

Understory composition and thermal environments of Quaking aspen
(*Populus tremuloides*): implications for wildlife in a changing climate

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ABSTRACT

Climate predictions for the west predict warmer and drier environments in the future. I studied how understory composition and cavity temperatures in quaking aspen (*Populus tremuloides*; hereafter referred to as aspen) might change as a function of changing climates. We sampled 47 aspen stands and characterized understory composition. Results suggest that some plant species are more indicative of different aspen successional stages and were strongly associated with aspect and TWI (topographic wetness index). Aspen tree characteristics [diameter at breast height (DBH), canopy cover, orientation] and ambient temperature influenced maximum temperatures in tree cavities. Cavity microclimates can provide physiological advantages for optimal embryonic development (between 36°C and 40°C) but embryo mortality might occur at temperatures of > 40°C after a minimum of an hour of exposure. Approximately 13 % of the cavities were between 36°C - 40°C for a least one hour and ~ 8% were in this temperature range for more than an hour. A small proportion of cavities exceed temperatures above 40°C for at least an hour (<5%). Understanding the factors influencing tree cavities and understory composition, which supports a myriad of wildlife, can have broad implications in the context of changing climates.

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CHAPTER 1

ASPEN STAND AND UNDERSTORY COMPOSITION ALONG TOPOGRAPHICAL GRADIENTS

Abstract

Quaking aspen (*Populus tremuloides*) is experiencing a region-wide decline that is exacerbated on south facing aspects in the semi-arid regions of the western United States. Hydrological evidence suggests topography, such as elevation, landscape curvature, aspect and a topographical wetness index (TWI), can be used to understand the spatial distribution of plant species on the landscape. We used these topographic variables to identify aspen presence in two parks in southern Idaho and we found significant influences of elevation and aspect. We examined understory plant community composition in combination with these topographic variables to understand observed landscape patterns and relate them to changes in density of aspen stands, classified as regenerating, stable or declining. Multivariate analysis identified understory species composition along gradients related to TWI and aspect. Our analysis suggests that aspen is selecting for higher elevations (> 1970 m; $p < 0.001$) and cooler aspects (east; $p = 0.005$). In addition, results suggest that some understory plant species are more indicative of regenerating, stable, and declining stands. A holistic view of the aspen plant community may benefit management strategies by identifying which stands are potentially more vulnerable to climate induced drought based on understory species composition and stand characteristics.

Introduction

Aspen (*Populus tremuloides*; hereafter referred to as aspen) communities function as keystone habitat (Stohlgren et al. 1997) supporting some of the highest diversity of flora and fauna compared to surrounding habitat types (Hansen et al. 2000); however, it is experiencing a region-wide decline (Rehfeldt et al. 2009) in the western contiguous United States. Causes of this decline may be impacts of conifer encroachment, fire suppression, drought, and rapid die-off from SAD “sudden aspen decline” (Bartos 2001;

Worrall et al. 2008). Bioclimatic models show that within 50 years approximately 40% of western aspen stands may no longer have a suitable climate (Rehfeldt et al. 2009). Aspen populations in the south-western portion of its range are thought to be particularly vulnerable to climate change, and genetic analysis has shown these populations are thought to be the most valuable in terms of evolutionary potential and conservation value (Callahan et al. 2013). Beyond a general warming trend, changes in climate have also shifted areas from snow dominated precipitation regimes to rain dominated regimes (Nayak et al. 2010) in many areas. This loss of moisture through the growing season may cause aspen mortality and loss of stands since seed regeneration is thought to be unreliable in comparison to suckering in the West (Mitton and Grant 1996).

Topography influences the distribution of hydrological variation on the landscape (Sorensen et al. 2006). Patterns of hydrology have been used to characterize biological processes (White and Running 1994) and understand the spatial distribution of vascular plant communities, including their species diversity and composition (Zinko et al. 2005; Irl et al. 2015). For instance, drought tolerant plant communities are more often associated with arid environments whereas drought intolerant communities are associated generally with wetter environments (Peterson et al. 2014).

Climate change may exacerbate and compound existing stressors on plant communities such as fire, insects, pathogens, and invasive species (McKenzie et al. 2009). Furthermore, increasing temperatures, decreasing snowpack and prolonged droughts are creating multiple new patterns and trends on the landscape (Solomon et al. 2007). Understanding the processes and patterns of plant communities and their interactions with environmental gradients gives us a holistic approach to maintain or restore of ecosystems, such as aspen woodlands.

Plant communities that might be indicative of hydrological patterns can serve as indicators of climate change, which may include changes in rain accumulation, snow melt timing, etc. (Rogers et al. 2013). These indices provide a valuable tool for managers who are developing and implementing adaptation projects in response to resource sensitivity to climate change. Jimenez-Alfaro et al. (2014) identified that plant communities as whole entities were influenced by altitude but individual species were more influenced by local topographic variables such as the topographical wetness index, slope, and solar

radiation. The use of topography and other environmental variables influencing community-based ecology may allow managers to efficiently apply focused management decisions to support resilient ecosystems.

Measurements of understory composition can be correlated to wind and water erosion (Herrick et al. 2005) and may be indicative of potential changes seen through the aspen stand experiencing varying degrees of stress from drought. Drought-stressed aspen can become more vulnerable to secondary insects and disease agents that typically cause insignificant damage under normal conditions (Worrall et al. 2008). In Idaho, the climate models indicating temperature increases and moderate precipitation increases appears to be most pronounced in the Intermountain, Middle and Southern Rockies Ecoregions (Klos et al. 2014). Understanding the relationship between understory composition and environmental variables may help predict changes in aspen distribution and assist managers in early detection of health changes due to drought. Additionally, understory vegetation is an important component of wildlife forage and habitat. Understanding how understory vegetation might change can be important for ungulates and other species who are sensitive to the floristic composition of the understory for forage (Beck and Peek 2005).

To further explore topographic drivers of aspen habitat and understory composition we aim to 1) identify the topographic factors influencing aspen presence 2) classify understory plant community composition and identify the topographic variables influencing observed patterns on the landscape 3) identify the topographical influences on stands classified as regenerating, stable, or declining. Topographic variables will focus on those influencing hydrological processes (Sorensen et al. 2006) since water availability is an important mechanism influencing vegetation composition (Peterson et al. 2014). This study identifies the topographic niche selection of aspen and provides a reference point in the understanding of patterns and processes affecting understory plant distribution in stands. Results from this study might also allow for an evaluation of whether certain species might be indicators, such as *Thelypteris palustris* and *Symplocarpus foetidus* indicating wetland health (Adams and Gara 2013). Potential benefits to management strategies include the ability to determine which stands might be

potentially more vulnerable to climate induced drought based on topographic position, understory and stand characteristics.

Methods

Study area

We conducted our study in quaking aspen stands found in the Pioneer Mountains of Blaine and Butte County, Idaho (approximately 43° 27 N, 113° 37 W) and Albion Mountains of Cassia County (approximately 42°04 N 113°42 W) (Figure 1.1). Land ownership federal lands such as Craters of the Moon National Monument and Preserve (CRMO), and areas of joint management between state and federal lands such as City of Rocks National Reserve (CIRO).

The region is considered a high desert ecosystem (1300 – 2700 m) comprised of sagebrush steppe (*Artemisia* spp.) semi-arid lands, and mountain riparian areas. Common shrub species include mountain snowberry (*Symphoricarpos oreophilus*), western chokecherry (*Prunus virginia*), and wax current (*Ribes cereum*); common grasses include Idaho fescue (*Festuca idahoensis*), Sandberg bluegrass (*Poa secunda*), and basin wildrye (*Leymus cinereus*); and common perennial forbs include leafy aster (*Aster foliaceus*), lupine (*Lupinus* spp.) and arrowleaf balsamroot (*Balsamorhiza sagittata*). Tree species include Douglas-fir (*Pseudotsuga menziesii*) and limber pine (*Pinus flexilis*) at CRMO and singleleaf pinyon pine - juniper (*Pinus monophylla* and *Juniperus* spp.) in CIRO. None of the sampled stands were dominated by conifer species and conifers were absent or composed of seedlings or saplings in most stands where they were present.

Although CRMO is known for its large basaltic lava, the substrate where aspen grows is Paleozoic sedimentary rocks with fine to course textured soil that is either silt and/or sandy loams (Bell et al. 2009). CIRO, with its granite formations has a variety of soil types due to the on-going weathering of bedrock. A majority of the soils are Ola-rock outcrops and loamy course sand, which have low moisture retention (Erixson and Cogan 2011). The differences in geology and soil composition could potentially influence how ground water is absorbed, drained, and stored to be used by vegetation.

Typically, areas where aspen is located receive 40 cm and up to 100 cm of precipitation; however in the west, distribution is closely associated with snowpack that

produces run-off (DeByle 1990). It is important to note that the stands in both locations are characterized by low annual precipitation (360-490 mm typically in the form of snow fall during the winter months) which is at the lower range which supports aspen. Temperatures range from an average of 29°C (85°F) in July to an average low 7°C (19°F) in January (Bell et al. 2009; Erixson and Cogan 2011).

Aspen is an important resource to CIRO and CRMO because of its biological and aesthetic significance. Although aspen comprise only a small percentage of the land cover in the parks, the community type contributes significantly to species diversity and richness (Bartos 2001; Strand and Bunting 2010). These sites are important and potentially sensitive to climate change since the stands are located on the lower edge of the precipitation and evapotranspiration range required to maintain aspen, and several stands are likely subject to higher pressures from drought.

Field methods

For 41 aspen stands (0.32 – 6.6 ha in size; mean 1.2 ha), we conducted transects to identify and quantify understory vegetation from May through August 2015 and 2016. We selected stands identified by Strand et al. (2009) for the Upper Columbia Basin Network (UCBN) Aspen Monitoring Program. The UCBN have extensive aspen monitoring programs in both locations to identify the current status and long-term trends in aspen regeneration, conifer density, and aspen abundance. Plot locations, identified by permanent rebar markers from the UCBN monitoring plots, were used as starting points for transects (CRMO: n = 17; CIRO: n = 24).

To document plant community composition, we used long-term monitoring protocol (Herrick et al. 2005; Heady et al. 1959) to identify percent canopy cover, frequency, and percent basal cover of shrubs, forbs and grasses along 30 m line-point intercepts or transects. This method included plants ≤ 1 m in height; trees along the transect were recorded for frequency but do not accurately represent overstory canopy cover for the stand. We also determined the percent bare ground using this method, which can be related to wind and water erosion and water infiltration.

We further incorporated aspen stem count data (collected 2007 - 2016) from the UCBN Aspen Monitoring Program to understand how trees, at various life stages, were

interacting with understory composition. Trees, classified by Strand et al. (2009), quantified status and density (stems per ha) into four categories: suckering, regenerating, mature, and dead (Table 1.1). In this study, we categorized the stand regeneration status, as regenerating, stable, or declining based on sapling changes from 2007-2008 to 2015-2016. Regenerating stands are those that increase in saplings stem counts more than 500 stems per hectare; stable stands were those with ± 500 saplings per hectare; and declining stands had a decrease of 500 or more saplings over time. To explore if understory patterns or composition were different among these categories, the mean canopy cover of individual understory species was calculated.

