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A COMPARISON OF WILDFIRE ADAPTIVE TRAITS IN JUVENILE CONIFERS OF THE NORTHERN ROCKIES

Andie Sonnen
University of Montana, as136907@umconnect.umt.edu

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BY

ANDIE SONNEN

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Introduction

Wildfire is an important ecological disturbance that continues to shape the ecosystems of the northern Rocky Mountains through varying patterns of frequency and severity. Given precipitation and vegetation patterns, the northern Rockies are characterized by a diversity of fire regimes including high frequency, low severity fire in lower elevation ponderosa pine forests with a mean fire return interval of approximately 5-25 years; moderate frequency, mixed severity fires in mixed conifer forests with a mean fire return interval of 15-40 years; and low frequency, high severity fires in subalpine forests with a mean fire return interval of 100-300 years (Hood 2021). However, due to historical fire suppression and the hotter and drier conditions brought upon by anthropogenic climate change, wildfire frequency, severity, and season length are increasing (Abatzoglou 2016 and Abatzoglou 2021). These changes in wildfire patterns will likely alter the vegetation composition and structure of the northern Rockies through changes in the ability of species to regenerate following wildfires (Moritz 2012). The ability of species, especially conifers, to regenerate following high severity fires is crucial for maintaining forest structure and composition (Rodman 2020). With more frequent low-severity fires, the ability of these forests to regenerate is in part dependent on the ability of juveniles to survive repeated fires (Stephens 2013).

Individual plant traits, especially those that reduce fire-related mortality, can offer insight into how these vegetation communities will shift (Rodman 2020). The three iconic fire-adapted conifers of the northern Rockies, western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menzeisii*), and ponderosa pine (*Pinus ponderosa*), all have differing physiological tolerances that allow their survival in the dry mountain forests of the west (Bigelow 2011, Stevens 2020, Rodman 2020). One of such tolerances is the ability to survive wildfire. Wildfire causes mortality through heat transfer via convection, conduction, and radiation to the tree crown, stem, and root tissue (Dickinson and Johnson 2001, Hood 2018). Damage to the crown occurs when heated air kills foliage and vascular tissues, in particular the bud tissue (Van Wagner 1973). If a tree experiences 100% bud mortality, the tree will die (Dickinson and Johnson 2001). Damage to the crown can cause mortality, but damage to the stem is the most common cause of fire-related mortality, particularly in younger and smaller trees or thin-barked species (Lawes 2011). Heat damage to stems can harm the vascular tissues that provide the crown with water and nutrients, both of which the tree cannot survive without (Midgley 2011). Thicker bark can offer protection from heat damage to the vascular tissue, and thus is an important determinate of tree resistance to fire (Lawes 2011). Given the two largest causes of fire mortality: damage to the crown and damage to the stem, juvenile trees are more at risk of fire mortality than mature trees.

Trees can survive fire by increasing bark thickness to protect vascular tissues and by growing more rapidly to protect bud tissue. Western larch, Douglas-fir, and ponderosa pine are all characterized as having very thick bark and high resistance to wildfire at maturity. Western larch is the most fire adapted species with the thickest bark and a high and open crown, followed by ponderosa pine and Douglas-fir (Hood 2018). While these species-specific survivability traits have been studied in adult conifers, little research has been done to examine survivability traits in juvenile (5-30 year old) conifers. Given that these younger trees are more vulnerable to mortality from wildfires, and given that wildfire frequency is increasing, it is important to examine what traits ponderosa pine, Douglas-fir, and western larch juveniles that established after fires possess to survive wildfire. In the southern Rockies, ponderosa pine juveniles are found to have both thicker bark and more rapid growth than Douglas-fir (Rodman 2020), but little is known about western larch and its plant traits. Identifying these individual plant traits across the three species in the northern Rockies will offer insight into which species may be more successful in a future with more frequent fires and thus which species could be prioritized for replanting after fires. Therefore, I will address the following three questions:

1. How does bark width and tree height vary among ponderosa pine, Douglas-fir, and western larch juveniles (5-30 years old) that established following wildfire in the northern Rockies? Because ponderosa pine had the most rapid height growth in the southern Rockies, I hypothesize that ponderosa pine will have the most rapid height growth in the northern Rockies as well. I predict western larch will have the thickest bark due to its thick bark as an adult, and I predict that Douglas-fir will have the thinnest bark and slowest height growth.

