Factors Influencing Lodgepole Pine Cone Openness

Dawn M. Harfmann
McCall Outdoor Science School
University of Idaho
December 2012

Abstract
1. Lodgepole pine cone serotiny is commonly thought to be an adaptation to fire dominated ecosystems.
2. This study tested the hypothesis that lodgepole pine cone openness can be influenced by incident solar radiation and tree age.
3. Two approximations of solar radiation (aspect and distance to nearest neighboring tree canopy) were used.
4. Tree age was approximated by tree diameter.
5. Cone angle of attachment was also tested.
6. There was a statistically significant difference ($p<0.05$) between cones on the north and south facing sides of the trees.
Synthesis: Results support the hypothesis that incident solar radiation influences cone openness. This study serves as a model for future studies that could investigate cone serotiny and the effects of incident radiation on cone openness in surrounding areas. Such information taken together with local disturbance history would increase understanding of the interplay between environmental factors and genetic predisposition for serotiny.

Key Words
Aspect, cone, disturbance, fire, lodgepole pine, openness, serotinous, serotiny

Introduction

Lodgepole pine trees (*Pinus contorta*) are known for their ability to regenerate after fires. The primary adaptation that trees of this species have to survive fires is a serotinous cone habit. Serotinous cones are closed and exhibit a waxy coating that is melted away by the heat of a fire. The closed cone serves as a heat-resistant capsule and protects the seeds contained within from being scorched by fire. Once the coating is removed, the cones are free to open via hygroscopic forces (Hellum and Barker 1980, Lotan and Critchfield). Serotinous cones thereby ensure that seeds are protected during a fire and not released until conditions are appropriate. This may be advantageous to lodgepole trees because of the potentially elevated nutrient content of the soil following fire, as well as the reduced competition from other less fire-adapted species (Anderson 2003). Further, since serotinous cones remain on trees for about fifteen years (and sometimes twice that long), the seed bank within the canopy is built up over many years and seeds from all serotinous cones are released in a very brief time following fire (Smith and Fischer 1997; Anderson 2003; Schoennagel et al 2005). Serotiny in lodgepole pines can have direct impact on vegetation composition and succession following fire, and is of interest to both ecologists and land managers.

Fire, however, is not the only mechanism by which lodgepole pine cones can open; heat without fire has been shown to successfully open lodgepole pine cones (Knight 1994). Moreover, while this environmental factor (heat) can cause a cone to open, not all cones have the same initial degree of openness. Not all lodgepole pine cones are serotinous; in other words, some cones are open initially without any need for added heat. It is proposed that serotiny can be best described on a continuum that can be broken into classifications based on temperature required to attain open cones. Thus, some cones are nonserotinous and are open initially. Some require lower temperatures (35-50 ºC) to open, and others require higher (40-60 ºC) temperatures (Perry and Lotan 1977).

A single lodgepole tree is typically either dominantly serotinous (producing mostly serotinous cones) or not (producing mostly nonserotinous cones) (Schoennagel et al 2005). Tree serotiny can vary geographically, to different degrees at different geographic scales (Tinker et al 1994). Such variation may be caused by stand age and disturbance history, as well as tree age (Schoennagel et al 2005). Fire has been shown to select for serotinous cone habit (Perry and Lotan 1977) by allowing for opening of serotinous cones and thus planting of the seeds from those cones. These seeds may contain genetic information coding for serotiny. By contrast, in years in which no fire impacts an area, seeds from nonserotinous or mildly serotinous cones will preferentially establish because they are open and seeds are able to be released.

Degree of serotiny for a given tree can also vary by tree age (Schoennagel et al 2005). Rocky Mountain lodgepole pines do not produce seeds until between five and fifteen years of age (Anderson 2003). Once they begin producing cones, even serotinous trees actually produce open cones for the first thirty to sixty years of their life, after which point they begin to produce serotinous cones (Anderson 2003). Then, once a cone is produced, its degree of openness may also be affected by its own maturity, as well as hygroscopic forces (Hellum and Barker 1980). Furthermore, weathering may affect openness by weakening cells in the cone scales.