Topographical calculations

To examine the response of vascular plant species patterns on the landscape, we used a raster DEM (grid size 10 m), derived from USGS to obtain environmental variables. We used ArcMap 10.3 (ESRI 2015) to identify elevation (m), aspect (cosine transformed; radians), curvature and a TWI (topographic wetness index; Jimenez-Alfaro et al. 2014; Sorensen et al. 2006) for each stand (Table 1.2). Curvature values were positive (convex surface), negative (concave surface) or zero (indicating a flat surface). TWI is based on the upslope area draining into the start point of the transect. We used Sorensen et al. (2006) recommendations to best capture the hydrological process on the landscape and have better predictions for plant species datasets. TWI values were relativized by maximum and ranged from 0 (low TWI) to 1 (high TWI). Because all aspen stands were situated within a relatively narrow range of precipitation and temperatures, we did not include climate variables in our analysis. Topographical variables were divided into three percentiles: low (lower 30th percentile), moderate, and high (upper 30th percentile) for curvature (-5.00 - -2.50; -0.49- 0.029; 0.03- 2.85), elevation (1700-1810 m; 1811-1970 m; 1971-2600 m) and TWI (0.00-0.133, 0.134-0.210, 0.211-1.00) for further evaluation.

Analytical procedures

To identify topographic variables indicative of aspen presence, we performed analysis on occupied versus available habitat within the study areas. Using ArcMap 10.3

(ESRI 2015), random points in stands (4 per stand; $n = 365$) and within the boundaries of the study sites ($n = 624$) were identified. Within the CRMO we included the wilderness area of the original monument and the western edge (managed by the Bureau of Land Management); this excluded the portion of the park dominated by lava fields where the establishment and maintenance of aspen is not likely. Comparisons of occupied versus available habitat was performed for topographic variables including curvature, elevation, aspect and TWI. A Chi-square test was conducted to evaluate significance.

The understory compositional patterns at each stand were summarized using nonmetric multidimensional scaling (NMS) in PC-ORD v. 6.22, (McCune and Grace 2002). We chose this ordination method because of the non-linearity of species community datasets. Species with fewer than 2 non-zeros were excluded from analysis, resulting in a matrix of 32 species in 47 stands. To reduce the number of species excluded, we lumped to genus when applicable, for example Lupinus (*L. argenteus* and *L. leucophyllus*) and Osmorhiza (*O. berteroi*, *O. chilensis*, and *O. occidentalis*). Environmental variables were relativized by maximum to reduce the influence of higher values associated with elevation. We followed McCune and Grace (2002) recommendations to use the Sorensen (Bray-Curtis) distance measure for the species ordination, and for comparison of environmental variables Euclidean distances was used. We conducted 500 runs (250 actual data, 250 random), stability was reached after 69 iterations. Starting coordinates were random numbers and the maximum number of iterations equaled 200.

To evaluate the differences between stands classified based on regeneration status (regenerating, stable and declining), aspen stems density and understory composition (data from 2015-2016) was analyzed using Multi-Response Permutation Procedures (MRPP) in PC-ORD v. 6.22 (McCune and Grace 2002). This method is a non-parametric multivariate test of differences between groups; groups included stand status (regenerating, stable or declining) and location. The effect size is defined by the p-value and the A statistic; when $A = 1$ sample units within the group are more homogenous; when $A = 0$ groups are more heterogenous than would be expected by chance. We also performed a multivariate analysis of variance (MANOVA; R Core Team (2015) to further determine if environmental variables influenced the stand status and understory

composition. Due to the possible influences of geology and soil composition, a MMRP and NMS was also performed to compare between locations.

Results

Elevation and aspect significantly influenced presence of aspen ($n = 988$, $X^2 = 71.49$, $p = < 0.001$; $X^2 = 15.12$, $p = 0.002$) (Figure 1.2). Differences in presence at mid-elevations were not observed; however, aspen was less likely to be present at lower elevations (< 1811 m; $p = < 0.001$) and increased likely presence at higher elevations (> 1970 m, $p = < 0.001$). Selection for east facing aspects ($p = 0.005$) and decreased presence on south facing aspects ($p = 0.05$) was observed. Although not significant to 0.05, less than expected by random presence was identified on west facing aspects ($p = 0.06$).

The use of topography, due to its influence on hydrology, can help identify moisture patterns influencing plant communities on the landscape. The NMS procedure found a significant (randomized test $p = 0.039$) two-dimensional solution with a final stress level of 11.53 after verifying consistency among several NMS solutions. The variance in the plant community data represented by NMS ordination was 54.9% (axis 1 = 38.9%; axis 2 = 16.0%) for the two dimensions (Table 1.3). The ordination of the species aligned to the TWI (axis 1) and aspect (axis 2) identifying both hydrological and solar radiation gradients (Figure 1.3). Plants associated with a lower TWI (topographically drier locations) on warmer aspects (south/west) included *Solidago canadensis* (SOCA6), *Koeleria macrantha* (KOMA), and *Osmorhiza* (OSMO). *Mahonia repens* (MARE11) was also found at higher cover levels on the warmer aspects (Table 1.4). Species such as *Poa pratensis* (POPR), *Veratrum californicum* (VECA2) and *Eleocharis palustris* (ELPA3) were found in areas of high TWI (topographically wetter locations; Figure 1.3). *Symphoricarpos oreophilus* (SYOR2) was abundant across TWI and aspect gradients (Table 1.4).

To understand the differences between the status of a stand (regenerating, stable, or declining) of the size classes, the MRPP confirmed plant community heterogeneity across the status types and indicate that there is no difference in plant community composition ($p = 0.232$; $A = 0.015$). Curvature was important as indicated by the MANOVA [highest significance was the combined product of curvature, aspect, and

elevation ($p = 0.005$) and second most significant was curvature ($p = 0.012$)]. These results continue to support that curvature is important for the maintenance of aspen but influences of tree class composition is complex. Grouping by stand status identified regenerating stands encompassing four understory species: *Veratrum californicum* (VECA2), *Juniperus scopulorum* (JUSC2), *Eleocharis palustris* (ELPA3), *Taraxacum officinale* (TAOF) (Figure 1.3). Stable stands occurred predominantly on north/east aspects and declining stands occurred towards the low TWI and warmer aspects (Figure 1.3). Mean canopy cover of understory plant species varied among stand status, aspect and TWI (Table 1.4).

The comparison between locations, due to different geology and soil composition, identified that the understory composition was found to influence by TWI and aspect (Table 1.4). The NMS procedure did not find a significant (randomized test $p = 0.019$) two-dimensional solution with a final stress level of 16.47 after verifying consistency among several NMS solutions. The variance in the plant community data represented by NMS ordination was 49.1% (axis 1 = 23.8%; axis 2 = 25.3%) for the two dimensions. The ordination of the species and locations aligned to TWI (axis 1) and aspect (axis 2) but the two sites did not overlap. The MRPP confirmed that there is no more heterogeneity within groups than expected by chance ($p = < 0.001$; $A = 0.146$).

Discussion

We identified decreased aspen presence in lower elevations and on south facing aspects; while selecting for higher elevations and east facing aspects in CRMO and CIRO. This may not hold true for all locations where aspen is found. On the northern edge of aspens distribution, Whitebeck et al. (2016) identified greater abundances on south facing aspects with increasing latitude in Canada. Although latitude effects temperature and photo period, topographical features in the southern distribution may be providing a similar microclimate for the persistence of aspen in this area. Topography influences hydrological sources for aspen and include surface water, for example springs and ground water, and snow which influence stand growth (Sorenson et al. 2006; Peterson et al. 2014). Warming climate trends, influencing the duration of snow fall may cause water limitations during the latter part of the growing season (Kirkey 2014). Stands

of potential concern in semi-arid regions are ones receiving moisture during the dry season from snow-melt. Cessation or decline of spring/summer snow-melt could inhibit growth and regeneration of stands. Snow may persist longer in areas of increased topographic curvature, higher elevations, and cooler aspects (north and east).

The influence of topography, especially TWI and aspect, on understory species within aspen stands can improve our understanding of responses to climate change. The ordination axes explained 54.9% of the variation in the data, which was correlated with TWI and aspect. Although no understory species were found exclusively on south and west aspects, the mean canopy cover for these species was lower on the warmer aspects (Table 1.4). Plants on these warmer aspects are subject to higher solar radiation thus increasing evapotranspiration rates (Worrall et al. 2008). The mean canopy cover on south-west aspects could be an indicator for stands experiencing moisture stress and be more vulnerable to climate induced drought (Worrall et al. 2013). Plant communities associated with increased wetness could be used as an indicator since these locations have been correlated with aspen growth (Hogg et al. 2005). Decreased wetness with the combination with increased temperatures may limit aspen longevity and distribution (Hogg et al. 2008; Rehfeldt et al. 2009).

When addressing the overall stand status there was no significant difference in plant community composition between stands classified as regenerating, stable or declining. This may be due to the cyclic nature of stand development in aspen where rapid natural thinning periodically occurs causing a surge in mortality that is disproportionate to the number of trees in the stand and is later replaced by sucker growth (DeByle 1990). Rogers et al. (2010) observed differences in regeneration of stable stands but overall, they identified a lack of systematic monitoring in these types of stands. Systematic monitoring of aspen stands has been implemented in CRMO and CIRO (Strand et al. 2009) where stem density by size class is measured every five years. Such a monitoring effort will likely shed light over the long-term relationship between stand structure and regeneration and potentially result in a better understanding of the cyclic stand development.

The different study locations were associated with a distinct pattern of plant species on the landscape that were influenced by the TWI and aspect. Although there was

some overlap between the locations, there was a defined difference between the study locations which could be due to the distinctive geology and soil composition in those locations. Craters of the Moon with its silt and/or sandy loams soils and basalt geomorphology, may have increased absorption rates which may contribute to the site difference observed. Vegetation can also influence the flow of water over the landscape and absorption rates into the soil.; however, canopy cover and species density (based on root masses) were not compared between the two locations.

Climate change is expected to profoundly alter structure and composition of vegetation (Peterson et al. 2014) which may influence wildlife habitat and forage availability. Aspen communities provide critical food and cover resources for wildlife. It is an important habitat for a variety of species of special interest, including ruffed grouse (*Bonasa umbellus*; Kouffeld et al. 2013), elk (*Cervus elaphus*; Beck et al. 2013), and a variety of other ungulates. Seasonal forage of forbs, grasses and shrubs are used by elk, mule deer (*Odocoileus hemionus*; Beck and Peek 2005), and moose (*Alces alces*; Hilde and Hjeljord 2010). Preferred forage for ungulates include *Amelanchier alnifolia* (Stewart et al. 2011), *Lupinus* species (Beck and Peek 2005), and *Poa* species (Stewart et al. 2002). Aspen is particularly important winter forage for elk and connectivity of aspen landscapes may be important for maintaining high quality movement corridors for elk migrations (Kirkey 2014). Our research indicates that areas with higher TWI on north and east facing slopes may be more receptive to adaptive management actions and provide a greater impact on wildlife in semi-arid regions.

