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

by

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ABSTRACT

Limber pine (*Pinus flexilis*) populations in the Kananaskis Valley of Alberta appear to have regional structure: discontinuous habitat, effective seed dispersal (by the Clark's nutcracker, *Nucifraga columbiana*), and an extinction mechanism (wildfire). Using dendrochronology, the regional processes of extinction and recolonization were detected within the local populations by reconstructing the recruitment and mortality of individuals. High intensity wildfires have caused catastrophic mortality and local population extinction within these populations. The Clark's nutcracker, the only effective seed disperser of limber pine, disperses seed between the local populations and is responsible for their rapid recolonization following fire. Within local populations, there is a steady recruitment of trees and low mortality rates following establishment, making extinction from negative population growth appear unlikely. Therefore, the limber pine populations are regionally persistent because rare extinction events are promptly recolonized by seed dispersal between local populations.

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On the road of life, I hope our paths cross often. Happy trails!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Most plant populations do not exist in complete isolation because seed often disperses between local habitat patches. Therefore, within a local population, individuals will recruit and die, and regionally, local populations will go extinct and be recolonized. There are two important consequences for 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 not be independent of each other. Second, seed dispersal will allow recolonization 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 and Simberloff 1997) assume that: 1) the local populations are isolated so that their local dynamics are independent of each other; 2) there is limited and random dispersal between populations; and 3) all the populations are subject to frequent 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 and 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 and 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 and Wolin 1989, Hastings 1991, Gyllenberg and 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. core-satellite dynamics) (Harrison and Taylor 1997).

Limber pine (*Pinus flexilis*, James, 1823) in the Canadian Rocky Mountains is an example of a set of populations where extinction and colonization events should be important. First, it exists as fairly distinct, open-canopied populations, occupying small, discontinuous areas on xeric habitats along ridges, scree slopes, and gravel creek-beds. Second, the wingless limber pine seeds cannot be dispersed by wind since they are inlaid on the cone scales. The only effective seed disperser for limber pine in this area is the Clark's nutcracker (*Nucifraga columbiana*, Wilson, 1811), who harvests seeds from the cones and scatterhoards them between the local populations (Tomback 1978, Lanner and VanderWall 1980, Tomback and Kramer 1980). Finally, these local limber pine populations exist within the subalpine zone of the Rocky Mountains where large, high intensity wildfires are recurrent within the lifespan of most canopy trees. These stand replacing fires could result in catastrophic mortality and potentially lead to the local extinction of these discontinuous limber pine populations (Fryer and Johnson 1988, Johnson and Larsen 1991, Johnson and Wowchuk 1993). Alternatively, local extinction

could occur due to the fluctuation in environmental conditions on these extremely dry sites. Unfavourable periods may cause low recruitment and high mortality, resulting in negative population growth rates.

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 (Henry and Swan 1974, Oliver and Stephens 1976, Johnson and Fryer 1989) 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 on the xeric habitat. However, since small trees, which have died in the past, decompose quickly and are largely absent in the reconstruction (Johnson and Greene 1991), experiments on seed and first year seedling mortality were used to determine the amount of early establishment mortality.

Extinction is indicated in the local population reconstruction when all the individuals in the population have died. If extinction is a result of catastrophic disturbance, tree mortality will correspond to the known date of a disturbance (e.g. wildfire). Alternatively, if extinction is due to a negative population growth rate, the population will progressively decrease in size due to low recruitment, high mortality or a combination of both. Recolonization is indicated in the local population reconstruction when trees establish in the population following extinction. Alternatively, a colonization

event is indicated in the reconstruction when trees establish on habitat that has never been occupied. Therefore, prior to recolonization there must not be any surviving, reproductive limber pine, nor a seed bank which could provide a source of seed.

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METHODS

Study Area

The range of limber pine is from the southern Canadian Rocky Mountains, to northern New Mexico in the United States (Critchfield and 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 (Rowe 1972). The limber pine populations sampled in this study are located within the north-east section of the Kananaskis Valley watershed, from latitude 50°55' to 51°03' and 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, which include limber pine, have continuously existed in this area 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" (Statham and Francis 1986), which in the front ranges of the Rocky Mountains are orientated 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 continues to accumulate below, increasing the slope angle. The maximum slope angle is determined by the shearing resistance, and ranges from 35° for limestone gravel,

to 38 - 40° for coarse, hard-rock debris (Statham and Francis 1986). A scree slope may slump as it weathers, due to decreased hydraulic conductivity in the fine top slope sediments, which results in an increased porewater pressure within the degrading 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 rock downstream. Mountain streams widen and deepen when they level off in the valleys, which decreases the water velocity and results in the deposition of rocks collected upstream (Gardner et al. 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*, Parry 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) and shrubby cinquefoil (*Potentilla fruticosa*, L.) are the most common shrubs, while bearberry (*Arctostaphylos uva-ursi*, (L.) Spreng.) and white camas (*Zygadenus elegans*, Pursh) are common herbs.

The climate of the Kananaskis Valley is transitional plains-cordilleran with cold winters (average January temperature -10°C), warm summers (average July temperature 14°C), and well-defined summer precipitation maxima (in June and August) and winter

minimum (in November) (Johnson and Fryer 1989). The average annual precipitation at the Barrier Lake Kananaskis Field Station (elevation 1390 m), located at the north end of the valley, is 618.1 mm. In general, the amount of precipitation in the valley increases by about 20 mm for each 100 m increase in elevation. Fryer and Johnson (1988), Johnson and Wowchuk (1993) and Hallsworth and Chinnappa (1997) provide more detail on the climate and geology of the study area.

