(\phi_{j[i],k}\right) &= \alpha_{\phi_j} + \left(\beta_{\phi 1} RM_j + \beta_{\phi 2} RF_j + \beta_{\phi 3} UM_j + \beta_{\phi 4} UF_j\right) RA_{j[i],k} + \\
&\quad \left(\beta_{\phi 5} RM_j + \beta_{\phi 6} RF_j + \beta_{\phi 7} UM_j + \beta_{\phi 8} UF_j\right) BD_{j[i],k} + \\
&\quad \left(\beta_{\phi 9} RM_j + \beta_{\phi 10} RF_j + \beta_{\phi 11} UM_j + \beta_{\phi 12} UF_j\right) RGR_{j[i],k}, && (5)
\end{aligned}
$$

where the above logit-link functions included one or more of the following stem-level covariates: stem reproductive status (RA), a discrete variable that equaled one when a stem was reproductive and zero otherwise, stem size (BD), a continuous variable standardized across all stems in all years to have a mean of one and a standard deviation of zero, and stem growth rate (RGR), a continuous variable standardized across all stems in years $k = 2...3$

to have a mean of one and a standard deviation of zero. I assumed that while the effect of the stem-level covariates did not vary across plants, the habitat and sex of the plant on which the stem was found did affect weevil attack in the initial year, and also affected colonization and re-attack rates in later years. To capture these varying effects, I used four plant-level binary predictors that each equaled one (for one of the four groups based on plant habitat and sex), riparian-male (RM), riparian-female (RF), upland-male (UM), and upland-female (UF), and zero otherwise. These four predictors interacted with each stem-level covariate. Representing each of the state variables (ψ, γ, ϕ) from Equations 3–5 with a dot and generically referring to them as weevil attack rates, the parameters $\beta_{.1} - \beta_{.4}$ were the expected effects of reproduction on weevil attack rates, on the logit scale, for each sex in riparian zones and upland areas. The parameters $\beta_{.5} - \beta_{.8}$ and $\beta_{.9} - \beta_{.12}$ specified the slopes of the logit-linear relationship between weevil attack rates and stem size and relative growth rate, respectively, for each sex in riparian zones and upland areas. Each linear predictor included $j = 1...277$ plant-specific intercepts that represented the baseline probability of weevil attack, on the logit scale, for an average-sized non-reproductive stem of average growth on the $\mathrm{j_{th}}$ plant.

At the plant-level, the $j = 1...277$ plant-specific intercepts used in Equations 3-5 were constrained to come from the normal distributions, whose hyperparameter means were conditional on plant habitat and sex:

$$\prod_{j=1}^{277} \text{Normal} \left(\alpha_{\psi j} \mid \mu_{\psi} = \eta_{\psi 1} RM_j + \eta_{\psi 2} RF_j + \eta_{\psi 3} UM + \eta_{\psi 4} UF_j \sigma_{\psi}\right) \tag{6}$$

$$\prod_{j=1}^{277} \text{Normal} \left(\alpha_{\gamma_j} \mid \mu_{\gamma} = \eta_{\gamma 1} RM_j + \eta_{\gamma 2} RF_j + \eta_{\gamma 3} UM + \eta_{\gamma 4} UF_j, \sigma_{\gamma}\right) \tag{7}$$

$$\prod_{j=1}^{277} \text{Normal} \left(\alpha_{\phi_j} \mid \mu_{\phi} = \eta_{\phi 1} RM_j + \eta_{\phi 2} RF_j + \eta_{\phi 3} UM + \eta_{\phi 4} UF_j, \sigma_{\phi}\right). \tag{8}$$

Using the same notation as above, the parameters $\eta_{.1} - \eta_{.4}$ were the hyperparameter means for each sex in riparian zones and upland areas. Plant habitat and sex affected weevil attack rates in two different ways; at the stem-level, the effect of each vigor covariate could vary depending on the habitat and sex of the plant on which a stem was found (Equations 3-5), while in the plant-level, the baseline probability of weevil attack for each plant was drawn from a distribution whose mean depended on its habitat and sex (Equations 6-8).

Observational process model

The observational process model (Equation 1) was linked to the biological process model through the assumption that the observations of weevil larvae in stems ($\boldsymbol{w}$) were i.i.d. Bernoulli random variables conditional on the true occurrences of weevil larvae in stems $(\boldsymbol{z})$ and the probability these larvae are detected in my survey (p),

$$\prod_{i=1}^{1986}\prod_{s=1}^{2}\prod_{k=1}^{3}\text{Bernoulli}\left(w_{j[i],s,k} \mid z_{j[i],k}p_{j[i],k}\right), \tag{9}$$

where $w = 1$ when a larvae was observed in a stem and $w = 0$ when they were not observed. Based on my experience surveying in the field, I estimated the probability of weevil detection in the $\mathrm{i_{th}}$ stem on the $\mathrm{j_{th}}$ plant as in the $\mathrm{s_{th}}$ survey of the $\mathrm{k_{th}}$ year as,

$$\text{logit}\left(p_{j[i],k}\right) = \alpha_{p1} + \beta_{p2}PH_j + \beta_{p3}BD_{j[i],k} + \beta_{p4}PH_jBD_{j[i],k}, \tag{10}$$

where the logit link function included the covariates stem size (BD) and plant habitat (PH). The intercept α_{p1} represented the detection probability, on the logit scale, for an average-sized stem found in riparian habitat. The parameter β_{p2} was the deviation from β_{p1} in the detection probability due to the stem being surveyed in upland habitat. The parameter β_{p3} specified the slope of the logit-linear relationship between the detection probability and stem size for riparian stems, whereas the parameter β_{p4} was the deviation from β_{p3} in the detection probability due to the stem being surveyed in upland habitat.

Estimation and model evaluation

I estimated the posterior distributions for all parameters ($\boldsymbol{\Omega}$) and stem states ($\boldsymbol{z}$) in my hierarchical stem-occupancy model (Equation 1) using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 (Plummer, 2013a) with the rjags package (Plummer, 2013b) in the R computing environment (R Development Core Team, 2013). I chose all priors to be noninformative:

$$\begin{gathered}
\prod_{t=1}^{8} \mathrm{N}\left(\beta_{\psi t} \mid 0, \sigma = 10^2\right) \prod_{t=1}^{12} \mathrm{N}\left(\beta_{\gamma t} \mid 0, \sigma = 10^2\right) \mathrm{N}\left(\beta_{\phi t} \mid 0, \sigma = 10^2\right) \times \\
\prod_{t=1}^{4} \mathrm{N}\left(\beta_{pt} \mid 0, \sigma = 10^2\right) \mathrm{N}\left(\eta_{\psi t} \mid 0, \sigma = 10^2\right) \mathrm{N}\left(\eta_{\gamma t} \mid 0, \sigma = 10^2\right) \times \\
\prod_{t=1}^{4} \mathrm{N}\left(\eta_{\phi t} \mid 0, \sigma = 10^2\right) \mathrm{Uniform}\left(\sigma_{\psi} \mid 0, 100\right) \times \\
\mathrm{Uniform}(\sigma_{\gamma} \mid 0, 100) \mathrm{Uniform}\left(\sigma_{\phi} \mid 0, 100\right). \qquad (11)
\end{gathered}$$

I computed three chains for each parameter, all with different initial values. After a burn-in period of 100,000 iterations, I accumulated 50,000 samples from each chain, keeping every 10th sample. I evaluated convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman (Brooks and Gelman, 1998). I assessed model fit with posterior predictive checks comprised of two test statistics appropriate for binary response data (M. Kéry, personal communication):

$$
\begin{aligned}
T^{obs} &= \sum_{i=1}^{1998}\sum_{k=1}^{3} \frac{(\sum_{s=1}^{2} w^{obs}_{j[i],s,k} - \sum_{s=1}^{2} \bar{w}_{j[i],s,k})^2}{\sum_{s=1}^{2} \bar{w}_{j[i],s,k}} && (12)\\
T^{rep} &= \sum_{i=1}^{1998}\sum_{k=1}^{3} \frac{(\sum_{s=1}^{2} w^{rep}_{j[i],s,k} - \sum_{s=1}^{2} \bar{w}_{j[i],s,k})^2}{\sum_{s=1}^{2} \bar{w}_{j[i],s,k}}, && (13)
\end{aligned}
$$

where $\overline{w}$ was the expected number of surveys per stem where weevils were observed, w^{obs} was the observed number of surveys per stem where weevils were observed, and w^{rep} was the simulated number of surveys per stem where weevils were observed from my stem occupancy model's posterior predictive distribution. Using these test statistics, I confirmed that the Bayesian p-value, defined as the probability that the simulated data were more extreme than the observed data, was indicative of a good model fit (Gelman et al., 2013). The Pearson correlation coefficient between the two continuous stem-level covariates in my stem-occupancy model, stem size and relative growth rate, was small, suggesting that collinearity between my explanatory variables was not an issue. I examined the degree of overlap between these two continuous covariates to insure that the data ranges for which I made inferences were due to direct support from the data and not model extrapolation (Gelman and Hill, 2007). Appendix E details the posterior predictive checks.

Hypothesis testing

I purposefully chose to fit only my global model and retained all covariates regardless of their effect sizes. I justify this approach by noting that the covariates were selected intentionally as part of my original survey design to test long-standing biological hypotheses regarding how plant vigor, stress, and sex affect insect herbivory. The model's structure was also chosen based on biological considerations, specifically to account for the non-independence of stems found on the same plant and to understand how the effects of the stem-level covariates were context-dependent with respect to plant habitat and sex. While this resulted in a large number of parameters, the size of the willow weevil dataset provided the needed replication for parameter estimation. I recognize that ignoring model uncertainty renders my inferences conditional upon my chosen model, however my specific *a priori* interest in each parameter trumps the need for a model selection approach.

I assessed the importance of the stem-level covariates reproductive status and relative growth rate to the vital rates (γ, ϕ) by examining their standardized model coefficients on the logit scale. For each stem-level covariate in Equations 4–5 I tested four additional hypotheses by computing derived quantities from the posterior distributions of the model coefficients (Gelman and Hill, 2007). Within each sex, I tested whether the effects differed between riparian zones and upland areas. Likewise, within each habitat I tested whether the effects differed between male and female stems.

For the plant-level covariates, habitat and sex, in Equations 7–8, I computed similar derived quantities. Modeled coefficients at the stem-level and all derived quantities were considered unimportant to the processes being modeled if the Bayesian 95% credible interval of their posterior distributions overlapped zero, and important otherwise. A positive effect for reproductive status was interpreted as support for the plant vigor hypothesis, whereas an important positive effect of habitat at the plant-level was interpreted as support for the plant stress hypothesis. The stem-level effects could be context dependent with respect to habitat and plant sex. Important sex-based differences for any of the stem-level covariates or an important sex effect at the plant-level was considered evidence of sex-biased herbivory.

I relied on three allometric relationships to determine whether weevils responded positively to vegetative vigor. First, I investigated how stem sink strength scaled with respect to stem size. I estimated the scaling coefficient for upland vegetative sink strength (which I assumed was proportional to aboveground biomass) with respect to basal stem diameter as $B = \pi c_1 (BD)^{n_1}$, where B is aboveground stem biomass, BD was stem basal diameter, n_1 was the scaling coefficient, and c_1 was a proportionality constant. Nutrients are translocated through the cambium, making the the flux of nutrients to aboveground vegetative structures proportional to the basal stem stem diameter such that $F = B/\pi(BD) = c_1(BD)^{n_1 - 1}$, where F equals nutrients $\cdot$ time^{-1} $\cdot$ area^{-1}. In September 2010, I harvested one stem each on 40 Pumice Plain upland plants, where plants were selected in a haphazardous manner from three randomly chosen sites, and stems were selected using a stratified approach based on basal diameter to capture the range of upland stem sizes available for weevil colonization. I was unable to collect riparian stems or enough large upland stems to properly estimate allometry of upland stems available for re-attack. Prior to harvesting I recorded basal diameters (BD) as described for tagged stems in my willow-weevil database. I dried stems in a drying oven at 65 C for one week prior to weighing each stem's biomass (B). I used regression analysis to estimate the scaling coefficient (n_1) as the slope of the log-linear relationships between stem biomass and stem size. I estimated the slope using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 (Plummer, 2013a) with the rjags package (Plummer, 2013b) in the R computing environment (R Development Core Team, 2013). I chose all priors to be non-informative and computed three chains for each parameter, all with different initial values. After a burn-in period of 5,000 iterations, I accumulated 2,000 samples from each chain, keeping every sample. I evaluated convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman (Brooks and Gelman, 1998). I used residual plots to confirm that variances between groups and years were homogeneous. I used the posterior distribution of the scaling coefficient (n_1) to estimate the scaling coefficient for stem nutrient flux $(n_1 - 1)$ as a derived quantity.

Second, I used the stem size coefficients from Equations 4–5 to estimate the scaling coefficients for the expected number of weevil larvae colonizing or re-attacking stems with respect to stem size in both habitats. While late instars feed in a stem's interior, oviposition and feeding by early instars feeding occurs in the cambium near a stem's base, regardless of its basal diameter, making my stem size measurements proportional to the portion of a stem's surface area utilized by early instars. I assumed that the expected number of weevil larvae per stem (λ) were i.i.d. Poisson random variables such that $Pr(0) = e^{\pi H c_2 (BD)^{n_2}}$, where $Pr(0)$ was the probability of a stem not being colonized or re-attacked over successive seasons by weevil larvae, BD was stem basal diameter, n_2 was the scaling coefficient, c_2 was the product of the proportionality constant, and H and the maximum height from the base of a stem or branching point where early weevil instars are found. I used the Hmisc package (Harrell Jr, 2014) to compute weighted 95% quantiles (where the weights are explained in section 2.5) that delineated the range of stem sizes available for colonization and re-attack in each habitat. I then estimated each scaling coefficients (n_2) as the slope of the double logarithmic linear relationship between these complementary probabilities and stem size. For riparian stems available for re-attack, this relationship was nonlinear and I used piecewise regression in the segmented package

(Muggeo, 2008) to estimate a single break point (BD_b) and two separate scaling coefficients. Third, I estimated the scaling coefficients for the expected weevil density colonizing upland stems with respect to stem nutrient flux as $\lambda = c_3 B^{n_2/(1-n_1)}$. I used the point estimate of the stem sink strength scaling coefficient (n_1), as the precision of this estimate was very high compared to (n_2). By retaining all samples from the stem size posterior distributions, I propagated the uncertainty in the my stem size model coefficients throughout this process, enabling us to construct 95% Bayesian credible intervals for all scaling coefficients. All analyses were carried out in the R computing environment (R Development Core Team, 2013). A positive weevil response to vegetative vigor required disproportionate scaling of weevil attack and sink strength to stem size $(n_1 > 1, n_2 > 1)$ and and proportional scaling of weevil attack with respect to nutrient flux $(n_2/(1-n_1) \geq 1)$. I justify my rationale for this approach to measuring vegetative vigor in section 4.1.

Effect of willow habitat and sex on weevil metapopulation dynamics

My third study question asked how annual changes in the size, relative growth rate, and reproductive status of stems available for colonization or re-attack were associated with annual weevil attack and vital rates for male and female stems in riparian zones and upland areas on the Pumice Plain. I retained posterior distributions from my stem-occupancy model for each stem's annual predicted state variables (ψ, γ, ϕ). Using these posterior distributions, I computed derived quantities representing annual weevil attack and vital rates for each of the four groups based on plant habitat and sex. I tested habitat and sex effects using the same approach as in my stem-occupancy model. Within each sex, I tested whether each of the predicted state variables differed between riparian zones and upland areas. Likewise, within each habitat I tested whether each of these state variables differed between male and female stems. In similar fashion, I also tested for yearly differences for each group.

I used weighted linear regressions for stem size and relative growth rate, and binomial linear regression for stem reproductive status to determine how each of these covariates varied annually with respect to plant sex and habitat for two pools of stems: 1) those not attacked the previous year and therefore available for colonization or 2) those attacked the previous year and therefore available for re-attack. To determine to which of these two pools a stem belonged in a given year, I retained the posterior distribution from my stem-occupancy model for the stem's predicted state (z) in the previous year and computed its mean. I used this mean value as the basis for including or excluding the stem from a pool (when its value equaled one), or to weight the influence the stem should have on the regression estimates (when its value was between zero and one). For reproductive status, I excluded or included stems using the observed weevil surveys in the previous year, as there was no convenient way to weight individual observations in a binomial linear model. All six regressions had eight binary predictors that each equaled one (for one of the four groups based on plant habitat and sex), riparian-male (RM), riparian-female (RF), upland-male (UM), and upland-female (UF), in 2010 or 2011 and zero otherwise. I log-transformed stem size and relative growth rate as these distributions had all positive values and were heavily skewed. I tested habitat, sex, and year effects on these three covariates using the same approach as for the annual attack and vital rates. I estimated parameter values for each regression using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 (Plummer, 2013a) with the rjags package (Plummer, 2013b) in the R computing environment (R Development Core Team, 2013). I chose all priors to be non-informative and computed three chains for each parameter, all with different initial values. After a burn-in period of 2,000 iterations, I accumulated 2,000 samples from each chain. I evaluated convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman (Brooks and Gelman, 1998). I used residual plots to confirm that variances between groups and years were homogeneous.

Effect of willow habitat and weevil phenology on weevil oviposition

My fourth study question was to determine whether counts of weevil larvae or eggs within stems differed by habitat between the two temporally distinct larval cohorts: senescent-feeding early instars oviposited in late summer/early fall and flush-feeding larvae oviposited in the spring. To remove the confounding effects of habitat differences in weevil colonization or re-attack rates, I conditioned my data by only retaining attacked stems from the weevil phenology database for analysis. To separate individuals by larval cohort, I assumed that 1) eggs or early instars found in late summer/ early fall were unlikely to have been oviposited in the spring of the current year, and 2) eggs or early instars found in the late spring were unlikely to have been oviposited the previous year. I analyzed the count data for eggs and early instars separately, using a series of Poisson t-tests to determine whether the expected number of eggs or early instars per stem differed by habitat in June and July of 2008, September and October of 2008, and June and July of 2009. I tested and corrected for over-dispersion in the count data by adding a normally distributed random effect to the linear predictor for the Poisson rate parameter (Millar, 2009). For each t-test, I estimated the posterior distributions for its three parameters, the intercept, the habitat effect, and the variance of the random effect term, using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0

(Plummer, 2013a) with the R2jags package (Su and Yajima, 2013) in the R computing environment (R Development Core Team, 2013). I chose all priors to be non-informative and computed three chains for each parameter, all with different initial values. After a burn-in period of 50,000 iterations, I accumulated 10,000 samples from each chain, keeping every 5th sample. I evaluated convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman (Brooks and Gelman, 1998). I used posterior predictive checks based on actual and replicated squared residuals and residual plots to confirm each model's assumptions and fit.

1.3 RESULTS

Detection of weevil larvae within stems

Although the probability of detecting weevil larvae in stems was quite high, the detection rate was affected by covariates also important to the biological process model (Equation 2). The detection rate was 90% (95% CI: 88%, 92%) for average sized upland stems and 87% (95% CI: 85%, 89%) for average sized riparian stems. Both habitat and stem size had an effect on the detection rate, with the effect of stem size varying by habitat. For average sized stems, the detection rate was 12% lower than in riparian zones

(95% CI: 9%, 15%) than in upland areas. Stem size had a positive effect on the detection of weevils in upland stems, where a one standard deviation increase in stem size (centered around the average upland stem size) was associated with a 13% increase in weevil detection (95% CI: 8%, 19%). In comparison, a one standard deviation increase in stem size (centered around the average riparian stem size) was associated with a 5% increase in weevil detection (95% CI: 3%, 8%).

Weevil colonization of previously unattacked stems

In order of importance, colonization by weevil larvae was associated with plant habitat, stem size, reproductive status, and relative growth rate (Figure 4A). In riparian zones, weevils successfully colonized flowering stems more often than non-reproductive ones, but reproduction did not have an effect on weevil colonization rates in upland areas (Figures 4A, 5A). For riparian stems of average size and growth rate, reproduction increased exposure to weevil colonization by 24% (95% CI: 16%, 32%). Weevils responded positively to stem size in both habitats, but how colonization scaled with respect to stem surface area differed by habitat. For riparian stems, expected weevil density per stem was invariant with respect to its surface area for stems below 32.7 mm in basal diameter (95% CI: 31.4, 34.4), whereas for stems above this size weevil density scaled proportionately with respect to stem surface area (Figure 6A). In contrast, expected weevil density per upland stem was disproportionately higher than would be expected by chance, given the stem's surface area available for attack (Figure 6A). For colonizable upland stems, stem sink strength scaled disproportionately with respect to stem size, while expected weevil density per stem scaled proportionately to nutrient flux (Figure 6). Weevil colonization was negatively correlated with fast-growing stems, but this effect was smaller than that of stem size (Figure 4A). For upland stems of average size, an increase of one standard deviation in relative growth rate (centered around the average upland relative growth rate) was associated with a 15% reduction in weevil colonization (95% CI: 6%, 25%). In contrast, for upland stems of average relative growth rate, a one standard deviation increase in stem size (centered around the average upland stem size) was associated with a 75% increase in weevil colonization (95% CI: 50%, 92%). The marginal effect of upland habitat on weevil colonization for stems of average relative growth rate was positive for all observed stem sizes both above and below the overall mean stem size (26.35 mm) (Figure 7A). This result was only possible if there was an effect of habitat itself at the plant-level, beyond any differences between habitats due to the interaction between habitat and stem size. I did not observe any sex effects at the plant- or stem-level. Weevil responses to stem size, reproduction, and relative growth rate were often habitat-dependent, but were the same for each sex within habitats (Figure 4A). Average plant-level baseline colonization rate did not vary by sex (Figure 4A).

Weevil re-attack of previously attacked stems

Unlike colonization, re-attack of stems by weevil larvae from year to year was largely invariant to stem size (with the exception of female upland stems) and relative growth rate, but was positively associated with plant habitat, riparian reproduction, and plant sex, in order of importance (Figure 4B). In riparian zones, weevils successfully re-attacked flowering stems more often than non-reproductive ones, but reproduction did not affect weevil re-attack in upland areas (Figures 4B, 5B). For riparian stems of average size and growth rate, reproduction increased exposure to weevil re-attack by 23% (95% CI: 6%, 40%). The poorer precision of the coefficient for the effect of riparian flowering for males as compared to females caused its Bayesian 95% credible interval to overlap zero. However, because the coefficient itself was similar in magnitude to that for females, and there was no sex-effect, I inferred that reproduction increased exposure to weevil re-attack for both sexes in riparian zones. Weevil re-attack was positively associated with increased stem size for female upland stems only (Figure 4B), but male and female attack did not scale differently with respect to stem surface area and I pooled their results. For riparian stems, expected weevil density per stem were invariant to its surface area, whereas in upland habitat weevil density was disproportionately lower than would be expected by chance based on stem surface area (Figure 6B). Male upland plants had higher baseline levels of attack as compared to female upland plants. For non-reproductive upland male stems of average relative growth rate and size, plant sex increased this baseline exposure to weevil attack by 10% (95% CI: 1%, 20%). For stems of below average size, this sex effect was even greater given the stronger logit-linear relationship between weevil re-attack and stem size for female as compared to male stems. The marginal effect of upland habitat on weevil re-attack for stems of average relative growth rate was positive for all observed stem sizes both above and below the overall mean stem size (Figure 1). As in the case of weevil colonization, this result was only possible if there was an effect of habitat itself at the plant-level, beyond any differences between habitats due to the size-dependent re-attack rates for female upland stems.

Willow habitat and sex differences

Stems available for colonization or re-attack differed considerably by habitat and year, and to a lesser degree by sex, in their stem-level covariates (Table 1,2). In 2010 and 2011, upland stems available for weevil colonization or re-attack tended to be smaller, faster-growing, and flowered less frequently than riparian stems (Table 1,2). In either habitat, stems available for weevil colonization in 2011 tended to be larger in size, slower-growing (with the exception of riparian male stems whose relative growth rate remained unchanged across years), and flowered more frequently than stems available for colonization stems in 2010 (Table 1). Stems available for re-attack in 2011 flowered more frequently than their counterparts in 2010, however differences in their size and relative growth rate between years did not show a clear pattern and varied depending on habitat and sex (Table 2). For each of the stem-level covariates, there were isolated cases of sex differences within habitats for certain years. In 2010, upland female stems available for weevil colonization were slightly larger than male stems, whereas riparian male stems available for re-attack were much larger than female stems (Table 1,2). Although upland male stems flowered more than female stems in 2010, upland reproduction was not a plant trait that weevils responded to (Table 12, Figure 5). In 2011, male and female stems available for colonization or re-attack did not differ in stem size or frequency of reproduction in either habitat (Table 1,2).

Weevil metapopulation dynamics

Whereas upland stems were attacked more frequently each year than riparian stems, stems in both habitats showed similar inter-annual trends that unambiguously mirrored inter-annual variation in colonization rates (Figure 8). The largest difference in annual weevil attack rates was due to habitat, as upland stems were attacked 19% more (95% CI: 15%, 23%) than riparian stems across sexes and years. Colonization rates were 35% greater (95% CI: 30%, 39%) in upland areas than in riparian zones across sexes and years. Re-attack rates were 23% greater (95% CI: 10%, 35%) in upland areas than riparian zones for males across both years, although for females there was no difference between habitats in either year. While colonization rates differed across years, male and female re-attack rates were stable and did not differ from one another by habitat or year. In 2010, low weevil colonization in both riparian zones and upland areas reduced annual attack by weevil larvae on stems in both habitats (Figure 8). This change was more pronounced in upland areas, which showed an 11% reduction (95% CI: 8%, 15%) in attack rates compared to a 7% (95% CI: 4%, 10%) drop in riparian zones. In 2011, colonization rates increased in both habitats, and overall weevil attack rates in both habitats rose to their 2009 levels (Figure 8). In addition to the male difference in re-attack rates between habitat, I observed two other sex-differences in weevil metapopulation dynamics: upland female stems were colonized 6% more than male stems 2010 (95% CI: 1%, 11%) and female stems were attacked 6% more (95% CI: 1%, 11%) than male stems in 2009.

Willow habitat and weevil phenology affect weevil oviposition

Weevil preference was greater for upland as compared to riparian stems for the fall senescent-feeding larval cohort, but these differences were attenuated for the preceding and following flush-feeding spring larval cohorts (Figure 9). For individuals oviposited in the late summer and early fall of 2008, the expected number eggs per stem was 3.4 times greater (95% CI: 1.21, 7.8) for upland stems than for riparian stems, whereas the expected number of early instars per stem was 3.5 times greater (95% CI: 1.8, 6.3) for upland stems than for riparian stems (Figure 9). For individuals that oviposited in the spring of 2008 and 2009, the differences in expected number of early instars between habitats were reduced in magnitude, or eliminated, in the case of eggs in 2009 (Figure 9).

1.4 DISCUSSION

Towards quantifying vigor for herbivores that live between sinks and sources

Vigorous plants (or plant parts) are defined as those that are greater than the population average in terms of size or relative growth rate, whereas plants of below average size are considered chronically stressed (Price, 1991). Using this definition to evaluate the plant vigor hypothesis requires careful consideration of size measurements relative to herbivore phenology, avoiding circular inferences when herbivory itself affects host plant relative growth rates, and properly interpreting how herbivory metrics scale with respect to sink strength and size. Traditionally, vigor comprises two components, size and relative growth rate, both of which are positively associated host plant quality (Price, 1991). When these traits are correlated, the relationship between herbivore attack and size is conditional on the time of sampling. For example, herbivores may preferentially oviposit in small, fast-growing stems which then outgrow larger, slower-growing stems during larval development (Faria and Fernandes, 2001). Sampling stem size only at the time of eclosion would avoid this problem, but only if all plants or plant parts present during sampling were also previously available for attack (Faria and Fernandes, 2001), and if herbivory does not have a large impact on growth rate. Herbivory can affect plant growth directly, by removing tissue or by causing physical damage that disrupts physiological processes, or indirectly through trade-offs between growth and defense (Herms and Mattson, 1992), although these effects can potentially be compensated for (McNaughton, 1983). If herbivory impedes growth, it is not possible to make strong inferences about herbivore response to plant vigor using only size data (see Santos and Almeida-Cortez, 2011; White, 2011; Santos et al., 2011). I avoided sampling issues by tracking all available stems on tagged willow plants over multiple seasons, adding and tracking new stems prior to when they were large enough for weevil attack, and bracketing the portion of each weevil generation where larvae inhabit willow stems with measurements of stem size. To separate the negative effect of weevil herbivory on relative growth rate from the attractive effect of willow stem size on herbivore presence, I included both stem size and relative growth rate in my stem-occupancy model.

Willow stems grew slower when colonized by weevil larvae (Figure 4A), whereas re-attacked stems did not show similar reductions in relative growth rate (Figure 4B) but grew slower than previously un-attacked stems (Table 1,2). This suggests that weevils have an immediate and lasting effect on willow stem growth, weakening stems beyond just the initial year of attack regardless of re-attack in future years. This is not unexpected, given the observed intensity of weevil attack and resulting stem mortality, and the degree to which girdling damage from weevil feeding impairs stem physiological functioning. Reduction in growth rate might also be affected by activation of dormant buds along along the base of attacked stems. Stems that survive weevil attack tend to become branchier, and resources devoted to these later stems likely precludes growth along the 1st order or tagged 2nd order stems I used to calculate relative growth rates.

Higher rates of herbivory on larger plants or plant parts does not, in and of itself, provide conclusive support for the plant vigor hypothesis. I suggest it is necessary to determine how herbivore attack of plants or plant parts (sinks) scales with respect to sink size (the unit area or unit volume of sink available to the herbivore), and with respect to the sink strength (the flux of nutrients into the sink). The sink competition hypothesis provides a way to structure this question for herbivores that feed directly on plant sinks, and can be extended to those herbivores, such as *C. lapathi* larvae, that intercept nutrients moving through the vascular system to sinks located more distantly (Larson and Whitham, 1997). Sink strength is not just a function of sink size, but also the ratio of sinks to sources in independent plant units (IPU's), defined as portions of a plant that are autonomous from one another due to vascular architecture (Larson and Whitham, 1997; Watson and Casper, 1984). Consequently, I treated each stem as an IPU and assumed fluxes of nutrients through the bark at the base of the stem was proportional to the total amount of aboveground biomass supported by that stem, i.e., the sum of all sinks on a stem. By feeding in localized areas of the bark, early weevil instars intercepted nutrients that were translocated seasonally between roots, bark and leaves. Although weevil larvae were not sedentary, movement was slow and required consumption of the bark itself. In this way, weevil larvae were limited to a greater degree by the flux of nutrients in their local environment than by the total area of bark available as a resource. Given this, three conditions must be met to confirm that weevil larvae responded positively to stem vigor:

1. Herbivore attack must scale disproportionately with respect to sink size. This ensures that larger stems were not attacked more simply because they were larger (Faria and Fernandes, 2001).

2. Sink strength must scale disproportionately with respect to sink size. Isometric scaling of a stem's canopy, in terms of its aboveground biomass, to its basal diameter would cause nutrient flux to remain constant across stem sizes. This would preclude weevil larvae from experiencing differences in plant quality in their local environment with respect to stem size.

3. The scaling coefficient for herbivore attack with respect to sink nutrient flux must be $\geqq 1$. A scaling coefficient of < 1 indicates that over some range of stem sizes, weevil larvae did not respond to willow stem vigor.

Note that one can omit conditions (2) and (3) in the special case where herbivores feed exclusively on the entire sink and that sink is the only one located within an IPU.

Weevil attack and leaf biomass of colonizable upland stems scaled disproportionately with stem size (satisfying conditions 1 and 2), while the distribution of weevil larvae within these stems scaled proportionately to bark nutrient fluxes (satisfying condition 3) (Figure 6). For riparian plants, observed herbivory of larger stems is likely due to stems simply being larger, whereas for upland plants larger stems might be of higher quality due to higher sink strength caused by an increased number of vegetative buds. These results are consistent with weevil herbivory patterns observed at other locations in its geographic range, suggesting that stem vigor is likely to be a generally important factor for *C. lapathi* host plant preference or performance. For example, in a survey of of *C. lapathi* attack patterns on 17 *Salix* species across 45 sites in British Columbia, Broberg and Borden (2001) found disproportionately higher attack of larger *Salix* stems than would be expected by chance. In addition, weevil colonization rates were higher on reproductive, as opposed to vegetative, riparian stems (Figure 5). Reproductive buds serve as strong nutrient sinks as well (Dawson and Ehleringer, 1993a,b; Kozlowski, 1992) and contribute positively towards stem sink strength. Taken together, these results show that weevil larvae responded positively to vegetative vigor when colonizing upland willow stems and reproductive vigor when colonizing or re-attacking riparian willow stems. Differences in willow phenology and reproductive allocation between habitats in relation to weevil phenology could be responsible for the effects of reproductive and vegetative vigor. Willow flowered in upland areas on the Pumice Plain from roughly late May to early June, and females set seed by early July. In riparian zones, willow reproductive phenology was usually, perhaps delayed due to lingering snow that accumulates during winter in stream beds. Riparian stems flower more frequently than upland stems (Table 1,2) and their reproductive allocation (quantified in terms of number of catkins, catkin mass, and catkin nitrogen and phosphorus concentrations) greatly exceeded reproductive allocation by upland stems (unpublished data). It is possible that compared to upland areas, reproduction in riparian zones was better synchronized with weevil oviposition, resulting in large nutrient pulses better timed with early instar feeding within stems. My results suggest that weevils imposed an ecological cost on reproduction for riparian willows by making flowering stems more susceptible to weevil attack and possibly more apparent to weevils (Prins et al., 1992; Courtney, 1985). Ecological costs associated with reproduction remains a largely unexplored topic, despite its importance as a selective force on plant life-history (Miller et al., 2008; Obeso, 2002; Klinkhamer et al., 1997). Although weevil larvae do not feed directly on reproductive structures (compared to other studies of ecological costs imposed by herbivorous insects; Miller et al., 2006; Rose et al., 2005), weevil herbivory probably imposes a demographic cost on flowering riparian plants. Weevil attack impacts stem growth rates both in the year of attack and future years (Table 1,2, Figure 4), as well as changing stem architecture. Once attacked, a riparian stem becomes more susceptible to re-attack in future years (Figures 7,8). These factors are likely to reduce future reproductive allocation and seed viability.

