

University of Montana

## ScholarWorks at University of Montana

---

Graduate Student Theses, Dissertations, &  
Professional Papers

Graduate School

---

2013

### Effects of Disturbance on Tree Community Dynamics in Whitebark Pine Ecosystems

Jeremy Travis Amberson  
*The University of Montana*

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

**Let us know how access to this document benefits you.**

---

#### Recommended Citation

Amberson, Jeremy Travis, "Effects of Disturbance on Tree Community Dynamics in Whitebark Pine Ecosystems" (2013). *Graduate Student Theses, Dissertations, & Professional Papers*. 4224.  
<https://scholarworks.umt.edu/etd/4224>

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

EFFECTS OF DISTURBANCE ON TREE COMMUNITY DYNAMICS IN WHITEBARK  
PINE ECOSYSTEMS

By

JEREMY T. AMBERSON

Bachelor of Arts in Philosophy, The University of Montana, Missoula, 2006  
Bachelor of Arts in Biology, The University of Montana, Missoula, 2006

Thesis

presented in partial fulfillment of the requirements  
for the degree of

Master of Science  
in Forestry

The University of Montana  
Missoula, MT

May, 2014

Approved by:

Sandy Ross, Dean of The Graduate School  
Graduate School

Cara R. Nelson, Chair  
College of Forestry and Conservation

Robert E. Keane  
US Forest Service

Andrew J. Larson  
College of Forestry and Conservation

Anna Sala  
Division of Biological Sciences

## ABSTRACT

Amberson, Jeremy, M.S., Spring 2014

Forestry

Effects of disturbance on tree community dynamics in whitebark pine ecosystems

Chairperson: Cara R. Nelson

### Abstract

Whitebark pine (*Pinus albicaulis*), a keystone species of high-elevation ecosystems of western North America, is warranted for listing under the Endangered Species Act due to the combined threats of fire exclusion, white pine blister rust (*Cronartium ribicola*), and increased pressure from insects due to climate warming. Despite widespread knowledge of the potential causes of the tree's decline, there is limited understanding of its ecology, including successional dynamics in forests disturbed by white pine blister rust and mountain pine beetle. Specifically, there is a need for more information on successional replacement by subalpine fir and whitebark seedling regeneration dynamics. I assessed changes in forest composition and structure and seedling regeneration dynamics over a 22-year period (1990-2012) at 19 sites in the Cascade Mountains of Washington State (USA). Over the two decades analyzed, 26% of sites experienced wildfire, 58% were disturbed by mountain pine beetle, and 68% were infected by white pine blister rust. Only one of 19 sites showed no evidence of disturbance by these agents. Tree community composition changed significantly during the study period, primarily due to a significant decline in mature ( $\geq 20$ -cm DBH) whitebark pine. Despite loss of mature whitebark pine, I found little evidence of successional replacement by other tree species. I also found insignificant correlation between whitebark seedling density and basal area of mature whitebark pine. Seedling density was positively correlated with herb and shrub cover. These observed regeneration dynamics appear to contradict the conventional view that seedling establishment is contingent on local seed production and microsites free of competing vegetation. Additional, long-term studies are needed to comprehensively quantify the effects of novel disturbances on successional trajectories in whitebark pine ecosystems.

**Keywords:** *Cronartium ribicola*; *Dendroctonus ponderosae*; forest succession; mountain pine beetle; *Pinus albicaulis*; regeneration; white pine blister rust; whitebark pine

## 1. Introduction

Whitebark pine (*Pinus albicaulis*), a keystone species (Paine, 1969) in high-elevation ecosystems of the western United States and Canada (Arno and Hoff, 1990; Keane et al., 2012), is declining due to widespread outbreaks of a native insect, mountain pine beetle (*Dendroctonus ponderosae*) (Logan and Powell, 2001), an invasive fungal pathogen that causes white pine blister rust (*Cronartium ribicola*), and altered fire regimes (Arno and Hoff, 1990). There is concern that changes in disturbance regimes are contributing to successional replacement of whitebark pine by killing whitebark pine trees and facilitating recruitment of late-seral species such as subalpine fir. Increases in late-seral species may also reduce the availability of canopy openings which are thought to be necessary for whitebark seedling recruitment (Tomback, 1982; Schwandt, 2006; Keane and Parsons, 2010). Despite evidence that mountain pine beetle, white pine blister rust, and altered fire regimes could contribute to successional replacement of whitebark pine by more shade-tolerant conifers in some areas (Keane, 2001; McKinney et al., 2009; Kegley et al., 2010), the rate and extent of this replacement across the tree's range is unknown (Rochefort, 2008; Larson and Kipfmüller, 2012). Moreover, there is little understanding of how interacting disturbance affects seral and climax whitebark pine ecosystems. Even with a high degree of interest in whitebark pine conservation and restoration, long-term data on tree community dynamics in relation to disturbance are lacking.

Whitebark pine ecosystem responses to attack by mountain pine beetles are shaped by interactions that have occurred over millennia (Brunelle et al., 2008). Recently, mountain pine beetle activity has intensified in high-elevation ecosystems due to temperature increases that have ameliorated climatic controls on beetle populations (Logan and Powell, 2001; Negrón et al., 2008; Logan et al., 2010; Jamieson et al., 2012). Since mountain pine beetle preferentially attack

trees that have sufficiently thick phloem to support beetle reproduction (Amman, 1972; Bartos and Gibson, 1990; Perkins and Roberts, 2003), there are concerns that increased mortality of mature trees following beetle attack could shift overstory dominance in whitebark pine stands to other tree species while reducing regeneration potential due to loss of cone production (McKinney et al., 2009).

Unlike the mountain pine beetle, the non-native blister rust kills trees of all sizes (Arno and Hoff, 1990; Keane and Arno, 1993; Tomback and Resler, 2007). Blister rust is also thought to indirectly affect successional processes by reducing cone production, both through mortality of cone-bearing trees and by killing cone-bearing branches of live trees (Tomback et al., 1995; Tomback and Achuff, 2010). It is unclear, however, how rust-induced mortality of cone-bearing branches or trees is affecting regeneration dynamics in whitebark pine stands and how rust is interacting with MPB to change successional dynamics.

With increasing mortality from rust and beetles, there is concern about the ability of whitebark pine to produce adequate seed stocks for regeneration. Some investigators have found correlations between basal area of live, cone-bearing whitebark pine and regeneration at the stand level (Tomback et al., 1995; McKinney et al., 2009; Kegley et al., 2010). Mature tree basal area estimates may not always be highly predictive of within-stand rates of regeneration, however, because Clark's nutcrackers (*Nucifraga columbiana*), the primary seed dispersers for whitebark pine (Hutchins and Lanner, 1982; Tomback, 1982), transport seeds over distances exceeding 30km (Lorenz et al., 2011). Furthermore, mortality of overstory whitebark pine trees could serve as a trigger for whitebark pine population renewal by freeing resources for seedling establishment and for release of established seedlings (but see Keane et al., 2007). There is some evidence of relatively high densities of whitebark seedlings and saplings in stands where the

majority of overstory whitebark pines have been killed by mountain pine beetle, suggesting that beetle-caused overstory mortality can create conditions that are favorable for whitebark pine regeneration (Larson, 2009; Larson and Kipfmüller, 2010). It is also possible that, at local scales, the negative effects of whitebark pine mortality agents on cone production may be less important than their positive effects on the increased growing environment for seedlings. Long-term data on the response of whitebark pine populations to mountain pine beetle and blister rust are lacking, however, and to date it is unclear how these disturbances affect seedling density.

Another aspect of whitebark pine regeneration dynamics requiring further study concerns suitable microsites for seedling establishment. Baker (1950) categorized whitebark pine as “very-intolerant” of shade. This description is echoed in later publications, including whitebark pine planting guidelines (Tomback, 1982; McCaughey et al., 2009) which recommend the removal of all vegetation from planting sites to provide openings for seedlings and to reduce competition from other vegetation (but see Perkins, 2004). Despite some apparent resistance to discard old ideas about the required growing conditions for whitebark, other researchers have characterized whitebark pine as moderately shade tolerant (Arno and Hoff, 1990) and capable of surviving and regenerating in closed canopy forests (Campbell and Antos, 2003). Neighboring vegetation may facilitate whitebark seedling establishment and growth in high-elevation ecosystems by ameliorating harsh environmental conditions (*sensu* Callaway, 1998). In fact, studies from the Rocky Mountains of Wyoming, USA show that whitebark pine seedling germination and early survival are higher near and beneath other vegetation (e.g. herbs, shrubs, and tree canopies) that block exposure to direct sunlight than they are in more exposed microsites (Maher et al., 2005; Maher and Germino, 2006). While the facilitative effects of rocks, stumps, and logs that provide a physical barrier against harsh conditions, including intense insolation and snow damage, have

been documented (Tomback et al., 1993; Izlar, 2007; McCaughey et al., 2009), the effects of neighboring vegetation, including overstory tree cover, on whitebark pine regeneration dynamics have been largely ignored (but see Campbell and Antos, 2003; Perkins, 2004; Maher et al., 2005; Maher and Germino, 2006). Yet, examination of the relative importance to seedlings of microsites created by neighboring vegetation compared to those created by rocks, stumps or logs could have important implications for whitebark pine restoration and management. Successful conservation and management of whitebark pine requires an understanding of patterns of succession and regeneration in the face of novel disturbance regimes (Kipfmüller and Kupfer, 2005). To date, studies of successional dynamics in whitebark pine ecosystems have relied largely on dendrochronology (Campbell and Antos, 2003; Kipfmüller and Kupfer, 2005) and computer-based modeling (Keane, 2001). This is the first study to use long-term re-measurement data to assess community and population-level trends in tree abundance and response to disturbance in whitebark pine communities.

I analyzed long-term re-measurement data collected over a 22-year period from whitebark pine stands in the eastern Cascade Mountains of Washington State (USA), an area where whitebark pine is understudied, to examine the frequency of disturbance to seral and climax whitebark pine stands by bark beetles and blister rust, as well as their effects on tree community composition and whitebark pine population and regeneration dynamics. Specific research questions are:

- 1) Has tree community composition changed within whitebark pine stands over the last 20-25 years? If so, are changes related to mountain pine beetle or white pine blister rust incidence?
- 2) Has basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of mature trees, poles, or saplings, or density ( $\#/ha$ ) of large seedlings changed over the last 20-25 years for common tree species (whitebark pine, subalpine fir, and

Engelmann spruce)? If so, are changes related to mountain pine beetle or white pine blister rust incidence?

3) Is current whitebark pine seedling density related to mountain pine beetle, white pine blister rust, or to other variables such as stand basal area?

4) Is current whitebark pine seedling density related to basal area of cone-producing whitebark pine trees?

5) Is seedling density higher than would be expected in particular microsite types (rocks, stumps, logs, herbs or shrubs, or beneath tree canopies) given the prevalence of that microsite type?

## **2. Materials and Methods**

### **2.1. Site selection**

This study was conducted on Current Vegetation Survey (CVS) research plots established by the US Forest Service (hereafter “USFS”) on the Okanogan-Wenatchee National Forest (hereafter “Forest”) in the early 1990s for the purpose of characterizing vegetation and assisting with landscape-level planning and monitoring. All CVS plots were established from a random point within the Forest and placed systematically across the landscape on a 2.74-km grid. Following the first re-measurement of these plots, the CVS program was subsumed by the USFS Forest Inventory and Analysis program.