This study investigated various factors that may affect cone openness. Preliminary trials using a heat lamp confirmed that cones could, indeed, be opened by these lower temperatures (Figure 1). Next, a field study to test for correlation between incident heat and tree age, and cone openness, was conducted. Two surrogate measurements were used to approximate incident radiation: cone aspect and distance between canopies of the study tree and its nearest neighbor. It was expected that a northerly or southerly aspect may well approximate incident radiation, with southern directions attaining more solar radiation in northern latitudes. Distance between canopies was used as an approximation of canopy cover, which would affect incident radiation. Tree age was approximated (albeit roughly) by tree diameter at breast height (dbh). Angle of cone attachment has also been shown to correlate with cone openness (Tinker et al 1994) and was analyzed in the present study. It was expected that cone openness will depend on angle of attachment, solar radiation, and tree dbh (rough measurement of tree age).

Methods

Two lodgepole pine trees in a sagebrush meadow in Ponderosa State Park, McCall, ID were selected as sample trees based on accessibility of lowest branches and general impression of tree health and cone intactness. Both trees had a relatively open growth habit with sprawling branches. As cone opening can be stimulated by increased temperatures that can be found at or near the ground (Lotan and Critchfield), only cones that remained on the tree were selected for measurement. Eight cones were measured from one tree and ten from the second tree. Cones were selected for their proximity to North and South, but cones that were not intact or were difficult to access using a stepladder were disregarded. Due to height limitations, most cones resided in approximately the same horizontal plane.

Two metrics for quantifying cone openness were developed and used in parallel. A value representing average distance between scales, termed "gap distance," was calculated by summing the space between scales in a single "row" of adjacent scales. (Henceforth the term "row" will be used to signify this diagonally curving row.) Given the morphology of a lodgepole pine cone (Figure 1), each row of adjacent scales wraps diagonally around and up the cone. The space between scales was defined as the region that appeared black between two successive scales in a row, and was measured with a millimeter ruler. Gap distance was determined as follows:

Gap distance = Sum of distances between scales / number of scales in a row

The second metric utilized was the percent of closed scales. For each cone, the number of scales in the sample row that were closed (showed no space between it and the next) were counted and normalized as follows:

Percent closed scales = (number of closed scales in a row/total number of scales in the row)*100

Factors that were to tested for include: aspect, angle of attachment, tree diameter at breast height (dbh) and distance to nearest neighboring canopy. Angle of attachment was measured using a protractor, branch diameter was measured using a millimeter ruler, and aspect was determined by identifying heading to the center of the tree trunk from the location of each cone. Tree dbh and distance to nearest neighboring canopy were measured using a meter tape. For each cone, height and width dimensions and cone color were also recorded; data are not shown. Canopy distance and angle of attachment were analyzed via linear regression models. Aspect and tree dbh were analyzed to test for a statistically significant difference between north and south aspects, and between dbh sizes, using Welch's independent sample t-tests. All statistical analysis was performed using the open source software package R (R Development Core Team, 2011).

Results

Most cones on the sample trees were not fully intact, with seed predation being the suspected cause. Even after cone selection was derandomized to preferentially select whole cones, five cones included in the study were not fully intact.

As shown in Figure 2, the two metrics for quantifying cone openness had only a moderate degree of correlation ($p=0.02$, $r^2 = 0.25$), so they could not be used interchangeably with confidence. Therefore, both techniques were utilized for subsequent analyses, in order to determine if the tested parameters correlated well with either technique. As shown in Figure 3, the north and south facing cones had statistically significantly different cone openness according to both gap distance (df =14.3, $p=0.014$) and percent closed scales (df=10.3, $p=0.047$). Canopy distance had no significant correlation with cone openness according to either metric (r^2 values were less than 0.2); scatter plots are shown in Figure 4. Figure 5 presents data for angle of attachment, which had a moderate correlation with cone openness for gap distance ($p=0.01$, $r^2 = 0.28$) and percent closed scales ($p=0.03$, $r^2 = 0.21$). Figure 6 illustrates that tree dbh is not a statistically significant predictor of cone openness via gap distance (df = 8.56, $p=0.29$) or percent closed scales (df = 10.17, $p=0.51$).

