Effect of Two Years of Nitrogen Deposition on Shoot Growth and Phenology of Engelmann Spruce (*Picea engelmannii* Parry ex Engelm.) Seedlings

A. W. Schoettle

INTRODUCTION

As a result of anthropogenic combustion processes, ecosystems in the eastern and western United States and Europe have experienced elevated atmospheric deposition of nitrogen for most of this century and have begun to show symptoms of decline. If there is a cause and effect relationship between nitrogen deposition and ecosystem decline, one would expect that the current symptoms are a result of the cumulative effect of years of deposition. Deposition of anthropogenically produced nitrogenous compounds has increased along the Colorado Front Range in the past decades as a result of increased urbanization (Sievering et al., 1992, 1996; Williams et al., 1996). Annual pollutant deposition rates increase with elevation (Gilliam et al., 1996) due to the greater amount of precipitation at high elevations. There-

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A. W. Schoettle is affiliated with the Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, CO 80526 (E-mail: Schoettl@lamar.colostate.edu).

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fore, the health of high elevation Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests may be at risk from sustained nitrogen inputs.

In the Colorado Rocky Mountains, the nitrogen deposition rate currently ranges from 3 to 6 kg N ha^{-1} y^{-1} at sites above 2700 m elevation. These deposition rates are low compared to maximum rates in Europe (58.8 kg N ha^{-1} y^{-1}, see Wright and Rasmussen, 1998), the eastern U.S. (10-20 kg N ha^{-1} y^{-1}, Gilliam et al., 1996), and the western U.S. (35-45 kg N ha^{-1} y^{-1}, Fenn et al., 1996). However, even the low nitrogen deposition rates in Colorado may exceed the nitrogen demand by high elevation plants since nitrogen requirement is limited by a short growing season. It has been hypothesized that excess nitrogen inputs may change shoot phenology by prolonging growth in fall (Friedland et al., 1984). This study quantified shoot growth and phenology of Engelmann spruce seedlings over two years in response to four levels of wet nitrogen deposition.

METHODS

Plant Material and Culture

Engelmann spruce seedlings were grown at the Mt. Sopris Nursery from seeds from a stand at 2888 m elevation on the White River National Forest, Colorado, USA. The seeds were planted in the spring of 1984. In June of 1986, the two-year-old seedlings were transplanted to 15 cm × 40 cm fiber pots with sieved forest soil (Darling series) collected from a spruce forest on the Fraser Experimental Forest in Fraser, Colorado. The plants were placed under an acrylic reinforced fiberglass open-air rain shelter in the understory of a *Pinus contorta* Dougl. forest at 3000 m elevation in southern Wyoming. During the growing seasons of 1986 and 1987, the plants were protected from ambient rain by the shelter and received only treatment solutions. At the end of October 1986 and 1987, the treatments were stopped, the shelter was removed, the pots were bermed with wood chips in a random arrangement with respect to treatment, and the plants were left to be covered with snow in winter.

Treatments

Two hundred and forty seedlings were randomly assigned to four nitrogen deposition treatments. The treatments were delivered in solution form to the surface of the soil for fifteen weeks per growing season. The treatment solutions were composed of reagent grade chemicals in combination with de-ionized water to simulate the rain chemistry that was collected during June-September in 1984 and 1985 in Rocky Mountain National Park, Colorado (Schoettle and Hubbard, 1992). The four treatments were prepared to represent ambient rain (1 ×), ambient rain containing ten times ambient nitrogen concentration (10 ×), ambient rain containing thirty times ambient nitrogen concentration (30 ×), and ambient rain containing fifty times ambient nitrogen concentration (50 ×) (Table 1). One hundred and seventy mL of solution was applied once a week to each pot and was the only water the seedlings received through the growing seasons. The quantity of treatment solution delivered to each pot was equal to the natural deposition rate of rainfall in subalpine forests at 3000 m in the central Rocky Mountains (National Atmospheric Deposition Program). The plants showed no sign of water stress.

Measurements

Bud break in spring of the second year was monitored weekly on the forty seedlings per treatment from mid-May until mid-July when all the seedlings had initiated growth. In both years, after growth was initiated, terminal shoot length and the length of the needles on the terminal shoot were recorded weekly until growth ceased. In fall of both years, the number of new shoots and lateral buds per seedling were counted.

Twenty plants per treatment were harvested after the first growing

TABLE 1. Summary of the nitrogen characteristics of treatment solutions. Deposition rates are for fifteen weeks of treatment each year between July and October. For complete chemical composition of simulated rain solutions, see Schoettle and Hubbard (1992).

Treatment	Nitrate concentration (mg L^{-1})	pH	Nitrogen deposition (kg N ha^{-1} growing $season^{-1}$)
1 ×	1.68	4.9	0.55
10 ×	16.82	4.2	5.48
30 ×	50.40	3.5	16.44
50 ×	84	2.9	27.38

season. Current-year and preexisting foliage from each seedling were oven dried at 65°C for 48 h. The mass per needle of current-year foliage was measured. The current-year and preexisting foliage were ground separately in a Wiley Mill (40 mesh) and analyzed for nitrogen by the micro-Kjeldahl method (Parkinson and Allen, 1975).

