The importance of regional dynamics in local populations of limber pine (Pinus flexilis)1

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Abstract - Limber pine (Pinus flexilis) populations in the Kainanuk Valley of Alberta have many of the traits of patchy populations based on the constancy of the dynamics of 13 local populations. The populations exist on an expected basis on high stress habitats of rocky ridges, scree slopes, and gravel creek beds. All populations showed continuous recruitment and low mortality. No population showed any evidence of local extinction as a result of negative population growth. Wildlife caused varitey in populations from extinction of the local populations to little or no effect. Populations extinguished by fire were quickly recolonized. Seed dispersed by the Clark's nutcracker (Nucifraga columbiana) appears to be responsible for this rapid recolonization following wildfire. Limber pine does not persist in the seed bank for more than two years. Therefore, the limber pine populations are regionally persistent because rare extinction events (wildfires) are followed by prompt recolonization by seed dispersed by Clark's nutcracker from other local populations.

Keywords: extinction, mortality, metapopulation, Nucifraga columbiana, patchy population, Pinus flexilis, population dynamics, recruitment, seed dispersal.

Introduction

Most plant populations do not exist in complete isolation because seed often disperses between local habitat patches. Therefore, within a plant species with regional population structure. First, seed produced in one local population may disperse and recruit into another local population. Therefore, local populations will be independent of one another. Second, seed dispersal will allow colonization following extinction events. Therefore, a species will persist regionally even when there are local extinctions. The amount of dispersal between populations and the probability of local population extinction will determine if the system acts more like a classic metapopulation, with low dispersal and high extinction (Levins, 1969), or a patchy population, with high dispersal and low extinction (Harrison, 1991). Historically, the classic metapopulation models (following Hanski & Simberloff, 1997) assume that: i) the local populations are isolated so that their local dynamics are independent of one another; ii) there is limited and random dispersal between populations; and iii) all the populations are subject to extinction. Although these strict criteria are important simplifying assumptions for tractable mathematical models, empirical studies have shown that these assumptions are unrealistic in natural populations (Harrison & Taylor, 1997). For example, the amount of migration between local populations is likely quite high since species must have good dispersal mechanisms to live in patchy habitats (Hamilton & May, 1977). A high rate of dispersal between local populations will result in a rapid recolonization following extinction, but will also affect the amount of local recruitment (Hastings & Wollin, 1989; Hastings, 1991; Gyllenberg & Hanski, 1992). Additionally, each local population is likely to have a different extinction rate, which depends on the ratio of mortality to recruitment (e.g., source-sink dynamics), or on the susceptibility to external disturbance (e.g., tree-satellite dynamics; Harrison & Taylor, 1997).

Limber pine (Pinus flexilis James) forms distinct open-canopied populations, occurring small, discontinuous areas on xeric sites along ridges, scree slopes, and gravel creek-beds throughout the subalpine zone. Their seeds cannot be

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dispersed by wind since they are wingless and are inhaled in the cone scales. The most effective seed disperser for limber pine in this area is the Clark’s nutcracker (Nucifraga columbiana Wilson), which harvests seeds from the cones and scatters them in open environments with shallow snow cover (Lanner & VanderWall, 1980; Tombback & Kraeaer, 1980). Many other animals eat limber pine seeds but the seeds are usually destroyed in the process. In this region, high-intensity wildfires are a recurrent event (Frey & Johnson, 1988; Johnson & Larsen, 1991; Johnson & Wowchuk, 1993). These stand-replacing fires are capable of causing extensive mortality and can lead to the local extinction of limber pine populations. Local extinction may also be caused by prolonged negative population growth rates resulting from long periods of unfavourable environmental conditions.

These observations alone are not sufficient to accurately classify limber pine as a type of metapopulation since careful estimates of the dispersal distributions and extinction probabilities are needed (Hashbad & Barrett, 1996; Harrison, 1991; Harrison & Taylor, 1997; Ludwig, 1996). However, data on dispersal and extinction probability distributions are exceedingly difficult to obtain.

The objective of this research is to determine how the regional processes of colonization and extinction affect limber pine. In order to detect extinction and recolonization within local populations, the population history was reconstructed (Johnson & Fryer, 1985) by aging the live trees, cross-dating the dead trees (Fritts, 1976), and dating fire scars. These limber pine populations could be reconstructed over a long period of time since the decomposition of most trees is slow in the xeric habitat.

