An Efficient Design for Studies of Plant Species Interactions: An Example with White Spruce and Alder

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Abstract

An experiment that examines plant species interactions under controlled conditions is described. The plantation lay-out is a combination of Nelder plots and a classical replacement series. Densities within individual plots range over four orders of magnitude, and the experiment as a whole includes plots with five different species ratios (100:0, 75:25, 50:50, 25:75, and 0:100). The experiment considers two common species of the boreal forest of Alaska: white spruce and green alder. Four growing seasons after planting, there was a highly significant density effect on both the height and diameter growth of the spruce trees, but species ratio did not have an ecologically important effect on growth.

Key words: *Nelder plots, replacement series, boreal forest*

Introduction

A Nelder plot is an experimental plantation lay-out in which plants are arranged in concentric circles or portions of circles (referred to here as 'arcs') (Nelder 1962). The distance between the arcs increases in a geometric progression, so that the area available to an individual plant increases from one arc to the next by the same factor (figure 1). Nelder plots are an efficient means of examining the effects of density on plant growth in that trials of many different densities can be done in a small amount of space. They have been used in studies of a variety of crop plant species, including maize (Bunting 1971, 1973), lettuce (Sale 1966), potatoes (Lynch and Rowberry 1977), and broccoli (Salter *et al.* 1984), and in a few studies of tree growth (Cripps et al. 1975, Belanger and Pepper 1978, Thomson 1986). Cole and Newton (1986) combined the Nelder plot design with the classical replacement series design used in experiments on interspecific competition (de Wit 1960). Their so-called 'Nel-Rep' experiments employ a replicated series of Nelder plots through which the proportions of two species, Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and red alder (*Alnus rubra* Bong.), are varied.

This paper describes the early results of a similar study of interactions between white spruce (*Picea glauca* Moench. Voss) and green alder (*Alnus crispa* (Ait.) Pursh) in the boreal

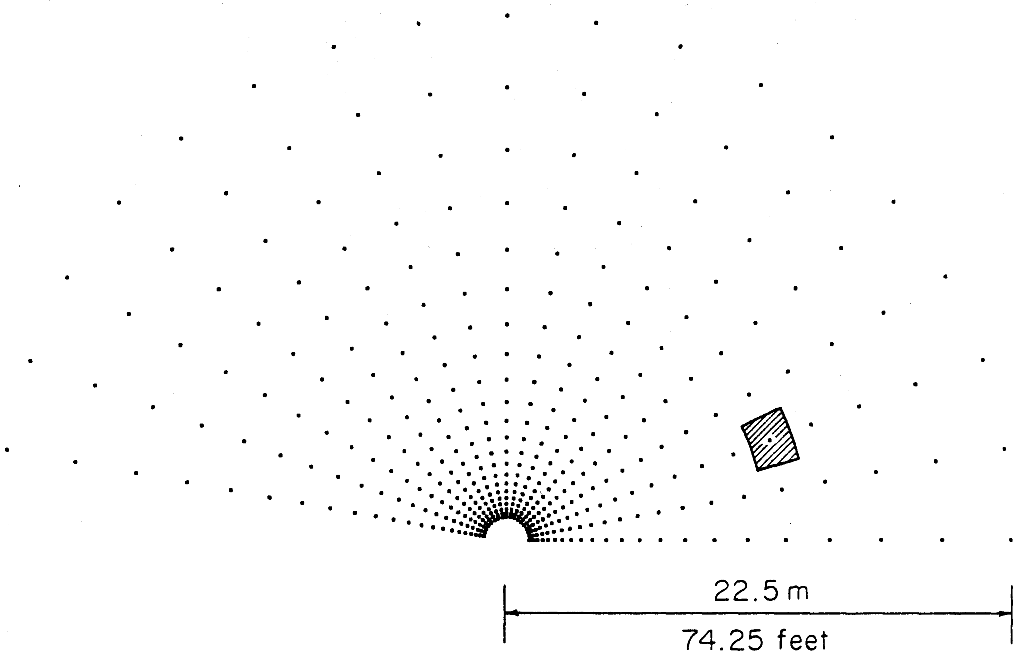


Figure 1: The Nelder plots used in this study each have 22 arcs and 18 spokes, with a 10° angle of separation between spokes. Shaded area is the space available to an individual in the seventeenth non-buffer arc

forest region of Alaska. At present, white spruce is the most commercially valuable tree species in this region, while green alder is a shrubby species with no commercial value.

