The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga

JOSHUA P. SCHIMEL[1,*], REX G. CATES[2] & ROGER RUESS[3]
[1]*Dept. Ecology Evolution and Marine Biology, Univ. California, Santa Barbara CA 93106, USA;* [2]*Dept. Botany and Range Science, Brigham Young University, Provo, UT 84602, USA;* [3]*Inst. Arctic Biology, University of Alaska, AK 99775, USA (*Corresponding author: Phone: (805) 893-7688; Fax: (805) 893-4724; E-mail: Schimel@lifesci.lscf.ucsb.edu)*

Abstract. The vegetation mosaic of the Alaskan taiga is produced by patterns of disturbance coupled to well-defined successional patterns. In primary succession on river floodplains, one of the critical transitions in succession is that from thinleaf alder (*Alnus tenuifolia*) to balsam poplar (*Populus balsamifera*). This is the shift from a N_2-fixing shrub to a deciduous tree. Through this transition there are major changes in N cycling including a decrease in N_2-fixation, mineralization, and nitrification. Most models of plant effects on soil processes assume that these changes are caused by shifts in litter quality and C/N ratio. This paper reviews several studies examining the effects of balsam poplar secondary chemicals on soil nutrient cycling. Balsam poplar tannins inhibited both N_2-fixation in alder, and decomposition and N-mineralization in alder soils. Other poplar compounds, including low-molecular-weight phenolics, were microbial substrates and increased microbial growth and immobilization, thereby reducing net soil N availability. Thus, substantial changes in soil N cycling through succession appear to have been mediated by balsam poplar secondary chemicals.

The boreal forest, including the taiga forest of Alaska, is composed of a complex mosaic of plant communities (Van Cleve et al. 1993). The controls on the pattern of boreal vegetation has been an area of research for at least several decades (Van Cleve et al. 1986), and is of global concern since the region contains approximately 20% of the total global soil C pool (Post et al. 1985). Changes in vegetation are accompanied by changes in soil C storage. Thus, the processes that control the structure of vegetation and changes in it are of interest both for understanding the basic ecology of the taiga and for understanding changes in the global C cycle.

The primary driving force causing the complex vegetation mosaic is disturbance. There are several disturbances that occur in the Alaskan taiga that can damage plants enough to restructure plant communities. The most common and widespread is fire, with return frequencies ranging widely from 30–400 years (Dyrness et al. 1986). Fires in the taiga tend to kill trees, which are not

fire resistant, though shrubs in muskeg regenerate quickly from belowground stems if the fire isn't severe. The major rivers have extensive floodplains and they periodically change their courses, cutting banks and dropping trees into the river, while depositing bare alluvial bars in their wake (Van Cleve et al. 1993). Additional disturbances that can affect the structure of taiga communities are insect outbreaks and unusual winter storms. In recent years there have been serious outbreaks of spruce budworm and spruce bark beetles that may eventually lead to the demise of large stands of white spruce (*Picea glauca*). Stand damaging winter storms have occurred both unusually early (Sept. 1992), prior to leaf fall, which bowed over many birch and aspen trees from the weight of snow, or very late (April 1992) when ice storms caused major damage to white spruce.

These infrequent disturbances leave long-term legacies on the landscape. When fire or river migration destroys a mature white spruce stand, it takes several hundred years to reestablish. The recovery processes involve patterns of plant succession that, while different in upland secondary- and floodplain-primary succession, are well documented and repeated. Thus, any individual piece of the taiga landscape is usually in some state of recovery from a past disturbance, rather than being in equilibrium.

Plants induce changes in soil characteristics and processes (both biotic and abiotic; see other papers in this issue), and these changes in turn affect the vegetation through altered water and nutrient availability, altered soil temperature, and other characteristics. These feedbacks may be complex and in the constantly changing ecosystems of the taiga, the feedbacks may affect both the direction and rate of succession. As vegetation changes, the nature of the plant–soil feedbacks change and this in turn may drive some of the changes in vegetation and ecosystem structure. This has been a major thrust of work done at the Bonanza Creek Long Term Ecological Research site near Fairbanks, Alaska.

One particular focus of our recent work has been on understanding the changes in soil properties that occur during primary succession on river floodplains. Newly established river bars are initially colonized by willow (*Salix*) and *Equisetum* species. Over a decade or so, these are largely replaced by thinleaf alder (*Alnus tenuifolia*). Balsam poplar (*Populus balsamifera*) saplings establish in the first decade but don't reach canopy dominance for about 40–60 years. White spruce (*Picea glauca*) usually dominates a site within 150–200 years. Eventually white spruce may be replaced by black spruce muskeg (*Picea mariana*; Viereck et al. 1993) though there is currently debate over whether this is common (Mann et al. 1995).

