

# A MARKOV ANALYSIS OF TREE ISLANDS AT ALPINE TREELINE

Lynn M. Resler *and* Mark A. Fonstad

---

## Contents

1. Introduction	151
2. Methods	154
2.1. Markov chain analysis	154
2.2. Embedded Markov chains	157
2.3. First-order Markov chains	157
3. Results	158
3.1. Spatial sequence of conifer establishment	158
3.2. Stability at treeline	158
4. Discussion	159
4.1. Establishment characteristics	160
4.2. Treeline stability	161
5. Conclusions	163
References	163

## 1. INTRODUCTION

Tree islands are an important and dynamic component of the alpine treeline landscape in Glacier National Park (GNP), Montana. Composed of an individual tree or several conifers of varying species, tree islands are landscape elements distinct from the upper subalpine continuous forest cover in terms of composition, pattern, and function. Pattern across the alpine treeline ecotone in GNP is often manifest as a transition from upright, closed canopy trees to dwarfed flagged trees or stunted trees, to tundra interspersed with sparse krummholz trees, and eventual replacement by krummholz (Allen and Walsh, 1996; Bekker, 2005). Tree islands of varying sizes may be found throughout the alpine treeline ecotone, and conifers in tree islands may assume any of these growth forms.

Though alpine treeline dynamics are often researched from a landscape scale perspective with emphasis on the relationship between adult tree growth and

abiotic drivers such as mean temperature (Daubenmire, 1954; Tranquillini, 1979), topography (Brown, 1994), and disturbance factors (Butler and Walsh, 1994), analysis of fine-scale components of alpine treeline, such as tree islands, may reveal information on treeline stability from the perspective of establishment, survival, and mortality of conifers. Specifically, the establishment and survival of seedlings is important to the geographic position and spatial pattern of treeline on a landscape scale (Callaway, 1995; DeAngelis et al., 1986), because such fine-scale processes ultimately determine the upslope migration of trees (Germino et al., 2002; Hattenschwiler and Smith, 1999).

Tree islands at alpine treeline in GNP provide shelter and ameliorate local climate conditions, thereby aiding in subsequent conifer establishment (Bekker, 2005; Resler et al., 2005). The sheltering effects of tree islands have also been shown at other western treelines (Germino et al., 2002). In this regard, the establishment of a conifer at alpine treeline might be dependent, at least to some degree, upon the presence of a preexisting conifer. In an abiotically stressful environment, such as alpine treeline, trees experience greater climatic stresses than those at lower elevations (Körner, 1999). Therefore, the moderating effects of existing conifers and surface microtopography are particularly important for seedling establishment and survival (Figure 1) because they expand local resource availability through shading and offering structural protection from wind (Benedict, 1984; Marr, 1977), increase the water-holding capacity of soils (Lamb and Chapman, 1943; Pérez, 1987, 1991), and serve as seed or sediment traps. In highly exposed tundra locations, conifer establishment is patchy and new seedlings are found growing in sheltered locations, such as in the lee of microtopographic features such as boulders (Figure 2), periglacial patterned ground, and topographic



**Figure 1** A seedling growing in the lee of a larger tree island at Lee Ridge; a common phenomena at alpine treeline in GNP. Predominant wind direction is from the west (top of the photo).



**Figure 2** Pine establishing in the lee of a boulder at upper limits of the alpine treeline ecotone, Lee Ridge study site.

hollows that serve as shelter (Resler et al., 2005). Research by Callaway et al. (2002) has indicated that the relative importance of positive plant interactions such as facilitation (as opposed to resource limiting interactions such as competition) increases in increasingly stressful abiotic environments. Many tree islands in GNP are composed of conifer species that, under less stressful conditions, would not likely coexist. For example, *Pinus albicaulis*, *Pinus contorta*, and *Larix lyallii* have been found coexisting in a single patch, within a relatively small area (Resler, 2004).

