Possible role of disturbance in shaping the northern distribution of *Pinus resinosa*

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Abstract. The objective of this study is to determine the factors responsible for the distribution of *Pinus resinosa* (red pine) at its northern limit in northwestern Québec. *Pinus resinosa* is found only on islands and protected lake shores at its northern distribution boundary. The influence of climate on the germination of *P. resinosa* seed and on the phenology of *P. resinosa* was investigated in the Lake Duparquet region of northwestern Québec. The results indicate that *P. resinosa* seed readily germinates at island- and inland sites, which indicates that germination is not responsible for the distribution of *P. resinosa* in the Lake Duparquet region. Also, cones and seeds developed normally at island sites and an inland plantation, which suggests that seed production is not hindering the expansion of *P. resinosa* . These results, together with other studies in the literature, suggest that no climatic factor could explain the present distribution of *P. resinosa* nor its northern limit. The fire regime appears to be responsible for the restriction of *P. resinosa* to lake environments and hinders the northward expansion of *P. resinosa*. The typical crown fire regime of the boreal forest is not conducive for *P. resinosa* regeneration and restricts the species to fire-sheltered locations such as islands and protected lake shores.

Keywords: Climate; Fire regime; Germination; Québec; Phenology; Red pine.

Introduction

Many factors may be responsible for the northern distribution limit of boreal tree species. These factors include climate, disturbance, soil and nutrient status, and competition. Several studies suggest that this limit is controlled by climatic factors, including winter minimum temperature and growing season warmth (Sakai & Weiser 1973; Woodward 1987; Arris & Eagleson 1989). For many tree species the critical phase in the life cycle will be the reproduction phase. For example, Black & Bliss (1980) determined that there was insufficient warmth during the growing season for *Picea mariana*

seeds to germinate at its northern limit. Disturbance regimes, particularly fire in the boreal forest, have been responsible for the distribution and abundance of vegetation (Payette 1992; Suffling 1995). Bergeron & Gagnon (1987) were the first to hypothesize that the crown fire regime in the boreal forest was limiting the northward expansion of *Pinus resinosa* (red pine).

The objective of this paper is to illustrate the possible role of climate and fire disturbance in shaping the northern limit of boreal forest tree species using *P. resinosa* as an example. *P. resinosa* extends from southern Manitoba eastward to Newfoundland and as far south as West Virginia (Burns & Honkala 1990; Roberts & Mallik 1994). In northwestern Quebec, *P. resinosa* reaches the northern limit of its range, whereas it occurs only scattered within 300 km of this limit (Haddow 1948). The species is typically found near lakes, either on islands or protected lake shores (Van Wagner 1970; Bergeron & Gagnon 1987; Bergeron & Brisson 1990; Bergeron 1991).

The fire regime is an integral part of the ecology of *P. resinosa*. The fire regime has six components: (1) fire intensity, (2) fire frequency, (3) timing (season) of the fire, (4) fire extension, (5) fire severity (duff removal) and (6) fire type (surface or crown) (Weber & Flannigan 1997). Recent studies have confirmed that *P. resinosa* is a fire-dependent species (Bergeron & Brisson 1990; Engstrom & Mann 1991; Mallik & Roberts 1994; Roberts & Mallik 1994). This dependence on fire is the result of several factors. First, the species is intolerant of shade and requires at least partial removal of the canopy for regeneration. Second, *P. resinosa* prefers mineral soil exposure for seedling establishment. Lastly, competition is a major hindrance for regeneration and needs to be temporarily removed during the regeneration step. Fire is the most effective natural agent to fulfil all these requirements. Fire can open up the canopy, reduce or eliminate the organic layer and remove the competition. Mature *P. resinosa* has a thick bark and is able to

survive all but the most intense fires (Johnson 1992). The ideal disturbance environment for *P. resinosa* is one of semi-regular moderate-intensity surface fires.

We examine two hypotheses regarding the northern distribution of *P. resinosa*. The first hypothesis is general and proposes that some climatic factor adversely affects the species during a critical development stage. The second, more specific hypothesis forwarded by Bergeron & Gagnon (1987) and Bergeron & Brisson (1990) states that the crown fire regime (lethal) that prevails in the boreal forest limits the northward distribution of *P. resinosa*. We will illustrate the possible role of climate and fire regime in synthesizing past research and by presenting some new data. This paper will test, in part, the climate hypothesis as it relates to climate interaction with reproductive processes in *P. resinosa*.

