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Competition causes regular spacing of alder in Alaskan shrub tundra

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Summary. Alders (*Alnus crispa*) in shrub tundra in northern Alaska showed significant regularity of spacing. Removal of neighboring alder shrubs stimulated nutrient accumulation and growth of remaining alders but did not stimulate nutrient accumulation or growth of any other shrub species. This demonstrates that neighboring alders competed with one another and that, when alders were removed, the resources made available were used preferentially by remaining alders rather than by the community in general. Neither patterns of seedling establishment nor patterns of frost-related features could explain the regular distribution of alder. We suggest that regular patterns of plant distribution are restricted to sites of low-resource availability, because in these habitats (1) there is strong competition for a scarce resource, and (2) there are only one or a few dominant species to compete for these resources in a given canopy height or rooting depth.

Key words: Alder – Competition – Growth – Regular spacing – Tundra

In most natural communities, plants show a random or clumped distribution. Consequently, the few documented examples of regular distribution of plants have stimulated considerable interest (Pielou 1960). In American deserts, *Larrea tridentata* shows a distribution that becomes increasingly regular as precipitation declines (Woodell et al. 1969; Phillips and MacMahon 1981). Although Ebert and McMaster (1981) suggested that this apparent regularity might be a sampling artifact, the pattern appears robust (King and Woodell 1984) and is probably caused by competition for water (Fonteyn and Mahall 1978, 1981). Similar regular spacing has been reported in other desert shrubs (Beals 1968; Waisel 1971; King and Woodell 1973).

Forest ecologists have noted that tree distribution goes from clumped to random to regular as succession proceeds (Cooper 1961; Laessle 1965; Christensen 1977; Schlesinger and Gill 1978; Nakagoshi et al. 1983), due mainly to high mortality of small, suppressed individuals near large dominant trees (Christensen 1977). Thus, as in deserts, competition is thought to be the major cause of regular plant distributions in forests. Despite frequent reference to competition as the cause of regular spacing, only one study (Fonteyn and Mahall 1978, 1981) has demonstrated experimentally the existence of competition among plants that have a regular distribution. In this study, the intensity of competition among regularly distributed individuals of *Larrea* was minor compared to interspecific competiton.

Regular patterns of distribution of plant *communities* have frequently been observed in tundra. However, these patterns reflect the presence of ice wedge polygons or other frost features that produce distinct microenvironments near their centers and edges and that are themselves regularly spaced due to the physics of the freeze-thaw process (Britton 1967; Webber 1978; Walker et al. 1987). These frost features are thought to be the major cause of a small-scale pattern in tundra vegetation.

Alder (*Alnus crispa*) is a dominant shrub in many areas of tundra south of the Brooks Range in north-central Alaska (Viereck and Little 1972). To our casual observation, individual alder shrubs appeared to be regularly spaced (Fig. 1), a phenomenon not previously reported for any tundra species. We developed three alternative hypotheses to explain this apparent pattern. (1) Competition among established alder individuals leads to a regular spacing, (2) competition between seedlings and established individuals leads to recruitment only at a great distance from established individuals, or (3) a polygonal pattern concealed beneath the vegetation permitted seedling establishment only in certain microsites (e.g., intersections of polygons). Here we document the regularity of that spacing in alders and

Fig. 1. Regularly spaced alder shrubs in Alaskan shrub tundra

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demonstrate that the pattern reflects competition among neighboring individuals.

Methods

Our major study site was an area of alder shrub tundra 16 km south of Gobbler's Knob on the Dalton Highway in north-central Alaska (66°39′N, 150°40′W, 300 m elevation). The community was dominated by scattered individuals of *Alnus crispa* with an understory of dwarf shrubs (*Betula nana, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum, V. vitis-idaea*, and *Rubus chamaemorus*), graminoids (*Carex bigelowii, Eriophorum vaginatum*, and *Calamagrostis canadensis*), and mosses (*Sphagnum* spp., *Aulacomnium* spp.). At this site we measured the distance from 62 random points to the nearest alder (regardless of size) and measured the distance from that alder to its nearest neighboring alder (Greig-Smith 1964). We then measured the height and diameter of both alder shrubs. From these data we calculated the ratio of point-plant: plant-plant distances to determine whether shrubs exhibited a clumped (ratio >0.88), random (ratio $=0.88$), or regular (ratio <0.88) distribution (Batcheler 1971). Since there are distributional problems associated with statistical analysis of ratios, we tested the significance of pattern on arcsine transformed proportions ((plant-plant distance)/(plant-plant + point-plant distances)). Significant regularity of pattern was recognized when this proportion was significantly less than 0.468 (or the arcsine transformed proportion <0.487 radians). Alders are multi-stemmed individuals in these sites. We considered all stems emanating from the same root crown to have been produced by a single individual. In general, we had little difficulty deciding whether a given stem belonged to the same or a different individual. Alder does not spread vegetatively and fragment, as does *Larrea tridentata* (Cox 1987). Errors in recognizing individuals (Ebert and McMaster 1981) are thus unlikely to cause artifacts in determining the regularity of alder distribution (King and Woodell 1984, Cox 1987).

