Spatial dynamics of forest decline: the role of neighbouring trees

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Abstract. Changes in horizontal structure and the influence of neighbours on tree vitality were studied in a spruce forest under air pollution stress. Five permanent plots along an altitudinal gradient in the Krkonoše Mts., Czech Republic, were monitored for 18 years. Digitized maps of each plot were used for the analysis: the health of each tree, expressed by the defoliation degree was recorded each year, the biometrical characteristics were measured at five-year intervals. Various indices of neighbourhood competition were used to evaluate the interference with neighbours. The results show that the suppressed trees are most susceptible to other environmental stresses, particularly to the air pollution stress. Similarly, tree damage is more severe in plots near the natural timberline, where the trees are close to their natural environmental limits. The spatial pattern of surviving trees changes towards regularity at a scale of 2 - 5 m (*K*-function analysis) when the suppressed trees, usually those with close neighbours, die.

Introduction

Forest decline under air pollution stress is considered to be one of the most important environmental threats in Central Europe; *Picea abies* (Norway spruce) forests, both indigenous and planted, are the most severely damaged ecosystems, particularly in mountain areas (Kubíková 1991; Balcar et al. 1994). The process is studied at various hierarchical levels — from mechanisms influencing photosynthetic activity to changes in ecosystem processes (Zimmermann et al. 1988; Atkinson & Winner 1990; Schultze 1989; Abrahamsen et al. 1994a, b). Forest decline is studied less frequently at the population and community level; for example, opening up of the forest canopy can speed up the spread of the damage (Wolak 1981, Smith 1981); on the other hand, we have shown (Vacek & Lepš 1987) that suppressed trees are more susceptible to other stress factors, both natural and those caused by air pollution. Quednau (1989) demonstrated a similar effect of neighbours in damaged forests in the Frankenwald area, Germany.

Spatial pattern is an important characteristic of a population. Although the underlying processes cannot be deduced directly from observed patterns (Lepš 1990), time changes in spatial pattern are highly indicative of certain processes. For example, an increase in regularity is evidence for dependence of mortality on local population density (Lepš & Kindlmann 1987; Chapin et al. 1989).

The present study is based on long term (18 yr) observations of permanent plots in an area severely damaged by air pollution. The aim of this study is to find answers to the following questions:
1. How is the performance of a particular individual and its changes under air pollution stress influenced by its neighbours?
2. How does the spatial pattern of a *Picea* population change under air pollution stress.

Study area and Methods

Sampling

Five permanent plots were established along an altitudinal transect in the Labsk□důl valley, Krkonoše Mountains (Giant Mountains, Krkonoše National Park, Eastern Bohemia, Czech Republic) on the area of autochthonous *Picea abies* forest in 1976. The plots, labelled A, B, C, D, E (50 m × 50 m each) were established at 1220, 1170, 1120, 1050 and 990 m a.s.l. respectively (Table 1); the timberline in the area is at about 1250 m a.s.l. The climate is cold, wet and windy: annual mean temperature = 4.0 °C; from April to September: 9.5 °C; precipitation = 1322 mm/yr; from April to September: 650 mm; 156 days/yr of snow cover; prevailing northwestern winds, average speed 7.2 m/s at the closest meteorological station at 922 m a.s.l. The climate becomes rapidly harsher with increasing altitude: at 1310 m mean annual temperature is only 2.2 °C, with nearly the same precipitation: 1308 mm. The length of the vegetation season (when the temperature is above 10 °C) is 102 days in plot E, but only 60 days in plot A.

Table 1. Basic characteristics of the plots under study in 1976 and 1991: number of living trees per plot, mean and maximum height of trees, their mean and maximum dbh, their mean and maximum age, and basal area.

Plot	A		B		C		D		E	
Elevation (m a.s.l.)	1220		1170		1120		1050		990	
Year	76	91	76	91	76	91	76	91	76	91
No. of living trees	74	39	76	47	84	66	60	47	61	23
Mean height (m)	10.8	14.4	19.3	21.3	25.6	27.1	31.0	31.5	32.7	35.6
Max. height (m)	20.5	20.5	25.5	26.5	33.0	34.5	38.5	39.0	38.5	39.5
Mean DBH (cm)	30.0	39.0	42.1	47.4	45.5	49.6	51.6	53.9	54.2	62.2
Max DBH (cm)	66.5	69.1	65.4	68.4	83.9	87.9	84.8	88.2	78.7	79.6
Mean age (yr)	135	174	189	200	186	203	198	211	211	229
Max age (yr)	224	239	216	231	247	262	236	247	247	262
Basal area (m^2/ha)	26.7	21.1	45.2	37.4	58.1	52.5	53.1	48.8	59.5	23.2

The increase in air pollution in the area arose mainly from power plants at the German-Polish border (50 - 60 km WNW of the Krkonoše Mts.), which have been in operation since 1972. Data on SO_2 levels are available since 1979 from the monitoring station at Labská bouda (Fig. 1). It should be noted that values over 20 μg/m^3 are considered dangerous, and that the harmful effects are amplified under extreme climatic conditions.

