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Aspen root dynamics, aspen productivity with and without understory spruce and seed dispersal of white spruce in aspen stands

SFM Network Project: Mortality and regeneration of aspen in mixedwood stands

by

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ABSTRACT

This project, supplemented with industry funds mostly from Alberta Pacific Forest Industries and several other contributors was able to complete three sets of research projects since 1996. The first set of projects examined roots and growth dynamics of aspen in cold soil conditions and in association with Calamagrostis canadensis. Findings were that aspen has virtually no root growth at 5ºC, minimal root growth at 12ºC but massive growth in roots, leaf area and leaf size at 20ºC. The colder temperatures are typical spring and summer temperatures under beds of Calamagrostis. Experiments also indicated that Calamagrostis is an important competitor of aspen and its litter, besides insulating the soil likely has allelopathic agents that restrict aspen growth. Root water flow is reduced in cold soils because water channel proteins are less active, perhaps because of reduced respiration in cold soils. This is summarized in 4 refereed publications. The second set of projects examines the growth of aspen stands with and without understory spruce in 29 pairs of stands. The aspen biomass and productivity were lower in the mixed than the pure stands, however, when the spruce was added to the total, there was a 10 % increase in total biomass and 12% increase in annual biomass increment in the mixed stands. The amount of spruce biomass in the stand could not be related to the difference in the productivity of the aspen between the pure and the mixed stands. This is published in a refereed journal. The third set of projects measured the dispersal of white spruce seed in mature aspen stands both by tallying the amount of white spruce seedlings surrounding seed tree groups within pure stands of aspen, and secondly by measuring the dispersion of confetti dropped from a tower within a pure aspen stand. Less than 1% of seed was dispersed greater than 100 m from the source and dispersal was greatest downwind. There was significant established seedlings (100/ha) up to 250 m from a seed source, suggesting that dispersal is under conditions of high wind, perhaps with updraft conditions.

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GROWTH OF ASPEN IN ASSOCIATION WITH *CALAMAGROSTIS CANADENSIS*

Simon Landhäusser and Victor Lieffers

INTRODUCTION

As the grass, *Calamagrostis canadensis* is usually established in the understory of aspen-dominated mixedwood stand prior to disturbance, it can quickly spread and dominate the site after logging. While aspen regenerates from suckers immediately after logging or fire, observations show that its height growth is gradually suppressed in the first four years, if the stand is quickly dominated by *Calamagrostis*. Suppression occurs even if the aspen is taller than the grass. There are several theories as to why this suppression takes place. 1) Competition for water and nutrients from *Calamagrostis* may limit the growth of the trees. 2) Litter buildup from the grass is known to delay soil warming in the spring and reduce the summer maximum temperatures (Hogg and Lieffers 1991). The cooler soil temperatures may suppress water uptake in the aspen. 3) The litter from the grass may contain allelochemicals that suppress the growth of the aspen. With a series of controlled environment experiments we tested each of these different theories.

METHODS

<u>Competition</u>: Aspen seedlings were transplanted into pots with or without well-established beds of *Calamagrostis*. The leaves of the grass did not shade the leaves of the aspen. These were grown for two months, harvested and weighed. <u>Temperature</u>: Dormant spring, plug planting stock of aspen was grown in pots placed in waterbaths where the temperature was maintained at 6 12 and 20ºC. Seedlings were grown for 8 weeks and harvested. <u>Allelopathy</u>: Aspen planting stock was grown in pots with or without a layer of *Calamagrostis* litter on top and each of these were fertilized with either a high or low nutrient fertilization regime, in 2X2 factorial experiment. Pots were watered from the top through the litter layer. The seedlings were harvested after 4 months.

RESULTS

<u>Competition</u>: There was a decrease in root growth and leaf of the grass as a result of the competition from the grass. There was virtually no stem growth of the aspen in the pots with *Calamagrostis* while ring increment was 2 mm in the control pots. <u>Temperature</u>: There was no root growth at 6ºC and massive root growth at 20ºC. In the 6 C treatment the aspen flushed the pre-formed buds and then set but soon after. At 20ºC the shoots kept on elongating producing a continuous addition of new leaves. Total leaf area per plant and leaf size increased dramatically in the 20ºC treatment compared to the 6ºC. <u>Allelopathy</u>: The litter treatment showed a striking decrease in aspen stem, root and leaf area growth compared to the control. The addition of

fertilizer appeared to counteract some of the negative effects of the *Calamagrostis* litter but not all.

