NOTE / NOTE

Response of *Gaultheria shallon* and *Epilobium angustifolium* to large additions of nitrogen and phosphorus fertilizer

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Abstract: A study was established in coastal British Columbia to determine if repeated nitrogen (N) and phosphorus (P) fertilization negatively influences the reestablishment of salal (*Gaultheria shallon* Pursh) on cleared and burned cedar–hemlock (*Thuja plicata* Donn ex D. Don – *Tsuga heterophylla* (Raf.) Sarg.) forests. Fertilizers were applied for 3 years, and the biomass of ground vegetation and conifer seedling survival and growth were measured. Salal biomass decreased with high levels of N application (1000 kg N/ha), but not when 400 kg P/ha was added with 1000 kg N/ha. The addition of 500 kg N/ha, with or without P, stimulated salal growth. The biomass of fireweed (*Epilobium angustifolium* L.) increased with the addition of N + P but not with N alone. In the high N and N + P treatments, conifer seedling survival and heights were reduced. These results confirm earlier reports that salal responds negatively to high N applications and that this negative response can be alleviated with simultaneous additions of P. The response of fireweed to N + P, but not to N alone, suggests that the abundance of this species is more indicative of P than N availability.

Résumé : Une étude a été entreprise dans la région côtière de la Colombie-Britannique afin de vérifier si l'ajout répété d'azote (N) et de phosphore (P) nuit au rétablissement de la gaulthérie (*Gaultheria shallon* Pursh) dans des forêts bûchées et brûlées de cèdre et de pruche (*Thuja plicata* Donn ex D. Don – *Tsuga heterophylla* (Raf.) Sarg.). Les fertilizants ont été appliqués pendant 3 ans et la biomasse de la végétation du sous-bois ainsi que la survie et la croissance des semis de conifères ont été mesurées. La biomasse de la gaulthérie a diminué avec un taux d'application élevé de N (1000 kg N/ha) mais n'a pas diminué lorsque 400 kg P/ha était ajouté avec 1000 kg N/ha. L'ajout de 500 kg N/ha, avec ou sans P, a stimulé la croissance de la gaulthérie. La biomasse de l'épilobe (*Epilobium angustifolium* L.) a augmenté avec l'ajout conjoint de N et P mais pas avec N seul. Avec le taux élevé de N et de N + P, la survie et la hauteur des semis de conifères ont été réduites. Ces résultats confirment les rapports antérieurs faisant état de la réaction négative de la gaulthérie à l'application de taux élevés de N et de l'atténuation de cette réaction négative par l'addition simultanée de P. La réponse de l'épilobe à N + P, mais non à P seul, indique que l'abondance de cette espèce est un indice de la disponibilité de P plus que de N.

[Traduit par la Rédaction]

Introduction

Salal is an ericaceous evergreen shrub that dominates nitrogen-poor sites in coastal British Columbia. Through rapid rhizome spread, extensive root systems, morphological plasticity to light, and dense aboveground cover, salal can be a serious competitor with trees regenerating on cutovers (Messier and Kimmins 1991). Competition and possible allelopathic effects of salal are thought to be partly responsible for poor nutrition and growth of planted and natural conifers (Fraser et al. 1995; Preston 1999), a situation analogous to conifer growth check observed on other ericaceous sites in the U.K., Ireland, and eastern Canada (Weatherell 1954; Carey 1977; Titus et al. 1995).

During measurement of two repeated fertilization trials in coastal British Columbia and Washington State, a very obvious reduction in salal biomass was observed in plots that had been repeatedly fertilized with nitrogen (N) (Prescott et al. 1993). At the Pack Forest in Washington, salal was eliminated in a plot that received N alone (1540 kg N/ha over

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32 years), but remained abundant in a plot that received N (1082 kg N/ha) with phosphorus (P) and sulfur (S). In a fertilization trial on Vancouver Island, salal was absent in plots that had received only N (600 kg N/ha), but was still present in plots where both S and N were applied. Unlike the heathlands of northern Europe (Pearson and Stewart 1993), the reduction in salal did not appear to be a function of competition, as the salal response was not related to the increased crown biomass or growth of other species of ground vegetation. Based on these observations, it was hypothesized that N may have a direct negative effect on growth and survival of salal, which is alleviated when other nutrients such as P or S are also applied. This hypothesis was further supported by results of a subsequent trial near Nanaimo on Vancouver Island (B. D'Anjou, unpublished data), in which salal cover was markedly reduced after two additions of N totaling 800 kg N/ha.

