

Magnificence in motion:
Climate and forest composition in Glacier National Park

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INTRODUCTION

Forests and disturbance in a changing climate

Worldwide climate is changing, resulting in altered patterns of temperature and precipitation (IPCC 2007). In the Northern Rockies, downscaled climate projections predict increased year-round temperature and a shift from summer to winter precipitation (Bartlein et al. 1997, Hall and Fagre 2003). As climate changes, significant shifts in ecosystems may be inevitable, and adaptive management strategies will be critical to address ecosystem responses as scientific knowledge expands (Baron et al. 2009).

Climate change will impact forest ecosystems in two distinct ways: indirectly through altered disturbance regimes, and directly through effects on plant mortality, recruitment, and growth. Current research reflects widespread concern over the effects of climate on patterns of disturbance. Fluctuations in climate have caused changes in the synchrony (Swetnam 1993), frequency (Johnson and Larsen 1991, Westerling et al. 2003), and extent of disturbance events (Schoennagel et al. 2005, Flannigan 2009), and recent studies have shown that disturbance regimes may already be responding to climate change (Westerling et al. 2006, Thompson and Spies 2009). For example, the relationship between unhistorical climate patterns and the extent of the current outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) in western North America has been a well-publicized topic of research (Carroll et al. 2004, Thomson 2009).

Models suggest that disturbance can short-circuit the process of gradual species overturn in response to climate change (Overpeck et al. 1990). In particular, climate-triggered changes in fire severity can have major consequences for forest ecosystems, as disturbance severity is strongly related to the timing and abundance of post-disturbance plant reestablishment (Turner et al. 1999). In the Rocky Mountain subalpine zone, fire occurrence and severity are closely related to drought conditions (Romme and Despain 1989, Renkin and Despain 1992, Sibold et al. 2006,

Thompson and Spies 2009), and regional fire data suggest that the Northern Rockies are particularly vulnerable to increased drought stress from climate change (Westerling et al. 2006). There is concern that structural variables, including fuel buildup from fire exclusion and extensive mortality from insect outbreaks, may be interacting with climate, leaving forests ripe for high-severity fire events. Climate-induced shifts in disturbance regimes would have widespread implications for forest composition and dynamics.

Climate also directly influences forest composition through effects on mortality, recruitment, and growth. Whereas mature trees are generally resistant to minor environmental fluctuations (with exceptions: e.g. van Mantgem et al. 2009), regeneration niches are often extremely sensitive to climate (Grubb 1977). After a disturbance, current climate conditions may favor the establishment of species that were not historically dominant, accelerating shifts in ecosystem responses to climate change (Turner 2010). For shade intolerant species that are able to establish following disturbance, seedling growth rates influence an individual's likelihood of outcompeting other species at the site and surviving to maturity. While several studies have modeled climate envelopes associated with current species distributions (Stephenson 1998, Pearson et al. 2002, Rehfeldt et al. 2006), the climate conditions required for seedling establishment and growth may be more valuable indicators of potential species range shifts in response to climate change in disturbance-prone ecosystems (Johnstone et al. 2010, Landhausser et al. 2010).

Few studies have directly investigated the role of climate for regeneration. In the absence of fire, variability in temperature and precipitation has been shown to initiate pulses of plant recruitment or periods of decreased establishment (Brown and Wu 2005, Shinneman and Baker 2009). Weather has been assumed to be the driver of initial post-fire regeneration in western

Montana (Tomback et al. 1993), but no studies have compared post-disturbance regeneration under varying weather conditions. Seedling growth rates are strongly related to soil moisture availability and thus to climate (e.g. Running 1980), and shade intolerant seedlings must rely on rapid growth to reach the canopy before being shaded out by their neighbors. By regulating interspecific rates of establishment and seedling growth, post-disturbance climate exerts a strong influence on the composition of the future forest.

Uncertainties about the implications of climate change are particularly alarming for Glacier National Park (GNP), where recent large, high-severity fire events have burned an unprecedented proportion of forest cover: over the last 23 years, approximately 23% of GNP has burned at least once (GNP Fire Atlas 2009). This dramatic rate of forest turnover corresponds to the recession of many of GNP's glaciers, which has been attributed to changes in climate patterns (Hall and Fagre 2003). Burned forests will be regenerating under climate conditions that are likely very different from those experienced during their last major disturbance event. The extent to which the recent stand-replacing fires are producing synchronous post-fire landscapes will influence the forests' resilience to future change (Millar et al. 2007), potentially creating a feedback loop that further accelerates the rate of ecosystem transition.

Synergistic influences of climate change on disturbance regimes and regeneration could have significant implications for forest landscapes. Because initial post-disturbance species compositions often determine the long-term trajectories of forest structure and process (Turner et al. 1998), the interaction of disturbance severity and post-fire weather may have impacts lasting well beyond the initial post-fire period. Current trends in GNP toward earlier spring snowmelt and hotter, drier growing seasons (Bartlein et al. 1997, Hall and Fagre 2003) could simultaneously increase the occurrence of stand-replacing disturbance and influence post-

disturbance establishment and growth, significantly altering species composition at the landscape scale. Moreover, resulting forest mosaics will undoubtedly influence the occurrence, spread, and severity of future disturbance events.

In this study, I examine the influence of post-fire climate on competition between two tree species in Glacier National Park. Western larch (*Larix occidentalis*) and lodgepole pine (*Pinus contorta* var. *latifolia*) are fire-adapted species that cohabit the subalpine zone of western GNP. While lodgepole pine and western larch both have clear strategies for regenerating after fire, they exhibit distinct approaches for maintaining fitness in fire-prone ecosystems. Lodgepole pine exhibits a “type A” response (Clark 1991): its serotinous cones ensure a pulse of post-fire recruitment even when mature trees are killed. Early and prolific seed production helps ensure that trees reach reproductive maturity before the next fire, and allow relatively young stands to regenerate a burned site (Fischer and Bradley 1987). In contrast, western larch displays a “type B” response (Clark 1991): mature trees have thick, fire-resistant bark and can quickly replace burned foliage through epicormic branching (Barrett et al. 1991), allowing individuals to better survive fire. Western larch is a deciduous conifer, meaning that defoliation by fire is less traumatic than for other coniferous species (Fischer and Bradley 1987).

The primary landscape-shaping disturbances in this forest type are stand-replacing fires, so post-fire forest composition depends on post-fire seedling establishment and successful recruitment to a canopy position. Species composition and annual growth increments were recorded at 73 sample sites stratified by fire year, fire severity, and elevation (Figure 1). Post-fire seedling establishment was usually abundant for both species, consistent with previous observations (Barrett et al. 1991). However, both species are shade intolerant (Schmidt et al. 1976), and extensive density-dependent mortality during canopy recruitment means that the

seedlings that grow the fastest will be most likely to survive to the forest canopy. If seedlings of one species have consistently superior growth rates, that species would be expected to comprise a greater proportion of the future forest.

In Chapter One, I evaluate the use of terminal bud-scar counts for aging seedlings and measuring annual growth increments for four conifer species in GNP, including western larch and lodgepole pine. This analysis shows that terminal bud scars are reliably identifiable indicators of the location on the stem at which one year of growth ends and the next begins, but that the accuracy of the method varies by species. Method accuracy and error are more strongly related to seedling age and height for fast-growing species (western larch and lodgepole pine) than for slower-growing species (Engelmann spruce and Douglas-fir). Even when it is not possible to determine a seedling's exact age using bud-scar counts, terminal bud scars from recent years of growth can be dependably used to estimate annual growth increments.

Chapter Two examines the role of differential responses to site and climate in the coexistence of lodgepole pine and western larch in GNP. I used vertical growth measurements (the distance between successive terminal bud scars) to develop a Bayesian hierarchical model of seedling growth for each species. The results of the models show that lodgepole pine seedlings prefer high elevations and dry years following wet winters, while western larch seedlings prefer low elevations and warm, wet growing seasons following wet, cool years. Climate projections for GNP, including increased year-round temperature and a shift from summer to winter precipitation (Bartlein et al. 1997), could reduce the survival of western larch seedlings at heterospecific post-fire sites by supporting relatively faster growth rates for lodgepole pine. Although differential responses to environmental variability may have historically promoted

coexistence between these species, climate changes that increase disturbance frequency and shift regeneration niches for these species may lead to a regional decline of western larch.

The implications of this study for land management are considerable. Ecosystem adaptation to climate change will occur both gradually and rapidly, but high-severity disturbance events will likely be central drivers of rapid shifts in forest composition (Overpeck et al. 1990, Turner 2010). The resulting ecological responses, including shifts in forest species composition, could potentially lead to reductions in valuable ecosystem services and trigger unforeseen reactions in related systems. It is probable that climate impacts on disturbance regimes will interact with post-disturbance climate to significantly influence regeneration, potentially altering long-term trajectories of forest composition.

Climate projections have left land managers with the difficult task of developing flexible approaches that can strike a balance between maintaining historic landscapes and facilitating ecosystem adaptation to global change. A lack of consensus over appropriate management responses to climate change is compounded by a poor understanding of its true ecological consequences. Research should prioritize broadening our knowledge of potential ecosystem responses to climate change in order to inform managers of realistic possibilities they may face in the near future. Determining the potential mechanisms through which a changing climate may alter forest composition will be invaluable for land managers in GNP and elsewhere.

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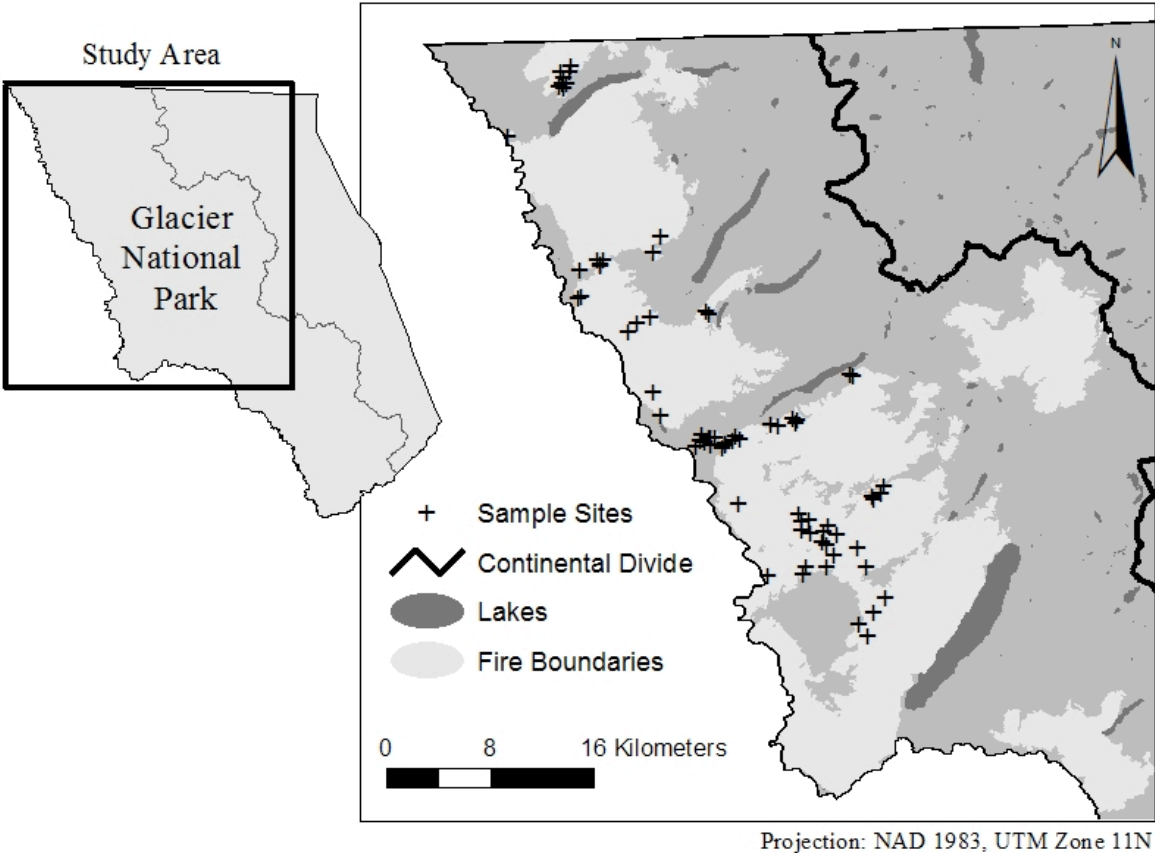


Figure 1. Distribution of sample sites within Glacier National Park.