The complete results of this work are published (Landhäusser and Lieffers 1998).

MANAGEMENT APPLICATIONS AND IMPLICATIONS

- Low soil temperatures such as might be found under a bed of *Calamagrostis* with several years of accumulated litter are likely to have a large negative effect on the growth of aspen.
- Direct competition from *Calamagrostis* and allelochemical impacts of its litter slow the growth rates of spruce.
- Heavy suckering of aspen to establish early, a dense layer of shading leaf to suppress the growth of the grass may be a strategy to limit the impacts of *Calamagrostis* (Lieffers et al. 1999). Alternatively, a grass specific herbicide needs to be developed.

WATER UPTAKE AND ROOT HYDRAULIC CONDUCTIVITY OF ASPEN ROOTS IN RELATION TO SOIL TEMPERATURE

X. Wan, J. Zwiazek, S. Landhäusser and V.J. Lieffers.

INTRODUCTION

The above work with aspen and Calamagrostis shows that aspen root, above ground and leaf area growth is negatively affected by cold soils. Since cold soils are one of the fundamental characteristics of boreal forests it is imperative to have a better understanding of the reaction of tree roots to cold soils. This section describes three different sets of experiments that give us a better understanding of processes affecting water uptake and flow through roots of aspen (*Populus tremuloides* Michx.) roots grown in cold soils.

OBJECTIVE A

To determine the rate of hydraulic conductivity of aspen roots from plants that had been grown at 5, 10 or 20ºC and determine if the roots of these plants responded differently to cold temperatures during the time of measurement.

METHODS

Aspen seedling (1 year-old bareroot stock) were planted into a hydroponics system for 2 weeks and then they were grown for another 30 days at either 5, 10, or 20ºC root temperature but 20ºC air temperatures. Root hydraulic conductivity, stomatal conductance, shoot water potential, above and below ground growth and root water flow were measured periodically during this 30 days. At day 30, the root water flow was measured on the remaining seedlings at 5, 10 and 20ºC temperatures.

RESULTS

Root water flow was very low at all temperature until day 10 of the treatments. At this time the 20ºC treatment had a strong increase in water flow and stomatal conductance. This coincided with the time of new root growth. It took until the 30 day for noticeable increase in root water flow in the 10ºC treatment. The cold treatments severely restricted root and leaf growth of the seedlings. When the seedlings grown at the various temperature were tested over a range of temperatures, it indicated that root water flow was strongly dependent upon the amount of new roots but plants grown at 20ºC had more than a 3 fold decline in root water flow when measured at 5ºC. This reduction is much greater than simple increases in water viscosity at the cold soils. This project is further described in Wan et al. 1999.

OBJECTIVE B

This work examines the impact of water channel proteins on root water flow and plant water relations. The effects of water channel inhibitor (mercuric chloride) were tested on the roots.

METHODS

One-year-old aspen seedlings were grown in solution culture containing half-strength modified Hoagland's solution. Root water flow was measured using the hydrostatic pressure method at different temperatures and after treating the roots with mercury chloride. Root systems were gradually pressurized to a constant pressure of 0.3 MPa and the root water flow was measured before and after adding different concentrations of mercuric chloride. In some experiments, the effects of mercuric chloride on root respiration were measured using a Clark-type electrode. Arrhenius plots were determined by measuring root water flow at the temperatures gradually changing from 25°C to 4°C and back to 25°C in 3°C steps. To examine the proportion of apoplastic to symplastic and cell-to-cell transport, Rhodamine B fluorescent dye, which is transported only through the apoplast, was added to the root incubating solution. Xylem sap was collected from the cut root surface and its fluorescence measured with the fluorometer. In a separate experiment, the effects of mercuric chloride on stomatal conductance were measured in excised shoots and intact seedlings.