Methods

Two experiments were carried out in the Lake Duparquet region, NW Québec (79° 21' 79° 13' W and 48° 26' 48° 30' N). The first was a germination experiment that was located at two sites, one on an island in Lake Duparquet (Ile à Jacques) and one ca. 10 km northwest of Lake Duparquet near the town of Roquemaure. The second experiment was a phenology experiment that used *P. resinosa* trees from two islands in Lake Duparquet along with *P. resinosa* trees in a plantation ca. 15 km northwest of Lake Duparquet. The absence of natural populations of *P. resinosa* inland meant that trees from a *P. resinosa* plantation had to be used in the phenology study.

The germination experiment used three provenances of *P. resinosa* seed along with one seed source of *P. banksiana* (jack pine) (Table 1). *Pinus banksiana* seed was included as a control because this species is found naturally at both sites, around the lake and inland, and

has a northern range limit exceeding that of *P. resinosa*. At both sites seeds were placed in a sand/peatmoss mixture contained in a 1.2×2.4-m frame in the autumn of 1991 with no vegetation present. The seeds were sited in the fall rather than the spring to simulate the actual seed fall that occurs in autumn. Both sites were situated in a clearing. Four randomly assigned groups of 50 seeds for each of the four provenances were placed on top of the sand/peatmoss mixture in the 1.2×2.4-m area. The seeds were covered with screening in order to prevent herbivory by birds or animals. Germinated seeds were counted in May and June of 1992. Ungerminated seeds were tallied as well to insure the total of each group of seeds equalled 50.

For the phenology study, 10 dominant trees were selected at the inland plantation and also on two islands on Lake Duparquet. Trees at the plantation site were 25 yr old. Similar aged trees were selected on the islands. These trees were at an age when *P. resinosa* trees begin to reach sexual maturity and are capable of seed production. Older trees (50 - 60 yr of age) would have been preferable, but no older inland plantations were present. Male and female cones were counted on the top eight whorls of each tree during the spring/summer of 1991 and 1992 at weekly intervals. Cone development is a two-year process with fertilization occurring in July of the second year (Lyons 1956) more than one year after pollination (Dickman & Kozlowski 1969). After fertilization, seeds from the female cones will be released in the autumn. Insect and disease damage to the cones were recorded.

At each site a weather station was established. Parameters recorded included the air temperature, relative humidity, wind speed and direction at 10 m above-ground and precipitation every hour on a Campbell Scientific CR10 data logger. The weather was monitored in 1991 and 1992 from early May to early October.

Table 1. Seed lot characteristics.

Provenance	Year collected	Origin	Latitude (°)	Longitude (°)	Elevation a.s.l. (m)	Weight per 1000 seeds(g)	Percent germinated
1	83	Alexander Bay, Nfl	49	54	120	7.49	95[a]
2	89	Chalk River, Ont.	46	77	180	9.48	85
3	90	Upper Peninsula, MI	47	86	240	10.33	97
4[b]	78	Garibaldi Township, Ont.	47	81	380	3.17	95

[a] Percentage germinated following a standard test conducted at the National Tree Seed Centre, Petawawa National Forestry Institute. The standard test for *P. resinosa* includes four replications of 100 seeds with a 16-h photoperiod, day temperatures of 30 °C (8 h) and night temperatures of 20 °C. Seeds are reported as having germinated only if they have high vigour, i.e., the radicle must be at least four times as long as the seed after 3 weeks.
[b] Provenances 1 - 3 are *P. resinosa* and provenance 4 is *P. banksiana*.

Results and Discussion

Results from the field germination are shown in Table 2. A total of 308 seeds were not accounted for at the inland site whereas 117 seeds were missing at the island site at the end of the experiment. A total of 800 seeds were sown at each site. Results are presented in two ways, (1) as the percentage of germinated seeds, using only the seeds that were located by the end of the experiment, and (2) as the percentage germinated, using all the seeds that were sown in the previous fall. Percent germinated ranges from 91 to 100 % using the located seeds versus 53 to 89 % for the total number of seeds sown.

Germination of *P. resinosa* seeds in large quantities occurred at both locations. In terms of the percentage of germinated seeds there is little difference between the two sites (Table 2). There was more germination at the island site if related to the total number of seeds sown in the experiment. However, with this method of assessment it is assumed that all the missing seeds failed to germinate. Anyway, germination occurred at both sites. The provenance of the seed had little effect on the germination results; this is not surprising given that the species is genetically depauperate (Fowler & Lester 1970). Seed of *Pinus banksiana* readily germinated at both sites. The larger number of missing seeds at the inland site cannot be explained. Seeds were missed due to settling and shifting in the soil during the extended time period the seeds were in the field and perhaps to some predation despite the preventive screening.