The purpose of this study is to characterize fine-scale attributes of alpine tree-line, such as conifer establishment characteristics, species associations, and conifer

growth in tree islands at three alpine treeline study locations in GNP, Montana. Specific objectives of this research are (a) to characterize the species-specific patterns of conifer establishment in tree islands throughout the alpine treeline ecotone using Markov chains, a statistical technique useful for analyzing sequences of data and (b) to determine whether there are predictable patterns to the spatial establishment of conifers in exposed patches. We are interested in the characteristics and dynamics of conifer establishment in tree islands for what they may reveal about landscape-scale ecotone dynamics. Because each conifer species at alpine treeline has different environmental tolerances, reproductive strategies, and susceptibility to environmental impacts, each has different potential to effect community structure, diversity, and ultimately, the stability of alpine treeline.



## 2. METHODS

We chose three representative sites (Lee Ridge, Divide Mountain, and Cataract Creek Basin) in GNP, Montana, immediately above alpine treeline, on the eastern slopes of the Continental Divide. Slopes east of the Divide are typically dominated by a dry, continental climate regime (Finklin, 1986). All sites are windswept periglacial environments and are found at elevations ranging from 2,050 to 2,150 m. Tree islands, including individual trees and islands with multiple trees, are typically found in conjunction with boulders, other vegetation (such as *Salix* spp. or trees), or microtopography created by the presence of periglacial features that form a step-like pattern on slopes with gradients from 3 to 7° (Resler et al., 2005). Tree islands may range in species composition from one species to several species. Elevation and relative topography at the sites precluded Pleistocene glaciations, and seedlings have grown in the last 50 years (Alftine and Malanson, 2004). While each site is similar with regard to microtopography, macrotopography differs. Variation in macrotopography among sites influences variation in predominant wind directions. These variations in wind directions result in patches of different shapes at each site and likely influence seed dispersal patterns.

Sampling boundaries at each study site were delineated by placing a 30 m × 30 m quadrat in each of five elevation zones (beginning near the edge of closed forest, moving upslope). Species intercepts along transects oriented lengthwise along each tree island captured species richness and abundance data that detailed the establishment characteristics of each tree island (Mueller-Dombois and Ellenberg, 1974). Measurements along transects began with the edge of the shelter source, where the measurement was considered zero.

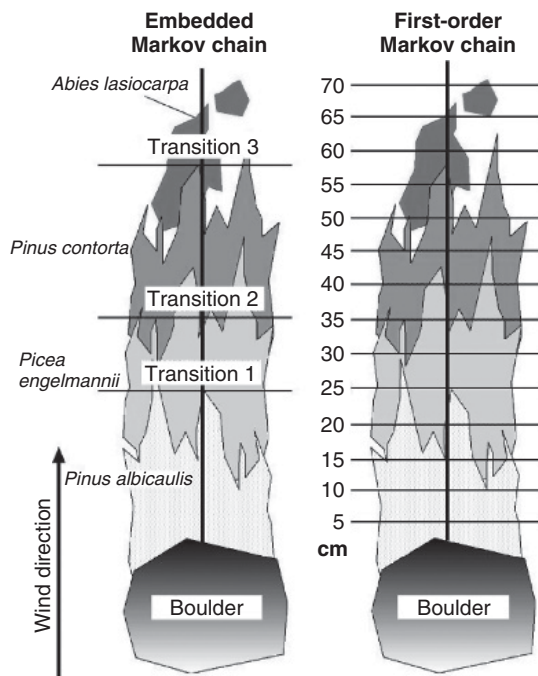
### 2.1. Markov chain analysis

Markov chains, when used in conjunction with probability statistics, are useful for testing data sequences for nonrandom arrangements in ordered successions of mutually exclusive states (Davis, 1973; Stevens, 1990). Markov chain analysis determines whether a series of data have the Markov property, the property that

each successive data point is interdependent with the preceding data point. A series may be a sequence of data measured at uniform spatial or temporal intervals (first-order Markov chains) or they may be a sequence of categorical transitions (embedded Markov chains).

In this particular study, we are interested in analyzing the sequence of conifer species establishment in tree islands. Embedded and first-order Markov chains assessed spatial patterns of plant establishment (Figure 3). Embedded chains determined whether fine-scale patterns to conifer establishment are predictable. In many conifer establishment sites, especially those located on Lee Ridge, a sequence to plant establishment within a linear microsite would suggest that the establishment of a species is dependent upon the previous establishment of another species to improve its local environment. First-order Markov chains are used to characterize the geographic variability of conifer growth and ecotone stability among each study site.