Lightening-caused wildfire is the major large-scale disturbance affecting vegetation in this area and is characterized by high intensity and high rate-of-spread (Fryer and Johnson 1988). The fire cycle in the Kananaskis Valley (Reed et al. 1998) from about 1730 to present is 144.6 years (confidence interval around Maximum Likelihood estimate is 99.2 to 222.3 years) and prior to 1730 is 44.6 years (confidence interval around ML estimate is 19.9 to 151.2 years).

Field sampling

Thirteen populations of limber pine were sampled in the study area (Figure 1 and Table 1). The sites chosen for sampling had to have a density of at least 5 limber pine per 100 m^2 and be at least one hectare in size. Within each site a circular plot of 15 m radius was established. All the live limber pine trees greater than 5 cm diameter were cored to the pith on three different radii, as close to the base as possible. All limber pine less than 5 cm diameter, and all standing and fallen dead trees were cut at the base to obtain a full cross-sectioned disc. Fire scars were located by examining trees in the area, being careful

Figure 1   The location of the 13 limber pine populations sampled in the Kananaskis

Valley, Alberta, Canada.

N

115°07' E 51°03' N

HM

Barrier Lake

JR

SS

BAC

OS

BP

Kananaskis River

ML

PC NP

MC

WR

SP

Highway 40

Highway 68

Powderface Trail

BRC

1 cm = 1 km

114°56' E 50°54' N

Table 1   Site characteristics of the 13 limber pine populations sampled.

Population	Population Name	Northing (UTM)	Easting (UTM)	Elevation (m)	Slope (°)	Aspect (°)	Density of Limber pine (number per 100 m²)	Total tree Density (number per 100 m²)	Percent Limber Pine Composition	Age of oldest tree (yr)	Fire evidence (char or fire scar)
BAC	Baldy Creek	5652390	635876	1605	33	171	5.9	8.9	66	101	yes
BP	Baldy Pass	5650080	638366	1944	19	332	9.8	48.5	20	76	yes
BRC	Bryant Creek	5642106	643209	1930	37	225	11.5	24.1	48	386	yes
HM	Heart Mountain	5656548	631673	1854	36	246	8.5	19.2	44	*200	yes
JR	Jewel Ridge	5654836	634470	1564	38	140	9.8	13.2	74	283	no
MC	McDougall Ridge	5647388	632721	1608	39	221	5.2	11.7	44	294	no
ML	Mount Lorette	5649120	632411	1507	26	142	11.7	15.4	76	*156	yes
NP	North Porcupine	5648553	636593	1769	31	194	17.4	20.4	85	*258	yes
OS	O'Shaughnessy Falls	5651450	635658	1606	32	237	9.1	9.7	93	*161	yes
PC	Porcupine Creek	5648892	634844	1454	5	315	5.5	9.6	57	163	yes
SP	South Porcupine	5646907	636115	1611	35	190	14.4	17.1	84	641	no
SS	Stoney South	5653907	633617	1651	36	147	5.9	13.9	42	*420	yes
WR	Wasootch Ridge	5646554	635399	1908	26	197	9.5	13.7	69	*526	no

*=dead

to watch 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.

Dendrochronology

All the 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 tracheids (Core et al. 1979). The date of recruitment of live 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 within each

stand. Each master chronology was developed by first measuring the widths of annual

rings (to 0.001 mm accuracy) on 10-15 of the oldest live trees within each population,

with the aid of the Velmex-Acurite measuring system and Metronics software. Next, the

ring-width series of the live trees were combined using ARSTAN (Cook 1985). Finally,

dead trees within each population were cross-dated to the master chronology using

COFECHA (Holmes 1992), and checked with skeleton plotting (Fritts 1976).

Population Reconstruction

Evidence of extinction is determined by examining the mortality of individuals

within each local population reconstruction. Evidence of colonization is determined by

examining recruitment data obtained from both the population reconstruction and

experiments on germination and establishment (see section on *Local Recruitment and*

Recolonization). The local population reconstructions were summarized using Lexis diagrams (Keyfitz 1968). A Lexis diagram tracks all live and dead individuals (those which have not yet decomposed) from the year of recruitment until the year of death. In the Lexis diagram, each individual is represented by a 45° angle line which gains a year in age (y axis) for every year it lives (x axis). A vertical line through any year will give the age distribution of the population at that time. Mortality rates can be calculated using the death dates of trees over an interval, which can be seen on the Lexis diagram.

Extinction

Lexis diagrams demonstrate an extinction event when all individuals in the population have died. If extinction is the result of catastrophic mortality from a wildfire, the date of death of the trees should correspond to the date of wildfire determined from fire scar data. Extinction which results from a negative population growth rate requires a detailed examination of local recruitment and mortality rates.

Local Mortality

To examine local age-specific mortality in the absence of disturbance, the deaths of individuals within a single cohort are followed through time. A cohort is defined as a group of individuals who recruit at the same time, experience similar conditions, and thus are subjected to a similar mortality schedule. The age-specific mortality is estimated over the interval equal to the time span of the cohort, Δt:

$$\hat{h}\ (t) = \frac{N_{t,\ \Delta t}}{(N_t)\ (\Delta t)} \tag{1}$$

where N_t is the number of trees alive at the beginning of the interval and $N_{t,\Delta t}$ is the

number of trees dying during the interval (Lee 1980). This method of estimating mortality

includes information from the Lexis diagram on the age of the dead individuals in the

cohort, as well as the age of the live individuals in the cohort. Specifically, the age-specific

mortality was estimated for the oldest cohort 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.