To determine whether seedlings might preferentially establish mostly at some distance from adult shrubs and thus create the regularity of pattern, we measured the distance of 114 alder seedlings (individuals <0.3 m tall) to the nearest non-seedling alder shrub and compared its distance with the random point-to-plant distance. Seedlings were relatively uncommon (none of the 124 randomly selected alders in the community). The mean distances of random points and seedlings from alder shrubs were compared with a t-test. Even if means were found to be the same, the distributions of distances could be different. Therefore to determine whether distributions were different, the number of seedlings observed in each of four distance classes (0–0.99, 1–1.99, 2–2.99, 3–3.99) was determined and compared with the number expected (based on random point-to-plant distances) using a G-test (Sokal and Rohlf 1981).

Table 1. Density, height, and diameter of randomly sampled *Alnus crispa* in Alaskan tundra. Data (±SE) are based on 62 random points and 124 shrubs. A regular distribution of shrubs is indicated by point-plant: plant-plant ratio <0.88

Density (shrubs m^{-2})	0.06
Point-plant: plant-plant ratio	0.81 **
Plant height (m)	1.82 ± 0.04
Plant diameter (m)	1.76 ± 0.07

** Indicates significant departure from random at $P<0.01$, as determined by *t*-test

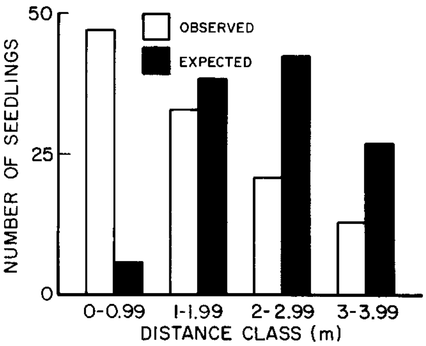

Fig. 2. Observed and expected distributions of distances of alder seedlings from the nearest non-seedling alder shrub. $G=138$, $P<0.001$

To determine whether competition among adjacent alders significantly affected their growth, we haphazardly selected 16 alder shrubs. From half of these shrubs we removed the 5 closest alder neighbors by chopping off all stems at the root crown in June 1983. On 19 August 1983, five current year's long shoots were randomly selected from each treated (i.e., shrub with five nearest neighbors removed) and control shrub. We separated these shoots into leaves and stems, oven-dried them at 70° C, and weighed and saved them for nutrient analysis. On 23 July 1984, we repeated these harvests on the same individuals with ten shoots per alder shrub and also measured the length and weight of current-year's growth of 20 long shoots from each of 4 species of dwarf shrubs (*Betula, Ledum, Vaccinium uliginosum*, and *V. vitis-idaea*) sampled within 1 m of the root crown of each of the 16 alder shrubs. Leaves and stems from each shrub sample were separetely ground in a Wiley mill (# 40 mesh), digested in selenous-sulfuric acid, and analyzed for nitrogen by microKjeldahl, phosphorus by phosphomolybdate, potassium, calcium, and magnesium by atomic absorption (Jonasson and Chapin 1985), and molybdenum and cobalt by plasma emission spectroscopy.

We were unable to detect presence of ice-wedge polygons in our main study site through observation of surface features and therefore could not use this site to relate alder distribution to subsurface topography. At a site on Gobbler's Knob (16 km N of our study site), a pattern of high-centered ice-wedge polygons was clearly evident from the distinctive surface microtopography. At this latter site we made qualitative observations about the position of alder shrubs relative to the patterned ground.

Results

Alders at our study site showed regularity of spacing among individuals, as indicated by point-plant: plant-plant ratios significantly less than 0.88 (Table 1). Nearest neighbor distance was positively correlated with shrub diameter ($r=0.31$, $P=0.023$), indicating that larger shrubs were more widely separated from one another than were small shrubs.