RESULTS

When mercuric chloride was applied to the roots, reduced pressure-induced water flux and root hydraulic conductivity in the roots of one-year-old aspen seedlings by about 50%. The inhibition was reversed with 50 mM mercaptoethanol suggesting that water channels play an important role in controlling root hydraulic conductivity in aspen. Mercurial treatment reduced the activation energy of water transport in the roots when measured over the 4°C - 25°C temperature range. An increase in Rhodamine B concentration in the xylem sap of mercury-treated roots suggested a decrease in the symplastic transport of water. Electrical conductivity and osmotic potentials of the expressed xylem sap suggested that 0.5 mM $HgCl_2$ and temperature changes over the 4°C - 25°C range did not induce cell membrane leakage. The 0.5 mM $HgCl_2$ solution applied as a root drench severely reduced stomatal conductance in intact plants and this reduction was partly reversed by 50 mM mercaptoethanol. In excised shoots, 0.5 mM $HgCl_2$ did not affect stomatal conductance suggesting that the signal which triggered stomatal closure originated in the roots. To determine, whether the inhibition of root water flow at low temperatures is triggered by stress-induced abscisic acid, we have conducted as series of experiments which failed to find any effect of exogenously applied abscisic acid on root water flow. The results of the project have allowed us to formulate a new model for root hydraulic conductivity regulation in woody plants. This work is published in Wan and Zwiazek (1999).

OBJECTIVE C

To test the hypothesis that abscisic acid, produced by plants at low soil temperatures, inhibits root water flow by its effect on water channels and induces stomatal closure.

METHODS

Aspen seedlings were grown in solution culture as described above and treated with abscisic acid (ABA). Stomatal conductance and root water flow were measured as previously in treated and control plants at the temperatures ranging from 4 to 25^{o}C.

RESULTS

Results are forthcoming. In summary, ABA supplied through the roots was effective in inducing stomatal closure, but had no effect on root hydraulic conductivity. We conclude that the regulation of water channel proteins in roots does not involve ABA. The manuscript is in preparation and will be submitted by the end of 1999 to the Journal of Experimental Botany.

MANAGEMENT APPLICATIONS AND IMPLICATIONS

- Aspen is highly sensitive to cold soil conditions both by slow development of new roots but also reduced root activity and water flow at cold soil temperatures. The need for increasing soil temperatures for good growth of regeneration is as least as important for aspen as for spruce.
- Root water flow at cold temperatures is inhibited more than can be accounted for by simple increases in water viscosity.
- Water channel proteins are responsible for most of the root water flow.
- Knowledge of the mechanisms controlling root water flow in cold soils could be applied in breeding programs.

GROWTH OF ASPEN WITH AND WITHOUT UNDERSTORY SPRUCE

Dan MacPherson, Victor Lieffers and Peter Blenis

INTRODUCTION

Based upon ecological theory (vandermeer 1989), there are numerous reasons why mixtures of trees species such as white spruce might yield more in mixture than single species stands. These ideas are reviewed by Man and Lieffers 1999 and can be summarized as follows: When two species have dissimilar structure and growth strategies they should have reduced levels of competition compared to individuals of the same species. 1) In the case of white spruce and aspen, juvenile spruce are capable of growth under an aspen canopy using the light not utilized by the aspen. 2) Because the canopies of aspen and spruce are physically separated, in theory more leaf area can be packed in a stand making the capture of light energy more efficient. 3) Because spruce is capable of photosynthesis in spring and fall during periods of aspen leaf-off, the stand should have greater seasonal use of solar energy if there is understory spruce under the aspen canopy. 4) With rapid expansion of aspen leaf area followed by a slow development of the eventually massive leaf area of spruce stands, the natural successional processes should result in higher average stand leaf area over a rotation than if only one species were grown. 5) Since aspen is more deeply rooted than spruce, different levels of the soil can be explored by a mixture of the two. Facilitative Production is a result of improved growing conditions related to the presence of a second species. There are several theoretical reasons for Facilitative Production with mixtures of aspen and spruce. 1) Aspen is noted to cycle nutrients faster than white spruce. 2) The shelter from aspen is noted to reduce the level of summer frost on spruce establishment and growth and reduces vapour pressure deficits which allow greater stomatal conductance and photosynthesis. 3) Mixed stands are noted to have reduced levels of insect attack.

While the above factors have been suggested to result in greater productivity, there is little empirical evidence that such a benefit exits. FORECAST model runs (Wang et al. 1995) suggest that there is increased production and there is weak evidence that mixed stands usually have more volume than pure stands of aspen.

Objectives of the study were to determine if aspen stands with an understory of white spruce had greater total productivity than pure stands.

METHODS

In the Northeastern portion of Alberta, 29 aspen dominated stands where selected for examination. Selection criteria were that stands be maturing, have a healthy and uniform aspen canopy and be large and on uniform topography. Each stand also had pure aspen stands immediately adjacent to similar aspen stands with an understory of white spruce. Plots were then established in the pure and mixed portions of the stand and the total biomass and biomass increment were determined (using increment cores). The pairs of stands were then analyzed for differences in total biomass and biomass increment over a 5 year period.