Local Recruitment and Recolonization

Lexis diagrams show the date of recruitment of live individuals and the date of

recruitment for the dead individuals that have not yet decomposed. Trees that have

decomposed are missing from the population reconstruction, despite the fact that they

recruited into the population. The population reconstruction cannot differentiate between

the mortality and subsequent decomposition of newly recruited trees and the absence of

recruitment, since young trees decompose quickly upon death. Consequently, the

reconstruction provides a conservative estimate of the number of trees that recruit. To

compensate for this limitation, lab and field experiments were designed to look at seed

survivorship through dormancy, germination success under different temperature,

stratification and scarification treatments, and first-year establishment survivorship. The

ability of a seed to remain viable and dormant for more than one winter, thus forming a

seed bank, can prevent extinction in the event of a disturbance, since a store of seeds are available for germination.

The aim of the lab experiments was to determine the range of temperatures that limber pine seeds could germinate under and the special treatment required for limber pine germination that may indicate whether a seed bank could form. Experimental batches of 25 seeds were exposed to different temperatures (5°, 10°, 15° and 20° C) and different treatments (wet stratification, seed coat scarification and prolonged, 17 month storage) for a total of 150 seeds. Ideally, the different treatments should be performed at each temperature, however seed availability limited the experimental combinations. Seeds were collected in the field during late summer of 1996 from trees with ripe cones. Only intact seeds, at least 0.07 mg were used in the experiments. This was to ensure that the embryo was not damaged, and that the seed was viable. All seeds were buried in moist, coarse sand with a 12 hour light regime. Germination was noted when the radicle protruded beyond the seed coat.

For the 20° C germination trials, all 50 seeds had been in cold, dry storage (refrigerator at 3-4° C) for approximately 5 months. To determine if seed coat abrasion hastened germination, 25 of the seeds were scarified by clipping the micropyle end of the seed coat with a razor blade and the other 25 seeds were left entire. For the 15° C germination trial, 25 seeds had been in cold, dry storage for 17 months. This treatment examined if germination was affected by extended storage. Additionally, after germination

the radicle length was measured every few days to examine the rate of radicle elongation. For the 11° C germination trial, all 25 seeds had been in cold, dry storage for 7 months. There were no additional manipulations done at this temperature. For the 5° C germination trials, all 50 seeds had been in cold, dry storage for 5 months. To examine if cold stratification (mimicking early spring conditions) enhances germination, 25 seeds were exposed to cold, wet stratification for 4 months. The other 25 seeds remained in the cold, dry storage for a further four months. The cold, wet stratification was performed by placing the seeds between layers of wet paper towels, in breathable plastic bags, loosely covered with tin foil to exclude light.

The field experiments examined seed and seedling survivorship. In these experiments three circular arrays of 19, 3" diameter pots, were filled with local soil (gravel, sand and some organic material) and each pot was buried 1 m apart with the rim level to the ground. The experimental site was located within a limber pine population in an open, unshaded area. Three limber pine seeds were planted at approximately 2 cm depth in each pot. These conditions mimic Clark's nutcracker caching behaviour (Lanner and Vander Wall 1980). Within each array, nine of the nineteen pots were completely covered with wire mesh and randomly assigned positions in the array. Therefore, each of the three plots had 27 seeds covered and 30 seeds uncovered, for a total of 171 seeds. Each array was separated by distance of between 10 and 200 meters. The sites were prepared in September 1996 and were monitored approximately every 3 weeks for the emergence, persistence and disappearance of seedlings throughout the spring and summer

of 1997.

Establishment survivorship was estimated using the non-parametric Product-Limit method (Kaplan and Meier 1958, Lee 1980). This method is useful when there are small to moderate sample sizes and when the exact survival time is not known because some individuals are still alive. The expected survivorship is estimated by:

$$\hat{S}(t) = \prod_{t_{(r)} \leq t} \frac{n-r}{n-r+1}$$

(2)

and the variance estimated by:

$$Var\,[\hat{S}(t)] = [\hat{S}(t)]^2 \sum_r \frac{1}{(n-r)(n-r+1)}$$

(3)

where n is the number of individuals and r is the rank from shortest to longest survival time (t).

RESULTS

Extinction from catastrophic mortality caused by wildfire.

The limber pine populations disturbed by wildfire appear to exhibit varying degrees of mortality and therefore they have been organized into three categories: 1) populations that show extinction (Figure 2 a); 2) populations that show catastrophic mortality without extinction (Figure 2 b); and 3) populations that show little mortality from fire (Figure 2 c). However, the interpretation of mortality within a local population can be confounded by the consumption of live and dead trees in the fire, the rate of wood decomposition and the downslope movement of dead debris. For example, small live trees and trees already dead at the time of the fire will likely be completely consumed in a fire, or fragmented such that they decompose quickly. Since those small individuals cannot be detected, they will be missing in the population reconstruction. The large trees, which take the longest to decompose, will be the easiest to detect. However, the sapwood areas of the bole may decompose faster than the heartwood area, giving a conservative estimate of the date of death. Finally, steep slopes experience debris shifts and flows, frost creep and gelifluction which may displace dead trees downslope of the sampling site.

The population reconstructions of BAC and ML appear to represent a recolonization following wildfire, while the population reconstruction of BP appears to represent recolonization or invasion into a recently unoccupied habitat (Figure 2 a). All three populations show the sudden appearance of trees on the site and an absence of dead

Figure 2 a   Lexis diagrams for the populations that show evidence of extinction

followed by recolonization, BAC and ML, or colonization of habitat not

recently occupied, BP. Each black line within a graph represents an

individual. Where each line intersects the x axis indicates the year of

recruitment, and the end point of each line indicates the year of death (x

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.