In addition to aspect and TWI, considerations of genetic variability might influence the focus of management objectives. Higher levels of genetic variation have been found in the south-western distribution of aspen (Callahan et al. 2013). Although more isolated, these stands collectively may represent the greatest amount of genetic diversity and have adaptive traits not found in the remainder of the range (Callahan et al. 2013). In these drier climates, this variation may contribute to the species ability to form large clones (asexual reproduction) where seed dispersal (sexual reproduction) is considered rare; as opposed to mesic areas where sexual reproduction is more prevalent (Mitton and Grant 2005, Long and Mock 2012; Callahan et al. 2013). Stands in the south-western region (Callahan et al. 2013) could potentially provide managers with seed

sources for aspen genetically suited for responding to major disturbances and future climates.

It is a challenge to foster resilient, diverse, and adaptive ecosystem management approaches in response to climate change. For aspen monitoring, focus has been on aspen stand structure and abundance at the individual plot and stand level. This study augments efforts by including the understory plant community composition for these stands with an understanding of how environmental variables affect their distribution on the topographically variable landscape. Factors influencing understory plant composition will be important as climate change continues to influence aspen woodland communities. If aspen can no longer maintain dominance in a stand because of changes in climate conditions, a different species will occupy the upper canopy, such conversion would be expected to occur on a stand by stand basis. Dominant species are those that are successfully competing for resources, such as moisture and light, and often exhibit high canopy cover and deeper root systems (Barbour et al. 1999). Identifying the understory plant community can provide managers insight on what vegetation may take the place of aspen on a stand by stand basis in a changing climate. For example, if sagebrush is dominant in the understory and in surrounding areas, conversion to sagebrush steppe could be likely; whereas conversion to a mesic shrubland could be expected if mountain snowberry or western chokecherry is the dominant species present. Conversion to a conifer woodland could be expected if conifers are expanding into and becoming dominant in the aspen stand.

We find that plant communities in aspen organize along hydrological and solar radiation gradients within the two parks we studied. In the semi-arid western mountains, aspen is sensitive to water limitations but may be more likely to persist in areas of concave curvature and cooler aspects to overcome this. An approach that fosters holistic understanding of plant community assemblages, their relationship to environmental conditions and natural processes may better prepare decision making for the preservation of our valued ecosystems.

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Figure 1.1 Location of Craters of the Moon National Monument and Preserve (CRMO; north) and the City of Rocks National Reserve (CIRO; south) in the state of Idaho, U.S.A.

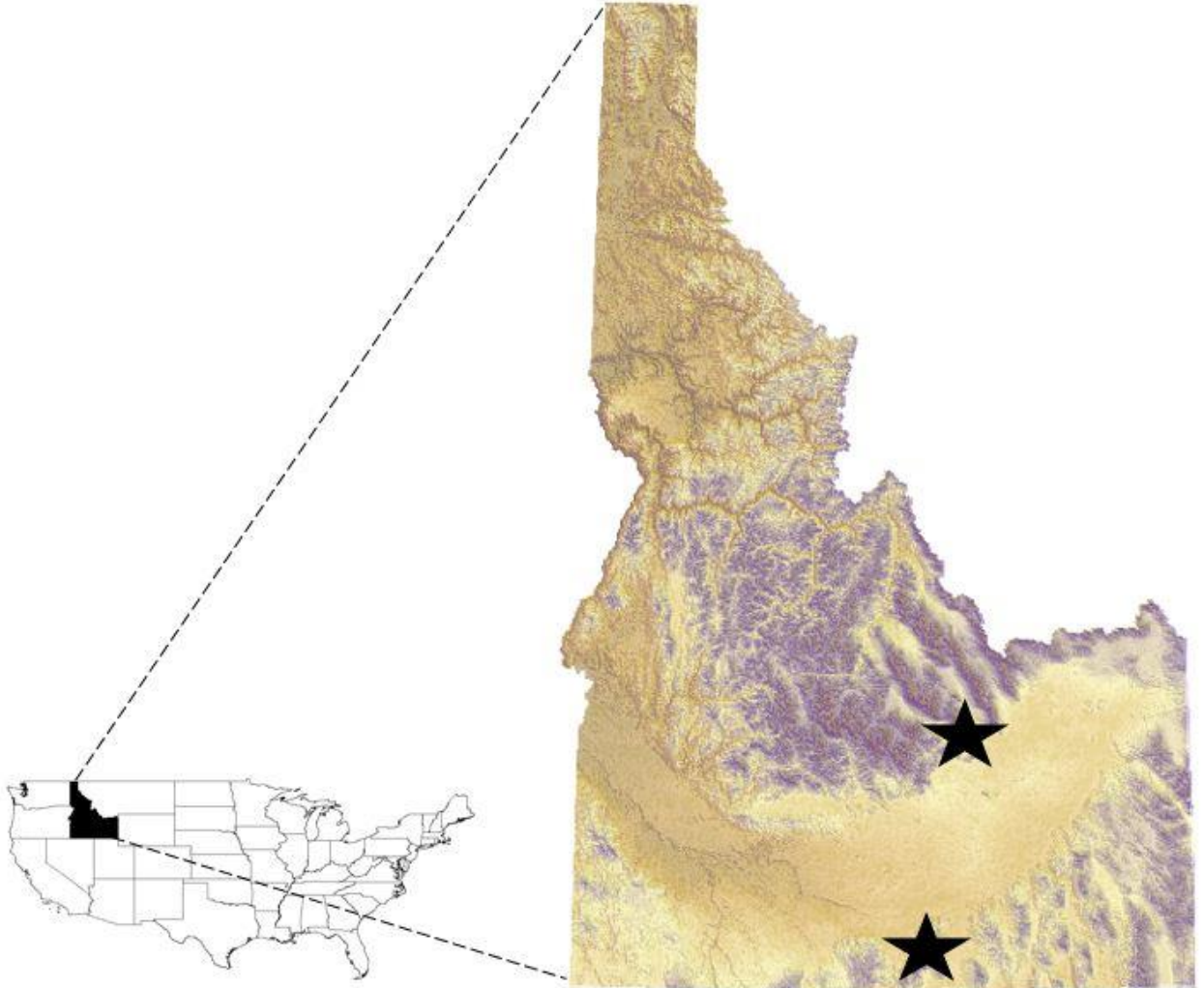


Figure 1.2 Proportional occupancy of aspen stands, compared to random samples in the study area, with regards to landscape curvature, elevation, topographic wetness index (TWI) and aspect. Significant differences at $p=0.05$ are marked with an asterisk (*).

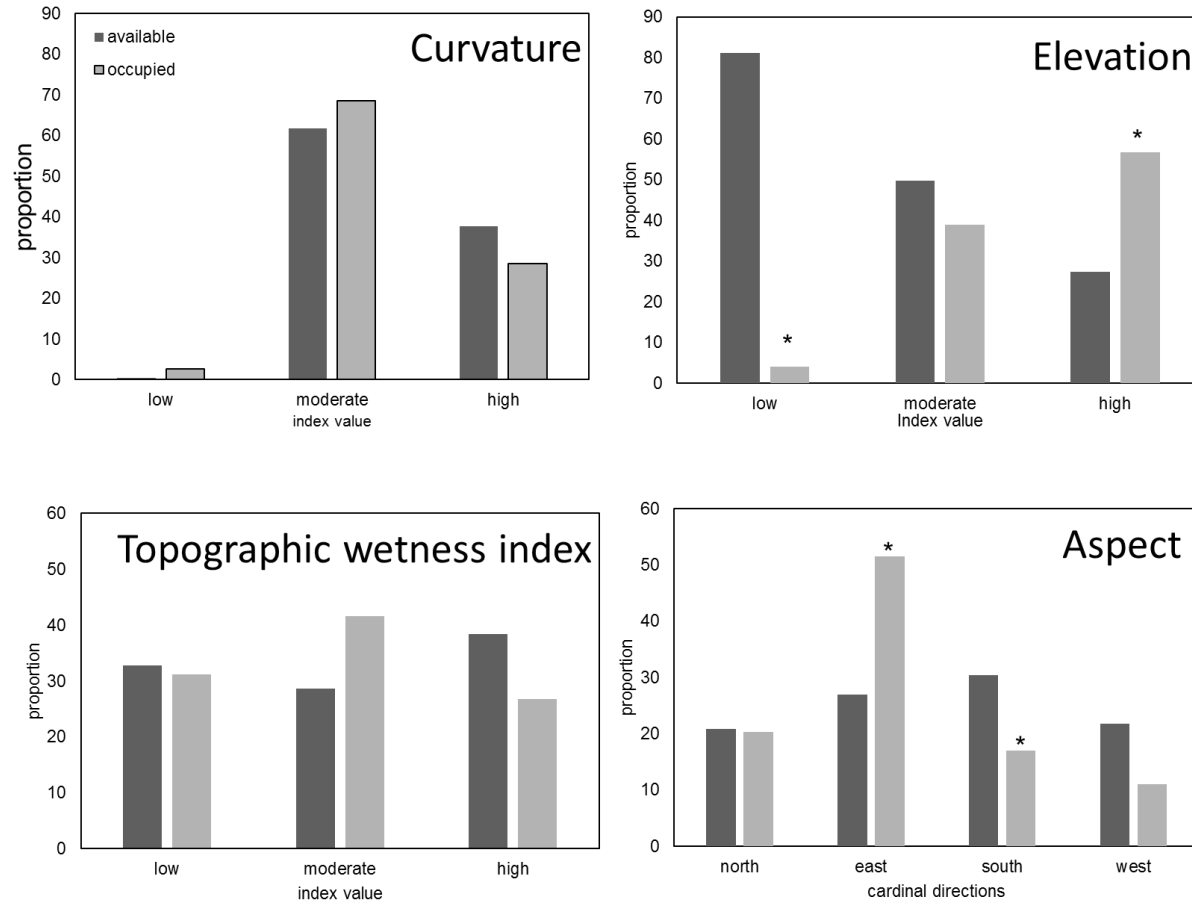


Figure 1.3 Display of the two-dimensional solution produced by the Nonmetric Multidimensional Scaling (NMS) gradient analysis. Axis 1 correlates with moisture (the topographic wetness index; TWI) and axis 2 correlates with aspect as indicated by the vectors in red; the two axes explain 54.9% of the variation in the data. Polygons indicate the regeneration stand status, 1=regenerating, 2=stable, 3= declining. See Table 1.4 for species codes.