During primary succession, there are major changes in nutrient cycling and soil C accumulation (Van Cleve et al. 1993). In the alder stage, rapid
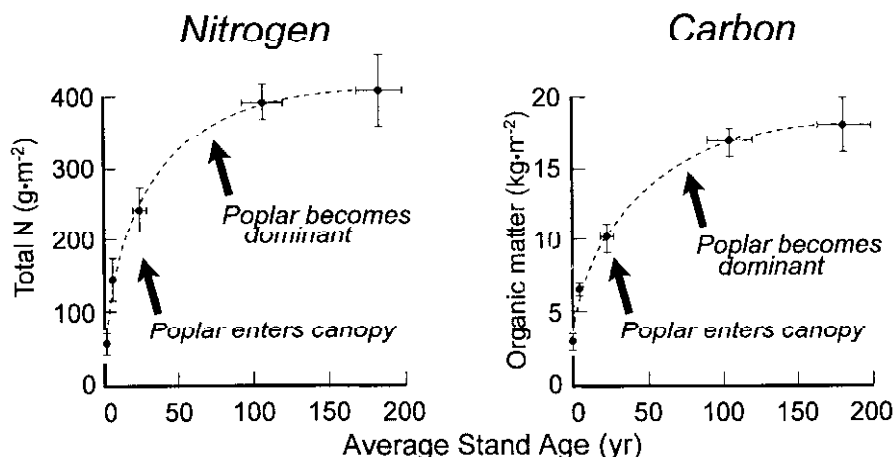
Nitrogen

Carbon

Figure 1. Soil nitrogen and carbon dynamics through succession. Data taken from Van Cleve et al. 1993.

N_2-fixation and litter production (Viereck et al. 1993; Van Cleve et al. 1993) account for most of the C and N accumulation in the forest floor over the lifespan of the forest (Figure 1). The N cycle during the alder stage is dominated by inputs from N_2-fixation, and turnover through mineralization and nitrification is rapid (Clein & Schimel 1995; Schimel et al. 1996). As balsam poplar takes over the stand, however, C accumulation slows and the N cycle changes as well, becoming dominated by the internal recycling processes of NH_4^+ mineralization-immobilization (Clein & Schimel 1995).

Two questions driving our research, and the topic of this paper, are: 1) what causes the changes in N cycling as poplar replaces alder during primary succession on these river terraces? and 2) what effects does this have on the transition from alder to poplar during succession? There are several possible mechanisms for the plant effects on N cycling. The first is through controlling litter quality (Swift et al. 1979; Aber et al. 1990). Balsam poplar produces lower quality litter than alder, with lower N and a much higher C/N ratio (senesced alder C/N = 24; senesced poplar C/N = 80.5). It is therefore possible that as balsam poplar litter becomes the dominant input to the forest floor that N mineralization and nitrification decline, simply because N availability in the litter substrate declines.

An alternate mechanism, however, is that poplar may produce compounds that directly alter microbial activity (e.g. substrates, toxins, or compounds that complex substrates and make them unavailable for microbial attack). Plant secondary chemicals, including tannins, low molecular weight phenolics, and terpenes may inhibit nitrification under some conditions (Baldwin et al. 1983; Thibault et al. 1982; Lodhi & Killingbeck 1980; White 1986). Tannins can

also act as inhibitors of soil microbial activity (Lewis & Starkey 1968; Benoit et al. 1968; Benoit & Starkey 1968; Swain 1979; Baldwin et al. 1983; Field & Lettinga 1992). Secondary metabolites may control decomposition and mineralization (Palm & Sanchez 1990, 1991; Gallardo & Merino 1992; Irons et al. 1991), and may also control the amount of N and the balance of inorganic vs. organic N present in soil solution (Northrup et al. 1995).