BAC

n=59

Fire
1890

ML

n=105

Fire
1890

Fire
1936

BP

n=83

Figure 2 b   Lexis diagrams for the populations that show catastrophic mortality

resulting from a wildfire that did not cause local extinction. A solid vertical

black line indicates the date of the most recent known fire and a dashed

vertical black line indicates the most probable date of the recent fire (fire

evidence is missing).

HM — n=66 — Fire 1910
SS — n=63 — Fire 1865
NP — n=156 — Fire 1936
BRC — n=90 — Fire 1778

Figure 2 c   Lexis diagrams for the populations that showed little mortality from wildfire. A solid vertical black line indicates the date of the most recent known fire and a dashed vertical black line indicates the most probable date of the recent fire (fire evidence is missing).

OS

SP

MC

WR

Figure 2 d   Lexis diagrams for the populations that do not fit any of the other three

categories because of the uncertainty in the date of fire and the absence of

dead wood. A dashed vertical black line indicates that the most probable

date of the recent fire (fire evidence is missing).

JR

PE

wood predating the live trees (except for one individual in ML). In the population

reconstruction of BAC, the date of the fire is certain (as indicated by a solid vertical line at

1890), and its historical presence is confirmed by fragments of decomposed limber pine

collected at the site. The population reconstruction of ML shows only a single individual

surviving the 1890 fire. The 1936 fire left a fire scar on one of the individuals but did not
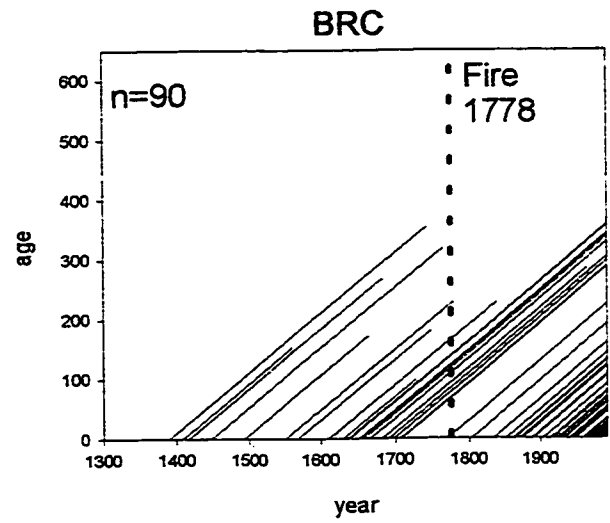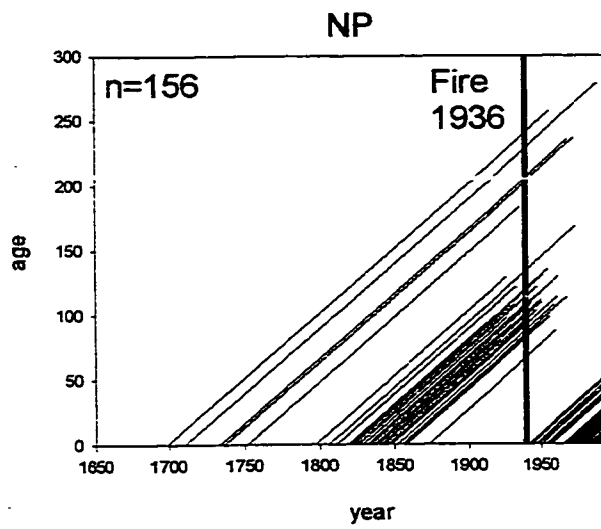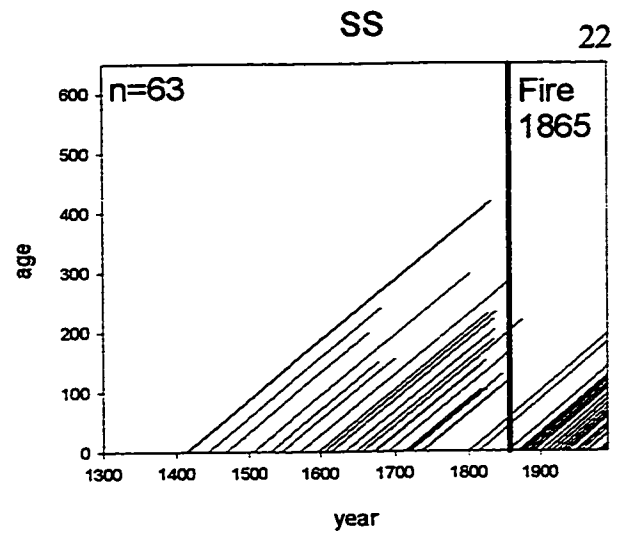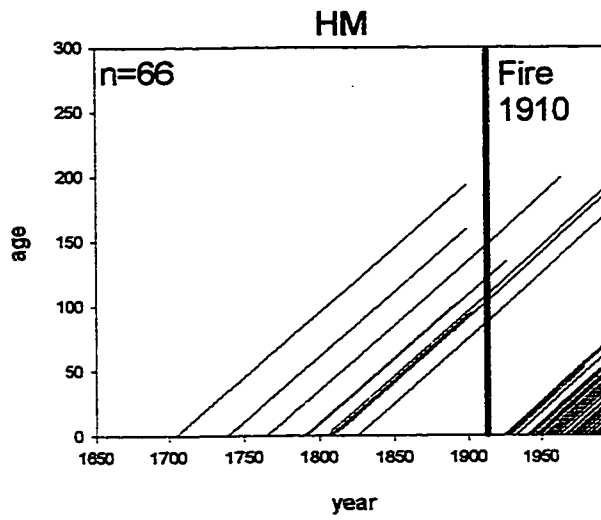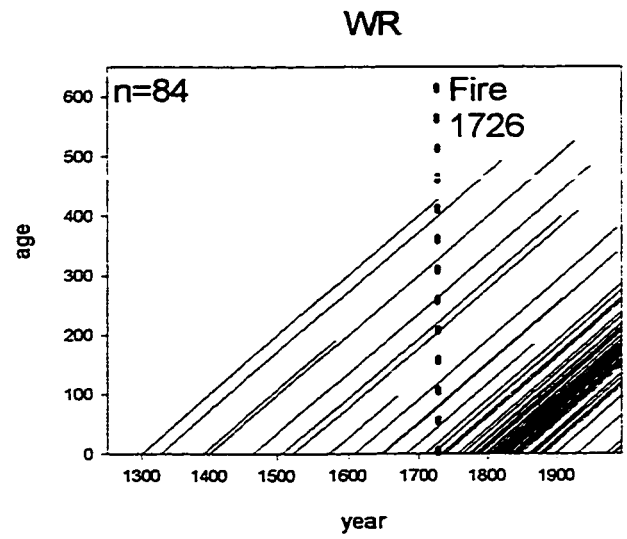
appear to significantly affect the rest of the population. The absence of pre-1820 wood