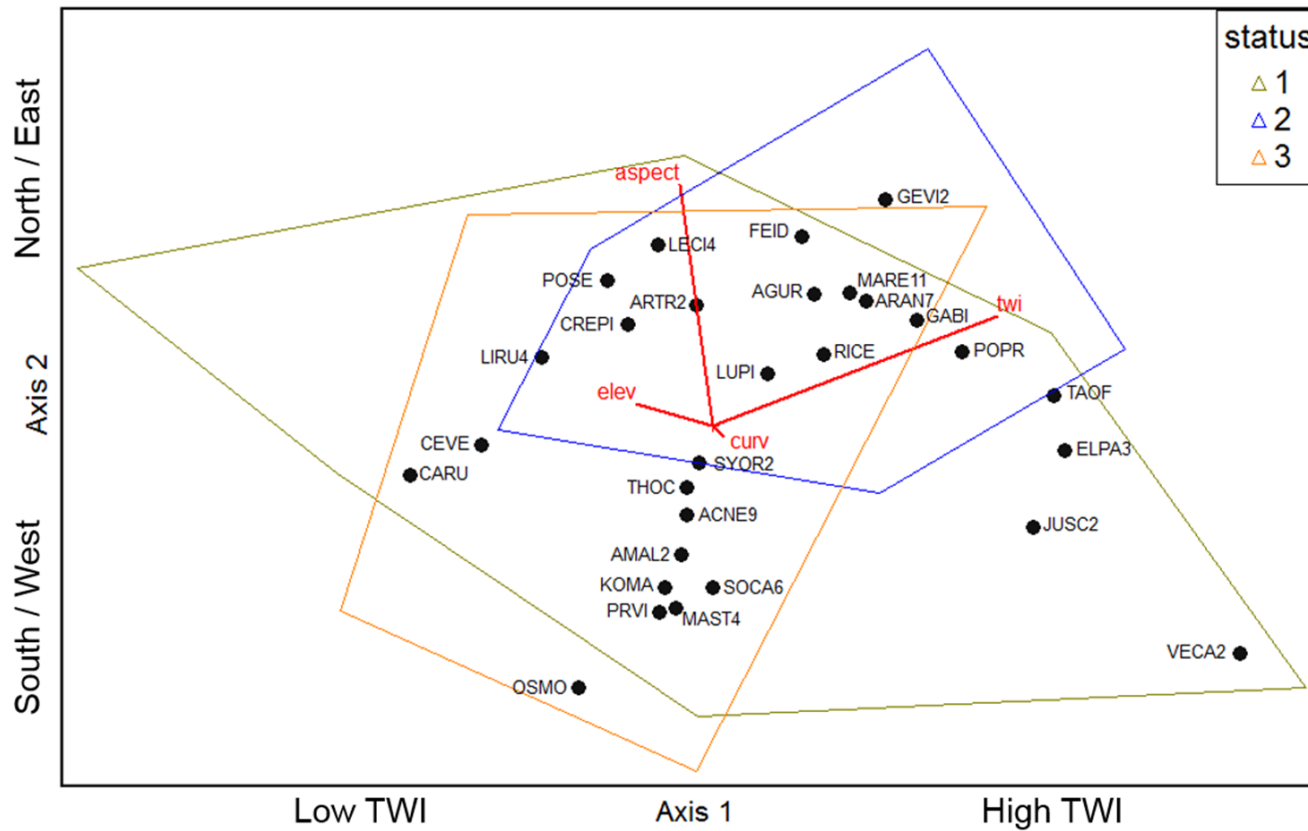


Figure 1.4 Display of the two-dimensional solution produced by the Nonmetric Multidimensional Scaling (NMS) gradient analysis. Axis 1 correlates with moisture (the topographic wetness index; TWI) and axis 2 correlates with aspect as indicated by the vectors in red; the two axes explain 49.1% of the variation in the data. Polygons indicate the two study locations, 1= City of Rocks National Reserve, Idaho, 2= Craters of the Moon National Monument and Reserve. See Table 1.4 for species list. codes.

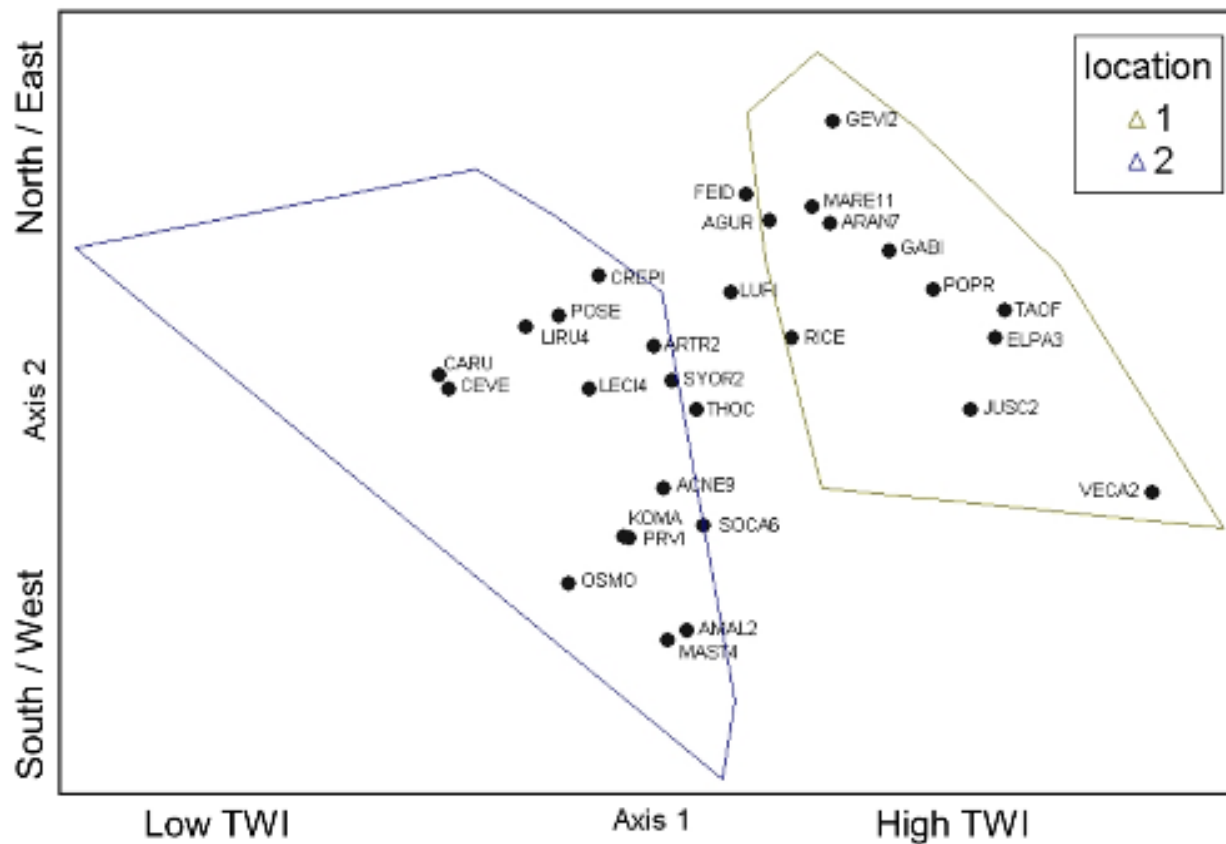


Table 1.1 Size classes of aspen from the Upper Columbia Basin Network Aspen Monitoring Program for Craters of the Moon National Monument, Idaho and City of Rocks, Idaho, U.S.A.

Class	Description
Suckers	Suckers or seedlings < 152 cm (5 ft) tall. A sucker is an aspen shoot originating from vegetative sprouting from another aspen tree.
Regeneration	Trees greater than 2.5 cm (1 inch) in diameter at breast height (dbh) and shorter than 75% of the stand height
Mature	Trees greater than 2.5 cm (1 inch) in dbh and taller than 75% of the stand height
Dead	Dead stems > 2.5 cm (1 inch) in dbh

Table 1.2 Description of parameters used to examine understory composition in Pioneer and Albion Mountains, Idaho, U.S.A. 2015-16.

Variable	Parameter	Description/ Hypothesized association with hydrological processes
Canopy cover	USDA species code	% canopy cover Species specific hydrological requirement
Elevation	Elev	m / Higher values retain snow longer
Aspect	Asp	radians; cosine transformed /North facing would retain snow longer
Curvature	Curv	radians per meter *100 Negative values (convex topography) would retain moisture
Topographic Wetness Index	TWI	$\ln(\text{flow accumulation}/\tan(\text{slope}))$ high values (higher accumulation rates with gentler slopes) would retain more moisture

Table 1.3 The pattern of understory composition in relation to environmental variables where 54.9% of the variation is explained by both Axis 1 (TWI) and Axis 2 (Aspect). The R^2 provides the explanatory power of the Axes.

	Axis 1	Axis 2
R^2	0.389	0.160
Curv	0.041	-0.024
Asp	-0.078	0.221
Elev	-0.125	0.065
TWI	0.240	0.148

Table 1.4 Species list for Pioneer and Albion Mountains, Idaho, U.S.A. 2015-16. The mean canopy cover and standard error is identified for each species for stand status, aspect and TWI. Stand status includes regenerating (stands that increased in saplings stem counts > 500 stems per hectare), stable (\pm 500 saplings per hectare), and declining (decrease of 500 or more saplings). Aspect is identified as N/E (north and east) and S/W (south and west). TWI [topographic wetness index; $\ln(\text{flowacc}/\tan(\text{slope}))$] is categorized as low (L; lower 30 percentile), moderate (M) and high (H; higher 30 percentile).