The potential to reduce salal competition through repeated N fertilization is of particular interest for the reforestation of N-poor cutovers of cedar–hemlock (*Thuja plicata* Donn ex D. Don – *Tsuga heterophylla* (Raf.) Sarg.) forests on northern Vancouver Island (Prescott et al. 1996). Salal typically reoccupies cedar–hemlock cutovers 5–7 years following clearing and burning and coincides with the development of foliar chlorosis in regenerating conifers (Weetman et al. 1989). Although chlorosis and poor growth of the conifers can be temporarily relieved by the application of 100 kg N/ha, and to a much greater degree by 300 kg N/ha + 100 kg P/ha (Weetman et al. 1989), both fertilization regimes also appear to stimulate salal growth on cedar–hemlock sites. Thus, in 1996, a study was installed on a recently clear-cut and burned cedar–hemlock site to determine if repeated N fertilization, with and without P, would inhibit salal reestablishment. We tested the hypotheses from earlier studies that high N additions inhibit salal and that the addition of P together with N offsets the negative effects of N on salal. The response of salal was determined through aboveground biomass assessments 2 years after the final fertilizer application. Aboveground biomass of all other ground vegetation was also measured to determine the potential role of competing vegetation in salal's response. The survival, height, and diameter of cedar and hemlock seedlings were measured to determine seedling responses to the fertilization treatments.

Materials and methods

The study site was near Port McNeill, on northern Vancouver Island, B.C. (50°60′N, 127°35′W) in the Coastal Western Hemlock very wet maritime (CWHvm) biogeoclimatic subzone (Green and Klinka 1994). At this location, the annual average precipitation is 1700 mm, and the mean daily temperatures range from 3.0 °C in January to 13.7 °C in July. Topography is gently undulating, and soils are well to poorly drained Ferro-Humic Podzols on unconsolidated morainal and fluvial outwash materials. An old-growth western redcedar and western hemlock forest occupied the site prior to being clear-cut and slash-burned in 1996. Cedar seedlings were planted in 1996 (1200 stems/ha) and hemlock seedlings (1 +0 PSB 313) were interplanted (1200 stems/ha) in May 1997 to give a final density of 2400 stems/ha. In the summer of 1996, 20 plots, each 20 m × 20 m, were established in the clearcut and randomly assigned to the following treatments in a completely randomized design with four replicates of each treatment.

(1) 500 kg N/ha
(2) 1000 kg N/ha
(3) 500 kg N/ha and 200 kg P/ha
(4) 1000 kg N/ha and 400 kg P/ha
(5) Control (no fertilizers applied)

The N fertilizers were applied as ammonium nitrate and the P as triple super phosphate. Each of the fertilizer additions was applied over 3 years: the spring of 1998, the spring of 1999, the fall of 1999, the spring of 2000, and the fall of 2000. Applications of 500 kg N/ha were added as 300 kg N/ha in spring of 1998 with subsequent additions of 50 kg N/ha at the times listed above. The 1000 kg N/ha treatment was applied as 600 kg N/ha in spring 1998 with subsequent additions of 100 kg N/ha. The additions of 200 kg P/ha were applied as 100 kg P/ha in 1998 with subsequent additions of 25 kg P/ha. The 400 kg P/ha treatment was added as 200 kg P/ha in 1998 with subsequent additions of 50 kg P/ha.