Simultaneous support for plant vigor and stress hypotheses

I found that weevil herbivory was positively associated with both vegetative and reproductive vigor, and with the seasonally water-stressed upland habitat. Simultaneous support for the plant vigor and plant stress hypotheses has been observed in other systems, generally where flush-feeding herbivores prefer or perform better on the most vigorous plants or plant parts in xeric habitat, as opposed to those in mesic locations. For example, Fernandes et al. (1992) found that while the abundance of *Aciurina trixa* galls on rabbitbrush (*Chrysothamnus nauseous*) was much greater for plants in dry compared to moist sites, females preferred to oviposit and galls developed more frequently in the longest shoots on plants in dry sites (Fernandes, 1992). A similar pattern was observed for various undescribed Cecidomyiidae galling species on Goncalo alves (*Astronium fraxinifolium*) leaves found in harsh cerrado compared to moist forest understory (Jesus et al., 2012). Despite outbreaks of pinyon sawflies (*Neodiprion edulicolis*) occurring most frequently in populations of water-stressed pinyon pine (*Pinus edulis*), *N. edulicolis* females reared on watered and fertilized trees within these populations had the greatest reproductive potential (Mopper and Whitham, 1992). In these cases, mortality factors differed between and within habitats, with different selective forces simultaneously shaping herbivore distribution patterns at different scales. At the habitat scale, predation risks and plant defensive responses were lower in xeric as opposed to mesic habitat (Fernandes and Price, 1992; Fernandes, 1992; Mopper et al., 1991), yet within xeric habitat, flush-feeders preferred or performed better on vigorous plants or plant parts for reasons predicted by the plant vigor and plant stress hypotheses (White, 2009, 1993; Price, 1991; White, 1984).

Although studies are sparse or taxonomically limited, wood-borers show similar patterns to herbivores from other guilds that respond simultaneously to both host plant stress and vigor. Increased performance on water-stressed host trees is usually associated with reduced plant defenses, whereas positive responses to large or fast-growing plants or plant parts are seen for borers whose larvae spend part of their life cycle as flush-feeders. At the guild-level, wood borers respond positively to plant stress (see reviews by Huberty and Denno, 2004; Koricheva et al., 1998; Larsson, 1989). Several studies have documented increased bark beetle (Scolytidae) and longhorn beetle (Cerambycidae) abundance and survivorship on stressed *Pinus* and *Eucalyptus* hosts, respectively (Caldeira et al., 2002; Hanks et al., 1999; Dunn and Lorio, 1993; Hanks et al., 1991; Sjodin et al., 1989; Miller et al., 1986; Lorio and Hodges, 1977). These results have generally been attributed to reductions in constitutive or inducible host plant defenses under water-stress, namely oleoresin exudation pressure (which physically prevents tree access by Scolytid beetles; Hodges and Lorio, 1971), bark moisture (which drowns Cerambycid eggs or young larvae; Hanks et al., 1999, 1991), and hypersensitivity response (which dissuades herbivory by causing necrosis in the cells surrounding scolytid larval galleries; Christiansen et al., 1987). Far fewer studies have examined how wood-borers respond to plant vigor (Cornelissen et al., 2008). Of these, Feller and Mathis (1997) found that the stem-boring cerambycids (*Elaphidion mimeticum* and other *Elaphidion* sp.) responded positively to plant vigor, as these herbivores were more abundant on red mangrove (*Rhizophora mangle*) experimentally fertilized with phosphorus or naturally growing on local nutrient hotspots. Similarly, the shoot-boring moth *Hypsipyla robusta*, whose early instars are flush-feeders within growing shoots, occurred in greater abundance on taller red cedar (*Toona ciliata*) trees (Cunningham and Floyd, 2006; Verma and Kaul, 1996).

I hypothesize that stress-induced differences in the nutritional quality of bark consumed by *C. lapathi* early instars were responsible for weevil herbivory dynamics being simultaneously associated with both host plant stress and vigor. I base this hypothesis on the following points:

1. There is little evidence to suggest that the reductions in host plant defenses that cause wood-borers to show greater abundance on stressed plants were important factors in *C. lapathi*'s preferential colonization and re-attack of seasonally water-stressed *S. sitchensis*. Sap flow did not cause early instar larval drowning or egg pitching in well-watered *Populus* hybrid clones attacked by *C. lapathi*, and the most susceptible clones had the highest bark water content during *C. lapathi* oviposi-

tion (Broberg et al., 2010). Although resistant poplar hybrid clones displayed *C. lapathi* early instar larval antibiosis (Broberg and Borden, 2005; Broberg et al., 2005), a detailed investigation of known susceptible and resistant clones found no clearly defined differences in primary and secondary metabolites, suggesting that resistance likely involves a non-salicylate mechanism (Broberg et al., 2010). There is one reported case of hypersensitivity in *Salix*, where the gall midge *Dasineura marginemtorquens* induces hydrogen peroxide production in galled *Salix viminalis* leaves (Höglund et al., 2005). Hypersensitivity responses to insect herbivores are somewhat rare, and are mainly restricted to sessile-feeders that cannot physically evade such responses (Fernandes, 1992). Although *C. lapathi* early instars are endophytic, their girdling indicates they do move around in the bark while feeding.

2. Early instars often represent the most vulnerable of insect life-stages, and in the case of *C. lapathi* this is likely the case as well (Broberg and Borden, 2005; Zalucki et al., 2002). Early instars typically have the highest relative growth rate and consumption rate, but the lowest gross growth efficiency of all larval stages (Scriber and Slansky, 1981). In many invertebrate species, food nitrogen content is positively correlated with gross growth efficiency, a limiting factor on relative growth rate (Mattson, 1980). Unsurprisingly, early instars show greater selectivity for high quality foods, and increased mortality for early, but not

later, instars, with reductions in plant quality (see reviews by Zalucki et al., 2002; Scriber and Slansky, 1981). Larval antibiosis observed in resistant hybrid poplar clones prevented xylem penetration by *C. lapathi*, indicating that weevil early instars are highly susceptible to bark conditions (Broberg and Borden, 2005).

3. Plant quality should be especially important to early instars of wood borers because faster growth lowers mortality due to mandibular wear by reducing the time interval between molts (Raupp and Denno, 1983). This problem should be exacerbated for young larvae, as their mandibles are less effective for consuming woody plant tissues (Bergvinson et al., 1995). Weevil larvae harvested from willow stems during the course of this study showed high amounts of mandibular wear and a large proportion of mandibles from collected individuals were in apposition, rendering them unable to feed (unpublished data).

4. Bark nutrient content on stressed trees was associated with higher colonization rates of the bark beetle *Phoracantha semipunctata* on blue gum (*Eucalyptus globulus*) (Caldeira et al., 2002) and emerald ash borer (*Agrilus planipennis*) on green ash (*Fraxinus pennsylvanica*) and black ash (*Fraxinus nigra*) (Chen et al., 2011). Also, one of the two *Populus* clones susceptible to *C. lapathi* herbivory had elevated levels of nitrogen, total carbohydrates, and protein during the time

females normally oviposited, suggesting that nutrient content may be important to early instar survival (Broberg et al., 2010).

5. *C. lapathi* preferentially attack stressed plants in dry sites across their geographic range. Broberg and Borden (2001) found that the intensity of weevil attack on *Salix scouleriana* in British Columbia increased drastically on sites that experienced summer drought. In North Dakota, *Salix planifolia* populations that experienced high levels of *C. lapathi* herbivory occurred in dry locations, but weevil pressure was released when these sites received increased soil moisture (Froiland, 1962). Similar patterns of increased *C. lapathi* attack on stressed trees were observed in other studies (Kistek, 1989; Woods et al., 1982).

Weevil adult eclosion occurred late each summer, and coincided with the seasonal dry-down experienced by upland plants (Figures A1,A2). These adults mated and oviposited their first cohort of offspring before overwintering in the leaf litter beneath willows. After hatching, early instars fed in stems prior to overwintering themselves. This feeding occurs at the end of the growing season, when deciduous plants typically re-mobilize leaf nitrogen and phosphorus, exporting amino acids and phosphate via the phloem to perennating structures, such as stems and roots, where it is stored during winter as protein or inorganic phosphorus (Cooke and Weih, 2005). While no information exists on nutrient remobilization in *S. sitchensis*, von Fircks et al. (2001) found that *Salix dasyclados* translocated roughly 40-50% of its leaf nitrogen and 60% of its leaf phosphorus at conclusion of the growing season into stem bark for winter storage. Early instars from this cohort, could be characterized as senescent-feeders, intercepting nutrients moving through the phloem away from senescing leaves. Upland plants experiencing transitory water stress are predicted by the plant stress hypothesis to be of higher host plant quality to senescent-feeders than riparian plants, leading to preferential oviposition or higher performance by early instars in upland plants (White, 2009, 1993, 1984). Higher weevil colonization and re-attack rates in upland stems (Figure 4), a higher overall level of weevil attack on upland stems in all years (Figure 8), and greater numbers of eggs and early instars found in upland stems for the fall cohort only (Figure 9), supported the predictions of the plant stress hypothesis for weevils ovipositing in the late summer and early fall.

After exiting diapause in late spring, adults oviposited a second cohort of offspring before dying. Oviposition of and feeding by early instars in this second cohort of offspring coincides with flowering and vegetative bud burst, but not conditions of drought stress (Figures A1,A2). Early instars from this early season larval cohort, can be characterized as flush-feeders, intercepting nutrients being translocated through the phloem from roots and stems to vegetative and reproductive buds (Cooke and Weih, 2005; von Fircks et al., 2001). Large reproductive stems would be predicted by the plant vigor hypothesis to be of higher host plant quality to flush-feeders than small vegetative stems (White, 2009; Price, 1991). Weevils would preferentially oviposit in such stem, and early instars would show higher performance thereon. Disproportionate colonization of upland stems based on size (Figure 6), proportional scaling of expected larval density with respect to stem nutrient flux (Figure 6), and a colonization and re-attack preference for reproductive, as opposed to vegetative, riparian stems (Figure 5), suggest that the numbers of reproductive and vegetative buds were positively associated with weevil colonization. These results supported the predictions of the plant vigor hypothesis for weevils oviposited in the spring.

The simultaneous response of weevils to willow vigor and water-stress highlights how the plant stress and vigor hypotheses are, at their core, phenological explanations for herbivorous insect abundance dynamics. Both assume synchronization of host plant resources with the stage of an herbivore's population that has the largest impact on its intrinsic rate of growth (usually early instars) as a necessary condition for stress to affect herbivore population dynamics. White refers to insects that change feeding mode over the course of their life-cycle as "double-dippers" (White, 2009). *C. lapathi* is a different kind of double-dipper, as its semi-voltinism, combined with host plant conditions at the times of oviposition, resulted in a portion of its offspring being senescent feeders while others are flush-feeders. I suggest this alternating feeding mode as the reason why weevil response to both transitory water stress and chronic nutrient stress was consistent with the predictions of both the plant stress and vigor hypotheses.

In general, herbivorous insects simultaneously responding to host plant stress and vigor, such as the weevil-willow interaction examined in this study, do more than highlight the false dichotomy of the plant stress and plant vigor hypothesis (White, 2009). They raise the issue that these hypotheses are being over-extended in regards to predicting herbivore response to stress. The plant stress and plant vigor hypotheses were originally conceived to explain how stress affects nutrient availability to herbivores. I disagree with White (2009) that other host physiological responses, such as changes in water content or turgor pressure (see reviews by Huberty and Denno, 2004; Larsson, 1989), should not also be considered as part of the plant or pulse stress hypotheses. These physiological responses are relevant, as they dictate whether herbivores can physically access enhanced nutrient availability in plant tissues experiencing transitory stress or metabolically benefit from increased plant quality once these tissues are consumed. However, the degree to which stress affects trophic interactions and plant defenses (excluding the case of nutrient quality as a form of plant defense) should remain outside the domain of these hypotheses. In the case of plant defense, there is already a substantial body of theory devoted to explaining plasticity in physical and chemical defenses due to acute environmental stress or chronic resource scarcity (Herms and Mattson, 1992). A better approach would be to consider plant defenses and nutrient quality as simultaneous factors affecting herbivorous insect response to stress, as opposed to subsuming defense responses within the stress/vigor paradigm. Also, the plant stress and vigor hypotheses should be integrated into a single framework regarding herbivore response to stressed host plants. This integrated hypothesis need not be new, but rather a combination of the sink-competition hypothesis (Larson and Whitham, 1997), which has added a mechanistic basis to the original plant vigor hypothesis, and, in the case of water stress, the pulse-stress hypothesis (Huberty and Denno, 2004), which focuses on how herbivores deal with several plant responses to stress besides nutrient remobilization.

Effects of sex-biased herbivory were limited

Dioecious host plants often experience sex-biased herbivory, with the common pattern being that males suffer greater damage than females (Cornelissen and Stiling, 2005; Ågren et al., 1999). In this study, sex-biased weevil attack was caused by two phenomena: 1) sexual dimorphism in traits related to plant quality (stem size and reproductive status), and 2) sexual dimorphism in weevil response to plant quality (due to unknown third-party traits that differ between the sexes). For example, female host plants may grow faster early in the growing season to compensate for the high reproductive cost of fruit production (see review by Obeso, 2002). As a result, for stems of any given size, flush-feeding weevil larvae may prefer or perform better on the sex whose allocation to vegetative growth is better synchronized with their larval development. My stem-occupancy model allowed us to parse these two phenomena for both weevil colonization and re-attack of willow, and scale their effects up to the Pumice Plain willow population.

I observed limited sexual dimorphism in the stem-level vigor covariates, stem size and frequency of reproduction, and weevil response to stem size and reproductive frequency did not vary by sex, except in the case of re-attack of upland stems. This lack of a sex-difference in weevil response to reproduction is counter-intuitive considering there were large differences in nutrient allocation to reproduction between male and female riparian willows. However, it is possible that nutrients needed for setting seed were remobilized from leaves and shoots near reproductive structures (Bañuelos and Obeso, 2004), and were not accessible to early weevil instars feeding at the base of stems. In upland areas, the disproportionate increase in weevil colonization with respect to stem size was the same for both male and females (Figure 6), implying that constitutive defenses (measured as the complement of the colonization probability) do not differ by sex. This result is contrary to the often observed male-biased herbivory in *Salix* (Boecklen et al., 1994; Hjältén, 1992; Danell et al., 1991; Boecklen et al., 1990; Alliende and Harper, 1989; Elmqvist et al., 1988; Danell et al., 1985, but see

Mosbacher et al., 2013; Fritz et al., 2003; Kopelke et al., 2003; Predavec and Danell, 2001). However, this is the first study of sex biased herbivory in Salicaceae by stem-borers and sex biased herbivory in *Salix* has been shown to depend greatly on herbivore species (Boecklen et al., 1994). In contrast, female upland stems had lower levels of re-attack than males, implying that delayed inducible defenses (measured as the complement of the re-attack probability) do differ by sex (Figure 4B). This effect was habitat-specific, with males differing in induced resistance between riparian and upland zones, whereas female induced resistance remained the same in each habitat. Overall, my results are consistent with the pattern of male-biased herbivory observed in the few papers that have studied inducible defenses (Mooney et al., 2012).

Sex-biased herbivory at the host-plant population level reflects the cumulative effects of sexual dimorphism in plant quality traits as well as herbivore response to these traits. These combined effects need not be reinforcing. In my case, higher colonization rates on upland female stems in 2010 (due to their being larger than upland male stems), offset greater delayed inducible defenses. (Table 1, Figure 8). Sex-biased herbivory has been implicated as a cause of biased sex ratios (Elmqvist et al., 1988) often observed in dioecious plant populations (Allen and Antos, 1993; Bierzychudek and Eckhart, 1988; Lloyd and Webb, 1977). However, this can be difficult to establish, as sex-based differences in reproductive costs (Allen and Antos, 1993; Elmqvist et al., 1991) and spatial segregation of sexes can contribute to such biases. It is unlikely that sex-biased weevil herbivory caused the female bias in willow numbers on the Pumice Plain. Indeed, over the three years of my study, I only observed sex-biased herbivory at the population level once (in 2009, and that was in the opposite direction from expectations with females attacked more than males). Instead, I argue that weevil attacks were driven not by sex per se but by the 'availability' of willow stems. Annual variation in stem availability is, in turn, driven by the sex-dependent demographic processes of willow, which hinge on reproductive allocation, reproductive costs, and compensatory mechanisms. Both the demographic and metapopulation dynamics governing herbivory must be simultaneously modeled to infer if sex-biased herbivory results in sex-biased populations (Ågren et al., 1999).

Weevil resource regulation differs by habitat

Weevil attack dynamics differed considerably between plants in riparian zones and upland areas, resulting in contrasting resource regulation patterns and potentially altering successional trajectories. Annual weevil attack in each habitat was cyclical, with a reduction in attack rates in 2010 followed by a recovery in 2011 (Figure 8A). This was caused by a lower colonization rate in 2010 due to small stem sizes and a low rate of riparian flowering

(Table 1, Figure 8). In 2011, stems available for colonization had become larger and riparian flowering was more frequent, and colonization increased in both habitats (Table 1). Rates of re-attack remained constant across years, indicating that colonization is the dynamic process driving annual variation in weevil herbivory.

The importance of weevil colonization highlights the role resource regulation plays in weevil herbivory dynamics on the Pumice Plain. Weevil attack on upland willow stems results in the juvenilization of willow plants, as stem-boring sustains a positive feedback cycle that replenishes the pool of stems available in future years for later weevil generations on the same plant (Craig, 2010; Craig et al., 1986). Weevil attack caused stems to become branchier, as lateral stems increased in size on attacked stems that survived until the next growing season. Weevil attack also activated dormant buds on the caudex of attacked plants resulting in 1st order stem recruits. In contrast to other examples of juvenilization caused by phytophagous insects (see review by Craig, 2010), weevil resource regulation did not immediately benefit weevil larvae the following year, as stems usually take two or more seasons to become large enough to be attacked. This lag effect was responsible for cyclical weevil herbivory patterns observed in upland areas, and, to a lesser extent, riparian zones. Studies of resource regulation for wood borers are extremely limited (Duval and Whitford, 2008; Utsumi and Ohgushi, 2007), making generalizations difficult. Utsumi and Ohgushi (2007) found that the the swift moth *Endoclita excrescens*, which bores out stems in various willow species, removes apical dominance without feeding on directly apical buds. I found a similar pattern of attack, as weevil larvae galleries occurred at the base of stems or at nodes, yet apical dominance was released. Moreover, the pattern of auxiliary bud activation observed in relation to weevil damage is consistent with both hormonal disruption (Utsumi and Ohgushi, 2007) and direct stimulation from physical damage, an otherwise adaptive response in Salicaceae to flood damage (Karrenberg et al., 2002).

In riparian zones, newly recruited stems were colonized much less frequently be weevils than in upland areas (Figure 7) and the colonization rate did not vary much with size (Figure 6). This change in weevil colonization as compared to upland areas had a profound effect on willow density and structure, as riparian stems grew to a size where stem-level tolerance for weevil herbivory became more important than plant-level resource regulation by weevils through juvenilization. I attribute this difference in stem mortality to lower densities of weevil larvae in riparian stems, as senescent feeding fall cohort was largely restricted to seasonally water stressed upland stems (Figure 9). These contrasting colonization patterns underpin the pronounced differences in willow spread on the Pumice Plain. In riparian zones, willows form dense canopies and are the dominant woody shrub. In upland areas, often only a few meters away, willow plants are sparse and shrubby. Other studies of primary succession have found that fast-growing competitive woody plants, such as willow, become established before giving way to seres dominated by slower-growing stress-tolerant woody plants (Walker and Chapin, 1986; Walker et al., 1986). It is likely that the juvenilization of upland willows by weevils is delaying the establishment of a willow dominated sere, allowing for alternative community trajectories.

Why detection matters in plant herbivore studies

Since their introduction a decade ago, statistical methods accounting for detection errors in observational studies (MacKenzie et al., 2003; Tyre et al., 2003; MacKenzie et al., 2002) have become widely used throughout ecology. One exception is insect population ecology, where few studies have modeled detection when investigating questions of occurrence or dynamics (Chiari et al., 2013; Govindan et al., 2012; Russo et al., 2011; Kéry et al., 2009; Sileshi, 2007). Instead, detection is usually assumed to be perfect in observational studies of insect herbivory, despite the fact that insects are often cryptic and easy to miscount. When the detection rate is < 1, species distribution models are modeling the apparent, as opposed to true, species distribution, which biases estimates of occupancy or vital rates towards zero (Kéry et al., 2010). Even low levels of non-detection biases the estimated relationship between these state variables and model covariates, reducing parameter precision (Gu and Swihart, 2004). Furthermore, model covariates that are also confounded with detection leads to biased predictions of species distributions (Kéry et al., 2010). This last issue may be crucial for studies that focus on how vegetation architecture and texture affect insect herbivore abundance, as these factors are also likely to be confounded with detection of insects in experimental plots or survey sites.

My study provides a cautionary tale of why it is important to model detection even when the detection rate was very high, in my case over 90% in both upland and riparian habitat for stems of average size. Detection of weevil larvae in riparian zones was lower than in upland areas due to fact that in the riparian zone (where the cramped, tangled complex of stems impeded both movement and visibility) observers had a difficult time inspecting all portions of a stem for evidence of weevils (Figure 2). Upland willows grew more sparsely and plant architecture was less complicated allowing observers easy access to all sides of a stem. In addition, stem size had a large positive effect on detection rates for upland stems, but less so for riparian ones. Detection was likely correlated with underlying weevil larvae abundance in stems; large upland stems had many exit holes and large amounts of frass making detection relatively easy. For smaller stems, the observer might have to locate very few or even a single exit hole. The interaction between habitat and size on detection was consistent with the fact that the scaling coefficient for expected larval density in riparian stems was small (Figure 6), meaning there were fewer cases in riparian zones of large stems riddled with exit holes. Despite the high detection rates in both habitats, if I had assumed that detection was perfect, I would have predicted that weevil larvae were not disproportionately attacking larger upland stems. As a consequence, I would have inferred that weevil larvae did not respond to vegetative vigor, a finding which would have substantially changed the conclusions of this study.

Table 1: Mean stem size, relative growth rate, and flowering frequency for male and female stems in each habitat each year that are available for colonization by weevils. Geometric means are reported for stem size and relative growth rate. Error bars represent Bayesian 95% credible intervals of posterior distributions of the group means. The first set of letters is for pairwise comparisons between male and female stems within habitats and years. The second set of letters is for pairwise comparisons between riparian and upland stems within sexes and years. For stems in each sex and habitat, I compare mean values across years. Different or bolded (in the case of comparisons across years) letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero.

			Colonization					
	Habitat	Sex	2010			2011		
Size	Riparian	Male	20.53	(18.73 – 22.39)	**a,a**	26.35	(23.95 – 29.00)	**a,a**
	Riparian	Female	21.97	(20.04 – 23.99)	**a,a**	28.71	(26.29 – 31.33)	**a,a**
	Upland	Male	11.97	(11.29 –12.64)	**a,b**	14.30	(13.15 – 15.48)	**a,b**
	Upland	Female	13.23	(12.62 –13.84)	**b,b**	15.71	(14.64 – 16.78)	**a,b**
RGR	Riparian	Male	0.16	(0.15 – 0.18)	a,a	0.18	(0.16 – 0.19)	a,a
	Riparian	Female	0.17	(0.15 – 0.18)	**a,a**	0.15	(0.14 – 0.16)	**b,a**
	Upland	Male	0.44	(0.41 – 0.47)	**a,b**	0.27	(0.24 – 0.29)	**a,b**
	Upland	Female	0.41	(0.39 – 0.43)	**a,b**	0.30	(0.27 – 0.32)	**a,b**
Flowering	Riparian	Male	0.47	(0.40 – 0.55)	**a,a**	0.63	(0.54 – 0.70)	**a,a**
	Riparian	Female	0.47	(0.40 – 0.55)	**a,a**	0.69	(0.62 – 0.75)	**a,a**
	Upland	Male	0.24	(0.18 – 0.31)	**a,b**	0.46	(0.36 – 0.56)	**a,b**
	Upland	Female	0.16	(0.12 - 0.20)	**b,b**	0.34	(0.27 – 0.42)	**a,b**

Table 2: Mean stem size, relative growth rate, and flowering frequency for male and female stems in each habitat each year that are available for re-attack by weevils. Geometric means are reported for stem size and relative growth rate. Error bars represent Bayesian 95% credible intervals of posterior distributions of the group means. The first set of letters is for pairwise comparisons between male and female stems within habitats and years. The second set of letters is for pairwise comparisons between riparian and upland stems within sexes and years. For stems in each sex and habitat, I compare mean values across years. Different or bolded (in the case of comparisons across years) letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero.

			Re-attack					
	Habitat	Sex	2010			2011		
Size	Riparian	Male	46.99	(43.69 – 50.55)	a,a	48.57	(44.67 – 52.61)	a,a
	Riparian	Female	39.79	(37.5 – 42.33)	**b,a**	46.32	(42.98 – 49.92)	**a,a**
	Upland	Male	22.71	(21.05 – 24.53)	a,b	23.08	(20.91 – 25.36)	a,b
	Upland	Female	24.55	(23.30 – 25.79)	a,b	26.00	(24.46 – 27.53)	a,b
RGR	Riparian	Male	0.10	(0.09 – 0.10)	**a,b**	0.12	(0.11 – 0.13)	**a,a**
	Riparian	Female	0.11	(0.10 – 0.12)	b,a	0.11	(0.11 – 0.12)	a,a
	Upland	Male	0.23	(0.21 – 0.25)	**a,b**	0.17	(0.16 – 0.19)	**a,b**
	Upland	Female	0.21	(0.19 – 0.22)	**b,b**	0.17	(0.16 – 0.18)	**a,b**
Flowering	Riparian	Male	0.81	(0.73 – 0.88)	**a,a**	0.95	(0.89 – 0.99)	**a,a**
	Riparian	Female	0.71	(0.64 – 0.78)	**a,a**	0.85	(0.77 – 0.92)	**b,a**
	Upland	Male	0.37	(0.26 – 0.50)	**a,b**	0.81	(0.69 – 0.91)	**a,b**
	Upland	Female	0.42	(0.34 – 0.50)	**a,b**	0.70	(0.61 – 0.78)	**a,b**

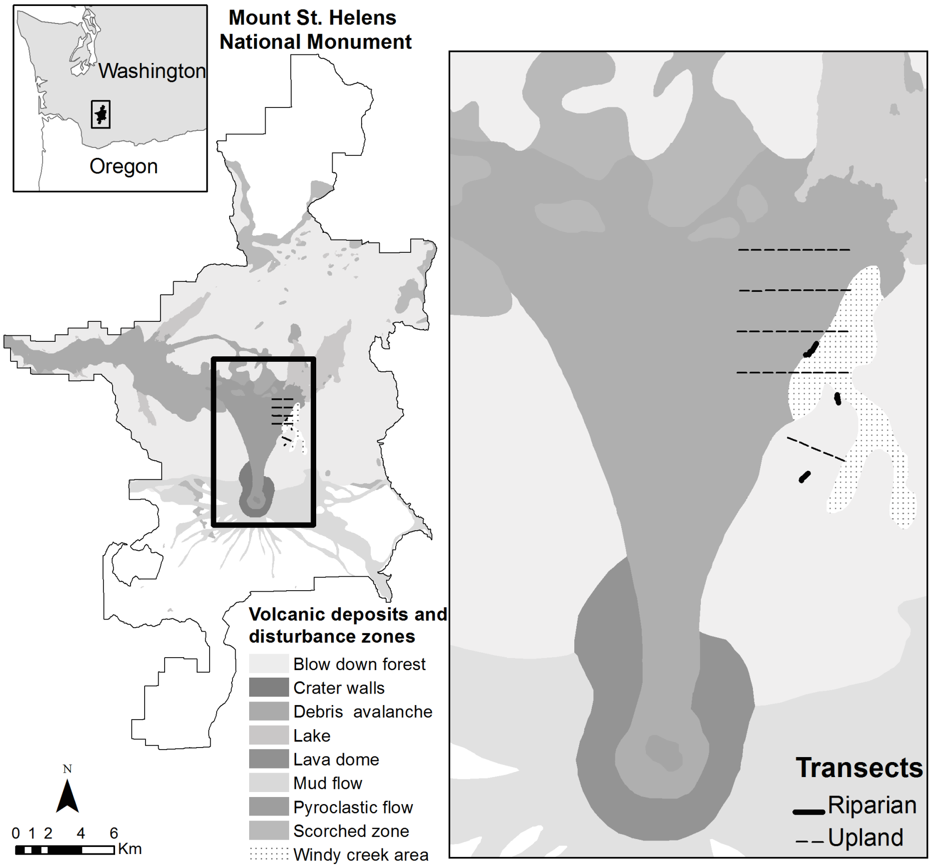

Figure 1: Distribution of primary volcanic deposits and disturbance zones of the 1980 Mount St. Helens eruptions (Adapted from Swanson and Major, 2005). The Pumice Plain is the eastern lobe of the pyroclastic flow and the Windy creek deposit. I denoted the upland transects (hatched lines) and riparian transects (solid lines) along which I tagged plants for my willow-weevil surveys.

Figure 2: (A) *Salix* growing densely along narrow perennial riparian zones and sparsely in seasonally dry upland habitat in 2010. (B) Visible damage to willow stems from *C. lapathi* larval galleries. Pictured are exit holes packed with weevil frass from galleries excavated in a *S. sitchensis* stem by *C. lapathi* larvae in 2009. Photographs courtesy of Charlie M. Crisafulli.

Figure 3: (A) Mating *C. lapathi* adults in spring 2009 near galleries excavated by weevil larvae oviposited in summer 2008 by adults from the same generation. Early instars oviposited in spring 2009 were flush-feeders while those from the previous summer were senescent feeders. (B) Damage to *S. sitchensis* stems from *C. lapathi* larval galleries. Pictured is a late stage weevil larvae just prior to pupation in summer 1992. Photographs courtesy of Charlie M. Crisafulli.