Green alders are aggressive colonists of recently harvested sites, quickly producing a dense shady canopy, and their presence can seriously impact on the establishment and early growth of a regenerating stand of crop trees. Yet they are also the primary nitrogen fixers of Alaska's boreal forest. Their roles are pivotal in soil amelioration in every sequence of forest succession thus far described for the region (Van Cleve and Viereck 1981). For example, in the first 20 years of primary succession on interior Alaska floodplain sites, alders fix 70% of the nitrogen needed by the system for the next 200 years. Further, scattered alders that remain in the understorey of mature white spruce stands can indicate 'nitrogen hotspots' in the soil mosaic, affecting the long-term productivity of the site (Wurtz, 1995).

The role of alders in managed forest stands may thus shift from being primarily competitive in the early stages of stand regeneration to primarily facilitative as the crop trees mature. The Nel-Rep experimental design is used here to examine the balance of positive and negative interactions in the early stages of stand development.

Method

The study is being conducted at the University of Alaska Fairbanks Agriculture and Forestry Experiment Station Farm (lat. 64°53'N; long. 148°0'W). The site has been managed for agricultural experimentation since the 1930s. The soil is Tanana silt loam, a mixed, non-acid Pergelic Cryaquept. The climate in the Fairbanks area is cold and semi-arid: mean annual temperature is -3.3 °C and mean annual precipitation is 285 mm. Growing seasons are short, usually lasting from 1 June to 1 September.

The dimensional attributes of Nelder plots can be varied to meet the sample size requirements, space limitations, and range of densities desired by the researcher. The 15 plots used in this study each have 22 arcs and 18 spokes, for a total of 5940 trees. The innermost and outermost arcs and the outermost spokes are considered buffer strips; trees in the buffer strips are not measured. The relationship defining the distances from the centre of the circle to each arc is:

$$r_n = r_0\alpha^n$$

where r_n is the distance from the centre of the circle to the nth arc; r_0 is the distance from the centre to the first arc; α is a constant, which for these plots was given the value 1.16 (Nelder 1962). In these plots there is a 10° angle of separation between spokes. Thus the area available to trees in these plots ranges from 0.034 m^2 at the innermost non-buffer arc to 9.785 m^2 at the outermost non-buffer arc.

The field lay-out is a randomised complete block design. Five plots were installed in each of three blocks, with spruce:alder ratios of 100:0, 75:25, 50:50, 25:75, and 0:100. In the 50:50 plots, spruce and alder occupy alternate locations as one proceeds around an arc or along a spoke. In the 75:25 and 25:75 plots, arcs made up entirely of one species alternate with arcs of alternating spruce and alder.

Containerised, one-year old white spruce seedlings from a Fairbanks area seed source were planted into the experiment in June 1990. The spruce seedlings were 10–20 cm tall at time of planting. Bare-root alder wildlings were collected from nearby roadsides and gravel pits just prior to bud break in May 1991. They ranged in height from 30 to 70 cm, and most were nodulated. They were planted into the experiment plots in June 1991. Mortality since the initial planting has been distributed evenly throughout the plots, regardless of seedling density, and thus appears to be the result of the establishment phase, rather than of competition. Consequently, dead seedlings have been replaced, with numbers that need to be replaced declining each year. Mortality was less than 2% in 1993. The plots are kept free of weeds by hand.

Though the growth of both spruce and alder is being measured, only spruce growth results are reported here.

A preliminary soil analysis was done in 1990. Soil samples were collected at 2 cm depth in all plots, and will be collected periodically throughout the study. Soil laboratory analyses were done at the University of Alaska Agriculture and Forestry Experiment Station Service Laboratory in Palmer, Alaska. Total nitrogen (N) was determined by ignition in a Leco CHN analyser; soil phosphorus (P) was extracted with a Mehlich 3 extract (Mehlich 1982, Michaelson *et al.* 1987) and analysed on an autoanalyser. Potassium (K) was extracted with a Mehlich 3 extract, and analysed with a Perkin-Elmer model 5500 atomic absorption spectrometer. Soil pH was measured in a saturated paste using an Orion combination pH electrode.

Growth results were initially expressed as both annual growth increment and relative growth rates (Hunt 1990). However, expressing the data in the form of relative growth rates did not assist in its interpretation, and actually seemed to obscure growth trends. Britt *et al.* (1991) also raised concerns about interpreting relative growth rates in trees. Consequently, only annual growth increments are presented here. Data were subjected to analysis of variance using the SAS system for personal computers (SAS Institute 1990).

Results

In the first full growing season, 1991, the diameter increment of the seedlings in the 100% spruce plots was unaffected by density (figure 2). In 1992, however, the effects of density became apparent, with the annual increment in the five most dense arcs declining or holding constant compared with 1991 levels. By 1993, the crowns of the trees in the five most dense arcs were touching. These trees grew markedly less than they had two years earlier, and growth in the sixth, seventh and eighth arcs had begun to decline from 1992 levels. Diameter growth in the ninth through the twentieth arcs continued to increase. The analysis of variance indicated a highly significant density effect on spruce diameter growth in 1993 (table 1).