Discussion and Future Research

Results from the present study suggest that aspect is a factor that influences cone openness. Both techniques for measuring cone openness yielded statistically significant differences between the north- and south-facing cones. The sagebrush meadow in which the sampled trees grow is open, and the differential effects of sunlight on north- and south-facing sides of a tree are not greatly masked by shading. The data support the hypothesis that aspect affects cone openness, and this effect may be due to the greater heating capacity of the sun on the southern exposure. It has been shown that heat increased the germination rates of serotinous cones and not of nonserotinous cones (Despain et al. 1996). Temperatures in the low end of the range required to open cones in the moderately serotinous category (35-50 ºC) (Perry and Lotan 1977) can be achieved during summer months in the McCall, Idaho area. The open character of the sagebrush meadow in which the sampled trees grow results in more drastic temperature fluctuations than do those of nearby forested areas. Biomass present in this meadow can thus be exposed to consistently high temperatures during summer months.

In this study, aspect was assumed to roughly represent the amount of incident solar radiation; some limitations of this approximation must be considered. Aspect is also known to correlate well with moisture; south-facing slopes are both sunnier and drier. Southern exposures of slopes tend to be drier than northern slopes. Once serotiny is broken in a cone, hygroscopic forces influence cone openness; cones open as they dry. It may be that the south-facing side of a tree is drier and stimulates cone opening. Nonetheless, heat may still be the reason for increased openness on south facing cones. To further support the results of the present study, and to eliminate other variables, more direct measurements of incident solar radiation would be essential. This could be accomplished using a solar radiation sensor or thermometer, with a logging device.

Distance between the canopy of each sample tree and its nearest neighbor was used as a secondary parameter to approximate incident radiation, as it was thought that radiation would increase as distance to nearest tree increased. Interestingly, canopy distance had no significant correlation with cone openness, but this may be explained. Each of the two trees samples only had one set each of north- and south-facing cones. Canopy distance was measured only once for each of these four sets. Therefore, each individual cone was paired with one of only four distances. This limited number of distances being compared with a relatively larger range of cone openness values reduces likelihood of statistical significance. Moreover, like aspect, canopy distance is an indirect way to measure incident radiation.

Tree dbh was not shown to predict openness. Again, this is quite an imperfect measurement of tree age; more accurate values could be obtained by using tree cores. Furthermore, analysis of this parameter was performed using tree dbh as a categorical variable (comparing one tree to the other), because only two trees were sampled. Thus, a t-test was used. If more trees were sampled and thus more dbh values were attained, it might make more sense to perform this test quantitatively using a regression model. It is not improbable that if actual tree age were used rather than the approximation, and if more trees were tested and analyzed via regression, statistically significant results could emerge.

Angle of attachment correlated slightly with cone openness. The reason for this may relate to seed predation. Benkman and Siepielski (2004) found that pine squirrels have a significant impact on diminishing the abundance of lodgepole pine cones. These squirrels are able to obtain seeds from serotinous cones (Benkman and Siepielski 2004). It may be that angles of cone attachment that best prevent seed predation are selected for as an additional adaptation in response to the coevolution of the pine trees and squirrels.

Alternatively, angle of attachment could correlate with openness because of incident sunlight. Certain angles of attachment of a cone may allow greater exposure to sunlight (Eitel, pers. comm.). If a particular tree has a predisposition for serotinous or nonserotinous nature, it may also select for certain angles of cone attachment to facilitate the amount of sunlight reaching each cone that is most conducive to achieving that condition. Angles of attachment varied from forty to seventy degrees in the present study. There is no statistically significant correlation according to a linear regression model conducted using Microsoft Excel software (r^2=0.03, p=0.24), but it is expected that if angle of attachment does depend in part on aspect, that it would also depend in part on the remainder of its three-dimensional location in space, such as the angle between the cone's branch and the ground. Conclusive statements about this potential relationship would require further research.