Our premise is that the local population integrates both local fecundity and mortality, and extinction and regional dispersal. Unlike many systems, our definition of a local population is clear, since limber pine populations occupy small, discontinuous habitats. Local extinction means the death of all individuals, reproductive or not, in the local population. This may occur in a single event, e.g., a stand replacing wildfire, or over a long period of time, e.g., if a population has a negative growth rate.

Recruitment in a closed population is dependent only on local fecundity, local dispersal and early establishment conditions. However, in an open population, where there is dispersal between populations, recruitment will also depend on the effectiveness of dispersal. The effect of dispersal will be most noticeable if recruitment continues when the local population is not capable of producing its own seeds, i.e., recolonization following extinction from wildfire, or when the trees are too young to be reproductive.

Material and methods

STUDY AREA

The range of limber pine in the Rocky Mountains of North America extends from the southern Rocky Mountains in Canada to northern New Mexico in the United States (Crichtfield & Little, 1966). In the Canadian Rocky Mountains, limber pine occurs on the eastern slopes of the front ranges and into the foothills of southwestern Alberta. The limber pine populations sampled in this study are located within the north-east section of the Kananaskis Valley, from about 114° 50' W to 114° 05' W and from longitude 114° 57' to 115° 08'. The valley is located in the front ranges of the Canadian Rocky Mountains, about 100 km west of Calgary, Alberta. The pollen record indicates that soft pines (subgenus Strobulis), which in this region include limber pine and to a lesser extent whitebark pine (Pinus albicaulis Engelm.), have continuously existed here for the past 10 400 years (MacDonald, 1989).

Limber pine in the Kananaskis Valley is found along rocky ridges, scree slopes and gravel creek beds, all of which are underlain by Paleozoic limestone. The ridge-line limber pine habitats are exposed bedrock with enough in situ weathered debris for limber pine to root. The scree slope habitats are found beneath the dip or tilted side of the mountains, i.e., the "headwalls," which in the front ranges of the Rocky Mountains are oriented in a south-west direction. A scree slope forms when rock erodes from the headwall and falls downslope. As the headwall decreases in size, the rock accumulates to become gradual, decreasing the slope angle. The maximum slope angle is determined by the shear strength, and ranges from 35° for limestone gravel to 35-40° for coarse, hard rock debris (Statham & Francis, 1986). A scree slope may slump as it weather, due to increased hydraulic conductivity in the fine top slope sediments; this results in an increased pore water pressure within the depositing scree through time. Scree slopes are considered fairly stable landforms and are further stabilized by the presence of vegetation. The gravel creek-bed habitat is formed by the fluvial transport of gravel. The Kananaskis Mountain stream widens and deepens when they level off in the valleys, decreasing the water velocity and resulting in the deposition of rocks collected upstream (Gardiner, Smith & Desloges, 1983). High post-glacial till loads combined with high post-glacial runoff most likely created the extensive creek beds that continue to receive rock input from upstream erosion and spring run-off.

On ridges, scree slopes and gravel creek beds, limber pine co-occurs with Engelmann spruce (Picea engelmannii Purry ex Engelm.), Lodgepole pine (Pinus contorta Loudon) and occasionally Douglas fir (Pseudotsuga menziesii [Mirb.] Franco). Common juniper (Juniperus communis L.), creeping juniper (J. horizontalis Moench), shrubby cinquefoil (Potentilla fruticosa L.), beaverberry (Arctostaphylos uva-ursi [L.] Spreng.) and white canna (Zigadenus elegans Pursh) are the most common shrubs and herbs.

The climate of the Kananaskis Valley is transitional Plains-Cordilleran with cold winters (average January temperature is -15°C), warm summers (average July temperature is 14°C), and well-defined summer precipitation maxima (in June and August) and winter minimum (in November; Johnson & Fryer, 1899). The average annual precipitation at the Barrier Lake Kananaskis Field Station, located at the north end of the valley (elevation 1390 m), is 618 mm. In general, the amount of precipitation in the valley increases by about 20 mm for each 100 m increase in elevation. Fryer & Johnson (1988), Johnson & Wowchuk (1993), and Hallsworth & Chinnappa (1997) provide more detail on the climate and geology of the study area.
Lightning-caused wildfire, characterized by high intensity and high rate of spread, is the major large-scale disturbance affecting vegetation in this area (Fryer & Johnson, 1988; Nash & Johnson, 1996). The fire cycle of the Kannaskis Valley from about 1750 to present is 144.6 years (confidence interval around the 95% confidence level (MLE) estimate is 99.2 to 222.3 years), and prior to 1750 is 44.6 years (confidence interval around MLE estimate is 19.9 to 151.2 years; Reed et al., 1998).

