Effect of sowing date on the germination and establishment of black spruce and jack pine under simulated field conditions

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Abstract: We used a diurnally and seasonally realistic simulation of seedbed conditions in a controlled environment chamber to test the dependence of seedling growth during the first year on the timing of spring germination in jack pine (Pinus banksiana Lamb.) and black spruce (Picea mariana [Mill.] BSP.). Jack pine germinated poorly under cold, early season conditions compared to black spruce. Survival in seedlings that did emerge was high and fairly constant through the early season in jack pine, and increased steadily as the season advanced in black spruce. Subsequent seedling development, measured as time to shedding of the seed coat, was slowed more by early season conditions in jack pine. Earlier emerging seedlings in both species achieved greater total biomass growth through the simulated season; jack pine seedlings consistently grew more than black spruce for all sowing dates. Height growth changed little with time of seedling emergence for jack pine, but increased greatly in earlier emerging black spruce. These results suggest that early season events can be important determinants of conifer seedling establishment and may help to explain the geographic limits of these two widespread boreal trees.

Keywords: Pinus banksiana, Picea mariana, timing of germination, early seedling growth, phytotron methods, range limits.

Résumé: Nous avons étudié l’effet du moment de la germination sur la croissance des semis du pin gris (Pinus banksiana Lamb.) et de l’épinette noire (Picea mariana [Mill.] BSP.), dans une chambre phytotronique où l’environnement du lit de semences a été simulé en utilisant des conditions journalières et saisonnières réalistes. Le pin gris a affiché une vitesse de germination moins rapide que l’épinette noire sous les conditions froides de la première partie de la saison de croissance simulée. La survie des semis qui ont émergé était élevée et constante pendant la première partie de la saison de croissance chez le pin gris, alors qu’elle a augmenté constamment pendant la saison chez l’épinette noire. Le développement des semis (mesuré comme le nombre de jours avant le délestage du tégument) a été ralenti par les conditions de début de saison d’avoisage chez le pin gris que chez l’épinette noire. Les semis des deux espèces ont émergé tôt dans la saison, mais les semis de pin gris ont poussé plus rapidement que les semis d’épinette noire, indépendamment de la date d’ensemencement. La croissance en hauteur était indépendante de la date de germination des semis de pin gris, alors qu’elle a augmenté fortement chez les semis d’épinette noire qui ont émergé tôt dans la saison. Ces résultats suggèrent que les événements de début de saison affectent la probabilité d’établissement des semis de conifères, et permettent d’expliquer les limites géographiques de ces deux espèces boréales.

Mots-clés: Pinus banksiana, Picea mariana, moment de la germination, la croissance des jeunes semis. méthodes phytotroniques, limites géographiques.

Introduction

Seed of boreal conifers matures in late summer and early fall, and, with the exception of serotinal seed, is primarily dispersed in late fall or early spring (Young, 1992; Farmer, 1997). Most dispersed seed germinates in the growing season after it is released (Fraser, 1976; Fleming & Mossa, 1994), typically in the spring or early summer as the seedbed warms (Haavisto, 1978; Vierreck & Dynness, 1979). Seedlings establishing in spring or early summer generally do better than those emerging later in the season (Richardson, 1972; Fraser, 1981; Vierreck & Johnston, 1990; Rudolph & Laidly, 1990; Van Damme, Buse & Warrington, 1990), perhaps because the seedbed tends to be moister early in the season and a longer growing season affords more time to develop a root system resistant to frost heaving. Apart from geographic variation in seasonality, there is also substantial local variation in the timing of snow melt and associated microclimatic conditions that characterize a species regeneration niche (Farmer, 1997). This leads to local variation in the earliest time when seed germinates and could affect differential success among seedlings within populations. We, therefore, investigated under controlled conditions whether such variation in the timing of germination in spring would lead to differences in seedling growth over the first growing season in jack pine (Pinus banksiana Lamb.) and black spruce (Picea mariana [Mill.] BSP.). While recognizing the importance of substrate type, substrate temperature and water regime for germination and seedling establishment in natural seedbeds (Black & Bliss, 1980; Thomas & Wein, 1985; Duchesne & Siros. 1995; Herr & Duchesne, 1995), we sought to isolate effects due to differing exposure to the seasonal progression of temperature and, to a lesser degree, insolation.

