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Résumé de l'article

Les structures d'âge des populations de pin rouge et de pin gris, échantillonnés dans deux sites du lac Duparquet (Abitibi), ont été corrélées avec la moyenne annuelle des températures et les précipitations annuelles enregistrées à Iroquois Falls, entre 1913 et 1986. Les structures d'âge montrent un patron commun caractérisé par une régénération faible avant 1930, un pic de régénération débutant au cours des années 30, une baisse importante autour de 1950, un second pic de régénération, quoique de moindre importance, dans les années 60 et une décroissance importante après 1970. L'abondance de la régénération est généralement positivement corrélée avec les précipitations et négativement corrélée avec la température, indiquant ainsi que le recrutement des individus serait négativement influencé par une couverture nivale faible ou une sécheresse prolongée. L'absence d'une corrélation positive avec la température indique que la limite nord du pin rouge serait déterminée par un changement dans le régime des feux et non par une baisse des températures.

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EFFECT OF CLIMATIC FLUCTUATIONS ON POST-FIRE REGENERATION OF TWO JACK PINE AND RED PINE POPULATIONS DURING THE TWENTIETH CENTURY

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ABSTRACT The age structure of two mixed red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.) forests located at Lac Duparquet, northwestern Québec, were correlated with mean annual temperature and total precipitation recorded at Iroquois Falls for the period between 1913 and 1986. The age structures of both pine species showed a common pattern of regeneration characterized by low regeneration before 1930, an important regeneration peak starting around the 1930s, a dip in the age structure around 1950, a second, though less important, regeneration peak in the 1960s, and an important drop, especially for red pine, after 1970. In general, high regeneration rates were positively correlated with precipitation and negatively with temperature, suggesting that pine recruitment is negatively affected by low snow cover and/or drought. The absence of correlation with temperature suggests that the red pine northern limit may be controlled more by a change in the fire regime than by increasing temperature.

RÉSUMÉ *Les conséquences des fluctuations climatiques au cours du XX^e siècle sur la régénération après feu du pin rouge et du pin gris.* Les structures d'âge des populations de pin rouge et de pin gris, échantillonnés dans deux sites du lac Duparquet (Abitibi), ont été corrélées avec la moyenne annuelle des températures et les précipitations annuelles enregistrées à Iroquois Falls, entre 1913 et 1986. Les structures d'âge montrent un patron commun caractérisé par une régénération faible avant 1930, un pic de régénération débutant au cours des années 30, une baisse importante autour de 1950, un second pic de régénération, quoique de moindre importance, dans les années 60 et une décroissance importante après 1970. L'abondance de la régénération est généralement positivement corrélée avec les précipitations et négativement corrélée avec la température, indiquant ainsi que le recrutement des individus serait négativement influencé par une couverture nivale faible ou une sécheresse prolongée. L'absence d'une corrélation positive avec la température indique que la limite nord du pin rouge serait déterminée par un changement dans le régime des feux et non par une baisse des températures.

ZUSAMMENFASSUNG *Der Einfluss klimatischer Schwankungen im 20. Jahrhundert auf die Regenerierung von zwei Graukiefer- und Rotkiefer-Populationen nach einem Brand.* Die Altersstrukturen von zwei Wäldern mit Rotkiefer (Pinus resinosa Ait.) und Graukiefer (Pinus banksiana Lamb.) am See Duparquet, nordwestliches Québec, wurden mit der durchschnittlichen Jahrestemperatur und den gesamten gemessenen Niederschlägen an den Iroquois Falls für die Zeit zwischen 1913 und 1986 in Beziehung gebracht. Die Altersstrukturen beider Kiefernarten wiesen ein gemeinsames Muster der Regenerierung auf, charakterisiert durch eine niedrige Regenierung vor 1930, einen bedeutenden Regenerierungshöhepunkt, der in den 30er Jahren beginnt, ein Sinken der Altersstruktur um 1950, einen zweiten, wenn auch weniger bedeutenden Regenerierungshöhepunkt in den 60er Jahren und einen bedeutenden Rückfall, besonders der Rotkiefer, nach 1970. Im allgemeinen wurden hohe Regenerierungsraten positiv mit Niederschlägen und negativ mit Temperatur in Beziehung gebracht, so dass man annehmen kann, dass die Zunahme von Kiefern durch eine niedrige Schneedecke und/oder Trockenheit negativ beeinflusst wird. Das Fehlen einer welchselseitigen Beziehung zur Temperatur lässt annehmen, dass die nördliche Grenze der Rotkiefer eher durch einen Wechsel im Vorkommen von Bränden als durch ansteigende Temperaturen kontrolliert wird.