In general, graphical representations of the data suggested that the growth trends in the mixed-species plots were similar to those in the 100% spruce plots (figure 2). Yet the analysis of variance indicated a highly significant interaction between density and species mixture (table 1).

Height growth in the 100% spruce plots showed somewhat different trends (figure 3). In 1991 and 1992, annual increment was greatest in the most dense portions of the plot. By 1993,

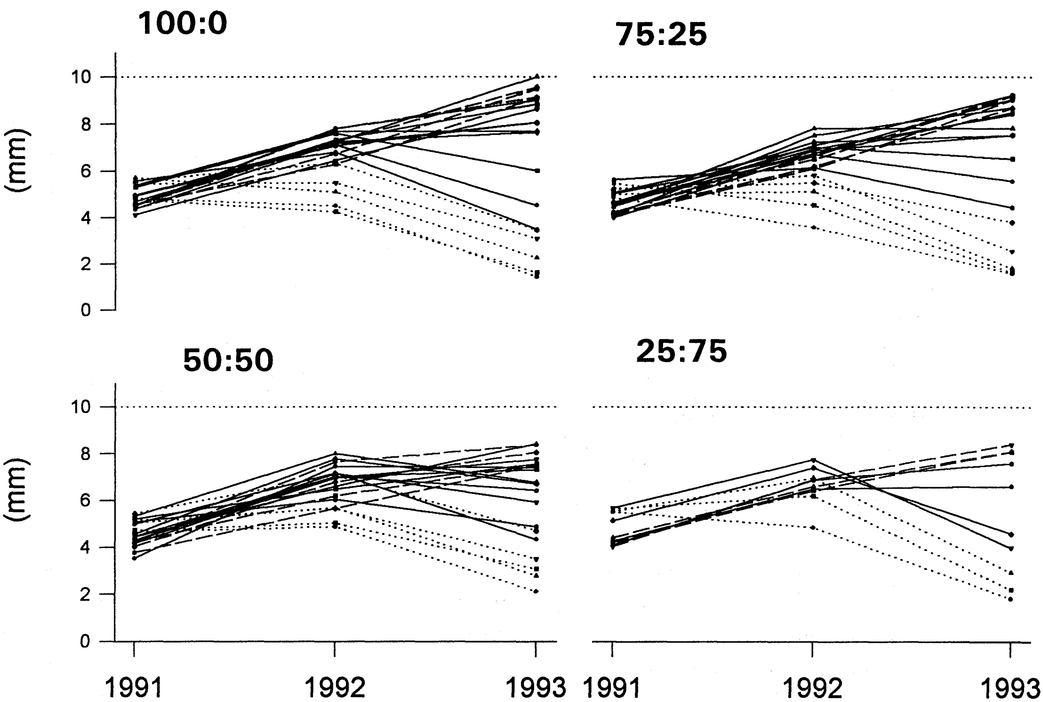


Figure 2: Annual diameter growth increment of spruce seedlings in the four different species mixture plot types: 100:0, 75:25, 50:50 and 25:75 spruce to alder respectively in each instance. Each line represents one of the 20 levels of density in each plot, except in the 25:75 plots, where only 10 of the 20 plot arcs contain spruce trees. Dotted lines represent the most dense arcs, and dashed lines represent the most widely-spaced arcs

Table 1: Sources of variation in 1993 diameter and height annual increment of spruce

	Diameter			Height		
Source of variation	**df**	**SS**	**F**	**df**	**SS**	**F**
Block	2	26.51	2.93	2	768.11	13.04***
Species mixture	3	8.49	0.94	3	102.80	1.16
Block x Species mixture (Error a)	6	9.04	10.18	6	176.72	4.18
Density	19	68.81	77.42****	19	397.13	2.96****
Density x Species mixture	47	1.57	1.77***	47	490.69	1.48*
Error (b)	132	117.33		132	930.93	
Total	209	1652.76		209	3082.02	

Note: SS sum of squares; * significant at $p = 0.05$; *** significant at $p = 0.001$; **** significant at $p = 0.0001$

Table 2: Mean values (to 1 SE) for soil nutrient data

Block	***n***	**pH**	**Total N (%)**	**Total P (%)**	**Total K (ppm)**
X	100	6.2 (0.04)	0.13 (0.002)	0.10 (0.001)	47.87 (0.82)
Y	100	6.3 (0.01)	0.14 (0.001)	0.10 (0.001)	53.87 (0.90)
Z	100	6.6 (0.02)	0.15 (0.002)	0.11 (0.001)	49.45 (0.85)

however, height growth in the five most dense arcs had begun to decline. The effects of density and block on height growth in 1993 were highly significant (table 1).