All CVS plots used for this study were located outside of designated wilderness areas to reduce travel time and maximize the number of plots sampled. Study sites were located along the eastern crest of the Cascade Mountain Range in Washington State on a ca. 200-km. north-south transect between 47°01’06”N and 48°48’09”N. Sites were located in a variety of environmental and ecological conditions, from mesic closed-canopy stands to relatively open xeric stands where



whitebark pine is the climax species. CVS plots chosen for this study were sampled once between 1991 and 1998 (hereafter, “Cycle I”) and again between 2001 and 2007 (hereafter, “Cycle II”) by USFS personnel. In 2012 (hereafter, “Cycle III”), I re-measured all CVS plots located on the Forest where: 1) whitebark pine was the dominant or co-dominant tree species at the time of establishment, 2) the site was sampled during both previous sample cycles, and 3) the site was located outside of designated wilderness areas. A total of 19 plots on the Forest met these criteria, 7 seral stands in which subalpine fir was the dominant tree species and 12 climax stands in which whitebark pine was the dominant species (Table 1; Figure 1).

## 2.2. Original Current Vegetation Survey Sampling Design

Each CVS macroplot (hereafter “macroplot”) consists of a 1-ha circular plot with five nested subplots: one at the center of the macroplot and the other four at cardinal directions and 15.6m inside of the 1-ha-macroplot boundary (Figure 2). Each of the five subplots contains three concentric microplots (radii = 3.6m, 7.3m, and 15.6m).

During each CVS sampling event prior to this study, all live trees  $\geq 2.54$ -cm DBH and all dead trees  $\geq 7.62$ -cm DBH within subplots were individually measured and tagged with unique identification numbers. Seedlings  $< 2.54$ -cm DBH but  $\geq 15$ -cm tall were tallied by group within the 3.6-m-diameter microplots but were not tagged individually. Species, DBH, and status (live or dead) were recorded for all individually tagged trees at Sample Cycles I and II (Johnson, 2003). Data on tree damage, including physical damage, damage from insects, and damage from pathogens, were also collected for all tagged trees. For each tree, up to three types of damage were recorded. Because of the three-damage-agent limitation, however, the actual number of trees damaged by specific agents is unknown. For this reason, I was not able to include CVS tree damage data in my analysis.

### 2.3. 2012 Field sampling

In 2012 (Cycle III), all trees  $\geq 2.54$ -cm DBH were re-measured according to size-classes as defined in original CVS protocol (Johnson, 2003). Additional data on whitebark pine trees, seedlings, and microsites were collected according to protocol developed for this study.

#### *2.3.1. Mature Trees and Poles*

At each macroplot, for all mature trees (trees  $\geq 20$ -cm diameter at breast height (hereafter “DBH”) and poles (trees  $\geq 7.62$ -cm DBH, but  $< 20$ -cm DBH) I recorded tag number, species, DBH, and status (live or dead). In addition, I inspected each mature whitebark pine tree (live or dead) for incidence of mountain pine beetle (*Dendroctonus ponderosae*) attack, and each live mature or pole-sized tree for incidence and severity of white pine blister rust (*Cronartium ribicola*), following the procedures below.

*Beetle attack*– Evidence of beetle attack was recorded for all mature whitebark pine trees based on observations of all areas of the tree bole visible with the un-aided eye from ground level based on presence of: *i*) “J”-shaped galleries beneath the bark of dead trees, *ii*) boring dust in bark crevices particularly around root collar of tree, *iii*) pitch tubes (mixtures of tree resin and beetle-produced boring dust), *iv*) small emergence holes ( $\approx 2$  mm diameter), and *v*) beetles actively chewing into bark (Safranyik et al., 1974). Bark was removed from dead trees with a hatchet to look for presence of “J”-shaped galleries if no other evidence was found.

For each mature whitebark pine tree with evidence of attack by mountain pine beetle, I assessed whether the attack occurred prior to or since Cycle I by referring to Cycle I data to determine if the tree was dead at that time; if so, that tree was considered attacked by mountain pine beetles prior to macroplot establishment. Trees that were alive at Cycle I, but were dead

with evidence of beetle attack at subsequent sample cycles, were considered to have been attacked after macroplot establishment. There was no evidence of recent beetle-attack on live whitebark pine trees at any macroplot during Cycle III.

*Blister rust*– To assess blister rust incidence and severity, I inspected all live mature or pole-size whitebark pine trees for presence of: *i*) active cankers with white aecial blisters or orange aeciospores present on branches or bole; *ii*) branch flagging; *iii*) rodent chewing at a suspected canker site; *iv*) roughened, dead bark; *v*) branch tissue with thin, smooth, or swollen sections; and *vi*) oozing sap (Hoff, 1992). Live whitebark pine trees with active cankers or with at least two other of the symptoms were considered to be infected and were further classified by the following severity categories: “1”= branch infection > 60 cm from tree bole; “2”= branch infections located between 15 and 60 cm from bole; “3”= bole infections, or branch infection  $\leq$  15cm from the tree bole (Johnson, 2003). Only one blister rust severity code representing the worst case of infection (highest number) was assigned to each tree. Examination for blister rust was done from the ground on all sides of the tree; I used binoculars to search for symptoms if areas of the bole were not clearly visible with the naked eye.

### 2.3.2. *Saplings*

Saplings (trees  $\geq$  2.54-cm DBH, but < 7.62-cm DBH) were measured in five 3.6-m radius microplots within each plot (Figure 1). For each sapling, I recorded the tag number (if previously measured), species, DBH, and status (alive or dead). In addition, I inspected each live whitebark pine sapling for incidence and severity of white pine blister rust.

### 2.3.3. Seedlings

Seedlings  $\geq 15$ -cm tall (measured as the length of the main stem) but  $< 2.54$ -cm DBH were tallied by species in each 3.6-m-radius microplot; this seedling category was used to assess differences in seedling densities of common trees over time (question 2 above). For analysis of relationships between recent whitebark seedling density and disturbance variables (Question 3 above), mature whitebark (question 4 above), and microsites (question 5), I also collected data on individual whitebark pine seedlings (alive and dead) in two height classes: large seedlings (“class 2”;  $\geq 15$ -cm tall but  $\leq 30$ -cm tall), and small seedlings (“class 1”;  $< 15$ -cm tall but at least one-yr. old without cotyledons). For each whitebark pine seedling in class 2 or 1, I recorded the status (alive or dead). For each live whitebark pine seedling, I recorded the incidence and severity of white pine blister rust using the categories defined above. For each live small whitebark pine seedling, I also recorded whether the seedling was beneath the drip-line of an overstory tree ( $\geq 20$ -cm DBH) (Cole and Amman, 1969), the species of the overstory tree, and whether the overstory tree was live, dead, and/or beetle-killed. In addition, for each live small whitebark pine seedling, I recorded whether the seedling was growing within a shaded microsite (within 15cm of a rock, stump, or log  $\geq 15$ cm in height or within 15cm of herbs or shrubs  $\geq 15$ -cm tall).

### 2.3.4. Microsites

To determine the proportion of each 3.6-m microplot containing potential seedling habitat (i.e. target microsities), I visually estimated the total area covered by individual microsite conditions by dividing the microplot into four quadrants, each covering a quarter wedge of the microplot. In each quadrant, I recorded the area ( $m^2$ ): 1) within 15cm of a rock, stump, log; 2) within 15cm of live herbs or shrubs that were at-least 15-cm tall, 3) beneath the drip-line of live

trees, and 4) beneath the drip-line of dead trees. For the latter, I recorded whether the dead tree was a whitebark pine and whether the tree was likely killed by mountain pine beetle. The area recorded for each microsite pertained to the area within the potential effective protection of each microsite in which it is possible for a seedling to germinate. Thus, the area of any solid surface such as a rock, stump, log, or the basal area (BA) of plant or tree stems was not included in the microsite area.

#### 2.3.5. *Wildfire*

At each plot I recorded recent (occurring since Cycle I) wildfire incidence and severity inside the 1-ha macroplot using the following codes: “0” = no signs of recent wildfire; “1” = < 50% mortality in overstory (previously tagged) trees over the entire macroplot; or “2” = >50% mortality in overstory trees over the entire macroplot.

#### 2.4. Statistical analysis

For analysis, all tagged (i.e. re-measured) trees were placed in one of three size-classes: mature ( $\geq 20$ -cm DBH), poles ( $\geq 7.62$ -cm DBH, but  $< 20$ -cm DBH), and saplings ( $\geq 2.54$ -cm DBH, but  $< 7.62$ -cm DBH). Seedlings were grouped as large ( $> 15$ -cm tall but  $\leq 30$ -cm tall) and small ( $\leq 15$ -cm tall but with no cotyledons).

To test for changes in tree community composition over time (Q1), for each tree species and size class (mature trees, poles, and saplings) on each macroplot (N=19) I calculated mean (n=5) relative BA (% of total for each species within each size class) at each of three sample cycles. Basal-area data were not collected for any seedlings (trees  $< 2.54$ -cm DBH), so they were not included in this analysis. I used principal components analysis (PCA; Joliffe, 2002) to visually assess temporal trends in species composition (relative  $\text{m}^2 \text{ha}^{-1}$ ) at the 19 macroplots. I

used Multiple Response Permutation Procedures (MRPP) (Biondini et al., 1988; Mielke, 1991), a multivariate approach for assessing differences among groups, to test for between-sampling-period (1990s to 2012) differences in species composition ( $\text{m}^2 \text{ha}^{-1}$ ). To test for relationships between changes in tree community composition over time (between Cycles I and III) and disturbance metrics (incidence of mountain pine beetle attack, and incidence and severity of white pine blister rust) at Cycle III, I first calculated percent dissimilarity (hereafter “Tree Community PD”) of tree BA for each macroplot (N=19) between Cycles I and III using the Bray-Curtis dissimilarity metric (Faith et al. 1987):

$$b_{ii'} = \frac{\sum_{j=1}^J |n_{ij} - n_{i'j}|}{n_{i+} + n_{i'+}}$$

Where dissimilarity is calculated between samples (rows)  $i$  and  $i'$ , species BAs are denoted  $n_{ij}$  and sample (row) totals are  $n_{i+}$ . I then used multiple linear regressions to determine if percent dissimilarity was related to these disturbance metrics. For this analysis, percent dissimilarity was log transformed to meet assumptions of normality.

To determine if there were among-sample-cycle differences in tree BA for the most common species (whitebark pine, subalpine fir, and Engelmann spruce) by size-class (mature trees, poles, and saplings), and density of seedlings, at each macroplot (N=19) (Q2), I used non-parametric Friedman tests for repeated measures (Demsar, 2006), with separate tests for each species and size-class (12 tests). In addition, I divided the 19 macroplots into seral (n=7) and climax (n=12) whitebark pine communities and repeated this analysis on each group (36 tests total). When significant differences were found, I used Wilcoxon rank-sum tests with bonferroni correction (Wilcoxon, 1945) to test for pairwise differences between sample cycles.