In order to use Markov chains in a geographic analysis, three types of data are needed: (a) a classification method that separates definable, individual states into time or space, (b) data to determine the transfer probabilities from one state to another, and (c) initial conditions. These conditions are met in the following ways. Mutually exclusive states are composed of individual conifer species, and the linear transects recorded such species information. Combined ordered species data



**Figure 3** Conceptual difference between sampling for embedded and first-order Markov chains.

determined the probabilities that one species follows another in space. Initial conditions are those conditions before the establishment of any conifer species in lee of a shelter. Because we had several sequences of observations from different locations within and among study sites, we calculated several transition chains for each location. Chi-square analyses ascertained whether the total combination of sequences composed of the linear vegetation data differed significantly from expected transitions from one state to another if the states were independent of each other (Davis, 1973).

In the field, we recorded information on 14 species and/or states found in tree islands at alpine treeline. Therefore, the species data along lengthwise transects were classified into 14 mutually exclusive states, as listed in Table 1. A  $14 \times 14$  transition frequency matrix generated from these data showed the number of times a species is succeeded by another species. A database contained the series of species measurements, with each species coded as a unique numerical category. Each data series began with an initial state, defined as whatever species occurs adjacent to the shelter. For example, if *P. albicaulis* was found growing in the immediate lee of a boulder, and this plant was followed by *Abies lasiocarpa*, the coding would be recorded as 3, 4. This type of coding reflects the change of one mutually exclusive state to another. Classified series included all transects with at least one transition. The total frequencies for all chains for each of the three study sites were added to form a total transition matrix representing the combination of species transitions of each chain, for each site. The counts for the total matrix became the input for the expected frequency matrix. Chi-square analysis allowed testing of the two matrices for the Markov property.

**Table 1** Mutually exclusive states, including species and topographic characteristics, and associated coding for Markov analysis

States	Code
Small herbaceous	1
<i>Salix</i> spp.	2
<i>Pinus albicaulis</i>	3
<i>Abies lasiocarpa</i>	4
<i>Picea engelmannii</i>	5
<i>Pinus contorta</i>	6
Dead <i>Pinus albicaulis</i>	7
Dead unknown	8
<i>Juniperus communis</i>	9
<i>Psuedotsuga menzesii</i>	10
<i>Juniperus horizontalis</i>	11
<i>Larix lyallii</i>	12
Bare	13
Rock	14

## 2.2. Embedded Markov chains

Embedded Markov chains are those in which observations are taken only when there is a change in state from one species to another (Figure 3). In embedded Markov chains, transitions cannot reflect change from one state to itself. Therefore, this type of model is ideal for testing the significance of conifer establishment sequences within each patch. For embedded models, coding required chains that did not reflect length of the patches but only transitions between states. Therefore, the species transects were recorded as a succession of different species in space.

Computation of embedded Markov chain models is different than that of first-order Markov chains to compensate for the restriction of no self-transition (Stevens, 1990). Davis (1973) outlines the computation of embedded Markov chains. In this research, a  $14 \times 14$  matrix is generated from observed species transitions based on the number and nature of transitions observed in the coded Excel Markov chains. The total number of possible transitions determined the  $14 \times 14$  size of the matrix. From this matrix and its associated transition probabilities, an expected transition matrix was generated, based on the assumption that, for example, if species 6 is independent of species 2, then  $P(6|2) = P(6)P(2)$ . The total of the column divided by the total number of transitions computed the occurrence probabilities of each transition. Once the two matrices are derived, a  $\chi^2$  test in the form of Equation (1)

$$\chi^2 = \sum_{i=1}^n \frac{(O_i - E_i)^2}{E_i} \quad (1)$$

that has (number of rows - 1)(number of columns - 1) degrees of freedom ( $13^2$  in this study) will test the chain to see whether a state at one part is partially dependent, in a probabilistic sense, on the preceding state, and thus check for the Markov property. This test compared the observed transition matrix to the matrix that would be expected if successive states were independent. If there is a significant difference between the observed and the expected matrices, then we can assume that the chain has the Markov property (Davis, 1973) and therefore can conclude that the establishment of one species lacks independence (in a probabilistic sense) with the preceding state.