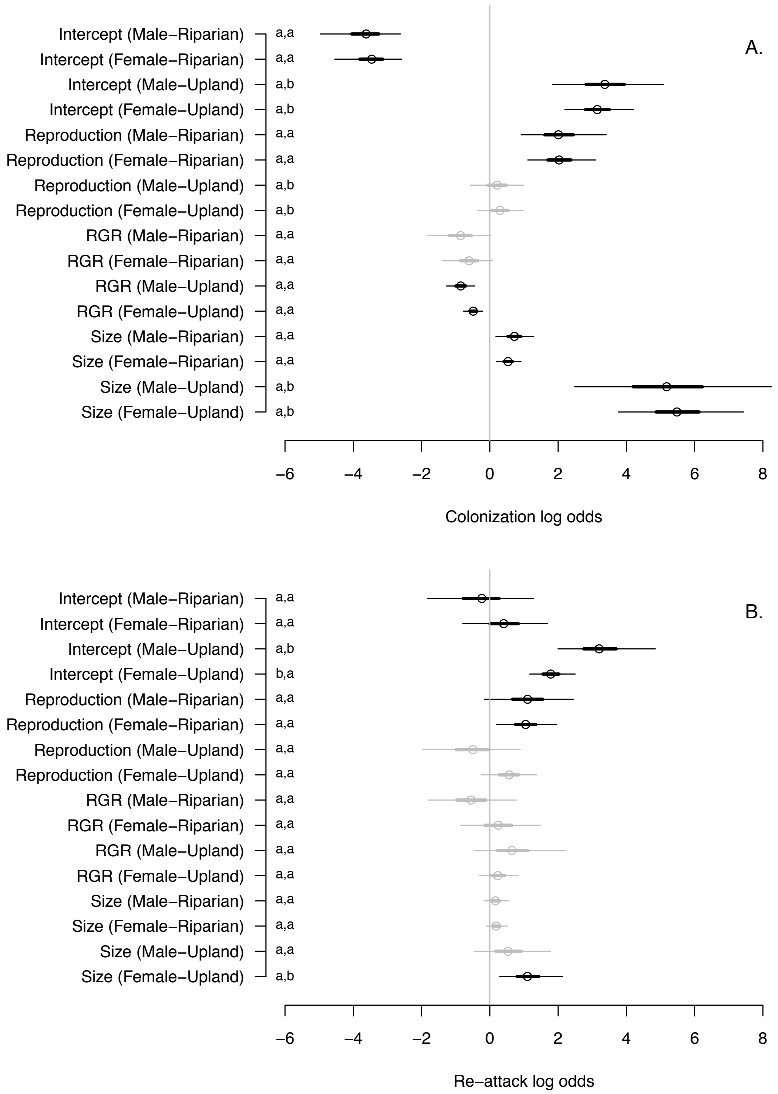

Figure 4: Mean (open circle) with 95% credible intervals (thin lines) and 50% credible intervals (thick lines), of each coefficient's posterior distribution from the stem-occupancy model fitted to observed weevil herbivory data from 2009-2011 for (A) colonization and (B) re-attack. Credible intervals that overlap zero are grayed out (except for intercepts). Intercepts are the plant-level hyperparameter mean colonization or re-attack rates for vegetative stems of average size and growth rate on male and female plants in riparian zones and upland areas. All stem-level parameters represent habitat and sex specific effects. Reproduction is the effect of stem flowering, RGR is the effect of stem relative growth rate, and size is the effect of stem size. All parameters are on the logit scale. Along the vertical axis I display four pairwise comparisons for each covariate (including the intercept). The first set of letters is for pairwise comparisons between male and female stems within habitats. The second set of letters is for pairwise comparisons between riparian and upland stems within sexes. Different letters indicate that the 95% credible interval of the posterior distribution of the difference between the two parameters being compared does not overlap zero.

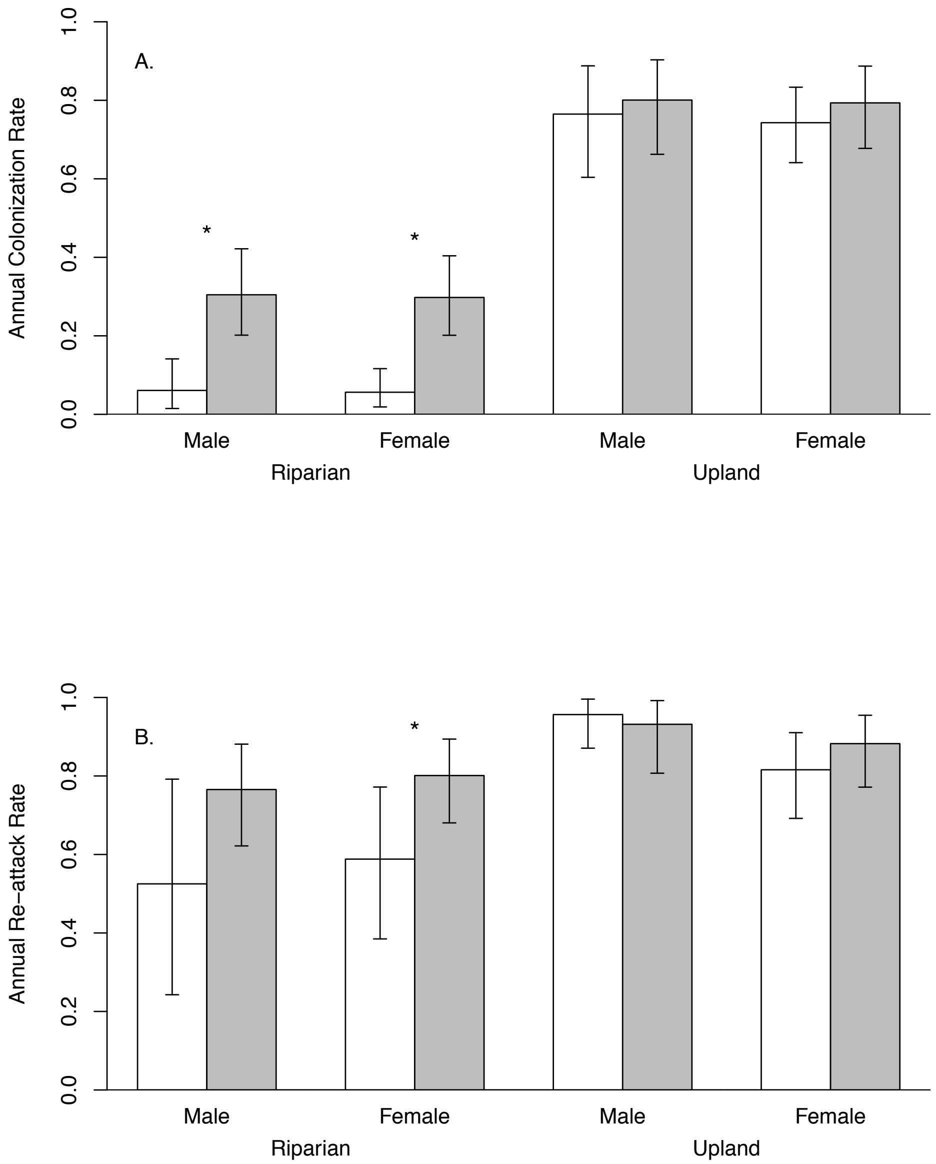

Figure 5: Mean (A) colonization and (B) re-attack annual rates by weevils on vegetative (white bars) and reproductive (gray bars) stems of average size and growth rate within each habitat. Means were calculated as derived quantities from the stem-occupancy model coefficients. Error bars represent Bayesian 95% credible intervals of posterior distributions of the means. Asterisks indicate that the 95% Bayesian credible interval of the posterior distribution for the effect of reproduction (measured as the difference in attack rate between vegetative and reproductive stems) does not overlap zero.

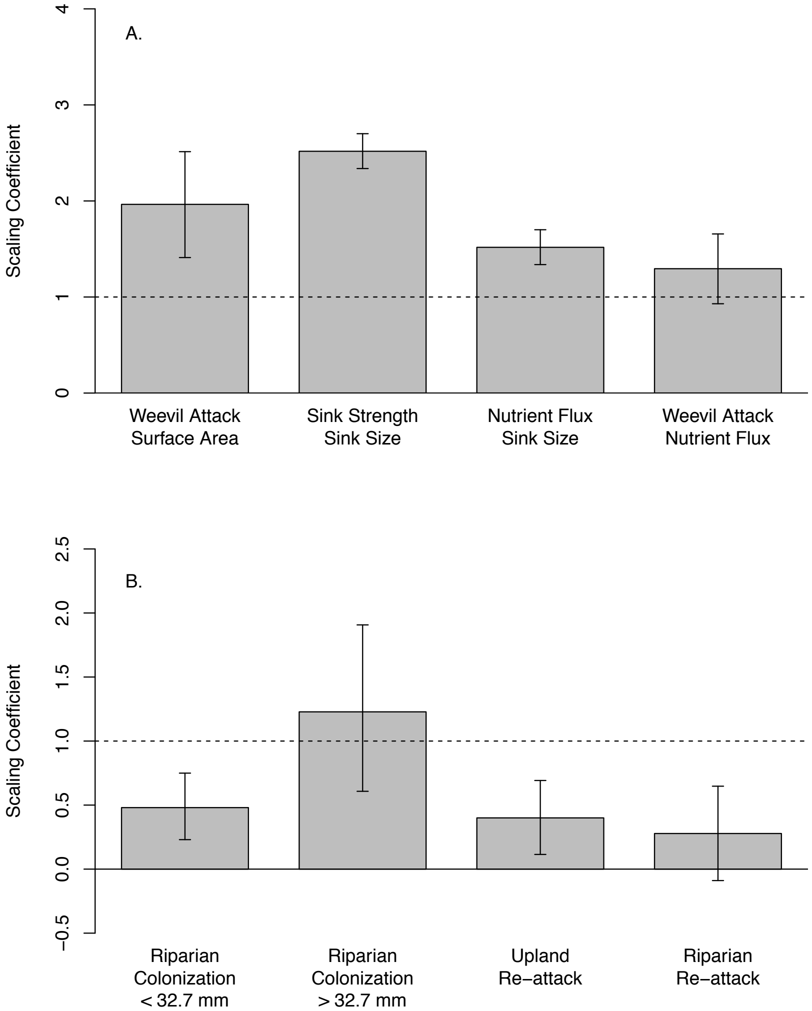

Figure 6: (A) Mean scaling coefficient of expected weevil larval density per stem with respect to stem surface area, stem sink strength with respect to stem size (basal diameter), stem nutrient flux with respect to stem surface area, and expected weevil larval density with respect to stem nutrient flux for upland vegetative stems available for colonization. (B) Mean scaling coefficients for riparian vegetative stems available for colonization for stems below and above the estimated break point (32.7 mm in basal diameter) and for upland and riparian vegetative stems available for re-attack. Upland and riparian colonization and re-attack rates were calculated for stems of average relative growth rate in each habitat and were averaged across sex prior to estimating the scaling coefficient. Credible intervals containing one (the dotted line) indicate proportional scaling. Credible intervals greater than one indicate disproportionate scaling, whereas credible intervals containing one indicate proportional scaling. The credible interval in (B) containing zero indicates expected weevil larval density per stem is invariant with respect to size. Error bars represent 95% credible intervals of the posterior distributions of the scaling coefficients.

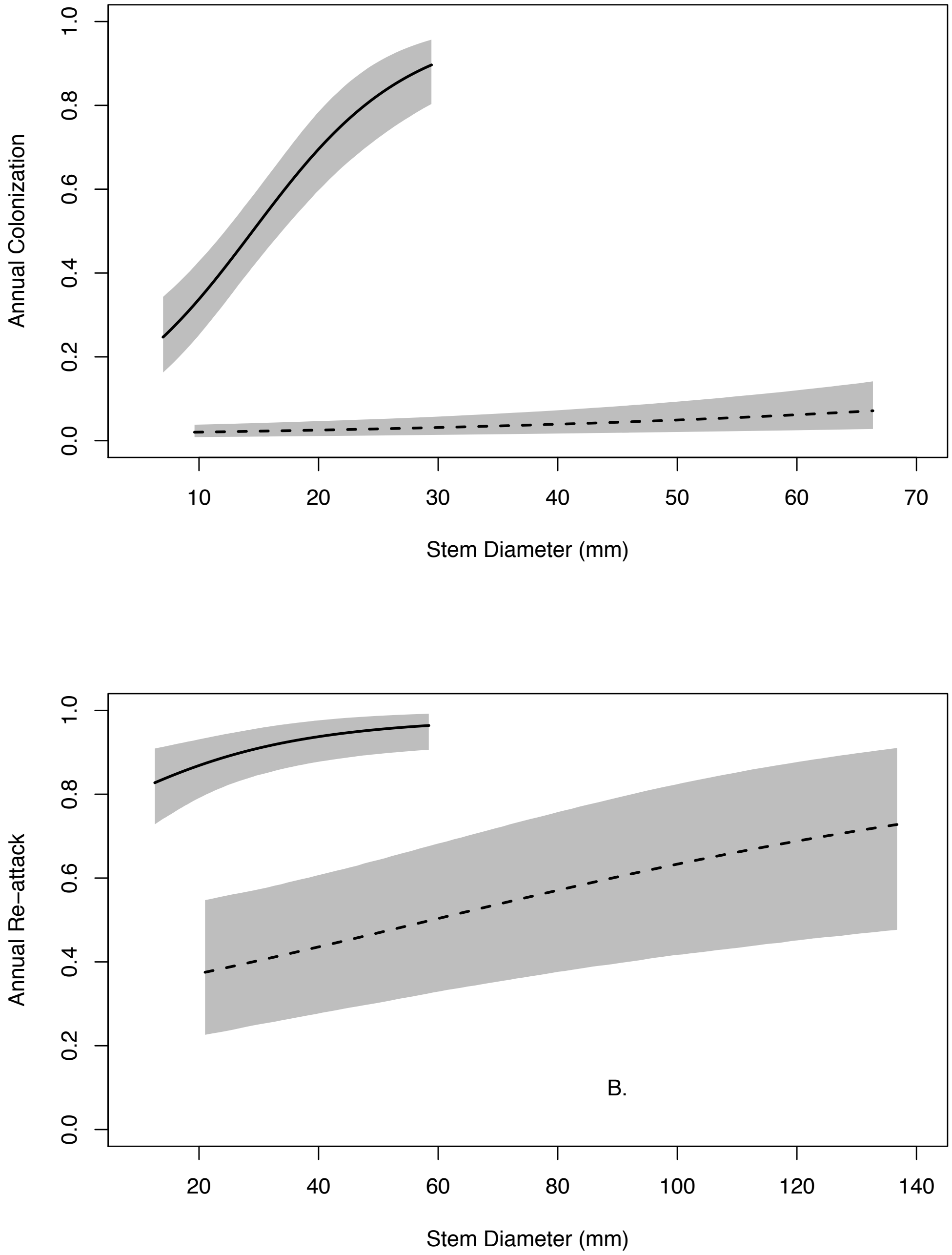

Figure 7: Mean annual (A) colonization and (B) re-attack rates by weevils on upland (solid) and riparian (dotted) stems of average relative growth rate in each habitat with respect to size. Vital rates were calculated as derived quantities from the stem-occupancy model coefficients. In each habitat, vital rates were averaged over male-vegetative, male-flowering, female-vegetative, and female-flowering stems for each size. Vital rates are shown over range of stems sizes available in each habitat for colonization and re-attack. Error bars represent 95% credible intervals of the posterior distributions of the vital rates.

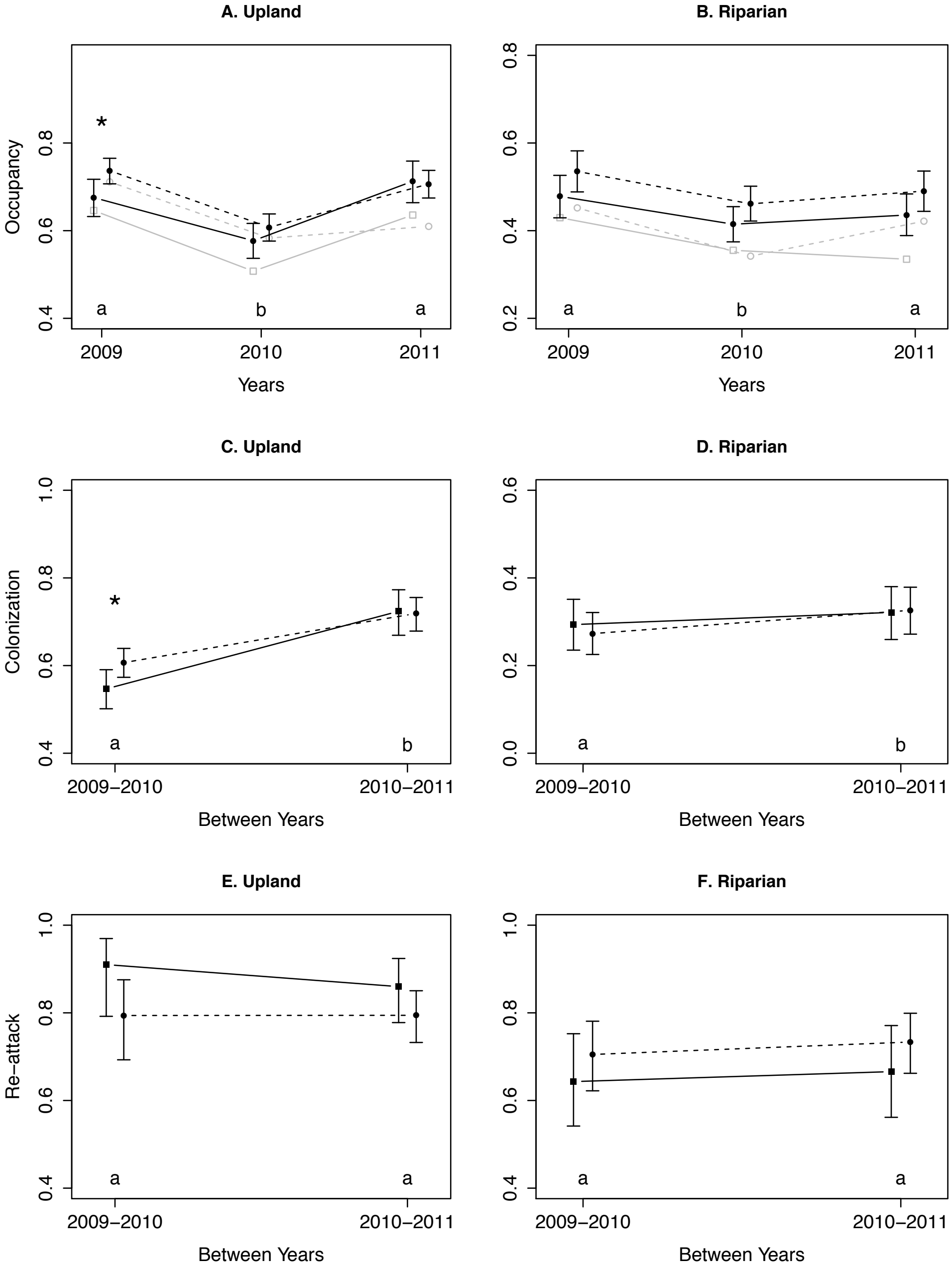

Figure 8: Mean annual attack and vital rates for male (solid) and female (dotted) stems in riparian zones and upland areas on the Pumice Plain. All means were calculated as derived quantities from the stem-occupancy model state parameters. Error bars represent 95% credible intervals of the posterior distributions of these derived quantities. Letters indicate pairwise comparisons between years. Different letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero. Asterisks indicate that the 95% Bayesian credible interval of the posterior distribution for the effect of sex does not overlap zero. Gray lines represent observed annual attack rates.

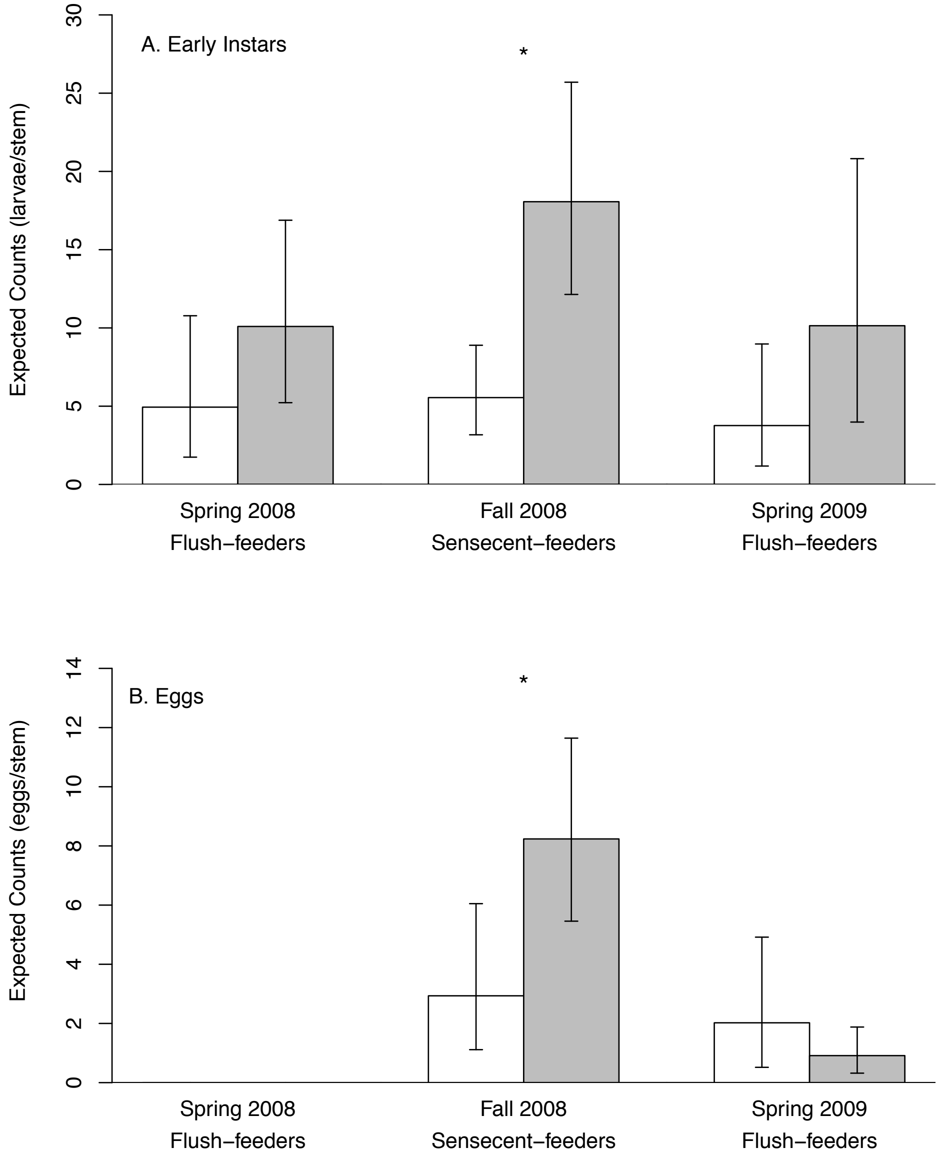

Figure 9: Expected number of (A) early weevil instars and (B) weevil eggs in attacked riparian (white) and upland (gray) stems from three distinct larval cohorts on the Pumice Plain. All means were calculated as derived quantities from Poisson t-tests. Error bars represent 95% credible intervals of the posterior distributions of these derived quantities. Asterisks indicate that the 95% Bayesian credible interval of the posterior distribution for the effect of habitat does not overlap zero.

2

WHAT CAUSES FEMALE BIAS IN THE SECONDARY SEX-RATIO OF *SALIX SITCHENSIS* COLONIZING A PRIMARY SUCCESSIONAL LANDSCAPE?

ABSTRACT

Sex ratios of *Salix* populations are often female-biased, although the mechanisms behind this bias are not well understood. Such biases are especially important for dioecious species in primary succession, as skewed sex ratios can introduce genetic or demographic bottlenecks affecting their ability to successfully invade new areas. I determined the riparian and upland secondary sex ratios of three populations of *Salix sitchensis* (Sitka willow), a dioecious pioneering woody shrub currently colonizing Mount St. Helens after the 1980 eruption, where two of the populations are found on spatially distinct primary successional surfaces and the third is a nearby relictual population serving as their seed source. For one of these populations, I tracked the mortality and flowering intensity of 266 *S. sitchensis* riparian and upland plants over three seasons. I quantified the amount of nitrogen, phosphorus, and carbon allocated to reproduction at the plant level for each sex in each habitat to test whether reproductive effort could result in sex-biased mortality that would bias *Salix sitchensis* secondary sex ratios. I also performed a field experiment, creating artificial streams to test whether vegetative expansion along riparian corridors via willow ramets was

sex-biased. I found a consistent $2:1$ female bias in all three populations, with no evidence of spatial segregation of the sexes by habitat or differences in sex ratio between the source population and the sink populations. Despite female *S. sitchensis* allocating more N, P, and C to reproduction in both riparian and upland habitat, there was no difference in adult mortality between the sexes. Lastly, the establishment rate of *S. sitchensis* vegetative ramets did not differ between the sexes, indicating that vegetative expansion was not injecting additional bias into secondary sex ratios in riparian zones. I suggest that secondary sex ratios in *S. sitchensis* depend on early acting genetic factors affecting the seed sex ratio, sex-biased germination, or seedling mortality, as opposed to late acting ecological factors.

2.1 INTRODUCTION

Dioecy (separate male and female individuals) occurs in a small but widely distributed number of angiosperm taxa, evolving independently multiple times from an ancestral cosexual state (Charlesworth, 2002; Heilbuth, 2000; Renner and Ricklefs, 1995). Natural dioecious plant populations often exhibit some form of biased sex ratio, typically measured as a sex-based difference in the frequency of flowering ramets (Field et al., 2013a; Sinclair et al., 2012; Delph, 1999). Of the cases where sex ratios are biased, the norm appears to be for male-bias, with female bias occurring half as often, and restricted mainly to clonal shrubs with abiotic pollen dispersal (Field et al., 2013a; Sinclair et al., 2012). What has remained unclear are the cause and maintenance of biased sex ratios, specifically does sex bias occur early on, as genetic or molecular factors alter the (primary) seed sex ratio, or later, as ecological factors affect the (secondary) sex ratio of the post-germination phase of a plant's life cycle, or both?

A diverse array of early-acting mechanisms have been advanced to explain deviations from 1:1 in primary sex ratios of dioecious plant populations, as predicted under the null models of negative frequency-dependent selection proposed by Düssing (Edwards, 2000) and Fisher (1930). These range from pre-zygotic factors, such as gametic viability selection (the certation hypothesis; Stehlik et al., 2008; Stehlik and Barrett, 2006, 2005; Taylor et al., 1999; Conn and Blum, 1981; Rychlewski and Zarzycki, 1975; Correns, 1922), X-chromosome meiotic drive (Taylor and Ingvarsson, 2003), Y-chromosome degradation (Stehlik et al., 2007; Smith, 1963), and sexual conflict (the restorer hypothesis; Werren and Beukeboom, 1998; Taylor, 1994), to post-zygotic factors, such as sex-based differences in seed viability. In addition, ecological factors affecting reproduction and dispersal can result in evolutionary stable biased seed sex ratios. For example, sib mating is predicted to cause female-biased seed sex ratios, while local resource competition can lead to a male-biased primary sex ratio when pollen dispersal distances exceed seed dispersal distances(de Jong et al., 2002; Bulmer and Taylor, 1980; Maynard Smith, 1978). Despite the potential importance of all these early-acting factors, limited data exists on seed sex ratios due to the length of time required to grow seed to sexually mature adults and the logistic difficulties in minimizing mortality during this process (but see Stehlik et al., 2008; de Jong et al., 2005; de Jong and Meijden, 2004; Taylor et al., 1999; Alström-Rapaport et al., 1997).

Late-acting ecological factors are rooted in the difference in reproductive allocation between the sexes, which in turn give rise to sexual dimorphisms in non-reproductive traits known to affect the frequency and distribution of each sex in a population at multiple spatial scales. Females typically allocate greater amounts of carbon or total biomass to reproduction than males, which can in turn lead to higher reproductive costs, such as delayed age of or size at first flowering, less frequent flowering, higher mortality following reproductive events, and lower rates of clonal growth (Obeso, 2002; Delph, 1999). These first three reproductive costs can cause male-bias in secondary sex ratios measures of flowering genets (Field et al., 2013a; Barrett et al., 2010). However, male allocation to reproduction may be higher than females for other resource currencies, such as nitrogen, raising the possibility that resources limiting plant growth are sex-specific (Ashman and Baker, 1992; Antos and Allen, 1990; Chapin, 1989). Such differences could lead to higher reproductive costs for males, especially in dioecious species where males allocate large amounts of nitrogen to pollen production (Harris and Pannell, 2008). In addition to early acting factors associated with pollen dispersal distance, higher male reproductive costs associated with pollen production may also be responsible for female-biased secondary sex ratios often observed in dioecious plants that disseminate pollen via wind (Field et al., 2013a; Sinclair et al., 2012). Females can display greater sensitivity to environmental stress than males (Escarré et al., 1990; Popp and Reinartz, 1988; Zimmerman and Lechowicz, 1982), causing broad-scale geographic variation in secondary sex-ratios as females are found less frequently in harsher sites (Li et al., 2007; Espírito-Santo et al., 2003; Marques et al., 2002; Pickering and Hill, 2002; Grant and Mitton, 1979). Male bias in less favorable environments is also seen at finer spatial scales, as the sexes often segregate by habitat (based on water availability) (Bierzychudek and Eckhart, 1988). This spatial segregation of the sexes (SSS) could be due to differential mortality between the sexes as a direct reproductive cost (Bierzychudek and Eckhart, 1988), habitat specialization as an adaptive response to overcome high reproductive costs (Dawson and Ehleringer, 1993b; Dawson and Bliss, 1989b), or niche partitioning as a means to reduce intersexual competition (Mercer and Eppley, 2010; Ågren, 1988; Cox, 1981; Freeman et al., 1976).

The act of colonization itself can also alter seed and secondary sex ratios through founder effects, and such sex biases can be persistent, depending on the degree of isolation between source and sink populations and the frequency of seed rain and establishment events (Field et al., 2013b). Despite this, studies examining how the sex ratios of colonizing dioecious plant populations change over time in primary or early secondary succession or comparing sex ratios between source and sink populations are extremely limited (Litrico et al., 2005; Alliende and Harper, 1989; Faliński, 1980). In colonizing populations (especially during primary succession) vegetative reproduction is often an important driver in species expansion (Walker and Del Moral, 2003; Krasny et al., 1988). While sex bias in clonal expansion of woody plants is well documented (see review by Obeso, 2002), no studies have examined whether sexual dimorphism exists in the establishment rate of asexual propagules in dioecious woody species, a phenomena that has the potential to regularly distort population secondary sex ratios. Vegetative expansion via asexual propagules is common in colonizing riparian woody plants, where ramets severed during flooding events root out downstream of parent plants or in drier sites on nearby floodplains (Karrenberg et al., 2002; Krasny et al., 1988). Sex-ratio bias, either in a colonizing population's founding members or their offspring, can have important genetic and demographic consequences for colonizing plant populations invading new habitats. Skewed sex ratios can reduce the effective population size, causing genetic bottlenecks that limit the ability of a population to adapt to a new environment and increase the role of drift over selection (Sinclair et al., 2012; Barrett et al., 2008). Biased secondary sex ratios can also introduce demographic bottlenecks, resulting in strong strong Allee effects and increasing the risk of local extinction (Xia et al., 2013; and sensu Elam et al., 2007; van Kleunen and Johnson, 2005).

In this study, I examined the adult genet secondary sex ratios of three populations of *Salix sitchensis* Bong. (Sitka willow), a dioecious pioneering woody shrub currently colonizing Mount St. Helens after the 1980 eruption, and investigated whether late acting ecological factors could be responsible for any observed sex ratio biases. The 1980 eruption involved a complex set of geophysical forces that acted singularly or in combination to radically transform a 600 km^2 area supporting forest, riparian and meadow habitats to a complex mosaic of disturbance types that differed dramatically in the types and abundance of biological legacies remaining in the post-eruption environment (Foxworthy and Hill, 1982; Lipman and Mullineaux, 1981). At one end of the disturbance gradient are areas immediately north and west of the crater where all vestiges of life were removed (debris avalanche and pyroclastic flow zones). A region of intermediate disturbance involved leveled forests with scattered and often isolated refugia that collectively contained most species assumed to be present in the pre-eruption landscape, but at vastly reduced abundances (blowdown zone). At the other extreme, beyond the impacts of the lateral blast, the eruption buried the understory community but plant survivorship was high(Dale et al., 2005). Here, I focus on *S. sitchensis* populations colonizing different disturbance zones (pyroclastic flow, debris avalanche and blowdown zones) that represent a gradient of disturbance intensities and biological legacies, as well as other environmental conditions. *S. sitchensis* in the blowdown zone serves as the initial seed source for Sitka willow colonizing the debris avalanche and pyroclastic flow, providing a unique opportunity to compare the sex ratios of two sink populations with their source population. I ask five questions: (1) Are the populations of *S. sitchensis* colonizing three disturbance zones on Mount St. Helens sex-biased? (2) Do *S. sitchensis* populations in these three disturbance zones exhibit spatial segregation of the sexes between upland and riparian habitat? For *S. sitchensis* colonizing the most heavily disturbed region, the pyroclastic flow, is sexual dimorphism in (3) adult survivorship, or (4) vegetative spread through severed ramets responsible for any observed sex bias seen in each habitat, and (5) does nutrient and carbon reproductive allocation differ by sex and habitat?

2.2 METHODS

Species description

Salix sitchensis is the dominant shrub species recolonizing Mount St. Helens after the 1980 eruption. *S. sitchensis* grows densely in hydric habitats near springs, perennial seeps, and watercourses while also occurring less frequently in upland habitat. In upland areas on the pyroclastic flow, flowering occurs over a period of several weeks in late May to early June, just prior to leaf emergence. Flowering in riparian zones on the pyroclastic flow is delayed by 1 – 2 weeks, while flowering occurs earlier in the lower elevation debris avalanche and blowdown zones. *Salix* is dual pollinated by wind and insects, although which mechanism predominates depends on the species and abiotic conditions during flowering (Tamura and Kudo, 2000; Sacchi and Price, 1988; Argus, 1974). For *S. sitchensis* colonizing Mount St. Helens, I do not know whether wind or insect pollination is more responsible for successful fertilization, but I have observed several unknown species of Diptera visiting flowers of *S. sitchensis* shrubs on the pyroclastic flow. *S. sitchensis* sets seed in early July on the pyroclastic flow, and seeds are dispersed by wind and running water (Karrenberg et al., 2002; Johnson, 2000). Seeds are short-lived, non-dormant, and depend critically on favorable microsites for germination (Densmore and Zasada, 1983). *S. sitchensis* also spreads asexually via underground runners and severed stems, and this latter form of propagule dispersal may be a necessary step in the colonization of new areas (Moggridge and Gurnell, 2009; Karrenberg et al., 2002).