For tree species and size classes that were found to change significantly over time, I used Kendall's tau rank-order correlations (Kendall, 1938) to assess relationships between percent change (Cycle I – Cycle III) in tree BA or density for that species and size class and the following measures of disturbance: BA ( $\text{m}^2 \text{ha}^{-1}$ ) of live whitebark pine trees with current blister rust incidence (“Recent WPBR-I”); current blister rust severity on live whitebark pine trees (“Recent WPBR-S”); BA ( $\text{m}^2 \text{ha}^{-1}$ ) of all whitebark pine killed prior to Cycle I with evidence of mountain pine beetle attack (“Initial MPB-I”); BA ( $\text{m}^2 \text{ha}^{-1}$ ) of all whitebark pine killed since Cycle I with evidence of mountain pine beetle attack (“Recent MPB-I”); and BA ( $\text{m}^2 \text{ha}^{-1}$ ) of all live whitebark pine (mature, sapling and pole) trees at Cycle I (“Initial PIAL”) and at Cycle III (“Recent PIAL”).

I used Kendall's tau rank-order correlations to assess relationships between whitebark pine seedling density (“PIAL Seedling Density,” seedling size classes “1” and “2” pooled) and recent and initial mountain pine beetle incidence, blister rust incidence and severity (N=19) (Q3), and density of mature whitebark pine trees at the time of plot establishment (“Initial Mature PIAL BA”) and at Cycle III (“Recent Mature PIAL BA”) (N=19) (Q4). I also tested for relationships between seedling density and initial total BA of live trees ( $\text{m}^2 \text{ha}^{-1}$  of all live trees  $\geq 2.54\text{-cm}$  DBH) (“Initial Tree BA”).

To test whether seedlings were more abundant than expected in particular microsite types (Q5) for each macroplot that had small whitebark pine seedlings (“PIAL Small Seedlings,” seedling size-class “1”) (N=12), I calculated mean (n=5): 1) percent of plot area covered by each microsite type (Log, Stump, Rock, ”Herb/Shrub,” “Live tree canopy [beneath the drip-line of live trees  $\geq 20\text{-cm}$  DBH], “PIAL-MPB canopy,” [beneath the drip-line of beetle-killed whitebark pine trees  $\geq 20\text{-cm}$  DBH]), and 2) percent of seedlings growing in each microsite type. I used

paired *t*-tests (Ott and Longnecker, 2010) to determine if there were differences between the mean proportion of plots covered by a particular microsite type and the mean proportion of seedlings growing within that microsite type, with separate tests for each microsite type.

MRPP analysis was completed using PC-ORD version 5.10 (McCune and Medford, 2005). All other analyses were completed using R software version 2.14 (R Development Core Team, 2011).

### 3. Results

Between Cycles I and III, 5 of 19 macroplots (26%) experienced wildfire (1 seral and 4 climax), 11 were disturbed by mountain pine beetle (58%) (2 seral and 9 climax), and 13 were infected by white pine blister rust (68%) (6 seral and 7 climax). Only one macroplot showed no evidence of disturbance by any of these disturbance agents. However, this macroplot did experience disturbance by avalanche.

Overall tree species composition changed significantly between Cycle I and Cycle III (MRPP:  $A=0.34$ ,  $P=0.001$ ). Variation in tree community composition among macroplots and sample cycles was primarily driven by BA of mature whitebark pine and mature subalpine fir: PCA axis 1 was significantly negatively correlated with relative BA of mature whitebark pine ( $\tau = -0.566$  and  $P < 0.001$ ; Figure 3) and PCA axis 2 was significantly negatively correlated with relative BA of mature subalpine fir ( $\tau = -0.309$  and  $P = 0.001$ ). The first two principal components explained 56 % of the overall variance in tree community composition over the three sample cycles (Figure 3).

Change in overall tree community composition (expressed as percent dissimilarity, “Tree Community PD”) between Cycles I and III was significantly related to incidence of white pine



blister rust and incidence of mountain pine beetle attack (adjusted  $R^2=0.57$ ). Stands that had lower BA of whitebark pine trees infected by white pine blister rust in Cycle III experienced greater change in tree composition than did those with higher rust incidence (“Recent WPBR-I” ;  $\beta = -0.560$  and  $P= 0.015$ ; Figure 4a). Similarly, stands that had lower cumulative total BA of trees killed by mountain pine beetle in any sample cycle had *greater* overall compositional change than did stands with higher total pine-beetle mortality (“Total MPB-I”,  $\beta = -0.517$  and  $P= 0.031$ ; Figure 4b), while stands that had lower BA of trees killed by mountain pine beetle during the 22-year sampling period (i.e. documented during sample Cycles II and III) had lower overall compositional change than did stands with higher recent pine-beetle mortality (“Recent MPB-I”,  $\beta = 0.844$  and  $p= 0.003$ ; Figure 4c).

Among sample cycles, the only species and size class to show significant differences in BA was mature whitebark pine, which on average, lost about 55% of BA between Cycles I and III at both climax and seral macroplots ( $\chi^2=9.15$ ,  $P=0.010$ ). Observed differences over time in mature whitebark abundance were significant when climax communities were analyzed separately ( $\chi^2=6.50$ ,  $P=0.039$ ), but not for seral stands when analyzed on their own. In addition, the differences between time periods in mature whitebark pine abundance were only significant between Cycles I and III (seral and climax pooled:  $P=0.002$ ,  $R = 0.421$ ; climax:  $P=0.040$ ,  $R = 0.529$ ), not between Cycles I and II or II and III (Figure 5). I did not detect significant differences among sample cycles in BA of pole or sapling size classes of whitebark pine, in density of large whitebark pine seedlings, or in any size class of subalpine fir or Engelmann spruce ( $P$ -values ranged from 0.066 to 0.911) (Figure 5).

Fire was an important factor in the reduction of mature whitebark pine, especially at high-elevation macroplots; of the five stands that experienced wildfire, four were in climax

communities. The five stands that burned showed the highest reductions in whitebark, with an average decline of 78%. When burned macroplots were removed from the analysis, BA of whitebark pine did not vary significantly among sample cycles.

Percent change in mature whitebark pine BA between Cycles I and III (climax and seral stands pooled) was significantly correlated to current BA of white pine blister rust-infected whitebark pine trees (“Recent WPBR-I”;  $\tau=0.416$  and  $P=0.047$ ; Figure 6a), BA of whitebark pine killed by mountain pine beetle prior to Cycle I (“Initial MPB-I”;  $\tau=0.433$ ,  $P=0.045$ ; Figure 6b), and BA of whitebark pine killed by mountain pine beetle since macroplot establishment (“Recent MPB-I”;  $\tau= -0.144$  and  $P=0.531$ ; Figure 6c). The significance of the relationship between percent change in mature whitebark pine BA and recent mountain pine beetle attack appears primarily due to three macroplots that lost  $> 8\text{ m}^2\text{ ha}^{-1}$  of mature whitebark pine to beetles over the study period. Beetle-caused whitebark pine mortality between Cycles I and III at other macroplots ranged between 0 and  $4\text{ m}^2\text{ ha}^{-1}$ . Six of the 14 non-burned macroplots had no whitebark pine mortality from beetles between Cycles I and III.

I did not detect a significant correlation between percent change in mature whitebark pine BA and either total BA of whitebark pine killed by beetles before and after macroplots were established (“Total MBP-I”;  $\tau=0.022$  and  $P=0.956$ ) or BA of mature whitebark pine living at the time of plot establishment (“Initial PIAL”;  $\tau= -0.033$  and  $P=0.912$ ).

Whitebark pine seedling density (large and small; classes 1 and 2) was significantly positively related to initial tree BA (“Initial tree BA”;  $\tau=0.390$ ,  $P=0.028$ ) (Figure 7a). I did not detect a significant relationship between seedling density and initial mature whitebark pine BA (“Initial PIAL BA”;  $\tau=-0.176$ ,  $P=0.331$ ) (Figure 7b), or BA of mature whitebark pine at Cycle

III (“Recent PIAL BA”;  $\tau=0.077$ ,  $P=0.690$ ) (figure 7c). There also was not a significant relationship detected between whitebark seedling density and either initial BA of beetle-killed whitebark pine ( $\tau=0.344$ ,  $P=0.072$ ) or current BA of blister rust infected whitebark pine trees ( $\tau=0.185$ ,  $P=0.322$ ).

Only one microsite type showed a positive association with small whitebark pine seedlings (seedling size-class “1”). Small whitebark pine seedling density was significantly higher than would be expected in microsites with herb and shrub cover ( $t=2.31$  and  $P=0.033$ ) (Table 2). Differences were not significant for the other five microsites tested (Table 2).

## **4. Discussion**

### 4.1. Successional dynamics

My analysis of 19 macroplots over a 22-year period indicates that tree community composition has changed significantly in whitebark pine stands in the Cascade Mountains, and that changes were primarily driven by mortality of mature whitebark pine trees. These findings are consistent with well-publicized concerns about increased rates of mortality in whitebark pine due to disturbance by mountain pine beetles and white pine blister rust (Schwandt, 2006; Keane et al., 2012). On average, these disturbances affected approximately 60-70% of stands in my study. Although my study was not designed to test wildfire effects, 26% of study stands burned between Cycles I and III, and BA of mature whitebark declined by over 77% at these sites.

Amid recent concern over the threat of successional replacement of whitebark pine by subalpine fir in seral communities, my results support the idea that this may not be a ubiquitous threat (Larson and Kipfmüller, 2010; 2012). Neither subalpine fir nor Engelmann spruce showed significant changes in abundance between Cycles I and III, perhaps because stand

development at these sites is too slow to detect shifts in species abundance over a 22-yr re-measurement cycle. Subalpine fir did have higher BA than whitebark pine for all size-classes at each of the three sample cycles, but the relative abundance of whitebark pine and subalpine fir was consistent over the ca. 22-yr period. Thus, even though whitebark occurred at lower relative abundance than subalpine fir in this study and elsewhere (e.g. Kegley et al., 2010), this pattern is not necessarily an indication of accelerated successional replacement. Rather, it suggests that whitebark is able to persist in stands dominated by subalpine fir or other species over long periods (Campbell and Antos, 2003). This persistence could be maintained by disturbance-induced mortality in other tree species (Frelich and Reich, 1995; van Mantgem et al., 2009) that would prevent the complete replacement of whitebark pine by competing species by reducing competition and maintaining the ecological niche of whitebark pine. To date, concerns about successional replacement of whitebark pine in seral communities have focused primarily on the effects of changing disturbance regimes on whitebark pine. However, disturbance regimes in other trees are also changing (Breshears et al., 2005; Bigler et al., 2007; van Mantgem et al., 2009). To understand successional dynamics in seral communities, it is necessary to consider the interacting effects of changing disturbance regimes among all species.

At the 12 climax macroplots, differences in BA of mature whitebark pine were significant between Cycles I and III; however, wildfire had a large effect on the overall trends observed in those sites. When macroplots that burned in recent wildfires were removed from analysis, there was no significant change in BA of mature whitebark pine. I also did not detect changes in abundance of whitebark pine in other size-classes or subalpine fir or Engelmann spruce in any size class. Since whitebark pine seedlings and saplings are more tolerant of harsh conditions at high-elevation sites, such as high wind, low growing season temperatures, and intense solar

radiation, than are seedlings of subalpine fir (Arno and Hoff, 1990; Maher and Germino, 2005; 2006), I expect whitebark to continue to dominate the climax stands in the study area.