## 2.3. First-order Markov chains

First-order Markov chains are those observations which occur at equal intervals in space or time (Figure 3). Therefore, first-order chains can reflect self-transitions. We coded first-order Markov chains in the same manner as embedded Markov chains and recorded observations at a regular interval rather than only at state transitions. Rather than testing the sequential establishment of species in a patch, first-order Markov chains served as an indicator of ecotone stability at the three study sites. A patch with several small individuals of different species may suggest the tendency of a patch to support multiple species and hence a level of dynamism that may not be present in a patch that has only one large patch of the same species. Absorbing states, those that show the tendency to remain in the same state, suggest a level of stability within a patch.

A critical part of Markov chain analysis is correctly choosing the appropriate sampling interval (in this case, distance along a lengthwise transect). Selecting an interval too large may miss important within-patch variability, and selecting an interval too small may suspiciously enhance the Markov property. In this study, we chose a 5-cm interval at which to take observations. This interval allowed measurement of the smallest individual at a site.

### 3. RESULTS

#### 3.1. Spatial sequence of conifer establishment

Results of the embedded Markov chain tests did not reveal a significant ( $p > 0.05$ ) spatial sequence to conifer establishment in exposed conifer patches at any of the three study sites. However, some important species-specific patterns of conifer establishment within patches did emerge. Species order indicated that initial conifer establishment, or position of occupancy found immediately adjacent to the shelter source, was occupied in most patches by *P. albicaulis* (Table 2). Cataract Creek Basin was the only site where *P. albicaulis* did not reflect the highest percentage of initial occupancy (Table 3). Here, *A. lasiocarpa* was the dominant initial colonizer. The total percent occupancy is shown in Table 3.

#### 3.2. Stability at treeline

First-order Markov chains assessed the within-patch dynamics of conifer species at treeline. State stability may be thought of as the tendency for a species to transition into the same state. Patches that exhibit a high degree of self-similarity (fewer species present, or large amounts of growth) are more stable or have more

**Table 2** Percent occupancy of initial position (position immediately adjacent to shelter source) in tree island transect sequences

Species	Percent (including dead conifers) $n = 128^*$	Percent (excluding dead conifers) $n = 128^*$
<i>Abies lasiocarpa</i>	19	23
<i>Juniperus communis</i>	5	6
<i>Juniperus horizontalis</i>	1	1
<i>Picea engelmannii</i>	19	24
<i>Pinus albicaulis</i>	30	39
<i>Pinus contorta</i>	4	5
<i>Pseudotsuga menziesii</i>	2	2
Dead	20	NA

\* Sample size reflects combined samples from each study site.

**Table 3** Percent initial position (position immediately adjacent to shelter source) occupancy for each study site, excluding dead conifers

Species	Percent, Lee Ridge <i>n</i> = 37	Percent, Cataract Creek Basin <i>n</i> = 53	Percent, Divide Peak <i>n</i> = 31
<i>Abies lasiocarpa</i>	3	41	10
<i>Juniperus communis</i>	8	9	0
<i>Juniperus horizontalis</i>	0	0	3
<i>Picea engelmannii</i>	3	39	16
<i>Pinus albicaulis</i>	70	6	71
<i>Pinus contorta</i>	16	0	0
<i>Pseudotsuga menziesii</i>	0	5	0

absorbing states. Those that show a high richness and transition numbers indicate dynamism within the establishment site through a tendency toward change. Geographic variability of sites may depend on a number of site conditions including wind, seed sources, and exposure.