The biomass of ground vegetation was measured in July 2002 (4 years after the initial fertilization and the second growing season after the last fertilization). Six sampling quadrats (0.75 m × 0.75 m) were randomly arranged within the inner 100 m^2 of each plot, and all living, aboveground, vascular vegetation was collected from within each quadrat. By mistake, vegetation in one plot of the 500 kg N/ha and 200 kg P/ha treatment was only sampled in three quadrats and one control plot was not sampled. The collected vegetation was separated by species and composited by plot. Samples were dried at 70 °C for 48 h, and the dry mass of each species was measured. Prior to drying, salal leaves were separated from the stems to determine foliar, stem, and total dry biomass. However, foliar and stem biomass results were similar and were therefore combined and presented as total salal biomass. Whole-plant aboveground biomass was measured for the other species, which included fireweed, deer fern (*Blechnum spicant* (L.) Sm.), bunchberry (*Cornus canadensis* L.), red huckleberry (*Vaccinium parvifolium* Sm.), and lady fern (*Athyrium filix-femina* (L.) Roth). Because fireweed accounted for a large proportion of the ground vegetation, its biomass results were analyzed and reported separately. The heights, diameters, and survival of all cedar and hemlock seedlings in the plots were assessed in April 2001.

Differences in the biomass of salal, fireweed, other ground vegetation, and the total ground vegetation among treatments were assessed using one-way analysis of variance (ANOVA) of plot means (n = 19). Because of the unbalanced experimental designs, the Tukey–Kramer multiple comparison test was then applied. Differences in seedling height and survival were assessed using one-way ANOVA, followed by Tukey's HSD multiple comparison test. Data were log transformed when necessary to meet the assumptions of ANOVA. Values presented are untransformed data, and the accepted alpha level was 0.05. The correlations between fireweed and salal biomass and between seedling heights and total ground vegetation biomass were determined using Spearman's correlation analysis. SAS Version 8.02 (SAS Institute Inc., Cary, N.C.) was used for all analyses.

Results

By July 2002, there were very obvious differences in the ground vegetation and conifer seedling responses among fertilizer treatments. The total aboveground biomass of ground vegetation was significantly higher in the 500 kg N/ha + 200 kg P/ha treatments than in the controls (Fig. 1). Biomass was significantly lower in the 1000 kg N/ha plots than in the remaining fertilizer treatments. Although not significant, biomass of species other than salal and fireweed was greater in the plots receiving only N.

Salal biomass decreased significantly with high levels of N application (1000 kg N/ha), but not when 400 kg P/ha was added with 1000 kg N/ha (Fig. 1). When N and P were combined at this high application rate, salal aboveground biomass in the treated plots was similar to that in the controls. The addition of 500 kg N/ha, with or without P, stimulated salal growth. Salal biomass was significantly lower in plots fertilized with 1000 kg N/ha than in plots receiving 500 kg N/ha + 200 kg P/ha. Fireweed biomass was significantly higher in the two N + P treatments than in the plots receiving N alone at 1000 kg N/ha (Fig. 1).

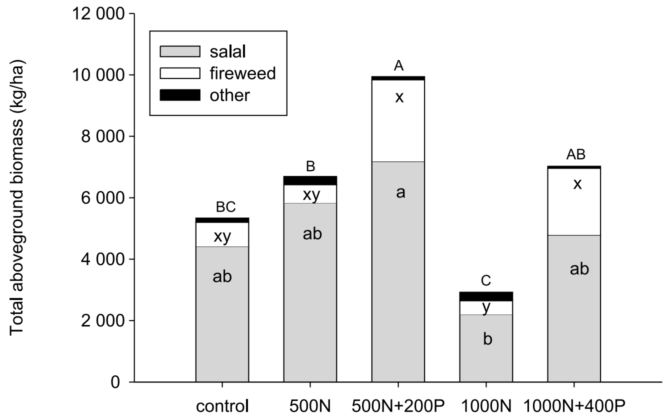
There was no relationship between biomass of salal and fireweed (r = –0.02, p = 0.81). There was no indication that the reduction in salal biomass in the 1000 kg N/ha plots was the result of increased competition from fireweed, as fireweed biomass was also low in these plots. The greatest biomass of fireweed was in the N + P plots, which also had large amounts of salal.