White pine blister rust was significantly related to changes in overall tree community composition and change in mature whitebark pine. Interestingly, macroplots with higher blister rust incidence during the most recent sampling period exhibited less overall community change and less mature whitebark pine mortality over the study period. One possible explanation for this is that the macroplots with low current blister rust incidence may have sustained high losses of mature whitebark pine prior to Cycle III and therefore had fewer potential host trees. Moreover, current blister rust incidence could have been low at these macroplots because of genetic resistance of remaining whitebark in those stands. On the other hand, the macroplots with high incidence of blister rust at Cycle III may have been exposed to the fungus relatively recently, and newly infected whitebark have not yet died from blister rust. I did not, however, have accurate blister rust data from previous sample cycles and, therefore, could not attribute mortality of mature whitebark that occurred prior to Cycle III to blister rust.

While not possible for blister rust, I was able to determine mountain-pine-beetle mortality on trees killed in previous sample cycles, allowing for greater understanding of its effects on overall community change and change in BA of mature whitebark pine. Across all macroplots, the majority of dead whitebark pine showed evidence of beetle attack, a trend which also was reported in recent studies in Montana, Idaho, Oregon, and Wyoming (Kegley et al., 2010; Larson, 2011). Disturbance by mountain pine beetle that occurred during the 22 year study period drove both change in overall tree community composition and change in BA of mature whitebark pine. This suggests that, as in the Greater Yellowstone Ecosystem (Logan and McFarlane, 2010), increased mountain pine beetle activity in the early-mid 2000s played a large

role in losses of whitebark pine in the Cascade Mountains. It is likely that interactions between white pine blister rust and mountain pine beetles had a synergistic effect on recent whitebark pine mortality at sites in this study (Six and Adams, 2006). Yet the role that rust infection may have played in increasing the susceptibility of whitebark pine to mountain pine beetle cannot be confirmed due to lack of data on rust incidence in Cycles I and II. The difficulty of interpreting the combined effects of beetles and rust on whitebark pine population and community change elucidates the need for more long-term re-measurements of the effects of disturbance on the dynamics of whitebark pine ecosystems.

Forest succession is sometimes viewed as a deterministic process of gradual replacement of shade-intolerant species by shade-tolerant species with changing light environment (Bergeron, 2000; Arevalo et al., 2000). This idea may be driving the concern that accelerated successional replacement of seral whitebark pine is occurring in stands where much of the overstory whitebark has died. Succession, however, can also be driven by stochastic mechanisms such as interactions of stand conditions with type, severity, and timing of disturbance (Harcombe et al., 2002). For instance, selective mortality of mature whitebark pine after mountain pine beetle attack could promote whitebark pine regeneration in gaps left by dead trees (Meyers and van Lear, 1998; Campbell and Antos, 2003) if another seed source is within the range of nutcrackers that visit the stand. But if all size-classes of whitebark are decimated over a large area, the stand may convert to late-seral dominance by subalpine fir. In addition, changing climate will likely have unexpected effects on succession in seral whitebark pine ecosystems. In western North America, wide-scale mortality of subalpine fir and Engelmann spruce has been linked to recent warm temperatures and drought, a trend that is likely to continue under the effects of climate change (van Mantgem et al., 2009; Bigler et al., 2007). Although I did not observe significant

mortality in firs or spruce in study stands, this phenomenon may limit successional replacement of whitebark pine by shade-tolerant firs. Thus, changing community dynamics in high-elevation ecosystems may add to the complexity of successional processes and result in unexpected ecological outcomes (Paine et al., 1998). My results illustrate the risk involved in making generalized range-wide predictions of whitebark pine community responses to disturbance. Without knowledge of long-term successional dynamics in whitebark pine communities at the scale of multiple-centuries or longer, it is unclear whether current declines are indicative of catastrophic ecological change or within the limits of millennial-scale variability in the whitebark pine population.

#### 4.2. Relationships between whitebark pine seedling density and mature whitebark pine trees

I did not find significant relationships between whitebark pine seedling density and either current BA of mature whitebark pine or BA of mature whitebark pine at the time of plot establishment. This finding is contrary to McKinney et al. (2009), who found a positive relationship between seedling density and BA of cone-bearing whitebark pine. The lack of a relationship between seedling density and stand-level BA of whitebark pine in this study suggests that within-stand cone availability may sometimes be decoupled from stand-level regeneration potential, potentially due to its obligate mutualism with Clark's nutcracker (Tomback, 1982). Recent findings from a study in the eastern Cascade Mountains show that, even in years of low cone production, a single nutcracker can cache approximately 4,800 whitebark pine seeds below-ground at sites that could potentially support whitebark pine, but only 3% of those seeds are cached within stands where they were originally harvested by nutcrackers. In addition, nutcrackers may carry seed in excess of 30km from harvest location to cache site (Lorenz et al., 2011); thus, stand-level cone production may be less important than

seed availability at landscape or even regional scales (Barringer et al., 2012). In this study, the variable that showed the strongest correlation to seedling density was initial stand BA (BA of all tree species combined) at plot establishment, suggesting that regeneration may be as contingent on overall site productivity as it is on local cone production or dispersal activity.

#### 4.3. Whitebark pine seedling-microsite relationships

Whitebark pine germination and survival is driven not only by seed availability and nutcracker behavior, but also by factors that influence seedling survival such as temperature, shade, and moisture availability (McCaughey and Weaver, 1990; Tomback et al., 2001). In this study, whitebark pine seedlings were more abundant than expected in microsites near or beneath herbs and shrubs. These neighboring plants may facilitate whitebark pine through above-ground mechanisms, such as by providing protection from sun, wind and frost (Hadley and Smith, 1986, Germino and Smith, 1999). Maher et al. (2005) and Maher and Germino (2006) found that whitebark seedlings growing near or beneath other vegetation or overstory trees that blocked exposure to the sky had higher photosynthetic rates and efficiency, as well as higher survival, likely due to the bright sunlight and frequent frost that occurs in high-elevation forests. Cache-site selection is also important for seedling establishment. Although caching in open sites has been referred to as the norm for Clark's nutcracker (Tomback et al., 2001), research suggests Clark's nutcrackers may preferentially cache seed away from canopy openings and beneath vegetation or beneath overstory trees, perhaps to avoid predation or to lessen the likelihood that caches will be inaccessible beneath winter snowpack (Tomback, 1982; Lorenz et al., 2011). Thus, sites near vegetation may be favorable for seed caching, as well providing protection necessary for seedling growth. It is unclear whether the observed higher-than-expected numbers of seedlings in areas with neighboring vegetation was due to a facilitative relationship, or if



nutcrackers preferentially cached seed near herbs and shrubs. Both scenarios, however, are supported in the literature (Tomback, 1982; Callaway, 1998; Maher and Germino, 2006; Lorenz et al., 2011).

I hypothesized that there would be a positive relationship between whitebark pine seedling density and recent tree mortality due to increased light and nutrients, as was noted in Larson (2009). I did not, however, find a seedling preference for microsites beneath trees. It may be that resource pulses following tree mortality affect seedling growth and recruitment into larger size-classes rather than improving survival. Although it is widely accepted that protection from the elements is important for whitebark seedlings, the potential for these protective benefits to come from growing in microsites near other plants has been mostly disregarded (McCaughey et al., 2009). From this study, however, it appears that the benefits provided to seedlings by neighboring plants may outweigh the disadvantages of sharing resources with other organisms.

## **5. Conclusions**

My results suggest a need to re-evaluate common assumptions about succession and seedling dynamics in whitebark pine ecosystems, both in general and in response to altered disturbance regimes. Range-wide, whitebark pine is facing novel conditions due to white pine blister rust, increased bark beetle presence, altered fire regimes, and climate change. These disturbance agents, and their interacting effects, will reduce the predictability of forest succession, especially given that, with climate change, patterns of disturbance from insects and disease on all tree species are likely to change (Breshears et al., 2005) and wildfires are likely to grow larger and more intense (Westerling et al., 2006). Moreover, the wide variation in

ecological conditions across the range of whitebark pine and the considerable genetic diversity of the species, add to the unpredictability of ecosystem responses to change and disturbance.

The high ecological diversity encountered across research sites in this study, and findings that are inconsistent with results from whitebark pine studies in other areas, highlight the importance of developing management strategies that take into account range-wide and regional variability of whitebark pine ecosystems. When prioritizing sites for whitebark pine restoration, managers must consider the continuum of ecological conditions and relationships that affect stand development, including patterns of tree regeneration and mortality, as well as disease and insect activity at local to regional scales, and among all tree species. Moreover, there is a growing body of evidence suggesting that the survivability of whitebark seedlings is not dependent on recently burned sites, vast canopy openings, or microsites free from competition by other tree or plant species. Thus, when implementing out-planting and restoration treatments, managers must be willing to experiment with a variety of site preparation techniques and planting microsites, and monitor outcomes over time to improve whitebark pine management over the long-term.

High variability in stand conditions also suggests the need for large sample sizes in order to detect trends in species composition over time. Due to the relatively short field season common in high-elevation whitebark pine ecosystems and the amount of time required to access sites, it is logistically difficult to include a large number of sites in whitebark pine studies. However, by assessing change over time using previously measured plots (rather than assuming similar initial conditions), I was able to document significant effects of disturbance on tree community composition. There may be additional, yet unexplored re-measurement opportunities that would allow for further investigation of the role of disturbance on succession range-wide;

resampling these areas and plots should be a high priority for those interested in successional dynamics in whitebark pine.

Information on regeneration of whitebark pine seedlings is a high priority for restoration and conservation, especially given increasing investment in out-planting rust-resistant seedlings (Tomback et al., 2001). Until we know more about regeneration dynamics across the range of conditions faced by whitebark pine, it will be difficult to make accurate predictions of regeneration potential based on a single variable such as within-stand capacity for cone production. Furthermore, given highly variable survival rates associated with out-planting seedlings (McCaughey et al., 2009), additional research is needed on the most suitable conditions for seedling survival and the mechanisms behind survival of naturally regenerated seedlings. My findings suggest that protected areas may be more important than previously thought for regeneration establishment, and that forest openings may not provide the only ideal sites for outplanting whitebark seedlings. To date, much of the research on whitebark seedling relationships with microsites (including my study) has focused on regeneration density. Although this knowledge is of critical importance, there is a need for more information concerning appropriate conditions for seedling germination, and long-term survival and growth to assist with selecting the most appropriate sites for restoration.