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INTRODUCTION

Red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.) seedlings are very shade-intolerant and have a low competitive capability. They must germinate and establish in open stands such as those recently cleared by fires (Cayford and MacClean 1983; Heinselman 1981; Van Wagner, 1971). In contrast to the more stable microclimate of a closed forest understory, such open conditions make red pine and jack pine regeneration more sensitive to climatic fluctuations.

Important climatic variations have occurred in the northern hemisphere throughout the twentieth century (Jones *et al.*, 1982). Several investigations in the boreal zone, and along the altitudinal and the latitudinal tree line, have indicated a causal relationship between tree regeneration rates and twentieth century climatic changes (Kullman, 1979, 1986, 1987; Morin and Payette, 1984; Payette and Filion, 1985; Steijlen and Zackrisson, 1987). However, there has been little assessment of the effects of climatic fluctuation for population located well into the forested area. In this paper, we assess the relationship between climate and jack and red pine regeneration over the period between 1913 and 1986. Since red pine is reaching its northern limit at this latitude, it should be more sensitive to climatic fluctuations than jack pine, which is in the center of its geographical distribution (Fowells, 1965).

STUDY SITE

The two jack pine and red pine populations studied are located at Lac Duparquet located within the Abitibi region of northwestern Québec at 79°21′-79°13′W and 48°26′-48°30′N (Fig. 1). Lac Duparquet is part of a large watershed that drains northwards through Lake Abitibi to James Bay. It is located at the southern limit of the boreal forest (Rowe, 1972) characterized in the area by mature forests of balsam fir (*Abies balsamea* (L.) Mill.) with paper birch (*Betula papyrifera* Marsh.) and white spruce (*Picea glauca* (Moench) Voss), and successional communities dominated by trembling aspen (*Populus tremuloides* Michx.), paper birch and jack pine (Bergeron and Dubuc, 1989).

Site A is an island of 1.4 hectares, and site B is the distal half of a double-humped peninsula and covers 0.6 hectares. Both sites have an undulating topography, with a maximum elevation of 14 m over the summer water level of Lac Duparquet. Since 1914, red and jack pine establishment within these sites has been limited to xeric areas. The xeric areas are characterized by exposed bedrock and thin organic deposits within depressions. The vegetation is characterized by a very open overstory of jack pine and red pine, with scattered eastern white cedar (*Thuja occidentalis* L.), black spruce (*Picea mariana* (mill.) BSP) and white spruce. *Vaccinium angustifolium*, *Juniperus communis*, mosses and lichens are common in the understory.

Both sites have experienced several fires in the last two centuries (Bergeron and Brisson, 1990). On site A, the last fire occurred in 1914. On site B, the last large fire occurred in 1930 while a very small fire, covering only a few square metres, occurred in 1971. Other site disturbance has been minimal.

METHODS

The field study was undertaken during the summer of 1986. At each site, increment cores were obtained from all jack and red pine trees greater than 5 cm in diameter at the base. Each core was taken at an angle, at the base of the stems, to ensure sampling of the oldest growth rings. For individuals less than 5 cm, cross-sections were collected for age determination. All the individuals (301 jack pines and 259 red pines) that have germinated after 1913 were included in the analysis.

Stem cross-sections and increment cores mounted on supports were sanded to clearly expose rings. In most cases, the age determination is based on cross-sections or cores that included the pith. In the case where the pith was barely missed a correction was made according to curvature of the last visible rings (Arno and Sneck, 1977). The age structures were first transformed using a 5 year running average in order to take into account the error in the age determination.

Climatic data for Iroquois Falls over the 1913-1986 period were gathered from the Digital Archive of Canadian Climatological data (Phillips *et al.*, 1988). Iroquois Falls, located 105 km west of Lac Duparquet, is the closest meteorological station that has recorded climatic data for most of the twentieth century. Yearly mean temperature and total precipitation (rain and snow) data were correlated with the age structures.