Adult genet survivorship and catkin production

I tagged 261 *S. sitchensis* plants in 2009 on the pyroclastic flow and monitored their demography for three growing seasons (2009 – 2011). In upland habitat, I selected plants at 100 m intervals along 1 km subsets of four 2 km + one 1 km permanent transects. These transects form a grid overlaid on the pyroclastic flow, with each separated by a distance of 500 m (Figure 10). In 2009, I sexed (if possible) and marked the five *S. sitchensis* plants nearest to each transect point that had at least one ramet $\geq$ 15 mm in basal diameter. The minimum stem size requirement was to insure that I only tagged adult willow plants. I tracked marked non-reproductive plants in my study even though I could not determine their sex initially, because flowering in future years would allow us to later sex a subset of these plants. Individual upland plants could usually be distinguished visually, but when plants were located very close to one another, or when I was unable to see an obvious caudex due to burial of stems by sediment, I traced shallow roots from each plant to group ramets by genet. In riparian habitat I established paired riparian transects 100 – 140 m in length along both sides of three permanent streams dominated by dense *Salix* and *Alnus* thickets (Figure 10). Visual separation of ramets by genets was not possible due to the high density of *Salix* in riparian zones. To ensure that marked plants represented different individuals, I searched for plants at 5 m intervals, and sexed and marked only plants that had at least one ramet $\geq$ 15 mm in basal diameter and whose ramets all could be clearly traced back to its caudex. I visited all plants twice each season for up to three years. In June of 2010 and 2011, I recorded the whether or not the plant was flowering, and, if so, the number of catkins produced. In August of each year, I recorded plant survivorship and ramet basal diameter. Plants were scored as "alive" if they possessed any ramets with living foliage and "dead" otherwise. For each plant, I standardized its annual catkin production by plant size by dividing the total catkins produced by the sum of the ramet basal diameters each year.

Adult genet sex ratios

I conducted *S. sitchensis* genet sex surveys in 2011 on the pyroclastic flow along the same transects used for tagging and monitoring adult plants. I conducted similar surveys in riparian and upland habitat on the debris avalanche and blowdown zone. For all surveys, I scored plants that had at least one stem ≥ 15 mm in basal diameter as male, female, or unknown (non-reproductive) based on observations of catkins. To insure that I surveyed individual upland genets, I employed the methodology described in the previous section for tagging upland plants. On the pyroclastic flow I scored all adult plants within 25 m of each surveyed upland transect point. In the debris avalanche and blowdown zone I established two (blowdown zone) or three (debris avalanche) band transects (100 m × 10 m) in upland areas and scored all plants meeting the minimum size requirement within these bands. For riparian plants, I surveyed genets in three (pyroclastic flow and debris avalanche) or two (blowdown zone) riparian areas in each disturbance zone. Riparian transects varied in length from 100 – 320 m in length, depending on the stream length. The high density of *Salix* riparian thickets precluded us from sexing all adult genets individually along riparian transects. Instead, I randomly selected a single stem at 5 m intervals on each side of the stream, a distance great enough to safely assume that stems came from different genets. If the selected stem was non-reproductive, I traced it back to its caudex and searched for catkins on the genet's other stems to identify its sex. If no other stems were flowering I scored the plant as unknown (non-reproductive).

Catkin biomass and nutrient content

I collected catkins from male and female upland and riparian *S. sitchensis* plants on the pyroclastic flow, selecting only male catkins whose flowers had reached reproductive maturity but had not yet lost their pollen to wind or pollinators and female catkins whose seeds had matured but had not yet dispersed. Due to the shortness of these phenophases and the spatial and temporal heterogeneity in *S. sitchensis* flowering observed on and between individual plants on Mount St. Helens, collection was done opportunistically along a subset of the transects used for the genet sex surveys. For upland *S. sitchensis*, I harvested 1 – 5 catkins per plant from 25 male plants (June 2011) and 62 female plants (July 2011) located within a band 50 m in width centered on the transect points whose length matched the start and end point used in the genet sex surveys. For riparian *S. sitchensis*, I harvested a similar number of catkins from 20 male and 48 female plants (July 2012) along two of the pyroclastic flow riparian transects. I dried all catkins with 24 – 48 hours of collecting at 60°C for 3 – 5 days in a drying oven prior to weighing. I ground catkins using a Retsch ball grinder, pooling catkins by plant. I determined catkin %P by mass by placing a known mass ($\sim$ 2 mg) of dried, ground leaf material in a muffle furnace at 550°C for two hours (Miller, 1998), followed by colorimetric analysis using the ammonium molybdate method (Clesceri et al., 1998). I combusted samples for carbon and nitrogen elemental analysis with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA). I separated N_2 and CO_2 gases with a 3.0 m GC column (40°C) and analyzed for total area with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) or thermal conductivity detector on the elemental analyzer (Brenna et al., 1997).

Ramet establishment experiment

To test whether asexual colonizing ability is sex-biased, I created artificial streams to experimentally mimic conditions where *S. sitchensis* spreads vegetatively through severed stems. In the spring of 2007, I harvested 120 *S. sitchensis* ramets (60 males and 60 females) in three locations on the pyroclastic flow that had high densities of flowering willow plants. I selected a single living ramet per genet whose basal diameter ranged from 1.5 – 3.5 cm and was free of insect attack and other signs of cankers or injuries. I removed all side branches, trimmed cuttings to a length of 60 – 100 cm, and stored them submerged in cold water for several days prior to planting in an experimental plot located on the pyroclastic flow just south of Forsyth Creek's initial branch point on the northeast flank of Mount St. Helens (46.230881° N, 122.164084° W, elevation 1282 m). This plot contained two dried rill beds 10 m apart, each roughly 1 m wide, 65 m long, and several cm in depth (Figure 11). I used a gravity-fed irrigation system to continually deliver water from nearby Forsyth Creek to each rill at a rate of 1135 – 2270 L/hr during the dry summer months of July - early September from 2007 – 2009. The slope of the experimental plot and topography of the rills channeled the irrigated water in such a way as to create two artificial streams when these rills were watered. Using a completely randomized design, I planted equal numbers of male and female ramets centered along both streams randomized by sex and source location, where each ramet was separated by 50 cm. I inserted ramets to a depth of at least 50 cm and sprayed them twice annually with the broad spectrum pyrethroid bifenthrin (Onyx™ insecticide) to prevent stem attack by the poplar-willow weevil (*Cryptorynchus lapathi* L.), the primary willow herbivore on Mount St. Helens. To minimize elk browse, which is common during the late fall, I constructed an electrified fence around both streams. I allowed ramets to establish over two seasons and in August 2009 scored each ramet as "alive" or "dead" based on the presence of living shoots and foliage.

Data analysis

I used Bayesian binomial generalized linear models to estimate male and female survivorship in 2011 of the riparian and upland adult pyroclastic flow plants tagged in 2009, male and female survivorship in 2009 of the ramets planted in the establishment experiment, and riparian and upland flowering genet sex ratios of flowering plants (the proportion of flowering genets that were female) in each disturbance zone. I used Bayesian linear regressions to estimate male and female catkin production in 2010 and 2011 on reproductive adult plants, and average plant catkin biomass, %C, %N, and %P in each habitat. I estimated the posterior distributions for all parameters in all models using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 (Plummer, 2013a) with the rjags package (Plummer, 2013b) in the R computing environment (R Development Core Team, 2013). I chose all priors to be noninformative and computed three chains for each parameter, each with a different initial value. After a burn-in period of 10,000 iterations, I accumulated 5,000 samples from each chain. I evaluated convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman (Brooks and Gelman, 1998) and assessed model fits with posterior predictive checks (Gelman et al., 2013). I used residual plots to confirm that variances between groups were homogeneous, where appropriate.

All models were means-parameterized, and I computed derived quantities as the difference between two parameters' posterior distributions, or, in the case of reproductive allocation, as the difference between the product of several parameters' posterior distributions. I considered the effect of sex, habitat, or disturbance zone to be important if the Bayesian 95% credible interval of the derived quantity's posterior distribution did not overlap zero, and otherwise unimportant. I computed derived quantities to answer the five questions outlined in the Introduction. 1) To test whether *S. sitchensis* colonizing three disturbance zones on Mount St. Helens were sex-biased, I calculated the habitat-specific effects of disturbance zone on flowering genet sex ratio. 2) To test whether *S. sitchensis* exhibited spatial segregation of the sexes between upland and riparian habitat, I calculated the effects of habitat on the flowering genet sex ratio for each disturbance zone. 3) To test whether *S. sitchensis* adult survivorship on the pyroclastic flow was sex-biased or differed by habitat, I calculated the simple effects of sex and habitat on adult survivorship. 4) To test whether *S. sitchensis* asexual colonization was sex-biased, I calculated the effect of sex on ramet survivorship. Lastly, 5) to test whether *S. sitchensis* investment in reproduction is sexually dimorphic or differed by habitat for different resource currencies, I calculated the simple effects of sex and habitat on catkin-level and plant-level reproductive allocation. In this last case, allocation to reproduction is first computed as the product of catkin mass, catkin production, and concentration of N, P, and C.

A substantial number of genets surveyed were non-reproductive, potentially biasing the population genet sex ratio if the non-reproductive class was disproportionately one sex. Taking advantage of the 2011 reproductive data collected on tagged pyroclastic flow plants, I employed Bayes' Theorem to calculate the unconditional proportion of pyroclastic flow *S. sitchensis* genets in riparian and upland habitat that were female as,

$$P(F) = \frac{P(F \mid R)\, P(R)}{P(R \mid F)}, \tag{14}$$

where $P(R)$ is the probability that a plant was reproductive, $P(R \mid F)$ is the probability that a reproductive plant was female, and $P(F \mid R)$ is the flowering genet sex ratio. I used Bayesian binomial generalized linear models to estimate $P(R)$ and $P(R \mid F)$ in the same manner as described above. I computed the population genet sex ratio, $P(F)$, as a derived quantity, incorporating the uncertainty in my estimates of the probabilities on the right-hand side of Equation 14. Alternatively, I could have used $P(R)$ from the flowering genet survey itself. However, the degree to which the population sex ratio departs from the flowering sex ratio is determined by the ratio of $P(R)$ to $P(R \mid F)$. Temporal heterogeneity in *S. sitchensis* flowering on Mount St. Helens could artificially influence this ratio, given that the pyroclastic flow genet sex survey was conducted later in the growing season than the reproductive survey of tagged plants. I computed the effect of habitat on population genet sex ratio as a derived quantity to test whether *S. sitchensis* exhibited spatial segregation of the sexes between upland and riparian habitat on the pyroclastic flow.

2.3 RESULTS

S. sitchensis flowering genet sex ratios were female-biased approximately $2:1$ in the riparian and upland habitats of all three disturbance zones (Figure 12). Within each habitat, there was no evidence that flowering genet sex ratios differed across disturbance zones (Figure 12). Within each disturbance zone, flowering *S. sitchensis* did not exhibit spatial segregation of sexes across habitats (Figure 12). The population genet sex ratios on the pyroclastic flow were almost identical to the flowering sex ratios observed in each habitat with no evidence of spatial segregation of the sexes, as 69% of the adult genets in riparian and upland habitat were female (riparian 95% CI: 60%, 81%, upland 95% CI: 60%, 83%). Adult survivorship of *S. sitchensis* adult plants on the pyroclastic flow was extremely high and not sex-biased in either riparian or upland habitat (Figure 13). Similarly, the asexual colonizing ability of *S. sitchensis* ramets via severed stems did not vary by plant sex, as roughly equal fractions of experimentally planted male and female ramets established in the artificial streams (Figure 13). In 2010, catkin production differed neither by sex nor habitat, but in 2011 riparian females produced 35% (95% CI: 0%, 85%) more catkins than riparian males and 130% (95% CI: 48%, 321%) more catkins than upland females (Figure

14). Male catkins had higher concentrations of N and P than female catkins in riparian and upland habitat, but female catkins were substantially larger (Table 3). At the plant-level, females allocated more resources to seed set than males did to flowering across all resource currencies measured (C, N, and P) in 2010 and 2011 (Figure 14).

2.4 DISCUSSION

Biased population sex ratios can be caused by genetic or ecological factors that occur sequentially during the life cycle of an organism, and by the act of colonization itself (Field et al., 2013b; Stehlik et al., 2007; de Jong et al., 2002; Obeso, 2002; Delph, 1999; Bulmer and Taylor, 1980; Maynard Smith, 1978; Lloyd and Webb, 1977; Smith, 1963; Correns, 1922; Darwin, 1877). Surveys of flowering genet sex ratios, which typically examine the adult reproductive stage due to ease of sex determination, reflect the cumulative effect of these potential biases. Such surveys make it difficult to disentangle the magnitude and direction of individual effects that function as series of filters as a population cohort moves from gametophyte to adult plant. For example, an observed female bias in a population where females experience higher adult mortality than males could be due to sex-biased adult mortality but also to an (unobserved) female bias in the seed sex ratio or seedling mortality. The use of long-term demographic modeling has been proposed as strategy for understanding how sex-based differences in life-history traits affect secondary sex ratios (Ågren et al., 1999; Waser, 1984). However, this task becomes difficult when a population is not at equilibrium, such as for pioneering dioecious plants that are colonizing new areas where sex bias may be partially determined by the high levels of stochasticity associated with the act of colonization itself. Despite the inability to self-fertilize, dioecious plants are well suited as early colonizers, as they often are wind-dispersed, rely on wind or generalist insect pollinators, and produce large quantities of seed due to their long lifespans (Pannell, 2006).

In this study I quantified the secondary sex ratios of three *S. sitchensis* populations currently colonizing Mount St. Helens, two populations occupying two distinct primary successional landscapes and one relictual population that served as their initial seed source. In all three disturbance zones, I observed a strong $2:1$ female bias (Figure 12), similar to other studies of secondary sex ratio bias in *Salix* (Myers-Smith and Hik, 2012; Hughes et al., 2010; Ueno et al., 2007; Dudley, 2006; de Jong and Meijden, 2004; Predavec and Danell, 2001; Rottenberg, 1998; Alström-Rapaport et al., 1997; Dawson and Bliss, 1989b; Alliende and Harper, 1989; Elmqvist et al., 1988; Crawford and Balfour, 1983; Faliński, 1980), but inconsistent with the generally observed trend (outside of *Salix*) that male plants are more common than female plants on highly disturbed or stressful sites (Li et al., 2007; Espírito-Santo et al., 2003; Marques et al., 2002; Pickering and Hill, 2002; Grant and Mitton, 1979). Researchers have advanced a variety of explanations to explain the consistent female sex ratio bias in *Salix*, ranging from differential mortality due to herbivory, to spatial segregation based on stress gradients, to group selection. Here I investigated potential sexual dimorphism in reproductive allocation, adult mortality, and vegetative reproduction through severed stems as possible explanations for the observed secondary sex ratios. In addition, I examined differences between habitats as well as source and recipient *S. sitchensis* populations to determine if spatial segregation of the sexes or the colonization process itself causes variation in secondary sex ratios. While I recognize that these efforts can only provide an incomplete picture of the causes and maintenance of sex bias these populations, I am able to rule out several factors that are not strong contributors to the consistent female bias in this system.

Reproductive allocation and adult mortality

Sex-biased mortality as a consequence of differing reproductive costs, either directly or indirectly through sex-biased herbivory, is often implicated as a mechanism underlying biased secondary sex ratios in dioecious plants (Obeso, 2002; Delph, 1999; Ågren et al., 1999; Åhman, 1997; Allen and Antos, 1993; Lovett-Doust and Lovett-Doust, 1987; Lloyd and Webb, 1977; Waser, 1984). Typically, females plants allocate more biomass to reproduction than males (see review by Obeso, 2002), resulting in male-biased secondary genet sex ratios (Field et al., 2013a; Sinclair et al., 2012). However, Field et al. (2013a) hypothesized that in the case of dioecious species with wind-dispersed pollen, male allocation to reproduction could possibly exceed females when other resource currencies are considered (Harris and Pannell, 2008), resulting in female-biased secondary sex ratios. I found no support for sex-biased reproductive allocation or mortality influencing *S. sitchensis* secondary sex ratio bias. Although male catkins were more nutrient-rich than female catkins, the larger size and more numerous production of female catkins resulted in female *S. sitchensis* on the pyroclastic flow allocating more N, P, and C to reproduction than do males (Figure 14, Table 3). Despite greater female allocation to reproduction, I did not observe sex-biased mortality for established genets on the pyroclastic flow (Figure 13). Higher reproductive allocation in terms of biomass, N, and P have been observed in natural populations of other *Salix* species (Dudley, 2006; Ueno and Seiwa, 2003; Turcotte and Houle, 2001). While greater female reproductive costs have been documented experimentally in *Salix alaxensis* (Fox and Stevens, 1991), investigations from correlative phenotypic studies into reproductive costs in other *Salix* species have provided mixed results (Ueno et al., 2006; Ueno and Seiwa, 2003; Obeso, 2002; Turcotte and Houle, 2001; Åhman, 1997; Alliende and Harper, 1989; Dawson and Bliss, 1989b).

Interestingly, in cases with data on secondary sex ratios and reproductive allocation for the same *Salix* population, the results are consistent with my findings of a female-biased secondary sex ratio despite greater female reproductive allocation (Ueno et al., 2007, 2006; Dudley, 2006; Ueno and Seiwa, 2003; Turcotte and Houle, 2001). This disparity suggests that 1) sex ratio bias in *Salix* is likely to occur in earlier life stages, such as the gametophyte, seedling, or juvenile plants, and 2) compensatory mechanisms employed by female *Salix* species to offset reproductive costs help reduce sex-biased mortality in reproductively mature plants. For example, female *Salix sachalinensis* and *Salix integra,* both commonly found in riparian areas in Northern Japan, compensated for relatively higher reproductive costs compared to males by increasing the resource gathering capacity of vegetative shoots through a variety of physiological mechanisms (Tozawa et al., 2009; Ueno et al., 2006; Ueno and Seiwa, 2003).

Colonization signature

Colonization of new areas by dioecious plant species, either at the edge of species' ranges or when habitat becomes available through disturbance, can potentially alter colonizing population seed and secondary sex ratios from those in their source populations (Field et al., 2013b; Barrett et al., 2008). The sex ratio of dioecious species' initial colonists are the result of stochastic draws from their donor population's sexual or asexual propagules, whose sex ratios may well differ from one another. These draws can be few in number, even a single chance event, and the number of colonizing individuals may be small, leading to high variability in the sex ratios of early colonizing plant populations. Founder effects are especially pronounced in primary successional seres. Individuals colonizing these landscapes are often long distance colonists , and persistent, as early colonists may often remain non-reproductive for long periods of time and colonization events can be very rare (Walker and Del Moral, 2003). Founder effects alter genetic controls over the seed sex ratio produced by a colonizing population's initial members. This can occur when (in the case of nuclear sex determination) only a subset of sex-determining alleles are either introduced into or drift to fixation in small colonizing populations, and epistasis or dominance is lost (sensu Naciri-Graven and Goudet, 2003; Willis and Orr, 1993).

The sex ratios of colonizing *S. sitchensis* populations on two spatially distinct primary successional surfaces, the pyroclastic flow and the debris avalanche, were initially governed by the seed sex ratio of relictual *S. sitchensis* plants in the blowdown zone that survived the 1980 eruption (pers.

comm. C. Crisafulli). On both the pyroclastic flow and debris avalanche, establishment first occurred in riparian zones shortly after the eruption (1983–1984), after which these colonizers expanded vegetatively along riparian corridors (pers. comm. C. Crisafulli). Although *Salix* seed rain from the blowdone zone was high (Wood and del Moral, 2000), the limited availability of "safe sites" resulted in only a small number of mass synchronous colonization events. These events, which occurred in years with cool, wet summers, were responsible for *S. sitchensis* spread into dry upland areas (pers. comm. C. Crisafulli). In this way, these three *Salix* populations resemble a paired island-mainland system, with limited but recurrent colonization due to establishment barriers, despite consistent seed rain (del Moral and Jones, 2002).

The genet sex ratios of mature adults from these three populations were all equally female-biased (Figure 12). This congruity occurred even though all three populations differ from one another in terms of the relative importance of disturbance frequency, vegetative reproduction along riparian corridors from fragmentation, ecological constraints on invading adjacent upland habitat, and historical contingencies associated with the 1980 eruption. It is possible that the genetic or ecological factors discussed below obviated differences in sex ratio due solely to the colonization process. Alternatively, the colonization signature on sex ratio bias may have been erased through continued immigration onto the debris avalanche and pyroclastic flow from the blowdown zone. However, even if such events transpired, the consistent female bias still suggests that the process of colonization itself does not have a strong persistent effect on *S. sitchensis* secondary sex ratios.

Vegetative reproduction

Pioneering populations in primary successional environments often succeed using vegetative reproduction (Walker and Del Moral, 2003). For example, vegetative expansion was the main contributor to *Salix* spread into upland areas or riparian zones subject to frequent flooding during primary succession along an Alaskan river floodplain (Krasny et al., 1988). Sexual dimorphism in the establishment rate of asexual propagules, such as severed stems, would bias a colonizing population's secondary sex ratios towards the sex that spreads better vegetatively in habitat. Episodic flooding caused by heavy rain events onto snow are the primary source of post-eruption disturbance, although the effects were felt most strongly on the debris avalanche (pers. comm. C. Crisafulli). A single 100-year flooding event (1996) relocated all riparian zones in the Clearwater drainage, resulting in vast areas of fragmented *Salix* stems on the debris avalanche and the pyroclastic flow near Spirit Lake, a portion of which subsequently established. Smaller 5-year flash-flood events scoured riparian areas in both of these disturbance zones, causing further stem fragmentation and re-establishment (pers. comm. C. Crisafulli). I did not find experimental evidence for sexual dimorphism in the establishment from severed stems based on my artificial stream experiment, indicating that asexual reproduction should not inject additional sex ratio biases during colonization (Figure 12). To my knowledge, this is the first study that has tested for sexual dimorphism in vegetative expansion, despite its importance as a means of spread in colonizing *Salix* populations. While I experimentally excluded sex-biased vegetative establishment in riparian habitat, I did not investigate whether vegetative reproduction in upland areas is sex-biased, as all the experimentally planted ramets were well-watered during the dry summer months.

Spatial segregation of sexes

Although male *Salix* plants are more drought-tolerant and more abundant in drier upland sites compared to females (Dudley, 2006; Dawson and Bliss, 1989b), I did not find evidence for moisture-related spatial segregation of the sexes in any of the three disturbance zones, as the sex ratios did not differ between riparian and upland habitat (Figure 12). These results are largely consistent with other studies that find no evidence or weak support for spatial segregation of the sexes along a gradient perpendicular to riparian corridors (Hughes et al., 2010; Ueno et al., 2007; Ueno and Seiwa, 2003; Alliende and Harper, 1989). It is possible that *S. sitchensis* on Mount St. Helens are segregating with respect to some other niche dimension (such as nutrient availability; Dudley, 2006) or that different ecological processes may be at work in each habitat (for example, competitive exclusion in one habitat or differential juvenile mortality in the other). However, an additional explanation might be that the process of upland invasion by *S. sitchensis* is so heavily dependent on microsite availability and seasonal weather conditions as to preclude sex-biased mortality during establishment. If *S. sitchensis* must establish in years where conditions are less stressful, sex-differences in stress tolerance may have a weak effect on survival. This type of colonization process is consistent with the low observed *Salix* mortality in both upland and riparian areas (Figure 13) as well as *Salix* mass establishment events historically observed on the pyroclastic flow and debris avalanche (pers. comm. C. Crisafulli).

Early acting factors implicated

Secondary sex ratios in *S. sitchensis* colonizing Mount St. Helens may depend on either early acting genetic factors affecting the seed sex ratio, or a sex-bias in seed viability or seedling mortality, as opposed to late acting ecological factors. Sex determination in *Salix* appears to be genetic and not environmentally controlled (Alström-Rapaport et al., 1997). None of the 261 tracked *S. sitchensis* plants demonstrated diphasy or produced hermaphroditic flowers over the three year course of my study. Sex chromosomes have not been observed in *Salix*, and the seed sex ratios in experimentally controlled crossings of *Salix viminalis* clones were best explained by a multi-locus autosomal sex determination (Alström-Rapaport et al., 1998, 1997). Lack of sex chromosomes precludes a variety of early acting mechanisms known to bias seed sex ratios, such as certation, X-chromosome meiotic drive, and Y-chromosome degradation. Seed sex ratio bias for dioecious plants where sex determination is under autosomal control is predicted to be the summation of two offsetting phenomena that can lead to different evolutionary stable biased seed sex ratios (de Jong and Klinkhamer, 2005; de Jong and Meijden, 2004; de Jong et al., 2002). High levels of sib mating associated with low seed dispersal can cause female-biased seed sex ratios (Maynard Smith, 1978), while increased pollen relative to seed dispersal distance may reduce local resource competition and promote a male-biased seed sex ratio (Bulmer and Taylor, 1980). Although reported seed sex ratios do not generally support the predictions based on pollen and seed dispersal distance, the lack of sex chromosomes in *Salix* may minimize intragenomic conflict that has been proposed to cause conflicting results in other taxa (see de Jong and Klinkhamer, 2005). For example, of the two studies on *Salix* seed sex ratios, both report strong female bias (de Jong and Meijden, 2004; Alström-Rapaport et al., 1997). Although Salix seeds may disperse great distances, *S. sitchensis* on the pyroclastic flow are heterogeneously distributed because successful establishment hinges on seeds landing in favorable microsites, and could result in high levels of sib mating due to clumping. Also, pollen dispersal distances are likely to be reduced by the wet weather conditions on Mount St. Helens that regularly coincide with pollen availability (Che-Castaldo et al., Chapter 1).

In addition to female-biased seed sex ratios, sex-biased seed germination and seedling mortality could also drive secondary sex ratios. Studies of *Salix* seed sex ratios report no differences between the sexes in seed viability (de Jong and Meijden, 2004; Alström-Rapaport et al., 1997). However, these studies were conducted in such a way as to maximize germination rate for obvious reasons, making it difficult to infer whether sex bias in seed viability exists in natural settings. Male-biased seedling herbivory by small mammals has been proposed as a mechanism explaining female-biased *Salix* secondary sex ratios, leading to the prediction that in *Salix* populations where small mammal herbivory is high, willow populations should be more female-biased (Hjältén, 1992; Danell et al., 1991; Elmqvist et al., 1988; Danell et al., 1985). I did not find evidence for such differential sex ratios on the pyroclastic flow, as small mammal subnivean herbivory is high in riparian zones, but almost non-existent in nearby upland areas, and yet the willow genet sex ratios remain nearly identical (Figure 14). I hypothesize that the strong *S. sitchensis* adult genet female bias observed in all habitats and disturbance zones on Mount St. Helens is caused by female bias in the seed sex ratio. This testable conclusion is similar to those derived in other studies of secondary sex bias in several other willow species (Myers-Smith and Hik, 2012; Ueno et al., 2007), suggesting that female-biased seed sex ratios are common, if not the norm, within *Salix*.

Table 3: Mean number of catkins per mm of stem basal diameter in 2010 and 2011, catkin nutrient content (%C, %N, and %P), and mass by habitat and sex for *S. sitchensis* plants or catkins from the pyroclastic flow. Error bars represent Bayesian 95% credible intervals of posterior distributions of the group means. The first letter in each pair is for pairwise comparisons between male and female plants or catkins within each habitat. The second letter in each pair is for pairwise comparisons between riparian and upland plants or catkins within each sex. When present, different letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero.

	Habitat	N	Male			Female		
2010	Riparian	53,58	0.49	(0.37 – 0.61)	a,a	0.38	(0.27 – 0.49)	a,a
	Upland	26,52	0.28	(0.12 – 0.44)	a,b	0.27	(0.15 – 0.39)	a,a
2011	Riparian	60,58	0.79	(0.59 – 0.98)	a,a	1.07	(0.87 – 1.26)	b,a
	Upland	26,49	0.60	(0.31 – 0.89)	a,b	0.47	(0.26 – 0.67)	a,b
%C	Riparian	20,48	44.61	(44.26 – 44.96)	a,a	45.07	(44.84 – 45.30)	b,a
	Upland	25,62	45.69	(45.38 – 46.01)	a,b	44.63	(44.43 – 44.83)	b,b
%N	Riparian	20,48	3.57	(3.41 – 3.74)	a,a	2.69	(2.59 – 2.80)	b,a
	Upland	25,62	3.60	(3.46 – 3.75)	a,a	1.89	(1.80 – 1.98)	b,b
%P	Riparian	20,32	0.62	(0.58 – 0.67)	a,a	0.48	(0.44 – 0.51)	b,a
	Upland	25,54	0.67	(0.63 – 0.71)	a,a	0.49	(0.47 – 0.52)	b,a
mass	Riparian	20,48	38.64	(33.80 – 43.36)	a,a	204.86	(171.75 – 236.71)	b,a
	Upland	25,62	27.90	(23.63 – 32.19)	a,b	126.76	(98.11 – 155.87)	b,b

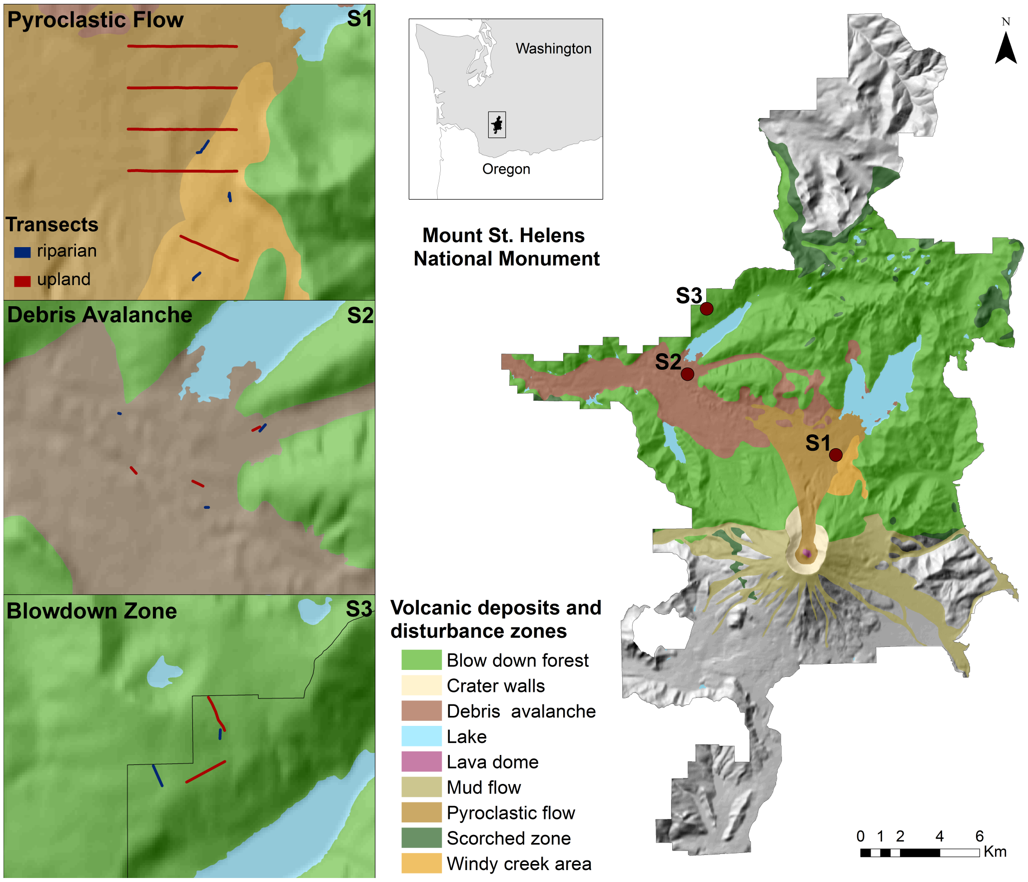

Figure 10: Distribution of primary volcanic deposits and disturbance zones of the 1980 Mount St. Helens eruptions (Adapted from Swanson and Major, 2005). I denoted upland (red lines) and riparian (blue lines) transects along which genet sex surveys were conducted in 2011, and in the case of the pyroclastic flow, where plants were tagged and monitored from 2009–2011 and catkins were collected in 2011 and 2012.

Figure 11: Layout of the ramet establishment experiment in summer 2009, just after measuring ramet survivorship. The colored flags mark surviving ramets in the eastern rill.