CHAPTER ONE

Non-destructive aging of post-fire seedlings for four conifer species in
northwestern Montana

ABSTRACT

Several methods are commonly used to determine the age of seedlings, and destructive aging methods are often assumed to be the most reliable. Terminal bud-scar counts can be used as a non-destructive alternative for aging seedlings, although clear criteria for which this method is appropriate are not well known. This article evaluates the use of terminal bud-scar counts for aging seedlings of four conifer species in Glacier National Park, Montana. The results of our study suggest that terminal bud scars are reliable indicators of annual vertical growth, but that the accuracy of the method is limited to varying degrees by the age and height of seedlings. Method accuracy and error are more strongly related to seedling age and height for fast-growing species (western larch and lodgepole pine) than for slower-growing species (Engelmann spruce and Douglas-fir).

KEYWORDS

terminal bud scar, western larch, lodgepole pine, Engelmann spruce, Douglas-fir

1 INTRODUCTION

2 Determining the precise age of tree seedlings is a useful and often necessary component
3 for a wide range of inquiries. In forest stand assessments, seedling ages aid in the calculation of
4 growth rates (e.g. Maguire et al. 2002) and provide information on the impacts of overstory
5 removal on growth (e.g. Murphy et al. 1999). In the monitoring phase of restoration projects, the
6 timing of seedling establishment can be an indicator of the effectiveness of reseedling methods or
7 the effect of grazing on tree recruitment (e.g. Miller and Halpern 1998). In ecological research,
8 knowledge of the age and growth rates of seedlings at a site provides critical insight into
9 regeneration dynamics (e.g. Girardin et al. 2002).

10 Methods to age seedlings can be classified as either destructive or non-destructive.
11 Destructive methods are considered the most accurate way to identify the exact year of
12 germination (Telewski and Lynch 1991). This approach involves removing a seedling from the
13 ground, locating the root-shoot interface, and counting the number of annual rings to the pith at
14 this location. The ‘serial sectioning’ method of locating the root-shoot interface requires cutting
15 minute cross sections from the root end until the pith becomes visible within the xylem (League
16 and Veblen 2006, Daniels et al. 2007). Another method involves uprooting a seedling and
17 splitting it longitudinally to reveal the precise location of the root-shoot boundary (Nigh and
18 Love 1999).

19 While destructive aging methods are extremely accurate (except when growth is
20 suppressed; see Parent et al. 2002), there are practical limitations to their application. First,
21 locating the precise root-shoot boundary is time-consuming and requires specialized equipment
22 to process and analyze samples. Unless there is significant soil erosion or sedimentation
23 (Telewski 1993), the root-shoot boundary is usually located just above the root collar (League

1 and Veblen 2006), and a seedling can often be accurately dated by counting annual rings at this
2 location, significantly reducing the time required for sample processing. A second limitation of
3 destructive methods is that they require, by definition, destroying a seedling in order to age it,
4 which is unacceptable for studies in long-term plots, for rare or endangered tree species, and
5 within protected areas such as National Parks.

6 Two primary methods provide non-destructive alternatives for aging seedlings. Core
7 samples removed with an increment borer can be used to determine the age of a seedling based
8 on the same dendrochronological principles as destructive aging: a core that intercepts the pith at
9 the base of a tree provides the same information as a cross section of the stem at that location
10 (Stokes and Smiley 1968). However, this method has limitations. Specifically, even with the
11 smallest marketed increment borer (4.3 mm diameter), only large seedlings and saplings can be
12 cored without significant risk of fatal damage. It can be difficult to intercept the pith at the root
13 collar, and coring above the tree base can result in the underestimation of a tree's age.

14 In contrast to ring counts, terminal bud scars can be counted along the stem of a seedling
15 to estimate the year of establishment while eliminating the possibility of damage to the tree.
16 Terminal bud scars are formed annually when the scales protecting the bud of the terminal leader
17 fall off; the resulting stem scar indicates the location at which one year of growth ends and the
18 next begins (Figure 1). Although counts of branch whorls can be used to determine age in certain
19 species (Husch et al. 2003), the development of secondary and tertiary branch whorls makes
20 simple whorl counts problematic. Counting terminal bud scars results in identical establishment
21 dates to those obtained by dendrochronological methods for some species (Williams and Johnson
22 1990). For balsam fir (*Abies balsamea*), bud-scar counts have been shown to be more accurate

1 than annual ring counts, especially where high rates of soil development result in the formation
2 of adventitious roots above the true root-shoot boundary (Parent et al. 2000).

3 However, terminal bud-scar counts are only viable as accurate records of tree age when
4 scars are visible. As a seedling's stem expands radially, terminal bud scars are healed over until
5 they are unrecognizable (Hett and Loucks 1976). The point at which scars become obscured is
6 unclear and likely varies by species. Limits of the use of bud-scar counts have been identified
7 qualitatively in the literature, but clear criteria for which this method is appropriate have yet to
8 be determined. Daly and Shankman (1985) found that age estimates based on bud-scar counts
9 were "comparable" to those from ring counts for limber pine in the Rocky Mountain Front
10 Range, with higher accuracy for small seedlings on sheltered microsites, but this inference was
11 made from a sample size of only four trees. Battles and Fahey (2000) reported "confidence" in
12 identifying terminal bud scars for only the last three years of seedling growth for "all species" in
13 the hardwood/spruce-fir transition zone in the northeastern United States, but they offered no
14 explanation of their arrival at this threshold.

15 When counting terminal bud scars is a viable option to accurately date the year of
16 establishment, the method has several advantages over other aging methods. The risk of damage
17 to aged seedlings is negligible, the method takes a fraction of the time required for other methods,
18 and it can be performed in the field without specialized equipment. Even when seedling age
19 cannot be determined, terminal bud scars for recent years of growth may still be accurately
20 identified, and vertical growth rates can be obtained for past years without direct measurements
21 in each year. The ability to dependably measure annual growth opens up many research
22 questions related to the relationships between seedling growth and management actions, climate,
23 or site conditions.

1 In order to apply this method across the full range of its potential, it is critical to know
2 when terminal bud scars can produce an accurate estimate of annual seedling growth. Past
3 research suggests that the accuracy of bud-scar identification is primarily associated with bud-
4 scar age, and that younger trees can be aged non-destructively more reliably. It is also possible,
5 however, that seedling height is a limiting factor for method accuracy, and that fast-growing
6 seedlings at productive sites would more quickly heal over their bud scars.

7 The objective of this research is to investigate the use of terminal bud-scar counts for
8 aging post-fire seedlings in Glacier National Park, Montana. We compare establishment dates
9 derived from bud-scar counts with annual ring counts to determine the accuracy of the method
10 for four conifer species. Relationships between the method's accuracy and seedling age and
11 height will be examined in order to identify potential sources of measurement uncertainty. We
12 then examine the accuracy of individual bud-scar identification in relation to bud-scar age for
13 two fast-growing species.

14

15

MATERIALS AND METHODS

16

Study Area

17

18 The study was conducted in an approximately 750 km² area west of the continental divide
19 in the northwest quadrant of Glacier National Park (GNP), Montana, USA. The climate of
20 northwest GNP is dominated by moist air masses originating in the northern Pacific and moving
21 across the Pacific Northwest region. Average annual precipitation is 750 mm (Western Regional
22 Climate Center) and typically experiences two peaks: one in January, in the form of snow, and
23 another in June, in the form of rain. The west side of GNP receives more precipitation than
similar elevations east of the continental divide, and stable soils on glacial till support denser

1 forests. Forests are predominantly characterized by even-aged post-fire cohorts of western larch
2 (*Larix occidentalis*) and lodgepole pine (*Pinus contorta*) and by uneven-age stands of
3 Engelmann spruce (*Picea engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*). Sample sites
4 ranged in elevation from 1000 m to 1500 m and varied with respect to aspect and slope.

5

6 *Field Methods*

7 Sampling took place in the summer of 2010 from sites located within areas that burned
8 between 1988 and 2003. The center points for seventy-three 40 m transects were stratified by fire
9 severity and elevation within six fire perimeters using a GIS. We selected 1-5 post-fire seedlings
10 of each species (based on overall abundance at the site) from fifteen 1 m² plots distributed along
11 transects using random number generation for distance between plots. The first five seedlings of
12 each species we encountered were selected to be aged, and seedlings with obvious stem damage
13 were avoided. Since neither soil erosion nor sedimentation was observed at the sample sites, we
14 assumed the location of the root collar, and thus the root-shoot interface, to be at the level of the
15 ground (Telewski 1993). We uprooted several seedlings of each species to verify this assumption
16 and found the ground level to be an appropriate proxy for the location of the root collar.

17 For each selected seedling, all terminal bud scars were identified and their height on the
18 stem was recorded. Bud scars were recognized as narrow horizontal scars visible around the
19 entire circumference of the stem (Figure 1). While the identification of terminal bud scars would
20 have likely been more accurate in the lab, measurements taken in the field provided a more
21 realistic representation of the common use of this aging method. We also recorded the estimated
22 year of establishment, based on a count of terminal bud scars. Smaller seedlings were cut at the

1 ground level using garden shears, and seedlings with base diameter ≥ 5 cm were cored at the
2 ground with an increment borer. In total, we collected samples from 378 seedlings (Table 1).

3
4 *Lab Methods*

5 We dried all cut seedlings and removed a disc from the base of the stem. The bottom side
6 of each disc, the location at ground level where the seedling was cut, was finely sanded. Core
7 samples were glued to wood mounts and sanded finely. For all samples, we counted annual rings
8 under a microscope from the outermost ring (year of sampling) to the pith to determine the year
9 of establishment. The difference between the bud-scar estimated and actual year of establishment
10 of each tree was recorded: an error of -1 indicated that the bud-scar age was one year less than
11 the ring age, and an error of +1 indicated that the bud-scar age was one year greater than the ring
12 age. Although error is possible in annual ring counts (Stokes and Smiley 1968), ring counts are
13 considered the most accurate representation of tree age (Telewski and Lynch 1991), and false or
14 absent rings are not common in this region (Barrett and Arno 1988).

15 For harvested lodgepole pine and western larch seedlings, we also verified the location of
16 each identified terminal bud scar (Table 1). We marked the location on the stem of all bud scars
17 identified in the field, and a disc was removed just above each identified scar. Between two and
18 seventeen bud scars were identified on each seedling. The bottom side of each disc was sanded,
19 and annual rings at each segment of the stem were counted under a microscope. We then
20 compared our estimate of the date of bud-scar formation with the count of annual growth rings at
21 each identified bud scar. If terminal bud scars had been accurately identified, each segment
22 would be expected to have one more annual ring than the segment above it. We verified the “age”
23 of the stem at each segment of a tree in the same way as the establishment year: an error of -1

1 indicated that the date of a segment's first growth was one year prior than had been estimated
2 based on bud-scar counts.