Results of the  $\chi^2$  test for the Markov property for first-order Markov chains for Lee Ridge ( $\chi^2 = 39,540.53$ ), Cataract Creek Basin ( $\chi^2 = 1,024.42$ ), and Divide Peak ( $\chi^2 = 11,428.29$ ) were found to be significant at the  $p < 0.0001$  level for 169 degrees of freedom. The results of this test indicate that when factoring in length of the transitions as a measure of growth of a species and allowing for self-transitions, transects at the three study sites do exhibit the Markov property. Self-transitions reflect the amount a species can grow before it is replaced by another species in a sequence. A high number of self-transitions may indicate that the establishment site has reached an absorbing state, and growth of one species dominates a patch's dynamics. Therefore, a high number of transitions between states of species may indicate that the site is dynamic and is suitable for establishment by numerous species. Interspecies transitions are therefore an indicator of species richness.

Among the three sites, Lee Ridge reports the highest number of transitions (104) from one state to another, indicating that its species composition is the highest and the site is the most dynamic of the three. Divide Peak showed 51 total interstate transitions, and Cataract Creek Basin showed only 29, indicating that a large portion of the patches have a very low species richness, and many large patches are occupied by one species only, in this case, *A. lasiocarpa*.

## 4. DISCUSSION

This study examines fine-scale attributes of alpine treeline, such as conifer establishment characteristics, species associations, and within-patch conifer growth, which may reflect coarse-scale ecotone dynamics in GNP. Based upon the results,

three major findings of this study are as follows: (a) establishment order of conifers within a tree island is not statistically predictable, (b) *P. albicaulis* is an important initial treeline colonizer, and (c) there is geographic variability among study sites in terms of patch occupancy and treeline stability.

#### 4.1. Establishment characteristics

First, this study demonstrates that the establishment of conifers within a patch does not follow a predictable spatial sequence. For example, *P. albicaulis*, which has extremely hardy seedlings (Mellmann-Brown, 2005; Tomback et al., 2001) is not always followed in spatial sequence by the less hardy *P. contorta*. This finding suggests that the spatial order of conifer establishment in tree islands is based on stochastic events, such as seed dispersal in favorable microsites. This is particularly true for *P. albicaulis* seedlings, which are dispersed primarily by Clark's nutcrackers. Nutcrackers often cache seeds in microsites near objects, such as at the base of rocks, trees, or logs (Tomback, 1978, 1998), which provide shelter against wind or shade (Mellmann-Brown, 2005).

The finding that there is no predictable sequence to conifer establishment within a tree island also suggests that the operating processes within a conifer patch above treeline are not successional in nature to the extent that competitive exclusion is the predominant operative process. Rather, what is evident on the landscape in GNP is a number of conifers that exist in a small location that would normally not exist together under alternative conditions more amenable to growth. Dominant controlling processes may be more abiotic than biotic in areas of high stress (Callaway, 1995, 1998; Callaway and Walker, 1997; Callaway et al., 2002; Choler et al., 2001) and facilitation is important to overall treeline patterns, even if this facilitation is structural in nature (Smith et al., 2003). The physical presence of a plant or rock may expand local resources necessary for conifer growth (Grabherr et al., 1995), acting as an ecosystem engineer (Jones et al., 1994). Additionally, the facilitating influence of mycorrhiza to conifers at alpine treeline may complement microclimatic amelioration at the local scale (Hasselquist et al., 2005).

##### 4.1.1. Initial establishment

Conifer establishment in high-elevation and highly exposed sites at alpine treeline in GNP is often in the lee of periglacial shelters such as surface boulders or periglacial patterned ground (Butler et al., 2004; Resler et al., 2005). We found that the initial position next to a shelter source, that is, the position immediately adjacent to the shelter, is most frequently occupied by *P. albicaulis*. Again, this is a pattern explained by the selection of suitable caching sites of the Clark's nutcrackers (Tomback, 1978, 1998). In addition, the microsites for initial tree island establishment must also be conducive to long-term survival of the tree (Resler et al., 2005). The hardiness of whitebark pine seedlings (Mellmann-Brown, 2005; Tomback et al., 2001) suggests that a whitebark pine may have a better ability to establish and survive in these microsites at treeline than other treeline conifer species.