In Alaska, balsam poplar foliage and other tissues have high concentrations of condensed tannins (76 mg/g dry wt. in foliage; Schimel et al. 1996), as well as large concentrations of low-molecular-weight phenolics (120 mg/dry wt.; Cates et al. 1997), which may act as C sources (Sugai & Schimel 1993). It is also possible that either foliage or roots release other chemicals (sugars etc.) that may affect microbial activities as well. All of these chemicals may affect N cycling and soil processes and thereby feed back to the vegetation, possibly affecting the shift from alder to poplar. In this paper we review work that addresses how balsam poplar affects soil processes in an alder-dominated stand. This work has included both laboratory research to determine the specific mechanisms of effect and field work to test the applicability of those mechanisms to the 'real world'. There have been two foci to the work we have done: effects on soil mineralization dynamics and effects on N_2-fixation in alder.

Mineralization-lab studies

To study the effects of balsam poplar chemicals on microbial processes in alder soils, we extracted and purified poplar tannins and low molecular weight phenolics (Schimel et al. 1996; Cates et al. 1997). These chemicals were sorbed onto silica gel to facilitate their addition to the soils. We then applied the chemicals (20 or 50 mg/g soil) to alder soil in laboratory incubations. We also used cellulose as a control to supply C without having other specific physiological effects. We measured respiration rates and N-mineralization/ nitrification dynamics over a two week incubation period.

All carbon amendments reduced net N mineralization at the 20 mg/g level and caused net immobilization at the 50 mg/g addition level (Figure 2a; Schimel et al. 1996). This could be explained either by the compounds acting as microbial growth substrates thereby causing immobilization, or by inhibiting decomposition and gross mineralization. The mechanism responsible was determined from the microbial respiration. Both cellulose and phenolics increased soil respiration, indicating they were used as microbial substrates. Poplar tannins, however, inhibited respiration by 40% (Figure 2b), indicating that they inhibited microbial activity. In other experiments, alder tannin did not inhibit respiration in alder soils, indicating that poplar tannins do not
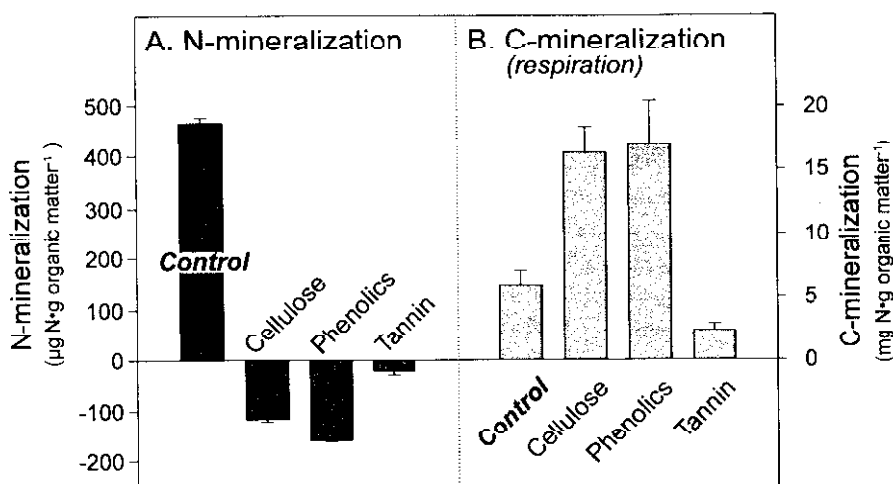
Figure 2. Effects of poplar chemicals (50 mg/g) and cellulose on N-mineralization and microbial respiration in soil from an alder stand. Data from Schimel et al. (1996).

merely replace alder tannins but introduce a new effect on N-cycling. These results suggest that balsam poplar secondary chemicals could reduce soil N availability by simultaneously reducing gross mineralization (tannins) and enhancing gross immobilization (phenolics). The question remained to what extent these effects occur in the field, as poplar becomes dominant in an alder stand.

Mineralization-field evidence

To test how poplar secondary chemicals affected soil processes in the field, we did a reciprocal transplant study. This allowed us to determine how changing the chemical environment of the soils would alter their C and N dynamics. We placed alder soils in a poplar site to simulate the changes in the chemical environment as poplar becomes dominant in an alder site.

We collected bulk samples of O horizon soil from both alder and poplar sites, homogenized the soil and packed it into polypropylene mesh 'cages' (5 cm diam. × 10 cm height, 6.4 mm mesh). The cage design was to contain the soil for sampling but to allow water and root movement into the soils. Replicate sets of cages were placed in the field in pairs, each pair having one alder and one poplar soil cage. They were placed in an alder stand and a mature balsam poplar stand in July 1992. In August 1992 and monthly through the summer of 1993 we collected cores and analyzed them for nitrification potential (chlorate slurry, Belser & Mays 1980), respiration potential

(CO_2 production over 30 days lab incubation), and N-mineralization potential (mineralization over the 30 day lab incubation).