3

4 *Data Analysis*

5 Separate uncertainty analyses were performed for estimates of seedling establishment and
6 individual bud-scar identification. For both analyses, differences between bud-scar age and ring
7 age were used to compute species-specific estimates of percent accuracy, mean error, and root
8 mean squared error (RMSE). Percent accuracy is the proportion of accurately aged terminal bud
9 scars (for estimates of seedling establishment, the age of the first bud scar is estimated). Mean
10 error is the average difference between bud-scar age and ring age; since error is represented as
11 either positive or negative, mean error represents the average estimation bias. RMSE, which
12 omits the direction of error through a squaring term, represents the average magnitude of error.
13 RMSE will always be greater than or equal to mean error, and greater differences between the
14 metrics indicate greater variance in individual errors.

15 Calculated uncertainties for estimated seedling establishment were plotted against
16 seedling age (Figure 2) and height (Figure 3), and calculations for bud-scar identification were
17 plotted against bud-scar age (Figure 4). For all plots, individual y-values represent a cumulative
18 average of the x-coordinate and all lesser values. For example, calculated error for a five-year-
19 old seedling included results from seedlings five years old and younger. This approach was
20 chosen to emphasize underlying trends and thresholds in the use of the bud-scar method, and
21 cumulative plots reduce noise caused by unbalanced data. Our randomized approach to sample
22 selection and post-fire establishment pulses resulted in a sample set that did not represent all
23 seedling ages and height classes evenly, and particularly for seedling ages and height classes

1 with very low sample sizes, error estimates were extremely sensitive to atypical individual
2 results. Graphs were generated using the standard plot package in R (R Development Core Team
3 2007).

5 RESULTS

6 *Establishment Year*

7 For all species combined, slightly more than 50% of the samples were accurately aged
8 using bud-scar counts (Table 2). Bud-scar estimations underestimated establishment age by an
9 average of 0.79 years (mean error), and the average magnitude of error from the bud-scar count
10 method was 2.14 years (RMSE). The appropriateness of using bud-scar counts to estimate
11 seedling establishment year varied greatly between species (Table 2). All statistics for data
12 subsets based on seedling age or height reported in this section represent cumulative averages.

13 Western larch

14 For all western larch samples combined, approximately 45% were accurately aged with
15 the bud-scar method (Table 2). Seedling age was underestimated by an average of 1.25 years
16 (mean error), and the average magnitude of estimation error (RMSE) was 2.70 years (Table 2).

17 Western larch showed a strong relationship between the accuracy of age estimation and
18 seedling age (Figure 2a). 100% of establishment year estimations based on bud-scar counts were
19 identical to those based on annual rings for 3-year-old seedlings; this proportion decreased for
20 older trees and declined to less than 50% when seedlings ≤ 13 years old were included. With
21 increasing age, RMSE increased and mean error steadily became more negative. RMSE was less
22 than 1 year for seedlings ≤ 11 years old and more than 2 years when seedlings 20 years old and
23 greater were included.

1 The relationship between age estimation accuracy and seedling height was less obvious
2 for western larch (Figure 3a). The accuracy of bud-scar ages for western larch declined slightly
3 with increased height, and percent accuracy fell from 67% for seedlings ≤ 30 cm to less than
4 50% when seedlings ≥ 220 cm were included. Mean estimation error became more negative and
5 RMSE increased with greater seedling height. RMSE was less than 1 year for seedlings ≤ 70 cm
6 tall and greater than 2 years when seedlings ≥ 200 cm were included.

7 Lodgepole pine

8 For all lodgepole pine samples, slightly more than 45% were accurately aged with the
9 bud-scar method (Table 2). Seedling age was underestimated by an average of 1 year (mean
10 error), and the average magnitude of estimation error (RMSE) was 2.27 years (Table 2).

11 Lodgepole pine showed the strongest relationship between age estimation accuracy and
12 seedling age (Figure 2b). Percent accuracy declined from 100% for seedlings ≤ 3 years old to
13 less than 50% when seedlings ≤ 10 years old were included. Mean error and RMSE trended
14 farther from zero with greater seedling age, meaning that older seedlings were, on average, more
15 difficult to age using bud-scar counts. RMSE was less than 1 year for seedlings ≤ 8 years old and
16 greater than 2 years when all samples were included.

17 For lodgepole pine, there was also a strong inverse relationship between the accuracy of
18 age estimation and seedling height (Figure 3b), and small seedlings were aged much more
19 accurately than tall seedlings. Estimation accuracy fell from 100% for seedlings ≤ 20 cm tall to
20 under 50% for seedlings ≤ 250 cm. Mean error and RMSE trended away from zero with greater
21 seedling height, as the age of taller seedlings was more likely to be underestimated. RMSE was
22 less than 1 year for seedlings ≤ 110 cm and more than 2 years when all samples were included.

23

1 Engelmann spruce

2 More than 62% of all Engelmann spruce samples were accurately aged with the bud-scar
3 method, seedling age was underestimated by an average of 0.34 years (mean error), and the
4 average magnitude of estimation error (RMSE) was 0.98 years (Table 2).

5 There was no consistent relationship between estimation accuracy and seedling age for
6 Engelmann spruce seedlings (Figure 2c). The accuracy of establishment year estimation
7 remained relatively constant as older seedlings were included in the analysis, fluctuating between
8 60% and 72%. Mean error became slightly more negative and RMSE trended slightly upward
9 with increasing age, but both error measurements remained within 1 year for all samples
10 combined.

11 Estimation accuracy for Engelmann spruce did not appear to be affected by seedling
12 height (Figure 3c). Mean error and RMSE trended slightly away from zero with increased
13 seedling height, although neither exceeded 1 year.

14 Douglas-fir

15 Approximately 55% of Douglas-fir samples were aged accurately using terminal bud-scar
16 counts (Table 2). Seedling age was underestimated by an average of 0.18 years (mean error), and
17 the average magnitude of estimation error (RMSE) was 1.83 years (Table 2).

18 Douglas-fir estimation accuracy showed a non-linear relationship with seedling age
19 (Figure 2d), and accuracy was greatest for seedling ≤ 14 years old. Percent accuracy fluctuated
20 between 44% and 59% as older seedlings were included. Mean error became increasingly
21 negative with increased seedling age. RMSE was less than 1 year for seedlings ≤ 11 years old,
22 and increased as older seedlings were included.

1 There was no obvious relationship between estimation accuracy and seedling height for
2 Douglas-fir (Figure 3d). For all height categories, percent accuracy was between 36% and 58%.
3 Mean error became increasingly negative with greater seedling height. RMSE fluctuated with
4 seedling heights ≤ 90 cm and then increased as taller seedlings were included.

5

6 *Identification of terminal bud scars*

7 For all western larch and lodgepole pine disc samples combined, more than 86% of
8 terminal bud scars were accurately aged using counts of bud scars from subsequent years (Table
9 2). Bud-scar estimations underestimated establishment age by an average of 0.17 years (mean
10 error), and the average magnitude of error from the bud-scar count method was 0.73 years
11 (RMSE). All statistics for data subsets based on bud-scar age reported in this section represent
12 cumulative averages.

13 Western larch

14 More than 80% of terminal bud scars from all western larch seedlings were accurately
15 identified (Table 2). Bud-scar age was underestimated by an average of 0.21 years (mean error),
16 and the average magnitude of estimation error (RMSE) was 0.88 years (Table 2).

17 For western larch, there was a steady decrease in bud-scar identification accuracy as bud-
18 scar age increased, which corresponded to a more negative mean error (Figure 4a). Bud scars
19 that formed in the last 3 years were accurately aged more than 97% of the time, declining to less
20 than 90% when bud scars ≤ 7 years old were included. Mean error became increasingly negative
21 and RMSE increased with age for bud scars ≤ 13 years old. On average, bud scars that formed in
22 the 7 years prior to sampling were aged to within 0.5 years of the actual date of their formation

1 (RMSE), and the year of their formation was underestimated by a mean of 0.07 years (mean
2 error).

3 Lodgepole pine

4 More than 90% of terminal bud scars from all lodgepole pine seedlings were accurately
5 identified (Table 2). Bud-scar age was underestimated by an average of 0.09 years (mean error),
6 and the average magnitude of estimation error (RMSE) was 0.40 years (Table 2).

7 For lodgepole pine, there was a slight decrease in bud-scar identification accuracy with
8 increased bud-scar age for bud scars ≤ 7 years old (Figure 4b), after which identification
9 accuracy held constant near 92%. Mean error declined from 0 years for bud scars ≤ 2 years old to
10 -0.09 years when bud scars ≤ 7 years old were included, and RMSE increased from 0 to 0.40
11 years.

12

13 DISCUSSION

14 Terminal bud-scar counts are commonly used to non-destructively age tree seedlings in
15 the field (Telewski and Lynch 1991), but the limits of this method have not been clearly
16 identified. Past research has examined the accuracy of bud-scar counts to age seedlings of
17 specific species with very limited sample sizes (Daly and Shankman 1985, Williams and Johnson
18 1990, Battles and Fahey 2000). Ours is the first study to our knowledge to quantitatively
19 examine the reliability of terminal bud scars identified in the field. When it is reliable, the
20 terminal bud-scar method is faster and less destructive than methods involving annual ring
21 counts. Even when seedling age cannot be determined, recent bud scars may still be accurately
22 identified, allowing for the development of seedling growth chronologies (Maguire et al. 2002).

1 In order to confidently use this method in the field, it is critical to know when terminal bud scars
2 produce an accurate estimate of annual seedling growth.

3 The results of our study suggest that terminal bud scars are reliable indicators of annual
4 vertical growth on post-fire seedlings for the four species examined. However, constraints on the
5 accuracy of the method vary by species. For all samples combined, using terminal bud scars to
6 estimate seedling age (Table 2) was most accurate for Engelmann spruce (62%), followed by
7 Douglas-fir (55%), lodgepole pine (46%), and western larch (45%). Mean error and RMSE
8 (Table 2) were lowest for Douglas-fir (-0.18 and 1.83 years respectively) and Engelmann spruce
9 (-0.34, 0.98 years), and greatest for lodgepole pine (-1.00, 2.27 years) and western larch (-1.25,
10 2.70 years).

11 Although it has been assumed that the reliability of identifying terminal bud scars
12 declines with bud-scar age (Battles and Fahey 2000) and height (Daly and Shankman 1985),
13 these relationships appear to be species-specific. In general, the use of bud-scar counts to
14 determine seedling age was more limited by age (Figure 2) and height (Figure 3) for fast-
15 growing species (western larch and lodgepole pine) than for slower-growing species (Engelmann
16 spruce and Douglas-fir). Variation in terminal bud morphology and corresponding scale scars is
17 likely an additional source of species-specific differences in aging accuracy.

18 For western larch and lodgepole pine, the accuracy of seedling age estimates based on
19 bud-scar counts decreased and the magnitude of bias (mean error) and error (RMSE) increased,
20 with greater seedling age (Figure 2a-2b) and height (Figure 3a-3b). In other words, bud-scar
21 counts consistently underestimated the age of taller and older seedlings. The reliability of field-
22 detection of bud scars decreased when the analysis included older and taller seedlings. Bud-scar

1 misidentification was also more likely for older seedlings, as the probability of stem damage
2 increases proportional to exposure time.

3 We also examined the accuracy of our field identification of individual terminal bud scars
4 for western larch and lodgepole pine seedlings, species for which the accuracy of bud-scar age
5 declined with greater seedling age and height. Even when bud-scar estimations of total seedling
6 age had low accuracy, our results indicate that the most recent years of growth were reliably
7 identified (Figure 4). However, we found important differences between western larch and
8 lodgepole pine when we analyzed the identification of individual bud scars. For western larch
9 (Figure 4a), more recently formed bud scars were accurately identified more often than older
10 scars, indicating that scars lower on the stem were the first to be obscured. This finding is
11 consistent with our field observations that bark formation towards the base of the stem was the
12 primary constraint to bud-scar identification.