The initial position next to the shelter represents a very important position in terms of environment, niche, and positive feedbacks. The first conifer species to establish next to a shelter initiates a positive feedback cycle whereby the local environment is moderated to allow for subsequent establishment and survival. Positive feedback mechanisms have been shown to generate pattern in ecotones in general (Malanson, 1999; Wilson and Agnew, 1992) and specifically, vegetation patterns at the alpine (Alftine and Malanson, 2004; Bekker, 2005; Zeng and Malanson, 2006) and arctic (Svienbjörnsson et al., 2002) treeline ecotone. Furthermore, conditions had to be appropriate for initial establishment to occur. The plant occupying the niche is indicative of environmental conditions at this particular site at the time it was established, and therefore, initial establishment of a conifer at treeline is species-specific due to varying environmental tolerances among species. The establishment of a hardy conifer such as *P. albicaulis*, for example, may enable the subsequent establishment of less resilient conifer species, resulting in increased conifer diversity at treeline. Knowledge about the species that occupies the first spatial position next to the shelter may be indicative of local conditions at the time of establishment.

Initial occupancy by *P. albicaulis* and subsequent establishment by other species implies that (a) local microclimatic conditions improve following establishment by *P. albicaulis* and (b) that post-Little Ice Age (LIA) conditions were less favorable for conifer establishment than they are currently. The former observation indicates the importance of positive feedback mechanisms in the amelioration of local site quality. The latter is especially apparent at Lee Ridge, where establishment sites lower in elevation are typically richer in diversity and larger in size than high-elevation sites where establishment sites often consist of a single individual (typically a spruce or a pine). Butler (1986) reported similar results in the Lemhi Mountains, Idaho. There, *Pinus flexilis*, an initial post-LIA colonizer in subalpine meadows, was replaced by other conifer colonizers as conditions became milder.

Establishment of *P. albicaulis* at treeline has significant implications for the treeline environment of GNP. Despite current regeneration at highly exposed treeline locations, the long-term potential for *P. albicaulis* to contribute to the treeline and lower elevation ecosystems is uncertain given the mortality of whitebark pine at treeline due to blister rust, an invasive and introduced fungal pathogen (Resler and Tomback, 2008; Tomback and Resler, 2007). Given the potential importance of whitebark pine as a tree island initiator (Resler, 2004; Resler and Tomback, 2008; Tomback and Resler, 2007), the pattern of tree islands on the alpine treeline landscape in GNP could be altered, as well as conifer diversity and composition at alpine treeline.

#### 4.2. Treeline stability

The results of the first-order test, allowing for transitions from one state to itself, indicate that transects at the three study sites do exhibit the Markov property. Although we cannot assume anything about the sequential nature of establishment from these results, we may make inferences about conifer growth and patch diversity. Conifer diversity at treeline may be indicative of ecotone stability.

Hacker and Gaines (1997) suggest that positive plant interactions can increase landscape biodiversity, resulting in increased ecotone stability.

Growth of conifer species within each conifer patch number is indicated in the Markov chains as the number of self-transitions. Diagonal dominance on a transition matrix suggests relative stability among the states (Dale et al., 2002). It implies that the local conditions are right for its self-perpetuation and thus occupancy and dominance of the niche by one or few conifer species. Diagonal dominance also suggests competitive advantages; a conifer has a high amount of resources and may compete for the most space in a patch. A large patch with 100% foliar cover by one species alone suggests that while it may not be in equilibrium in terms of growth, it may be stable and less dynamic than one with five different species. Dynamism may tell us that there are numerous species that can thrive in a particular patch, implying a potential for increased treeline biodiversity. If biodiversity is an important indicator of ecosystem health (Tilman, 1999), then site stability as recorded by interspecies transitions suggests that there is important geographic variability among the three study sites in terms of ecosystem health. Where species richness and patch dynamism are high (such as at Lee Ridge), there may be greater potential for treeline advance than at sites with lower species richness (such as Cataract Creek Basin and Divide Peak). Low richness sites may be more susceptible to stochastic disturbance events that would disrupt conifer establishment and survival.

