Short Communication

Changes in the Horizontal Structure in a Spruce Forest over a 9-year Period of Pollutant Exposure in the Krkonoše Mountains, Czechoslovakia

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ABSTRACT

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The influence of neighbours on tree vitality was studied, comparing the nearest-neighbour distance with tree vitality. In 1976, before the massive impact of air-pollution stress, the distance to the nearest neighbour was seen to increase with tree vitality, indicating the prevailing effect of neighbours' competition. In 1985, under a strong influence of air pollution, a certain optimal distance to neighbours can be found in the most-affected plots, allowing ecological sheltering as a type of mutual protection among trees, but not leading to strong competition. The surviving trees are spaced more evenly than is the whole population.

INTRODUCTION

Forest decay under emission stress represents one of the most difficult problems in contemporary forest ecology. In this paper, we deal with the influence of neighbouring individuals on the extent of injury to a particular tree. It is usually supposed that, under favourable environmental conditions, a very important factor influencing the vitality of trees is the competition of neighbouring individuals (see, e.g., Keister, 1972; Whipple, 1980). However, under environmental stress, the individual may be protected by the neighbours; some 'mutualistic relationships' among neighbouring individuals (ecological sheltering) may take place (Smith, 1981). In this case the neighbours (or the

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neighbours' configuration) are supposed to modify the environment by diminishing the environmental stress.

The competition among neighbouring individuals leads to their more regular distribution or a decrease in clumping (Laesle, 1965: Lepš and Kindlmann; 1987). Mutualisms among neighbours would have the opposite effect (Kershaw, 1973). Changes in the horizontal structure, or the dependence of the state of an individual on the distance to a neighbouring individual, may be taken as indices of the type of relationships among individuals.

STUDY AREA AND METHODS

The paper is based on 10 years' data (1976–1985) from five permanent plots in the Krkonoše Mountains (Giant Mountains, Eastern Bohemia, Czechoslovakia). The plots A, B, C, D, E (size 0.25 ha) were laid down along an altitudinal transect (1220, 1170, 1120, 1050 and 990 m a.s.l., respectively) in the Labský důl valley, near the town of Špindlerův Mlýn. The area is covered by autochthonous Norway spruce (*Picea abies* Karst.) forest. The climate is wet and cold (annual average temperature 4.7°C and sum of precipitation 1322 mm, both measured at the Špindlerův Mlýn meteorological station, 922 m a.s.l.). The plots are located above the station, hence the temperature is still lower there and obviously further decreases with elevation. Ecological characteristics vary considerably with elevation. The following tree characteristics decrease monotonically with elevation: mean age (ranging from 135 to 210 years), mean height (11-32 m), maximum height (20.5-38.5 m), mean dbh (30.0-54.3 cm), and growing stock (42.2-211.1 m³); all as 1976 values.

The area is now under heavy emissions stress (SO₂: 30 μ g m⁻³ average for the period of 1981–1984, at the Labská bouda station, 1320 m a.s.l.). At the beginning of the study in 1976, the forest was without any visible injury. (A small percentage of dead trees is an expected feature of natural forests here, depending on the developmental stage of the plot within the natural regeneration cycle.) The first visible symptoms of injury appeared in 1979, followed by rapid decay in the early eighties (see Vacek, 1984). The density of 240–392 live trees per ha in 1976 decreased to 172–300 in 1985. The rate of dying off increases with the elevation. The estimated plot half-lives (expected times by which one half of the population will die off) vary from 7.2 years in plot A to 23.8 years in plot D (details in Lepš and Vacek, 1986). Under normal conditions (i.e., without air pollution) the life-span of trees reached 300 years. Forest die-back is often accompanied by outbreaks of pest populations. In our case, plot E was massively infested by bark-beetle (*Ips typographus* L.).

In all plots, the location of all individual trees taller than 1.30 m was noted and the individuals were measured (dbh, height). The health condition of each individual was evaluated by defoliation degree, using the scale of Tesař and Temlová (1971). The scale is used routinely in Czechoslovak forestry and may The distance to the nearest neighbour may be considered as a rough measure of biotic influence. If competition prevails, the strongly influenced individuals (i.e., individuals with a high defoliation degree) are expected to have closer neighbours than the healthy individuals. In the case of mutual protection, the opposite trend is expected. Strictly speaking, the particular distances are not independent random items (all distances from each tree in each plot were recorded). However, we consider the ordinary statistical analysis (one-way AN-OVA) to be sufficiently robust to give reasonable indication of real trends.