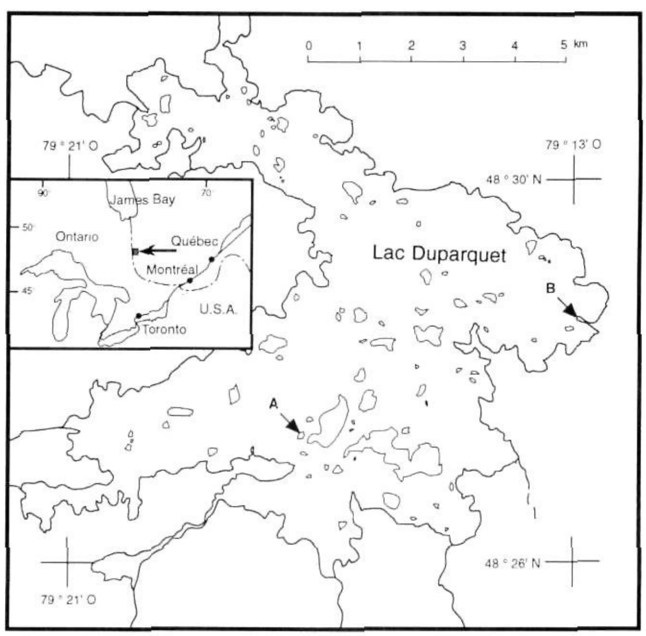

FIGURE 1. Map of Lac Duparquet showing the location of the two sites studied.

Carte du lac Duparquet montrant les deux sites à l'étude.

RESULTS AND DISCUSSION

PINE REGENERATION

Except for jack pine at site A and red pine at site B, regeneration patterns are significantly correlated (Table I). Correlations are influenced principally by low regeneration before 1930, around 1950, and, especially for red pine, after 1970. An important regeneration peak starting around the 1930s followed by a less important peak in the 1960s also characterized all age structures (Fig. 2a,b,c,d).

Red pine and jack pine are generally considered to be dependant upon fire for successful regeneration (Ahlgren, 1976; Heinselman, 1981). Our results show important peaks of regeneration for both pine species following the 1914 and 1930 fires. On site A, although the fire occurred in 1914, the regeneration peaks for jack pine and red pine were centered around 1930 (Fig. 2a and b) as in site B, suggesting that adequate climatic conditions for establishment were not met immediately following the 1914 fire.

The positive effect of fire may last for several years, but it cannot explain the successful regeneration observed many decades after fire. Due to the presence of bedrock, these sites may only support a low density of trees and a discontinuous layer of mosses and shrubs. These conditions provide the luminosity and the seedbed needed for a low, but constant pine reqeneration even without fire.

The fact that all age structures show common fluctuations despite differences in site, species, and fire years suggests that similar climatic factors may affect pine regeneration.

CORRELATIONS WITH TEMPERATURE AND PRECIPITATION

Both mean annual temperature and precipitation registered at Iroquois Falls showed large fluctuations during the 1913-1986 period (Fig. 3a and 3b). Precipitation and temperature were significatively negatively correlated (Pearson's $r = -.37$, $p < .01$) during the observed period.

All age structures were significantly correlated with temperature and precipitation (Table II). Pine regeneration was positively correlated with precipitation in all cases. Except for red pine in site B, regeneration was negatively correlated with temperature. Total pine regeneration (including both sites; Fig. 3c) shows a very good correlation with precipitation

TABLE I

Pearson's correlation coefficients for all pairs of age-structure comparisons between jack pine and red pine populations in sites A and B

Between sites		Within sites (jack pine and red pine)	
Jack pine	0,27*	site A	0.59***
Red pine	0.34**		
		site B	0.30*
Jack (A) and Red (B)	-0.01		
Jack (B) and Red (A)	0.51***		