13 For lodgepole pine (Figure 4b), there was not a strong relationship between bud-scar age
14 and identification for the 12-year range of bud-scar ages in our sample. This result appears to
15 contradict the finding that the accuracy of age estimates (the identification of a seedling's first
16 bud scar) declined with the age of the first scar (Figure 2b). However, this contradiction is
17 understandable in the context of our field observations, which documented consistent difficulties
18 identifying the first terminal bud scar on lodgepole pine seedlings. For most of the lodgepole
19 pine seedlings within our study, the bud scar lowest on the stem was not usually associated with
20 a primary branch whorl, making it more difficult to identify. While it is possible that bud scar
21 identification declines with bud-scar age, this pattern was not strong in lodgepole pine for the
22 range of ages in our sample of harvested seedlings. Instead, our findings suggest that the
23 identification of the *first* bud scar declined with seedling age and height.

1 The effect of age and height on the accuracy of this method was less clear for Engelmann
2 spruce and Douglas-fir seedlings. Seedling age was not an obvious determinant of the overall
3 accuracy of bud-scar counts for either species (Figure 2c-d), although older seedlings had greater
4 RMSE and mean error. Seedling height had no consistent effect on the accuracy of Engelmann
5 spruce age estimations (Figure 3c), but mean error and RMSE were marginally lower for the
6 smallest seedlings. Mean error and RMSE were unaffected by height for small Douglas-fir
7 seedlings (Figure 3d) and increased only slightly as taller trees were included.

8 The absence of a relationship between estimation accuracy and seedling age or height for
9 Douglas-fir and Engelmann spruce was likely a result of slower growth rates. Young seedlings of
10 these species are more tolerant of shade than the other species in our study, and although
11 Douglas-fir is considered fast-growing in some ecosystems (e.g. Spies et al. 1990), radial and
12 vertical growth for both of these species were observed to be very slow during the first decades
13 after establishment. Field observations showed that terminal bud-scar identification for these
14 species was more often limited by extremely narrow growth increments than by scars obscured
15 by bark formation. It is possible that the relatively young, small seedlings in our study had not
16 yet begun to form bark over their early bud scars.

17 Our results show that the confidence with which this method can be employed depends
18 greatly on the study objective. When a mean error of 0.8 years (RMSE of 2.1 years) is acceptable
19 for age estimations, bud-scar counts provide an acceptable alternative to destructive methods for
20 all of the seedlings in our study (Table 2). If greater precision is required, the seedlings included
21 in a study can be limited by species, age, or size in order to reach the necessary level of accuracy.
22 Even when a seedling is too old or too tall to be aged reliably, terminal bud scars for recent years
23 of its growth may still be accurately identified for analyses of annual growth. The ability to

1 develop seedling growth chronologies has implications for many applications within forestry and
2 ecological research, including analyses of growth responses to management treatments,
3 disturbance, and climate.

4 While our results provide general support for the use of terminal bud scars to non-
5 destructively age seedlings of these four species, specific levels of accuracy and error likely
6 depend on the ecological context of a particular site. All of the seedlings in our study established
7 following fire, so our results may not be representative of seedlings growing in other conditions.
8 Additionally, the effect of site quality on growth rates likely influences the accuracy of this
9 method by promoting or slowing the healing of bud scars. Future studies requiring precise
10 estimates of estimation error and accuracy should include site-specific verifications of this
11 method.

12

13

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8
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Table 1. Number of samples collected.

Species	Establishment Year Estimation			Bud-Scar Identification
	Cores	Discs	Total	Bud Scars
 Number of samples			
Western larch	18	87	105	607
Lodgepole pine	52	77	129	398
Engelmann spruce	1	76	77	-----
Douglas-fir	3	64	67	-----
Total	74	304	378	1005

Table 2. Percent accuracy, mean error and RMSE for all samples combined.

Species	Establishment Year Estimation			Bud-Scar Identification		
	Mean Error ^a	RMSE ^b	Accuracy ^c	Mean Error ^a	RMSE ^b	Accuracy ^c
 Error (yr)		(%) Error (yr)		(%)
Western larch	-1.25	2.70	44.76	-0.21	0.88	82.70
Lodgepole pine	-1.00	2.27	45.74	-0.09	0.40	92.21
Engelmann spruce	-0.34	0.98	62.34	-----	-----	-----
Douglas-fir	-0.18	1.83	55.22	-----	-----	-----
Total	-0.79	2.14	50.53	-0.17	0.73	86.47

^a Mean error is the average difference in years between bud-scar age and ring age; negative error indicates that ring age was *n* years greater than bud-scar age, and positive error indicates that ring age was *n* years less than bud-scar age.

^b Root mean squared error (RMSE) is the average magnitude of error in years.

^c Percent accuracy is the proportion of seedlings whose age was accurately determined by counting terminal bud scars.

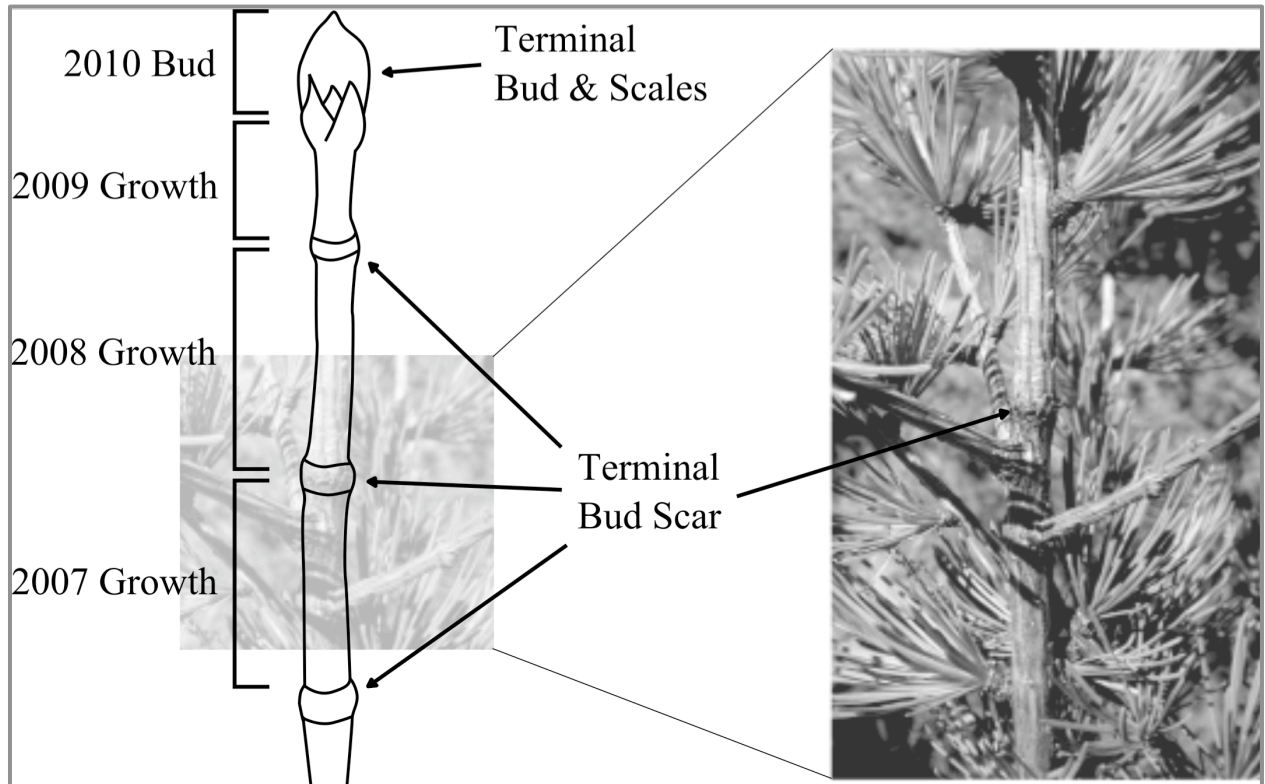


Figure 1. Diagram of terminal bud-scar formation and the use of scars to estimate annual vertical growth.

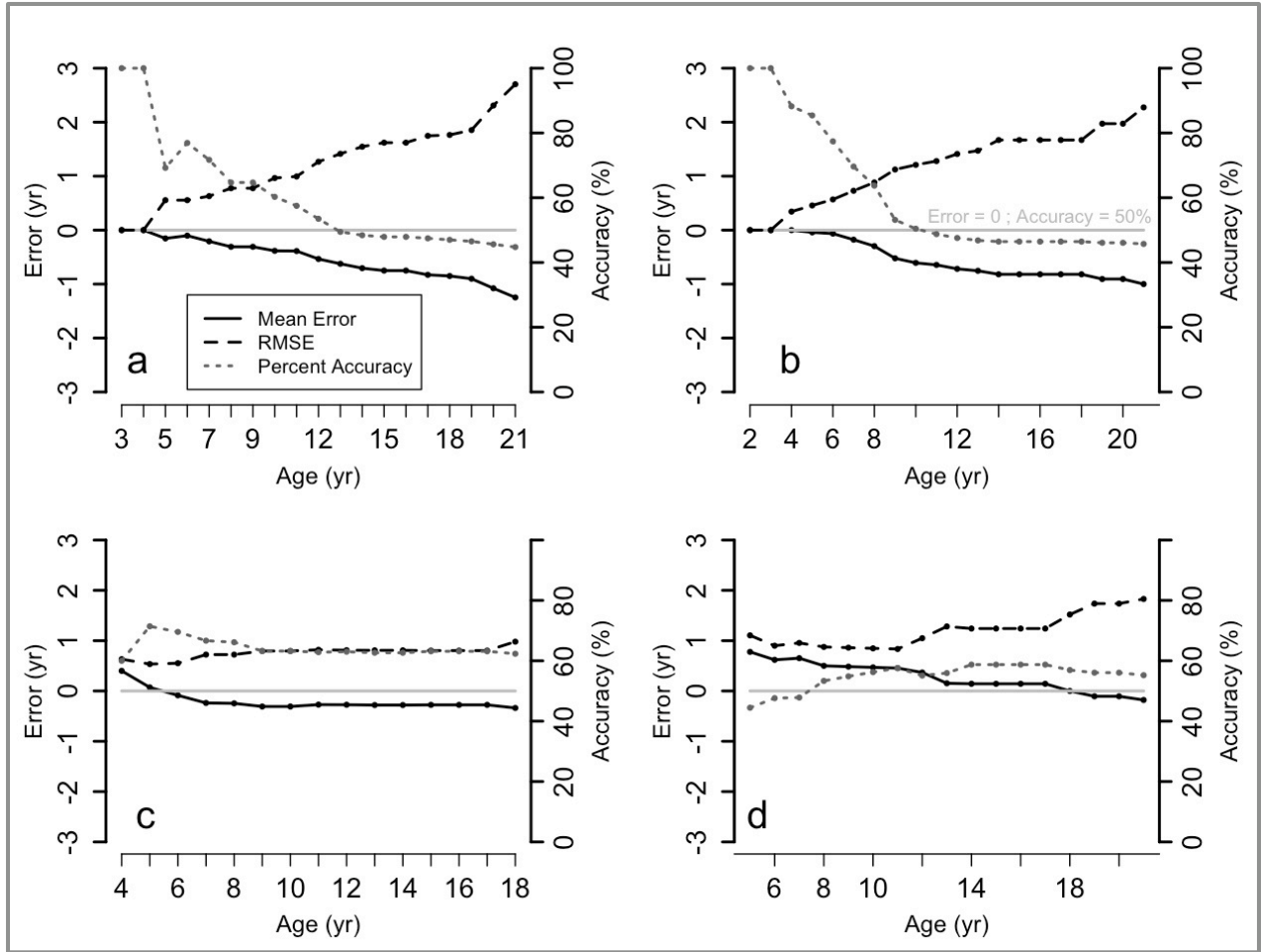


Figure 2. Percent accuracy, mean error, and RMSE of bud-scar age by ring age for all species.