2. Are there tradeoffs associated with thicker bark or more rapid height growth? That is, do species with thicker bark have slower height growth and vice versa? I hypothesize that generally, species either put their energy into increasing bark width or increasing height growth.

3. Which species is best adapted to more frequent fires at the juvenile stage? I hypothesize that ponderosa pine is the most adapted species, followed by western larch, followed by Douglas-fir.

Methods

Study Area and Field Sites:

To obtain tree data, we established plots following recent (1995-2015) wildfires throughout the northern Rockies and Interior Northwest (Montana, Idaho, Oregon, and Washington). All fires burned sometime within the months of May-October and at varying degrees of severity from 0% mortality to 100% mortality. Climatic conditions varied among sites, with annual average precipitation between 318 and 878mm and mean annual temperatures between 3.3 and 8.4℃. Within the fire perimeters, we established field plots based on the following conditions: within western larch/Douglas-fir/ponderosa pine range, within an area that burned with moderate to high severity, and not replanted following the wildfire. There were 43 plots total, in 30 different fires. Within these plots, a 60 meter belt transect was set directly uphill, and all seedlings within an established distance from the transect were destructively sampled with the goal of approximately 30 seedlings per plot. We measured and recorded height, diameter, and point on the transect for each seedling, and we removed the area on the stem surrounding the root collar to take back to the lab for further processing.

Lab Measurements:

We cut each seedling was into 2cm cross sections from 2cm below the first root to above the first branch. We sanded the cross sections, and then counted the tree rings. For each seedling, we scanned the oldest cross-sections. We selected the seedlings of each species to measure using stratified random sampling. It was not feasible to measure all the seedlings we sampled, so we split the larch seedlings into two categories based on diameter size: over 6cm and under 6cm. We randomly selected fifty larch from the under 6cm size class and fifty larch from the over 6cm size class. We did the same for Douglas-fir with a 3cm diameter break, and ponderosa pine with a 7cm diameter break. The size classes varied by species due to the difference in the range of diameters between species and to maximize the number of large seedlings we measured from each species. From the scans, I measured tree bark width for the selected trees in four places: at 0˚, 90˚, 180˚, and 270˚ using the computer program ImageJ. I measured diameter in two places: at 0˚ and at 90˚.

Statistical Analysis:

Because height and relative bark thickness are both indicators of the ability to survive wildfire, it was important to do two separate analyses. I compared heights of all the seedlings to age, and then the bark width of each seedling to age. To assess whether the relationship between height and age varied between species, we used a multiple linear regression model. We logged transformed the response, and did the same for the model of bark width.

Results

We found significant differences between the heights of western larch, ponderosa pine, and Douglas-fir after approximately ten years (table 1). Western larch had the most rapid height growth, followed by ponderosa pine, followed by Douglas-fir (figure 1). At age 10, western larch is approximately 16% taller than ponderosa pine. At age 15, western larch is approximately 67% taller, and at age 20, western larch is approximately 140% taller than ponderosa pine. At age 10, ponderosa pine is approximately 14% taller than Douglas-fir, 39% taller at age 15, and 71% taller at age 20.

Table 1. Results from the statistical analysis using a multiple linear regression model comparing the relationship between height (cm) and age (yr) between western larch, Douglas-fir, and ponderosa pine. Ponderosa pine is the reference level for species. The relationship between height and age was also significantly different between western larch and Douglas-fir (β=-0.11, SE=0.024, t=-0.047, p<0.0001).