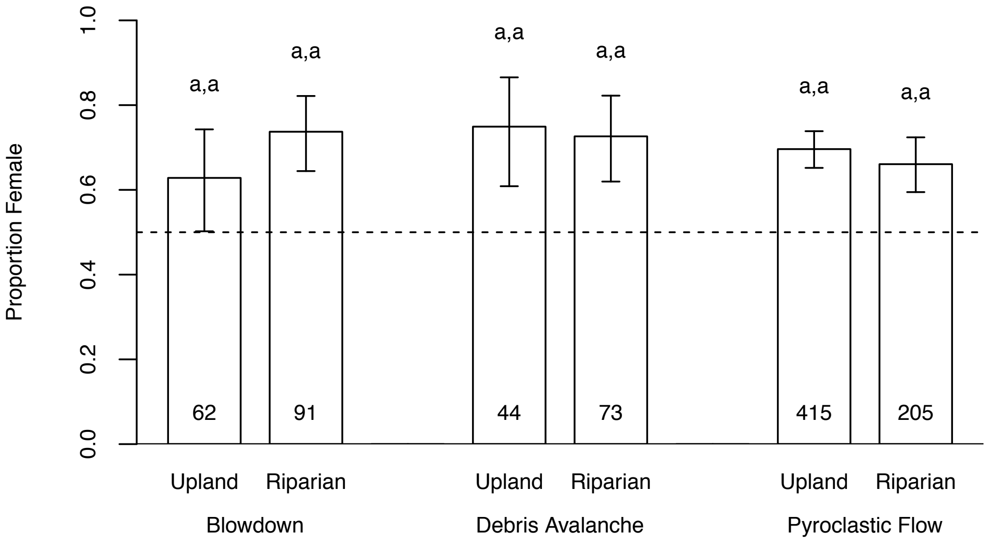

Figure 12: Mean proportion of flowering genet sex ratios for adult riparian and upland *S. sitchensis* plants in three disturbance zones that are female in 2011. Error bars represent Bayesian 95% credible intervals of posterior distributions of the means. The first letter in each pair is for the pairwise comparison between riparian and upland sex ratios within each disturbance zone. The second set letter in each pair is for pairwise comparisons between disturbance zones for each habitat. The same letters for each pairwise comparison indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared overlaps zero.

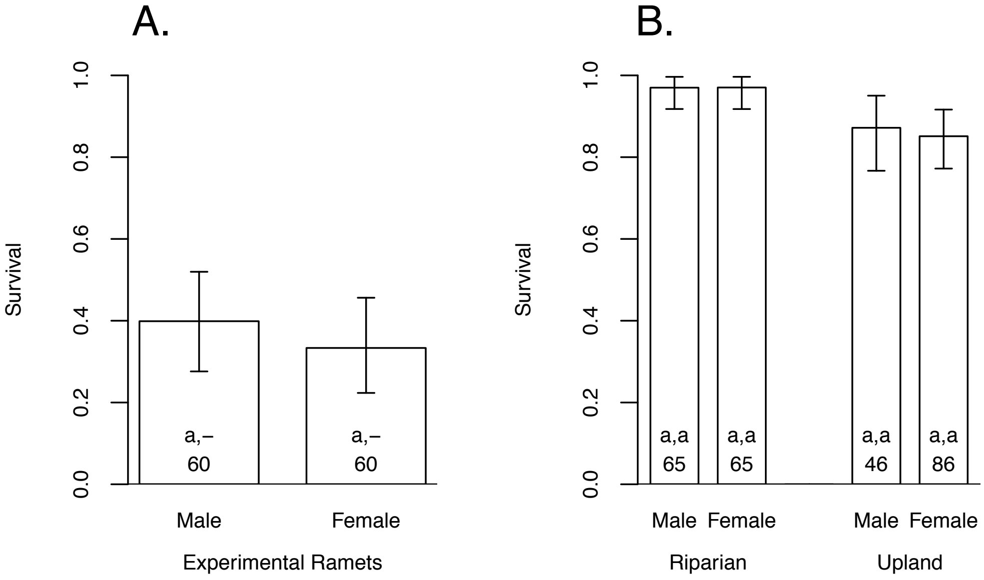

Figure 13: Mean survival rate of (A) experimentally planted *S. sitchensis* ramets and (B) naturally growing adult riparian and upland *S. sitchensis* pyroclastic flow plants by sex from 2009 to 2011. Error bars represent Bayesian 95% credible intervals of posterior distributions of the means. The first letter in each pair is for the pairwise comparison between male and female plants (within each habitat in the case of naturally growing plants). The second letter in each pair is for pairwise comparisons between riparian and upland habitat for each sex (this is not applicable for the experimental ramets and is designated as a dash). When present, different letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero.

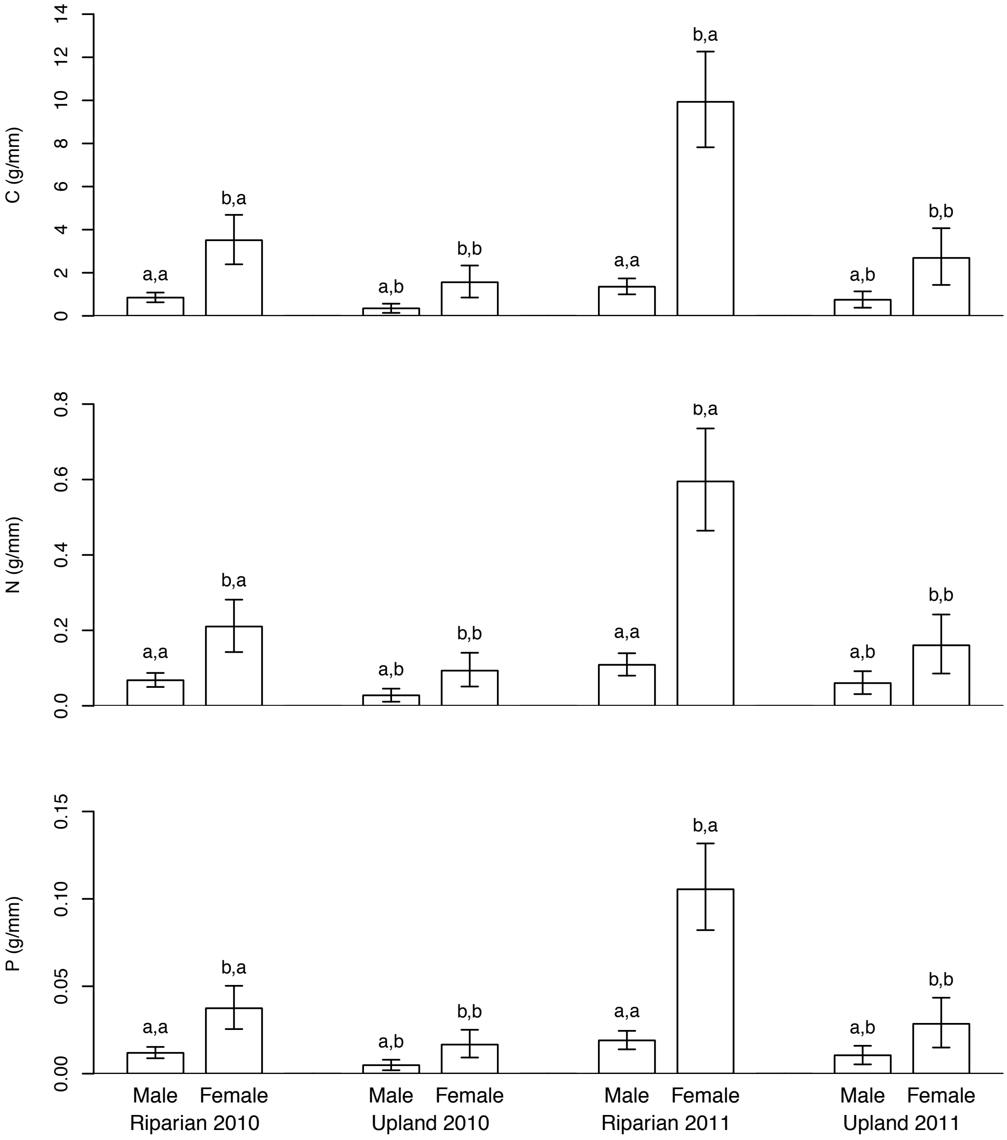

Figure 14: Mean C, N, and P allocated to reproduction per mm of stem basal diameter in 2010 and 2011 for male and female *S. sitchensis* pyroclastic flow plants by habitat. Error bars represent Bayesian 95% credible intervals of posterior distributions of the means. The letter in each pair is for pairwise comparisons between male and female plants within each habitat and year. The second letter in each pair is for pairwise comparisons between riparian and upland plants or catkins within each sex and year. When present, different letters indicate that the 95% credible interval of the posterior distribution of the difference between the two means being compared does not overlap zero.

3

THE EFFECT OF WILLOW STEM-BORER HERBIVORY ON LITTER NUTRIENT CONTENT, DECOMPOSITION RATE, AND NUTRIENT CYCLING

ABSTRACT

Herbivore mediated nutrient cycling has been shown to both inhibit plant succession in highly productive environments dominated by plant species able to tolerate herbivory, and promote succession in unproductive environments where palatable species are preferred over unpalatable ones. However, few studies have examined the ecosystem consequences of insect herbivory on ecosystem processes in primary successional environments, where pioneering or ruderal plant species invade areas characterized by extreme nutrient limitation. At the same time, studies of herbivore mediated nutrient cycling in insects has been almost entirely restricted to folivorous herbivores. I quantified the effect of stem-boring insect herbivory by larvae of *Cryptorynchus lapathi* (the poplar-willow weevil) on the leaf litter nutrient quality *Salix sitchensis* (Sitka willow), a dioecious pioneering woody shrub currently colonizing Mount St. Helens after the 1980 eruption. I performed a field experiment to quantify the effect of leaf litter type, weevil frass, and

root zone environment on litter decomposition rate using litter bags and the NH_4^+, NO_3^-, and PO_4^+ nutrient supply rate using ion exchange resin. I found that stems attacked by weevils were associated with a 50% reduction in the phosphorus content of leaf litter and a 65% reduction in the mass of individual leaves. Leaf litter from attacked plants decomposed 50% faster than leaf litter from unattacked stems or leaf litter from attacked stems mixed with frass. The differences in leaf litter nutrient composition were reflected in nutrient supply rates, as resin available PO_4^+ was three times higher for leaves from unattacked stems as compared to leaves from attacked stems. I suggest that weevils either prefer or perform better in drought stressed stems that have prematurely remobilized foliar P, or that stem damage from herbivores has prevented P translocation during the growing season or remobilization at the end of the growing season. I conclude that weevil herbivory is decelerating nutrient cycling for P, a nutrient known to limit plant growth on Mount St. Helens, and is this is likely accelerating successional change.

3.1 INTRODUCTION

During terrestrial primary succession, plant community establishment occurs simultaneously with soil development (Gill et al., 2006; Halvorson and Smith, 1995; Jenny, 1941), and numerous studies have focused on their interaction (see Vitousek, 1999; Lichter, 1998; del Moral and Bliss, 1993; Gorham et al., 1979; Vitousek and Reiners, 1975). Independently, a recent body of literature has highlighted the importance of feedbacks between aboveground and belowground communities mediated by plant physiological responses to herbivory and by herbivores themselves (Bardgett et al., 2005; Bardgett and Wardle, 2003; Chapman et al., 2003; Wardle, 2002; Hobbie, 1992). These studies on herbivory feedbacks have focused on either low nutrient environments dominated by stress-tolerant plant species (Ritchie et al., 1998; Pastor and Naiman, 1992; Bryant et al., 1991; Leibold, 1989; Pastor et al., 1988; Naiman et al., 1986) or nutrient-rich environments dominated by fast growing plant species (Chapman et al., 2003; Singer and Schoenecker, 2003; Belovsky and Slade, 2000; Ritchie et al., 1998; Hobbie, 1992; Holland et al., 1992; Chapin et al., 1986; McNaughton, 1985) and has led to two general hypotheses concerning herbivore effects on plant succession (Ritchie et al., 1998). In communities where plants preferred by herbivores have the capacity to replace lost tissues by increasing nutrient uptake and relative growth rate, consumption of plants can increase the quality and quantity of decomposer resources. This can accelerate nutrient cycling, as the physiological changes in plants due to herbivory and the elimination of high quality animal waste initiates a positive feedback that continues to accelerate nutrient cycling, plant production, and competitive dominance of these plants (Singer and Schoenecker, 2003; Ritchie et al., 1998). Conversely, in communities dominated by slow-growing, unpalatable plants or where palatable plants are unable to tolerate herbivory, consumption of palatable plants should decrease decomposer resource quality and quantity. This can decelerate nutrient cycling, increasing the proportion of litter from unpalatable plants which decomposes more slowly, further decreasing the consumed plant's ability to regrow lost tissue. This also initiates a positive feedback that continues to decelerate nutrient cycling, reducing palatable plant production, and increases environmental stress until palatable plants are unable to persist (Singer and Schoenecker, 2003; Ritchie et al., 1998).

Aboveground-belowground interactions are poorly understood in terrestrial primary succession despite their fundamental importance to community development and successional dynamics (Van der Putten et al., 2009). Studies of herbivore-mediated nutrient cycling in primary successional would provide a unique perspective, as these environments are typically extremely nutrient poor, but are inhabited by plant communities comprised of both fast-growing pioneer species as well as stress tolerant ruderal species (Walker and Del Moral, 2003; Chapin et al., 1994; del Moral and Wood, 1993; Walker and Chapin, 1986; Walker et al., 1986; Connell and Slatyer, 1977). Given this general lack of knowledge about the ecosystem consequences of herbivory in primary succession, I examine how herbivory by larvae of the poplar-willow weevil (*Cryptorynchus lapathi* L.) (Curculionidae: Coleoptera) on Sitka willow (*Salix sitchensis* Bong.) (Salicaceae: Malpighiales) on the Mount St. Helens Pumice Plain, a 15 km^2 primary successional landscape of rock and ash formed and sterilized by pyroclastic flows during the 1980 eruption, affects nutrient cycling and litter decomposition, two key ecosystem processes. Alteration of these processes by herbivory would have profound implications for plant-available inorganic nutrients and community development in successional landscapes. At Mount St. Helens, nutrient limitation drives the spread of both native and invading plants and their herbivores (Fagan et al., 2005, 2004; Bishop, 2002; Fagan and Bishop, 2000). I address two specific questions: 1) Is *C. lapathi* herbivory associated with differences in *S. sitchensis* leaf litter nutrient quality and mass? 2) Does *C. lapathi* frass, the root environment of *S. sitchensis* attacked by *C. lapathi*, and *S.*

sitchensis leaf litter from stems attacked by *C. lapathi* accelerate or decelerate leaf litter decomposition rates and the nutrient supply rate of nitrogen and phosphorus to plants?

3.2 METHODS

Study System

Salix sitchensis (hereafter willow) is the dominant shrub species recolonizing the Mount St. Helens Pumice Plain, but is being attacked heavily by *C. lapathi* (hereafter weevils). Willow grows frequently in hydric habitats near springs, perennial seeps, and watercourses while also occurring less frequently in upland habitats. Field observations on the Pumice Plain from 2004 – 2011 demonstrated that weevils were present at very high densities and were the primary willow herbivores. Willow stem mortality due to weevil herbivory was extremely high, ranging from 50 – 90% annually. Adults feed on leaves and stems but do minimal damage. The first three weevil instars girdle directly underneath the bark, feeding on the cambium and phloem tissue. In contrast, later instars excavate galleys that penetrate the sapwood and heartwood. Larvae kill the stems directly via girdling or indirectly by providing access to fungal pathogens (Broberg et al., 2001; Abebe et al., 1990; Harris and Coppel, 1967; Primm, 1918; Matheson, 1917).

Willow provides large amounts of annual litter inputs on the Pumice Plain, which often collects directly beneath willow plants forming discrete resource hotspots. Weevil larval herbivory likely affects both the quantity and quality of stem and leaf litter inputs. Without herbivory, leaves are shed each fall. However, after being attacked, leaves senesce prematurely and stems often break off and fall to the ground during the growing season. Herbivore-induced alterations in leaf and stem quality, as well as changes in root exudation patterns and fine root turnover, provide a possible mechanism for changes in nutrient supply rates as a consequence of herbivory (Bardgett et al., 2005; Bardgett and Wardle, 2003; Chapman et al., 2003; Wardle, 2002; Belovsky and Slade, 2000). In addition to these direct consequences of herbivory, stem-borers also generate large quantities of frass that accumulate beneath plants over the course of the growing season (Figure 15). Other studies of insect frass have shown that the relatively labile forms of carbon and nitrogen in frass affect nutrient cycling rates over very short times scales (Frost and Hunter, 2007, 2004).

Leaf Litter Nutrient Composition

In fall 2009, I harvested leaves after senescence but before abscission from attacked ($n = 25$) and unattacked ($n = 25$) stems on naturally established willow plants growing on the Pumice Plain, and collected current year weevil frass from exit holes on attacked stems and from beneath attacked plants. I homogenized the leaves by type (attacked vs. unattacked), before drying the leaf litter and frass at 60°C for 7 days in a drying oven. To compare leaf nutrient content between these two types, I sampled leaves at random ($n = 5$) from the homogenized attacked and unattacked leaf litter pools for chemical analysis. I randomly selected leaves from these same pools to compare leaf mass ($n = 10, 8$). I ground leaves for chemical analysis using a Retsch ball grinder and determined leaf %P by mass by placing a known mass ($\sim$ 2 mg) of dried, ground leaf material in a muffle furnace at 550°C for two hours (Miller, 1998), followed by colorimetric analysis using the ammonium molybdate method (Clesceri et al., 1998). I combusted samples for carbon and nitrogen elemental analysis with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA). I separated N_2 and CO_2 gases with a 3.0 m GC column (40°C) and analyzed for total area with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) or thermal conductivity detector on the elemental analyzer (Brenna et al., 1997). Using the remaining leaf litter, I inserted 7 g of dried leaves from either attacked or unattacked stems into 15 cm x 15 cm plastic litter bags with a mesh size of 1 mm^2. I passed the weevil frass through #5 and #10 mesh filters to remove non-frass material. All litter bags and frass were dried periodically and stored in the open air until the following summer.

Experimental Design

I used a completely randomized split plot design to experimentally test whether willow responses to weevil herbivory (specifically altered leaf litter quality and root exudation and fine root turnover dynamics) affected litter decomposition rates and the nutrient supply rates of N and P to plants. In the spring of 2008, I marked 10 willow plants in a designated experimental site on the pyroclastic flow south of Forsyth Creek's initial branch point on the northeast flank of Mt. St. Helens (46.231418° N, 122.163908° W, elevation 1275 m). I randomly selected half of the tagged plants and applied bifenthrin, a synthetic pyrethroid insecticide sold as Onyx™ (FMC Inc.), used at a concentration of 0.25 ml active ingredient/L of water, until stems were dripping, as recommended on the product label. I sprayed stems in late June or early July and late August, when weevils were observed ovipositing. I did not control for water addition because spraying was minimal relative to recent rainfalls. The treatment did not eradicate existing infestation, but completely prevented subsequent attack. Onyx™ is a blend of bifenthrin ($C_{23}H_{22}ClF_3O_2$), sulfonate salts, nonylphenol ethoxylate, standard paraffinic solvents and esters of glycerin, and contains no fertilizer constituents (FMC ProSolutions, personal communication). Therefore it is unlikely to cause any sustained stimulation of growth in nutrient-limited soils, nor could I find any literature reports of direct effects on plant growth. Because bifenthrin is non-systemic and I focused my spray on stems during a specific seasonal window, the pesticide treatment was unlikely to strongly impact other arthropods or vertebrate herbivores (such as elk, *Cervus elaphus*) associated with willow. On 30 June 2010, I randomly selected whole plots within the experimental site that were either root environments beneath sprayed plants ($n = 5$), root environments beneath unsprayed plants whose stems were currently attacked by weevil larvae ($n = 5$), or plant interspaces outside the rooting environment of any plants ($n = 5$). Within each whole plot, I established four sub plots at intervals of 90 degrees around the center point of each plant or interspace. For all plants, I selected sub plots that were far enough from the plant so as to not be near pre-existing leaf litter and frass that had naturally accumulated beneath these plants but still within the root environment based on the plant's dripline. I randomly assigned to each sub plot either a litter bag with willow leaves from stems that were not attacked ($n = 15$), a litter bag with willow leaves from stems that were attacked ($n = 15$), a litter bag with willow leaves from stems that were attacked placed on top of 5 g of weevil frass ($n = 14$), or an empty litter bag ($n = 15$) (Figure 16B). I placed 6 g of cation–anion exchange resin (Amberlite IRN-150 ion-exchange resin) in 3.8 cm circular discs enclosed on both sides with 120 micron nylon mesh cut into small 5.6 mm thick plexiglass sticks (hereafter resin stick) 10 cm beneath each litter bag (Figure 16A). I accomplished this by digging several centimeters away from each litter bag and inserting the resin stick parallel to the litter bag before replacing the excavated soil (Figure 16C). I used this technique in order to collect and replace resin sticks without disturbing the soil above and around the slit containing the resin stick itself. In total I emplaced three sets of resin sticks beneath each litter bag over the course of this experiment (30 June 2010 – 05 Sep 2011), with the first set for summer 2010, the second set for fall 2010 through spring 2011, and the third set for summer 2011. On 05 Sep 2011, I collected the last set of resin sticks and the litter bags. I immediately dried the litter bag contents at 60°C for 7 days in a drying oven prior to weighing the remaining leaf material. I extracted the resin with 100 ml of 2 M KCl and analyzed the extracts colorimetrically for NH_4^+, NO_3^-, and PO_4^+ (Westco SmartChem 200 Discrete Analyzer, Unity Scientific, Brookfield, Conn., USA). For the first and second time period, NO_3^- concentrations were usually below detection threshold and I excluded these data from my analysis.

Data Analysis

All data analyses were generated using SAS statistical software, version 9.3 by the SAS Institute (2010). I used t-tests to compare attacked and unattacked leaf litter mass, C, N and P concentrations (PROC REG). I used separate mixed model ANOVAs to measure the effect of root environment (whole plot factor), litter type (sub plot factor), and their interaction on 1) willow leaf litter decomposition rate and 2) NH_4^+, NO_3^-, and PO_4^+ supply rates in each time period (PROC MIXED). For all analyses, I treated plot as a random effect nested within root environment, and I used the Satterthwaite method to calculate the degrees of freedom and the variance components covariance structure. For the litter decomposition response variable, I calculated the decomposition rate constant for willow leaf litter as $X_0/X_{1.184} = e^{-k \cdot 1.184}$, where X_0 is the mass (g) of the leaf litter prior to the experiment, $X_{1.184}$ is the mass (g) of the leaf litter at the conclusion of the experiment, and k is the decomposition rate constant expressed in 1/ year (Karberg et al., 2008). For nutrient supply rate response variables, I used the mass (g) of each ion recovered per g of ion exchange resin in each time period. Of the 413 ion exchange resin observations, I excluded three observations due to mold that had grown in the extractant solution and five observations as extreme values prior to analysis. I did not exclude any of the willow leaf litter observations. I used a significance level of $P \leq .10$ for all omnibus F-tests due to the high microsite variability associated with soil nutrient studies in nutrient-limited environments (Gill et al., 2006) and a significance level of $P \leq .05$ for all mean comparisons. If the interaction term in a mixed model was significant, I conducted planned comparisons between a subset of the least square cell means using protected LSD tests (LSMEANS option). If the interaction term in a mixed model was not significant, I removed it from the model. Conditional on its F-value being significant in the additive model, I conducted planned comparisons of the main effect marginal group means means using protected LSD tests (LSMEANS option). For all analyses, I visually determined that the variances were homogenous by plotting the residuals versus the predicted values, and checked for normality using normality probability plots and residual histograms.

3.3 RESULTS

Weevil herbivory had a positive effect on willow leaf litter decomposition under attacked and unattacked plants and on bare ground, but only in the absence of weevil frass. Leaves from attacked stems decomposed 50% faster than either leaves from unattacked stems or leaves from attacked stems placed over weevil frass, while root environment did not affect the decomposition rate constant (Table 4, Figure 17). Weevil herbivory was associated with differences in willow leaf litter nutrient content, which in turn affected nutrient supply rates, but these effects depended on the root environment, season, and nutrient identity. Leaves from stems attacked by weevil larvae were smaller than leaves from unattacked stems (52.2 ± 15.4 mg vs. 123.7 ± 17.2 mg; t-student=6.19, df = 16, P <.001). While leaves from attacked and unattacked stems had similar %C (46.69 ± .46% vs. 46.05 ± .46%; t-student=2.01, df=8, P=.08) and %N (2.09 ± .17% vs. 1.93 ±

.17%; t-student=1.46, df=8, P=.19), leaves from attacked stems had roughly half the %P as leaves from unattacked stems (.16 ± .025% vs. .32 ± .025%; t-student=8.979, df=8, P=<.001). Resin available NH_4^+ did not differ by root environment or litter type during either the initial summer (Jul 2010 – Aug 2010) the litter bags were emplaced, or the following summer (Jul 2011 – Aug 2011) (Table 4). From Sep 2010 – Jun 2011, resin available NH_4^+ was higher under both attacked and unattacked plants as compared to bare ground, but there was not an effect of litter type (Table 4, Figure 17). Resin available NO_3^- was below detection limits until the second summer of the experiment (Jul 2011 – Aug 2011), where there was an interaction between root environment and litter type (Table 4). However, there were no differences in any of the biologically meaningful planned comparisons, other than a slightly lower amount of resin available NO_3^- under attacked leaf litter as compared to bare ground (Figure 19). Resin available PO_4^+ did not differ by root environment or litter type during either the initial summer (Jul 2010 – Aug 2010) the litter bags were emplaced, or the following summer (Jul 2011 – Aug 2011) (Table 4). From Sep 2010 – Jun 2011, there was an interaction between root environment and litter type for resin available PO_4^+ (Table 4), as in the root environment of attacked plants there was roughly three times as much PO_4^+ available under leaf litter from stems not attacked by weevils as compared to under leaf litter from attacked stems or bare ground (Figure 20A). This effect was not seen in the root environment of plants not attacked by weevils or in interspaces between plants (Figure 20B,C).

3.4 DISCUSSION

Litter nutrient content and decomposition rate

While studies connecting the effect of insect herbivores on foliar chemistry with leaf litter quality and decomposition rates are more limited in comparison to those for mammalian browsers, folivorous insects can both accelerate and decelerate litter decomposition rates (Ibanez et al., 2013; Frost et al., 2012; Uselman et al., 2011; Sariyildiz et al., 2008; Schweitzer et al., 2005; Chapman et al., 2003) This is likely due to two opposing effects concerning plant responses to leaf herbivory (Chapman et al., 2006). In evergreens, herbivory causes a disruption of a plant's ability to reabsorb nutrients into the stem or roots prior to leaf abscission, increasing litter nutrient quality and decomposition rates (Uselman et al., 2011; Sariyildiz et al., 2008; Chapman et al., 2003). For example, herbivory by the moth *Dioryctria albovittella* and scale *Matsucoccus acalyptus* on *Pinus edulis* needles is hypothesized to accelerate senescence or damage vascular tissue, preventing pines from reclaiming nutrients prior to litterfall and resulting in increased high quality litter and faster decomposition (Chapman et al., 2003). In comparison, in deciduous trees secondary metabolites can decrease litter quality and slow decomposition rates (Ibanez et al., 2013; Frost et al., 2012; Schweitzer et al., 2005).

Here, I investigate how stem borers, which do not feed directly on leaves but rather along the vascular tissues responsible for nutrient translocation to and from leaves, affect leaf litter quality and decomposition. I find that while weevil herbivory is associated with reduced leaf litter P and mass (logically resulting in reduced litterfall), litter decomposition rates are highest for leaves from attacked stems decomposing in the absence of frass (Figure 17). In short, weevil herbivory accelerates decomposition of willow leaf litter, although the leaf litter itself is of reduced quality. I hypothesize that differences in litter quality could occurs for several reasons: 1) weevils may target stems that are experiencing summer drought stress that are prematurely remobilizing nutrients (White, 2009, 2003, 1993, 1984), 2) plants may be able to reabsorb nutrients in response to weevil herbivory prior to stem death, or 3) weevil herbivory may reduce leaves from acquiring nutrients in the first place. These hypotheses may not be mutually exclusive, as the response of stem boring insects to stressed plants could be occurring simultaneously with their physiological disruption of nutrient translocation. This question could be addressed by experimentally tracking seasonal changes in leaf chemistry in attacked and unattacked leaves, something I did not attempt in this study.

Herbivore mediated nutrient cycling

Herbivores can alter nutrient cycling rates by changing the quantity of resource available to decomposers in the root environment of attacked plants (through fine root turnover and alteration of root exudation patterns) and the quality of resources (through changes in plant litter nutrient content; Bardgett and Wardle, 2003). Plant nutrient supply as measured by resin sticks showed that the reduced P content of leaf litter from attacked stems translated into reduced availability of PO_4^+ to plants during the fall through spring following the deployment of the leaf litter bags (Figure 20A). While I did not observe differences in nutrient supply rates between attacked an unattacked plants for N or P, the root environment *x* litter type interaction indicated that the effects of litter quality occurred only under attacked plants while plants not attacked by weevil larvae and in open areas PO_4^+ supply rates did not differ (Figure 20B,C). Since the majority of plants in upland areas of the Pumice Plain are attacked by weevils, this reduction in PO_4^+ availability is likely to be a widespread phenomena. Although frass did not have a positive effect on litter decomposition rates, it did appear to attenuate the reduction in PO_4^+ availability as there was no difference between resin available PO_4^+ under leaves from unattacked stems and leaves from attacked stems placed over frass. Frass can enhance nutrient decomposition and immobilization, but these effects depend on the ratio of litter to frass as well as the nutrient quality of the frass itself (Kagata and Ohgushi, 2012a,b). While insect frass is often recycled quickly and made available to plants in the same season it is generated (Frost and Hunter, 2007), weevil frass is of low nutrient content, as it is largely undigested wood (unpublished data), raising the question of the degree to which it could enhance nutrient cycling rates even when present in very large quantities. These results suggest that weevil herbivory was associated with (and perhaps causes) decelerated nutrient cycling on the Pumice Plain with respect to P, a limiting nutrient for net primary production in this system.

Successional consequences

Weevil herbivory on willow is likely accelerating succession in upland areas on the Pumice Plain from from areas dominated by willows to those composed primarily of *Alnus*. This is accomplished through preferential weevil herbivory on willow over *Alnus sinuata*, a common woody species on Mount St. Helens that has already encroached on willow in many of the Pumice Plain riparian zones. The transition from a willow to alder dominated sere has been observed in other primary successional systems, and is attributed to differences in species life history traits as well as mammalian herbivory (Bryant, 1987; Bryant and Chapin, 1986; Walker and Chapin, 1986; Walker et al., 1986; Bryant et al., 1985). In contrast, on Mount St. Helens, preferential weevil herbivory on willow over alder is causing the juvenilization of willow plants in upland areas (Che-Castaldo, chapter 1), resulting in plants of reduced size and competitive ability. Weevil mediated nutrient cycling reinforces this negative effect on willow biomass by decelerating the cycling of PO_4^+ under attacked plants. While other studies of herbivore nutrient cycling in primary succession have found positive effects of herbivory on litter quality and decomposition, surprisingly this has translated into slowing soil development (Classen et al., 2013, 2006). While this may be occurring on the Pumice Plain in the short term, the potential willow-to-alder transition should significantly increase the nitrogen supply to this nutrient poor landscape, having broad scale community and ecosystem level consequences. In primary succession on Alaskan silt bars, alder N-fixation adds roughly 60% of total N found in these developing soils (Kielland and Bryant, 1998;

Figure 15: *C. lapathi* frass accumulates beneath attacked *S. sitchensis* plants during the growing season. During the fall, both attacked and unattacked *S. sitchensis* leaves collect under these plants forming resource hotspots.

Kielland et al., 1997), and it seems probable that alder will have a similar affect on the Pumice Plain. This highlights the fact that soil development in primary succession depends both on positive feedback loops associated with nutrient cycling as well as the identity of new species that come to dominate as a result.

Table 4: Split-plot ANOVAs for the effect of root environment (whole plot), leaf litter type (sub plot), and their interaction on willow litter leaf decomposition constant (k) and nutrient supply rates for NH_4^+, NO_3^-, and PO_4^+. All degrees of freedom are based on Sattherthwaite approximations and significant F-values ($P < .10$) are denoted with an asterisk.