Lastly, the lack of correlation between the two techniques used to measure cone openness prevents definitive conclusions being drawn from this dataset alone. If the two techniques correlated, it could be reasonably argued that they are a good approximation of openness. Given the lack of relationship between the two, at least one of them must be faulty. Potential improvements on the techniques could include performing measurements for more than one row of scales. For the gap distance technique, a more consistent way of measuring the gap between two scales would be desirable (for example, perhaps measurements could be conducted from scale tip to scale tip). Using calipers instead of a millimeter ruler would also facilitate this process.

Many further questions arise. Additional, more direct methods of measuring incident radiation and tree age, with greater replication, would strengthen these analyses. Further exploration of the north/south aspect distinction would also be interesting and could also help determine whether aspect is, in fact, a usable approximation of incident radiation. It would be helpful to control or at least monitor humidity at each aspect to eliminate moisture as a secondary variable. Studies conducted earlier in the season, when cones are first produced, would be helpful in order to determine with certainty what serotiny habits are exemplified by which sample trees. Following cone openness throughout the course of a season seems like it would be especially valuable. Serotiny at the whole-tree level would be interesting to explore at different areas of Ponderosa State Park (not just the sagebrush meadow from which the samples examined here were taken) and could inform broader ecosystem studies regarding how serotiny in Ponderosa State Park correlates with disturbance history and how environmental and innate serotinous nature interact to affect cone openness.

Acknowledgements

Thanks are never enough, but much gratitude goes to my family and friends, to Dr. Jan Eitel for his guidance and encouragement during this project, to the MOSS grad team for their support and smiles, and to Elinor Israel for her camaraderie and friendship and for carrying the ladder back.

Works Cited

Anderson, M. D. (2003) Species: Pinus contorta var. latifolia. *Fire Effects Information*. <http://www.fs.fed.us/database/feis/plants/tree/pinconl/all.html>

Benkman, C. W. and A. M. Siepielski. (2004) A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology*, **85(8)**, 2082-2087.

Despain, D. G., D. L. Clark, J. J. Reardon. (1996) Simulation of crown fire effects on canopy seed bank in lodgepole pine. *International Journal of Wildland Fire*, **6(1),** 45-49.

Eitel, J. (December 5, 2012). Personal communication. McCall Outdoor Science School, McCall, ID.

Hellum, A. K. and N. A. Barker. (1980) Cone moisture content influences seed release in lodgepole Pinus Contorta var. Latifolia. *Canadian Journal of Forest Research*, **10(3)**, 239-244.

Knight, D. H. (1994) *Mountains and plains: the ecology of Wyoming landscapes*. Yale, New Haven, CT.

Lotan, J. E. and W. B. Critchfield. Lodgepole Pine. *USDA Forest Service Publications and Products*. <http://www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/contorta.htm>

Perry, D. A. and J. E. Lotan. (1997) *Opening temperatures in serotinous cones in lodgepole pine USDA Forest Service Research Note INT-228.* USDA, Intermountain Forest and Range Experiment Station, Ogden, UT.

R Development Core Team (2011). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Schoennagel, T., M. G. Turner, W. H. Romme. (2003) The influence of fire interval and serotiny on postfire lodgepole density in Yellowstone National Park. *Ecology*, **84(11)**, 2967-2978.

Smith, J. K. and W. C. Fischer. (1997) *Fire ecology of the forest habitat types of northern Idaho General Technical Report INT-GTR 363.* Rocky Mountain Research Station, Ogden, UT.

Tinker, D. B., W. H. Romme, W. W. Hargrove, et al. (1994) Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research*, **24(5)**. 897-903.

Figures

Figure 1: Cone openness prior to (top) and following (bottom) approximately five hours of incident radiation via a heat lamp. Lodgepole pine cones are the twelve smallest.