FIELD SAMPLING

We sampled thirteen populations of limber pine at 13 different sites in the study area (Table 1). The sites chosen for sampling had a minimum density of at least five limber pine per 100 m² and had to be at least one hectare in size. Within each site, a circular plot of 15 m radius was established. All live limber pine trees greater than 5 cm basal diameter were cored to the pith, as close to the base as possible, at three different radii. All limber pine less than 5 cm basal diameter and all dead trees (standing and fallen) were cut at the base to obtain a full cross-sectional disc. Five scars were located by examining trees in the area, particularly watching for fire scars which had become overgrown. If no fire scars were found within the population, fire scars were sampled from trees in the neighbouring closed-canopy forest.

LOCAL POPULATION RECONSTRUCTION

All cores and discs were sanded so that individual cells could be discerned. Dead trees were identified to species by microscopic examination of the pattern of cross-field pitting on the trachoids (Core, Cité & Day, 1979). The date of recruitment of five trees was determined by counting the annual rings on tree cores. To determine the date of recruitment and death of dead trees, a master chronology was developed for each species within each stand. Each master chronology was developed by first measuring the widths of annual rings (to 0.0001 mm accuracy) on 10-15 of the oldest live trees within each population, with the aid of the Velnex-Acurite measuring system and Metronics software. Dead trees within each population were cross-dated to the master chronology using COFECHA (Holmes, 1992), and checked with skeleton plotting (Fritts, 1976). Finally, the local recruitment and mortality were summarized using Leslie diagrams (Keyfitz, 1965, methods in Myerscough & Alho, 1994), which show the date of recruitment of five individual and the date of recruitment and death of the dead individual that have not yet decomposed. Dead limber pine within the populations are well preserved due to the dry site conditions and high wood resin content that inhibit decay in organisms (Harmon, 1986; Panahi & De Zeeuw, 1980).

To examine each age-specific mortality, individuals within a single cohort are followed through time from recruitment to death or present (if still alive). A cohort is defined as a group of individuals who are recruited at the same time, experience similar environmental conditions, and are thus subjected to a similar mortality schedule. The age-specific mortality h(t) is estimated over the interval Δt:

\[
h(t) = \frac{N_{t+1}}{(N_{t})(Δt)}
\]

\[
Var h(t) = \frac{h(t)(Δt - h(t))}{N_t}
\]

where \(N_t\) is the number of trees alive at the beginning of the interval and \(N_{t+1}\) is the number of trees dying during the interval (Lee, 1992). The age-specific mortality was estimated for the oldest cohort (Table 1) in BAC, ML, and WR and the two oldest cohorts of OS, all of which had not been affected by fire and had at least 14 individuals. The cohort time interval varied from 20 to 36 years. There is a trade-off in making the time interval short enough so that the individuals experience similar conditions at the same life stages, yet long enough so that a reasonable mortality estimate can be calculated. Hence, age-specific mortality levels can only be compared within populations where time intervals are the same.

**Results**

The pattern of recruitment in each population is reasonably constant over time (Figure 1), but becomes more sporadic further back in the reconstruction. This is probably a result of individuals who were recruited but were not included in the population reconstruction due to decomposi-

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**Table 1. Characteristics of the study sites and populations of limber pine**