Code; Scientific name	Stand status			Aspect		TWI		
	Regenerating	Stable	Declining	N/E	S/W	L	M	H
ACNE9; <i>Achnatherum nelsonii</i>	1.78(1.12)	0.00(0.00)	3.33(1.60)	2.18(0.91)	2.22(2.22)	3.00(1.68)	1.48(0.01)	2.05(1.53)
AGUR; <i>Agastache urticifolia</i>	0.00(0.00)	0.83(0.83)	0.51(0.35)	0.34(0.19)	0.00(0.00)	0.33(0.33)	0.00(1.13)	0.51(0.35)
AMAL2; <i>Amelanchier alnifolia</i>	0.44(0.30)	0.83(0.83)	2.31(1.82)	1.15(0.81)	2.22(2.22)	1.33(0.74)	2.96(1.48)	0.00(0.00)
ARAN7; <i>Argentina anserina</i>	0.67(0.48)	0.00(0.00)	0.51(0.35)	0.46(0.27)	1.11(1.11)	0.67(0.44)	0.37(0.98)	0.51(0.51)
ARTR2; <i>Artemisia tridentata</i>	2.44(1.24)	4.16(3.15)	0.00(0.00)	1.84(0.79)	0.00(0.00)	3.33(1.79)	0.00(0.00)	1.54(1.04)
CARU; <i>Calamagrostis rubescens</i>	6.44(4.35)	12.49(9.46)	15.88(6.38)	12.17(3.78)	0.00(0.00)	7.99(4.87)	14.06(0.37)	11.27(5.86)
CEVE; <i>Ceanothus velutinus</i>	0.67(0.67)	0.00(0.00)	0.77(0.77)	0.69(0.48)	0.00(0.00)	1.00(1.00)	0.00(0.00)	0.77(0.77)

<i>CREPI;</i> <i>Crepis acuminata</i> <i>Crepis intermedia</i>	0.22(0.22)	0.83(0.83)	0.26(0.26)	0.23(0.16)	1.11(1.11)	0.33(0.33)	0.74(0.00)	0.00(0.00)
<i>ELPA3;</i> <i>Eleocharis palustris</i>	1.33(0.78)	1.67(1.67)	0.26(0.26)	1.03(0.47)	0.00(0.00)	1.00(0.71)	0.37(0.00)	1.28(0.89)
<i>FEID;</i> <i>Festuca idahoensis</i>	2.00(0.91)	12.49(4.59)	9.48(4.38)	6.55(2.18)	4.44(4.44)	3.00(1.95)	8.88(0.49)	7.17(2.16)
<i>GABI;</i> <i>Galium bifolium</i>	0.67(0.48)	0.00(0.00)	0.51(0.51)	0.34(0.25)	2.22(2.22)	0.67(0.67)	0.74(0.37)	0.26(0.26)
<i>GEVI2; Geranium</i> <i>viscosissimum</i>	0.00(0.00)	0.00(0.00)	0.51(0.35)	0.11(0.11)	1.11(1.11)	0.33(0.33)	0.37(0.00)	0.00(0.00)
<i>JUSC2;</i> <i>Juniperus scopulorum</i>	4.00(1.73)	3.33(1.92)	0.00(0.00)	2.53(0.97)	0.00(0.00)	3.00(1.60)	1.48(0.00)	2.31(1.57)
<i>KOMA;</i> <i>Koeleria macrantha</i>	0.67(0.67)	0.00(0.00)	0.77(0.41)	0.34(0.19)	3.33(3.33)	0.00(0.00)	1.85(0.49)	0.26(0.26)
<i>LECI4;</i> <i>Leymus cinereus</i>	4.22(3.16)	0.83(0.83)	0.26(0.26)	2.30(1.65)	1.11(1.11)	5.99(4.70)	0.74(0.37)	0.26(0.26)
<i>LIRU4;</i> <i>Lithospermum ruderale</i>	1.55(1.17)	1.67(1.67)	0.00(0.00)	1.03(0.64)	0.00(0.00)	1.67(1.67)	0.74(0.00)	0.51(0.51)
<i>LUPI;</i> <i>Lupinus argenteus</i> <i>Lupinus leucophyllus</i>	0.22(0.22)	5.00(2.15)	0.77(0.55)	0.92(0.43)	2.22(2.22)	1.00(1.00)	1.11(0.74)	1.02(0.58)
<i>MARE11;</i> <i>Mahonia repens</i>	0.44(0.44)	0.00(0.00)	2.05(1.10)	0.80(0.46)	3.33(3.33)	0.67(0.67)	1.11(6.16)	1.28(0.89)
<i>MAST4;</i> <i>Maianthemum stellatum</i>	0.00(0.00)	0.00(0.00)	0.77(0.41)	0.23(0.16)	1.11(1.11)	0.33(0.33)	0.37(0.37)	0.26(0.26)

<i>OSMO;</i> <i>Osmorhiza berteroi</i> <i>Osmorhiza chilensis</i> <i>Osmorhiza occidentalis</i>	1.11(1.11)	0.00(0.00)	1.02(0.79)	0.92(0.66)	1.11(1.11)	1.33(1.02)	1.85(1.11)	0.00(0.00)
<i>POPR; Poa pratensis</i>	9.32(4.54)	8.33(5.00)	9.22(4.62)	9.88(3.09)	2.22(2.22)	7.33(3.54)	1.85(0.00)	15.63(6.03)
<i>POSE; Poa secunda</i>	0.89(0.69)	0.83(0.83)	1.54(0.72)	1.15(0.48)	1.11(1.11)	1.33(1.02)	0.74(0.00)	1.28(0.71)
<i>POTR5;</i> <i>Populus tremuloides</i>	NA	NA	NA	NA	NA	NA	NA	NA
<i>PRVI; Prunus virginia</i>	1.11(0.90)	0.83(0.83)	0.51(0.35)	0.80(0.49)	1.11(1.11)	0.00(0.00)	2.22(0.00)	0.51(0.35)
<i>RICE; Ribes cereum</i>	1.55(0.79)	2.50(1.59)	1.54(1.11)	1.84(0.65)	0.00(0.00)	2.00(1.13)	0.00(0.00)	2.56(1.14)
<i>SOCA6;</i> <i>Solidago canadensis</i>	2.44(1.24)	4.16(2.50)	2.56(1.89)	1.61(0.61)	13.32(6.93)	4.66(2.39)	2.59(1.25)	1.28(0.89)
<i>SYOR2;</i> <i>Symphoricarpos</i> <i>oreophilus</i>	8.88(2.81)	18.32(4.81)	7.17(2.47)	8.84(1.73)	14.43(11.27)	5.66(2.63)	10.73(0.00)	11.27(2.86)
<i>TAOF;</i> <i>Taraxacum officinale</i>	0.89(0.61)	0.00(0.00)	0.00(0.00)	0.46(0.32)	0.00(0.00)	0.67(0.67)	0.00(0.00)	0.51(0.51)
<i>THOC;</i> <i>Thalictrum occidentale</i>	0.00(0.00)	0.00(0.00)	1.54(0.89)	0.69(0.42)	0.00(0.00)	0.00(0.00)	0.37(0.11)	1.28(0.89)
<i>VECA2;</i> <i>Veratrum californicum</i>	1.55(1.17)	0.00(0.00)	0.00(0.00)	0.80(0.61)	0.00(0.00)	0.00(0.00)	1.85(0.74)	0.51(0.51)

CHAPTER 2
THERMAL ENVIRONMENTS WITHIN TREE CAVITIES OF QUAKING
ASPEN (*POPULUS TREMULOIDES*) DURING SUMMER:
IMPLICATIONS FOR BREEDING BIRDS

Abstract

Selection for optimal cavity microclimates can influence species using those cavities during the summer. Although species specific, temperatures providing physiological advantages for embryonic development and optimal development are provided for through incubation and cavity microclimate. Our study aimed to identify the environmental variables influencing the thermal microclimate (i.e. temperature) during the breeding season in aspen tree cavities created by woodpeckers in the Middle Rockies ecoregion. We examined how environmental variables, tree, and cavity characteristics might influence 1) maximum cavity temperatures, 2) the amount of time a cavity exceeds temperatures $\geq 26^{\circ}\text{C}$ and $\geq 36^{\circ}\text{C}$, and 3) the temperature differences between a cavity and external environment within a twenty-four-hour period. The two top competing models explaining the maximum cavity temperatures included tree diameter, canopy cover, cavity orientation, and ambient temperature. Warmer cavities were positively associated with warmer ambient temperatures, SW facing cavities, low canopy cover, and smaller diameter at breast height. Ambient temperature alone was the top model for the number of hours a cavity was $\geq 26^{\circ}\text{C}$ ($p < 0.001$) and $\geq 36^{\circ}\text{C}$ ($p < 0.001$). The global model best explained the temperature difference between the external environment and the cavity. Cavities that experiences more fluctuation in temperature were negatively associated with canopy cover, cavity volumes and the area of cavity entrance. Because cavities in aspen are an important resource for multiple species, understanding the factors that influence the microclimate of tree cavities can have broad implications for cavity using species in the context of changing climates.

Introduction

Tree cavities are an important resource used by at least 100 species of vertebrates in western North America (e.g. Aitken and Martin 2007). Tree cavities are used at various times by birds and other animals throughout the year for roosting sites, and breeding sites (Boyles 2007). Cavity selection has been thought to provide favorable microclimates for physiological advantages and increased fitness (Conway and Martin 2000, Boyles 2007, Wiebe 2010). Due to the multiple uses of cavities by different species, variation in available microclimates and longevity of cavities is important.

The thermal environment within a cavity can both positively and negatively influence species using those cavities during the breeding season. The temperature thresholds which may negatively influence animals can vary by species but there are critical upper bounds that adversely affect either the adult or the embryo (Conway and Martin 2000). Depending on the duration of exposure, this can influence embryo survival and/or cause the adult to change its behavior (e.g. relocate and/or abandon the nest/den) for its own survival (Webb 1987). Since breeding typically occurs for most cavity dwelling species in the late spring and early summer, individuals are most likely responding the maximum ambient and cavity temperatures. This may be due to the influence of temperature on processes such as embryonic development which can be sensitive to temperature thresholds that are surpassed or maintained for extended periods (Webb 1978). The process at which initiation or resumption of embryonic development occurs is defined as physiological zero, and this occurs between 24°C and 26°C for most bird species as identified by Reyna and Burggren (2012) in nest box studies. Lundy (1969) identified optimal development for chickens occurring between 36°C and 40°C; however, at upper lethal temperatures (e.g. >40°C), Webb (1987) identified the occurrence of developmental malformations and death in some bird species.

Although negative effects of increased temperatures are possible, avian studies have shown that temperature within specific ranges can positively influence egg development (Webb 1987), nestling growth rates (Quinney et al. 1986) and energy consumption of nestlings (Webb and King 1983). Recent studies have shown that individuals select for cavities with stable and moderate thermal regimes (Rhodes et al. 2009, Robertson 2009). This was closely associated to tree health, diameter at cavity height, cavity orientation

(Coombs et al. 2010, Wiebe 2001) and entrance width (Rhodes et al. 2009). Multiple studies have also indicated that ambient temperature strongly affect the internal temperatures of tree cavities (Coombs et al 2010, Clement and Castleberry 2013).

Bioclimatic models are predicting temperature increases in the Northwest (Mote et al. 2014) and shifts from snow dominated to rain dominated regimes (Nayak et al. 2010) thus increasing the importance of understanding the factors influencing tree cavity microclimates. In Quaking aspen (*Populus tremuloides*; hereafter referred to as aspen), up to 10% of mature stands in the West, are dying with no apparent regeneration in the form of suckering (Strand and Bunting 2010). Bioclimatic models predict that within 50 years approximately 40% of western aspen stands will no longer have a suitable climate (Rehfeldt et al. 2009). Several studies support the idea that aspen communities function as a keystone habitat in that they contribute disproportionately to the biological diversity (Stohlgren et al. 1997, Bartos 2001). The diversity associated with aspen stands is due in part to woodpeckers which excavate cavities that might be used by opportunistic species (Bunnell 2013).