One of the critical data sets from this experiment was the ratio of C to N mineralized in the lab after soils were collected from the field. This ratio is an indicator of the relative extent of C or N limitation to the soil microbial community (Schimel 1986). A high ratio of C to N mineralized indicates a N limited community, that is either processing N poor material or immobilizing a large portion of the mineralized N; a low ratio indicates a C limited community that has excess N relative to its needs. In alder soils, the ratio ranged between 10 and 24 (depending on sampling date and the site soil was incubated in), while the ratio for poplar soil ranged between 30 and 60 (Clein & Schimel 1995). These data indicate that alder soil microbial communities are relatively C limited while poplar communities are N limited.

One explanation for the relative C vs. N limitation between the two soils is indicated by the lab incubation respiration data (Table 1). Because these incubations were carried out under optimal conditions, they provide an indication of the availability of C to the microbial community. Poplar soil always respired more than the alder soil that had been incubated in the alder site, indicating that there was a ready supply of C to microorganisms in the poplar site. The highest respiration rates, however, were generally in the alder soils that had been incubated in the poplar site (Table 1; Clein & Schimel 1995). The increased respiration compared to the alder soils incubated in the alder site indicates that the poplar site was supplying labile C to the alder soils. Thus, in the poplar site, low N contents coupled to high amounts of available C led to N limited microbes.

Indices of net N availability (extractable inorganic N and nitrification potentials) in the field were always higher in alder soil than poplar soil at a given site, and were always higher in the alder site than in the poplar site for a given soil (Table 1). Thus, alder soil had greater native N availability than poplar. Transplanting alder soil to the poplar site decreased its N availability, while transplanting poplar soil to the alder site increased net N availability. The C and N data together suggest that the extra inputs of C the soils were receiving in the poplar site were responsible for increasing microbial growth and immobilization and thereby decreasing N availability.

Surprisingly, however, after cages were collected and soils were incubated in the laboratory for 30 days, N-mineralization in the alder soils was higher in soils that had been in the poplar site than in the alder site. Given that *in situ* net N availability was lower in alder soils incubated in the poplar site, this was surprising. The explanation likely involves the C inputs the alder soils receive in the poplar site (Figure 3). In the field, inputs of labile C would cause net N immobilization. After removing any inputs by incubating the

Table 1. Properties of poplar and alder soils that had been incubated in the field for approximately one year. Values are the average of measurements from at least three samplings spread over the 1993 growing season. Data are from Clein and Schimel (1995). All values are presented as means and standard errors.

Soil treatment	Soil inorganic N at sampling[1] μg N·g O.M.$^{-1}$	Nitrification potential μg N·g O.M.$^{-1}$·h^{-1}	C respired in a 30 day lab incubation μg N·g O.M.$^{-1}$	N mineralized in a 30 day lab incubation μg N·g O.M.$^{-1}$	Ratio of C/N mineralized in a 30 day lab incubation
Alder soil/Alder site	455 ± 120	3.6 ± 0.41	5920 ± 840	538 ± 59	11.0
Alder soil/Poplar site	73 ± 9.9	1.8 ± 0.30	7430 ± 980	705 ± 105	10.5
Poplar soil/Alder site	287 ± 141	1.5 ± 0.23	7140 ± 630	245 ± 37	29.1
Poplar soil/Poplar site	66 ± 14.2	1.0 ± 0.30	7420 ± 870	242 ± 41	30.7

[1] Inorganic is mostly NO_3^-. NH_4^+ values were only 23, 27, 23, and 31 μg N·g O.M.$^{-1}$ for the four treatments.

$$C \searrow \qquad\qquad \nearrow CO_2$$

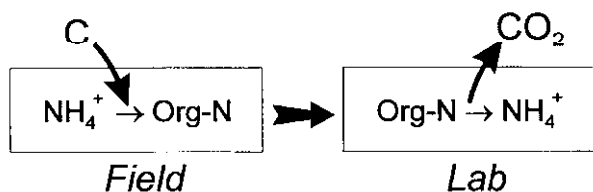| $NH_4^+ \to Org\text{-}N$ | ⟹ | $Org\text{-}N \to NH_4^+$ |

Field   *Lab*

Figure 3. Mechanism by which transplanting alder soils to a poplar site decreases N availability in situ, but increases N-mineralization in lab incubations.

soils in the lab, that C would be respired away, and the N associated with it would be mineralized.