Indicators of species richness, namely species richness counts and the number of interspecific transitions as shown in the Markov chains, determine that the lowest level of dynamics occur at Cataract Creek Basin. Species richness is 5, and transitions from one species to another are only 29 for the entire site. The transition transfer number indicates that the majority of patches found at Cataract Creek Basin are composed only of one species. Additionally, Cataract Creek Basin is the only site of the three where *Pseudotsuga menziesii* was established. This is likely due to the site's location adjacent to the Continental Divide and the moister site conditions at Cataract Creek. The western portion of the park has a higher occurrence of *P. menziesii* than does the east, and therefore the seed source is likely from trees residing on the western ranges.

Indicators of species richness, namely species richness counts and the number of interspecies transitions as shown in the Markov chains, demonstrate the dynamics intermediate between those at Cataract Creek Basin and Lee Ridge. Species richness is 5, and transitions from one species to another are 51 for the entire site. Divide Peak does not contain any unique species.

Lee Ridge is the most dynamic treeline site of the three chosen for this study. Indicators of species richness include species richness counts (simply the number of different conifer species per site) and the number of transitions from one species to another, as shown in the results of the first-order Markov chains. Lee Ridge shows the highest conifer richness (with a total of seven conifer species). Additionally, Lee Ridge exhibits more than twice as much change from one species to another than does Cataract Creek Basin or Divide Peak. Lee Ridge is the only study site where *Larix lyallii* was recorded. Additionally, it is the only site among the three where *P. contorta* is found. A likely source for *L. lyallii* is Canada, as Lee Ridge lies only

4 miles from the Canadian border. An even-age stand of lodgepole pine dominate the lower portions of the ridge below the subalpine zone.

This study indicates geographic variability in patch diversity among the three study sites, all located on the eastern slopes of GNP. This finding suggests that varying fine-scale factors may result in different landscape scale treeline patterns in different places, depending upon how the geography of a site influences establishment, growth, and survival.

## 5. CONCLUSIONS

Fine-scale factors of alpine treeline, specifically species-specific characteristics of tree islands such as growth, and conifer establishment patterns were examined using Markov chains. Results of the Markov analyses revealed that establishment order of conifers within tree islands is not statistically predictable, indicating that stochastic processes and modification of local climate in sheltered sites are important for establishment of conifers. *P. albicaulis* was found to be the conifer species most frequently located immediately adjacent to a shelter source – a function of both nutcracker caching and hardy seedlings. Fine-scale characteristics of conifer establishment in tree islands may be important in making links between local and landscape level dynamics, given the unique environmental tolerances of each conifer. It will be interesting to see how tree island composition in GNP responds as our environment continues to change.

## REFERENCES

- Alfline, K.J., Malanson, G.P., 2004. Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science* 15, 3–12.
- Allen, T.R., Walsh, S.J., 1996. Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing* 62, 1261–1268.
- Bekker, M.F., 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 37, 97–107.
- Benedict, J.B., 1984. Rates of tree-island migration, Colorado Rocky Mountains, USA. *Ecology* 65, 820–823.
- Brown, D.C., 1994. Comparison of vegetation-topography relationships at the alpine treeline. *Physical Geography* 15, 125–145.
- Butler, D.R., 1986. Conifer invasion of subalpine meadows, central Lemhi Mountains, Idaho. *Northwest Science* 60, 166–173.
- Butler, D.R., Walsh, S.J., 1994. Site characteristics of debris flows and their relationship to alpine treeline. *Physical Geography* 15, 181–199.
- Butler, D.R., Malanson, G.P., Resler, L.M., 2004. Turf-banked terrace treads and risers, turf exfoliation, and possible relationships with advancing treeline. *Catena* 58, 259–274.
- Callaway, R.M., 1995. Positive interactions among plants. *Botanical Review* 61, 306–349.
- Callaway, R.M., 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82, 561–573.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., et al., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848.

- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: Asynthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82, 3295–3308.
- Dale, M., Dale, P., Edgoose, T., 2002. Using Markov models to incorporate serial dependence in studies of vegetation change. *Acta Oecologia* 23, 261–269.
- Daubenmire, R.F., 1954. Alpine timberlines in the Americas and their interpretation. *Butler University Botanical Studies* 11, 119–136.
- Davis, J.C., 1973. *Statistics and Data Analysis in Geology*. John Wiley, New York.
- DeAngelis, D.L., Post, W.M., Travis, C.C., 1986. *Positive Feedback in Natural Systems*. Springer, New York.
- Finklin, A.I., 1986. *A Climatic Handbook for Glacier National Park with Data for Waterton Lakes National Park, Intermountain Research Station, U.S.D.A. Forest Service, Ogden, Utah*.
- Germino, M.J., Smith, W.K., Resor, A.C., 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162, 157–168.
- Graherr, G., Gottfried, M., Gruber, A., Pauli, H., 1995. Patterns and current changes in alpine plant diversity. In: Chapin, F.S., Körner, C. (Eds.), *Arctic and Alpine Biodiversity*. Springer Verlag, Berlin, pp. 161–181.
- Hacker, S.D., Gaines, S., 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78, 1990–2003.
- Hasselquist, N., Germino, M.J., McGonigle, T., Smith, W.K., 2005. Variability of *Cenococcum* colonization and its ecophysiological significance for young conifers at alpine-treeline. *New Phytologist* 165, 867–873.
- Hattenschwiler, S., Smith, W.K., 1999. Seedling occurrence in alpine treeline conifers: A case study from the central Rocky Mountains, USA. *Acta Oecologica* 20, 219–224.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Körner, C., 1999. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer, Berlin.
- Lamb, J., Jr., Chapman, J.E., 1943. Effect of surface stones on erosion, evaporation, soil temperature, and soil moisture. *Journal of the American Society of Agronomy* 35, 567–578.
- Malanson, G.P., 1999. Considering complexity. *Annals, Association of American Geographers* 89, 746–753.
- Marr, J.W., 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58, 1159–1164.
- Mellmann-Brown, S., 2005. Regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, U.S.A.: Spatial distribution and responsible agents. In: Broll, G., Keplin, B. (Eds.), *Mountain Ecosystems: Studies in Treeline Ecology*. Springer, Berlin, 97–115.
- Mueller-Dombois, D., Eldenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York.
- Pérez, F.L., 1987. Soil moisture and the upper altitudinal limit of giant paramo rosettes. *Journal of Biogeography* 14, 173–186.
- Pérez, F.L., 1991. Soil moisture and the distribution of giant Andean rosettes on talus slopes of a desert paramo. *Climate Research* 1, 217–231.
- Resler, L.M., 2004. *Conifer Establishment Sites at the Alpine Treeline Ecotone, Glacier National Park, Montana*. Doctoral Dissertation, Department of Geography, Texas State University-San Marcos.
- Resler, L.M., Butler, D.R., Malanson, G.P., 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography* 26, 112–125.
- Resler, L.M., Tomback, D.F., 2008. Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics, northern Rocky Mountains, Montana, USA. *Arctic, Antarctic, and Alpine Research* 40, 161–170.
- Smith, W.K., Germino, M.J., Hancock, T.E., Johnson, D.M., 2003. Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology* 23, 1101–1112.

- Stevens, R.L., 1990. Markov-chain analysis as a pedagogic tool. *Journal of Geological Education* 38, 288–293.
- Svienbjörnsson, B., Hofgaard, A., Lloyd, A., 2002. Natural causes of the tundra-taiga boundary. *Ambio* 30, 23–29.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80, 1455–1474.
- Tomback, D.F., 1978. Foraging strategies of Clark's nutcracker. *Living Bird* 16, 123–161.
- Tomback, D.F., 1998. Clark's nutcracker (*Nucifraga columbiana*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*. The Birds of North America, Inc., Philadelphia, No. 331.
- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., Mellmann-Brown, S., 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology* 82, 2587–2600.
- Tomback, D.F., Resler, L.M., 2007. Invasive pathogens at alpine treeline: Consequences for treeline dynamics. *Physical Geography* 28, 397–418.
- Tranquillini, W., 1979. *Physiological Ecology of the Alpine Timberline*. Springer-Verlag, New York.
- Wilson, J.B., Agnew, A.D.Q., 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23, 263–336.
- Zeng, Y., Malanson, G.P., 2006. Endogenous fractal dynamics at alpine treeline ecotones. *Geographical Analysis* 38, 271–287.