Alder *seedlings* were not spaced at random (G-test, $P<0.001$) with respect to individuals of adult alder (Fig. 2); they were closer to adult plants than expected (*t*-test, $P<0.001$). If subsequent growth and survival followed the same

Table 2. Length and weight of current year's shoots of shrubs sampled within 1 m of alder shrubs whose 5 nearest alder neighbors were intact (control) or removed the previous year. Data are means ± SE, $n=8$ alder shrubs. Each length and weight sample is the average of 20 shoots

	Shoot length (cm)		Shoot weight (mg shoot^{-1})	
	Control	Alders removed	Control	Alders removed
Alnus crispa	3.59±0.24	7.45±0.37***	794±70	1135±80*
Betula nana	3.97±0.24	3.84±0.21	105±10	88± 6
Ledum decumbens	1.47±0.08	1.33±0.07	51± 5	45± 5
Vaccinium uliginosum	2.85±0.19	2.52±0.17	64± 5	61± 4
V. vitis-idaea	2.66±0.10	2.17±0.10*	58± 4	43± 3*

* and *** indicate significant difference between treatment and control at $P<0.05$ and 0.001, respectively

pattern, this would lead to a clumped distribution of individuals. Thus, the pattern produced by early seedling establishment does not implicate a regular distribution of safe sites or early competition as causes of the regular spacing of adults.

At Gobbler's Knob, where we could readily distinguish the positioning of ice-wedge polygons, we could discern no pattern of adult alders with respect to centers or edges of polygons. Alders were abundant in both troughs and high centers, suggesting that, at least at this site, the pattern of polygonization did not readily explain the regular distribution of alders.

Removal of the 5 closest alders had no significant effect upon current shoot growth ($P>0.1$) of alder in samples collected two months after the removal (data not shown). However, by late July of the following year, alder shrubs whose nearest neighbors had been removed showed greater shoot growth than did controls (Table 2), indicating that neighboring alders were competing with one another. Growth of shrubs of other species situated beneath (i.e., within 1 m) alders was not stimulated by removal of neighboring alders, indicating that the competitive interaction was specific between the individual alders: removal of neighbors did not release resources that could be tapped by other shrub species in the community. Growth of *Vaccinium vitis-idaea* beneath alders was inhibited by the removal of neighboring alders, perhaps due to stimulation of growth of the canopy alder. Qualitative observations indicated that most alder roots were deeper than most roots of the dwarf shrubs, perhaps explaining why resources made available by removal of neighboring alders were more available to alders than to other species.

Leaves and stems of alder sampled in 1983 and 1984 did not differ ($P>0.05$) between removal and control treatments with respect to tissue concentrations of nitrogen, phosphorus, potassium, calcium, magnesium, cobalt, or molybdenum. Among understory shrubs sampled in 1984 the only significant difference in nitrogen or phosphorus concentration between treatment and control shrubs was a higher ($P<0.05$) stem nitrogen concentration in *Betula* sampled beneath alders whose neighbors were removed, relative to controls. Thus, out of 44 nutrient comparisons between treatment and control samples, onle one proved significant at the 0.05 level, a number that could be explained by chance. We conclude that there was no major change in the tissue nutrient concentrations of alder or understory shrubs as a result of removal of neighboring alders.

The pool size of nutrients accumulated in current year's shoots of alder was increased by removal of neighbors (shown for nitrogen and phosphorus only; Table 3). This was due entirely to the increase in shoot biomass rather than tissue element concentrations. This suggests that nutrients were among the resources for which neighboring alders competed.

Table 3. Pool size of nitrogen and phosphorus in leaves and stems of current year's shoots of alder shrubs whose 5 nearest alder neighbors were intact (control) or removed the previous year. Data are means ±SE, $n=8$ shrubs. Statistics as in Table 2

	Nitrogen (mg shoot^{-1})		Phosphorus (mg shoot^{-1})	
	Control	Alders removed	Control	Alders removed
Leaf	13.8±1.2	18.2±1.5	0.83±0.04	1.16±0.09*
Stem	5.7±0.8	7.9±0.7	0.57±0.08	0.79±0.07
Total shoot	19.5±1.9	26.1±1.8*	1.40±0.11	1.95±0.14*

Discussion

Our results indicate that adult alders are regularly spaced in our study site and that competition among neighboring adult alders is the most likely explanation for this spacing.