Our germination results are from one year only and cannot directly account for factors like intermittent drought years. However, Bergeron & Brisson (1994) assessed regeneration of *P. resinosa* as a function of climate for over 70 yr in our study area and found a correlation between drought and recruitment but regeneration was still occurring. Also, our results from the germination experiment support the laboratory results from Flannigan & Woodward (1993), namely that at the northern limit of *P. resinosa* lack of germination is not the factor determining the species range limit. Nor can the germination results explain the absence of *P. resinosa* inland at the northern extreme of the range of *P. resinosa*.

Phenological data show that more female seed cones were present at the island site whereas many more male conelets were present at the inland site (Table 3). A higher percentage of female cones reached maturity at the island sites – 40 % of 496 cones (1992 cones / 1991 conelets) – as compared to the inland site – 20 % of 167. The rate of development of both male pollen cones and female cones during the growing season was the same at all locations.

The phenology experiment shows that cones are produced at both sites. The difference in cone production between the two sites could be a response to different levels of sexual maturity between the trees at the two sites or perhaps due to differences in stand density (Stiell 1971). Stiell (1988) related cone production to height of the tree and previous cone production. The trees were all about the same height (8 - 10 m) therefore this attribute could not account for the difference in cone production though the trees in this study were young and still growing rapidly and there were no data on previous cone production. The numbers of male and female conelets produced in 1991 and 1992 were very similar at the different sites. No comparison of the quantity of mature cones is possible as they were not counted in 1991. A small number of cones were sampled from trees at both sites. Seed from these cones were viable, which is consistent with findings in the literature on seed viability at the northern limit of *P. resinosa*. Butson et al. (1987) found seed produced by a small stand of *P. resinosa* near Lake Nipigon was viable and Roberts (1989) found viable seeds in Newfoundland with the same germination and similar characteristics as shown in provenance 1.

According to the literature, seed production is quite variable with a good cone crop every three to 12 years (Horton & Bedell 1960). Unless data collection continues for a number of years, the classification of 1991 and

Table 2. Field germination results.

	% Germinated of seeds found	% Germinated (total seeds)
Island		
Provenance 1	100	89
Provenance 2	93	83
Provenance 3	99	89
Pinus banksiana	97	74
Inland		
Provenance 1	98	60
Provenance 2	100	53
Provenance 3	99	70
Jack Pine	91	55

Table 3. Phenology data.

	Male conelet	Female conelet	Cones
1991			
Island	486	496	n/a[a]
Inland	2968	163	n/a
1992			
Island	235	508	198
Inland	2726	167	32

[a] n/a represents not available. No mature cones were tallied in the first field season (1991).

1992 data will remain unknown. Some studies have shown that insects can damage 25 to 50 % of the cones (Mattson 1978). Only less than 1 % of the cones were damaged by insects in this study. At the weather stations two late frosts were recorded at the inland site in June 1992 that did not occur at the island sites. However, the frosts were light with temperatures of – 1 °C and did not coincide with the frost-sensitive period of the female flower. Schooley et al. (1986) have shown that late spring frosts can reduce the cone crop production of *P. resinosa* if the frosts coincide with the frost-sensitive period of the female flower. Indications from only two years of climate data suggest that frost is more likely to occur inland, which would be expected as a large body of water such as Lake Duparquet (ca. 5 × 5 km) would have a moderating effect on extreme minimum temperatures. However, the killing of female flowers by spring frost does not appear to be the mechanism that is restricting *P. resinosa* to the lake environment.

Results from these experiments suggest that seed germination and cone and seed production are not responsible for the northern limit of *P. resinosa* nor do these mechanisms explain the absence of *P. resinosa* in areas away from lakes.

Alternative explanations for the present distribution of *P. resinosa* might involve other climatic factors. Many studies suggest that the northward limit of a tree species is controlled by the minimum temperature that is regularly experienced (Sakai & Weiser 1973; George et al. 1974; Sakai 1978; Larcher & Bauer 1981; Woodward 1987; Arris & Eagleson 1989; Woodward 1990). Sakai & Weiser (1973) have shown that *P. resinosa* twigs were able to survive exposure to temperatures of – 80 °C, which would guarantee winter survival in any forest region of Canada. Flannigan (1993a) showed that entire seedlings subjected to temperatures of – 60 °C remained undamaged. Lack of summer warmth also could be an influencing factor. Kozlowski & Borger (1971) found that growth of *P. resinosa* seedlings was restricted when mean growing season temperatures were 10 °C or lower. However, summer temperatures average over 15 °C at the northern limit of *P. resinosa* in northwestern Québec (Anon. 1993). Bergeron & Brisson (1994) found no relationship between *Pinus* regeneration and low temperature, but did find that drought hindered regeneration. As the occurrence of drought does not increase northward, they concluded that *P. resinosa* was not limited by climate. Also, the presence of healthy plantations of *P. resinosa* 50 km north of the natural limit of *P. resinosa* suggests that climate does not hinder the growth of *P. resinosa*.