The lab data showed strong inhibition of soil microbial activity, particularly N mineralization, by poplar tannins, as well as strong enhancement of activity by simple phenolics. The field data, however, suggest that the primary effect of balsam poplar on microbial processes in alder soils is through enhancing microbial activity by supplying labile C to alder microbes. Thus, tannins may be important in litter decomposition, but any role of tannins in inhibiting forest floor microbial processes is outweighed by the enhancement from the inputs of labile C.

The combination of the lab and field studies shows that as poplar becomes dominant in an alder stand it reduces net N availability to plants. This occurs via two mechanisms. The first is the increasing dominance of poplar litter, which is low in N (0.55% in senesced litter), decomposes slowly (leaves remain relatively intact for several years), and immobilizes N for 3–4 years (data not shown). The second mechanism by which poplar affects soil N availability appears to be by releasing labile C into the soils and stimulating N immobilization. It is unclear whether the C released is from root exudation, foliar leaching, litter leaching, or some combination of these. Thus, the low quality litter produces a long-term N sink, while labile C inputs provide a short-term N sink.

This reduction in soil N availability, however, shouldn't have a significant effect on alder, since alder species are symbiotic N_2-fixers and generally appear to obtain more than 90% of their N from N_2-fixation (Binkley et al. 1992; Mead & Preston 1992). Thus, a reduction in soil N availability should only be noticeable to alder if N_2-fixation is reduced. To test for this, we have also examined the effects of poplar on N_2-fixation in alder.

N_2-fixation-lab studies

Cates et al. (1997) carried out laboratory studies to determine the effect of poplar chemicals on N_2-fixation in alder. They took 2-year-old alder
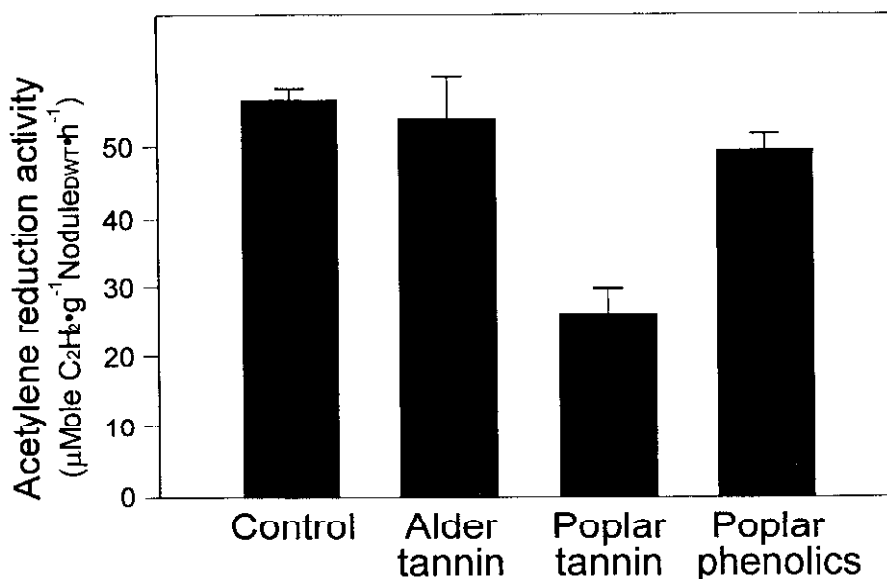
Figure 4. Effect of poplar chemicals on N_2-fixation in alder nodules. Data from Cates et al. (1997).

plants, put them into a hydroponic medium and applied poplar tannin, poplar phenolics, or alder tannin at concentrations of 0.1% w/w in the solutions. After 30 days incubation in the hydroponic system, they measured nitrogenase activity in excised alder nodules by acetylene reduction. While alder tannin and poplar phenolics had essentially no effect on N_2-fixation in alder nodules, poplar tannins significantly inhibited N_2-fixation ($p < 0.0001$; Figure 4). This suggests that poplar tannins have the potential to inhibit the ability of alder to fix N_2 *in situ*.