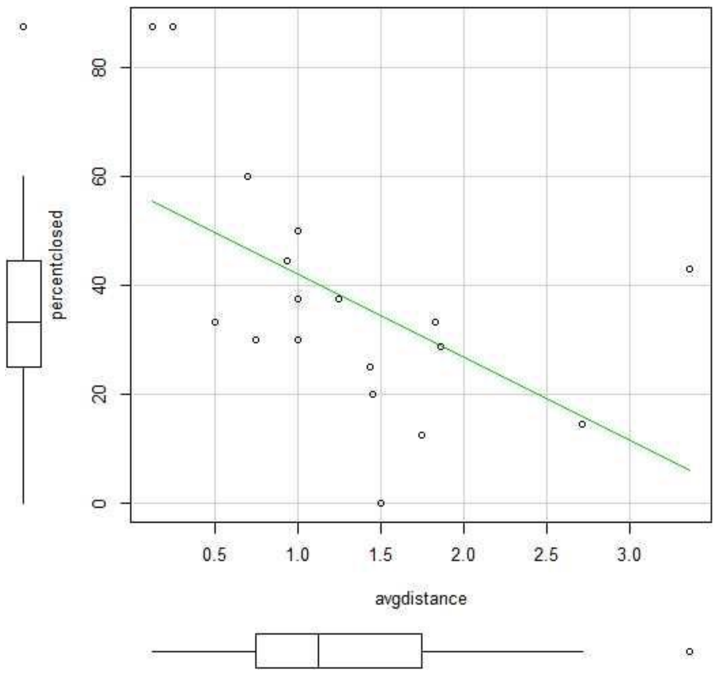

Figure 2: Comparison of two techniques for quantifying cone openness

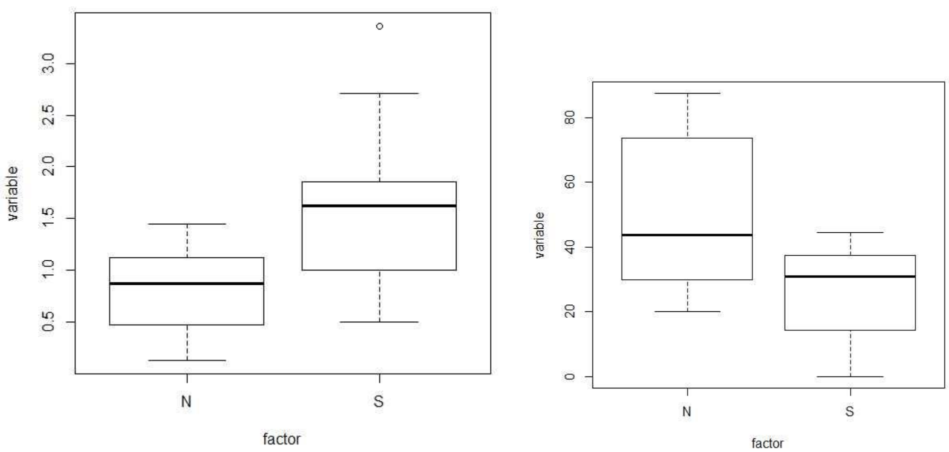

Figure 3: North and south aspect as a predictor of gap distance (left) and percent closed scales (right)