^a Figure 2a = western larch; 2b = lodgepole pine; 2c = Engelmann spruce; 2d = Douglas-fir.

^b Mean error is the average difference in years between bud-scar age and ring age; negative error indicates that ring age was n years greater than bud-scar age, and positive error indicates that ring age was n years less than bud-scar age.

^c Root mean squared error (RMSE) is the average magnitude of error in years.

^d Percent accuracy: % of seedlings whose age was accurately determined by counting terminal bud scars.

^e Age of seedling based on annual ring counts at the root collar.

^f Y-values represent a cumulative average of the x-coordinate and all younger seedlings.

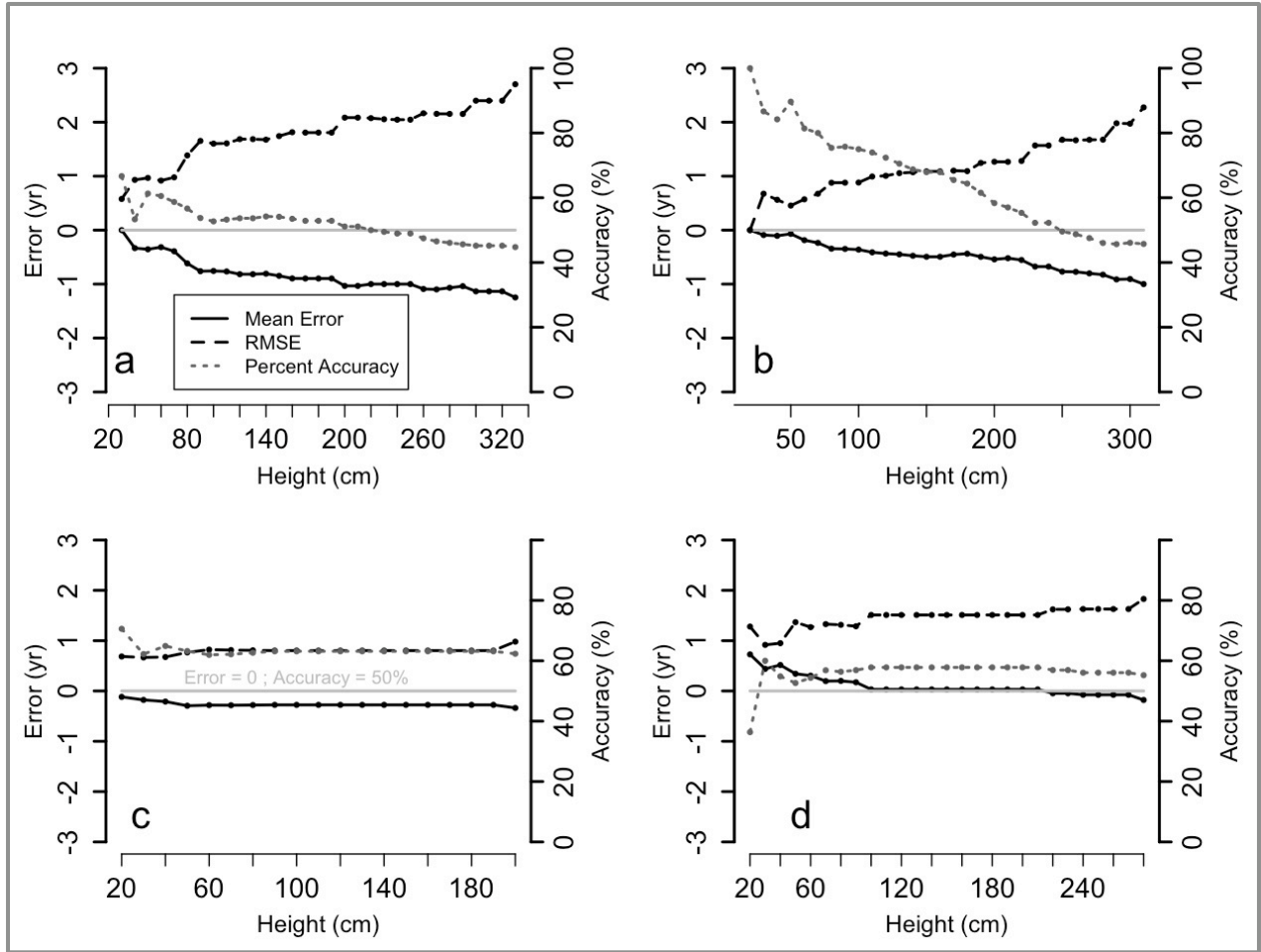


Figure 3. Percent accuracy, mean error, and RMSE of bud-scar age by seedling height for all species.

^a Figure 2a = western larch; 2b = lodgepole pine; 2c = Engelmann spruce; 2d = Douglas-fir.

^b Mean error is the average difference in years between bud-scar age and ring age; negative error indicates that ring age was n years greater than bud-scar age, and positive error indicates that ring age was n years less than bud-scar age.

^c Root mean squared error (RMSE) is the average magnitude of error in years.

^d Percent accuracy: % of seedlings whose age was accurately determined by counting terminal bud scars.

^e Seedling height was measured as the distance between the root collar and the beginning of 2010 growth, so height measurements do not reflect the timing of sampling during the 2010 growing season.

^f Y-values represent a cumulative average of the x-coordinate and all smaller seedlings.

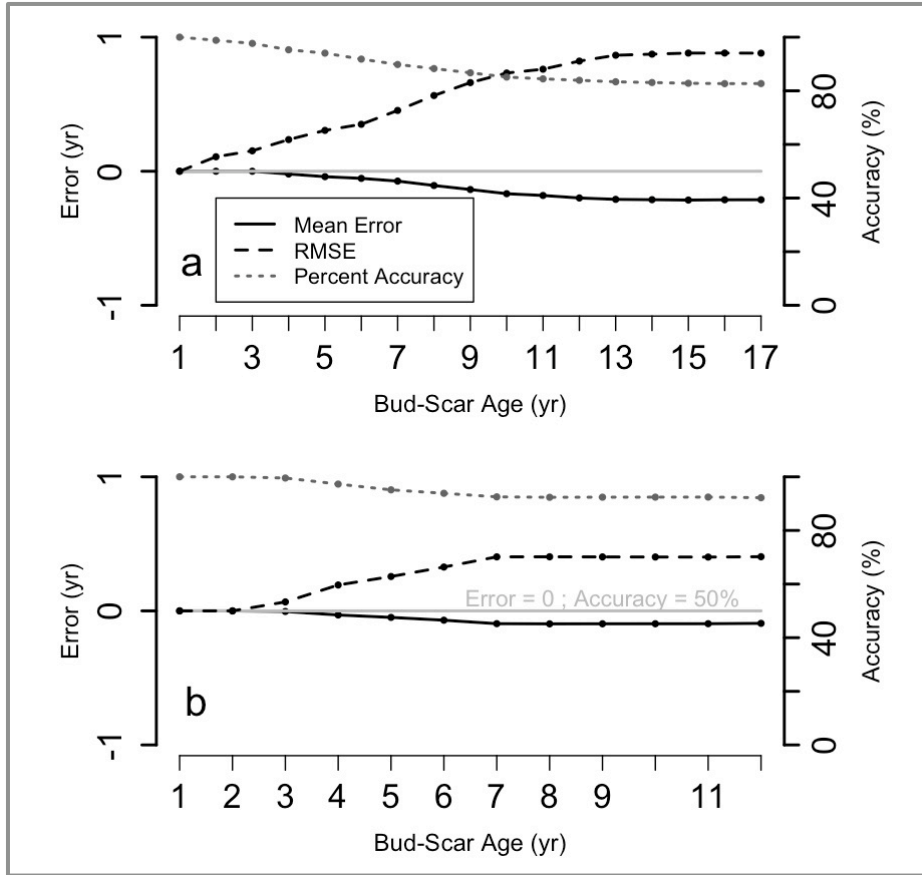


Figure 4. Accuracy, mean error, and RMSE of terminal bud-scar identification for western larch and lodgepole pine.

^a Figure 2a = western larch; 2b = lodgepole pine.

^b Mean error is the average difference in years between bud-scar age and ring age; negative error indicates that ring age was n years greater than bud-scar age, and positive error indicates that ring age was n years less than bud-scar age.

^c Root mean squared error (RMSE) is the average magnitude of error in years.

^d Percent accuracy is the proportion of bud scars whose age was accurately determined.

^e Age of bud scar based on annual ring counts just above the identified scar.

^f Y-values represent a cumulative average of the x-coordinate and all younger terminal bud scars.

CHAPTER TWO

Niche differentiation during canopy recruitment promotes coexistence between
shade intolerant conifer species

ABSTRACT

Larix occidentalis (western larch) and *Pinus contorta* var. *latifolia* (lodgepole pine) cohabit western Glacier National Park (GNP). Both species are shade intolerant, so following fire, seedling growth rates influence an individual's survival to the canopy and therefore future forest composition. We used vertical growth measurements to develop models of seedling growth based on site characteristics and climate. Since these species have similar requirements for establishment and growth, classical niche theory does not explain their coexistence in mature stands. However, spatio-temporal resource heterogeneity can allow for niche partitioning, and our results show that subtle differences in species' responses to environmental variability support coexistence. We found that *P. contorta* prefers high elevations and dry years following wet winters, while *L. occidentalis* prefers low elevations and warm, wet growing seasons following wet, cool years. Climate projections for GNP predict increased year-round temperature and a shift from summer to winter precipitation, which could reduce the survival of *L. occidentalis* seedlings at post-fire sites. While differential responses to environmental variability may have helped historically to promote coexistence between these species, climate changes that increase disturbance frequency and favor *P. contorta* following fire may destabilize that coexistence and lead to a regional decline of *L. occidentalis*.

KEY WORDS

coexistence, regeneration niche, canopy recruitment niche, climate change, niche partitioning, post-fire climate, *Larix occidentalis*, *Pinus contorta*, western larch, lodgepole pine

1 INTRODUCTION

2 The coexistence of plant species with similar ecological requirements is the subject of a
3 large body of theoretical literature in ecology. Classical niche theory (Hutchinson 1959, Tilman
4 1982, and many others) predicts that the species that tolerates the lowest level of resources will
5 competitively exclude other species when resources are constant. However, spatial and temporal
6 heterogeneity of available resources can allow plant species to partition space and time so that
7 each is the superior competitor under specific conditions (Tilman 1985, Chesson 2000, Barot and
8 Gignoux 2004). Spatio-temporal partitioning during even a single life stage can promote
9 coexistence, and niche differentiation during regeneration often maintains diversity among adult
10 individuals (Grubb 1977, Lavorel and Chesson 1995). Few empirical studies have directly
11 investigated the importance of spatio-temporal heterogeneity in species codominance (notable
12 examples include Latham 1992, Beckage and Clark 2003, Takahashi and Lechowicz 2008). In
13 this study, we examine the role of differential responses to site and climate in the coexistence of
14 two shade intolerant tree species in Glacier National Park. We expect that niche differentiation
15 during canopy recruitment is a key driver of broad-scale patterns of species distribution and
16 community composition following disturbance.