	Estimate	Standard Error	T value	Pr(>|t|)
Intercept	1.87847	0.19602	9.583	<2e-16
Age	0.17235	0.01201	14.348	<2e-16
LAOC	-0.57986	0.35691	-1.625	0.10543
PSME	0.28246	0.30518	0.926	0.35552
Age:LAOC	0.07262	0.02198	3.304	0.00108
Age: PSME	-0.04093	0.02005	-2.042	0.04215

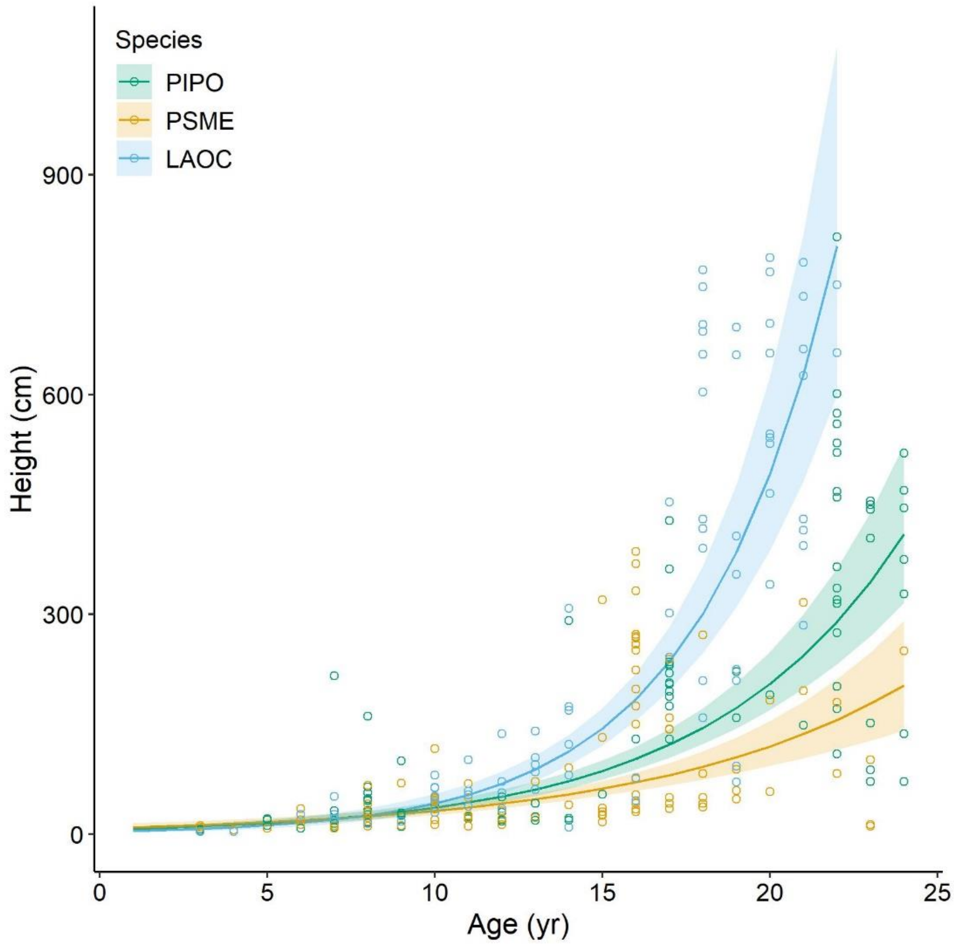

Figure 1. Fitted lines from the final multiple linear regression model comparing the relationship between height and age for western larch, Douglas-fir, and ponderosa pine. The solid lines are predicted values, the points represent the observed data, and the shaded region represents the 95% confidence interval. The adjusted R-squared value for this model is 0.6652.

We also found a significant difference between the bark width of western larch and the bark widths of ponderosa pine and Douglas-fir (table 2). Western larch has the thickest bark, but it is not statistically clear whether Douglas-fir or ponderosa pine has the next thickest (figure 2). Bark width appears to become significantly different around age 15. At age 15, western larch had approximately 15% thicker bark than ponderosa pine and Douglas-fir, and 50% thicker bark at age 20 (figure 2)

Figure 2. Results from the statistical analysis using a multiple linear regression model comparing the relationship between bark width (mm) and age (yr) between western larch, Douglas-fir, and ponderosa pine. Ponderosa pine is the reference level for species. The relationship between bark width and age was also significantly different between western larch and Douglas-fir (β=-0.04, SE=0.024, t=-1.865, p=0.0432).