## **6. Acknowledgements**

This project could not have been possible without the contribution of many individuals. I would like to thank my graduate advisor, Dr. Cara Nelson, for her support, guidance, and patience. Thanks to all the present and former members of the Restoration Ecology Lab for invaluable help and advice, especially Dr. Gunnar Carnwath, Colin Maher, Alexis Gibson, and Eva Masin. I would like to thank all of those who helped in the field, who allowed me to succeed

despite the enormous challenge of relocating and re-measuring long-abandoned research plots in the high mountains: Megan Keville, Abigail Marshall, Edie Dooley, Colin Maher, and Kevin Moore. Thanks to my committee members, Drs. Robert Keane, Andrew Larson, and Anna Sala, for their guidance, patience, and the wealth of knowledge they provided. Thanks to Dr. Dave Affleck for help with statistical analysis. Many thanks to the US Forest Service personnel who assisted me with selection of study sites, acquisition of macroplot information and previously collected data, and field logistics: Dr. Rod Clausnitzer, Betsy Peterson, Therese Ohlson, Pete Ohlson, and the personnel of the Okanogan-Wenatchee National Forest. Others who have contributed include Mark Vander Meer, Dr. John Maron, Dr. Dean Pearson, Dr. Judy Perkins, Dr. Matthew Germino, Dr. Evan Larson, Dr. John Schwandt and many others. This research was supported in part by funding from the US Forest Service Forest Health and Protection Program (Cooperative agreement # 11-DG-11010000-020). I offer my sincere apologies to those whom I have occasionally neglected and ignored over the course of this project. And finally, thanks to all of my closest family, friends, and companions who have always encouraged me to keep looking forward.

## **7. References**

- Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Jour. Eco. Ent.* **65**: 138–140.
- Arevalo, J.R., DeCoster, J.K., McAlister, S.D., and Palmer, M.W. 2000. Changes in two Minnesota forests during 14 years following catastrophic windthrow. *Jour. of Veg. Sci.* **11**: 833-840.
- Arno, S.F., and Hoff, R.J. 1990. *Pinus albicaulis* Englm. Whitebark Pine: *In* *Silvics of North America*. Bol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Handb. 654. pp. 530-554.
- Baker, F.S. 1950. *Principles of Silviculture*. McGraw-Hill Book Co., Inc. N.Y.

- Barringer, L.E., Tomback, D.F., Wunder, M.B., McKinney, S.T. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker. PLoS ONE. **7**(5): e37663. doi:10.1371/journal.pone.0037663
- Bartos, D. L. and Gibson, K. E. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. In: Schmidt, W. C. and McDonald, K. J. (eds) Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, 29–31 March 1989, Bozeman, MT. Ogden, UT: U.S. Dep.t of Agri., For. Serv., Gen. Tech. Rep. GTR-INT-270, Intermountain For. and Range Res. Stat.: 171–178.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology. **81**: 1500-1516.
- Bigler, C., Gavin, D.G., Gunning, C., and Veblen, T.T. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos. **116**: 1983-1994.
- Biondini, M.E., Mielke, P.W., Berry, K.J. 1988. Data-dependent permutation techniques for the analysis of ecological data. Veg. **75**(3): 161-168.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Kevin, P.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, L., Belnap, J., Anderson, J.J., Meyers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Nat. Acad. Sci. USA. **102**: 15144-15148.
- Brunelle, A., Rehfeldt, G.E., Bentz, B., and Munson, A.S. 2008. Holocene records of Dendroctonus bark beetles in high elevation pine forests of Idaho and Montana, USA. For. Ecol. Manage. **255**(3-4): 836-846. Doi:10.1016/j.foreco.2007.10.008.
- Callaway, R.M. 1998. Competition and facilitation on elevational gradients in subalpine forests of the northern Rocky Mountains. USA. Oikos. **82**: 561-573.
- Campbell, E.M., and Antos, J.A. 2003. Postfire succession in Pinus albicaulis - Abies lasiocarpa forests of southern British Columbia. Ca. Jour. of Bot. **81**(4): 383-397.
- Cole, W.E., and Amman, G.D. 1969. Mountain Pine Beetle Infestations in Relation to Lodgepole Pine Diameters. USDA For. Serv. Res. Note. INT-95. 7pp.
- Demsar, J. 2006. Statistical comparisons of classifiers over multiple data sets. J. Mach. Learn. Res. **7**:1-30.
- Faith, D.P., Minchin, P.R., and Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio. **69**: 57-68.
- Frelich, L.E, and Reich, P.B.. 1995. Neighborhood effects, disturbance, and succession in forests of the western Great Lakes Region. Ecoscience. **2**(2): 148-158.

- Germino, M.J., and Smith, W.K. 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell and Env.* 22: 407-415.
- Hadley, J.L., and Smith, W.K. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. *Ecology*. **67**(1): 12-19.
- Harcombe, P.A., Bill, C.J., Fulton, M., Glitzenstein, J.S., Marks, P.L., and Elsik, I.S. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *Ecology*. **90**: 947-957.
- Hoff, R.J. 1992. How to Recognize Blister Rust Infection on Whitebark Pine. USDA For. Serv. Res. No. INT-406.
- Hutchins, H.E., and Lanner, R.M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia (Berl.)*, **55**(2): 192-201.  
Doi:10.1007/BF00384487.
- Izlar, D.K. 2007. Assessment of Whitebark Pine Seedling Survival for Rocky Mountain Plantings. Thesis. The University of Montana, Missoula.
- Jamieson, M.A., Trowbridge, A.M., Raffa, K.F., and Lindroth, R.L. 2012 Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Pl. Phys.* **160**: 1719-1727.
- Johnson, M.D. 2003. Field Procedures for the Current Vegetation Survey. Natural Resource Inventory, Pacif. N. W. Reg., U.S. For. Serv., Port., OR., Ver. 2.05.
- Joliffe, I.T. 2002. Principal Component Analysis. Verlag-New York, Springer, Inc.
- Keane, R.E. 2001. Can the fire-dependent whitebark pine be saved? *Fire Mgmt. Today*. **61**: 17-20.
- Keane, R.E., and Arno, S.F. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year re-measurements. *W. Jour. of App. For.* **8**: 44-47.
- Keane, R.E., Gray, K.L., Dickinson, L.J. 2007. Whitebark Pine Diameter Growth Response to Removal of Competition. USDA, For. Serv., Intermountain Region, Ogden, UT, Research Note RMRS-RN-32.
- Keane, R.E., and Parsons, R.A. 2010. Restoring whitebark pine forests of the northern Rocky Mountains, USA. *Eco. Rest.* **28**: 56-70.
- Keane, R.E., Tomback, D.F., Aubry, C.A., Bower, A.D., Campbell, E.M., Cripps, C.L. et al. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). USDA For. Serv. Gen. Tech. Rep. RMRS-GTR 279.

- Kegley, S., Schwandt, J.W., Gibson, K., and Perkins, D. 2010. Health of Whitebark Pine Forests After Mountain Pine Beetle Outbreaks. USDA Forest Service, Northern Region Forest Health Protection, FHP Report 11-03. 14 p.
- Kendall, M. 1938. A new measure of rank correlation. *Biomet.* **30**(1-2): 81-89.
- Kipfmüller, K. F. and Kupfer, J. A. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. *Annals of the Assoc. Am. Geog.* **95**: 495–510.
- Larson, E.R. 2009. Status and Dynamics of Whitebark Pine (*Pinus albicaulis* Engelm.) Forests in Southwest Montana, Central Idaho, and Oregon, USA. Dissertation. University of Minnesota, Minneapolis.
- Larson, E.R. 2011. Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. *J. of Biogeo.* **38**: 453-470.
- Larson, E.R., and Kipfmüller, K.F. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. *Can. J. For. Res.* **40**(3): 476-487.
- Larson, E.R., and Kipfmüller, K.F. 2012. Ecological disaster or the limits of observation? Reconciling modern declines with the long-term dynamics of whitebark pine communities. *Geog. Compass.* **40**(3): 476-487.
- Logan, J.A., McFarlane, W.W., and Willcox, L. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Eco. App.* **20**(4): 895-902.
- Logan, J.A., and Powell, J.A. 2001. Ghost forest, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *Am. Ent.* **47**(3): 160-173.
- Lorenz, T. J.; Sullivan, K. A.; Bakian, A. V.; Aubry, C. A. 2011. Cache-site selection in Clark's nutcracker. *The Auk* 128:237-247.
- Maher, E.L., Germino, M.J., and Hasselquist, N.J. 2005. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Can. J. For. Res.* **35**: 567-574.
- Maher, E.L., and Germino, M.J. 2006. Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience* **13**(3): 334-341.
- McCaughey, W.W., Scott, G.L., and Izlar, K.L., 2009. Whitebark pine planting guidelines. *West. J. Appl. For.* **24**(3): 163-166.

- McCaughey, W.W., and Weaver, T. 1990. Biotic and Microsite Factors Affecting Whitebark Pine Establishment. USDA For. Serv. Gen. Tech. Rpt. **270**: 140-150.
- McCune, B., and M. J. Medford. 2005. PC-ORD, Multivariate Analysis of Ecological Data, Version 5 for Windows edition. MjM Software Design, Glenden Beach, Oregon USA.
- McKinney, S.T., Fiedler, C.E, and Tomback, D.F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. *Eco. Appl.* **19(3)**: 597-607.
- Mielke, P.W. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth Sci. Rev.* **31(1)**: 55-71.
- Meyers, R.K. and van Lear, D.H. 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *For. Ecol. And Mgmt.* **103**: 265-276.
- Negron, J. F., Bentz, B.J., Fettig, C.J., Gillette, N., Hansen, E.M., Hayes, J.L., Kelsey, R.G., Lundquist, J.E., Lynch, A.M., Progar, R.A., and Seybold, S.J. 2008. US Forest Service bark beetle research in the western United States: looking toward the future. *Jour. of For.* **106**: 325–331.
- Ott, L.R., and Longnecker, M. 2010. *An Introduction to Statistical Methods and Data Analysis*. Brooks/Cole. Belmont, CA, USA.
- Paine, R.T. 1969. A note on trophic complexity and community stability. *Am. Nat.* **103**: 91-93.
- Paine, R.T., Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems.* **1**:535-545.
- Perkins, J. L. 2004. *Pinus albicaulis* Seedling Regeneration After Fire. Dissertation. University of Montana. Missoula, Montana.
- Perkins, D. L. and Roberts, D. W. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *For. Ecol. and Man.* **174**: 495–510.
- Rocheftort, R.M. 2008. The influence of white pine blister rust (*Cronartium ribicola*) on whitebark pine (*Pinus albicaulis*) in Mount Rainier National Park and North Cascades National Park Service Complex, Washington. *Nat. Ar. Jour.* **28(3)**: 290-298.
- Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1974. Management of Lodgepole Pine to Reduce Losses from the Mountain Pine Beetle. *Can. For. Serv., Tech. Rep.*
- Schwandt, J.W. 2006. Whitebark Pine in Peril: A Case for Restoration. USDA For. Serv. Gen. Tech. Rep. R1-06-28.



- Six, D., and Adams, J. 2006. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). *J. Entomol. Sci.* **42**(3): 345-353.
- Team, R.D.C., 2011. R: A Language and Environment for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker – a mutualism hypothesis. *J. Anim. Ecol.* **51**(2): 451-467.
- Tomback, D.F., Sund, S.K., and Hoffmann, L.A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Can. J. For. Res.* **23**: 113-119.
- Tomback, D.F., and Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *Forest Pathology* **40**(3-4): 186-225.
- Tomback, D.F., and Resler, L.M. 2007. Invasive pathogens at alpine treeline: Consequences for treeline dynamics. *Phys. Geo.* **28**(5): 397-418.
- Tomback, D.F., Clary, J.K., Koehler, J., Hoff, R.J., and Arno, S.F. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: The Sundance burn of northern Idaho (U.S.A). *Con. Bio.* **9**(3): 654-664.
- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., and Mellmann-Brown, S. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology* **82**(9): 2587-2600.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. *Science*. **323**(5913): 521-524.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**(5789): 940-943.
- Wilcoxon, F. 1945. Individual comparisons by ranking methods. *Biomet. Bullet.* **1**(6): 80-83.