Because cavities in aspen are an important resource for multiple species, understanding the factors that influence the microclimate of tree cavities can have broad implications for cavity users in the context of changing climates. Wiebe (2001) identified that orientation of the cavity, diameter at cavity height, and tree health were the best predictors of stability and maximum temperatures experienced in the cavity. Studies of aspen microclimate are limited but it is assumed that the thermal environment is an important component associated with cavity selection since nest cavity characteristics have been positively associated with increased survival and reproductive success. From these studies, we can infer that wood hardness (Lorenz et al. 2014) of live aspen trees (Dobkin et al 1995) with large DBHs (Dobkin et al. 1995, Edworthy et al. 2012) are selected for by cavity dwelling species to ensure the longevity of the cavity structure (Edworthy et al. 2012), presumably to promote survival and reproductive success (Dobkin et al 1995, Wiebe 2001, Lorenz et al 2014).

The objective of this study is to identify the environmental variables influencing the thermal microclimate (i.e. temperature) of aspen tree cavities created by woodpeckers in the Middle Rockies ecoregion. This study will focus on the breeding season (June -

July) and we will examine how environmental variables might influence 1) maximum cavity temperatures, 2) the amount of time a cavity exceeds temperatures $\geq 26^{\circ}\text{C}$, and $\geq 36^{\circ}\text{C}$, and 3) the temperature differences between a cavity and external environment within a twenty-four-hour period. These temperature thresholds were chosen to modestly represent physical zero affecting embryonic development (26°C) and the lower limit for optimal development (36°C). Specifically, we aim to 1) identify how the role of tree, cavity and wood hardness characteristics influence cavity temperatures, and 2) quantify the proportion of cavities on the landscape that are experiencing different temperatures thresholds (26°C and 36°C) during the same time period.

Methods

Study area

We conducted our study in 2015 in quaking aspen stands found in the Pioneer Mountains of Blaine and Butte County, Idaho (approximately $43^{\circ} 27' \text{N}$, $113^{\circ} 37' \text{W}$). Land ownership included private lands managed by Lava Lake Land and Livestock ranch and federal lands which included Craters of the Moon National Monument (Figure 2.1). The region is considered a high desert ecosystem comprised of large basaltic lava fields, sagebrush steppe (*Artemisia* spp.) arid lands, and mountain riparian areas. Aspen was dominant, but other important plant species included douglas-fir (*Pseudotsuga menziesii*), mountain snowberry (*Symphoricarpos oreophilus*), and western chokecherry (*Prunus virginia*). Low annual precipitation of 380-510 mm, typically in the form of winter snows, characterizes the climate. Temperatures range from an average of 29.4°C (84.9°F) in July to an average low of -7.2°C (19°F) in January (Bell et al. 2009).

Field methods

Within 47 aspen stands (0.32 – 6.6 ha; mean 1.2 ha), we searched for cavities from June through August, 2015. We conducted cavity surveys by walking in parallel and perpendicular transects 30m apart every 7-10 days to identify excavated aspen tree cavities. Cavities were marked with a GPS, and DS1921G Thermochron iButtons were used to record temperatures. To reach the cavities, an extendable ladder was used, but if cavities were unsafe due to height and/or terrain, these cavities were excluded from the

study. The data loggers were calibrated to record temperature at 1 hour intervals. One iButton was inserted into the cavity and the other was attached to the tree exterior with a nail below the deepest part of the cavity; this represented a pair of iButtons. One hundred iButtons were paired and attached to one another with a fishing line for ease of extraction and the prevention of equipment loss if ejected. We constructed a thermal shield to cover the external iButton as Hubbert et. al (2005) noted that this is important to reduce excessive ambient influence from direct sunlight on the metal device. For the shield, we used light colored cardboard and in some cases pieces of bark. The shield was secured with a nail to create a bottomless tent to allow airflow (Hubber et al. 2005). iButton pairs were rotated to new cavities every 15-21 days. If the data download was incomplete, or the tree fell down during the study due to severe wind storms, the cavity was excluded from the study.

We measured predictor variables that could influence cavity temperatures (Table 2.1), and these variables were selected based on their use in previous studies or their hypothesized influences on tree cavity temperatures. We included variables that represented tree, cavity and wood hardness characteristics. Tree parameters included canopy cover, orientation, and DBH. Trees with a larger DBH are assumed to have greater insulative abilities. Canopy cover was measured with a spherical densitometer at the cavity entrance. Previous studies have identified that DBH (Coombs et al. 2010) and canopy cover (Dobkin et al. 1995) strongly influence tree cavity microclimates. An open reel measuring tape was used to measure DBH (cm) at the center of the cavity entrance. The orientation was measured with a compass to identify the cardinal direction on the tree where the cavity was excavated thus representing exposure to solar radiation. Nonrandom selection of cavity orientation by multiple species has been recognized and suggested to provide thermoregulatory advantages (Inouye 1981, Butcher 2002) such as limiting wind exposure (Haggerty 1995) and altering sun exposure (Inouye 1981, Inouye 1976). Additional tree variables that were measured included the height of the cavity entrance from the ground. We assumed that a cavity near the ground would be warmer because it would experience reduced winds and be closer to solar radiation from the earth's surface in comparison to a cavity higher on a tree.

Cavity variables included horizontal and vertical depth (mm), entrance height and width (mm), and sill width (mm). Clement and Castleberry (2013) identified cavity entrances as one of the most important factors to the internal temperature and thus influencing the microclimate. To determine entrance diameter, we assumed the cavity entrance was elliptical ($\pi * h * w$) where h is cavity entrance height and w is cavity entrance width, and used digital calipers to measure the entrance height and width at its narrowed points. We assumed that cavities with larger entrances would experience temperatures closer to the ambient temperature because of increased convective heat transfer. To calculate cavity volume a modified flex-cable tool was used to identify horizontal and vertical depth of the cavity. For horizontal depth, the distance from back of the cavity wall, but not including the cavity sill, was measured. To capture vertical depth, the measurement from the base of the cavity to the base of the cavity entrance was summed to the measurement from the top of the cavity to the base of the cavity entrance. Assuming the cavity was cylindrical, the measurements were used to calculate cavity volume ($\pi r^2 h$). We predicted that cavities with greater volumes would have cooler microclimates since it takes longer for external factors (e.g. ambient temperature) to influence these cavities.

Lorenz et al. (2015) identified wood hardness to be an influential factor in nest site selection for woodpeckers and other primary cavity excavators (PCEs). Multiple studies have identified that the use of decay classify, instead of a quantitative measure of wood hardness, is subjective and can provide inaccurate results (Saint-Germain et al. 2007, Lorenz et al. 2015). Due to the potential link between wood hardness and preferable microclimate, we used methodology developed by Matsuoka (2000) to characterize wood hardness in newton Meters (NM). A 9mm diameter hole was drilled approximately 15 cm into the tree, depending on the size of the tree. A torque meter was used to measure resistance every 1cm. In order to represent the wood hardness of the excavated cavity, Matsuoka (2008) proposed to drill 5 cm above the cavity. If the tree was hollow, measurements were recorded as zero. The torque required to turn the increment borer in the predrill hole was used to identify the wood hardness of the sill (from the tree surface to 3cm) and the body (3-10 cm within a tree's bole) of the cavity

used in the model. Including wood hardness is a novel concept for microclimate studies since, to our knowledge, it has not been used.

Statistical analysis

To represent the temporal signature of each tree without the influence of lag effects, only data from every third day was used in this study (Wiebe 2001). Every third day, the maximum ambient and internal temperatures over the 24-hour period was identified. During this time-period, we also recorded the number of hours that the cavity was $\geq 26^{\circ}\text{C}$ and $\geq 36^{\circ}\text{C}$. In addition, the difference between the ambient temperature and cavity temperature was calculated. This was done by identifying how many degrees ($^{\circ}\text{C}$) of change occurred in the cavity and the external environment within the 24-hour period. The difference between these degrees of change (external – internal) had either positive or negative values. Positive values indicated that the ambient temperature experienced more degrees of change than the cavity thus, indicating that the cavity characteristics are potentially providing a more thermally stable microclimate. A negative value indicated that cavity temperature fluctuated more than the ambient temperature, thus representing a less thermally stable microclimate in the cavity.

We used R Studio Version 0.98.1103 statistical software and the lme4 package (Linear Mixed-Effects Models using 'Eigen' and S4) for statistical analysis (Bates et al. 2015) and considered results significant at a $\alpha=0.05$. Using a linear mixed effect model, we ranked models based on Akaike's Information Criterion (AIC). Multiple models were evaluated, and the response variables included: maximum internal temperature, the number of hours $\geq 26^{\circ}\text{C}$, the number of hours $\geq 36^{\circ}\text{C}$, and the difference between internal and external temperatures. The tree was identified as a random effect to account for the multiple temperature measurements for the same tree. Variables used in the model were checked for correlations. Variables were excluded from the model if a significant ($p = 0.05$) correlation existed. To control for the ambient temperature effects, we included it in all models except for the null (Table 2.2). In order to identify significance, we restricted the log-likelihood ratio test (REML) to estimate model parameters for the best supported model. We identified the proportion of cavities experiencing temperatures over 26°C and 36°C and the duration spent at or above these thresholds. Although the

cavities described in this study were not all actively used by cavity nesters, this study can nevertheless suggest those variables which have the most influence on the cavity microclimate.

Results

We deployed 100 iButtons, and included 47 cavities within the study. The top ranked models that explain the difference in maximum internal cavity temperature included tree characteristics (tree diameter, canopy cover, and orientation), and ambient temperature (Table 2.3). Parameter estimates in the tree model that were significant included canopy cover and ambient temperature (Table 2.4). Canopy cover was negatively associated with maximum temperature, suggesting that as local canopy cover decreased, the maximum temperature within the cavity increased. Similarly, ambient temperature was positively associated with both the maximum temperature of the cavity.

The number of hours the cavity was greater or equal to 26°C and 26°C was strongly influenced only by ambient temperature (Table 2.3). This was the only parameter that was in the top model for the time spent above 26°C and the time spent above 36°C, and the time cavities were at these temperatures was positively and significantly associated with ambient temperature (Table 2.4).

Most cavities (64%) experienced temperature $\geq 26^{\circ}\text{C}$ for at least one hour during the breeding season (Figure 2.2a and 2.2b); of these cavities, roughly 57% experienced this temperature greater than an hour (Figure 2.2c). Fewer cavities experience temperatures $\geq 36^{\circ}\text{C}$ (13%); of these cavities, less than 8% experienced this temperature for more than 1 hour (Figure 2.2d), and an even smaller proportion of nests experienced temperatures $> 40^{\circ}\text{C}$ for more than an hour (Figure 2.2).

Temperature differences from the external environment and cavity were best explained by the global model (Table 2.3). Cavities that experiences more fluctuation in temperature were negatively associated with canopy cover (0.0203), cavity volume (0.0051) and the area of cavity entrance (0.0005).