*** p <0.000 ; ** p < 0.01; * p < 0.05

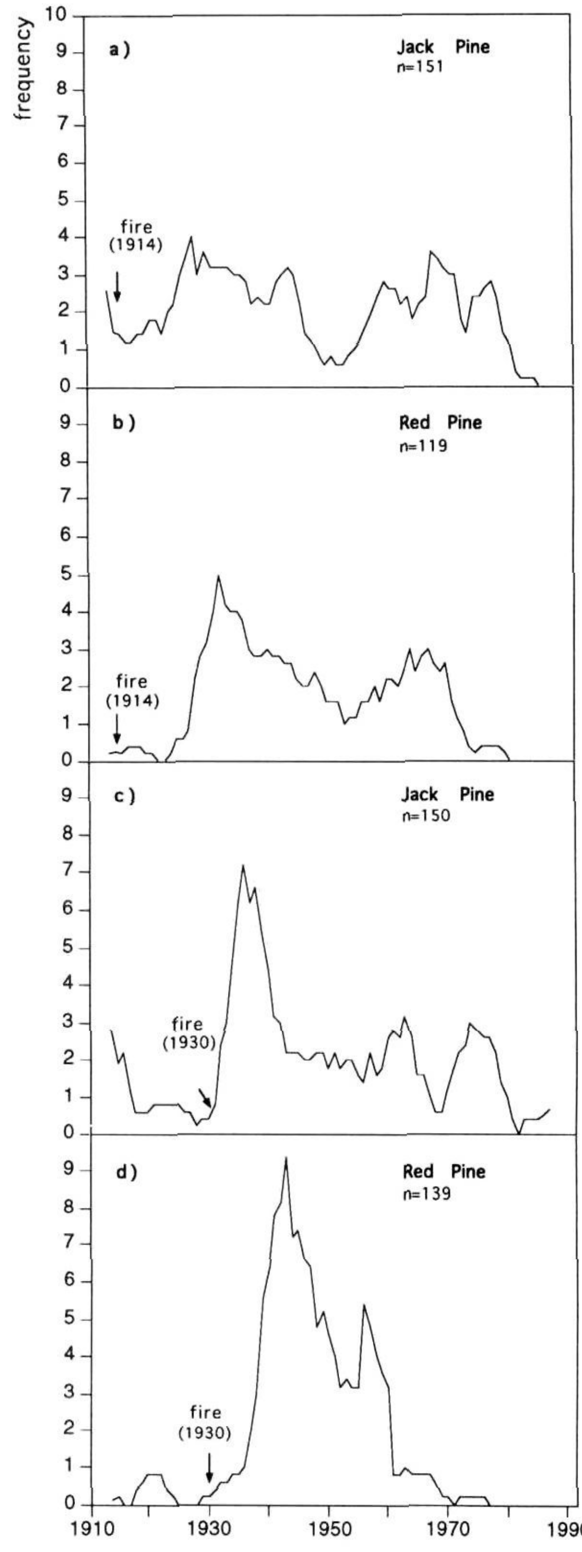

FIGURE 2. Age structure for (a) jack pine on site A; (b) red pine on site A; (c) jack pine on site B; (d) red pine on site B. Data were first transformed using a 5-year running mean.

Structure d'âge du (a) pin gris au site A; (b) du pin rouge au site A; (c) du pin gris au site B; (d) du pin rouge au site B. Les données ont d'abord été transformées par l'entremise d'une moyenne mobile établie sur 5 ans.