Material and methods

A Conviron PGW36-DE5 (Conviron. Winnipeg, Manitoba) growth chamber equipped for low temperature work in the McGill University Phytotron was programmed to simulate the temperature and relative humidity using

mean hourly values taken by the Atmospheric Environment Service for 1955 to 1990 at Val d'Or, Québec, Canada (48° 04' N, 77° 47' W). This simulation based on weather service data taken at screen height does not reproduce the most extreme events over this period, but rather focuses on the average progression of seasonal conditions. We started the seasonal simulation from April 15 when the mean daily soil temperature (5 cm depth) at Val d'Or is about 0°C; both species can germinate under snow at temperatures near zero (MacArthur & Fraser, 1963; Haavisto & Winston, 1974). At this time the mean daily air temperature is about 2.7°C with hourly means ranging from -1.0°C to 6.6°C, which are temperatures sufficient for seedling growth during some of the day on snow-free ground. Photoperiod and light intensity at 15 minute intervals were simulated for clear sky at Val d'Or following Brock (1981). The maximum photosynthetic photon flux density at the seedling level was about 600 μE/m²/s. This is only about one third of full sunlight at midday on cloudless days, but not uncharacteristic of partially shaded or cloudy conditions over the day as a whole. Allowing for overcast weather, we believe that the total seasonal photon flux density in the real and simulated seedbeds are reasonably comparable. Chamber CO₂ level was controlled at 350 μL·L⁻¹. Wang, Lechowicz & Potvin (1994) provide additional details on this type of dynamic climate simulation, which differs from the usual alternation of constant day/night temperatures on a fixed photoperiod typical of experiments in controlled environments. While simulations in controlled environments can never fully reproduce the energy balance of natural seedbeds, this protocol does a good job of reproducing a more natural diurnal and seasonal progression of temperatures and irradiance.

Seeds of black spruce and jack pine were obtained from the Ministère des Forêts du Québec, Pêpièriniere forestière de Berthierville, Berthierville, Québec. The seed originated from the vicinity of 48° 39' N and 77° w (J. Grenier, pers. comm.). Seeds of each species were randomly selected, and empty ones were discarded. They were individually placed in Microtrast III trays (Becton Dickinson Labware, Lincoln Park, New Jersey) with a disc of Whatman #1 filter paper wetted by 0.3 mL of deionized water. Seeds were cold-stratified for one week at 4°C and then planted on 4 different days in the simulated season at Val d'Or (April 15, May 6, 15, and 21), each separated by about 600 degree-hours (e.g., the summation of mean hourly temperatures above a 5°C threshold; Figure 1). At each planting date, 96 stratified seeds in one tray per species were planted, one per cell, at random positions in containers (IPL-45, 100 cm²/cell) filled with milled peat. The IPL containers positions were blocked and randomized to allow for spatial heterogeneity within the growth chamber (Potvin et al., 1990). The IPL-45 containers filled the entire floor of the chamber except for narrow gaps for air circulation; each cell was treated as an experimental unit. To facilitate checking of germination, the planted seeds were placed on the peat surface with a little seed coat visible at the radicle end and then covered with a small disc of Whatman #1 filter paper. To facilitate comparison to published results, additional seed were also tested for germination on moist filter paper at a constant temperature of 27°C.

During the entire germination period, we misted the seeds every morning and scored seed germination (defined by the radicle breaking the seed coat) as days after the end of cold stratification. We also recorded days taken to shed the seed coat as an index of seedling development. Unergerninated seeds were dissected to determine if they were solid (with white endosperm and embryo). The total germination percentage was calculated as 100 × (number of germinated seeds)/(number of full seeds) for the 96 seeds in each Microtrast tray. The cumulative germination was calculated as 100 × (total number of seeds germinated to a given day)/(total number of seeds germinated). Days from germination to shedding of the seed coat were obtained for all individual seedlings. Percent of seed coat shedding was calculated as 100 × (number of seedlings with seed coat shed)/(number of seedlings with and without seed coat shed).

After germination was complete and during the rest of the simulated growing season, we soaked the seedlings with de-ionized water once a week and also fertilized seedlings once a week with 5 mL of 100 ppm N fertilizer solution per seedling (Wang, Lechowicz & Potvin, 1994). This nitrogen fertilization is used for black spruce and jack pine seedlings in tree nurseries in the Abitibi-Témiscamingue forest region (F. Tremblay, pers. comm.). Fertilization was started as soon as seedlings had visible needles.

The experiment was terminated on August 18 in the simulated growing season. Seedling height from the peat surface to the seedling apex was measured. Seedling tops were cut at the peat surface and roots were carefully washed free from the peat. Tissues were dried at 70°C for 3 days.
and dry mass (top and root) recorded to the nearest 0.01 mg.

Growth parameters, and number of days taken for seed to germinate and for germinants to shed seed coats were analyzed by ANOVA with species and planting dates as fixed factors (SAS, 1990). Survival rates were not statistically analyzed because our estimates are unreplicated. However, the means by planting dates were plotted. Germination percentages always exceeded 90%, and percent of seedlings with seed coat shed ranged from 95% to 100% for all the treatments. Therefore, these data were not analyzed further.

Results

Temperature strongly influenced seed germination of jack pine and black spruce. The highest hourly mean temperature in the growth chamber during the germination period (April 15 to June 10) was 22.6°C. The mean daily air temperature over this period never reached the 16-27°C range reported to be optimal for black spruce germination or the 16-35°C optimal for jack pine (Fraser, 1970a, b; cf. Figure 1). Seed of both species germinated faster at 27°C than at the lower temperatures prevailing on the simulated seedbed; on average, it took only 2.2 days for a jack pine seed and 3.1 days for a black spruce seed to germinate at 27°C. Black spruce and jack pine differed significantly in germination speed (Gday) among planting dates (Table I). Both species germinated more quickly as planting dates became later (Figure 2a). Total germination was 93% for jack pine and 96% for black spruce on the simulated seedbed.