17 *Larix occidentalis* (western larch) and *Pinus contorta* var. *latifolia* (lodgepole pine) are
18 fire-adapted species that cohabit the subalpine zone of western Glacier National Park (GNP).
19 Fires in this forest type are typically stand replacing, so post-fire forest composition depends on
20 seedling establishment and successful recruitment to a canopy position. Both species require bare
21 mineral soil for germination and are capable of prolific and rapid seed dispersal following fire
22 (Barrett et al. 1991). *L. occidentalis* has wind-dispersed seeds and fire-resistant bark that allows
23 mature individuals to survive. *P. contorta* has serotinous cones that provide a seed source even

1 when mature trees are killed by fire. Post-fire seedling establishment is usually abundant for both
2 species. However, successful seedling establishment does not guarantee a place in the future
3 forest. Both species are extremely shade intolerant (Schmidt et al. 1976), and density-dependent
4 stand thinning during canopy recruitment is extensive in this forest type, where post-fire seedling
5 densities can reach >500,000 seedlings/ha (Kashian et al 2005). Provided that seedlings are able
6 to establish at a site, growth rates during the canopy recruitment period will determine the
7 probability of an individual's survival to maturity, exerting a strong influence on the composition
8 of the future forest. Since these species have similar requirements for establishment, classical
9 niche theory does not explain why they commonly coexist in heterospecific stands.

10 We hypothesize that niche partitioning is based on species-specific growth responses to
11 variability in water availability and temperature, and that the influence of climate may be
12 mediated by site characteristics. Previous studies have shown that *L. occidentalis* seedlings
13 conserve water less efficiently than *P. contorta* (Running 1980, Gower and Richards 1990). *L.*
14 *occidentalis*, a deciduous conifer, is more sensitive to growing season frosts (Fiedler and Lloyd
15 1992), reducing its fitness at higher elevations. We expect that *L. occidentalis* growth will be
16 favored during wet and cool growing seasons and at lower elevations, while *P. contorta* growth
17 will be favored during dry and hot years and at higher elevations. Even small differences in
18 species' growth requirements may allow for partitioning of spatio-temporal resources.

19 Understanding the drivers of species coexistence is particularly important in the current
20 context of rapid climate change (IPCC 2007). Differential growth responses will promote stable
21 coexistence between these species only when the range of environmental variability includes
22 conditions in which each species can outcompete the other. If the range of climate conditions
23 shifts enough to consistently favor the same species during canopy recruitment, niche

1 partitioning will no longer be possible, and coexistence will be destabilized. Significant changes
2 in climate have been observed in recent decades in Glacier National Park, and further shifts are
3 expected (Hall and Fagre 2003). Understanding these species' sensitivity to climate will be
4 imperative for predicting their potential response to climate change.

5 We used annual vertical growth measurements to develop predictive models of seedling
6 growth based on site characteristics, weather conditions, and seedling age in the year of growth.
7 These models characterize the optimum conditions for seedling growth, which we will refer to as
8 the "canopy recruitment niche" for each species. We compared parameter estimates from the best
9 fitting models for each species to site characteristics and historical climate ranges to produce
10 predictions of growth. We then compared species-specific model predictions for evidence of
11 spatio-temporal partitioning. While our study emphasizes the importance of climate and site,
12 stochastic processes such as ecological drift, immigration, speciation, and dispersal have also
13 been shown to influence coexistence (Hubbell 1997, Gravel et al 2006, etc.)

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MATERIALS AND METHODS

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Study Area

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The study was conducted in an approximately 750 km² area in the northwest quadrant of
Glacier National Park (GNP), Montana, USA (Appendix: Figure 1). Moist air bodies originating
in the northern Pacific and moving across the Pacific Northwest region drive the climate of
northwest GNP. Average annual precipitation in West Glacier, MT is 75 cm (WRCC 2011) and
typically experiences two peaks: one in January, in the form of snow, and another in June, in the
form of rain. Average temperature is highest in July at 17.6°C, and lowest in January at -5.4°C.

1 Temperate conditions west of the continental divide support denser, more productive forests than
2 at comparable elevations in eastern GNP. Forests in this area are predominantly characterized by
3 even-aged post-fire cohorts of *Larix occidentalis* and *Pinus contorta* and by uneven-age stands
4 of *Picea engelmannii* (Engelmann spruce) and *Pseudotsuga menziesii* (Douglas-fir).

6 *Study Design and Sampling*

7 Sampling took place in 2010 in areas that burned between 1988 and 2003. Transect
8 center points were situated within six fire perimeters with stratification by elevation and fire
9 severity. From each center point, a transect line was extended 20 m in each direction along a
10 randomly chosen azimuth. 15 1 m² sampling plots were distributed along each 40 m transect
11 using random number generation. Aspect and slope were estimated for each site using a compass
12 and inclinometer, and elevation was recorded from a GPS.

13 Within the 1 m² sampling plots, tree seedlings were identified and the stem height of
14 terminal bud scars on each seedling was recorded. Terminal bud scars are formed annually when
15 the scales protecting the terminal leader bud fall off, and the resulting scar indicates the end of a
16 year of growth. Starting at the top of a stem, we recorded the height of all bud scars on a stem or
17 until we could no longer confidently identify all scars. Annual growth was calculated by
18 subtracting the stem height of two consecutive bud scars. Estimated year of establishment was
19 based on a count of bud scars, and the age of a seedling at each bud scar was calculated by
20 subtracting the estimated year of establishment from the year of bud-scar formation.

21 Based on a dendrochronological analysis of the accuracy of field identifications of
22 terminal bud scars (Urza and Sibold, in review), we are confident that annual growth
23 measurements based on the distance between bud scars from at least 12 years prior to sampling

1 does not introduce significant error into our analysis. However, since bud-scar identification
2 error was found to increase with the age of the scar, during model evaluation we tested the
3 sensitivity of our results to the number of years of growth measurements included in the analysis.

4 In total, 73 sites were sampled, ranging between 1000 m and 1500 m in elevation. 13 of
5 these sites were not included in the analysis because either there were not seedlings of either
6 species or we were unable to confidently measure growth increments. Of the 60 sites included in
7 the analysis, 13 did not have *L. occidentalis* in their pre-fire composition and 1 did not have *P.*
8 *contorta* present before fire. 9 sites had no *L. occidentalis* seedlings establish following fire, and
9 12 sites had no *P. contorta* seedlings. Seedlings for which we could not confidently estimate the
10 year of establishment were excluded from models that included age as a predictor variable. Slope
11 angle was below 10° for most sites. Our final dataset included approximately 4,000 growth
12 measurements for *L. occidentalis* and 7,000 for *P. contorta* from a 12 year period (1998 – 2009).

13

14 *Climate Data*

15 Monthly climate data were acquired from the co-op weather station in West Glacier,
16 Montana (WRCC 2011). Records from this weather station were available from 1950 to 2010,
17 and the entire available record was used to determine the range of values from which to generate
18 model predictions of growth. Monthly precipitation values were separated into annual totals for
19 growing season precipitation (May through September) and winter precipitation (October
20 through April prior to the growing season). Since daily climate data were not available, growing
21 degree days (GDD) were calculated based on monthly averages of maximum (T_{\max}) and
22 minimum temperature (T_{\min}) from May to September (Eq. 1). Minimum temperature required for
23 growth (T_{base}) was assumed to be 0°C for subalpine ecosystems (CCSM 2011).

$$GDD = \sum_{mo=May}^{Sept} \left[\frac{T_{max} + T_{min}}{2} - T_{base} \right] * \# \text{ days}_{mo}$$

1 **(Equation 1)**

2

3 *Statistical Analysis*

4 We developed hierarchical Bayesian regression models of growth for each species.

5 Posterior probability distributions for all parameters were estimated with Monte Carlo Markov

6 Chain (MCMC) simulations using JAGS (Plummer 2011) through the R programming interface

7 (R Development Core Team 2009). We chose a Bayesian statistical approach both for the

8 potential for flexibility in model development as well as for the intuitive interpretation of

9 parameter estimates and credible intervals (Clark 2007).

10 We used multi-level regression models predicting annual growth increments with a site-

11 level ‘random’ intercept. Separate models were run for each species to allow for variability in

12 coefficient values at all levels of the hierarchy. Several dozen models were fit using different

13 combinations of predictor variables. Predictors were discarded if their estimated coefficients

14 produced diffuse posterior distributions, and the best models were selected based on agreement

15 between model predictions and data. The direction and magnitude of estimated parameter values

16 did not depend greatly on the choice of model. The final model is specified as follows:

$$P(\vec{\beta}, g_0, g_1, \tau_p, \tau_\alpha | \mathbf{y}, \vec{\mathbf{x}}, \mathbf{e}) \propto \prod_{j=1}^{n.j} [normal(\alpha_j | g_0 + g_1 e, \tau_\alpha)] \times \prod_{i=1}^{n.i} [lognormal(y_i | \alpha_j[i] + \vec{\beta}(\vec{\mathbf{x}}_i), \tau_p)]$$

$$\times uniform(\vec{\beta} | -10, 10) \times uniform(g_0 | -40, 40) \times uniform(g_1 | -40, 40)$$

$$\times gamma(\tau_p | .0001, .0001) \times gamma(\tau_\alpha | .0001, .0001)$$

17 **(Equation 2)**

1 Where: n_j is the number of sites, α_j is the intercept at site j , g_0 is the intercept at mean elevation,
2 g_1 is the regression coefficient for elevation e , n_i is the number of growth increments, y_i is
3 annual growth increment i , $\vec{\beta}$ is a vector of regression coefficients for a vector of explanatory
4 variables \vec{x}_i , and τ_p and τ_α are precision terms from each level of the regression. Uninformative
5 priors were used for all estimated parameters.

6 Estimated coefficient values at the level of growth represent each species' response to
7 conditions in the year of growth, such as climate and tree age. Coefficients were standardized
8 with z-scores so that the magnitude of covariate effects on growth can be easily compared
9 between predictors and models. Coefficient values represent the effect on growth of an increase
10 of the covariate by one standard deviation from its mean.

11 The final model included the following explanatory variables: elevation (predicting the
12 site-specific intercept), winter precipitation (October-April), growing season (GS) precipitation
13 (May-September), growing degree days (GDD), previous year's GS precipitation, previous
14 year's GDD, seedling age, and seedling age² (combining coefficients for age and age² allows for
15 non-linear relationship between seedling age and growth). Representing the site-level intercept as
16 a function of additional site characteristics such as aspect, slope, and latitude produced diffuse
17 coefficient posterior distributions, so these variables were not included in the final model.

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RESULTS

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Several climate variables were shown to have a strong relationship with annual growth (Table 1; Fig. 1a-e). Both species showed a positive relationship between growth and precipitation during the winter preceding growth, although the magnitude of the mean effect was greater for *P. contorta* ($\beta=0.24$) than for *L. occidentalis* ($\beta=0.16$). Growing season precipitation

1 had a slightly positive mean effect on *L. occidentalis* growth ($\beta=0.07$), but there was a 16.7%
2 probability that the effect was negative, suggesting a weak relationship. Growing season
3 precipitation had a strongly negative mean effect on *P. contorta* growth ($\beta= -0.50$). The mean
4 effect of growing degree days on growth was positive for both species and with nearly equal
5 magnitude (*L. occidentalis* $\beta=0.21$; *P. contorta* $\beta=0.22$).

6 For both species, climate in the previous growing season had a stronger explanatory
7 effect on growth than climate during the year of growth. The previous growing season's
8 precipitation had a positive mean effect on both species' growth, and the magnitude of the effect
9 was again greater for *P. contorta* ($\beta=0.68$) than for *L. occidentalis* ($\beta=0.38$). The previous year's
10 growing degree days had a negative mean effect on *L. occidentalis* growth ($\beta=-0.19$) and a
11 positive mean effect on *P. contorta* growth ($\beta=0.58$).

12 The model predictions for growth based on varying climate conditions (Fig. 2a-e)
13 consistently predict greater annual growth for *P. contorta* under most climate scenarios. At the
14 mean of all other variables, *P. contorta* is predicted to have greater growth than *L. occidentalis*
15 under the entire historic ranges of winter precipitation (Fig 2a), growing degree days (Fig. 2c),
16 and previous growing season precipitation (Fig. 2d). *L. occidentalis* growth is predicted to be
17 greatest under two conditions: when growing season precipitation is greater than 39 cm (Fig. 2b);
18 or in the year following a growing season with fewer than 2160 growing degree days (Fig. 2e).