Net photosynthesis of one current-year lateral shoot from the second upper-most whorl of five seedlings per treatment was repeatedly measured, intact, from August 30 through November 11, 1987 with an ADC LCA-2 infrared gas analysis system (ADC, England). Measurements were made in the ambient environment when full sun was available and air temperature conditions were 15°C ± 3°C (standard deviation). Net photosynthesis is expressed on a total leaf surface area basis (Thompson and Leyton, 1971).

The data met the assumptions of normality and equal variance and were analyzed by analysis of variance. Orthogonal contrasts were used to test for linear, quadratic, and cubic relationships among the treatments (SAS, Cary, NC, USA).

RESULTS

One season of nitrogen additions caused a significant linear increase in foliar nitrogen in both new and preexisting foliage (Figure 1). There was no effect ($p > 0.05$) of the treatments on the number of needles produced per new shoot or the number of new shoots per seedling during the first growing season. There was a slight, but not statistically significant ($p = 0.10$), increase in the mass per needle and length of new needles at the end of the first season for those plants that received elevated nitrogen inputs.

Nitrogen additions significantly increased the number of new shoots and new lateral buds per seedling after the second growing season (Figure 2). The terminal shoot length of seedlings increased linearly with increased nitrogen addition (Figure 3). Average needle length of the terminal shoot was slightly, but not significantly, greater in response to nitrogen additions during the second growing season ($p = 0.06$).

Nitrogen additions altered some, but not all, of the measured phenological events during the second year of treatment. In spring after the first growing season, the initiation of growth of terminal buds was

FIGURE 1. Linear response ($p < 0.001$) of foliar nitrogen in new and preexisting foliage to nitrogen additions in the first growing season. Each point (± standard error) is an average of five samples each composed of foliage from four seedlings.

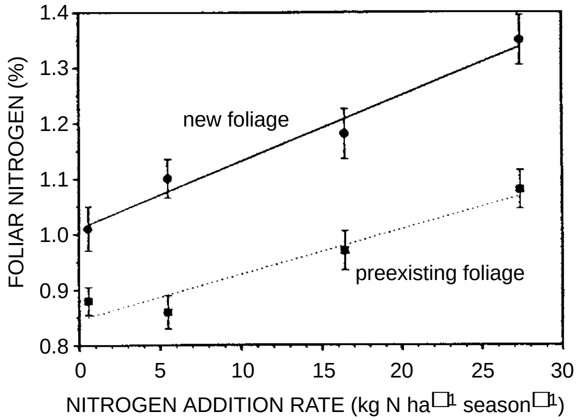


FIGURE 2. The effect of nitrogen additions on the number of new shoots (± standard error) and new lateral buds formed per seedling (± standard erro) in the second season of treatment. The relationships were linear ($p < 0.001$). The number of seedlings observed was 37, 37, 33, and 36 for the 1×, 10×, 30× and 50× treatments, respectively.

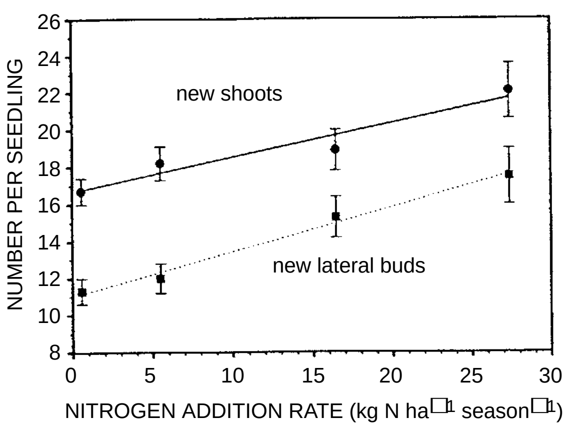
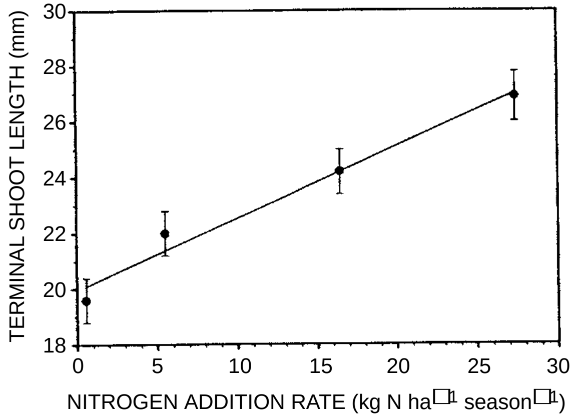


FIGURE 3. Length of the terminal shoot (± standard error) after the second season of nitrogen additions. The relationship was linear ($p < 0.001$). The number of seedlings observed was 37, 37, 33, and 36 for the 1×, 10×, 30× and 50× treatments, respectively.