<table>
<thead>
<tr>
<th>Population</th>
<th>Elevation (m)</th>
<th>Slope (%)</th>
<th>Aspect (°)</th>
<th>Density of limber pine (trees/100 m²)</th>
<th>Total tree density (trees/100 m²)</th>
<th>Percent limber pine composition</th>
<th>Age of oldest tree (years)</th>
<th>Fire occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAC</td>
<td>1605</td>
<td>33</td>
<td>171</td>
<td>5.9</td>
<td>8.5</td>
<td>66%</td>
<td>101</td>
<td>yes</td>
</tr>
<tr>
<td>BP</td>
<td>1944</td>
<td>19</td>
<td>332</td>
<td>9.8</td>
<td>68.5</td>
<td>20%</td>
<td>76</td>
<td>yes</td>
</tr>
<tr>
<td>HR</td>
<td>1834</td>
<td>36</td>
<td>246</td>
<td>8.5</td>
<td>19.2</td>
<td>44%</td>
<td>*200</td>
<td>yes</td>
</tr>
<tr>
<td>JR</td>
<td>1564</td>
<td>38</td>
<td>140</td>
<td>9.8</td>
<td>13.2</td>
<td>74%</td>
<td>283</td>
<td>no</td>
</tr>
<tr>
<td>MBR</td>
<td>1930</td>
<td>97</td>
<td>223</td>
<td>11.5</td>
<td>241</td>
<td>48%</td>
<td>386</td>
<td>yes</td>
</tr>
<tr>
<td>MC</td>
<td>1608</td>
<td>39</td>
<td>221</td>
<td>3.2</td>
<td>11.7</td>
<td>46%</td>
<td>294</td>
<td>no</td>
</tr>
<tr>
<td>ML</td>
<td>1537</td>
<td>26</td>
<td>142</td>
<td>1.7</td>
<td>15.4</td>
<td>76%</td>
<td>*156</td>
<td>yes</td>
</tr>
<tr>
<td>NP</td>
<td>1709</td>
<td>31</td>
<td>194</td>
<td>11.4</td>
<td>20.4</td>
<td>85%</td>
<td>*258</td>
<td>yes</td>
</tr>
<tr>
<td>OS</td>
<td>1606</td>
<td>32</td>
<td>227</td>
<td>9.1</td>
<td>9.7</td>
<td>93%</td>
<td>*161</td>
<td>no</td>
</tr>
<tr>
<td>PC</td>
<td>1454</td>
<td>5</td>
<td>315</td>
<td>5.5</td>
<td>9.6</td>
<td>17%</td>
<td>163</td>
<td>yes</td>
</tr>
<tr>
<td>SP</td>
<td>1611</td>
<td>35</td>
<td>190</td>
<td>14.4</td>
<td>17.1</td>
<td>84%</td>
<td>642</td>
<td>no</td>
</tr>
<tr>
<td>SS</td>
<td>1651</td>
<td>36</td>
<td>147</td>
<td>5.9</td>
<td>13.9</td>
<td>42%</td>
<td>*420</td>
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</tr>
<tr>
<td>WR</td>
<td>1908</td>
<td>26</td>
<td>197</td>
<td>9.5</td>
<td>13.7</td>
<td>69%</td>
<td>*226</td>
<td>no</td>
</tr>
</tbody>
</table>

* = dead
tion, that is, very young (small) trees that died, decomposed, and therefore cannot be detected. Therefore, the absence of trees in an age class, or the exact number presently occurring in an age class, does not necessarily represent an accurate account of the number recruited. The Lexis diagrams (Figures 3-6) indicate that no dead individuals are found younger than 40 to 60 years of age. As a consequence, our estimates of mortality do not start at the recruitment date of the cohort, but some years later.

The age-specific mortality (Figure 2) in the five oldest post-fire cohorts of BAC, ML, Wr and OS varies between 0.005 and 0.025 individuals per cohort interval but appears to show no trend with age. Periods of mortality appear to be higher in the 1950s in all but one cohort. The reconstructed populations can be organized into four categories based on wildfire-caused extinction and post-fire recolonization: i) populations that show wildfire-caused extinction, and recoloni-
zation from other populations (Figure 7); ii) populations

that show colonization of habitat not recently occupied (Figure 3), iii) populations that show excessive mortality from wildfire with no local extinction (Figure 4); and iv) populations that show little mortality from wildfire (Figure 5).

![Figure 1](image1.png)

**Figure 1.** Periods of recruitment for the (1) local timber pine populations. Data include live and dead individuals. Each vertical line indicates the last known fire date in the population.

![Figure 2](image2.png)

**Figure 2.** The age-specific mortality for the five oldest, post-fire cohorts within four populations. The years of recruitment for each cohort are shown in the legend. The bars are the standard error.

![Figure 3](image3.png)

**Figure 3.** Lexis diagrams for the populations that show evidence of extinction followed by recolonization. BAC and ML, a colonization of habitat not recently occupied, BP. Each black 4th line within the graphs represents one or more individuals. Where each line intersects the x-axis indicates the year of recruitment, and the end point of each line indicates the year of death (z-axis) and age at death (y-axis). Lines that intersect the right hand side of the graph are individuals that were alive at the time of sampling. A solid vertical black line indicates the date of the most recent known fire.
there appear to be no young trees prior to the fire. This is likely due to the young trees being killed and consumed by the fire or killed by the fire and decomposed, and not due to the absence of young trees in the pre-fire stands. Also, in HM and SS, the outer sapwood in some trees has decomposed and hence the dates of recruitment and death are likely inaccurate in those trees.