Discussion

This study, in aspen stands of potential concern in semi-arid regions, augments research on factors influencing cavity microclimates and additionally enhances efforts by incorporating wood hardness. It is important to note the limitations within our data set since many cavities during our study were not occupied at the time of data collection. We were unable to confirm if this was due to thermal unsuitability or a potential mismatch in the timing of data collection and actual cavity usage. Therefore, it is important to note that cavity availability on the landscape does not specifically correlate to thermally suitable microclimates.

We identified that tree characteristics and ambient temperature to best explain the internal cavity temperatures in aspen. Ambient temperature has been previously suggested to strongly affect the internal temperatures of tree cavities (Coombs et al 2010, Clement and Castleberry 2013). Although high temperatures might have negative consequences for some bird species, higher cavity temperatures might also benefit some species via providing climatic conditions enhancing fledgling growth rates (Dawson et al 2005) and may reduce the energetic costs to the young (Howe et al. 1987, Robertson 2009). With tree characteristics, (DBH, canopy cover, and orientation), the most significant parameters included canopy cover and ambient temperature. Clements and Castleberry (2013) identified that canopy cover affected cavity humidity more so than cavity temperature. Our study identified that increased canopy cover may be acting as a thermal buffer to reduce the effects of ambient temperature on a cavity's microclimate. With predictions of rising temperatures, this may suggest that the versatile importance of canopy cover could provide resiliency to a cavity's microclimate.

Variables that we excluded from the modeling included height of the cavity entrance from the ground (CE) due to the significant relationship with DBH ($p = 0.00167$; coefficient -0.4178). The role of DBH in cavity microclimates is equivocal with some studies suggesting its importance while other studies don't support this relationship (Inouye 1981, Wiebe 2001). Our top model of tree characteristics included orientation, although there was no significance associated with a specific cardinal direction with our study. Although species specific, multiple studies have identified the importance of cavity orientation. Since our study did not follow specific species, it was unlikely that

selection for non-random orientation would be identified. The selection for cavity orientation have been related to higher daily nest survival rates of secondary cavity nesters (Deng and Zhang 2015) and it is believed that cavities that warm rapidly in the morning following nights with frost may reduce embryonic mortality. The importance of cavity orientation has even been explored in Saguaro Cacti (*Carnegiea gigantea*; Inouye et al. 1981) to identify thermoregulatory advantages. Landler et al. (2014) suggests that regional climate forces may be influencing non-random cavity orientation patterns identified on a latitudinal and continental scale. Because of our limited latitudinal variation, this was not confirmed at our study site but the significant variables indicate the importance of climatic influences (i.e. ambient temperatures and potential solar radiation) on cavity microclimates.

The aspen stands in our study area predominantly receive moisture during the dry season from snow-melt and are potentially sensitive to climate change since they are located on the lower edge of the precipitation range required to the species. Our results in this ecosystem are similar to those identified by Wiebe (2001) in aspen stands of Canada, which are not likely subjected to higher pressures from drought. Their study also indicated the importance of cavity orientation and the diameter at cavity height affecting cavity microclimates. Multiple studies in aspen stands have been with tree characteristics associated with survival and reproductive success. Although our results are comparative to others indicating the importance of the influence ambient temperatures (Clement and Castleberry 2013), the different combination of influential variables further amplifies the complexities associated with cavity microclimates.

Parameters used in this study, although not all found to be significant, are similar to those selected in studies of different forest and habitat types. In mature temperate podocarp–hardwood forests of New Zealand, Rhodes et al. (2015) found that cavity entrance width was significantly associated with minimum cavity temperature used by secondary cavity nesters passerines. Cavities with smaller entrance diameters, which were higher above ground in subtropical Atlantic forests (semi-deciduous forests) have been found to provide higher survival rates in small birds (12-128g; Cockle et al. 2015); however, in our study, neither cavity entrance nor cavity volume was found to influence cavity microclimates. Nest site selection has been attributed to greater DBH (Joy 2000)

in high elevation coastal forests of western white pine (*Pinus monticola*), and hemlock (*Tsuga sp.*); while Lorenz et al. (2015) identified in ponderosa pine (*Pinus ponderosa*) and Douglasfir (*Pseudotsuga menziesii*) that wood hardness significantly influenced nest site selection for woodpeckers (*Picidae spp.*). In our study, wood hardness of the body and sill were found to be important influencers of the difference (in degrees of change) between the cavity and ambient temperatures. It is assumed that the selection for these cavity and tree characteristics are optimal for fitness and survival.

The thermal environments within tree cavities have important implications for breeding birds but also for other species that use these cavities during their life cycle. Cavities excavated by woodpeckers provide critical roosting and nesting habitat for a variety of animals who cannot excavate their own cavities (e.g. wrens (*Troglodytes spp.*), big-eared bats (*Corynorhinus townsendii*), and fishers (*Pekania pennanti*). A wide assumption is that tree cavities used by bats and birds (Conway and Martin 2000; Boyles 2007), are selected for in part because they have characteristics that provide favorable conditions which ultimately influences overall survival. Several laboratory studies have compared temperature selection of artificial structures for both birds and bats. Researchers found that with bats, selection for higher temperature provided acceleration of fetal development (Racey 1973), increased milk production (Wilde et al. 1995) and increased pup growth (Zahn 1999).

With future projections of rising temperatures associated with climate change, understanding the influence on tree cavities microclimates becomes increasingly important since they support a diverse community of both cavity nesting birds and mammals. Our study indicates that the ambient temperature is one of the top variables influencing high cavity temperature and the reason cavities experience these temperatures for extended periods. As temperatures are projected to rise 0.1°C to 0.6°C (0.2°F to 1.0°F) per decade (Mote and Salathé 2010), more cavities may become unsuitable for some species. It is unknown how this change may shift cavity usage amongst species or alter biological diversity associated with aspen communities as a whole. Variables influencing cavity temperatures are diverse, thus highlighting the complexities associated with understanding cavity microclimates. Identifying how these temperature projections

will alter the suitability, longevity and varying microclimates provided by cavities may be critical for the complex array of species using tree cavities.

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Figure 2.1 Location of study sites used to examine cavity characteristics in the Pioneer Mountains, Idaho, U.S.A. 2015.

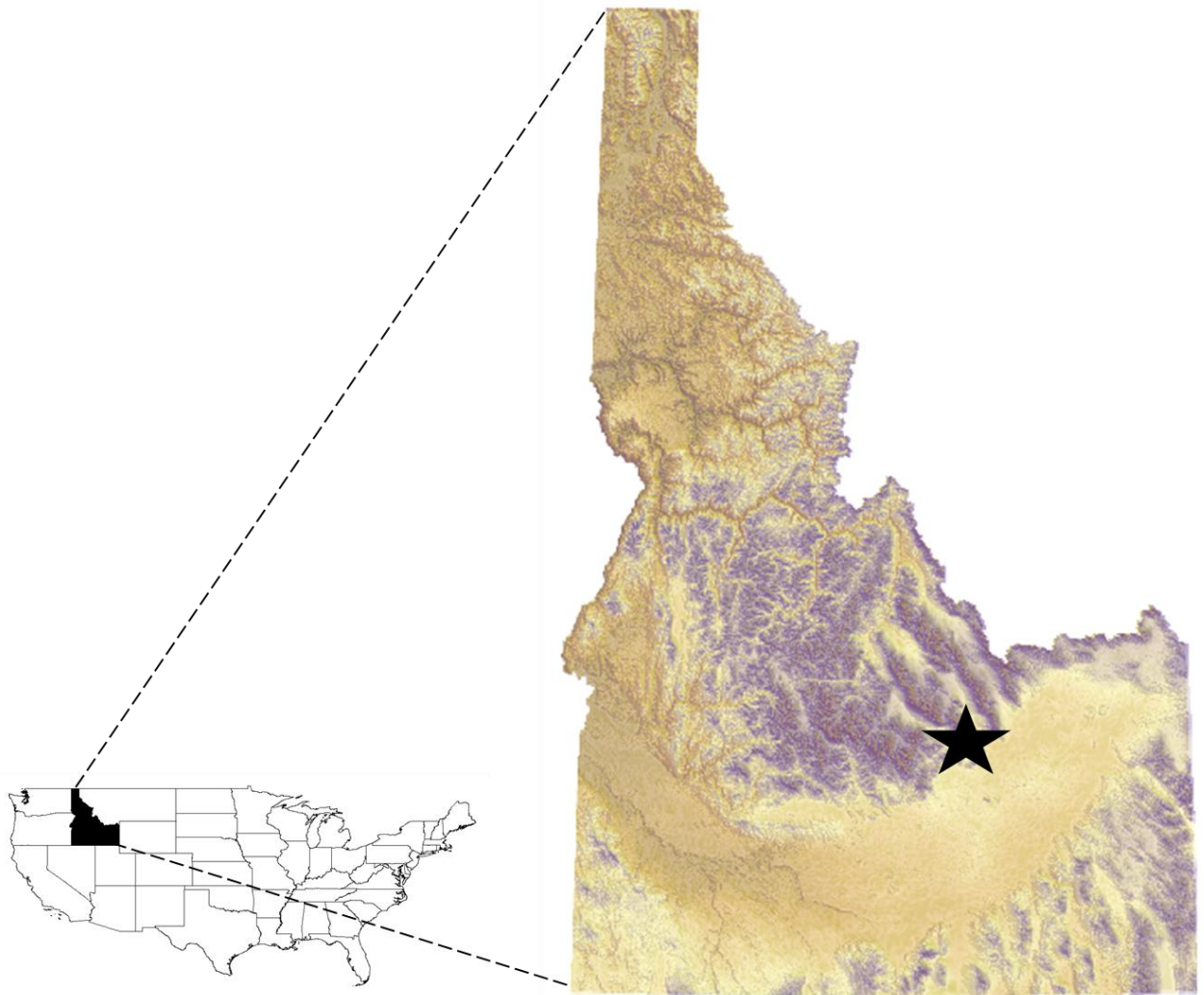


Figure 2.2 Proportion of cavities (n=47) experiencing maximum temperatures from 17-43°C from June to July b) Proportion of cavities that experiences temperatures $\geq 26^{\circ}\text{C}$ (physical zero affecting embryonic development) and $\geq 36^{\circ}\text{C}$ (the lower limit for optimal development) within a twenty-four-hour period. c) The duration (in hours) that cavities experience temperatures $\geq 26^{\circ}\text{C}$ over a twenty-four-hour period and d) temperatures $\geq 36^{\circ}\text{C}$. Cavities are in aspen trees within the Pioneer Mountains, Idaho 2015.