	Estimate	Standard Error	T value	Pr(>|t|)
(Intercept)	-2.111186	0.19906	-10.609	<2e-16
Age	0.12889	0.01220	10.566	<2e-16
LAOC	-0.71412	0.35455	-2.014	0.04493
PSME	-0.58981	0.30991	-1.903	0.05803
Age:LAOC	0.06677	0.02124	3.144	0.00184
Age:PSME	0.02233	0.02036	1.097	0.27357

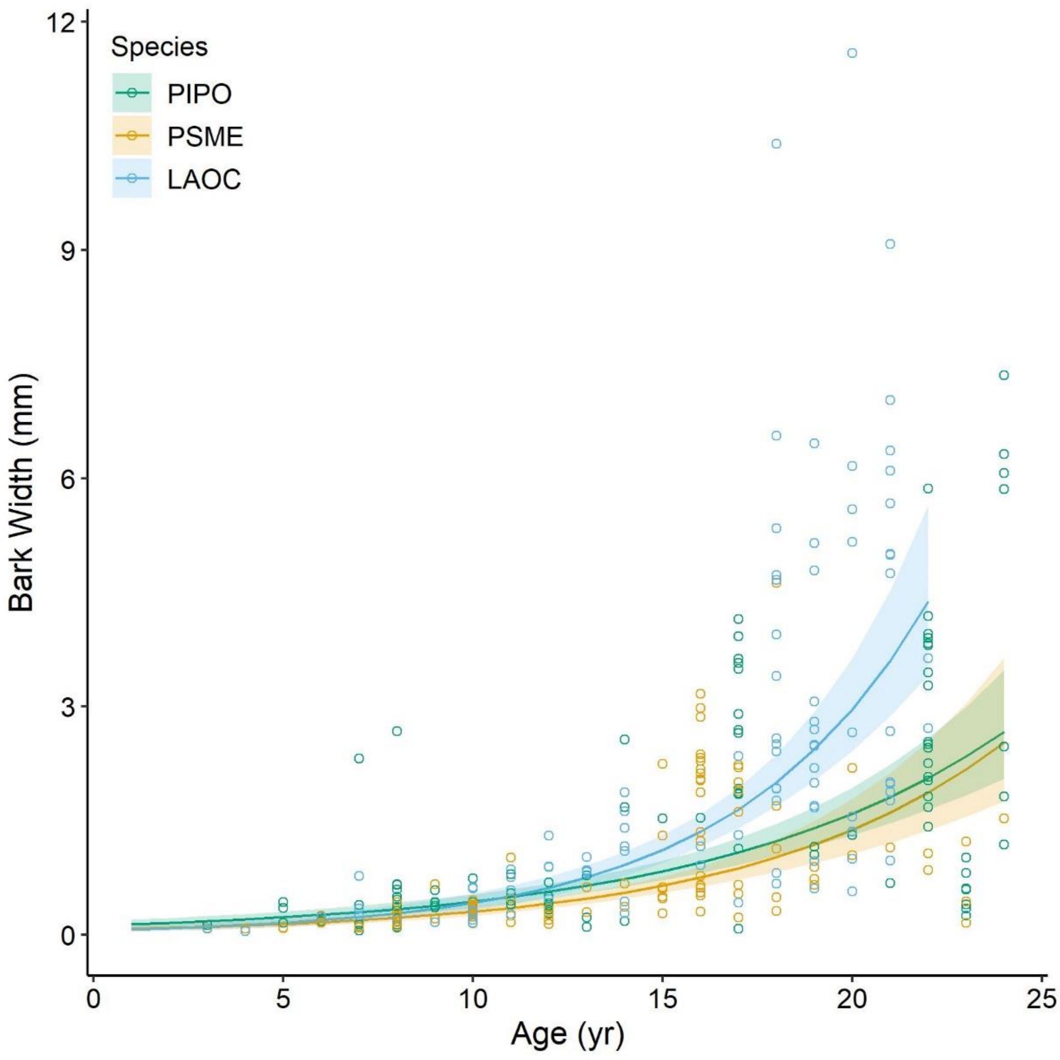

Figure 2. Fitted lines from the final multiple linear regression model comparing the relationship between bark width and age for western larch, Douglas-fir, and ponderosa pine. The solid lines