Patterns of seedling establishment do not provide a consistent explanation of regular distribution of adult alders. If competition between seedling and adult alders led to regular spacing, we would expect most seedlings to occur far from rather than close to adult shrubs. The clumping of seedlings near adult alders, which we observed, is most likely due to more abundant seed rain near adult shrubs (Fenner 1985) but could also reflect more favorable establishment conditions near the adult.

The lack of correlation between the distribution of alders and recognizable frost features at Gobbler's Knob suggests that alder seedlings do not establish preferentially in certain microsites within a system of ice-wedge polygons. Moreover, the seedlings we did find were in a variety of types of microsites, both vegetated and frost-disturbed. Thus, it seems unlikely that any concealed pattern of ice-wedge polygonization could produce safe sites (Harper 1977) favoring alder establishment, thereby explaining the regular pattern of adult alders. However, we could not see any polygonal pattern in our main study site, so we cannot definitively preclude the possibility that some hidden frost pattern contributed to the regular distribution of alder in that site.

The increased shoot growth in alders whose nearest neighbors were removed clearly indicates release from competition. The fact that various species of dwarf shrubs beneath the alders did not respond positively to the removal treatment suggests that alders had preferential access to resources released by the removed alders and that the resources were not equally available to all members of the community. In a similar experiment in the desert, removal of all shrubs except a single *Larrea* individual caused the water potential of the *Larrea* to decrease less than in control shrubs during drought. However, removal of only *Larrea* shrubs (except a single individual) enhanced water potential of the remaining *Larrea* individual only under conditions of severe drought, suggesting that the development of a regular pattern of spacing may have minimized competition among adjacent individuals of *Larrea* except under conditions of extremely low resource supply (Mahall and Fonteyn 1981).

In our tundra experiments, we do not known the resource for which alders were competing, although several considerations suggest that nutrients were important. The wide spacing of individual alders relative to their canopy width (Table 1) suggests that light competition was unimportant. Moreover, nearest neighbor distance was not correlated ($P > 0.5$) with shrub height. Soils in our study site were above field capacity, so it is unlikely that water directly limited growth of alders. A nutritional limitation is suggested by the fact that the larger shoots in plants with neighbors removed had more nitrogen, phosphorus, and other nutrients, although the proportions (concentrations) of these elements were similar in treated and control plants. An increase in growth without change in tissue concentration is the expected response of plants to partial release from nutrient limitation (Chapin 1980). Nitrogen is the macronutrient that limits plant growth in two tussock tundra sites near our study site (Shaver and Chapin unpublished work). However, alder supports symbiotic nitrogen fixation and was well nodulated in our study site. Moreover, cobalt and molybdenum, the micronutrients specifically required for nitrogen fixation (Epstein 1972), did not increase disproportionately in shrub tissues in response to removal of neighbors, nor did any macronutrient. Therefore, it seems likely that the alder shrubs adjusted the uptake of specific nutrients to compensate for changes in the balance of supply (Harrison and Helliwell 1979; Chapin 1980), perhaps explaining why we did not see increased tissue concentrations of any particular nutrient in response to removal of neighbors.

Competition has been implicated as the cause of regular spacing in all reported instances of this phenomenon in natural communities and has now been demonstrated experimentally in tundra (this study) and desert (Fonteyn and Mahall 1978, 1981). Regularity of spacing is most pronounced in low-resource environments. Spacing of trees in forests becomes more regular as succession proceeds, and as competition for light and other resources increases (Christensen 1977). In late successional forests, sub-dominant trees (which receive less light) die, and the remaining dominant trees become regularly spaced. In deserts, spacing is most regular in the driest sites. In all these studies regularity of spacing is most pronounced among individuals of a single species, generally the dominant (largest) plant in the community. If regularity of spacing does indeed reflect competition, why is regular spacing not more common among plant populations? First, mesotopographic heterogeneity is a major cause of non-regular pattern in most plant communities. Only in topographically uniform areas such as many deserts dominated by *Larrea tridentata* (Woodell et al. 1969) or the broad tundra slopes which we studied can regularity of distribution be detected. More importantly, we suggest that intraspecific competition is severe enough to override other causes of vegetation pattern only in those environments with lowest resource availability (e.g., deserts, tundra, and late successional forests), because in these environments growth, survival, and reproduction are clearly resource-limited. This conclusion directly contradicts Grime's (1977) hypothesis that competition is relatively unimportant in low-resource (stressful) environments. In less severe environments where there are more resources to support plant growth, other factors (e.g., seed rain, safe sites, stochastic factors regulating recruitment) may be more important than competition in determining vegetation pattern.