The population reconstructions of OS, SP, MC and WR (Figure 5) represent populations in which there is no evidence of fire-caused mortality, with some individuals reaching hundreds of years of age (maximum age of a live tree was 641 years in the SP population). Since there is no evidence of fire in these stands or in any of the immediate surroundings, the periods without trees in the Lexis diagrams may truly reflect episodes of poor recruitment or high mortality of young trees that have since decomposed. Note that the periods without trees do not appear to be synchronous between the four populations.

The population reconstructions of JR and PE (Figure 6) did not fit any of the previous categories. For these two populations, the date of the fire was uncertain and there were not many dead trees. As well, there is a long history of trees occupying the current sites. For instance, there are live individuals in three populations that are 282 years old (JR) and 180 years old (PE), and the few dead trees that are present were 153 years old (JR) and 201 years old (PE) at death. However, the lack of dead wood and the uncertainty in the fire dates make it difficult to interpret both the absence of individuals recruited during the late 1700s in PE and during the early 1800s in JR.

Population growth rate is a combination of the birth and death of all individuals in every cohort through time. Our ability to determine population growth rate for the populations studied here is severely limited, because individuals were lost through decomposition. Despite these problems, there are two important general trends in population growth that we can detect (Figure 3c). First, none of the populations show a long-term decrease in population size, i.e., negative population growth rates. In fact, most populations show an increase over time in the number of individuals since the last fire (ML, BP, HM, SS, NP, BRC, SP, JR, PE), although the increase may be an artifact of the presence of many small young individuals at the time of sampling who may soon die. In the remaining populations, population growth has either been fairly stable in recent times, or there have been some fluctuations in population size (BAC, OS, MC, WR). In many populations there appear to be high levels of recruitment following the fire (BAC, ML, HM, SS, NP, OS, SP).

Discussion

Our objective was to describe the dynamics of regional populations of limber pine from local population extinction and reacclimation via dispersal between populations. In other words, are local limber pine population dynamics largely governed by random dispersal patterns and frequent local extinction, or are the local populations either collectively or singly governed only by their birth and death rates?
Before we discuss the population dynamics, we need to consider the limitations of our data. Population reconstructions using both live and dead individuals (Johnson, Miyashita & Kiehl, 1994) do not assume that all cohorts have the same birth and death rates. However, our ability to look back into the history of individual cohorts is limited by the loss of individuals to decomposition or fire, and by the accuracy of aging individuals.

The success of population reconstruction depends on the ability to detect individuals that have died in the past, which is dependent upon the rate of wood decomposition. This decomposition limit is roughly equivalent to the earliest date that trees could be accurately cross-dated, in this study greater than 300 years (SS, BBC, WR). However, decomposition and consumption by fire varies depending on the size of the individual, whether a dead individual is standing or fallen, and how long the dead fallen tree has been on the ground (Johnson & Greene, 1991). Hence, the reconstruction will be missing individuals that have been dead for a long time, were very small at the time of death, or were consumed by fire.

Accurately determining recruitment dates depends both on crossdating, to locate missing or false rings (Fritts, 1976), and our ability to locate all growth rings laid down since recruitment. Crossdating has long been recognized as essential to aging individuals accurately. However, recently DesRochers & Gagnon (1997) have shown that aging a tree by simply counting the number of rings at the base rarely gives the actual date of recruitment. This is because rings laid down in the initial years are located below the basal core or disk, or there may be rings missing on any single cross-section (core or disk). Since we did not excavate the root-shoot interface to locate the initial growth rings, recruitment dates are likely earlier than stated.

Despite the limitations of the stand reconstructions, we conclude that limber pine in the Kananaskis Valley has dynamics similar to a patchy-population metapopulation (Harrison, 1991; Harrison & Taylor, 1997). That is, we have discrete local populations that are united by high inter-population dispersal rates, and wildfires are responsible for local population extinction.

Limber pine is found in relatively small, discrete, local populations separated from other populations by hundreds of meters to tens of kilometers. The local populations have low and constant age-specific mortality, i.e., a negative exponential survivorship. Individual trees can live more than 600 years. Such a long lifespan is possible in these rather severe environments because of a longer average fire return time compared to the closed canopy forest, low competition, and the ability of these trees to maintain a balance between conducting tissue and foliage by slow growth (0.02 cm y\(^{-1}\), cambial die-back, and foliage reduction (Pruden, Fryer & Johnson, 1987). Cambial die-back begins when trees are 200 or more years old. At this age, live cambium may account for as little as 4% of the basal area (Pruden, Fryer & Johnson, 1987). This reduction in cambium reduces the high respiration load of the sapwood (Waring & Schlesinger, 1985) caused by the geometric increase of sapwood area with increasing trunk diameter.