Other possible controls of the distribution of *P. resinosa* include habitat availability, competition and disturbance. *Pinus resinosa* is most commonly found on sandy or gravelly soils on terrace and outwash plains, but rock outcrops and lacustrine clays will also support the species. *Pinus resinosa* commonly occurs and grows satisfactorily on soils of low to moderate fertility. In the Lake Duparquet region there are numerous available sites for *P. resinosa* away from the lake environment (Bergeron et al. 1983); consequently, lack of habitat is not hindering the expansion of the range of *P. resinosa*. Farther north, site availability could be more of a problem although potential upland sites still represent a significant portion of the landscape (Gauthier et al. 1996). Competition does not appear to be a limiting factor as there are fewer competitors in comparison to more southern sections of the *P. resinosa* range where this species is more abundant and is not restricted to lake environments. However, the role of competition was not explicitly tested and cannot be dismissed completely without further research.

The second hypothesis that the fire regime is limiting the distribution of *P. resinosa* (Bergeron & Gagnon 1987; Bergeron & Brisson 1990) appears to be the best explanation. This hypothesis could not be tested explicitly, but by the process of elimination it appears to be the most plausible explanation. Fire regime is important in determining the northern limit of some tree species. Desponts & Payette (1992) showed that at the northern limit of *P. banksiana* a fire interval shorter than the average life time of *P. banksiana* is required to perpetuate *P. banksiana* populations. Payette & Gagnon (1985) show that both climate and fire regime are responsible for the tree line in Québec. Johnson (1992) stated that where fire occurs, fire behavior and population recruitment may control population abundance and distributions.

The distribution of other species in this region are also influenced by the fire regime. Diotte & Bergeron (1989) found that *Juniperus communis* is restricted to island sites because of the fire regime. Fire regime appears to be a key factor in the distribution and abundance of *P. resinosa* and is intimately linked with *P. resinosa* abundance. This close link is expected given that the regeneration requirements are typically and often most adequately met by fire; in particular, preparation of the seed bed, opening of the canopy and the removal of competitors and because *P. resinosa* is adapted to fire (through a flammable and thick bark). Flannigan (1993b) found that 70 % of the variation in the *P. resinosa* abundance (volume per unit area) was explained by fire regime factors.

The present day northern limit of *P. resinosa* could be the result of an earlier expansion (Horton & Bedell 1960) during a period when the disturbance environment was favourable for the regeneration and growth of *P. resinosa* . This expansion probably occurred during a

warm period ca. 7000 - 3000 yr before present (Liu 1990). This period was probably both wetter and milder than the present day climate, which resulted in a favourable fire regime of semi-regular moderate-intensity surface fires. We have no evidence of this expansion because of the difficulty in discriminating between *P. resinosa* pollen and *P. banksiana* pollen. After the period which we believe to be the favourable period for expansion ended, *P. resinosa* may have been eliminated over time from all sites that were unfavourable, i.e. from sites where the fire regime had become one of frequent intense forest fires (stand-replacing crown fires), a regime which is typical of the present day boreal forest. This left *P. resinosa* scattered in areas where forest fires would not be as intense. In particular *P. resinosa* seems to be found close to lakes near its northern limit, either on islands or protected mainland lake shores (Van Wagner 1970; Bergeron & Gagnon 1987; Bergeron & Brisson 1990; Bergeron 1991). Even in these favourable habitats, *P. resinosa* is not common and is not in equilibrium with the present fire regime (Bergeron et al. 1997). The present day *P. resinosa* populations are probably remnants of the earlier expansion. The existing populations of *P. resinosa* near the northern limit seem to be maintaining themselves i.e., regeneration approximates senescence (Bergeron & Gagnon 1987; Butson et al. 1987).

Climate has not directly limited the migration of *P. resinosa* and if the fire regime was more conducive to *P. resinosa* the species probably would be able to expand its range many hundreds of kilometers northward before climatic variables would directly influence the distribution of the species. However, the fire regime is very dependent on the climate (Swetnam 1993) and one could argue that climate is indirectly controlling the distribution of the species through the fire regime. If the climate does change, as is simulated by the General Circulation Models, with warmer and wetter summers the fire regime would be suitable for the migration of *P. resinosa* into sites away from the lake environment and would allow *P. resinosa* to migrate northward (Flannigan & Woodward 1994). The present distribution of *P. resinosa*, at its northern limit in the Lake Duparquet region of Québec, is probably a result of the fire regime.

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