1 Table 1. For each of the 19 study macroplots, location and stand characteristics including elevation (“Elev.”); northing and easting,  
 2 mean BA of all trees  $\geq 7.62$ -cm DBH at Cycle I (“Initial BA”); initial mean BA of all live whitebark pine trees  $\geq 7.62$ -cm DBH at  
 3 Cycle I (“Initial PIAL BA”); the initial mean BA of standing dead whitebark pine trees killed by mountain pine beetle at Cycle I  
 4 (“Initial PIAL MPB”), initial mean BA of all live subalpine fir trees  $\geq 7.62$ -cm DBH at Cycle I (“Initial ABLA BA”), fire activity  
 5 during the study period (year of fire or blank if no fire activity since Cycle I), and plant associations (Lillybridge et al. 1995).  
 6 Macroplots are numbered from south to north. Macroplot locations are approximate and are projected in North American Datum 1983.  
 7 Macroplots # 11, 14, 15, and 16 are located in UTM zone 11; all other macroplots are in UTM zone 10. “Climax” study sites are  
 8 located in *Pinus albicaulis* (“PIAL”) plant associations; seral sites are located in other plant association types.

		Northing,	Initial	Initial PIAL	Initial PIAL	Initial ABLA	Recent Fire History	
Macro-	Elev.	Easting	Basal area	Basal area	MPB Basal	Basal area	(Year of Wildfire or	
plot	(m)	(meters)	(m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	area (m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	blank)	Plant Association(s)
1	1798	5209096,	7.02	7.02	0.00	0.00		PIAL/CARU
		650589						
2	1707	5252903,	11.63	4.24	0.00	4.20		PSME/AGSP
		661536						

Table 1 continued

		Northing,	Initial	Initial PIAL	Initial PIAL	Initial ABLA	Recent Fire History	
Macro-	Elev.	Easting	Basal area	Basal area	MPB Basal	Basal area	(Year of Wildfire or	
plot	(m)	(meters)	(m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	area (m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	blank)	Plant Association(s)
3	1737	5255604,  650579	4.00	4.00	0.66	0.00		PIAL/JUCO6
4	1829	5269249,  664247	23.44	3.63	5.77	6.32		ABLA2/RHAL/LUHI
5	1859	5304797,  688821	20.33	5.43	6.00	7.11		TSME/RHAL-VAME, ABLA2/RHAL/LUHI
6	1981	5313060,  691632	22.23	2.45	19.34	11.74		ABLA2/VASC/LUHI, ABLA2/RHAL/LUHI

Table 1 continued

		Northing,	Initial	Initial PIAL	Initial PIAL	Initial ABLA	Recent Fire History	
Macro-	Elev.	Easting	Basal rea	Basal area	MPB Basal	Basal area	(Year of Wildfire or	
plot	(m)	(meters)	(m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	area (m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	blank)	Plant Association(s)
7	1737	5315809,  661506	12.21	6.81	0.00	3.61		ABLA2/VAME
8	1951	5318556,  672456	19.02	7.46	2.82	10.80		PIAL/VASC/LUHI
9	2103	5332217,  694367	15.45	14.69	1.62	0.76		PIAL/FEVI
10	2073	5337692,  694369"	5.24	5.24	0.00	0.00	2001	PIAL/FEVI
11	1920	5375519,  286651	31.40	8.59	0.00	10.65	2006	ABLA2/VASC

Table 1 continued

		Northing,	Initial	Initial PIAL	Initial PIAL	Initial ABLA	Recent Fire History	
Macro-	Elev.	Easting	Basal area	Basal area	MPB Basal	Basal area	(Year of Wildfire or	
plot	(m)	(meters)	(m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	area (m <sup>2</sup> ha <sup>-1</sup> )	(m <sup>2</sup> ha <sup>-1</sup> )	Blank)	Plant Association(s)
12	1798	5381529,  672472	6.59	4.60	0.65	1.26		PIAL/ JUCO6
13	1829	5384225,  672345	21.03	14.30	0.00	4.56		PIAL/CARU
14	2073	5389192,  285021	20.42	16.53	0.00	0.00	2006	PIAL/VASC/LUGLH
15	2073	5394648,  285457	52.39	26.71	0.85	2.87	2003	PIAL/VASC/LUHI
16	2256	5394851,  282732	17.76	9.65	0.00	0.00	2006	PIAL/VASC/LUHI, PIAL/CARU

Table 1 Continued

Macro-plot	Elev. (m)	Northing, Easting (meters)	Initial Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Initial PIAL Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Initial PIAL MPB Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Initial ABLA Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Recent Fire History (Year of Wildfire or blank)	Plant Association(s)
17	1768	5400583, 705281	23.58	8.23	0.00	0.00		PIAL/CARU
18	1707	5403326, 702607	38.31	2.51	8.61	24.19		ABLA2/VAME
19	2134	5408845, 697110	21.05	14.58	0.00	6.11		PIAL/VASC/LUHI

10 \* *Species codes are:* ABLA2 – *Abies lasiocarpa*; AGSP (now PSSP) – *Pseudoroegneria spicata*; CARU – *Calamagrostis rubescens*; FEVI –  
11 *Festuca viridula*; JUCO6 – *Juniperus communis*; LUHI – *Luzula hitchcockii*; PIAL – *Pinus albicaulis*; PSME – *Pseudotsuga menziesii*; RHAL –  
12 *Rhododendron albiflorum*; TSME – *Tsuga mertensiana*; VAME – *Vaccinium membranaceum*; VASC – *Vaccinium scoparium*.

13

Table 2. Mean proportion of subplots covered by each microsite type, mean proportion of all whitebark pine seedlings (<15-cm; seedling size-class “1”) in subplots growing within each microsite type, and P-values for paired t-tests of differences between proportion of subplots covered by and proportion of seedlings growing in each microsite type (significant values in bold font). “PIAL-MPB Canopy” refers to the area beneath the canopy drip line of beetle-killed whitebark pine.

Microsite type	Proportion of each microplot within microsite type	Proportion of PIAL Seedlings in microsite type	<i>P-value</i>
Herb/Shrub	<b>0.392</b>	<b>0.563</b>	<b>0.033</b>
Rock	0.031	0.221	0.062
Log	0.041	0.207	0.074
Stump	0.001	0.000	0.163
Live Tree Canopy	0.272	0.327	0.465
PIAL-MPB Canopy	0.099	0.085	0.700

## Figure Captions

Fig.1. Location of the 19 macroplots along the eastern crest of the Cascade Range, Washington, USA. Triangles = climax whitebark pine plots; circles = seral whitebark pine plots. Map inset shows extent of enlarged area.

Fig.2. Design of Continuous Vegetation Survey (CVS) sample units. Each 1-ha macroplot contains five 0.076-ha subplots. Each of the five subplots contains two smaller (0.017-ha and 0.004-ha) concentric microplots. The centroids for subplots 2-5 are located 40.8m at cardinal directions from the centroid of subplot 1. Dimensions given for microplots are radii.

Fig.3. Ordination (PCA) of macroplots based on relative BA ( $\text{m}^2 \text{ha}^{-1}$ ) of species and size-classes (mature, pole, sapling, large seedling) across the three sample cycles (1990s= circles, 2000s= squares, and 2012= triangles; plots in climax stands =black, and plots in seral stands=white). Symbols are sized relative to BA of mature whitebark pine.

Fig.4. Relationship between percent dissimilarity (PD) of overstory tree composition and mean BA of a) whitebark pine infected by blister rust at Cycle III (“Recent WPBR-I”), b) whitebark pine killed by mountain pine beetle in all sample cycles (“Total MPB-I”), and c) whitebark pine killed by mountain pine beetle between Cycles I and III (“Recent MPB-I”). Solid lines derived using locally weighted scatterplot smoothing techniques; dashed lines = +/- 1 standard error.

Fig.5. Mean change (+/- 1 SE) in BA of mature ( $\geq 20$ -cm DBH), pole ( $< 20$ -cm DBH but  $\geq 7.62$ -cm DBH), and sapling ( $< 7.62$ -cm DBH but  $\geq 2.54$ -cm DBH) trees and mean change (+/- 1 SE) in density of seedlings ( $\geq 15$ -cm tall but  $< 2.54$ -cm DBH) between Sample Cycles I and III for the three most common species (PIAL=whitebark pine, ABLA=subalpine fir, and PIEN=Engelmann spruce). Panel a= climax stands (n=12); Panel b=seral stands (n=7).



Fig.6. Relationships between percent change in BA of mature whitebark pine between Cycles I and III (“Mature PIAL change in BA”) and mean BA of a) recent whitebark pine infected by blister rust at Cycle III (“Recent WPBR-I”), b) initial beetle-killed whitebark pine at Cycle I (“Initial MPB-I”), and c) whitebark pine killed by beetles since plot establishment (“Recent MPB-I”); dashed lines = +/- 1 standard error.

Fig.7. Relationships between mean density of whitebark pine (PIAL) seedlings <30-cm tall (PIAL seedling size-classes “1” and “2” pooled) and a) total mean BA of all trees  $\geq 7.62$ -cm DBH (“Initial Tree BA”) at macroplot establishment in the 1990s, b) initial BA of mature whitebark pine  $\geq 20$ -cm DBH (“Initial PIAL BA”) , and c) recent mean BA of mature whitebark pine (“Recent PIAL BA”). Solid lines derived using locally weighted scatterplot smoothing techniques; dashed lines = +/- 1 standard error.

Fig. 1.