Response	Period Start		Period End	Effect	DF (n/d)	F-Value	Pr > F
k	30 Jun 2010	–	05 Sep 2011	root env.	2/11.7	2.19	0.15
				litter type	2/27	3.43	0.05*
NH_4^+	30 Jun 2010	–	10 Sep 2010	root env.	2/12.3	0.42	0.67
				litter type	3/39.2	1.62	0.20
NH_4^+	10 Sep 2010	–	01 Jul 2011	root env.	2/11.2	9.58	<.01*
				litter type	3/37.9	0.17	0.92
NH_4^+	01 Jul 2011	–	05 Sep 2011	root env.	2/12.4	0.40	0.68
				litter type	3/41.2	0.15	0.93
NO_3^-	01 Jun 2010	–	05 Sep 2011	root env.	2/11.7	1.15	0.36
				litter type	3/34.9	1.36	0.28
				interaction	6/34.9	2.10	0.08*
PO_4^+	30 Jun 2010	–	10 Sep 2010	root env.	2/12.6	0.40	0.68
				litter type	3/39.7	0.41	0.74
PO_4^+	10 Sep 2010	–	01 Jul 2011	root env.	2/12.2	0.73	0.50
				litter type	3/35.5	1.20	0.32
				interaction	6/35.4	2.20	0.07*
PO_4^+	01 Jun 2011	–	05 Sep 2011	root env.	2/12.2	0.94	0.42
				litter type	3/34.7	1.54	0.92

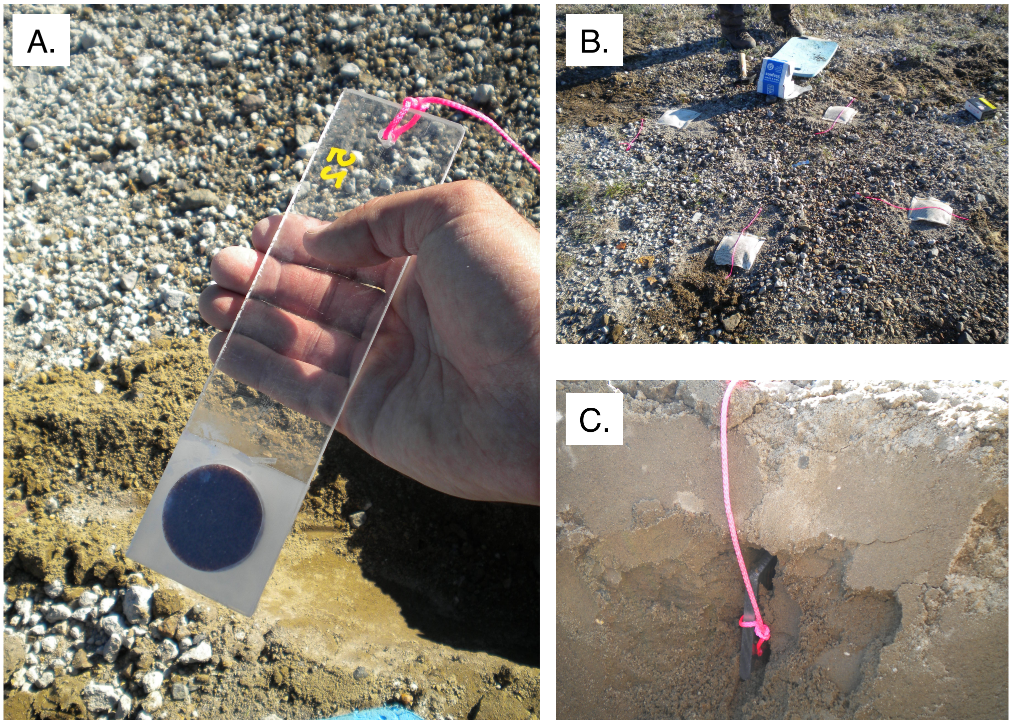

Figure 16: A) Resin stick made of plexiglass containing a cutout disk where ion exchange resin is inserted between two pieces of nylon mesh. B) Experimental layout for a replicate located in the interspace between plants. C) Method for emplacing and removing the resin stick from beneath the litterbags.

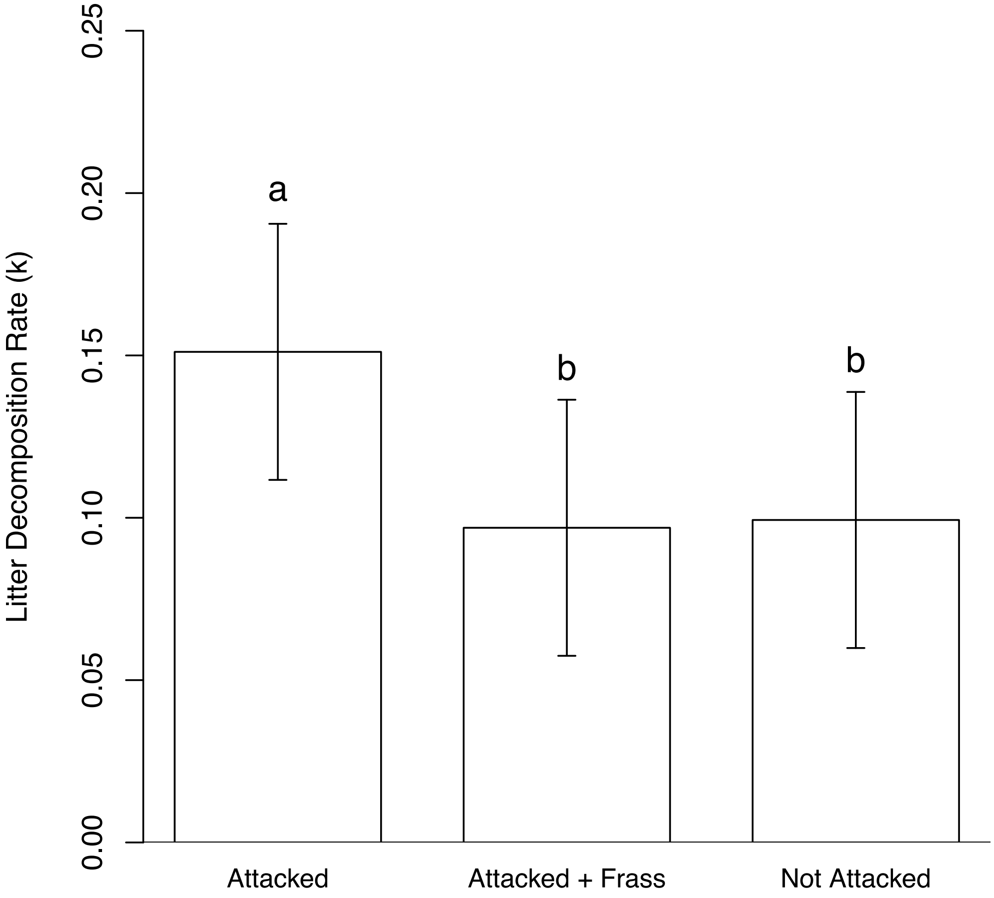

Figure 17: Mean willow leaf litter decomposition rate constant (k) of leaves from stems attacked by weevils, leaves from stems not attacked by weevils, and leaves from stems attacked by weevils placed on top of weevil frass. Bars show least square means and error bars represent 95% confidence intervals. Letters show significant differences ($P < .05$) in pairwise comparisons between the leaf litter treatment levels pooled across the root environment treatment levels.

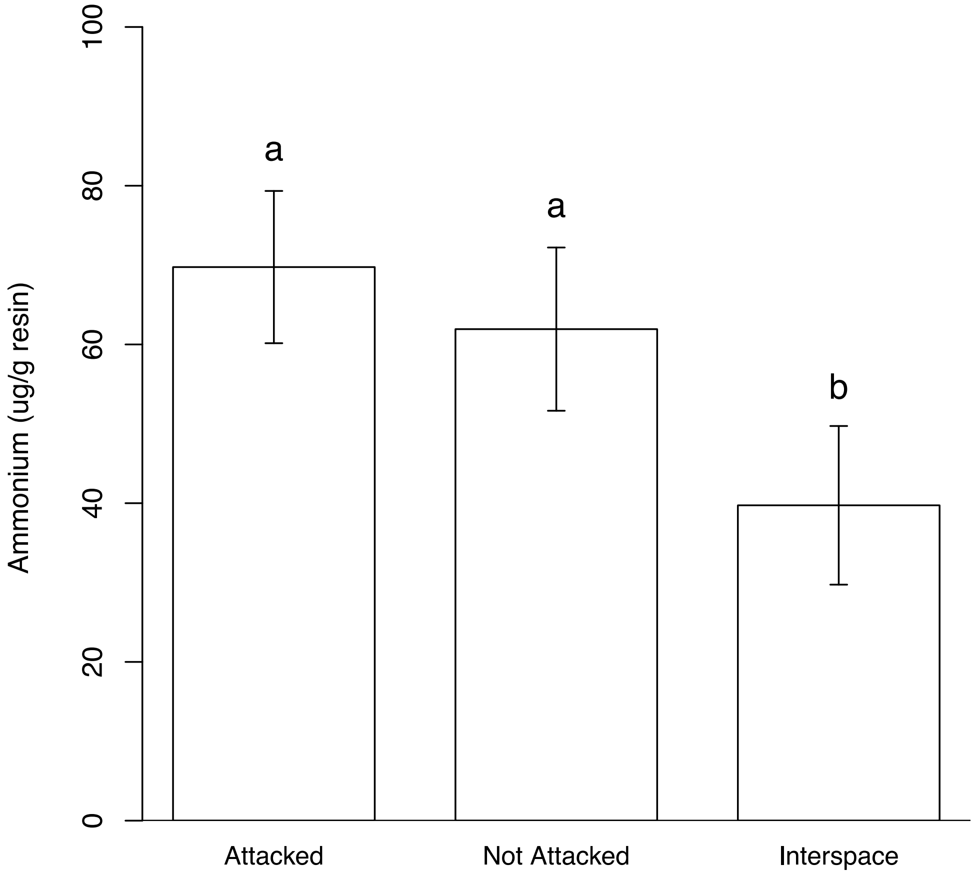

Figure 18: Mean NH_4^+ recovered from resin sticks emplaced from 10 Sep 2010 – 01 Jul 2011 in the root environment beneath willow plants attacked by weevils, willow plants not attacked by weevils, and in bare interspaces between plants. Bars show least square means and error bars represent 95% confidence intervals. Letters show significant differences ($P < .05$) in pairwise comparisons between the rooting zone treatment levels pooled across the litter type treatment levels.

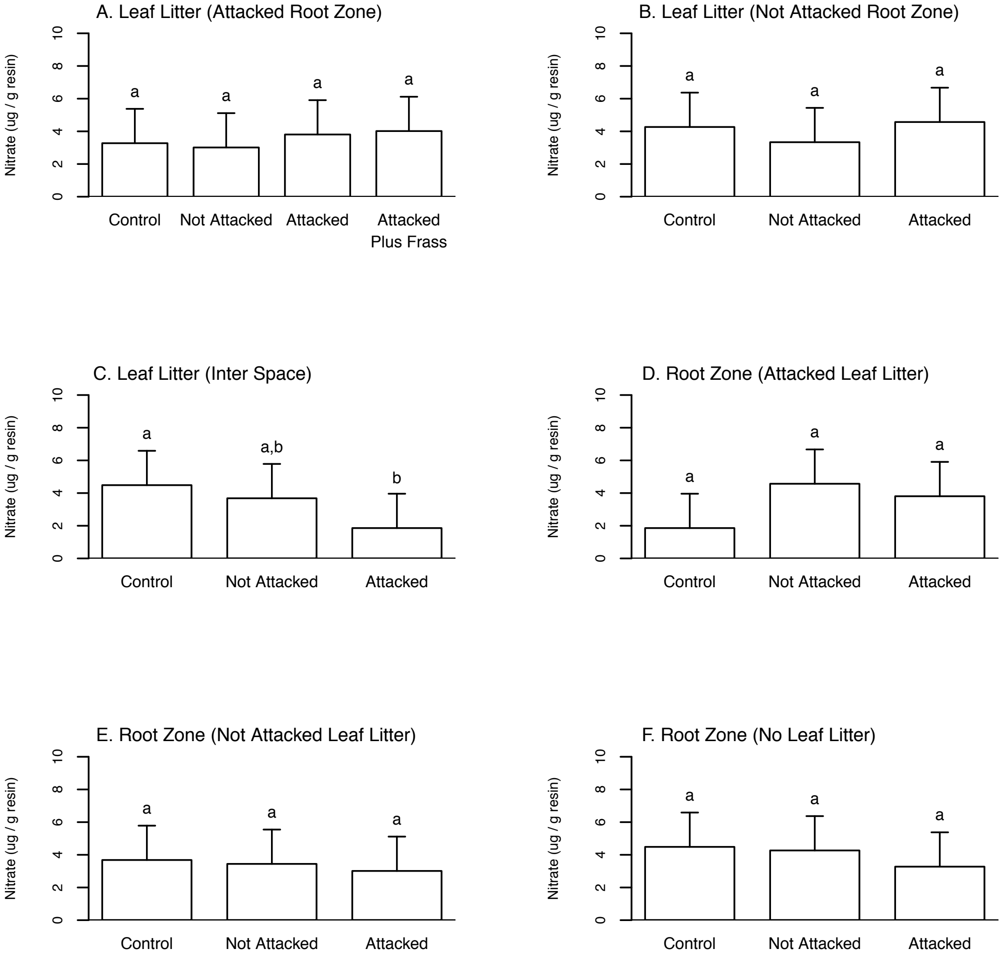

Figure 19: Mean NO_3^- recovered from resin sticks emplaced from 01 Jul 2011 – 05 Sep 2011 in A) under the litter type treatments in the root environment of attacked plants, B) under the litter type treatments (excluding attacked plus frass) in the root environment of plants not attacked by weevils, C) under the litter type treatments (excluding attacked plus frass) in the interspaces between plants, D) under leaf litter from stems attacked by weevils across the root environment treatments, E) under leaf litter from stems not attacked by weevils across the root environment treatments, and F) under bare ground across the root environment treatments. Bars show least square means and error bars represent 95% confidence intervals. Letters show significant differences ($P < .05$) in pairwise comparisons for all means within each panel.

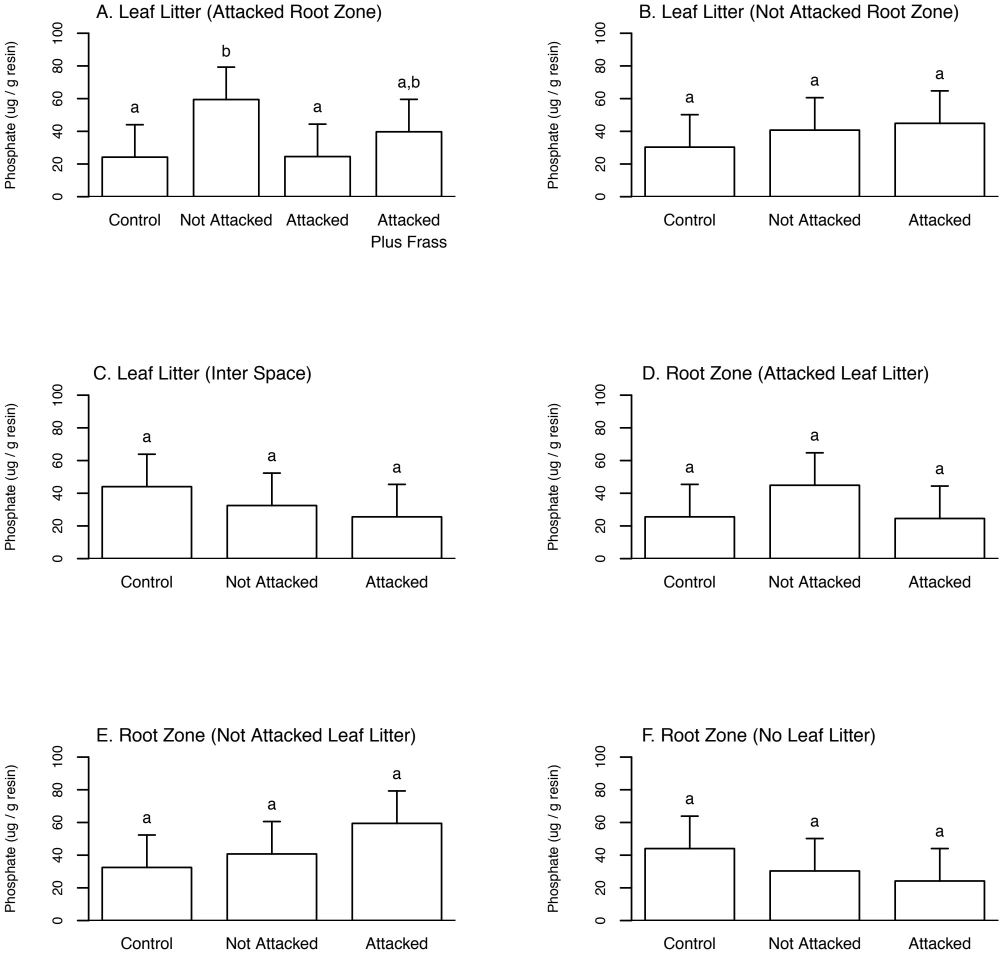

Figure 20: Mean PO_4^+ recovered from resin sticks emplaced from 10 Sep 2010 – 01 Jul 2011 in A) under the litter type treatments in the root environment of attacked plants, B) under the litter type treatments (excluding attacked plus frass) in the root environment of plants not attacked by weevils, C) under the litter type treatments (excluding attacked plus frass) in the interspaces between plants, D) under leaf litter from stems attacked by weevils across the root environment treatments, E) under leaf litter from stems not attacked by weevils across the root environment treatments, and F) under bare ground across the root environment treatments. Bars show least square means and error bars represent 95% confidence intervals. Letters show significant differences ($P < .05$) in pairwise comparisons for all means within each panel.

APPENDIX A: PUMICE PLAIN ENVIRONMENTAL CONDITIONS

I recorded temperature, relative humidity, precipitation, and soil volumetric water content on the Pumice Plain during the course of my study (2009–2011) using:

- 12 HOBO® U23 temperature/relative humidity data loggers located at 6 paired riparian and upland sites
- the Spirit Lake SNOTEL (Site Number: 777)
- 7 Decagon® EC-5 soil moisture sensors in a 20 m x 30 m upland plot near Forsyth Creek

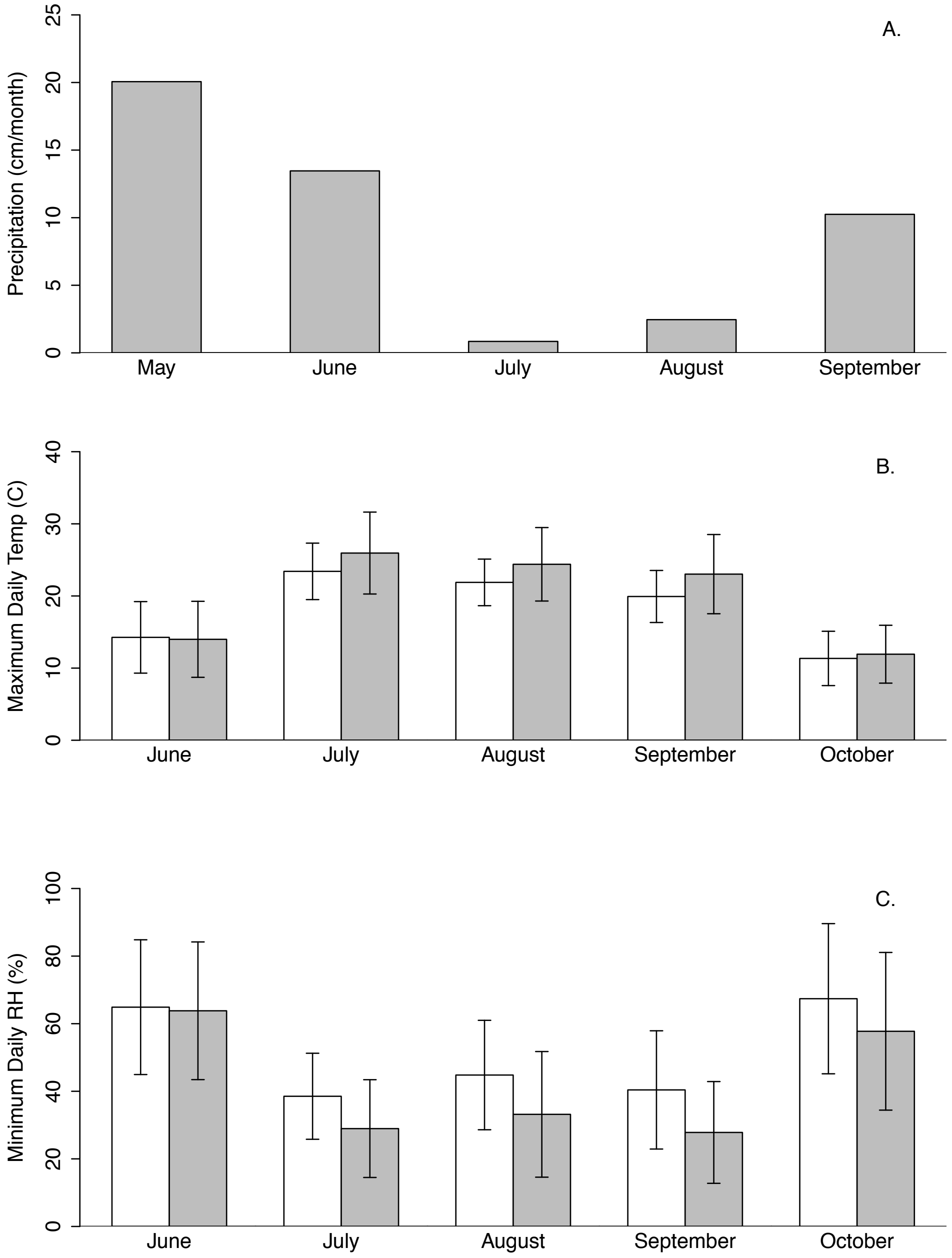

Figure A1: (A) Average monthly precipitation on the Pumice Plain from 2009 – 2011. Precipitation data were recorded by the Spirit Lake SNOTEL (Site Number: 777). (B) Average monthly maximum daily temperature and (C) minimum daily relative humidity for riparian zones (white bars) and upland areas (gray bars) on the Pumice Plain from 2009 - 2011. These data were recorded using 12 HOBO® U23 temperature/relative humidity data loggers located at 6 paired riparian and upland sites. Error bars on (B) and (C) represent ± 1 standard deviation.

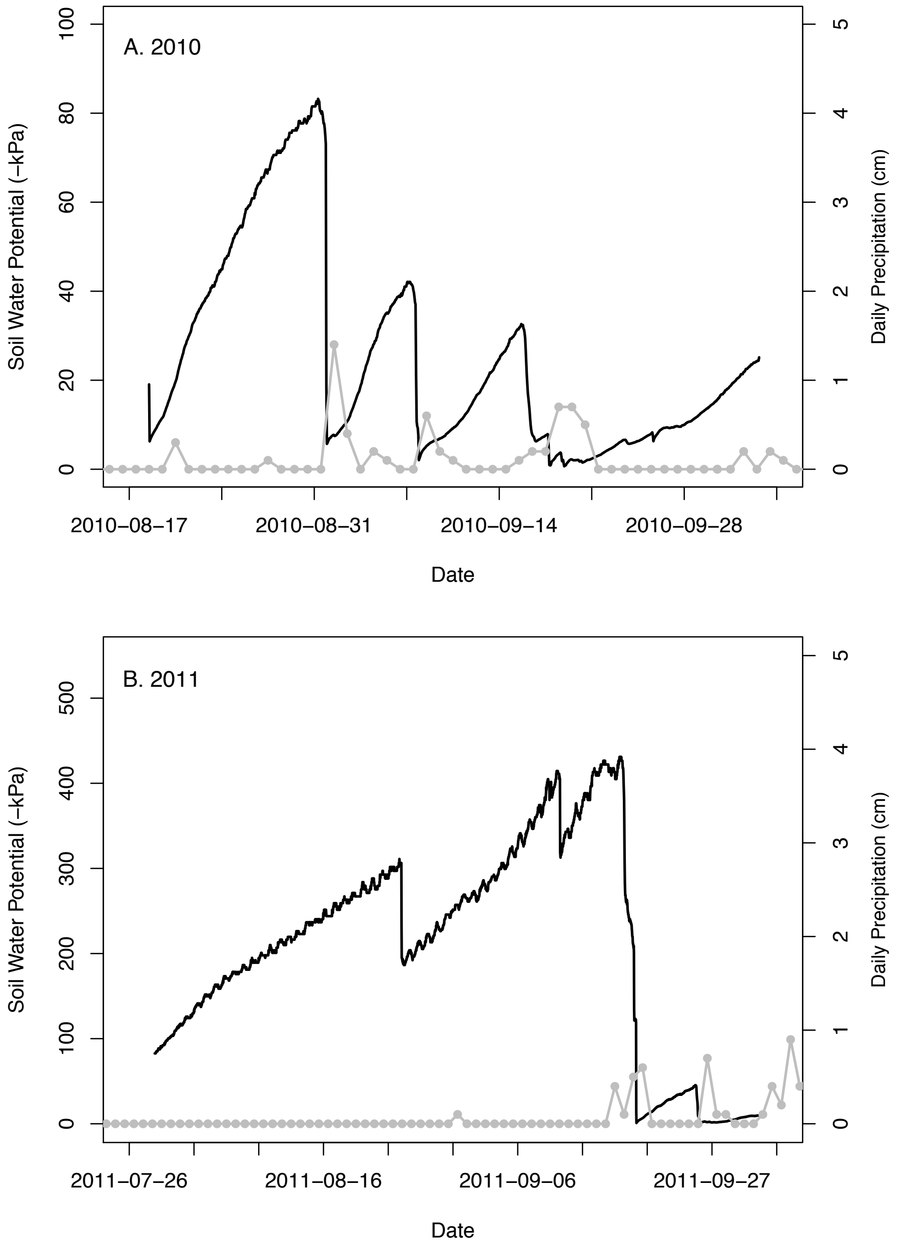

Figure A2: Soil water potential measured at a depth of 25 cm (black lines) and daily precipitation (gray lines) during a portion of the (A) 2010 and (B) 2011 summer dry-downs on the Pumice Plain. Soil volumetric water content was recorded hourly using 7 Decagon® EC-5 soil moisture sensors in a 20 m x 30 m upland plot. Volumetric water content was converted to soil water potential using a soil release curve estimated from soil cores taken in this plot. Precipitation data were recorded by the Spirit Lake SNOTEL (Site Number: 777).

APPENDIX B: QUANTIFYING WILLOW STEM TOPOLOGY

I treated willow plants as nested sets of stems. First order stems originated from the ground or caudex (which may be elevated above the soil due to erosion). Higher order stems are initiated from axillary buds, each located between a leaf and stem one order lower. This representation designated consistent and interpretable sites (branches) that weevils may have been attacked with a simple set of assignment rules that worked for all willow topologies observed in my sample. An n^{th} order stem was defined as a stem that branched from an n^{th} − 1 order stem. This process continued for n orders until the current annual growth (CAG) of any first order stem was reached. CAG, which I defined as the plant tissue extending from the previous year's terminal bud scar to an active meristem, was the only portion of a *S. sitchensis* stem that had living leaves attached during the growing season. Several methodological issues arose while implementing this approach:

1. At a branch point, it was sometimes difficult or misleading to identify the n^{th} order stem from the $n^{th} + 1$ order stem based on branch orientation or bud scars. This difficulty arose because the terminal branch did not always grow in a straight line, and older axillary and terminal bud scars were sometimes difficult to distinguish from one another. If an n^{th} order stem was elk browsed or damaged from weevil attack, a

higher order stem often outgrew the damaged stem, such that, after several seasons, the higher order stem resembled the n^{th} order stem. Alternatively, the damaged n^{th} order stem later broke off at or near the branching point with the new dominant higher-order stem. For these reasons, I defined a 1st order stem as a trace along a branch from caudex to tip that follows the thickest route at any branching point. The same rule applied to all higher-order stems. Thus, my geometrical representation of a stem did not necessarily reflect its historical growth process.

2. It was sometimes difficult to determine whether a stem originating close to the ground did so from caudex or was a 2nd order stem located close to the base of a 1st order stem. In such cases, the determining factor was to decide whether weevil attack on one stem could influence mortality of the other by damaging woody tissue below the second stem. If so, then one is a 2nd order stem from the other. In the case where a stem appeared to split evenly into two equally sized stems near the caudex, I treated both as 1st order stems.

3. Some 1st order stems included both dead and living tissue. These types of stems were separated into two groups, one where higher-order stems originated from epicormic buds near the base of the 1st order stem following severe damage to the stem, and the other where higher-order stems originated from axillary buds following abortion or removal of the apical shoot. In the first group, the damaged portion of the stem was treated as new caudex and all higher-order stems were re-categorized as order n-1. In the second group, the stem orders were

not re-categorized, but the damaged portion was excluded from size calculations based on basal diameters. Stems in both of these groups were excluded from all analyses.

4. Additional plants were added in 2010 to offset stem mortality. These were included in my hierarchical stem-occupancy model by pooling their 2010 data with the 2009 data from the remaining plants and so on. I did this because colonization and re-attack for any stem could not be estimated without knowing whether the stem was attacked in the previous year (the occupancy estimate from 2009 in my model). I were able to artificially categorized the added plants because I did not estimate year-specific covariates on colonization and re-attack. These plants were excluded from the calculation of annual occupancy, colonization, and re-attack by plant habitat and sex.

APPENDIX C: ESTIMATION OF ADJUSTED BASAL DIAMETERS

I modified Rüger and Condit's [1] statistical methodology to estimate routine errors associated with caliper measurements of willow stem basal diameters. In 2009, two independent observers conducted paired basal diameter measurements on willow stems of various sizes. I assumed that the routine measurement error was a linear function of the true, but unobservable, basal diameter. This was consistent with my experience in the field where it was usually more difficult to correctly position the calipers around the bases of large stems due to their complex geometries, whereas the bases of smaller linear stems were more conducive to accurate measurements. To estimate how this routine error changes with respect to stem size, I used the simple Bayesian model,

$$\begin{aligned}\mathrm{Pr}\left(\mathrm{a},\mathrm{b},\mathbf{z}\mid\mathbf{x}\right) \;\propto\; & \prod_{i=1}^{103}\prod_{j=1}^{2}\mathrm{N}\left(x_{i[j]}\mid\mu=z_i,\sigma=\mathrm{a}+\mathrm{b}z_i\right)\times \\ & \text{uniform}\left(\mathsf{a}\mid 0,100\right)\times\text{uniform}\left(\mathsf{b}\mid 0,100\right)\end{aligned} \tag{1}$$

where $\mathbf{x}$ is a vector of untransformed basal diameters, a and b are regression coefficients, and $\mathbf{z}$ is vector of true basal diameters. The subscript i indexes stems $(i = 1...103)$ and the subscript j indexes measurements $(j = 1, 2)$ on the i_{th} stem. Priors were chosen to be positive and uninformative uniform distributions. I obtained posterior distributions from the model using a hybrid Markov chain Monte Carlo (MCMC) algorithm implemented in the R computing environment [2], where parameter values were sequentially updated, as in the Gibbs sampler, whereas the acceptance criterion depended on the likelihood ratios, as in the Metropolis–Hastings algorithm [1,3,4]. I used a normal proposal distribution, whose mean was the value of the given parameter in the current iteration and whose standard deviation (step width) was adjusted during the burn-in period such that the acceptance rate remained roughly 25% [1]. Three chains were computed for each parameter with different initial values. I used a burn-in period of 10,000 iterations, after which I accumulated 10,000 samples from each chain. I assessed convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman [5].

For some stems in my study, basal diameter measurements across years yielded either negative or abnormally large positive growth increments, both of which were biologically unreasonable. I did not wish to exclude these stems from my study, nor did I wish to employ arbitrary rules to correct these data artifacts. Instead, I relied on my prior beliefs about growth increments and routine measurement error to adjust the observed basal diameters such that all growth increments were positive and biologically feasible. To accomplish this, I used the over-parameterized Bayesian model,

$$\begin{aligned} z_{i,j} &= \beta_{1,j}T_{1,j} + \beta_{2,j}T_{2,j} + \beta_{3,j}T_{3,j} && (2) \\ \Pr\left(\boldsymbol{\beta_1}, \boldsymbol{\beta_2}, \boldsymbol{\beta_3}, \mathbf{z} \mid \boldsymbol{x}, \mathrm{a}, \mathrm{b}\right) &\propto \prod_{i=1}^{3}\prod_{j=1}^{N} \mathrm{N}\left(x_{i,j} \mid z_{i,j}, \sigma = \mathrm{a} + \mathrm{b}z_{i,j}\right) \times && (3) \\ & \prod_{\mathrm{j}=1}^{\mathrm{N}} \mathrm{uniform}\left(\mathrm{fi}_{1,\mathrm{j}} \mid 0, 100\right) \times \end{aligned}$$

$$\prod_{i=2}^{3}\prod_{j=1}^{N}\text{gamma}\left(\beta_{i,j} \mid k_{s[j]}, \theta_{s[j]}\right) \times$$
$$\text{N}\left(\text{a} \mid 1.152, .299\right) \times$$
$$\text{N}\left(\text{b} \mid .0298, .0186\right),$$

where $\mathbf{x}$ is a vector of untransformed basal diameters, $\boldsymbol{\beta_1}$ is a vector of true stem diameters, $\boldsymbol{\beta_2}$ and $\boldsymbol{\beta_3}$ are vectors of growth increments, and $\mathbf{z}$ is a vector of adjusted basal diameters of the same dimension as $\mathbf{x}$. The subscript i indexes years $(i = 1...3)$, the subscript j indexes stems $(j = 1...N)$ in the i_{th} year, and the subscript s indexes groupings of stems $(s = 1...8)$ based on their genet's sex and habitat and the transition years (Table C1). N is the total number of tracked 1$^{\text{st}}$ and 2$^{\text{nd}}$ order stems in my study. The first binary indicator (T_1) equal one if a stem was alive in the i_{th} year and zero otherwise. The remaining two binary indicators, T_2 and T_3, equal one if the stem was alive during the transition between years i and $i-1$ and zero otherwise.