may indicate that the habitat had never been occupied before and that the current

population represents an invasion of limber pine onto the site. However, due to the

presence of one sampled individual established in 1820, a more likely explanation is that

the 1936 fire consumed any of the remaining, pre-1890 wood. The population

reconstruction of BP appears to represent the colonization of previously unoccupied

habitat beginning in the 1920's. The site had no clear evidence of fire and the surrounding

forests were last burned in the late 1600's or early 1700's.

The population reconstructions of HM, SS, NP and BRC appears to represent

populations that were disturbed by wildfire, but that did not go extinct (Figure 2 b). In

these four populations many individuals, regardless of their age, died in the fire or shortly

thereafter. These populations illustrate some of the difficulties in interpreting the local

dynamics when there has been wood decomposition and wood consumption by fire. For

example, in all four populations there is an absence of young trees prior to the fire, likely

because any young trees were killed by the fire. Also, notice in HM and SS that some

trees may have a conservative (i.e. earlier than in reality) date of death prior to the fire

because of the decomposition of the outer sapwood.

The population reconstructions of OS, SP, MC and WR appear to represent populations where fire has caused little mortality, with some individuals achieving hundreds of years of age (maximum age of a live tree was 641 years at SP) (Figure 2 c and Table 1). Since fire does not appear to play a significant role in structuring these populations, the periods without trees in the Lexis diagrams may truly reflect episodes of poor recruitment, or high mortality of young trees that have decomposed. Note that the periods without trees do not appear to be synchronous between the four populations.

The population reconstructions of JR and PE did not fit in any of the previous categories (Figure 2 d). 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 within the populations that are quite old (282 years old at JR and 180 years old at PE), and the few dead trees that are present are also old (153 years old at JR and 201 years old at PE). However, the lack of dead wood and the uncertainty in the fire dates makes it difficult to interpret both the absence of individuals during the late 1700's in PE and during the early 1800's in JR. Perhaps the wildfire was not intense enough to cause much mortality of the older trees, but killed smaller trees and partially consumed dead wood that has since decomposed.

Re-colonization following extinction.

For the eight populations in which the date of the last fire is known (BAC, ML, OS, NP, HM, SS, SP, and MC), the average time for recruitment to resume following disturbance was 6.0 years (S.E. +/- 1.5 years, n=8). The subset of these populations that showed the strongest evidence of extinction (i.e. BAC and ML), those that will be dependent on seed arrival from other populations, do not appear to take longer to re-initiate recruitment (6.5 years +/- 0.5 years, n=2) compared to the populations (i.e. OS, NP, HM, SS, SP and MC) with locally present source trees (5.8 years +/- 2.1 years, n=6). However, these are overestimates of the time for recruitment to resume because there will be high mortality among the newly recruited trees (as shown later in the seed germination experiments) as well as an age discrepancy between the root collar age and the age at which the tree was sampled (DesRochers and Gagnon 1997).

Local population dynamics.

Local Recruitment

The pattern of local recruitment (Figure 3) shows a steady recruitment of new trees into each of the local populations over time. This steady pattern of recruitment is controlled by the processes of seed dispersal, seed dormancy and seed and seedling survivorship. The length of seed dormancy determines *when* a new individual can germinate and recruit into the population. Seeds that can remain dormant for many years will form a seed bank, which will allow the local population to survive even if the current live trees are killed. Seed and seedling survivorship control *how many* individuals will

Figure 3   Periods of recruitment for the 13 limber pine populations. This graph

includes live and cross-dated dead individuals. Each vertical line indicates

the last known fire date in the population.

year of recruitment

recruit from the original number of seeds available.

Seed Dormancy and Germination

In the lab, the germination success of trials (Figure 4) with seeds that had been in

cold, dry storage for 5 to 17 months was 96% at 11°C (n=25), 87% at 15°C (n=30), 72%

at 20°C (n=25) and 48% at 5°C (n=25). When the cold, wet stratification treatment

followed cold, dry storage (performed only in the 5°C trial), the germination success

increased to 68%. The seed coat scarification treatment (performed only in the 20°C

trial), had no observable effect on germination success. Extended storage and subsequent

germination at 15°C had similar germination success as the 11°C and 20°C trials.