The spatial pattern of individuals was evaluated using indices of Clark and Evans (1954) and Hopkins and Skellam (1954). The computerized calculation of these indices was based on the digitized map of each plot. The index A (Hopkins and Skellam, 1954) was computed as follows:

 $A = a_1/a_2$

where a_1 is the mean square of an individual-to-neighbour distance over all individuals and a_2 is the mean square of point-to-individual distance over 100 randomly generated points. The index R (Clark and Evans, 1954) was computed as

 $R = 2\bar{r}\sqrt{\rho}$

where \bar{r} is the mean value of an individual-to-neighbour distance over all individuals and ρ is density. Both R > 1 and A < 1 indicate regularity, R < 1 and A > 1 indicate aggregated pattern.

RESULTS AND DISCUSSION

The average individual-to-neighbour distances for individuals showing various defoliation degrees are given in Table 1. In 1976, the distance decreased monotonically with defoliation degree in all plots, and individuals with higher defoliation degree were mostly absent. In other words, the individuals having a reduced foliage usually have close neighbours. This may be taken as evidence for neighbours' competition. The greatest differences were found in plots B and C, i.e., in plots with highest density of individuals. This roughly holds for 1985 also, but in the upper plots A, B and C, the less-damaged individuals do not exhibit the maximum distances to their neighbours. This suggests that individuals in plots exposed to the strongest environmental stress (combined both hard natural climatic conditions and air pollution) may partially profit from an intermediate proximity of a neighbour. However, the very close proximity results in stronger competition and tree vitality decreases. Competitive suppression seems to increase the sensitivity of individuals to air pollution.

TABLE 1

The average distance (m) to the nearest neighbour of trees of various defoliation degrees (D.D.)

| Plot year D.D. | Α | | В | | С | | D | | Е | |
|----------------------|----------|------|------|------|------|----------------|------|------|------|------|
| | 1976 | 1985 | 1976 | 1985 | 1976 | 1985 | 1976 | 1985 | 1976 | 1985 |
| 0 | 3.2 | | 4.3 | 2.7 | 3.3 | 2.8 | 5.1 | 5.2 | 4.4 | _ |
| 1 | 3.2 | 2.9 | 2.8 | 3.5 | 2.4 | 2.9 | 3.0 | 3.7 | 3.4 | 3.8 |
| 2 | 2.0 | 4.0 | 1.7 | 2.8 | 1.3 | 2.0 | 2.2 | 2.5 | 3.2 | 3.2 |
| 3 | _ | 2.5 | | 2.5 | | 1.4 | _ | 1.6 | | |
| 4 | _ | 2.7 | | 2.0 | | _ | _ | _ | _ | |
| 5 | — | 2.3 | | 1.6 | — | 1.8 | | 3.1 | | 3.3 |
| | P = 0.07 | NS | ** | * | ** | $P \!=\! 0.05$ | * | NS | NS | NS |

Only trees that were alive in 1976 were taken into account. The last row indicates the statistical significance of differences among means (one-way ANOVA). Meaning of symbols: *, P < 0.05; **, P < 0.01; NS, not significant; —, absent.

TABLE 2

Number of individuals (N) on plots A-E and characteristics of spatial pattern — values of R and A indices

| | | A | В | С | D | E |
|--------------------|---|------|------|------|------|------|
| All trees in 1976 | N | 85 | 108 | 116 | 93 | 96 |
| | R | 0.97 | 0.81 | 0.74 | 0.86 | 1.01 |
| | A | 1.29 | 1.77 | 2.45 | 1.39 | 1.51 |
| Live trees in 1976 | N | 74 | 78 | 84 | 60 | 61 |
| | R | 1.00 | 0.97 | 0.88 | 0.98 | 1.09 |
| | Α | 1.17 | 1.22 | 1.69 | 1.15 | 1.05 |
| Live trees in 1985 | Ν | 52 | 67 | 75 | 53 | 43 |
| | R | 1.14 | 1.04 | 0.94 | 1.01 | 1.11 |
| | A | 0.81 | 1.08 | 1.42 | 0.99 | 1.15 |

Indices of spatial pattern are given in Table 2. When comparing the spatial pattern of the whole population with that of live individuals, the live individuals are always spaced more evenly. Both indices in all plots indicate a decrease in the intensity of clumping or an increase in the regularity of pattern during the 1976–1985 period, with the exception of plot E, where the changes are negligible.

Tree damage under emission stress is a complex multi-causal process (Smith, 1981; Wentzel, 1984). The rate of damage increases when the pollution stress is combined with other stresses (e.g., natural environmental stress near the

timberline; see Vacek, 1984). We tried to evaluate the influence of neighbouring individuals on tree vitality. Two possible mechanisms are in question: competition and 'ecological sheltering' as a type of mutual protection. Our results suggest that competition prevailed in our plots. Under emission stress, the importance of ecological sheltering seems to increase. Then, some optimal distance to neighbours may be found, allowing ecological sheltering, but not leading to strong competition. Our conclusions are taken from forest stands forming a nearly closed canopy, where all individuals take the advantage of being protected within the canopy. The evidence for ecological sheltering will most probably increase in the case of appearance of large gaps, where trees would be directly exposed to winds.

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