The survival and height of the conifer seedlings was significantly lower in plots that received 1000 kg N/ha with or without P than in control plots (Fig. 2). This did not appear to be the result of increased competition from ground vegetation, as there was no relationship between total ground vegetation biomass and height of either the cedar (r = –0.08, p = 0.76) or hemlock seedlings (r = 0.25, p = 0.31).

Discussion

The results of this experiment are consistent with the hypothesis that salal reestablishment is reduced with high N loading. Six years after clearing and burning a cedar–hemlock site, salal aboveground biomass was lower on plots receiving 1000 kg N/ha. Reduction in ericaceous plants following chronic or repeated inputs of N have been reported in other N-poor systems. The heathlands of northern Europe have seen a decrease in *Calluna* and other heath species (Pearson and Stewart 1993), and repeated N fertilization of a jack pine forest in Quebec reduced the cover of *Kalmia angustifolium* (Prescott et al. 1995). Suggested mechanisms to account for the negative growth responses include induced competition resulting from a shift in soil fertility favouring plant species characteristic of more fertile conditions (Kellner 1993; Pearson and Stewart 1993), ammonia toxicity due to high concentrations of N in the rooting media (Kellner 1993; Pearson and Stewart 1993; De Graaf et al. 1998), and reduction in mycorrhizal roots and colonization in response to elevated N (Yesmin et al. 1996; Johansson 2000). In the current study, the reduction in salal biomass in the high-N plots was not the result of competition, as the biomass of other vegetation was also reduced in these plots.

Fig. 1. Total aboveground biomass of all ground vegetation in plots receiving different rates (kg/ha) of nitrogen (N) or nitrogen + phosphorus (N + P) fertilizer. Bars are divided to show the proportion of total biomass accounted for by salal, fireweed, and other ground vegetation. Each value is the mean of four plots (three for controls). Total aboveground biomass means with different uppercase letters are significantly different ($p \leq 0.05$) based on one-way ANOVA and Tukey–Kramer test. For salal and fireweed, means with different lowercase letters are significantly different ($p \leq 0.05$) based on one-way ANOVA and Tukey–Kramer test.