N_2-fixation-field evidence

Given the apparent lack of tannin activity in the field studies on mineralization, it seemed critical to test for poplar effects on N_2-fixation in alder in the field. Evidence suggests that the effects of poplar chemicals on N_2-fixation in the lab do occur in the field. A study measured N_2-fixation in alder nodules throughout the floodplain succession, from an open willow-alder stage; through a mature alder stage; a stage dominated by poplar, in which alder is an understory plant; and finally a mature white spruce stage, in which alder is also in the understory (Figure 5). N_2-fixation activity was measured by short-term acetylene reduction assays on excised nodules.
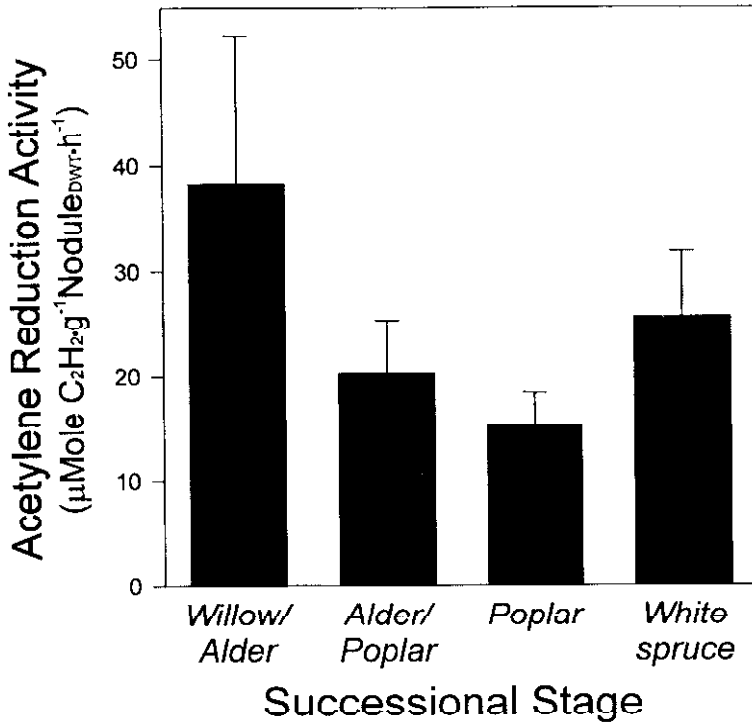
Figure 5. Changes in N_2-fixation activity in alder nodules through succession.

N_2-fixation per gram nodule declined through the stages from willow-alder through balsam poplar. This could result from the input of poplar secondary chemicals inhibiting N_2-fixation, or it could result from alder aging and becoming less active, some other resource becoming progressively more limited (either light from increased shading, or perhaps P becomes sequestered in biomass and organic matter), or from conditions becoming progressively worse in some other way, such as the soils becoming colder. However, N_2-fixation rates per gram nodule increased again into the oldest successional stage – the white spruce stage. In white spruce light remains very limited, soils are colder, and conditions appear generally less hospitable to alder (Viereck et al. 1993). This suggests that the increase in N_2-fixation in the white spruce stand was due to the demise of poplar, providing field evidence that the low N_2-fixation rates in the poplar stage are due to a specific poplar effect, probably mediated via tannins, as suggested by the lab studies.
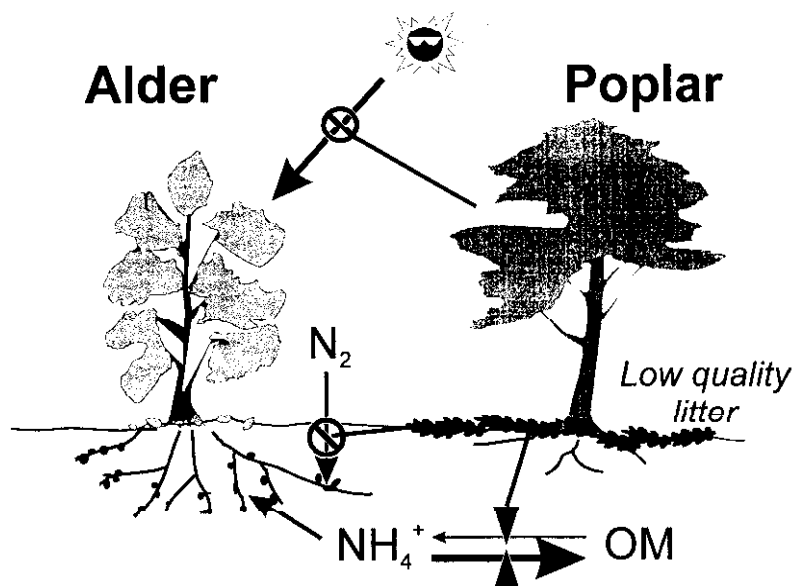
Figure 6. Mechanisms by which balsam poplar may affect thinleaf alder's access to nutrients and gain dominance through succession.