In height growth as well as diameter, there was some disparity between the graphical representations of the data and the analysis of variance. While graphing the data did not indicate an obvious effect of alder on the height growth of spruce, the ANOVA indicated a significant density by species mixture interaction.

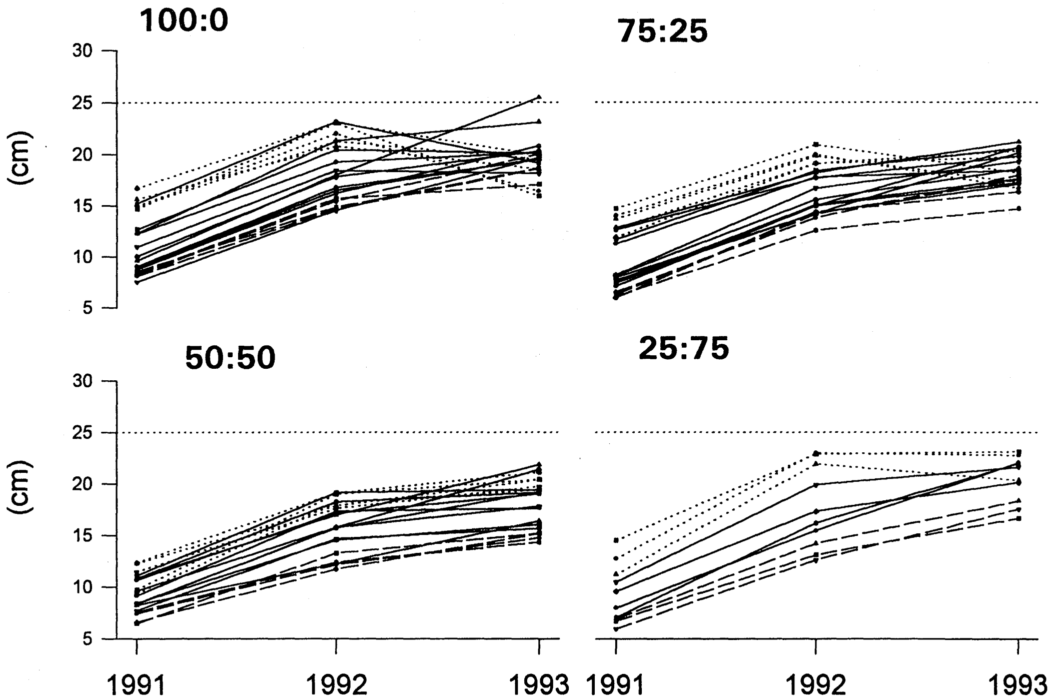
Results of the preliminary soil analysis are given in table 2.

Discussion

To date, most of the variability in the growth of the spruce trees in these plots can be attributed to density, with trends in height lagging a year behind trends in diameter. The relationship between cambial growth one year and extension growth the next year is well-documented in trees (Duff and Nolan 1953, Lanner 1985). In the mixed-species plots, the faster-growing alder may have created competition for light in the dense portions of the plots, encouraging the spruce trees there to allocate resources to extension growth.

The disparity between the ANOVA results and the graphical representations in mixed species plots may be due to the sensitivity of the density by species mixture test. This test is highly sensitive (as indicated by a 47:209 ratio of degrees of freedom), and though the effect is statistically significant, it may not yet be ecologically important.

However, the portion of the overall field (the block) in which trees were planted also significantly affected height growth. The block effect is likely to be explained by the block-to-block variation in soil characteristics, which in turn is probably a reflection of differences in the fertilisation history of the blocks prior to the



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start of this experiment. In any case, future positive effects of alders on the growth of spruce trees would likely be related to available soil N, and less benefit would be expected where background soil N levels were high.

One of the challenges of any long-term density study is mortality. Individuals within single arcs differed in initial size, and will differ in their competitive ability. As trees begin to die, they will release their immediate neighbours and effectively change the area available to individuals in that portion of the plot. I plan to deal with future density-dependent mortality in this study by designating buffer islands around dead seedlings; all trees in the islands will be omitted from the analysis. When mortality within an arc reaches a certain threshold, the entire arc will be omitted from the analysis.

Now that it is well established, this experiment provides an ideal environment to examine the relationship between density and a variety of additional environmental and plant growth measures, including canopy light penetration, soil moisture patterns, tissue nutrient content and, at least for the alders, reproductive output. Because tree morphology is markedly affected by density (Lanner 1985), there is an excellent opportunity for tree architecture studies. The integrity of the plots can be maintained during a limited number of destructive sampling episodes by collecting from spokes just inside the buffers, and then moving the buffer designation inward.

Acknowledgment

Tim Max, of the USDA Forest Service, PNW Research Station, assisted in the data analysis.

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