Seeds in the 5°C trial (Figure 4) took the longest time to initiate germination (28

days in cold, wet treatment and 29 days in cold, dry treatment), followed by the 11°C trial

(17 days) and 15°C trial (11 days). The 20°C trial initiated germination the fastest (9 days

for both scarified and non-scarified treatments). Although the 11°C trial was slower to

initiate germination, it had the highest rate of germination with 1.1 seeds germinating per

day. The rate of germination was slightly lower in the 20°C trial (0.9 seeds per day in the

unscarified treatment and 0.7 seeds per day in the scarified treatment) and the 15°C trial

(0.8 seeds per day). In these three trials (11°C, 15°C and 20°C) all the seeds had

germinated within a month and a half of planting. The rate of germination was much

slower in the colder 5°C trial (0.3 seeds per day in the cold, dry treatment and 0.4 seeds

per day in the cold, wet treatment), with some seeds continuing to germinate two and a

Figure 4   The rate of germination of limber pine seeds exposed to different

treatments as indicated.

half months after planting.

The field germination experiment (Figure 5) was designed to examine germination under field conditions and the amount of seed predation. Seeds that were covered with wire mesh to exclude predators had a winter survival and spring germination success of 64.2% (n=81). However, the seeds that were in uncovered pots, and thus available for predation, had a winter survival and germination success of 2.4% (n=90).

Seedling Survivorship

Following germination in the lab at 15°C (Figure 6), the seedlings increase the length of the radicle at a rate of 1.4 mm per day, reaching a length of 70 mm in approximately 50 days. After 50 days, root growth was predominantly in the form of lateral roots.

Seedling survivorship in the field (Figure 5) decreases after germination (May) at a constant rate of 9 individuals every three weeks, until approximately 100 days (mid August), when mortality decreases to 2 individuals every three weeks. By December, only 15% of those seeds that germinated were still alive (5 seedlings). The data on establishment is limited in that only a single set of planted seeds were followed through one growing season.

Figure 5   The survivorship of seeds from the time of planting in September 1996,

through germination (May 1997), the first growing season (summer 1997)

and second winter. Covered seeds (solid line) were planted in pots that

were protected with wire mesh to prevent predation of seeds. The

uncovered seeds (dotted line), were planted in pots that were not protected

with wire mesh. The error bars indicate the standard deviation around the

estimate.

Figure 6   Radicle elongation rate after germination for four seedlings. Radicle length

is scaled by dry seed weight to eliminate embryo size-related effects on rate

of growth.

Local Mortality

The field establishment study examined early seedling survival over the first growing season. After the initial establishment there is a period of time in which mortality cannot be estimated because small, young individuals may have died and decomposed and therefore cannot be detected in the population reconstruction. The age of the youngest dead individuals detected in the population reconstructions are between 40 and 60 years of age (the difference between the date the cohort recruited and the date for which mortality is first estimated in Figure 7). Although the mortality of young trees cannot be estimated, it is likely very low because there was little evidence of mortality in the young populations of BP and NP. The age-specific mortality (Figure 7) within the five oldest post-fire cohorts of BAC, ML, WR and OS was low, ranging between 0.005 and 0.025. The fluctuations in mortality corresponded to fluctuations in summer temperatures (Figure 8). In BAC, ML and the two cohorts of OS, mortality peaks during the 1950's when there was a series of cold summers. The WR cohort was old enough to show a peak in mortality during the cold period of the 1890's, as well as a smaller peak in the 1950's.

Figure 7   The age-specific mortality for the five oldest, post-fire cohorts of four

populations. The years of recruitment for the cohort is shown in the

legend.

Figure 8   The ten year moving average of summer temperature (averaged over May,

June, July, and August) from 1891 to 1988 from Banff, Alberta (source

World WeatherDisc 1990).

DISCUSSION

The accurate reconstruction of local limber pine recruitment and mortality was used to indicate extinction events and recolonization, and therefore the existence of regional structure. The dates of recruitment and death for individuals were not inferred from a static age distribution, which is a more common method to examine population structure. Inferring population dynamics from a static age distribution, unlike the population reconstruction method, assumes that all the cohorts behave the same (Johnson et al. 1994). However, this assumption is rarely met because cohorts often experience different growing conditions, whether it be in the understorey or the canopy, and experience different climate conditions through time. Therefore, population reconstruction is a good method to examine local population dynamics.

This method of reconstructing a population's history has two important limitations. The first is that the success of the method depends on our ability to detect individuals that have died in the past. The detection and accurate dating of dead individuals is limited by the rate of wood decomposition. This decomposition limit is roughly equivalent to the earliest date that trees can be accurately cross-dated. However, the individuals that have been dead for a long time or destroyed by fire, as well as small individuals that have already decomposed, will be missing in the reconstruction. The absence of these individuals underestimates the *amount* of recruitment and mortality, particularly the mortality of young trees in the population. To compensate for this

limitation, additional experiments should examine early survivorship during dormancy, germination and first year establishment. Ideally these experiments should be repeated over several years to determine the variation in the force of mortality (i.e. weather, predation, herbivory).

The second limitation of the population reconstruction is in the use of tree cores to determine the date of recruitment. The age of a tree is most accurate if determined at the root collar (i.e. root-shoot interface) where the initial growth rings will be found. This is often below the organic matter at the mineral soil interface. DesRochers and Gagnon (1997) found that by cross-dating black spruce (*Picea mariana*) trees down to the root collar, an additional 3-19 years were added to the age estimates taken from 30 cm above the mineral soil (typical coring height). The inability to detect these first few years means the true *date* of recruitment is earlier than what the age at coring height indicates, creating false time lags in the recruitment.