The posterior distributions of a and b from Equation 1 enter as fixed normal priors in Equation 3. The priors for $\boldsymbol{\beta_1}$ were positive and uninformative uniform distributions. I used informed gamma distributions for all $\boldsymbol{\beta_2}$ and $\boldsymbol{\beta_3}$ priors, where the maximum likelihood estimates of the shape (k) and rate (θ) parameters were computed for all observed positive growth increments in each of the s groups (Table C1) using the fitdistrplus package [6] in the R computing environment [2]. Whereas this informed prior was based on observed and not true basal diameters, the routine measurement error associated with these measurements should not have led to overly biased growth increments. All the informed priors in my model were derived from my field data and represented my best belief about the growth rates of *Salix* stems in my study and the routine errors associated with measuring their basal diameters. Equation 3 combined these prior beliefs with the observed sequence of basal diameter measurements for any given stem to insure that all growth increments were positive and to reduce overly large growth increments by partially attributing such observations to measurement error. I illustrate this correction method for two stems whose observed sequence of basal diameters was biologically inconsistent due to measurement error (Figure C1). In addition, Equation 3 used the informed priors to predict basal measurements for the year prior to tagging for stems recruited to plants in 2010 and 2011, when stems were smaller than my minimum basal diameter requirement for tracking. This avoided setting basal diameters in years prior to tagging to zero or some other arbitrary value. Equation 3 also predicted any missing basal diameter data in the few cases where basal diameters were accidentally not recorded for a tagged stem in a given year. This imputation was done for 30% of the 2010 relative growth rate calculations and 11% of the 2011 relative growth rate calculations. The number of imputations in 2010 is higher as I did not tag 2nd order upland stems in 2009.

I estimated posterior distributions for all basal diameters $\left(z_{i,j}\right)$ using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 [7] with the R2jags package [8] of the R computing environment [2]. Three chains were computed for each parameter with different initial values. I used a burn-in period of 5,000 iterations, after which I accumulated 3,000 samples from each chain. I assessed convergence through visual inspection of trace plots to assure stationarity and homogeneous mixing, and by using the diagnostics of Gelman [5]. For each basal diameter $\left(z_{i,j}\right)$, I used the posterior distribution's mean in the calculation of the adjusted basal diameter (referred to in the main text as " stem basal diameter") and relative growth rate covariates for all pooled individual plant units included in Equation 1 in the main text.

LITERATURE CITED

1. Rüger, N. and R. Condit, 2012. Testing metabolic theory with models of tree growth that include light competition. *Functional Ecology* **26**:759–765.

2. R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

3. Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin, 2013. Bayesian data analysis. CRC Press.

4. Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. A. U. N. Gunatilleke, C. V. S. Gunatilleke, P. Hall, K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. LaFrankie, S. L. de Lao, J.-R. Makana, M. N. S. Noor, A. R. Kassim, S. Russo, R. Sukumar, C. Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa, and T. Zillio, 2006. The importance of demographic niches to tree diversity. *Science* **313**:98–101.

5. Brooks, S. P. and A. Gelman, 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**:434–455.

6. Delignette-Muller, M. L., R. Pouillot, J.-B. Denis, and C. Dutang, 2013. fitdistrplus: Help to fit of a parametric distribution to non-censored or censored data.

7. Plummer, M., 2013a. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

8. Su, Y.-S. and M. Yajima, 2013. R2jags: A package for running jags from R.

Table C1: Group-level maximum likelihood estimates of the shape (k) and rate (θ) parameters governing the informed gamma priors for $\boldsymbol{\beta_2}$ and $\boldsymbol{\beta_3}$. These were computed from all observed positive growth increments in each of the s groups (each group's sample size is indicated by n). Groupings were based on stem habitat, sex, and transition years.

s	Habitat	Sex	Transition	k_s	θ_s	n
1	Upland	Male	2009–2010	2.592	0.506	128
2	Upland	Female	2009–2010	2.420	0.480	230
3	Upland	Male	2010–2011	2.193	0.489	116
4	Upland	Female	2010–2011	2.271	0.486	277
5	Riparian	Male	2009–2010	2.129	0.569	244
6	Riparian	Female	2009–2010	2.259	0.561	307
7	Riparian	Male	2010–2011	1.742	0.342	264
8	Riparian	Female	2010–2011	1.694	0.329	305

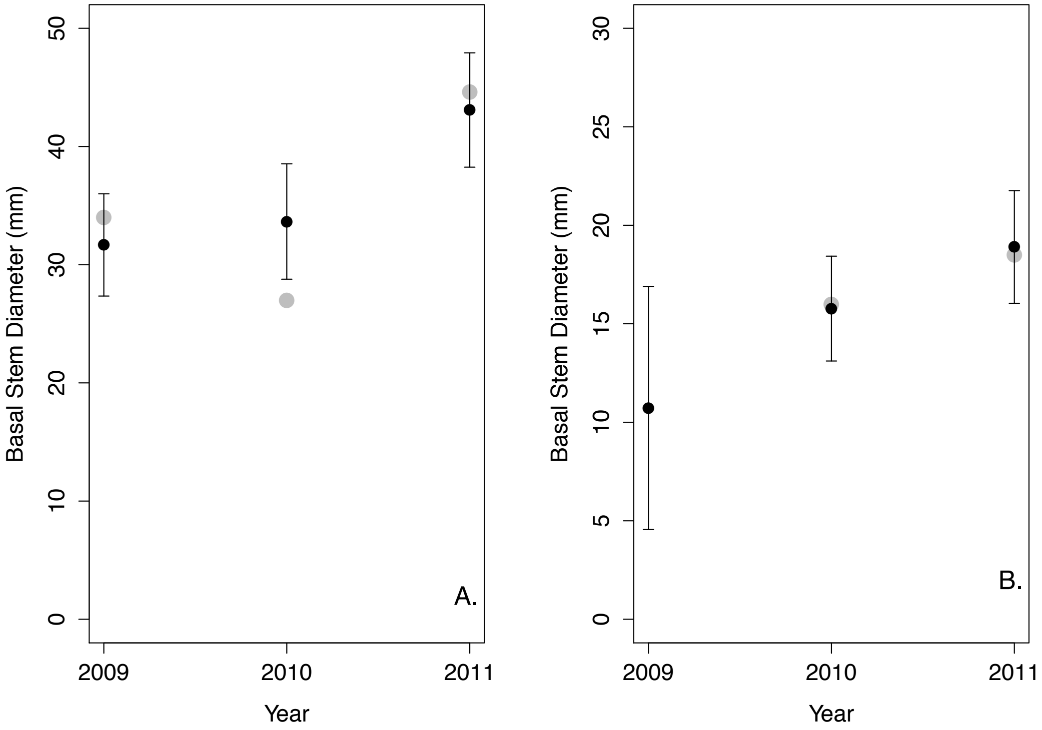

Figure C1: Observed (gray) and adjusted (black) basal stem diameters for (A) a stem with a negative growth increment from 2010–2011 and (B) a stem with a missing 2009 stem diameter measurement. Black circles and error bars represent the mean and 95% credible intervals of the adjusted stem diameter posterior distributions from Equation 3.

APPENDIX D: AGGREGATING WILLOW STEMS

We pooled the data for each 1st order stem and its associated 2nd order stems to create the individual plant units (hereafter "stem"). We summed a stem's 1st and 2nd order basal diameters and number of catkins each year to calculate the annual basal diameter, in millimeters, and catkin count as metrics for stem size and reproductive allocation, respectively (Figure D1). For each year, we created a binary indicator that equaled one if flowering stems had ≥ 3 catkins, and zero otherwise. After examining cumulative frequency plots of the number catkins per stem, we chose this cutoff to group stems that committed only superficially to reproduction with non-reproductive stems, as opposed to with those that invested heavily in flowering. We calculated the relative growth rate (yr^{-1}) for each stem as the difference in the log of stem size from year t to year $t+1$ for the sum of the 1st order stem and any 2nd order stems alive during the second visit of year t and first visit of year $t+1$. For each observer, a stem was scored as attacked if the presence of weevils was detected on any of its 1st or 2nd order stems.

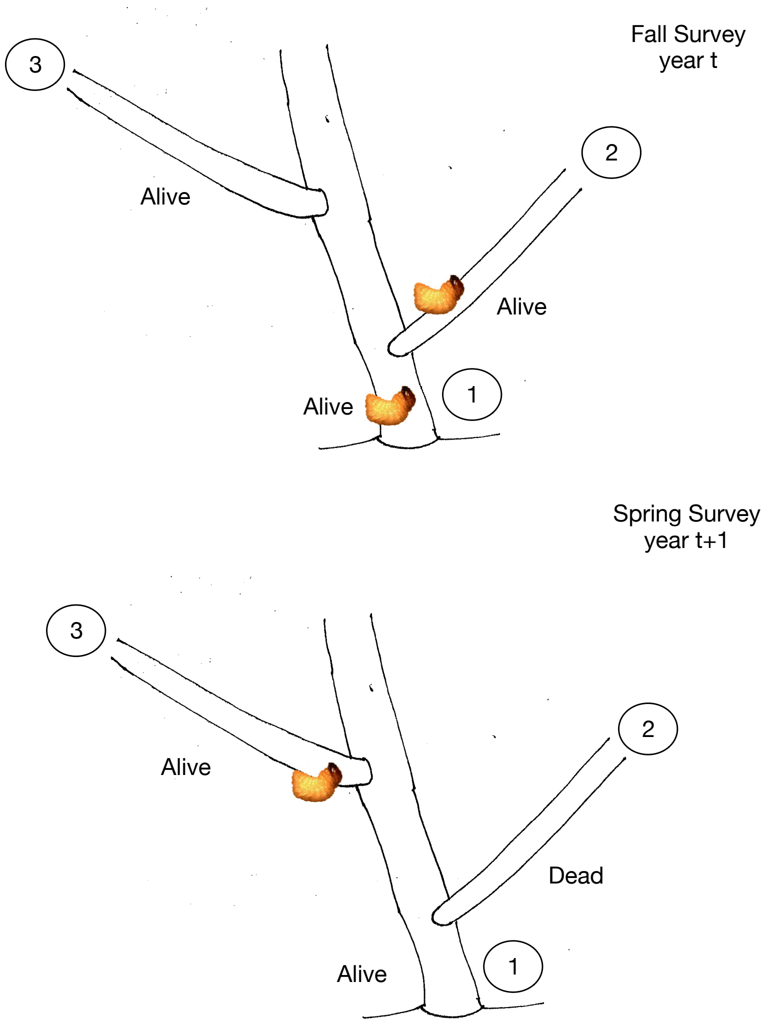

Figure D1: Diagram of willow stem surveyed in summer of year t and spring of year $t+1$. This stem had two 2^{nd} order stems (2) and (3). In year t the stem size would be calculated as the sum of basal diameters of the 1^{st} order stem (1) and the two 2^{nd} order stems (2) and (3). In year $t+1$, the stem size would exclude the dead 2^{nd} order stem (2). The relative growth rate would be calculated as the difference in the log of stem size where in both years only stem (1) and stem (3) are included in this calculation, as stem (2) is dead in year $t+1$. In both years, we would score the stem as attacked, as weevil larvae were observed in either the 1^{st} order stem or any of its 2^{nd} order stems.

APPENDIX E: STEM-OCCUPANCY MODEL PREDICTIVE CHECKS

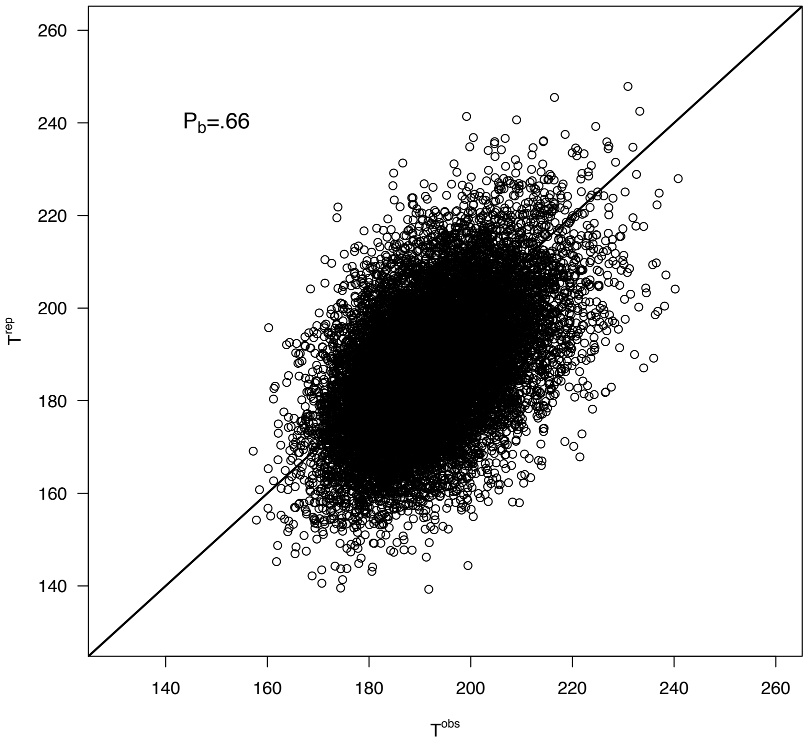

Figure E1: Posterior predictive checks of the dynamic stem occupancy model (Equation 1). Test statistics were calculated from the observed data plotted against test statistics calculated from simulated data bracket a line with intercept 0 and slope = 1, indicating adequate model fit. The proportion of points above the line give the Bayesian P value (P_b). Values of P_b near 1 or 0 indicate lack of fit.

BIBLIOGRAPHY

Abebe, G., J. H. Hart, R. Adams, et al., 1990. The relationship of site factors to the incidence of *Cytospora* and *Septoria* cankers and poplar and willow borer in hybrid poplar plantations. *General Technical Report-North Central Forest Experiment Station, USDA Forest Service* pages 163–171.

Ågren, J. K., 1988. Sexual differences in biomass and nutrient allocation in the dioecious *Rubus chamaemorus*. *Ecology* **69**:962–973.

Ågren, J. K., K. Danell, T. Elmqvist, L. Ericson, and J. Hjältén, 1999. Sexual dimorphism and biotic interactions. In M. A. Geber, T. E. Dawson, and L. F. Delph, editors, *Gender and sexual dimorphism in flowering plants*, pages 217–246. Springer, Berlin.

Åhman, I., 1997. Growth, herbivory and disease in relation to gender in *Salix viminalis* L. *Oecologia* **111**:61–68.

Allen, G. A. and J. A. Antos, 1988. Relative reproductive effort in males and females of the dioecious shrub *Oemleria cerasiformis*. *Oecologia* **76**:111–118.

Allen, G. A. and J. A. Antos, 1993. Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. *The American Naturalist* **141**:537–553.

Alliende, M. and J. Harper, 1989. Demographic studies of a dioecious tree. I. Colonization, sex and age structure of a population of *Salix cinerea*. *Journal of Ecology* **77**:1029–1047.

Alström-Rapaport, C., M. Lascoux, and U. Gullberg, 1997. Sex determination and sex ratio in the dioecious shrub *Salix viminalis* L. *Theoretical and Applied Genetics* **94**:493–497.

Alström-Rapaport, C., M. Lascoux, Y. Wang, G. Roberts, and G. Tuskan, 1998. Identification of a RAPD marker linked to sex determination in the basket willow (*Salix viminalis* L.). *Journal of Heredity* **89**:44–49.

Antos, J. A. and G. A. Allen, 1990. A comparison of reproductive effort in the dioecious shrub *Oemleria cerasiformis* using nitrogen, energy and biomass as currencies. *American Midland Naturalist* **124**:254–262.

Apple, J. L., M. Wink, S. E. Wills, and J. G. Bishop, 2009. Successional change in phosphorus stoichiometry explains the inverse relationship between herbivory and lupin density on Mount St. Helens. *PLoS ONE* **4**:e7807.

Argus, G. W., 1974. An experimental study of hybridization and pollination in *Salix* (willow). *Canadian Journal of Botany* **52**:1613–1619.

Ashman, T.-L. and I. Baker, 1992. Variation in floral sex allocation with time of season and currency. *Ecology* **73**:1237–1243.

Aspinall, D. and L. G. Paleg, 1981. Proline accumulation: Physiological aspects. In L. G. Paleg and D. Aspinall, editors, *The physiology and* *biochemistry of drought resistance in plants*, pages 205–241. Academic Press, New York.

Bañuelos, M.-J. and J.-R. Obeso, 2004. Resource allocation in the dioecious shrub *Rhamnus alpinus*: The hidden costs of reproduction. *Evolutionary Ecology Research* **6**:397–413.

Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt, 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution* **20**:634–641.

Bardgett, R. D. and D. A. Wardle, 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84**:2258–2268.

Barrett, S. C., R. I. Colautti, and C. G. Eckert, 2008. Plant reproductive systems and evolution during biological invasion. *Molecular Ecology* **17**:373–383.

Barrett, S. C., S. B. Yakimowski, D. L. Field, and M. Pickup, 2010. Ecological genetics of sex ratios in plant populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:2549–2557.

Bauerfeind, S. S. and K. Fischer, 2013. Testing the plant stress hypothesis: Stressed plants offer better food to an insect herbivore. *Entomologia Experimentalis Et Applicata* **149**:148–158.

Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka, 1987. Allocating resources to reproduction and defense. *BioScience* **37**:58–67.

Belovsky, G. and J. Slade, 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences* **97**:14412–14417.

Bergvinson, D. J., R. I. Hamilton, and J. T. Arnason, 1995. Leaf profile of maize resistance factors to European corn borer, *Ostrinia nubilalis*. *Journal of Chemical Ecology* **21**:343–354.

Bierzychudek, P. and V. Eckhart, 1988. Spatial segregation of the sexes of dioecious plants. *American Naturalist* **132**:34–43.

Bishop, J. G., 2002. Early primary succession on Mount St. Helens: Impact of insect herbivores on colonizing lupines. *Ecology* **83**:191–202.

Bishop, J. G., N. B. O'Hara, J. H. Titus, J. L. Apple, R. A. Gill, and L. Wynn, 2010. NP co-limitation of primary production and response of arthropods to N and P in early primary succession on Mount St. Helens volcano. *PloS ONE* **5**:e13598.

Boecklen, W. J. and M. T. Hoffman, 1993. Sex-biased herbivory in *Ephedra trifurca*: The importance of sex-by-environment interactions. *Oecologia* **96**:49–55.

Boecklen, W. J., S. Mopper, and P. W. Price, 1994. Sex-biased herbivory in arroyo willow: Are there general patterns among herbivores? *Oikos* **71**:267–272.

Boecklen, W. J., P. W. Price, and S. Mopper, 1990. Sex and drugs and herbivores: sex-biased herbivory in arroyo willow (*Salix lasiolepis*). *Ecology* **71**:581–588.

Brenna, J. T., T. N. Corso, H. J. Tobias, and R. J. Caimi, 1997. High-precision continuous-flow isotope ratio mass spectrometry. *Mass Spectrometry Reviews* **16**:227–258.

Broberg, C. and J. Borden, 2005. Hybrid poplar clones with *Populus maximowimii* parentage demonstrate postoviposition antibiosis to *Cryptorhynchus lapathi* (Coleoptera: Curculionidae). *Journal of Economic Entomology* **98**:2254–2259.

Broberg, C., J. Borden, and R. Gries, 2005. Olfactory and feeding preferences of *Cryptorhynchus lapathi* L. (Coleoptera: Curculionidae) among hybrid clones and natural poplars. *Environmental Entomology* **34**:1606–1613.

Broberg, C., J. Borden, and L. Humble, 2001. Host range, attack dynamics, and impact of *Cryptorhynchus lapathi* (Coleoptera: Curculionidae) on *Salix* (Salicaceae) spp. *Canadian Entomologist* **133**:119–130.

Broberg, C. L., J. H. Borden, and L. M. Humble, 2002. Distribution and abundance of *Cryptorhynchus lapathi* on *Salix* spp. in British Columbia. *Canadian Journal of Forest Research* **32**:561–568.

Broberg, C. L., J. A. H. Inkster, and J. H. Borden, 2010. Phenological and chemical differences among hybrid poplar clones (Salicaceae) varying in resistance to *Cryptorhynchus lapathi* (L.) (Coleoptera: Curculionidae). *Biochemical Systematics and Ecology* **38**:29–48.

Brodbeck, B. and D. Strong, 1987. Amino acid nutrition of herbivorous insects and stress to host plants. In P. Barbosa and J. C. Schultz, editors, *Insect Outbreaks*, pages 347–364. Academic Press, New York.

Brooks, S. P. and A. Gelman, 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**:434–455.

Bryant, J. and F. Chapin, 1986. Browsing-woody plant interactions during boreal forest plant succession. In K. Van Cleve, F. Chapin III, P. Flanagan, L. Viereck, and C. Dyrness, editors, *Forest ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*, pages 213–225. Springer, New York.

Bryant, J. P., 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. *Ecology* **68**:1319–1327.

Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. T. du Toit, 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* **22**:431–446.

Bryant, J. P., G. D. Wieland, T. Clausen, and P. Kuropat, 1985. Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology* **66**:1564–1573.

Bulmer, M. G. and P. D. Taylor, 1980. Dispersal and the sex ratio. *Nature* **284**:448–449.

Caldeira, M., V. Fernandez, J. Tome, and J. Pereira, 2002. Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. *Annals of Forest Science* **59**:99–106.

Chapin, F. S., P. M. Vitousek, and K. Van Cleve, 1986. The nature of nutrient limitation in plant communities. *The American Naturalist* **127**:48–58.

Chapin, F. S., L. R. Walker, C. L. Fastie, and L. C. Sharman, 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**:149–175.

Chapin, S. F., 1989. The cost of tundra plant structures: Evaluation of concepts and currencies. *The American Naturalist* **133**:1–19.

Chapin III, F. S., A. J. Bloom, C. B. Field, and R. H. Waring, 1987. Plant responses to multiple environmental factors. *BioScience* **37**:49–57.

Chapman, S. K., S. C. Hart, N. S. Cobb, T. G. Whitham, and G. W. Koch, 2003. Insect herbivory increases litter quality and decomposition: An extension of the acceleration hypothesis. *Ecology* **84**:2867–2876.

Chapman, S. K., T. G. Whitham, and M. Powell, 2006. Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees. *Oikos* **114**:566–574.

Charlesworth, D., 2002. Plant sex determination and sex chromosomes. *Heredity* **88**:94–101.

Chen, Y., T. Ciaramitaro, and T. M. Poland, 2011. Moisture content and nutrition as selection forces for emerald ash borer larval feeding behaviour. *Ecological Entomology* **36**:344–354.

Chiari, S., A. Zauli, A. Mazziotta, L. Luiselli, P. Audisio, and G. M. Carpaneto, 2013. Surveying an endangered saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands: A comparison between different capture methods. *Journal of Insect Conservation* **17**:171–181.

Christiansen, E., R. H. Waring, and A. A. Berryman, 1987. Resistance of conifers to bark beetle attack - Searching for general relationships. *Forest Ecology and Management* **22**:89–106.

Classen, A. T., S. K. Chapman, T. G. Whitham, S. C. Hart, and G. W. Koch, 2013. Long-term insect herbivory slows soil development in an arid ecosystem. *Ecosphere* **4**:art52.

Classen, A. T., J. DeMarco, S. C. Hart, T. G. Whitham, N. S. Cobb, and G. W. Koch, 2006. Impacts of herbivorous insects on decomposer communities during the early stages of primary succession in a semi-arid woodland. *Soil Biology and Biochemistry* **38**:972–982.

Clesceri, L. S., A. E. Greenberg, and A. D. Eaton, editors, 1998. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC.

Cobb, N. S., S. Mopper, C. A. Gehring, M. Caouette, K. M. Christensen, and T. G. Whitham, 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. *Oecologia* **109**:389–397.

Coley, P. D., J. P. Bryant, and F. S. Chapin III, 1985. Resource availability and plant antiherbivore defense. *Science* **230**:895–899.

Conn, J. S. and U. Blum, 1981. Sex ratio of *Rumex hastatulus*: The effect of environmental factors and certation. *Evolution* **35**:1108–1116.

Connell, J. H. and R. O. Slatyer, 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**:1119–1144.

Cooke, J. E. and M. Weih, 2005. Nitrogen storage and seasonal nitrogen cycling in Populus: Bridging molecular physiology and ecophysiology. *New Phytologist* **167**:19–30.

Cornelissen, T., G. W. Fernandes, and J. Vasconcellos-Neto, 2008. Size does matter: Variation in herbivory between and within plants and the plant vigor hypothesis. *Oikos* **117**:1121–1130.

Cornelissen, T. and P. Stiling, 2005. Sex-biased herbivory: A meta-analysis of the effects of gender on plant-herbivore interactions. *Oikos* **111**:488–500.

Correns, C., 1922. Sex determination and numerical proportion of genders in common sorrel (*Rumex acetosa*) (translated from German). *Biol. Zentralblatt* **42**:465–480.

Courtney, S. P., 1985. Apparency in coevolving relationships. *Oikos* **44**:91–98.

Cox, P. A., 1981. Niche partitioning between sexes of dioecious plants. *The American Naturalist* **117**:295–307.

Craig, T. P., 2010. The resource regulation hypothesis and positive feedback loops in plant–herbivore interactions. *Population Ecology* **52**:461–473.

Craig, T. P., P. W. Price, and J. K. Itami, 1986. Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* **67**:419–425.

Crawford, R. and J. Balfour, 1983. Female predominant sex ratios and physiological differentiation in arctic willows. *Journal of Ecology* **71**:149–160.

Crawley, M. J. and M. Akhteruzzaman, 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology* **2**:409–415.

Cunningham, S. A. and R. B. Floyd, 2006. *Toona ciliata* that suffer frequent height-reducing herbivore damage by a shoot-boring moth *Hypsipyla robusta* are taller. *Forest Ecology and Management* **225**:400–403.

Dale, V. H., F. J. Swanson, and C. M. Crisafulli, 2005. Disturbance, survival, and succession: Understanding ecological responses to the 1980 eruption of Mount St. Helens. In V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors, *Ecological responses to the 1980 eruption of Mount St. Helens*. Springer, New York.

Danell, K., T. Elmqvist, L. Ericson, and A. Salomonson, 1985. Sexuality in willows and preference by bark-eating voles: Defence or not? *Oikos* **44**:82–90.

Danell, K., J. Hjältén, L. Ericson, and T. Elmqvist, 1991. Vole feeding on male and female willow shoots along a gradient of plant productivity. *Oikos* **62**:145–152.

Darwin, C., 1877. The different forms of flowers on plants of the same species. John Murray, London.

Dawson, T. E. and L. Bliss, 1989a. Intraspecific variation in the water relations of *Salix arctica*, an arctic-alpine dwarf willow. *Oecologia* **79**:322–331.

Dawson, T. E. and L. Bliss, 1989b. Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: The physiological basis for habitat partitioning between the sexes. *Oecologia* **79**:332–343.

Dawson, T. E. and J. R. Ehleringer, 1993a. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* **74**:798–815.

Dawson, T. E. and J. R. Ehleringer, 1993b. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* **74**:798–815.

Dawson, T. E. and M. A. Geber, 1999. Sexual dimorphism in physiology and morphology. In M. A. Geber, T. E. Dawson, and L. F. Delph, editors, *Gender and sexual dimorphism in flowering plants*, pages 175–215. Springer, Berlin.

De Bruyn, L., 1995. Plant stress and larval performance of a dipterous gall former. *Oecologia* **101**:461–466.

de Jong, T. and P. Klinkhamer, 2005. Sex ratios in dioecious plants. In *Evolutionary ecology of plant reproductive strategies*, pages 175–183. Cambridge University Press, Cambridge.

de Jong, T. and E. Meijden, 2004. Sex ratio of some long-lived dioecious plants in a sand dune area. *Plant Biology* **6**:616–620.

de Jong, T., H. Nell, and G. Glawe, 2005. Heritable variation in seed sex ratio of the stinging nettle (*Urtica dioica*). *Plant Biology* **7**:190–194.

de Jong, T., F. Van Batenburg, and J. Van Dijk, 2002. Seed sex ratio in dioecious plants depends on relative dispersal of pollen and seeds: An example using a chessboard simulation model. *Journal of Evolutionary Biology* **15**:373–379.

del Moral, R. and L. Bliss, 1993. Mechanisms of primary succession - Insights resulting from the eruption of Mount St. Helens. In M. Begon and A. Fitter, editors, *Advances in Ecological Research*, volume 24 of *Advances in Ecological Research*, pages 1–66. Academic Press, London.

del Moral, R. and C. Jones, 2002. Vegetation development on pumice at Mount St. Helens, USA. *Plant Ecology* **162**:9–22.

Del Moral, R. and D. M. Wood, 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *American Journal of Botany* **80**:981–981.

del Moral, R. and D. M. Wood, 1993. Early primary succession on a barren volcanic plain at mount st. helens, washington. *American Journal of Botany* **80**:981–991.

Delph, L. F., 1999. Sexual dimorphism in life history. In M. A. Geber, T. E. Dawson, and L. F. Delph, editors, *Gender and sexual dimorphism in flowering plants*, pages 150–173. Springer, Berlin.

Delph, L. F., Y. Lu, and L. D. Jayne, 1993. Patterns of resource allocation in a dioecious *Carex* (Cyperaceae). *American Journal of Botany* **80**:607–615.

Densmore, R. and J. Zasada, 1983. Seed dispersal and dormancy patterns in northern willows: Ecological and evolutionary significance. *Canadian Journal of Botany* **61**:3207–3216.

Dudley, L. S., 2006. Ecological correlates of secondary sexual dimorphism in *Salix glauca* (Salicaceae). *American Journal of Botany* **93**:1775–1783.

Dunn, J. and P. Lorio, 1993. Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera, Scolytidae). *Environmental Entomology* **22**:948–957.

Duval, B. and W. Whitford, 2008. Resource regulation by a twig-girdling beetle has implications for desertification. *Ecological Entomology* **33**:161–166.

Edwards, A., 2000. Carl Düsing (1884) on *The Regulation of the Sex-Ratio*. *Theoretical Population Biology* **58**:255–257.

Elam, D. R., C. E. Ridley, K. Goodell, and N. C. Ellstrand, 2007. Population size and relatedness affect fitness of a self-incompatible invasive plant. *Proceedings of the National Academy of Sciences* **104**:549–552.

Elmqvist, T., R. G. Cates, J. K. Harper, and H. Gardfjell, 1991. Flowering in males and females of a Utah willow, *Salix rigida* and effects on growth, tannins, phenolic glycosides and sugars. *Oikos* **61**:65–72.

Elmqvist, T., L. Ericson, K. Danell, and A. Salomonson, 1988. Latitudinal sex ratio variation in willows, *Salix* spp., and gradients in vole herbivory. *Oikos* **51**:259–266.

Escarré, J., C. Houssard, and N. Vartanian, 1990. Comparison of water-balance regulation of populations of *Rumex-acetosella* along a postcultural successional gradient. *Canadian Journal Of Botany* **68**:428–434.

Espírito-Santo, M., B. Madeira, F. Neves, M. Faria, M. Fagundes, and G. W. Fernandes, 2003. Sexual differences in reproductive phenology and their consequences for the demography of *Baccharis dracunculifolia* (Asteraceae), a dioecious tropical shrub. *Annals of Botany* **91**:13–19.

Fagan, W. F. and J. G. Bishop, 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helen. *The American Naturalist* **155**:238–251.

Fagan, W. F., J. G. Bishop, and J. D. Schade, 2004. Spatially structured herbivory and primary succession at Mount St Helens: Field surveys and experimental growth studies suggest a role for nutrients. *Ecological Entomology* **29**:398–409.

Fagan, W. F., M. Lewis, M. G. Neubert, C. Aumann, J. L. Apple, and J. G. Bishop, 2005. When can herbivores slow or reverse the spread of an invading plant? A test case from Mount St. Helens. *The American Naturalist* **166**:669–685.

Faliński, J. B., 1980. Vegetation dynamics and sex structure of the populations of pioneer dioecious woody plants. *Vegetatio* **43**:23–38.

Faria, M. L. and G. W. Fernandes, 2001. Vigour of a dioecious shrub and attack by a galling herbivore. *Ecological Entomology* **26**:37–45.

Feller, I. C. and W. N. Mathis, 1997. Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. *Biotropica* **29**:440–451.

Fernandes, G. W., 1992. Adaptive distribution of gall-forming insects: Patterns and mechanisms. Ph.D. thesis, Northern Arizona University.