Young trees have a higher ratio of photosynthetic surface to respiring tissue compared to middle-age trees (Kramer & Korzukhina, 1960), and it appears that cambial retreat allows older trees to maintain a favourable ratio of conducting and foliage tissue.

Fire appears to be the primary means of causing local extinction, yet it rarely does. Fires in the Kananaskis generally range in size from 5 000 to 10 000 ha and are usually confined to one valley (Fryer & Johnson, 1988). Given both the scattered distribution of limber pine habitat on scree slopes, rocky ridges, and gravel creek beds, and the discontinuous fuel in the stands, fires rarely exterminate all limber pine stands in a valley. The populations studied show the full range of fire effects, from those in which fire caused local extinction or killed varying numbers of individuals, to those in which there is no evidence of fire in the life span of the present population.

Seed dispersal by Clark's nutcracker appears to be very efficient. The evidence for this is indirect but consistent. All populations showed continuous recruitment over a hundred years, and in sites where the local population was extirpated by fire, rapid recruitment, even when the nearest extant population was kilometers away. Also, the seedbank of limber pine in this area is not able to persist for longer than two years (Webster, 1998), showing that recruitment would have to come from dispersal.

Limber pine requires Clark's nutcracker to extract and disperse its seeds both within and between sites. Although much is known about Clark's nutcracker's ability to remember and retrieve buried seeds, only a little is known about the dispersal curve for the seeds. Tombback & Linhart (1990) and Tombach, Hoffman & Sund (1989) summarize the observational evidence that Nutcrackers disperse seeds tens of kilometers across a range of deviations. Evidence in this study suggests that the recolonization of most fire-extended limber pine sites is relatively rapid (see also Tombach, Hoffman & Sund, 1989). However, what we do not know is how the bird's home range, population numbers, and behaviour affect this recolonization.

In terms of population growth, there appears to be an increased period of successful recruitment following fire. This pattern may be the result of higher amounts of seed input by the Clark's nutcracker following a fire, and/or higher survivorship of the first post-fire cohort. There is no evidence for high survivorship of the post-fire cohort and it seems unlikely that the first cohort should have higher survivorship because the low density of trees in the stand changes very little over time. This is in contrast to closed canopy forests where the initial post-fire cohort has higher survivorship because the later arriving understory cohorts experience shading from the established canopy cohort (Johnson & Fryer, 1989). However, there is some evidence that there may be an increase in bird caching of seeds to post-burn sites (Lanser & VanderWall, 1980; Morgan et al., 1994; Tombach, 1986). It is unclear why the birds would increase the rate of dispersal of seeds to burned sites, although the completely open sites may allow easier retrieval of seeds during the winter since there is lower snow accumulation on open sites.
Following the initial re Colonization, recruitment continues to occur, and mortality appears to be fairly low and constant, allowing the population to increase steadily. Cold late-summer periods may cause a temporary increase in the mortality rates. However, since the continuous recruitment outweighs mortality, it seems clear that negative population growth has not led to local population extinction in the studied populations.

Conclusion

Limbic pines persist in discrete local populations which are subject to recurrent extinction by fire and rapid re-colonization because of seed dispersal from other discrete local populations. The open-canopied limber pine habitats are always available for recruitment, unlike closed-canopied conifer forests in which the majority of recruitment is limited to a brief period after disturbance (Charron, 1998; Greene & Johnson, 1998). This is because the tree density is always low and the forest floor is largely exposed mineral soil and scree, both of which are good recruitment surfaces.

Limb pine habitat is well drained and suffers extreme moisture stress and exposure to winds and snow which removes snow cover and melts snow early in the spring. Limb pine is well adapted to this environment, with its very slow growth and the ability of its stipule and leaf area to die back. This may result in the low and relatively constant mortality observed.

Although the local populations show somewhat synchronous regional stochastic (weather) mortality, this is not severe enough to cause extinction of all of the populations in the populations. Also, fire is not of a size or frequency to cause more than a few local populations to be extinguished in a century. When there is catastrophic mortality or local extinction, seed dispersal by the Clark's nutcracker allows rapid re-colonization.

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Literature cited