Wildfire as the extinction mechanism in the limber pine populations.

In the limber pine forests of the Kananaskis Valley, fire caused detectable mortality in 4 of the 13 populations. The populations that were affected by fire displayed a range of mortality, from only the youngest trees killed (HM), to many individuals killed (NP, SS), to local extinction (BAC). Fire behaviour often explains patterns of tree mortality (Johnson 1992), but there has been no observations of fire behaviour within these open-canopy limber pine forests. However, a post-burn description of a 1975 lightning initiated

fire in krummholz whitebark pine (*Pinus albicaulis*, Engelm.) (Tomback 1986), a

subalpine species similar to open-canopied limber pine, indicated that all the burned trees

were defoliated and killed, with some trees reduced to charred pieces [presumably the

trees dead at the time of the fire]. The few trees that escaped fire damage were located in

the center of the burn and on the ridgetop.

The fire behaviour in limber pine may have parallels to fire behaviour in black

spruce-lichen woodlands (*Picea mariana*, (P.Miller) B.S.P. - *Stereocaulon paschale*, (L.)

Hoffm.). In both limber pine forests and black spruce woodlands there is low tree density

on well-drained substrates. These open conditions lead to tree crowns with low branches

in both species. Fire may spread faster on the steep slopes which limber pines occupy,

because of the greater angle of flame tilt (Van Wagner 1977). However, an uneven rate of

spread is possible in the limber pine forest because of patchy ground cover, as opposed to

the uniform rate of spread through the continuous lichen ground cover of the spruce

woodlands (Alexander et al. 1991). Limber pine also occurs in small, isolated patches

often bordering closed-canopy forest on the downslope boundary, and open scree or

bedrock cliffs on the upslope boundary. Unfortunately, the change in fire behaviour

between forest types with different tree densities and different fuels is not well understood.

A range of fire intensities cause different fire behaviours in the black spruce-lichen

woodlands (Alexander et al. 1991). Surface fires cause negligible crown loss, intermittent

crown fires cause higher amounts of crown loss, and active crown fires cause complete

crown loss and extensive tree mortality. Surface fires occur under calm conditions. Intermittent crown fires occur when flame length increases with higher wind speeds, promoting short-distance spotting beyond the fire front. The preheating caused by spotting increases fire intensity and spread. Crown fires occur when tree density is high enough that the zone of radiation from one tree reaches the edge of the next (Alexander et al. 1991). A similar range in fire behaviour has been observed in another system similar to limber pine, the open pinyon pine-juniper woodlands (*Pinus monophylla,* Torr. & Frém. - *Juniperus osteosperma,* (Torr.) Little.) during prescribed burns (Bruner and Klebenow 1979).

If the fire behaviour in limber pine forests is similar to the fire behaviour observed in spruce-lichen woodlands, wildfires of varying intensities are possible. The most intense fires in these limber pine forest would likely be the wildfires that rapidly spread upslope from the closed canopy forests. In the 1936 Galatea fire in the Kananaskis Valley, crown fires in the closed-canopy forests were predicted to have been in excess of 30 000 kW/m (Fryer and Johnson 1988). Crown fires between 13 000 and 32 000 kW/m have also been observed in spruce-lichen woodlands (Alexander et al. 1991). Fires within this range of intensity would cause complete canopy mortality (Johnson 1992). Passive crown fires that are less intense will only cause intermittent tree mortality: larger trees with thicker bark and higher branches are more likely to survive (Van Wagner 1973). Low intensity surface fires may cause fire scars on larger trees, but small trees with thin bark and low branches will die (Gutsell and Johnson 1996). Therefore, the probability of extinction by

wildfire of a local limber pine population is influenced by characteristics of the local population (e.g. slope, tree density, tree size distribution and fuel loads), climate conditions prior to the fire (e.g. fuel moisture and wind speed), fire frequency and the spatial attributes of the limber pine populations (e.g. proximity to closed-canopy forest and degree of isolation). In effect there will be spatial differences between local populations in their resistance to extinction.

Clark's nutcracker as the recolonization mechanism in the limber pine populations.

Recolonization of limber pine populations occurred quickly after extinction by wildfire. In fact, recolonization probably occurred sooner after wildfire than the data seems to show, given the limitations of the reconstruction method. The rapid recolonization appears to be a result of seed dispersal by the Clark's nutcracker from other local populations and not by the germination of the seed bank.

There have been observations recorded in the literature that confirm that the Clark's nutcracker will bring seed to areas that have been burned (Lanner and VanderWall 1980, Tomback 1986). Studies on the foraging and caching behaviour of the Clark's nutcracker also indicate that the nutcrackers carry seed long distances (VanderWall and Balda 1977 and Tomback 1978). Personal observations during the fall harvest confirmed that birds foraging in an area often left the local area to cache. The rapid recolonization and the steady pattern of local recruitment suggest that seed dispersal is not limiting to this system. Basic studies on the size of resource territories, the amount of overlap in resource

territories with other birds and movements within the territories are essential to determine

the amount and distribution of seed between populations. However, determining the rate

of seed dispersal and the distribution of dispersed seed between local populations was

beyond the scope of this study.

Limber pine does not form a seed bank because of high seed predation rates and

high germination success, even though the seeds can remain viable for a long period of

time (greater than 17 months). Limber pine seeds likely suffer high predation (97.6%), in

part because of their high nutritive value (30 kJ/g) and large size (at least 0.07 g) which

make them a preferred food source (VanderWall and Balda 1977, Hutchins and Lanner

1982). The high germination success of limber pine over a range of temperature

conditions also suggests that seed banks do not form. Limber pine germination appears to

fit some of the generalities of tree germination, with slower germination rates at colder

temperatures and germination rates linearly related to temperature (Farmer 1997). Like

other pine species, limber pine did not require special treatments in order to germinate

successfully (Young and Young 1986).