19 The effect of elevation differed between the two species (Table 1; Fig. 1f). Elevation had
20 a positive mean effect on *P. contorta* growth ($\beta=1.85$), with a 1.3% probability of being negative.
21 Elevation's mean effect on *L. occidentalis* was negative ($\beta=-0.59$), although there was a 6.6%
22 probability that the actual effect was positive. There is no overlap between the species' 95%

1 credible intervals, which means there is at least a 95% probability that the effect of elevation is
2 more positive for *P. contorta* than for *L. occidentalis*.

3 The model predicts a clear tradeoff in the species' elevational optima, as growth for both
4 species shows a strong, while opposite, response to elevation. Mean *L. occidentalis* growth is
5 predicted to be greater than *P. contorta* at elevations less than 1180 m, while *P. contorta* growth
6 is predicted to be greater at higher elevations (Fig. 2f). At the highest elevations within the range
7 of our study, *P. contorta* annual growth is predicted to be more than twice that of *L. occidentalis*.

8 The relationship between annual growth and seedling age was qualitatively similar
9 between the species (Table 1, Fig. 1g-h). The mean effect of age on growth was positive for both
10 species (*L. occidentalis* $\beta=0.89$; *P. contorta* $\beta=2.55$), and the mean effect of age² was negative (*L.*
11 *occidentalis* $\beta=-0.26$; *P. contorta* $\beta=-0.37$). The predictions of annual growth based on seedling
12 age at the mean of all other variables (Fig. 2g) show a much steeper initial increase in growth for
13 *P. contorta* than for *L. occidentalis*, which is reflected in the large difference between the species'
14 estimated coefficients for age.

15 Sensitivity tests of the model including only the most recent nine and seven years of
16 annual growth data showed no significant changes in model predictions from the original model.
17 However, when only seven years of data are included, the threshold at which *L. occidentalis* is
18 predicted to have greater mean growth than *P. contorta* occurs at higher values of growing
19 season precipitation (> 45 cm) and at lower values of the previous year's growing degree days (<
20 2100 GDD). While the data subsets are likely to contain lower observation error than the full
21 dataset with twelve years of growth measurements, the full dataset was preferred because it
22 contained a greater range of climate conditions for use in parameter estimation.

23

1 DISCUSSION

2 Our results suggest that subtle differences in species' responses to spatio-temporal
3 environmental variability can support coexistence, providing support for theories of niche
4 partitioning. Even where the direction of both species' responses to a predictor was the same,
5 small differences in the magnitude of this response were shown to have a strong influence on
6 predicted growth rates. Ours is the first study to our knowledge to examine differential growth
7 responses in shade-intolerant tree seedlings, and one of few to empirically examine spatio-
8 temporal partitioning. Since canopy recruitment is often associated with extensive density-
9 dependent mortality, seedling growth rates have enormous significance for future forest
10 composition. In Glacier National Park, recent and widespread stand-replacing fires have resulted
11 in large areas of forest that are regenerating under shifting climatic conditions. Awareness of the
12 effect of climate on the coexistence of *P. contorta* and *L. occidentalis* provides critical insight for
13 projections of climate-related ecosystem change.

14 We found that *P. contorta* and *L. occidentalis* seedlings respond differently to climatic
15 and environmental conditions. *P. contorta* growth is favored by high elevations and dry years
16 following wet winters, consistent with our initial hypotheses. While growing season precipitation
17 is negatively associated with *P. contorta* growth during that year, the next year's growth is likely
18 to be greater than average. This may be related to the negative correlation between growing
19 season precipitation and sun exposure, so that a seedling would receive less light during a wet
20 summer but would be less likely to be damaged going into the next. *P. contorta* seedlings
21 respond positively to higher growing season temperatures in both the current and previous years.

22 *L. occidentalis*, in contrast, is favored by low elevations and warm, wet growing seasons
23 following wet, cool years. Since *L. occidentalis* is known to be less drought resistant than *P.*

1 *contorta*, it is not surprising to find a consistently positive relationship between growing season
2 precipitation and growth, consistent with our hypothesis. Although one would expect the positive
3 association between precipitation and growth to indicate a preference for the moist conditions on
4 north-facing slopes, aspect was not found to be a useful predictor in our models. We predicted
5 that cooler temperatures would be associated with greater growth rates, but higher growing
6 season temperatures were shown to have a positive effect on the current year's growth but a
7 negative effect on the following year's growth. The immediate growth benefit of higher
8 temperatures is likely due to increased photosynthetic rates, though hotter growing seasons may
9 tax a seedling's reserves, leading to reduced growth in the following year. The negative
10 relationship between *L. occidentalis* growth and elevation is likely a result of increased frost risk
11 at higher elevations.

12 Based on the predictions of our model, *L. occidentalis* mean annual seedling growth is
13 greater than *P. contorta* growth only in extremely wet growing seasons and following very cool
14 years. The conditions required for average seedling growth rates of *L. occidentalis* to exceed that
15 of *P. contorta* are at the extreme ends of historical climate ranges. *P. contorta* would be expected
16 to always dominate at higher elevations, and *L. occidentalis* would dominate at lower elevations,
17 if climate conditions favoring the other species did not occasionally occur. While seedling
18 growth rates are not indicators of future community composition in pure stands of either species,
19 our results suggest that *L. occidentalis* are likely to be outcompeted by *P. contorta* in
20 heterospecific post-disturbance stands under climate conditions typical of the last 60 years.

21 Downscaled climate projections for the Northern Rockies predict increased year-round
22 temperature and a shift from summer to winter precipitation in northwestern Montana (Bartlein
23 et al. 1997, Hall and Fagre 2003). Our model predicts that both decreased growing season

1 precipitation and increased mean temperature will strongly favor *P. contorta* seedling growth as
2 compared to *L. occidentalis* (Fig. 2a/b). These results are particularly significant given
3 observations of increased fire frequency and extent in the Northern Rockies (Overpeck 1990,
4 Westerling et al. 2006), which would produce more post-disturbance stands in which *P. contorta*
5 seedlings would likely be favored. This scenario coincides with existing models of species
6 distribution and climate, which predict a range contraction for *L. occidentalis* in northwestern
7 Montana under likely future climate scenarios (Bartlein et al. 1997). However, seedling growth
8 rates will not constrain *L. occidentalis* canopy recruitment in stands where it does not compete
9 with *P. contorta*, and increased temperatures may allow *L. occidentalis* to maintain its presence
10 in the region through upward movement of its range along elevational gradients.

11 While it is impossible to foresee how future changes in climate may produce previously
12 unseen ecosystem trajectories, disturbances are likely to be significant drivers of rapid ecological
13 change (Turner 2010). In GNP, climate shifts towards hotter, drier growing seasons could
14 simultaneously increase the occurrence of stand-replacing disturbance and greatly reduce the
15 chance that *L. occidentalis* seedlings will survive to the canopy at heterospecific sites. Although
16 differential responses to environmental variability may have helped historically to promote
17 coexistence between these two species, climate changes that increase disturbance frequency and
18 favor *P. contorta* following fire may destabilize that coexistence and lead to a regional decline of
19 *L. occidentalis*.

20

21

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Table 1. Mean and 95% range of estimated regression coefficients, and the corresponding probability of an opposite or nonexistent effect.

Parameter	<i>L. occidentalis</i>			<i>P. contorta</i>		
	β^a	(0.95 CI) ^b	$P(\beta \cap 0)^c$	β^a	(0.95 CI) ^b	$P(\beta \cap 0)^c$
Intercept	8.49	(7.51/9.51)	0	9.92	(7.29/12.65)	0
Winter precip	0.16	(0.02/0.30)	0.012	0.24	(0.10/0.37)	0
GS precip	0.07	(-0.08/0.22)	0.167	-0.50	(-0.67/-0.33)	0
GDD	0.21	(0.05/0.36)	0.004	0.22	(0.06/0.38)	0.004
Last GS precip	0.38	(0.21/0.55)	0	0.68	(0.44/0.92)	0
Last GDD	-0.19	(-0.35/-0.02)	0.013	0.58	(0.40/0.76)	0
Age	0.89	(0.71/1.08)	0	2.55	(2.38/2.73)	0
Age ²	-0.26	(-0.36/-0.16)	0	-0.37	(-0.40/-0.34)	0
Elevation	-0.59	(-1.36/0.19)	0.066	1.85	(0.23/3.42)	0.014

Notes: Coefficient values represent the effect on growth of an increase of the predictor by one standard deviation from its mean.

^a β = mean coefficient value.

^b 0.95 CI = range of 95% credible interval.

^c $P(\beta \cap 0)$ = probability that the coefficient posterior distribution overlaps with 0. This represents the probability that an explanatory variable has no effect or an opposite effect from the coefficient mean. Coefficient means are in **bold** if $P(\beta \cap 0) \leq 0.05$.

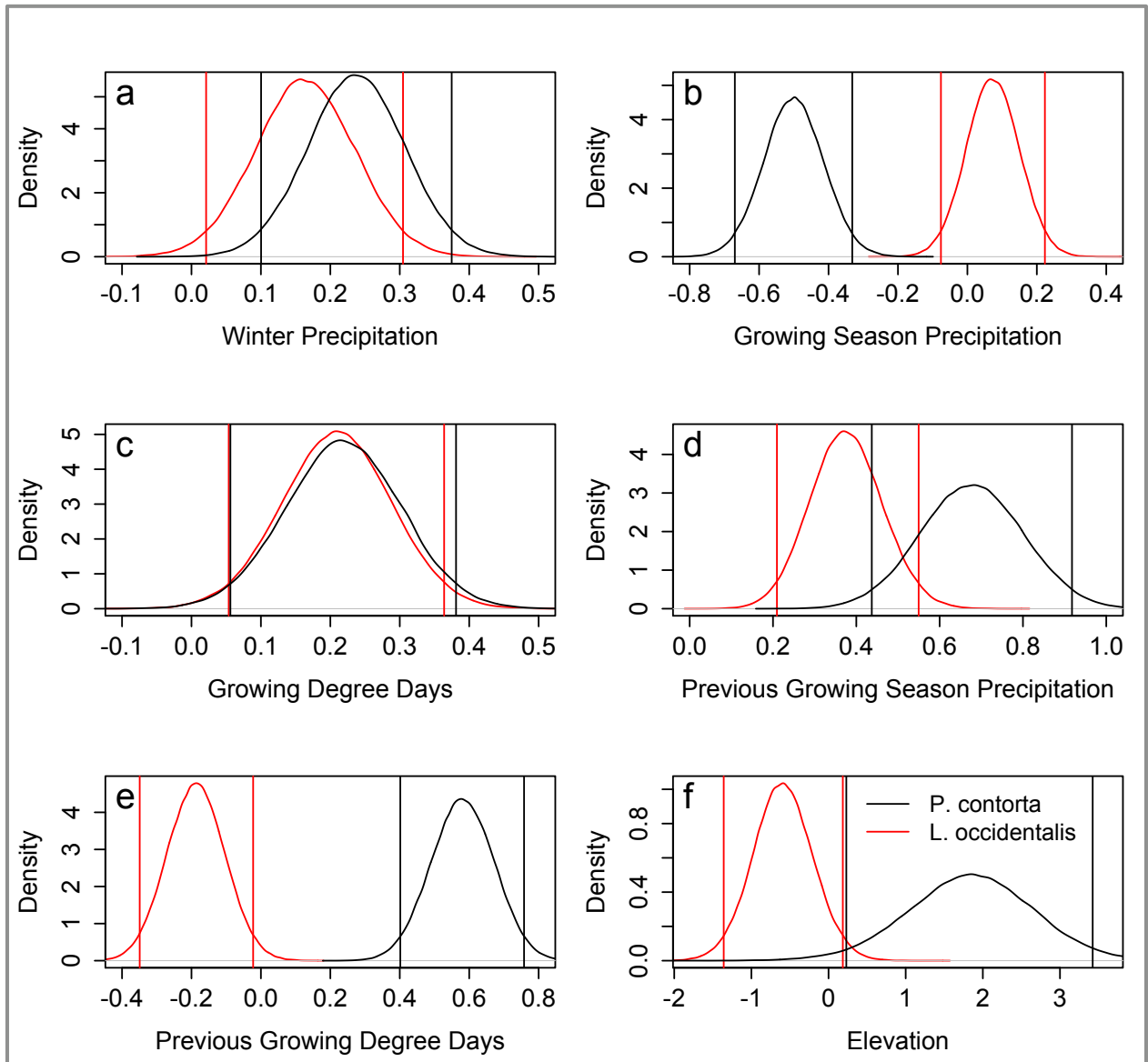


Figure 1. Estimated posterior distributions for regression coefficients.