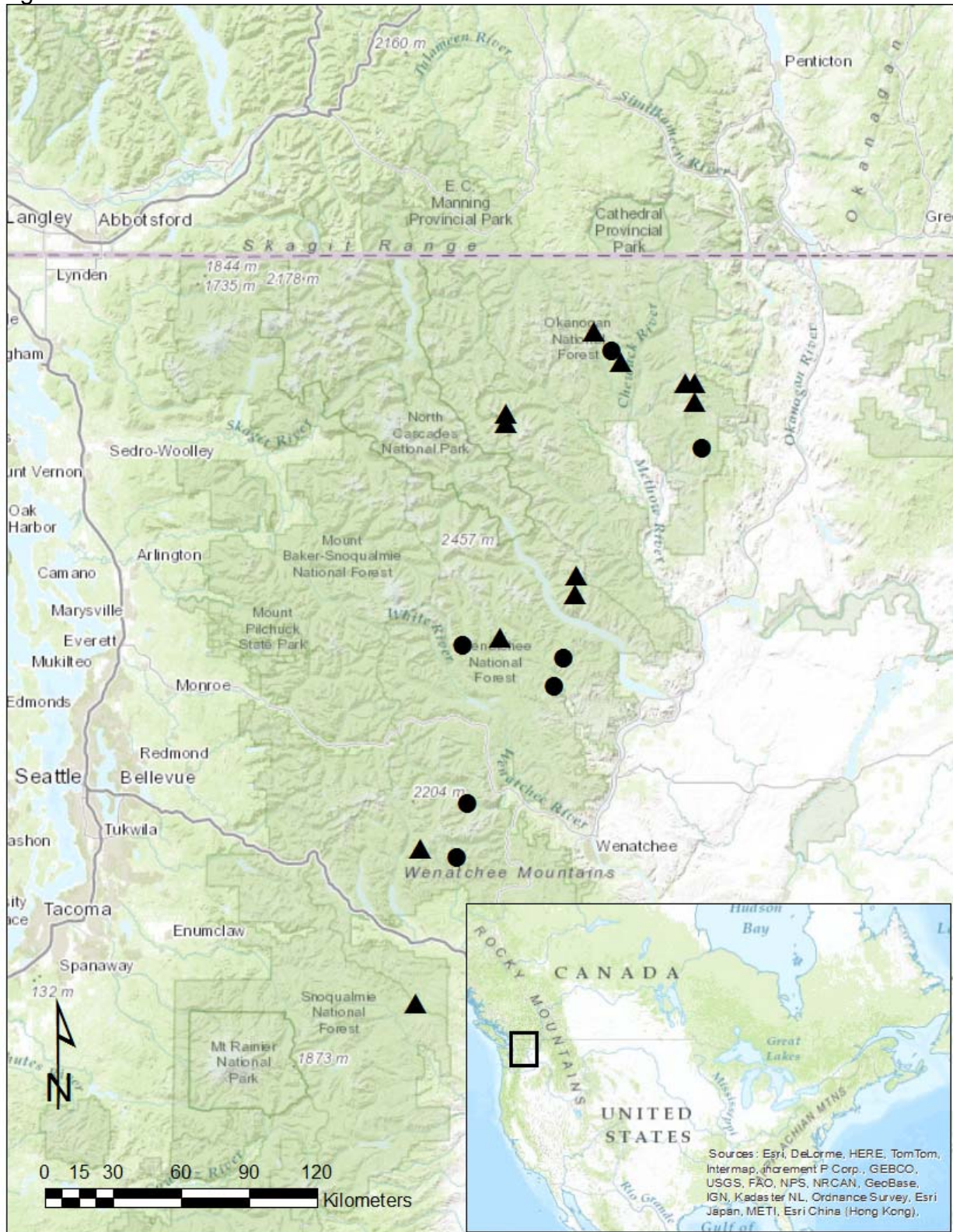


Fig. 2.

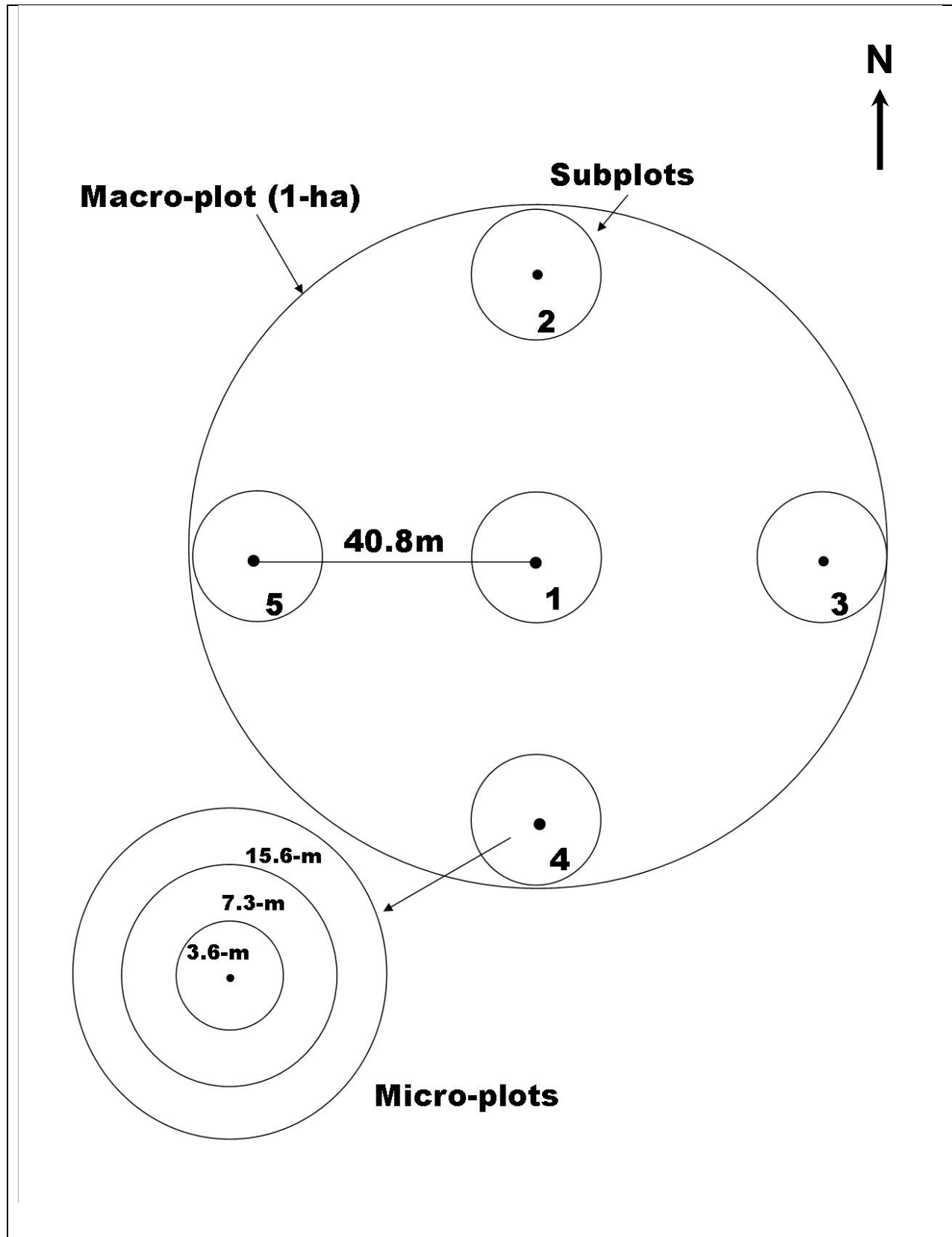


Fig. 3.

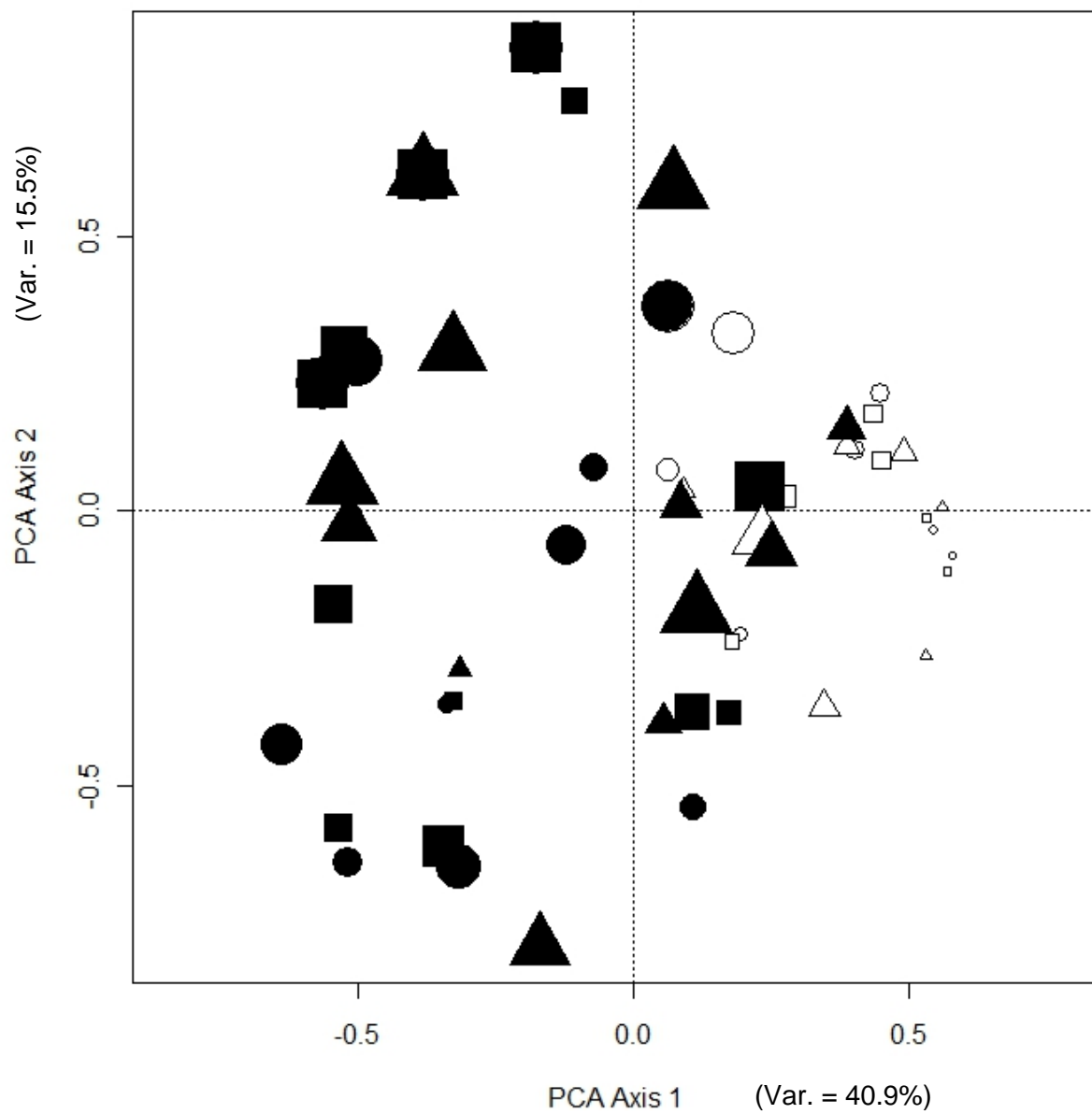


Fig. 4.