are predicted values, the points represent the observed data, and the shaded region represents the 95% confidence interval. The adjusted R-squared value for this model is 0.5773.

Discussion

As anthropogenic climate change alters temperature and precipitation patterns, and thus alters wildfire frequency and severity (Abatzoglou 2016 and Abatzoglou 2021), it is increasingly important to understand and quantify wildfire adaptive traits in northern conifers. Here, we show that western larch juveniles are more fire adapted than ponderosa pine and Douglas-fir by having both thicker bark and more rapid height growth. Ponderosa pine had the second thickest bark and second fastest height growth, and Douglas-fir had the thinnest bark and slowest height growth. This is important because the presence of these wildfire-adaptive traits (thicker bark and more rapid height growth) indicate a higher chance of survival in forests with increasing fire frequency.

Our results were consistent with the results of a similar study conducted on ponderosa pine and Douglas-fir in the southern Rockies. Like our study, this study found that juvenile ponderosa pine had thicker bark and more rapid height growth than Douglas-fir (Rodman 2020). However, this study did not include western larch, an iconic fire-resistant conifer of the northern Rockies. With these results, we fill that gap. Other studies (Hood 2018) examined these characteristics in adult western larch, ponderosa pine, and Douglas-fir, and partially confirmed our hypothesis that juveniles of these species follow the same patterns: adult western larch has the thickest bark, followed by ponderosa pine, followed by Douglas-fir. When examining specific adaptations, our results agree with the ecology of the species: western larch is shade-tolerant, and thus must keep above its competition and establish its wide and open crown. In contrast, Douglas-fir is more shade-tolerant, and thus may persist in the shade of the other two species.

This study is especially relevant as we consider post-fire management choices under ongoing climate change and increases in fire frequency. Based on our findings, western larch is the most adapted to wildfire at the juvenile stage. This may be valuable information when considering which species to replant following fires, given the increasing chance that sites planted post-fire may burn again before trees reach adulthood. However, other traits (shade tolerance, drought tolerance, etc.) would have to be considered too.

Despite our ability to capture the adaptive traits of all three species, there were limitations with our study. We recognize that when the seedlings are small (<100 cm tall), bark thickness and height will not stop mortality in the event of a wildfire. Ideally, we would have wanted more trees in the upper size class (>100cm tall) where bark width and height would be more likely to influence fire-induced mortality. Additionally, there were variations in the height on the stem that bark width was measured. Every measurement was within 10cm, but the further up the stem, the greater the relative bark width was. All bark width measurements were taken at the base of the seedlings, and it might be valuable to measure further up.

In summary, climate change is increasing fire frequency. This study provides valuable insight into which species will be most likely to survive in an ecosystem with more frequent fire. The first research questions asked how bark width and height vary across western larch, ponderosa pine, and Douglas-fir juveniles. We now know that western larch has the thickest bark and most rapid height growth, followed by ponderosa pine, followed by Douglas-fir. The second research question was concerned as to whether or not there are tradeoffs associated with possessing one trait (thick bark) over the other (more rapid height growth). Based on our findings, there are no tradeoffs between those two variables. Western larch had both the thickest bark and most rapid height growth, and thus is the species most likely to survive in an ecosystem with more frequent fire, followed by ponderosa pine, followed by Douglas-fir. An opportunity for further research could involve examining other wildfire adaptive traits (age of reproductive maturity, seed mass, juvenile crown structure, and self-pruning ability) to identify further tradeoffs associated with height and bark width.

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