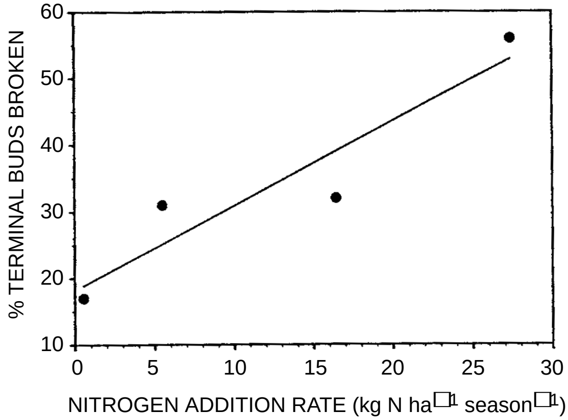
accelerated by nitrogen additions (Figure 4). The duration of terminal shoot elongation was not affected ($p > 0.05$) by the nitrogen treatments. The time course of the decline in net photosynthesis in the fall of the second year of treatment was not significantly affected by nitrogen additions (Figure 5).

DISCUSSION

During the first season of nitrogen additions, foliar nitrogen concentration in both the new and the preexisting foliage was significantly increased, demonstrating that the nitrogen delivered in the treatment solutions was available to the seedlings. As expected, there were no treatment effects on the number of needles or new shoots extended in the first growing season, because the number of needles and lateral buds per shoot are determined in the previous year for spruce.

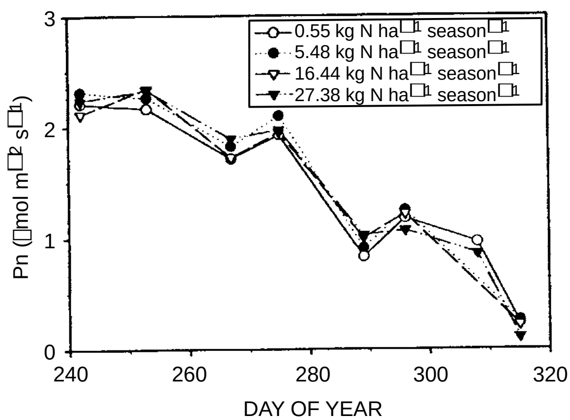
An increase in the growth of seedlings that received elevated nitrogen became evident in the second year. More new shoots were initiated during the second growing season on seedlings that received

FIGURE 4. Percentage of seedlings whose terminal buds had burst by June 12, 1987 as a function of nitrogen addition treatment. The number of seedlings observed was 37, 37, 33, and 36 for the 1 ×, 10 ×, 30 × and 50 × treatments, respectively. The relationship was linear ($p < 0.05$).



nitrogen deposition treatments. The number of new lateral buds per

FIGURE 5. The time course of the decline in net photosynthesis in the later portion of the second growing season. Measurements were repeatedly made on one shoot of each of five seedlings per treatment; the average standard error was 0.09 μmol m^{-2} s^{-1}. No readings were taken on plants treated with the 5.48 or 16.44 kg N ha^{-1} growing $season^{-1}$ treatments on Julian day 308.



seedling was also increased by nitrogen addition, as well, suggesting that the production of new shoots per year may continue to increase with sustained nitrogen treatment.

Nitrogen additions affected the phenology of Engelmann spruce seedlings during the second year. The growing season was lengthened by nitrogen additions. Contrary to the hypothesis of Friedland et al. (1984), the nitrogen additions in the present study extended the growing season for Engelmann spruce in the spring rather than fall. With increased nitrogen availability, growth was initiated earlier in the spring for Engelmann spruce, yet no effects were measured for the decline in physiological activity in the fall as estimated from net photosynthesis and shoot elongation. Although no effects were detected by Lumme and Smolander (1996) for Norway spruce (*Picea abies* Karst) seedlings until the nitrogen deposition rate approached the equivalent of 100 kg N ha^{-1} y^{-1}, they also observed that bud burst was accelerated by nitrogen addition. Acceleration of spring bud break by nitrogen additions indicates that nitrogen deposition at high elevations in the Rocky Mountains may expose seedlings to damage by late spring or early summer frost or cold periods.

CONCLUSIONS

These results suggest that the growth and phenology of Engelmann spruce seedlings are responsive to nitrogen inputs at deposition rates that could occur in Colorado. If nitrogen inputs continue to rise along the Front Range of Colorado, we may expect to see a change in the crown architecture of Engelmann spruce seedlings as well as an increase in damage to new foliage due to late frosts or abnormal cold periods in early summer. Further research is needed to assess Engelmann spruce seed source recommendations for regeneration plantings in areas with high nitrogen deposition and to evaluate the sensitivity of mature Engelmann spruce trees to nitrogen deposition.

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