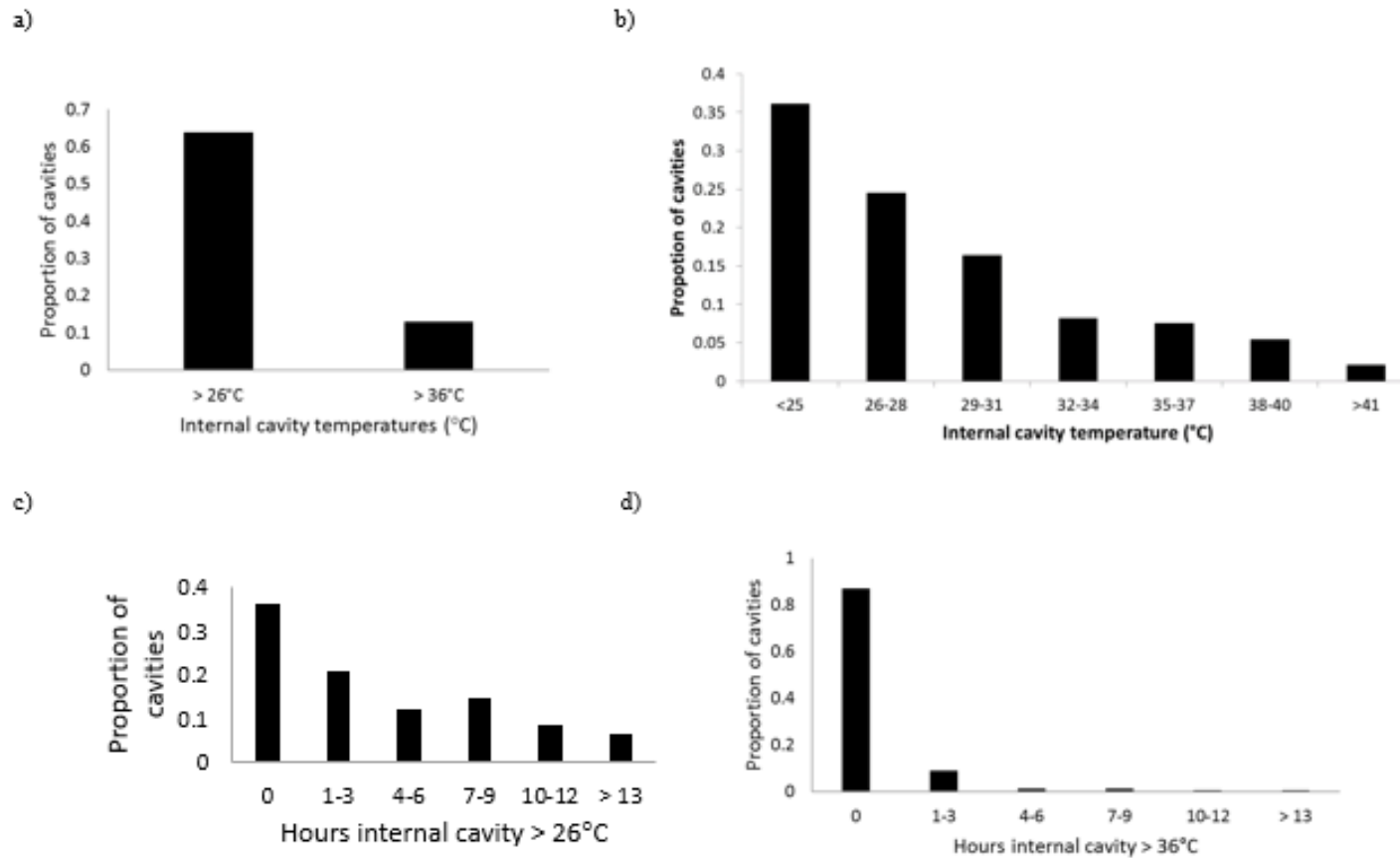


Table 2.1 Description of parameters used to examine tree cavity microclimate in the Pioneer Mountains, Idaho, U.S.A. 2015.

Parameter	Definition
Ambient temperature (°C)	Maximum temperature, within a 24-hour period, obtained from an iButton every third day directly outside the tree cavity
Temperature difference (°C)	Degrees of difference between the internal cavity temperature and external temperature within a 24-hour period, every third day (i.e. external – internal)
Entrance area (cm ²)	Area of entrance hole estimated from width and height ($A = \pi wh$) assuming entrances were ellipses
Cavity volume (cm ³)	Volume of cavity estimated from vertical and horizontal depth ($V = \pi r^2 h$) assuming cavities were cylindrical
Sill width (mm)	Width of the cavity wall
Tree diameter (cm)	Diameter of tree at cavity height
Canopy cover (%)	Percent cover directly above cavity estimated using densiometer
Orientation	Cardinal direction of cavity placement on the tree
Hardness body (N•m)	Torque required to turn increment borer into a pre-drilled hole, 3-10 cm within a tree's bole
Hardness sill (N•m)	Torque required to turn increment borer into a pre-drilled hole, from tree surface to 3 cm

Table 2.2 Models used to examine the effects of site characteristics on cavity microclimate for 47 cavities in the Pioneer Mountains, Idaho, 2015.

Model	Explanation	Parameters
1	Global	Ambient temperature, tree diameter, entrance area, cavity volume, sill width, canopy, orientation, hardness body, hardness sill
2	External	Ambient temperature
3	Cavity characteristics only	Ambient temperature, entrance area, cavity volume, sill width
4	Tree only	Ambient temperature, tree diameter, canopy, orientation
5	Hardness only	Ambient temperature, hardness body, hardness sill
6	Cavity characteristics and hardness	Ambient temperature, entrance area, cavity volume, sill width, hardness body, hardness sill
7	Tree and cavity characteristics	Ambient temperature, tree diameter, entrance area, cavity volume, sill width
8	Tree and hardness	Ambient temperature, tree diameter, hardness body, hardness sill
9	Null	Contained only the intercept term

Table 2.3 Support for models explaining difference in external and internal temperature for 47 cavities in the Pioneer Mountains, Idaho 2015. Parameters are explained in Table 2.1 and models are listed in Table 2.2. We computed temperatures using every third day to examine effects of cavity characteristics separately for maximum temperature days.

Model parameters	AIC _c	Δ_i	P-value
Maximum cavity temperature			
AT, tree diameter, canopy, orientation	627.39	0	< 0.001
AT (ambient temperature)	628.46	1.07	< 0.001
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width	630.81	3.42	0.12
AT, tree diameter, canopy, orientation, hardness body, hardness sill	631.19	3.80	0.91
AT, hardness body, hardness sill	632.00	4.61	0.79
AT, entrance area, cavity volume, sill width	632.63	5.24	0.24
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width, hardness body, hardness sill	633.83	6.44	0.61
AT, entrance area, cavity volume, sill width, hardness body, hardness sill	636.15	8.76	0.79
Null	765.49	138.10	
Temperature difference (external- internal)			
Tree diameter, canopy, orientation, entrance area, cavity volume, sill width, hardness body, hardness sill	689.38	0	0.008
Entrance area, cavity volume, sill width, hardness body, hardness sill	692.16	2.78	0.018
Hardness body, hardness sill	693.51	4.13	0.039
Tree diameter, canopy, orientation, entrance area, cavity volume, sill width	694.91	5.53	0.019
Null	695.97	6.59	
Entrance area, cavity volume, sill width	696.17	6.79	1
Tree diameter, canopy, orientation, hardness body, hardness sill	698.40	9.02	0.050
Tree diameter, canopy, orientation	700.38	11.00	1

Number of hours at $\geq 26^{\circ}\text{C}$

AT (ambient temperature)	633.12	0	< 0.001
AT, hardness body, hardness sill	636.38	3.26	0.69
AT, tree diameter, canopy, orientation	636.81	3.69	< 0.001
AT, tree diameter, canopy, orientation, hardness body, hardness sill	638.14	5.02	0.26
AT, entrance area, cavity volume, sill width	638.87	5.75	1
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width	640.72	7.60	1
AT, entrance area, cavity volume, sill width, hardness body, hardness sill	642.14	9.02	0.70
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width, hardness body, hardness sill	642.25	9.13	0.29
Null	713.46	80.34	

Number of hours at $\geq 36^{\circ}\text{C}$

AT (ambient temperature)	448.65	0	< 0.001
AT, hardness body, hardness sill	451.47	2.82	0.55
AT, entrance area, cavity volume, sill width	454.13	5.48	1
AT, tree diameter, canopy, orientation	455.37	6.72	< 0.001
AT, entrance area, cavity volume, sill width, hardness body, hardness sill	456.92	8.27	0.55
AT, tree diameter, canopy, orientation, hardness body, hardness sill	457.13	8.48	0.33
Null	459.45	10.8	
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width	460.39	11.74	1
AT, tree diameter, canopy, orientation, entrance area, cavity volume, sill width, hardness body, hardness sill	461.55	12.90	0.24

Table 2.4 Parameter estimates with confidence intervals and odds ratio with confidence intervals for top ranked models explaining differences between thermal environments and tree characteristics for 47 cavities in Pioneer Mountains, Idaho 2015.

Parameter	Estimate	Odds Ratio
Maximum temperature		
DBH	-0.001 (-0.015 – 0.013)	0.999 (0.985 – 1.013)
Orient (North)	-0.105 (-3.773 – 3.562)	0.900 (0.023 – 3.524e ¹)
Orient (South)	1.966 (-2.609 – 6.542)	7.146 (0.736 – 6.937e ²)
Orient (West)	1.284 (-2.324 – 4.893)	3.612 (0.978 – 1.334e ²)
Canopy cover*	-0.064 (-0.116 – -0.123)	0.938 (0.890 – 9.878e ⁻¹)
Ambient Temperature*	0.894 (0.791 – 0.998)	2.445 (2.205 – 2.712)
Temperature Difference (external – internal)		
Canopy cover	0.020 (-0.0249 – 0.065)	1.020 (0.975 – 1.068)
Cavity volume	0.0005 (-0.0002 – 0.001)	1.0005 (0.999 – 1.0013)
Area of cavity entrance	0.005 (0.003 – 0.007)	1.005 (1.003 – 1.008)

Number of hours $\geq 26^{\circ}\text{C}$

Ambient temperature*

0.584 (0.481 – 0.688)

1.794 (1.617 – 1.989)

Number of hours $\geq 36^{\circ}\text{C}$

Ambient temperature*

0.092 (0.043 – 0.141)

1.097 (1.044 – 1.152)

Table 2.5 Mean, standard deviation, range, and median temperature (°C) recorded on iButtons placed inside and outside 47 cavities in the Pioneer Mountains, Idaho 2105. The number of hours represents the duration (in hours) that cavities experience temperatures $\geq 26^{\circ}\text{C}$ or $\geq 36^{\circ}\text{C}$ over a twenty-four-hour period.

	Mean	SD	Min	Max	Median
All days					
External	27.55	-10.78	18.00	41.5	27.00
Internal	27.71	-11.75	17.50	43.00	27.00
Difference of internal vs external	1.24	4.93	-19.00	11.50	1.00
Number of hours $\geq 26^{\circ}\text{C}$	4.48		0.00	24.00	2.00
Number of hours $\geq 36^{\circ}\text{C}$	0.57		0.00	13.00	0.00