RESULTS

Over the 29 pairs of stands, there was approximately 10% increase in total biomass and a 11% increase in periodic biomass annual increment (averaged over the last 5 years) in the mixed stands compared to the pure aspen stand. The spruce component of the plots ranged from 11 to 119 t/Ha. The aspen component of the mixed stands had lower biomass and periodic annual increment compared to the aspen from the pure stand. There was not a significant relationship between the difference in the aspen biomass or increment compared to the amount of spruce in the stand. In other word, the plot pairs with high spruce biomass did not have a greater decline (pure aspen-mixed aspen) than the plot pairs with low spruce biomass in the mixed stand. A thesis and research paper on this topic are currently being prepared.

MANAGEMENT APPLICATIONS AND IMPLICATIONS

- In maturing aspen stand, there is a significant increase in total stand production when there is a spruce understory.
- There was no relationship between the amount of spruce in the stands and the amount of decline in the aspen biomass or increment (pure aspen-mixed). We have difficulty interpreting this issue but suggest that given some of the clonal differences in productivity of aspen, it is possible that in these fully stocked aspen stands, the spruce understory develops preferentially in some of the less productive aspen clones.

DISPERSAL OF WHITE SPRUCE SEED IN MATURE ASPEN STANDS

James D. Stewart, Edward H. Hogg, Patrick A. Hurdle, Kenneth J. Stadt,
Peter Tollestrup, and Victor J. Lieffers

INTRODUCTION

Natural regeneration of white spruce is limited by seed supply and appropriate seedbed conditions. The dispersion of and density of white spruce seed trees has been studied for seedcast from edge trees into clearcuts or burns (Dobbs 1976, Greene and Johnson 1996). To be able to predict the recruitment of seedlings under aspen canopies or in partial cut forests the dispersal distance of seed under canopies must also be known. The objectives of this work were to determine the natural seeding distances from isolated groups of mature white spruce into adjacent aspen stands. The differences in dispersal distance in times of aspen leaf on and leaf off conditions should also be known.

METHODS

Two approaches were undertaken.

1) Isolated groups of white spruce, with no other spruce trees capable of bearing seed within at least 500m, within maturing aspen stands, were identified by aerial photos and reconnaissance. Radial transects were established to 250m from the island and the regeneration of white spruce was tallied. Approximately 3 replicate stands were identified in the Lac La Biche and Whitecourt areas.

2) The dispersion seed from various heights above, at, or below the top of the aspen stand was estimated by dropping colored confetti from a tower located in an aspen stand near Grande Prairie Alberta. The confetti was dropped over a 10 minute period during moderate wind events during leaf on periods and after leaf off in mid October. It was counted on pulp sheets positioned at various distances downwind of the tower. Vertical and horizontal windspeeds were measured during the release of the confetti.

RESULTS

<u>Seed Tree Groups:</u> Dense recruitment of white spruce was found 10m upwind and up to 50 m downwind from the seed tree groups; recruitment declined to low levels by 100 m. Beyond this distance there were still about 100 tree/ha even up to 250 m from the seed sources. It is noteworthy that good spruce recruitment was not observed in aspen stands with heavy understories of Calamagrostis, green alder or beaked hazelnut. <u>Confetti:</u> The confetti had a faster fall speed than natural white spruce seeds with wings. Even after correcting for this difference dispersal distance of the dropped confetti was much shorter than the distances estimated from the seed tree groups. A model using horizontal and vertical windspeeds and the fall speed of the seed

indicates that under the moderate wind speeds observed during the drop of the confetti, less than 1% of the seed will go beyond 100m. Seeds were dispersed more widely during leaf-off conditions. This work is described in detail in Stewart et al. (1998).

MANAGEMENT APPLICATIONS AND IMPLICATIONS

- Seed trees must be within 100m and preferably upwind of microsites to be regenerated if heavy stocking is desired.
- Low densities of spruce (ca. 100 trees/ha) can be expected at distances greater than 250 m from seed sources, provided seed beds are appropriate.
- Understories of Calamagrostis, green alder or beaked hazel nut are unsuitable for significant natural regeneration of white spruce.
- Based upon the greater seeding distances surrounding the seed tree groups than the confetti drops, most of the seed is likely released from the trees during high wind events (perhaps with significant updrafts).

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