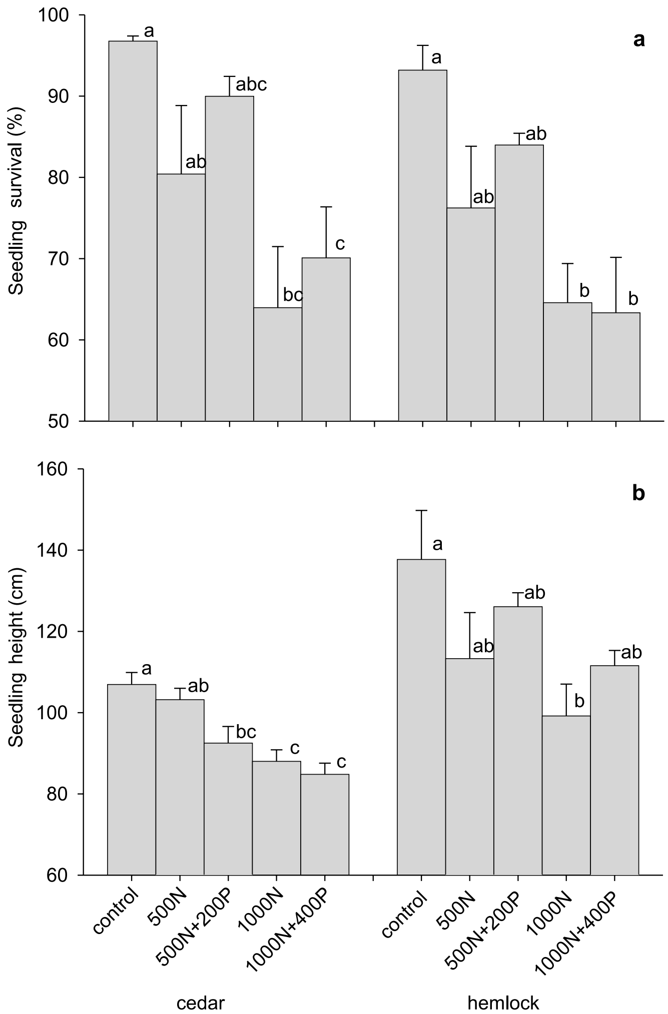


The decrease in salal, therefore, may have been a result of soil N concentrations in the high-N plots reaching levels that are inhibitory to root growth or mycorrhizal function. Root growth of most species is retarded at NH_4^+ concentrations greater than 0.1 mmol/L (Schenk and Wehrmann 1979). Although N concentrations in the forest floor solution were not measured, the greatest reductions in salal were in low-lying areas of the plots, where water and dissolved N would collect. Prescott and others (1993) also suggested that salal roots and mycorrhizae might be inhibited by the high concentrations of ammonium and nitrate in the forest floor, where fine roots of salal are concentrated (Bennett et al. 2002). Colonization of roots by mycorrhizal fungi can be reduced by fertilization and increased N concentrations in growth media (Pearson and Stewart 1993; Yesmin et al. 1996). Thus, large additions of inorganic N could interfere with the formation of ericoid mycorrhizae, which are believed to give salal a competitive advantage on these N-poor sites (Xiao and Berch 1996).

As hypothesized, the decrease in salal biomass in fertilized plots did not occur when P was added along with N. This indicates that the negative effect of large N additions may be the result of a nutrient imbalance, which is consistent with the larger growth response of conifers to additions of N + P than to N alone on other cedar–hemlock sites (Weetman et al. 1989). Elevated levels of soil P may also allow for greater immobilization of the added N by microbes and plants, thus keeping inorganic N concentrations in the forest floor below the level at which they inhibit roots and mycorrhizae.

The much greater response of fireweed to applications of N + P than to N alone was surprising, as fireweed abundance is usually considered to be indicative of sites with high N or nitrate availability (Tamm 1956; Klinka et al. 1989). Van

Fig. 2. Survival (*a*) and height(*b*) of western redcedar and western hemlock seedlings in each treatment (kg/ha) in 2001 (3 years after initial fertilization). Within a species, means with different letters are significantly different ($p \leq 0.05$) based on one-way ANOVA and Tukey's HSD multiple comparison test. The error bars shown are the standard error of the mean survival and height for each species.



Andel (1976) concluded that growth of *Epilobium* was independent of the level of P supply, and Chapin (1995) reported a large response of fireweed to fertilization with N only, no response to P only, and that fertilization with N and P did not differ much from N only. The effect of P alone was not tested in this study, but the large positive response of fireweed to N + P fertilization and its negative response to N alone indicate that its abundance on these sites is closely related to P availability. Fireweed rapidly invades areas in western North America that have been disturbed by wildfire or logging, and its presence is indicative of the post-disturbance nutrient flush (Kimmins 1996). Although this "assart flush" is often thought of in terms of high N availability, the responses of fireweed to fertilization in this study suggest that increased P availability may be largely responsible for postdisturbance changes in fireweed abundance.

In conclusion, the addition of a high cumulative dose of N alone inhibited salal regeneration on cedar–hemlock cutovers, as hypothesized. Growth of fireweed was also reduced in these treatments, indicating that the effect on salal was not the result of increased competition. In contrast, when P was included with the fertilization, the growth of salal and fireweed was stimulated, suggesting that P addition somehow reduced the deleterious effect of N and alleviated growth-limiting nutrient deficiencies. Additional work is necessary to elucidate the mechanisms behind the vegetation responses to large additions of N + P fertilizers.

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