Fernandes, G. W. and P. W. Price, 1992. Plant sex and habitat effects on the survivorship of insect galls within the geographical range of the host-plant. *Oecologia* **90**:14–20.

Field, D. L., M. Pickup, and S. C. Barrett, 2013a. Comparative analyses of sex-ratio variation in dioecious flowering plants. *Evolution* **67**:661–672.

Field, D. L., M. Pickup, and S. C. Barrett, 2013b. Ecological context and metapopulation dynamics affect sex-ratio variation among dioecious plant populations. *Annals of Botany* **111**:917–923.

Fisher, R. A., 1930. The genetical theory of natural selection. Oxford University Press, London.

Fox, J. F. and G. C. Stevens, 1991. Costs of reproduction in a willow: Experimental responses vs. natural variation. *Ecology* **72**:1013–1023.

Foxworthy, B. L. and M. Hill, 1982. Volcanic eruptions of 1980 at Mount St. Helens: The first 100 days. Number 1249. USGPO.

Freeman, D. C., L. G. Klikoff, and K. T. Harper, 1976. Differential resource utilization by the sexes of dioecious plants. *Science* **193**:597–599.

Fritz, R. S., B. A. Crabb, and C. G. Hochwender, 2000. Preference and performance of a gall-inducing sawfly: A test of the plant vigor hypothesis. *Oikos* **89**:555–563.

Fritz, R. S., B. A. Crabb, and C. G. Hochwender, 2003. Preference and performance of a gall-inducing sawfly: Plant vigor, sex, gall traits and phenology. *Oikos* **102**:601–613.

Froiland, S. G., 1962. The genus *Salix* (willows) in the Black Hills of South Dakota. Technical Report 1269, United States Department of Agriculture.

Frost, C. J., J. M. Dean, E. C. Smyers, M. C. Mescher, J. E. Carlson, C. M. De Moraes, and J. F. Tooker, 2012. A petiole-galling insect herbivore decelerates leaf lamina litter decomposition rates. *Functional Ecology* **26**:628–636.

Frost, C. J. and M. D. Hunter, 2004. Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology* **85**:3335–3347.

Frost, C. J. and M. D. Hunter, 2007. Recycling of nitrogen in herbivore feces: Plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia* **151**:42–53.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin, 2013. Bayesian data analysis. CRC Press, Boca Raton.

Gelman, A. and J. Hill, 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press.

Gershenzon, J., 1984. Changes in the levels of plant secondary metabolites under water and nutrient stress. In B. N. Timmermann, C. Steelink, and F. A. Loewus, editors, *Recent Advances in Phytochemistry*, pages 273–320. Springer, Boston.

Gill, R. A., J. A. Boie, J. G. Bishop, L. Larsen, J. L. Apple, and R. D. Evans, 2006. Linking community and ecosystem development on Mount St. Helens. *Oecologia* **148**:312–324.

Gorham, E., P. M. Vitousek, and W. A. Reiners, 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* **10**:53–84.

Govindan, B. N., M. Kéry, and R. K. Swihart, 2012. Host selection and responses to forest fragmentation in acorn weevils: inferences from dynamic occupancy models. *Oikos* **121**:623–633.

Grant, M. C. and J. B. Mitton, 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution* **33**:914–918.

Grinnan, R., T. E. Carter, Jr., and M. T. J. Johnson, 2013. Effects of drought, temperature, herbivory, and genotype on plant-insect interactions in soybean *(Glycine max)*. *Arthropod-Plant Interactions* **7**:201–215.

Gu, W. and R. K. Swihart, 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* **116**:195–203.

Gutbrodt, B., K. Mody, and S. Dorn, 2011. Drought changes plant chemistry and causes contrasting responses in Lepidopteran herbivores. *Oikos* **120**:1732–1740.

Halvorson, J. J. and J. L. Smith, 1995. Decomposition of lupine biomass by soil microorganisms in developing Mount St. Helens' pyroclastic soils. *Soil Biology and Biochemistry* **27**:983–992.

Hanks, L., T. Paine, and J. Millar, 1991. Mechanisms of resistance in *Eucalyptus* against larvae of the eucalyptus longhorned borer (Coleoptera, Cerambycidae). *Environmental Entomology* **20**:1583–1588.

Hanks, L., T. Paine, J. Millar, C. Campbell, and U. Schuch, 1999. Water relations of host trees and resistance to the phloem–boring beetle *Phoracantha semipunctata* F. (Coleoptera:Cerambycidae). *Oecologia* **119**:400–407.

Harrell Jr, F. E., 2014. Hmisc: Harrell Miscellaneous.

Harris, J. W. E. and H. C. Coppel, 1967. The poplar-and-willow borer, *Sternochetus* (= *Cryptorhynchus*) *lapathi* (Coleoptera: Curculionidae), in British Columbia. *The Canadian Entomologist* **99**:411–418.

Harris, M. S. and J. R. Pannell, 2008. Roots, shoots and reproduction: Sexual dimorphism in size and costs of reproductive allocation in an annual herb. *Proceedings of the Royal Society B: Biological Sciences* **275**:2595–2602.

Heilbuth, J. C., 2000. Lower species richness in dioecious clades. *The American Naturalist* **156**:221–241.

Herms, D. A. and W. J. Mattson, 1992. The dilemma of plants - To grow or defend. *Quarterly Review of Biology* **67**:283–335.

Hjältén, J., 1992. Plant sex and hare feeding preferences. *Oecologia* **89**:253–256.

Hobbie, S. E., 1992. Effects of plant species on nutrient cycling. *Trends in ecology & evolution* **7**:336–339.

Hodges, J. and P. Lorio, 1971. Comparison of field techniques for measuring moisture stress in large loblolly pines. *Forest Science* **17**:220–223.

Höglund, S., S. Larsson, and G. Wingsle, 2005. Both hypersensitive and non-hypersensitive responses are associated with resistance in *Salix viminalis* against the gall midge *Dasineura marginemtorquens*. *Journal of Experimental Botany* **56**:3215–3222.

Holland, E. A., W. J. Parton, J. K. Detling, and D. L. Coppock, 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist* **140**:685–706.

Houssard, C., J. Escarré, and N. Vartanian, 1992. Water stress effects on successional populations of the dioecious herb, *Rumex acetosella* L. *New Phytologist* **120**:551–559.

Hsiao, T. C., 1973. Plant responses to water stress. *Annual Review of Plant Physiology and Plant Molecular Biology* **24**:519–570.

Huberty, A. F. and R. F. Denno, 2004. Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology* **85**:1383–1398.

Hughes, F. M., M. Johansson, S. Xiong, E. Carlborg, D. Hawkins, M. Svedmark, A. Hayes, A. Goodall, K. S. Richards, and C. Nilsson, 2010. The influence of hydrological regimes on sex ratios and spatial segregation of the sexes in two dioecious riparian shrub species in northern Sweden. *Plant Ecology* **208**:77–92.

Ibanez, S., L. Bernard, S. Coq, M. Moretti, S. Lavorel, and C. Gallet, 2013. Herbivory differentially alters litter dynamics of two functionally contrasted grasses. *Functional Ecology* **27**:1064–1074.

Inbar, M., H. Doostdar, and R. T. Mayer, 2001. Suitability of stressed and vigorous plants to various insect herbivores. *Oikos* **94**:228–235.

Inbar, M. and S. Kark, 2007. Gender-related developmental instability and herbivory of *Pistacia atlantica* across a steep environmental gradient. *Folia Geobotanica* **42**:401–410.

Jenny, H., 1941. Factors of soil formation: A system of pedology. McGraw-Hill.

Jesus, F. M., J. O. Silva, M. Fagundes, and G. W. Fernandes, 2012. Differential female attack and larval performance of a galling cecidomyiid on the host, *Astronium fraxinifolium* (Anacardiaceae), in contrasting habitats. *Entomological News* **122**:10–21.

Jing, S. W. and P. D. Coley, 1990. Dioecy and herbivory: The effect of growth rate on plant defense in *Acer negundo*. *Oikos* **58**:369–377.

Johnson, C. W., 2000. Tree recruitment and survival in rivers: Influence of hydrological processes. *Hydrological Processes* **14**:3051–3074.

Kagata, H. and T. Ohgushi, 2012a. Non-additive effects of leaf litter and insect frass mixture on decomposition processes. *Ecological research* **27**:69–75.

Kagata, H. and T. Ohgushi, 2012b. Positive and negative impacts of insect frass quality on soil nitrogen availability and plant growth. *Population ecology* **54**:75–82.

Karberg, N. J., N. A. Scott, and C. P. Giardina, 2008. Methods for estimating litter decomposition. In C. M. Hoover, editor, *Field Measurements for Forest Carbon Monitoring*, pages 103–111. Springer, New York.

Karrenberg, S., P. Edwards, and J. Kollmann, 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* **47**:733–748.

Kéry, M., B. Gardner, and C. Monnerat, 2010. Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography* **37**:1851–1862.

Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio, 2009. Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology* **90**:1279–1290.

Kielland, K. and J. P. Bryant, 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* **82**:377–383.

Kielland, K., J. P. Bryant, and R. W. Ruess, 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos* **80**:25–30.

Kistek, J., 1989. Die populationsdynamik der forstschadinsekten als grundlage des integrierten forstchntzes gegen sie. In *Acta Universitatis Agriculturae Facultas Silviculturae (Brno) Series C*, volume 58, pages 47–83.

Klinkhamer, P., T. Kubo, and Y. Iwasa, 1997. Herbivores and the evolution of the semelparous perennial life-history of plants. *Journal of Evolutionary Biology* **10**:529–550.

Kolehmainen, J., H. Roininen, R. Julkunen-Tiitto, and J. Tahvanainen, 1994. Importance of phenolic glucosides in host selection of shoot galling sawfly, *Euura amerinae*, on *Salix pentandra. Journal of Chemical Ecology* **20**:2455–2466.

Kopelke, J.-P., J. Amendt, and K. Schönrogge, 2003. Patterns of interspecific associations of stem gallers on willows. *Diversity and Distributions* **9**:443–453.

Koricheva, J., S. Larsson, and E. Haukioja, 1998. Insect performance on experimentally stressed woody plants: A meta-analysis. *Annual Review of Entomology* **43**:195–216.

Kozlowski, T., 1992. Carbohydrate sources and sinks in woody plants. *The Botanical Review* **58**:107–222.

Kozlowski, T. T., 1979. Tree growth and environmental stresses. University of Washington Press, Seattle.

Krasny, M. E., K. A. Vogt, and J. C. Zasada, 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Ecography* **11**:210–219.

Krugner, R., R. L. Groves, M. W. Johnson, A. P. Flores, J. R. Hagler, and J. G. Morse, 2009. Seasonal population dynamics of *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in sweet orange trees maintained under continuous deficit irrigation. *Journal of Economic Entomology* **102**:960–973.

Larson, K. C. and T. G. Whitham, 1997. Competition between gall aphids and natural plant sinks: Plant architecture affects resistance to galling. *Oecologia* **109**:575–582.

Larsson, S., 1989. Stressful times for the plant stress - insect performance hypothesis. *Oikos* **56**:277–283.

Larsson, S. and O. Tenow, 1984. Areal distribution of a *Neodiprion sertifer* (Hym., Diprionidae) outbreak on scots pine as related to stand condition. *Ecography* **7**:81–90.

Leibold, M. A., 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* **134**:922–949.

Levitt, J., 1972. Responses of plants to environmental stresses. Academic Press, New York.

Li, C., G. Xu, R. Zang, H. Korpelainen, and F. Berninger, 2007. Sex-related differences in leaf morphological and physiological responses in *Hippophae rhamnoides* along an altitudinal gradient. *Tree physiology* **27**:399–406.

Lichter, J., 1998. Primary succession and forest development oncoastal Lake Michigan sand dunes. *Ecological Monographs* **68**:487–510.

Lipman, P. W. and D. R. Mullineaux, 1981. The 1980 eruptions of Mount St. Helens, Washington. Technical report, United States Geological Survey.

Litrico, I., T. Pailler, and J. D. Thompson, 2005. Gender variation and primary succession in a tropical woody plant, *Antirhea borbonica* (Rubiaceae). *Journal of Ecology* **93**:705–715.

Lloyd, D. G. and C. J. Webb, 1977. Secondary sex characters in plants. *Botanical Review* **43**:177–216.

Lorio, P. L. and J. D. Hodges, 1977. Tree water status affects induced southern pine beetle attacks and brood production. 135, USDA Southern Research Station, Asheville, North Carolina, USA.

Louda, S. M. and S. K. Collinge, 1992. Plant resistance to insect herbivores: A field test of the environmental stress hypothesis. *Ecology* **73**:153–169.

Lovett-Doust, L. and J. Lovett-Doust, 1987. Leaf demography and clonal growth in female and male *Rumex acetosella*. *Ecology* **68**:2056–2058.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin, 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm, 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248–2255.

Marques, A., G. Fernandes, I. Reis, et al., 2002. Distribution of adult male and female *Baccharis concinna* (Asteraceae) in the rupestrian fields of Serra do Cipó, Brazil. *Plant Biology* **4**:94–103.

Matheson, R., 1917. The poplar and willow borer. Technical report, Cornell University Agricultural Experimental Station, 388.

Mattson, W. J., 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**:119–161.

Mattson, W. J. and R. A. Haack, 1987. The role of drought stress in provoking outbreaks of phytophagous insects. In P. Barbosa and J. C. Schultz, editors, *Insect Outbreaks*, pages 365–407. Academic Press, New York.

Maynard Smith, J., 1978. The evolution of sex. Cambridge University Press, Cambridge.

McNaughton, S., 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological monographs* **55**:259–294.

McNaughton, S. J., 1983. Compensatory plant growth as a response to herbivory. *Oikos* **40**:329–336.

Mercer, C. A. and S. M. Eppley, 2010. Inter-sexual competition in a dioecious grass. *Oecologia* **164**:657–664.

Millar, R. B., 2009. Comparison of hierarchical Bayesian models for overdispersed count data using DIC and Bayes' factors. *Biometrics* **65**:962–969.

Miller, R. H., H. S. Whitney, and A. A. Berryman, 1986. Effects of induced translocation stress and bark beetle attack (*Dendroctonus-ponderosae*) on heat pulse velocity and the dynamic wound response of lodgepole pine (*Pinus-contorta* var *latifolia*). *Canadian Journal of Botany* **641**:2669–2674.

Miller, R. O., 1998. High-temperature oxidation: Dry ashing. In *Handbook of reference methods for plant analysis.*, pages 53–56. CRC Press, Boca Raton.

Miller, T. E., B. Tenhumberg, and S. M. Louda, 2008. Herbivore-mediated ecological costs of reproduction shape the life history of an iteroparous plant. *The American Naturalist* **171**:141–149.

Miller, T. E., A. J. Tyre, and S. M. Louda, 2006. Plant reproductive allocation predicts herbivore dynamics across spatial and temporal scales. *The American Naturalist* **168**:608–616.

Mody, K., D. Eichenberger, and S. Dorn, 2009. Stress magnitude matters: Different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. *Ecological Entomology* **34**:133–143.

Moggridge, H. L. and A. M. Gurnell, 2009. Controls on the sexual and asexual regeneration of Salicaceae along a highly dynamic, braided river system. *Aquatic Sciences* **71**:305–317.

Mooney, H. A., 1972. The carbon balance of plants. *Annual Review of Ecology and Systematics* **3**:315–346.

Mooney, K. A., A. Fremgen, and W. K. Petry, 2012. Plant sex and induced responses independently influence herbivore performance, natural enemies and aphid-tending ants. *Arthropod-Plant Interactions* **6**:553–560.

Mopper, S., J. B. Mitton, T. G. Whitham, N. S. Cobb, and C. K. M., 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental-stress. *Evolution* **45**:989–999.

Mopper, S. and T. G. Whitham, 1992. The plant stress paradox: Effects on pinyon sawfly sex ratios and fecundity. *Ecology* **73**:515–525.

Mosbacher, J. B., N. M. Schmidt, and A. Michelsen, 2013. Impacts of eriophyoid gall mites on arctic willow in a rapidly changing Arctic. *Polar Biology* **36**:1735–1748.

Muggeo, V. M. R., 2008. segmented: An R package to fit regression models with broken-line relationships.

Myers-Smith, I. H. and D. S. Hik, 2012. Uniform female-biased sex ratios in alpine willows. *American Journal of Botany* **99**:1243–1248.

Naciri-Graven, Y. and J. Goudet, 2003. The additive genetic variance after bottlenecks is affected by the number of loci involved in epistatic interactions. *Evolution* **57**:706–716.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie, 1986. Ecosystem alteation of boreal forest streams by beaver (*Castor canadensis*). *Ecology* **67**:1254–1269.

Nyman, T., R. Paajanen, S. Heiska, and R. Julkunen-Tiitto, 2011. Preference-performance relationship in the gall midge *Rabdophaga* *rosaria*: Insights from a common-garden experiment with nine willow clones. *Ecological Entomology* **36**:200–211.

Obeso, J., 2002. The costs of reproduction in plants. *New Phytologist* **155**:321–348.

Paine, T. D. and C. C. Hanlon, 2010. Integration of tactics for management of *Eucalyptus* herbivores: Influence of moisture and nitrogen fertilization on red gum lerp psyllid colonization. *Entomologia Experimentalis Et Applicata* **137**:290–295.

Pannell, J. R., 2006. Effects of colonization and metapopulation dynamics on the evolution of plant sexual systems. In L. D. Harder and S. C. H. Barrett, editors, *Ecology and evolution of flowers*, pages 223–238. Oxford University Press, Oxford.

Pastor, J. and R. J. Naiman, 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* **139**:690–705.

Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes, 1988. Moose, microbes, and the boreal forest. *BioScience* **38**:770–777.

Pickering, C. M. and W. Hill, 2002. Reproductive ecology and the effect of altitude on sex ratios in the dioecious herb *Aciphylla simplicifolia* (Apiaceae). *Australian Journal of Botany* **50**:289–300.

Plummer, M., 2013a. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

Plummer, M., 2013b. rjags: Bayesian graphical models using MCMC.

Popp, J. W. and J. A. Reinartz, 1988. Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum. American Journal of Botany* **75**:1732–1741.

Predavec, M. and K. Danell, 2001. The role of lemming herbivory in the sex ratio and shoot demography of willow populations. *Oikos* **92**:459–466.

Price, P. W., 1991. The plant vigor hypothesis and herbivore attack. *Oikos* **62**:244–251.

Price, P. W., H. Roininen, and J. Tahvanainen, 1987a. Plant age and attack by the bud galler, *Euura mucronata. Oecologia* **73**:334–337.

Price, P. W., H. Roininen, and J. Tahvanainen, 1987b. Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? *Oecologia* **74**:1–6.

Primm, J. K., 1918. The European poplar canker in the vicinity of Philadelphia, Pennsylvania. *Journal of Economic Entomology* **11**:129–133.

Prins, A. H., H. W. Nell, and P. G. Klinkhamer, 1992. Size-dependent root herbivory on *Cynoglossum officinale. Oikos* **65**:409–413.

Putwain, P. D. and J. L. Harper, 1972. Studies in the dynamics of plant populations: V. mechanisms governing the sex ratio in *Rumex acetosa* and *R. acetosella. The Journal of Ecology* **60**:113–129.

R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raupp, M. J. and R. F. Denno, 1983. Leaf age as a predictor of herbivore distribution and abundance. In R. F. Denno and M. S. McClure, editors, *Variable Plants and Herbivores in Natural and Managed Systems*, pages 91–124. Academic Press, New York.

Rehill, B. J. and J. C. Schultz, 2001. *Hormaphis hamamelidis* and gall size: A test of the plant vigor hypothesis. *Oikos* **95**:94–104.

Renner, S. S. and R. E. Ricklefs, 1995. Dioecy and its correlates in the flowering plants. *American Journal of Botany* **82**:596–606.

Ritchie, M. E., D. Tilman, and J. M. Knops, 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* **79**:165–177.

Roininen, H., P. W. Price, and J. P. Bryant, 1997. Response of galling insects to natural browsing by mammals in Alaska. *Oikos* **80**:481–486.

Roininen, H., P. W. Price, and J. Tahvanainen, 1993. Colonization and extinction in a population of the shoot-galling sawfly, *Euura amerinae*. *Oikos* **68**:448–454.

Rose, K. E., S. M. Louda, and M. Rees, 2005. Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology* **86**:453–465.

Rottenberg, A., 1998. Sex ratio and gender stability in the dioecious plants of Israel. *Botanical Journal of the Linnean Society* **128**:137–148.

Royle, J. A. and M. Kéry, 2007. A Bayesian state-space formulation of dynamic occupancy models. *Ecology* **88**:1813–1823.

Rüger, N. and R. Condit, 2012. Testing metabolic theory with models of tree growth that include light competition. *Functional Ecology* **26**:759–765.

Russo, D., L. Cistrone, and A. P. Garonna, 2011. Habitat selection by the highly endangered long-horned beetle *Rosalia alpina* in Southern Europe: A multiple spatial scale assessment. *Journal of Insect Conservation* **15**:685–693.

Rychlewski, J. and K. Zarzycki, 1975. Sex-ratio in seeds of *Rumex-acetosa* L. as a result of sparse or abundant pollination. *Acta Biologica Cracoviensia Series Botanica* **18**:101–114.

Sacchi, C. F. and P. W. Price, 1988. Pollination of the arroyo willow, *Salix lasiolepis*: Role of insects and wind. *American Journal of Botany* **75**:1387–1393.

Santos, J., C. Tavares, and J. Almeida-Cortez, 2011. Plant vigor hypothesis refuted: Preference-performance linkage of a gall-inducing weevil on small-sized host plant resources. *Brazilian Journal of Biology* **71**:65–69.

Santos, J. C. and J. Almeida-Cortez, 2011. Reply to galls on smaller leaves do not refute the plant vigour hypothesis. *Brazilian Journal of Biology* **71**:1028.

Sariyildiz, T., E. Akkuzu, M. Küçük, A. Duman, and Y. Aksu, 2008. Effects of *Ips typographus* (L.) damage on litter quality and decomposition rates of Oriental Spruce [*Picea Orientalis* (L.) Link.] in Hatila Valley National Park, Turkey. *European Journal of Forest Research* **127**:429–440.

SAS Institute, 2010. SAS software 9th edn, version 9.3. SAS Institute, Cary, N.C.

Schultz, J. C., 1983. Habitat selection and foraging tactics of caterpillars in heterogenous trees. In R. F. Denno and M. S. McClure, editors, *Variable Plants and Herbivores in Natural and Managed Systems*, pages 61–90. Academic Press, New York.

Schweitzer, J. A., J. K. Bailey, S. C. Hart, G. M. Wimp, S. K. Chapman, and T. G. Whitham, 2005. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos* **110**:133–145.

Scriber, J. M. and F. Slansky, 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* **26**:183–211.

Sileshi, G., 2007. A method for estimating insect abundance and patch occupancy with potential applications in large-scale monitoring programmes. *African Entomology* **15**:89–101.

Simpson, K. L. S., G. E. Jackson, and J. Grace, 2012. The response of aphids to plant water stress - The case of *Myzus persicae* and *Brassica oleracea* var. *capitata*. *Entomologia Experimentalis Et Applicata* **142**:191–202.

Sinclair, J. P., J. Emlen, and D. Freeman, 2012. Biased sex ratios in plants: Theory and trends. *The Botanical Review* **78**:63–86.

Singer, F. J. and K. A. Schoenecker, 2003. Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management* **181**:189–204.

Sjodin, K., L. M. Schroeder, H. H. Eidmann, T. Norin, and S. Wold, 1989. Attack rates of scolytids and composition of volatile wood constituents in healthy and mechanically weakened pine trees. *Scandinavian Journal of Forest Research* **4**:379–391.

Smith, B. D. and K. G. Stott, 1964. The life history and behaviour of the willow weevil *Cryptorhynchus lapathi* L. *Annals of Applied Biology* **54**:141–151.

Smith, B. W., 1963. The mechanism of sex determination in rumex hastatulus. *Genetics* **48**:1265–1288.

Stehlik, I. and S. C. Barrett, 2006. Pollination intensity influences sex ratios in dioecious *Rumex nivalis*, a wind-pollinated plant. *Evolution* **60**:1207–1214.

Stehlik, I. and S. C. H. Barrett, 2005. Mechanisms governing sex-ratio variation in dioecious *Rumex nivals*. *Evolution* **59**:814–825.

Stehlik, I., J. Friedman, and S. C. Barrett, 2008. Environmental influence on primary sex ratio in a dioecious plant. *Proceedings of the National Academy of Sciences* **105**:10847–10852.

Stehlik, I., P. Kron, S. C. Barrett, and B. C. Husband, 2007. Sexing pollen reveals female bias in a dioecious plant. *New Phytologist* **175**:185–194.

Su, Y.-S. and M. Yajima, 2013. R2jags: A package for running jags from R.

Swanson, F. J. and J. J. Major, 2005. Physical events, environments, and geological-ecological interactions at Mount St. Helens: March 1980–2004. In V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors, *Ecological responses to the 1980 eruption of Mount St. Helens*, pages 27–44. Springer, New York.

Tamura, S. and G. Kudo, 2000. Wind pollination and insect pollination of two temperate willow species, *Salix miyabeana* and *Salix sachalinensis*. *Plant Ecology* **147**:185–192.

Tariq, M., D. J. Wright, J. T. Rossiter, and J. T. Staley, 2012. Aphids in a changing world: Testing the plant stress, plant vigour and pulsed stress hypotheses. *Agricultural and Forest Entomology* **14**:177–185.

Taylor, D. R., 1994. The genetic basis of sex ratio in *Silene alba* (= *S. latifolia*). *Genetics* **136**:641–651.

Taylor, D. R. and P. K. Ingvarsson, 2003. Common features of segregation distortion in plants and animals. *Genetica* **117**:27–35.

Taylor, D. R., M. J. Saur, and E. Adams, 1999. Pollen performance and sex-ratio evolution in a dioecious plant. *Evolution* **53**:1028–1036.

Thompson, J. N. and O. Pellmyr, 1991. Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology* **36**:65–89.

Tozawa, M., N. Ueno, and K. Seiwa, 2009. Compensatory mechanisms for reproductive costs in the dioecious tree *Salix integra*. *Botany* **87**:315–323.

Tscharntke, T., 1988. Variability of the grass *Phragmites australis* in relation to the behaviour and mortality of the gall-inducing midge *Giraudiella inclusa* (Diptera, Cecidomyiidae). *Oecologia* **76**:504–512.

Tuomi, J., T. Hakala, and E. Haukioja, 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *American Zoologist* **23**:25–34.

Turcotte, J. and G. Houle, 2001. Reproductive costs in Salix planifolia ssp. planifolia in subarctic Québec, Canada. *Ecoscience* **8**:506–512.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham, 2003. Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. *Ecological Applications* **13**:1790–1801.

Ueno, N., H. Kanno, and K. Seiwa, 2006. Sexual differences in shoot and leaf dynamics in the dioecious tree *Salix sachalinensis*. *Botany* **84**:1852–1859.

Ueno, N. and K. Seiwa, 2003. Gender-specific shoot structure and functions in relation to habitat conditions in a dioecious tree, *Salix sachalinensis*. *Journal of Forest Research* **8**:0009–0016.

Ueno, N., Y. Suyama, and K. Seiwa, 2007. What makes the sex ratio female-biased in the dioecious tree *Salix sachalinensis*? *Journal of Ecology* **95**:951–959.

Uselman, S. M., K. A. Snyder, and R. R. Blank, 2011. Insect biological control accelerates leaf litter decomposition and alters short-term nutrient dynamics in a Tamarix-invaded riparian ecosystem. *Oikos* **120**:409–417.

Utsumi, S. and T. Ohgushi, 2007. Plant regrowth response to a stem-boring insect: A swift moth-willow system. *Population Ecology* **49**:241–248.

Van der Putten, W. H., R. D. Bardgett, P. De Ruiter, W. Hol, K. Meyer, T. Bezemer, M. Bradford, S. Christensen, M. Eppinga, T. Fukami, et al., 2009. Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia* **161**:1–14.

van Kleunen, M. and S. D. Johnson, 2005. Testing for ecological and genetic Allee effects in the invasive shrub *Senna didymobotrya* (Fabaceae). *American Journal of Botany* **92**:1124–1130.

Verma, T. D. and N. Kaul, 1996. Biology and impact of *Hypsipyla robusta* (Moore) on *Toona ciliata* M. Roem. in Himachal Pradesh. In R. B. Floyd and C. Hauxwell, editors, *Hypsipyla shoot borers in Meliaceae: Proceedings of an international workshop*, pages 81–84. Australian Centre for International Agricultural Research, Canberra.

Vitousek, P. M., 1999. Nutrient limitation to nitrogen fixation in young volcanic sites. *Ecosystems* **2**:505–510.

Vitousek, P. M. and W. A. Reiners, 1975. Ecosystem succession and nutrient retention: A hypothesis. *BioScience* **25**:376–381.

von Fircks, Y., T. Ericsson, and L. Sennerby-Forsse, 2001. Seasonal variation of macronutrients in leaves, stems and roots of *Salix dasyclados* Wimm. grown at two nutrient levels. *Biomass and Bioenergy* **21**:321–334.

Walker, L. R. and F. S. Chapin, 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology* **67**:1508–1523.

Walker, L. R. and R. Del Moral, 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, New York.

Walker, L. R., J. C. Zasada, and F. S. Chapin, 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* **67**:1243–1253.

Walter, J., R. Hein, H. Auge, C. Beierkuhnlein, S. Loeffler, K. Reifenrath, M. Schaedler, M. Weber, and A. Jentsch, 2012. How do extreme drought and plant community composition affect host plant metabolites and herbivore performance? *Arthropod-Plant Interactions* **6**:15–25.

Wardle, D. A., 2002. Communities and ecosystems: linking the aboveground and belowground components, volume 34. Princeton University Press, Princeton.

Waring, R. H. and G. B. Pitman, 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **66**:889–897.

Waser, N. M., 1984. Sex ratio variation in populations of a dioecious desert perennial, *Simmondsia chinensis*. *Oikos* **42**:343–348.

Watson, M. A. and B. B. Casper, 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* **15**:233–258.

Watt, A., 1994. The relevance of the stress hypothesis to insects feeding on tree foliage. In S. R. Leather, A. D. Watt, N. J. Mills, and K. Walters, editors, *Individuals, Populations and Patterns in Ecology*, pages 73–85. Intercept, Andover, UK.

Werren, J. H. and L. W. Beukeboom, 1998. Sex determination, sex ratios, and genetic conflict. *Annual Review of Ecology and Systematics* **29**:233–261.

White, T., 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* **50**:905–909.

White, T., 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* **16**:279–301.

White, T., 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* **63**:90–105.

White, T., 1993. The inadequate environment: nitrogen and the abundance of animals. Springer-Verlag, New York.

White, T., 2003. Nutrient retranslocation hypothesis: A subset of the flush-feeding/senescence feeding hypothesis. *Oikos* **103**:217.

White, T., 2009. Plant vigour versus plant stress: A false dichotomy. *Oikos* **118**:807–808.

White, T., 2011. Galls on smaller leaves do not refute the plant vigour hypothesis. *Brazilian Journal of Biology* **71**:1027–1027.

Whitham, T. G. and C. N. Slobodchikoff, 1981. Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: The adaptive significance of somatic mutations in plants. *Oecologia* **49**:287–292.

Williams, M. A. and J. T. Cronin, 2004. Response of a gall-forming guild (Hymenoptera: Cynipidae) to stressed and vigorous prairie roses. *Environmental Entomology* **33**:1052–1061.

Willis, J. H. and H. A. Orr, 1993. Increased heritable variation following population bottlenecks: the role of dominance. *Evolution* **47**:949–957.

Wood, D. M. and R. Del Moral, 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* **68**:780–790.

Wood, D. M. and R. del Moral, 2000. Seed rain during early primary succession on Mount St. Helens, Washington. *Madroño* **47**:1–9.

Woods, R. F., L. M. Moore, L. F. Wilson, M. E. Ostry, and D. I. Dickmann, 1982. Performance of 3-year old hybrid poplar clones in relation to soil texture, natural soil drainage and pest incidence. In J. Zavitkovski and E. A. Hansen, editors, *Proceedings of the North American Poplar Council 19th Annual Meeting*, pages 74–83, Rhinelander, Wisconsin. Kansas State University.

Xia, J., J. Lu, Z. Wang, B. Hao, H. Wang, and G. Liu, 2013. Pollen limitation and Allee effect related to population size and sex ratio in the endangered *Ottelia acuminata* (Hydrocharitaceae): Implications for conservation and reintroduction. *Plant Biology* **15**:376–383.

Zalucki, M., A. Clarke, and S. Malcolm, 2002. Ecology and behavior of first instar larval Lepidoptera. *Annual Review of Entomology* **47**:361–393.

Zimmerman, J. K. and M. J. Lechowicz, 1982. Responses to moisture stress in male and female plants of *Rumex acetosella* L. (Polygonaceae). *Oecologia* **53**:305–309.