Synthesis

The integration of these studies provides a complex picture of interactions between alder and poplar that are mediated through the soil and involve a variety of chemicals, not all of which have been characterized. Figure 6 shows the combination of interactions that we believe go on during the transition from alder to poplar dominance on Alaskan floodplains.

Poplar appears to reduce N availability to alder by both inhibiting alder's ability to fix atmospheric N_2, and by reducing the availability of soil N that alder could potentially use as a substitute for fixed N_2. Thus, it may be possible that by reducing alder's ability to acquire N, balsam poplar may limit alder growth and give poplar a competitive advantage in getting into the canopy. Once poplar becomes dominant in the canopy, it can shade out alder and complete the transition to poplar domination (Figure 6).

The common explanation for the transition between alder and poplar is based primarily on life history traits. Alder requires high light and only lives for several decades, while poplar is more shade tolerant and is longer lived (Viereck et al. 1993). Thus, poplar can naturally replace alder without requiring active mechanisms for interfering with alder. However, the chemical interactions between alder and poplar support a hypothesis that the changes in N cycling through the transition are caused, in part, by poplar secondary

chemicals. As nutrient dynamics may play a role in controlling the timing of the transition from alder to poplar, it is therefore possible that poplar secondary chemicals affect the timing of the transition from alder to poplar domination of the community.

Another effect of poplar's reducing soil N availability is that it retains N in the ecosystem by enhancing net immobilization. In the long-term perspective of these ecosystems' structure and function, this may be even more important than any effect of hastening the successional transition. The N cycle in the alder stage has rapid inputs and rapid losses. As poplar replaces alder, N inputs from N_2-fixation decline; if N losses were not also reduced there could be large net losses of N from the ecosystem. As inputs decline through succession, if there were large N losses during the alder-poplar transition, it would reduce the total N pool available to later stages of vegetation in succession. This could affect the structure and function of floodplain ecosystems for an extended period.

This work may raise the question of whether some of the evolutionary selection for secondary chemical production has been for the effects on below-ground conditions and interactions, rather than these being merely 'accidental' side effects of some primary purpose. This hypothesis would run counter to much of the theory explaining plant secondary chemical production, which has focused on protection from herbivores (Rosenthal & Berenbaum 1992). Beyond raising the possibility of selection for soil effects, however, we don't believe there is sufficient evidence to draw meaningful conclusions on this issue.

Conclusions

This body of research has shown that poplar secondary chemicals have substantial ecological significance, beyond their role as herbivore deterrents (Bryant et al. 1991). These chemicals appear to strongly affect nutrient cycling in the taiga floodplain ecosystem and on the changes in nutrient cycling that occur through primary succession. Balsam poplar tannins, it appears, may have roles in controlling litter decomposition and in inhibiting N_2-fixation in alder. Simple phenolics and possibly other chemicals are strong stimulators of microbial activity and cause extensive N-immobilization, thus reducing N-availability and reducing N-loss. These kinds of interactions, mediated by plant secondary chemicals, are rarely considered in models of ecosystem behavior or in plant–soil relationships. We believe that the work described here and in other studies cited, show that plant secondary chemicals may sometimes be an important factor in mediating the interactions between plants and soils.

Acknowledgements

References

Aber JD, Melillo JM & McClaugherty CA (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68: 2201–2208

Baldwin IT, Olson RK & Reiners WA (1983) Protein binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. Soil Biol. Biochem. 15: 419–423

Belser LW & Mays EL (1980) Specific inhibition of nitrite oxidation by chlorate and its use in assessing nitrification in soils and sediments. Appl Environ Microbiol. 39: 505–510

Benoit RE & Starkey RL (1968) Enzyme inactivation as a factor in the inhibition of decomposition of organic matter by tannins. Soil Sci. 105: 203–208

Benoit, RE, Starkey RL & Basaraba J (1968) Effect of purified plant tannin on decomposition of some organic compounds and plant materials. Soil Sci. 105: 153–158

Binkley D, Sollins P, Bell R, Sachs D & Myrold D (1992) Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73: 2022–2033

Bryant JP. Provenza FD. Pastor J. Reichardt PB, Clausen TP & du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. Ann. Rev. Ecol. Syst. 22: 431–446