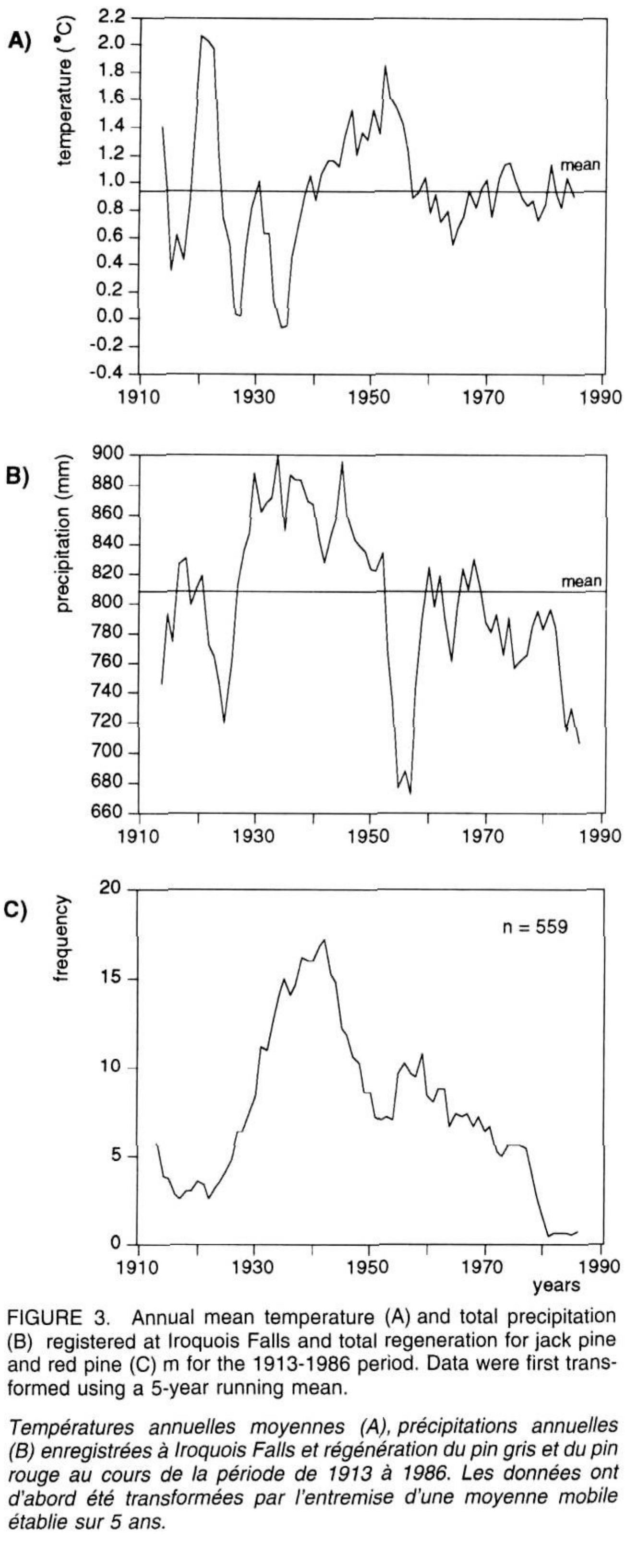

FIGURE 3. Annual mean temperature (A) and total precipitation (B) registered at Iroquois Falls and total regeneration for jack pine and red pine (C) m for the 1913-1986 period. Data were first transformed using a 5-year running mean.

Températures annuelles moyennes (A), précipitations annuelles (B) enregistrées à Iroquois Falls et régénération du pin gris et du pin rouge au cours de la période de 1913 à 1986. Les données ont d'abord été transformées par l'entremise d'une moyenne mobile établie sur 5 ans.

(Fig. 3b). Low recruitments were associated with below average precipitation whereas peaks of regeneration have occurred in periods where precipitation was above average. Although relatively strong, the relationship between pine regeneration and temperature is less clear. While the low recruitment observed before 1930 and in the mid-50s was associated with above average temperature, the low recruitment observed since 1970 was not associated with a major change in temperature (Fig. 3a).

TABLE II

Pearson's correlation coefficients between age structure, mean annual temperature and precipitation for the 1914-1986 period

		Temperature	Precipitation
Site A:			
	Jack pine	-0.43***	0.37**
	Red pine	-0.38***	0.62***
Site B:			
	Jack pine	-0.29*	0.47***
	Red pine	0.27*	0.29*

*** p <0.000 ; ** p < 0.01; * p < 0.05

The positive correlations with precipitation and negative correlations with temperature suggest that high evaporation combined with low precipitation is detrimental to pine regeneration. Drought is the most important limiting factor for germination and seedling development of red and jack pines (Horton and Bedell, 1960; Fowells, 1965). Considering the prevailing xeric conditions of these sites, it is quite likely that low regeneration is associated with drought periods. Seed germination and seedling survival may also fail in years of low snow cover. The seeds may be killed by alternating periods of freezing and thawing, and the seedlings may be damaged by frost and desiccation (Kramer and Kozlowski, 1979).

CONCLUSION

Results presented here show clearly the importance of climatic factors in shaping the age structure of red and jack pine populations on rocky outcrops. The fact that both species react in a similar manner suggest that climate may affect long term regeneration not only at the species northern limit (which is the case for red pine) but also well within the species range as is the case for jack pine. Precipitation appears to be the most limiting factor influencing recruitment.

This result contrasts with studies conducted at other tree species limits where low temperature was the most limiting factor (Kullman, 1979, 1986, 1987; Morin and Payette, 1984; Payette and Filion, 1985; Pigott and Huntley, 1981). Since drought conditions are not increasing northwards, our results suggest that the red pine northern limit is controlled by ecological factors rather than by decreasing temperature. The presence, in the boreal forest, of a fire regime characterized by large fires of high intensity may limit successfull post-fire regeneration, leading to the exclusion of red pine from areas climatically favourable (Bergeron and Gagnon, 1987; Bergeron and Brisson, 1992).

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