The role of local population dynamics in limber pine.

The local limber pine populations showed no evidence of prolonged negative

growth rates that could result in demographic extinction. This is likely the result of steady

recruitment and low mortality in the local population. Local recruitment was shown to be

steady despite the high predation and high establishment mortality. High establishment

losses are common among young seedlings of other tree species and are usually the result

of either heat damage to the hypocotyls or root growth that cannot keep up with rates of

soil moisture depletion (Farmer 1997). Haig et al. (1941) found that heat mortality was

greater than drought mortality at sites with complete exposure to the sun for a variety of

conifer species. However, Pomeroy (1949) found that slow radicle growth rate into

favourable substrate where water could potentially be obtained accounted for 83% of

seedling mortality. It is difficult to determine which may have caused seedling mortality in

these limber pine populations. However, in the lab experiment the radicle of seedlings

elongated at a rate of 1.4 mm per day at 15°C under constantly moist conditions. If the

summer moisture layer was at a depth of 5 cm it would take 36 days to reach that layer.

Therefore, since germination begins in May, there is plenty of time to reach a secure

moisture layer by the driest part of the summer in July and hence heat injury to the

hypocotyl may be more important.

Once limber pine became established, age-specific mortality was low, ranging only

between 0.005 and 0.025. The cohort age-specific mortality calculated by Johnson and

Fryer (1989) for closed-canopy subalpine species was higher than for limber pine. They

ranged from 0.002 to 0.9 for lodgepole pine and 0.03 to 0.3 for Engelmann spruce.

However, post-establishment mortality of limber pine does appear to fluctuate with

summer temperatures, with increased mortality during cold summer periods.

It was common to have individuals that lived greater then several hundred years

(WR, SP). Therefore, even a complete cessation of recruitment would mean a long lag time before the population would go extinct because of the long survival time of the remaining individuals (Eriksson 1996). Adult mortality would have to be much higher in order for negative growth rates to lead to local extinction.

The role of regional dynamics in limber pine

For there to be regional population structure the local populations must be sufficiently isolated so that all the local populations do not go extinct at once, yet not isolated enough that there is little chance of dispersal between the local populations. A population's isolation is a function of not only the geography of the habitat, but also of the seed dispersal distribution. For example, populations that are close to each other could still be isolated if seeds do not disperse far. Conversely, populations that are far apart may not be isolated if seeds easily disperse a great distance. From this definition a range of population structures are conceivable. At one extreme, if dispersal is extensive over the entire area, a large continuous or perhaps patchy population is formed (Harrison 1991). At the opposite extreme there will be many small and essentially independent populations (Harrison 1991). In between are the types of populations in which there is a sufficient amount of dispersal such that the local seed production can not predict the amount of recruitment. In this case, recruitment within the local population is the result of both locally produced seed and seeds from other populations within the dispersal region.

The limber pine of the Kananaskis Valley show evidence of regional structure.

Extinction is rare and is caused by wildfire disturbance, not from internal negative growth

rates. It was evident that the limber pine populations sampled are isolated enough that

they could not all be affected by the same fire. Even between populations the amount of

mortality that results from a wildfire varies. For limber pine, the most intense fires are

likely those that spread upslope from the closed-canopy forest. Therefore, the lower

elevation populations that are closer to the closed-canopy forest may have a higher

probability of extinction then the isolated or high elevation populations. Thus, the limber

pine appear to exhibit core-satellite regional extinction dynamics where some populations

have lower extinction probabilities (the core populations) than other populations (the

satellite populations) (Boorman and Levitt 1973). The local extinction probabilities may

also change over time if there is a shift in the fire frequency or if there are additional types

of disturbance (e.g. white pine blister rust or land clearing).

Seed dispersal between local limber pine populations appears to be high. This is

inferred from the rapid recolonization following extinction, and the subsequent recruitment

within a young population before local trees are old enough to produce seed. The pattern

and distance of seed dispersal by the Clark's nutcracker will determine if all the local

populations act as a single population or if they are isolated. Within the local population,

the amount of dispersal determines how much of the recruitment is the result of external

sources. The seed dispersal distribution for limber pine is not known, but behaviour

studies indicate long dispersal distances (22 km) are possible, although shorter dispersal

distances of several kilometers are more common (VanderWall and Balda 1977, Tomback

1978). Therefore, for most local populations within a bird territory (or home range), the amount of seed dispersed between local populations will be quite high, although a few peripheral areas (i.e. low priority cache areas) may not receive many seeds. For local populations located in different bird territories, the exchange of seed will be low, except perhaps in areas of territory overlap. Consequently, fluctuations in the Clark's nutcracker population could alter the amount of dispersal between the local populations.

In conclusion, despite the apparent spatial isolation of local limber pine populations, dispersal appears to be more than adequate to allow for prompt recolonization following wildfire in the local populations sampled. However, since the only sites that were sampled had live limber pine trees, it is possible that there may be sites that went extinct that have not been recolonized, thus potentially underestimating the amount of extinction. Additionally, the apparent high rates of dispersal between populations is the basis for the conclusion that dispersal is an important consideration in the interpretation of the local dynamics. However, further details on the limber pine seed dispersal distribution are required to indicate the specific effects of dispersal on the regional population structure and local recruitment.

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