In addition, high-resource environments may support several dominant species, so in these environments interspecific competition may be more important than intraspecific competition. Regularity of distribution implies that individuals of a given species compete strongly for resources not used by other species in the community, either because requirements of the regularly distributed species differ from those of other species (e.g., cobalt and molybdenum for nitrogen-fixers) or because the regularly distributed species taps resources from a different canopy height or rooting depth than do other species, as with the comparison between *Larrea* and desert annuals (Fonteyn and Mahall 1981).

Because regularity has been found in low-nutrient (tundra) and low-moisture (desert) environments, it also might be expected in low-light environments (e.g., under a dense forest), but there have been no reports of regular spacing in such environments. The absence of regular spacing there may be due to the very uneven distribution of light (and therefore of individual plants of a particular species) under a forest canopy, whereas, at the scale of an individual plant, moisture and nutrients are more uniformly distributed. We suggest that strong competition for soil nutrients may explain the regular distribution of alders in northern Alaska.

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References

Batcheler CL (1971) Estimation of density from a sample of joint point and nearest-neighbor distances. Ecology 52:703–709

Beals EW (1968) Spatial pattern of shrubs on a desert plain in Ethiopia. Ecology 49:744–746

Britton ME (1967) Vegetation of the arctic tundra. In: Hanson HP (ed) Arctic biology. Oregon State Univ Press, Corvallis, pp 67–130

Chapin FS III (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Christensen NL (1977) Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. Am Midl Nat 97:176–188

Cooper CF (1961) Pattern in ponderosa pine forests. Ecology 42:493–499

Cox GW (1987) Nearest neighbor relationships of overlapping circles and the dispersion pattern of desert shrubs. J Ecol 75:193–199

Ebert TA, McMaster GS (1981) Regular pattern of desert shrubs: a sampling artifact? J Ecol 69:559–564

Epstein E (1972) Mineral nutrition of plants: principles and perspectives. John Wiley and Sons, New York

Fenner M (1985) Seed ecology. Chapman and Hall, London

Fonteyn PJ, Mahall BE (1978) Competition among desert perennials. Nature 275:544–545

Fonteyn PJ, Mahall BE (1981) An experimental analysis of structure in a desert plant community. J Ecol 69:883–896

Greig-Smith P (1964) Quantitative plant ecology. Butterworth, London

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194

Harper JL (1977) The population biology of plants. Academic Press, New York

Harrison AF, Helliwell DR (1979) A bioassay for comparing phosphorus availability in soils. J Appl Ecol 16:497–505

Jonasson S, Chapin FS III (1985) Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. Oecologia 67:511–518

King TJ, Woodell SRJ (1973) The causes of regular pattern in desert perennials. J Ecol 61:761–765

King TJ, Woodell SRJ (1984) Are regular patterns in desert shrubs artifacts of sampling? J Ecol 72:295–298

Laessle AM (1965) Spacing and competition in natural stands of sand pine. Ecology 46:65–72

Nakagoshi N, Takamatsu S, Nehira K (1983) Post-fire vegetation at 21 years old stand in Otake, Southwestern Japan. Bull Biol Soc Hiroshima University 49:23–33

Phillips DL, MacMahon JA (1981) Competition and spacing patterns in desert shrubs. J Ecol 69:97–115

Pielou EC (1960) A single mechanism to account for regular, random and aggregated populations. J Ecol 48:575–584

Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman, San Francisco

Schlesinger WH, Gill DS (1978) Demographic studies of the chaparral shrub *Ceanothus megacarpus* in the Santa Ynez Mountains, California. Ecology 59:1256–1263

Waisel Y (1971) Patterns of distribution of some xerophytic species in the Negev, Israel. Isr J Bot 20:101–110

Webber PJ (1978) Spatial and temporal variation of the vegetation and its productivity, Barrow, Alaska. In: Tieszen LL (ed) Vegetation and production ecology of an Alaskan arctic tundra. Springer, Berlin Heidelberg New York, pp 37–112

Woodell SRJ, Mooney HA, Hill AJ (1969) The behavior of *Larrea divaricata* (Creosote Bush) in response to rainfall in California. J Ecol 57:37–44

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