Cates RG, Terry R, Zou J & Wood S (1997) The effect of tannins amd phenolics from Alaska taiga species on nitrogen-fixation in *Alnus tenuifolia*. Biochem. Syst. Ecol. (submitted)

Clein JS & Schimel JP (1995) Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. Soil Biol. Biochem. 27: 743–752

Dyrness CT, Viereck LA & Van Cleve K (1986) Fire in taiga communities in interior Alaska. In: Van Cleve K, Chapin FS, III, Flanagan PW, Viereck LA & Dyrness CT (Eds) Forest Ecosystems in the Alaskan Taiga (pp 74–86). Springer-Verlag, New York

Field JA & Lettinga G (1992) Toxicity of tannin compounds to microorganisms. In: Hemingway RW & Laks PE (Eds) Plant Polyphenols (pp 673–692) Plenum Press. NY

Gallardo A & Merino J (1992) Nitrogen immobilization in leaf litter at two Mediterranean ecosystems of SW Spain. Biogeochemistry 15: 213–228

Irons JG, Bryant JP & Oswood MW (1991) Effects of moose browsing on decomposition rates of birch litter in a subarctic stream. Can. J. Fish. Aquat. Sci. 48: 442–444

Lewis JA & Starkey RL (1968) Vegetable tannins, their decomposition and effects of decomposition of some organic compounds. Soil Sci. 106: 241–247

Lodhi MAK & Killingbeck KT (1980) Allelopathic inhibition of nitrification and nitrifying bacteria in a ponderosa pine (*Pinus ponderosa* Dougl.) community. Am. J. Bot. 67: 1423–1429

Mann DH, Fastie CL, Rowland EL & Bigelow NH (1995) Spruce succession, disturbance, and geomorphology on the tanana river floodplain, Alaska. Ecoscience 2: 184–199

Mead DJ & Preston CM (1992) Nitrogen fixation in Sitka alder by ^{15}N isotope dilution after eight growing seasons in a lodgepole pine site. Can. J. For. Res. 22: 1192–1194

Northrup RR, Yu Z, Dahlgren RA & Vogt KA (1995) Polyphenol control of nitrogen release from pine litter. Nature 377: 227–229

Palm CA & Sanchez PA (1990) Decomposition and nutrient release patterns of the leaves of three tropical legumes. Biotropica 22: 330–338

234

Palm CA & Sanchez PA (1991) Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biol. Biochem. 23: 83–88

Post WM, Pastor J, Zinke PJ & Stangenberger AG (1985) Global patterns of soil nitrogen storage. Nature 317: 613–616

Rosenthal GA, Berenbaum ME (1992) Herbivores: Their Interactions with Secondary Plant Metabolites. Volume II. Academic Press, San Diego

Schimel DS (1986) Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2: 345–357

Schimel JP, Van Cleve K, Cates RG, Clausen TP & Reichardt PB (1996) Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: Implications for changes in N cycling during succession. Can. J. Bot. 74: 84–90

Sugai SF & Schimel JP (1993) Decomposition and biomass incorporation of ^{14}C-labeled glucose and phenolics in taiga forest floor: effect of substrate quality, successional state, and season. Soil Biol. Biochem. 25: 1379–1389

Swain T (1979) Tannins and lignins. In: Rosenthal GA & Jansen DH (Eds) Herbivores: Their Interactions with Secondary Plant Metabolites (pp 657–682). Academic Press, New York

Swift MJ, Heal OW & Anderson JM (1979) Decomposition in Terrestrial Ecosystems. Univ. California Press, Berkeley

Thibault J-R, Fortin J-A & Smirnoff WA (1982) In vitro allelopathic inhibition of nitrification by balsam poplar and balsam fir. Am. J. Bot. 69: 676–679

Van Cleve K, Chapin FS, III, Flanagan PW, Viereck LA & Dyrness CT (1986) Forest Ecosystems in the Alaskan Taiga. Springer-Verlag, New York

Van Cleve K, Dyrness CT, Marion GM & Erickson R (1993) Control of soil development on the Tanana River floodplain, interior Alaska. Can. J. For. Res. 23: 941–955

Viereck LA, Dyrness CT & Foote MJ (1993) An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Can. J. For. Res. 23: 889–898

White CS (1986) Volatile and water-soluble inhibitors of nitrogen mineralization and nitrification in a ponderosa pine ecosystem. Biol. Fertil. Soils 2: 97–104