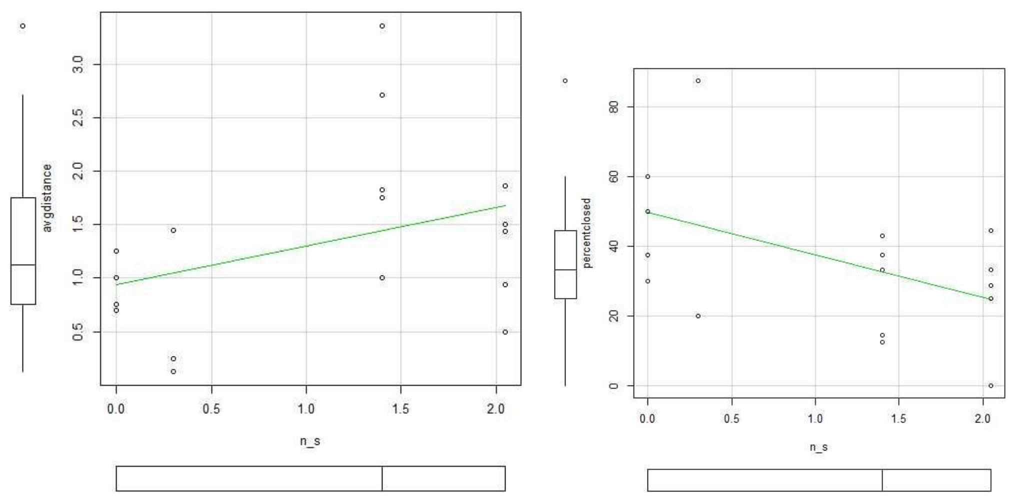

Figure 4: Canopy distance, as it correlates with gap distance (left) and percent closed scales (right)

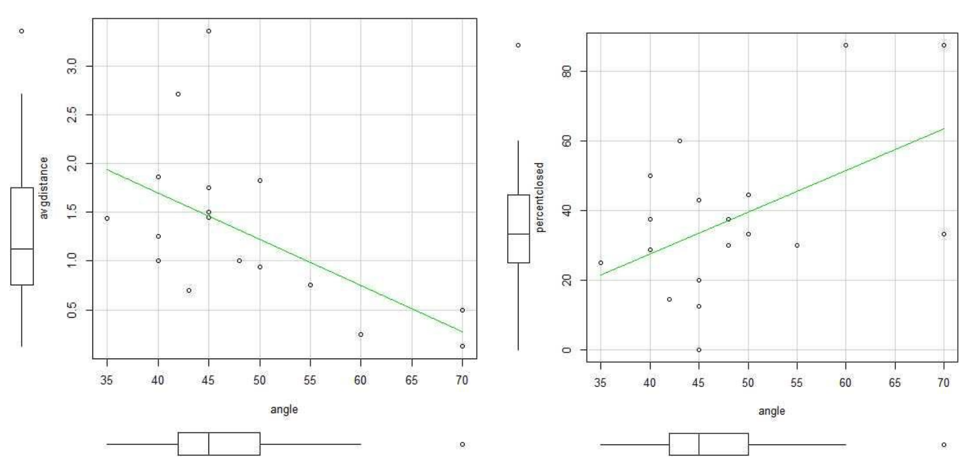

Figure 5: Angle of attachment, as it correlates with gap distance (left) and percent closed scales (right)

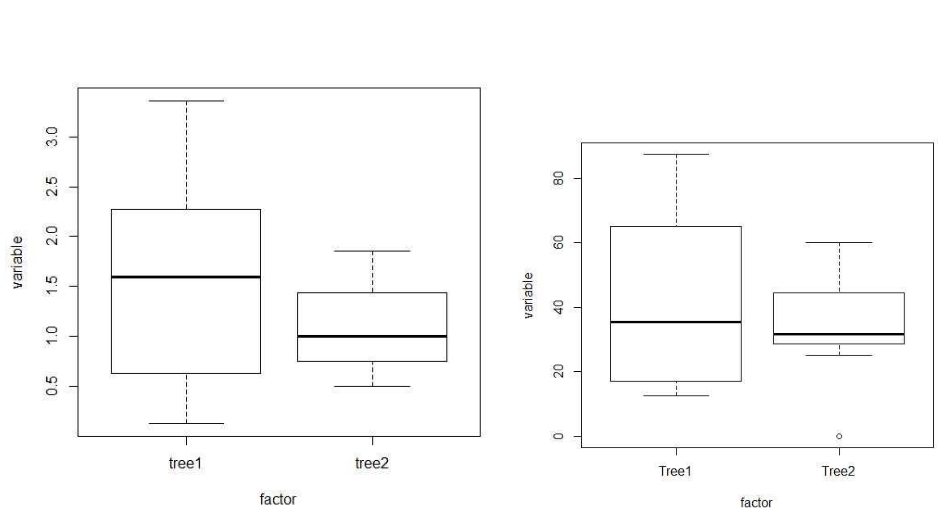

Figure 6: Diameter at breast height as a predictor of gap distance (left) and percent closed scales (right)