More than 95% of the seedlings of both species shed their seed coats during the growing period. Days from germination to shed seed coat varied significantly between black spruce and jack pine among planting dates (Table I). In general, as planting dates became later, seedlings took less time to shed their seed coats (Figure 2b). Jack pine seedlings took less time than black spruce seedlings to shed their seed coats, but as planting dates became later, days taken to shed seed coat decreased more in jack pine than in black spruce (Figure 2b).

Seedling survival varied with planting dates more in black spruce than in jack pine (Figure 3). As planting dates became later, seedling survival of black spruce increased steadily, but was relatively constant for jack pine.

Main effects and the interactions of species by planting dates were significant for most of the seedling growth parameters (Table I; Figure 3). Black spruce seedlings generally grew taller, and had higher top/root ratio but smaller dry mass than jack pine seedlings (Figure 3). In order to interpret these growth responses, it should be kept in mind that unless early season conditions had adverse effects, seedling growth in height or dry mass should increase as planting dates became earlier and, hence, the growing period became longer. As planting dates became later, black spruce seedlings had more marked reduction in height compared to jack pine (Figure 3). In other words, the height growth of jack pine in its first season can be reduced by earlier germination in the growing season. The effects of time of planting on dry mass do not show the same evidence of an adverse early season effect in jack pine. In general, the dry mass accumulated during the growing season increases with the longer period of growth achieved through earlier germination; this effect tapers off in black spruce as the season progresses, but not in jack pine. Both species show some depression in top/root ratio for seedlings germinating very early in the season, but this effect is weak in jack pine.

Discussion

In this study, jack pine seeds germinated faster than black spruce seeds at an artificially high temperature (27°C). This is consistent with results in standard germination trials which used an alternation of 8 hour days at 30°C with 16 hour nights at 20°C on a continuously moist medium; under these conditions jack pine has 54-86% ger-

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FIGURE 2. Days for seeds to germinate (a) and for the germinants to shed seed coats after germination (b) plotted against planting dates for black spruce and jack pine with 95% confidence intervals.
mination within 5-10 days, black spruce 57-85% within 10-19 days (Young, 1992). Lower temperatures are known to retard germination (Fraser, 1970a,b; Farmer et al., 1984; Stoehr & Farmer, 1986), but some seed of both species will germinate even near 0°C (MacArthur & Fraser, 1963; Haavisto & Winston, 1974). Our simulations give a better indication of the germination behavior of these two important boreal trees under the lower and fluctuating temperatures characteristic of seedbed environments during spring and early summer. Seed of neither species germinates rapidly on the cold seedbed early in the season, but the seasonal onset of germination in black spruce is more rapid than that of jack pine. Subsequent seedling development, as indicated by the time to shedding of the seed coat, also is less delayed in early germinating seed of black spruce than in that of jack pine. Finally, height growth in newly emerging jack pine seedlings was more reduced by chilling early in the growing season than was black spruce.

The somewhat greater tolerance of cold conditions during establishment by black spruce is consistent with, and may contribute to, differences in the geographic distribution of these two important boreal conifers. Black spruce reaches almost 70° N but jack pine only 65° N, and at comparable longitude black spruce always extends north of jack pine (Viereck & Johnston, 1990; Rudolph & Laidly, 1990). Black spruce also colonized far northern regions more quickly than jack pine after deglaciation (Desponts & Payette, 1993). These northern range limits do not appear to be set by air temperature limitations on productivity (Bonan & Sirois, 1992), and jack pine provenances grown somewhat north of their present localities actually do better (Mayyas & Yeatman, 1992). Similarly, modest increases in temperature in northern Finland substantially increase the germination and establishment of Pinus sylvestris (Kellomäki & Väisänen, 1995). An isolated arctic population of black spruce, which almost certainly established from long distance seed dispersal, is associated with a microsite having slightly warmer soils (Payette & Delwaide, 1994). Temperature effects on seed production, germination and establishment may be a more important control on the range limits for many northern conifers than is commonly appreciated (Piggott, 1992).

These results have a bearing on the design of ecophysiological studies of conifer seedlings in controlled environments. It is possible to simulate fairly realistically the diurnal and seasonal patterns of temperature, relative humidity and irradiance in growth chambers (Wang, Lechowicz & Potvin, 1994; 1995). This capability can be useful not only in studies of early seedling establishment but also in investigations of problems like the joint control of photoperiod and seasonal temperatures on phenological events such as flowering, leaf senescence or winter bud formation. Despite the difficulty of simulating temperatures much below 5°C except in specially equipped growth chambers, our results suggest the importance of simulating such early spring conditions if possible. Events in the early season can have substantial influence on traits measured at harvest, so species comparisons in controlled environments that ignore simulation of early season conditions can be misleading.

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Literature cited