Black lines indicate parameter values for *P. contorta*, and red lines indicate parameter values for *L. occidentalis*. Vertical lines represent 95% credible intervals for each parameter. Coefficient posterior distributions represent the effect on growth from: (a) winter precipitation; (b) growing season precipitation; (c) growing degree days; (d) previous growing season precipitation; (e) previous growing degree days; (f) elevation.

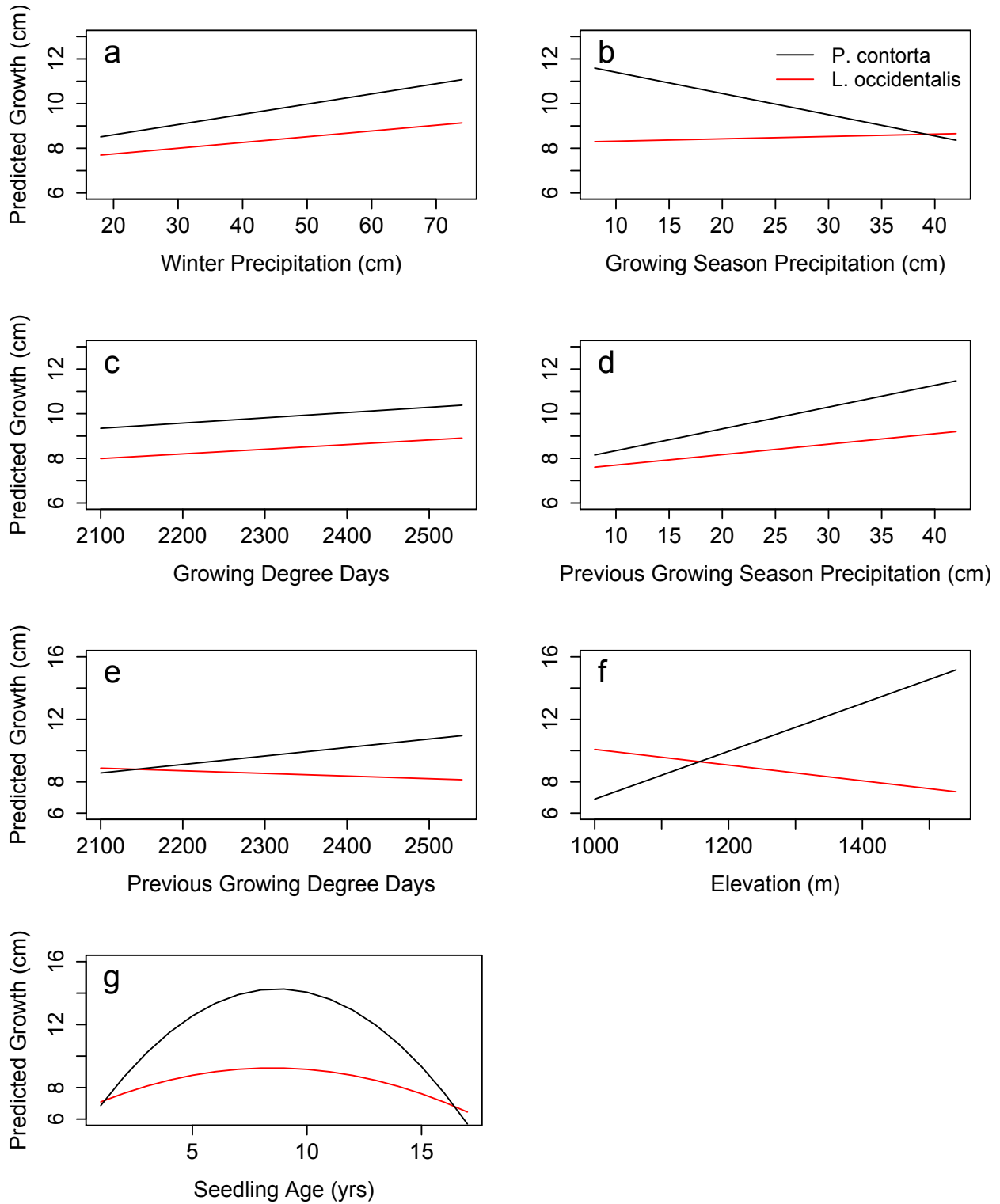


Figure 2. Mean model predictions of growth in response to varying explanatory variables.

(a) winter precipitation; (b) growing season precipitation; (c) growing degree days; (d) previous

growing season precipitation; (e) previous growing degree days; (f) elevation; (g) seedling age.

Black lines indicate parameter values for *P. contorta*, and red lines indicate parameter values for *L. occidentalis*. The range of climate values used for model predictions includes the historical range from the entire available climate record (1950-2010).

DISCUSSION

Implications and conclusions

The results of this study have multiple implications for forest science and management. At a practical level, Chapter One's assessment of field identifications of terminal bud scars will provide foresters and ecologists an estimate of the accuracy of this common field method. Chapter Two contributes to ecological theory by developing the concept of the "canopy recruitment niche," a particular instance of the broadly defined regeneration niche. This concept was then applied to a case study to explicitly investigate spatio-temporal niche partitioning and the historical coexistence of tree species in Glacier National Park (GNP) with broadly similar resource requirements. Finally, the results of the case study were interpreted in the context of current and projected climate to develop a data-driven forecast of possible ecosystem adaptation to climate change.

In Chapter One, I used harvested seedlings of four conifer species to quantitatively assess the accuracy and error of field identifications of terminal bud scars. Terminal bud scars are commonly used in forest research and management to estimate seedling age and measure annual vertical growth increments (e.g. Daly and Shankman 1985, Williams and Johnson 1990, Battles and Fahey 2000, Parent et al. 2000), and they provide a fast and cheap alternative to destructive aging methods. However, as a seedling grows, bud scars are healed over until they are unrecognizable (Hett and Loucks 1976), limiting the use of the method. I compared estimated dates of bud-scar formation derived from bud-scar counts with annual ring counts, and found that terminal bud scars are generally reliable indicators of annual vertical growth. The accuracy of bud-scar identification declined with bud-scar age and height for fast-growing species (western larch and lodgepole pine) but not for slower-growing species (Engelmann spruce and Douglas-fir). These results will provide informed estimates of error for future applications of this method.

In Chapter Two, I used annual growth increments, derived from the distance between successive terminal bud scars, to develop hierarchical models of canopy recruitment niches for western larch and lodgepole pine in GNP. This idea expands on the broad concept of the regeneration niche (Grubb 1977, Lavorel and Chesson 1995) by investigating the factors contributing to a specific stage in tree regeneration. The canopy recruitment niche models the climatic and environmental conditions that allow for maximum seedling growth during the period of seedling recruitment into the canopy. Since these species are intolerant of shade (Schmidt et al. 1976), post-fire seedling growth rates will greatly influence their chance of surviving to maturity. By comparing the canopy recruitment niches for two coexisting species with similar requirements for establishment and growth, I explicitly examine the possibility that differential responses to environmental variability are allowing for coexistence through spatio-temporal niche partitioning (Tilman 1985, Chesson 2000, Barot and Gignoux 2004). The results of the models suggest that within the range of climate experienced in the last 50 years, the differences between these species' canopy recruitment niches have allowed for their coexistence because each species can outcompete the other under periods of relative climatic advantage.

Based on the modeled canopy recruitment niches, projected regional climate change (Bartlein et al. 1997, Hall and Fagre 2003) would likely promote greater lodgepole pine growth relative to western larch. The model results suggest that under historic climate, western larch average growth rates exceed those of lodgepole pine at low elevations and only in extremely wet growing seasons following cool years. Even small shifts in climate towards hotter and drier growing seasons may eliminate the occurrence of conditions favorable to western larch seedlings, potentially leading to a destabilization of lodgepole pine-western larch coexistence. Increased frequency of high-severity fire (Overpeck 1990, Westerling et al. 2006) may induce rapid

ecosystem shifts (Turner 2010) by increasing the proportion of the landscape regenerating under a shifting climate. If lodgepole pine seedlings are able to consistently grow faster than western larch, fewer larch seedlings will survive to the post-fire canopy, and its presence on the GNP landscape will eventually be reduced. Western larch in GNP is already at the dry, eastern edge of the species' range (Gower and Richards 1990), and it may become confined to isolated pure stands if it is no longer able to compete with lodgepole pine at mixed post-fire sites. Increased temperatures may allow larch to migrate uphill within GNP, where environmental characteristics will resemble historic growing conditions, leaving it better able to compete with lodgepole during post-fire canopy recruitment.

The results of this study are enormously significant for land managers at GNP. Western larch is an iconic tree species within GNP, and a contraction of its range would have immense aesthetic consequences for the greater landscape. Reductions in western larch's presence on the GNP landscape would also likely have wide-ranging ecological effects. Effects on the hydrologic cycle could include reductions in the amount of annual precipitation that reaches the ground, since western larch intercepts less winter precipitation than evergreen conifers (Gower and Richards 1990). Disturbance regimes would be influenced in several ways by a diminished western larch component in larch-lodgepole stands: mountain pine beetle outbreaks would have a more thorough effect on the landscape, and the flammability of lodgepole pine (Schwilk and Ackerly 2001) is conducive to higher-intensity fires. Finally, wildlife species with specific requirements for food, nesting/roosting sites, and refuge will be inevitably impacted by a shift in forest composition.

Although we cannot predict future changes with certainty (Millar et al. 2007), awareness of the potential impacts of climate change on competitive dynamics between western larch and

lodgepole pine will leave GNP's managers better prepared to detect early ecosystem shifts. Land managers have the option of adopting either a passive or proactive approach to climate-induced ecosystem shifts. In GNP, a passive approach to lodgepole pine-western larch forests would ideally involve consistent monitoring in order to observe the direction and magnitude of ecosystem changes when they occur. Proactive tactics might include any combination of the following approaches: assisted uphill migration of western larch, active fire management to reduce the chance of high-severity fires in historically pure western larch stands, or mechanical elimination of post-fire lodgepole seedlings in targeted areas conducive to western larch survival. Successful management approaches to ecosystem transitions will likely include a flexible mixture of mitigation and facilitation (Seastedt et al. 2008).

If climate change continues at its current pace, ecosystems are inevitably going to respond, transitioning towards communities that are more suited to the new climate (Baron et al. 2009). Species ranges will expand and contract, resulting in regional extinctions and ecotone shifts (Allen and Breshears 1998, Thomas et al. 2004, Breshears et al. 2005). Our own ability to adapt to global change will depend partially on our ability to anticipate possible shifts in the ecosystem services on which we depend. By using field-based data to inform models of ecosystem adaptation, our ability to anticipate and prepare for the possible consequences of climate change can continuously progress.

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