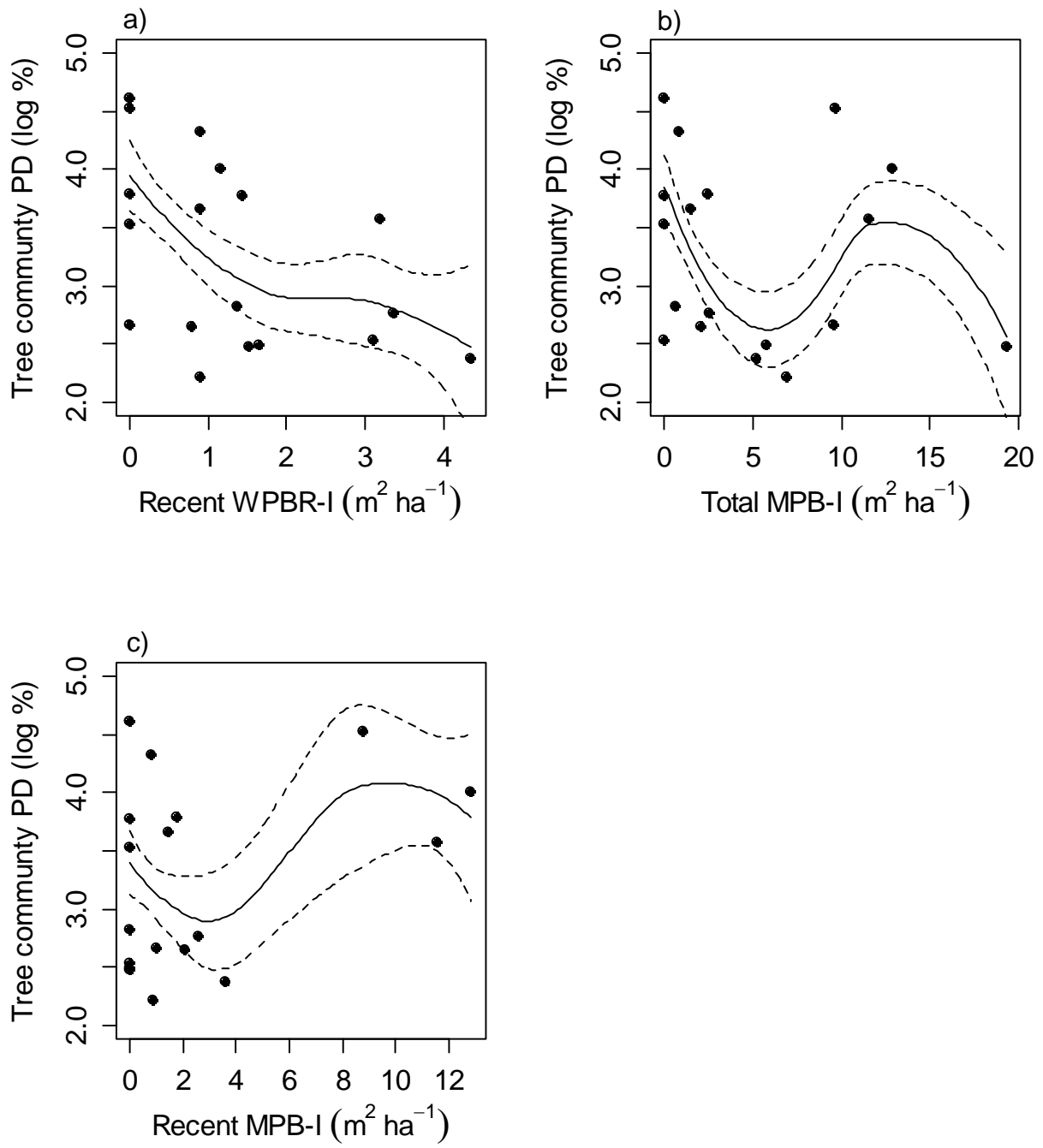


Fig. 5a

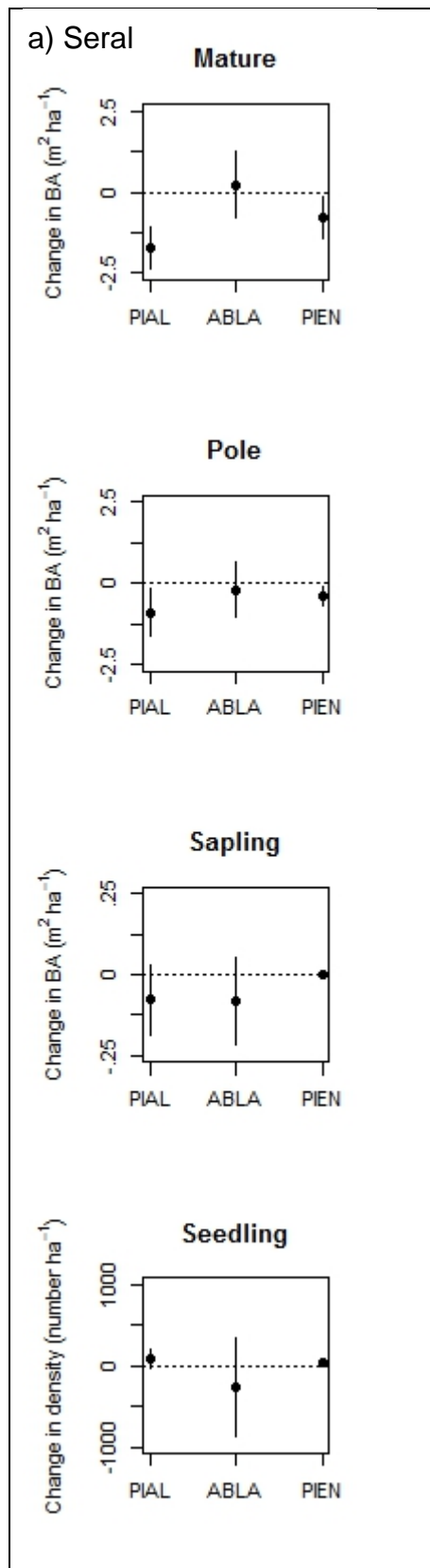


Fig. 5b

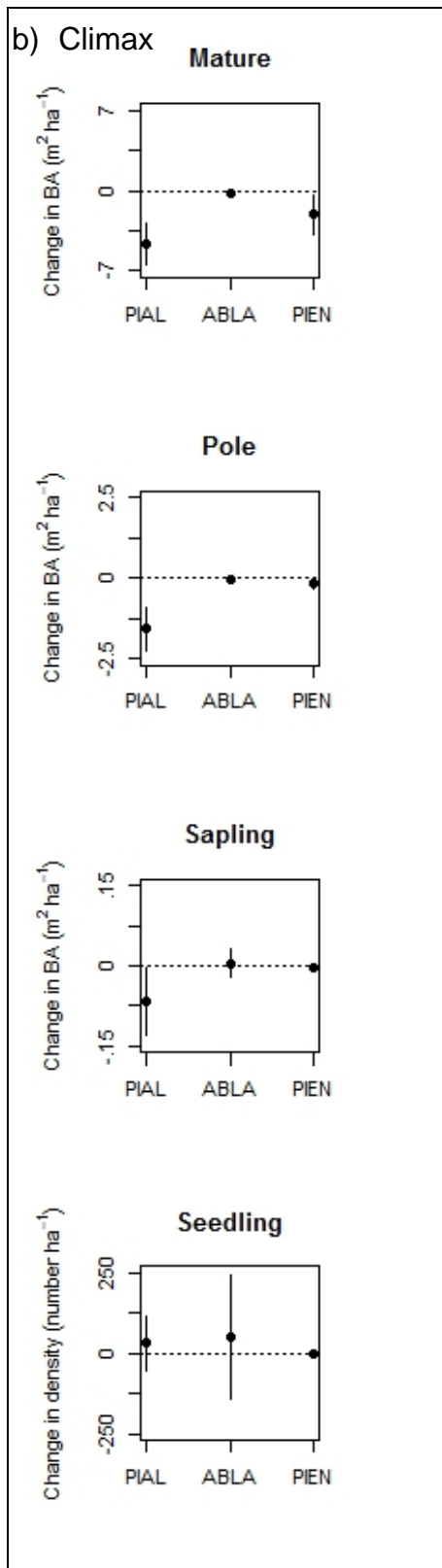


Fig. 6.

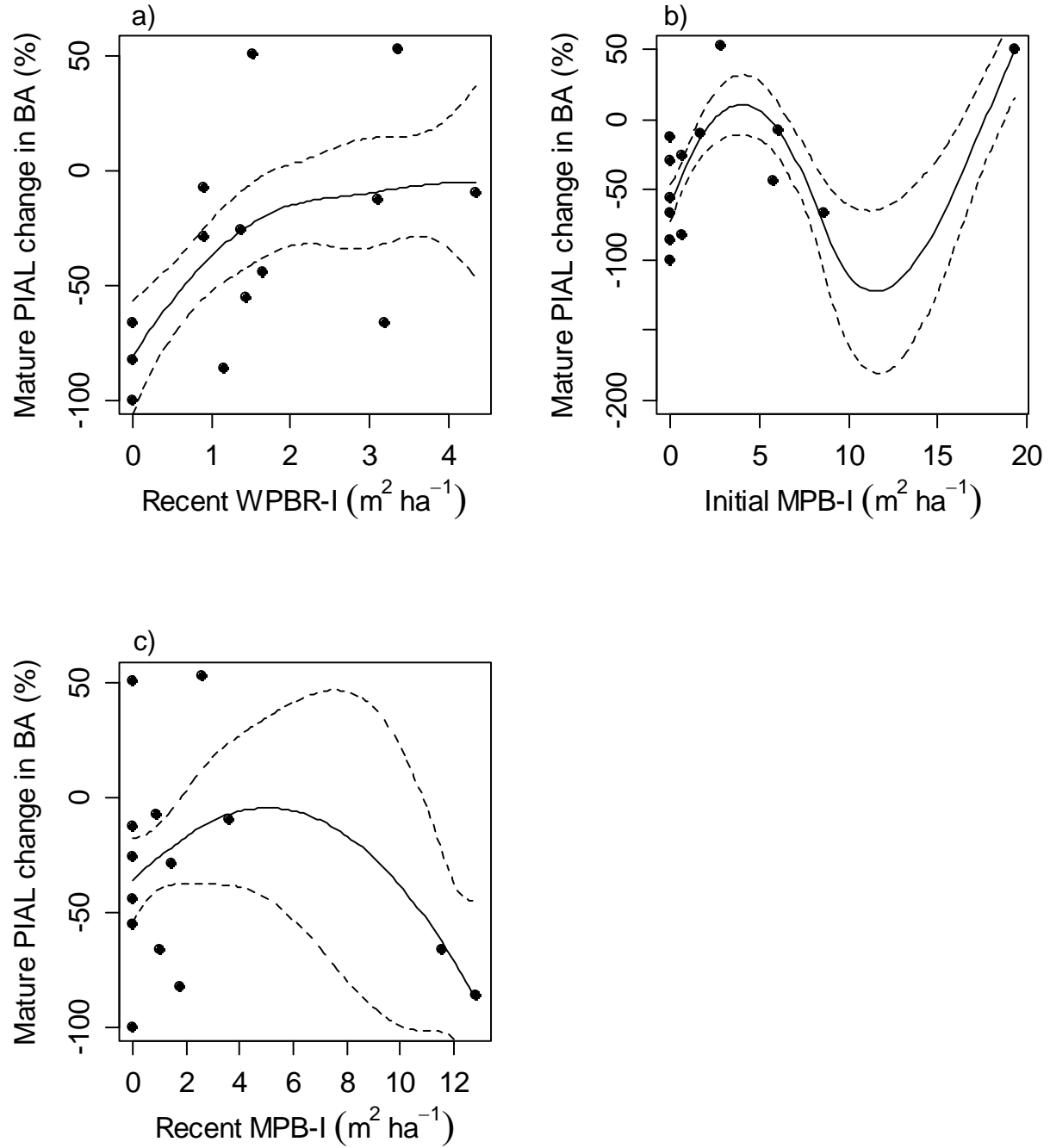




Fig. 7.