In 1976, detailed maps of all trees in the plots were made, and biometrical characteristics DBH, height, crown width, crown height and the health state were recorded. In 1977, all trees were cored for age determination (Vacek 1981). The health state was determined on the basis of the degree of defoliation, using the scale of Tesař & Temlová (1971), which indicates the proportion of living foliage as follows: state 0 = 100 - 91 %; 1 = 90 - 71 %; 2 = 70 - 51 %; 3 = 50 - 31 %; 4 = 30 - 1 %; 5 = 0 %: dead tree. Biometrical measurements were made at 5-yr intervals (i.e. 1976, 1981, 1986, 1991) and the health state has been estimated each year since 1976. The defoliation degree can be estimated relatively reliably by an experienced forester and the scale is routinely used in the Czech Republic. The estimations were made by the first author during the whole 18-yr period. In North America a similar scale is also used for visual estimation (e.g. Zedaker & Nicholas 1990). Digitized maps were used for all subsequent calculations. The plots always contained some dead trees (see Vacek & Lepš 1987), but the decay of dead trees is very slow. For this study only trees alive in 1976 were used.
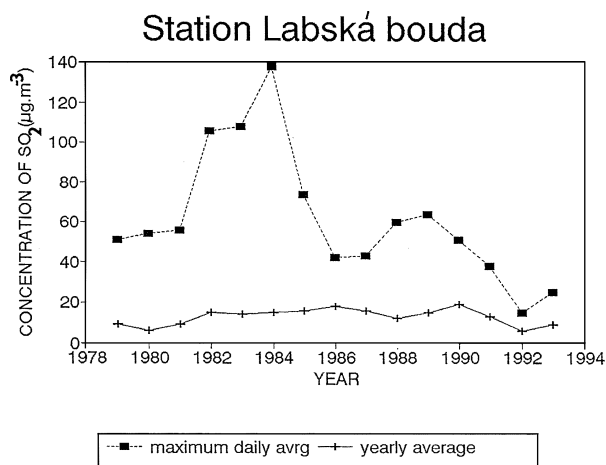
Measures of crowding

In communities of sessile organisms, each particular individual is influenced by its neighbours. In forests, this influence may operate in two directions: (1) the neighbours compete for light, water, nutrients, etc. and (2) a continuous canopy creates a typical forest micro-climate providing shelter to particular individuals (Wolak

1981; Smith 1981). As the growth and health characteristics of particular trees were known, it was important to learn how these characteristics are influenced by their neighbours. Many ways exist of expressing the configuration of neighbours; one usually speaks of index of neighbourhood competition, as competition is the most common interaction. These indices have been used both in evaluation of field experiments and observations, and in dynamic models of forest stands (Bella 1971; Keister 1972; Lorimer 1983; Weiner 1984; Lepš & Kindlmann 1987; Rejmánek & Messina 1990; Randall & Rejmánek 1993).

We used four measures of influence:
1. Distance from the target tree to its nearest neighbour.
2. Sum of basal areas of all trees growing closer than 4 m from the target tree (basal area). A similar measure was used by LeBlanc (1990) in a study on red spruce decline.
3. Unweighted crowding of tree crowns. The crowns were considered circular and symmetric. The area of

Station Labská bouda

Fig. 1. Maximum daily average and yearly average SO_2-concentration at the Labská bouda Station, 1320 m a.s.l.

overlap of the horizontal projection of the target tree crown with that of each of its neighbours was calculated as overlap of two circles. The overlapping crown projections with those of all the neighbouring trees were totalled. This sum was divided by the projected crown area of the target tree. The resulting value is zero if the target tree is solitary and does not overlap with any of its neighbours. The value can exceed 1 if the tree is crowded, with overlapping crowns of many trees which also have mutually overlapping crowns. As the width of the crown is usually correlated with that of the root system (Vinš & Šika 1977), the value although calculated on the basis of crowns may also reflect below-ground interference.
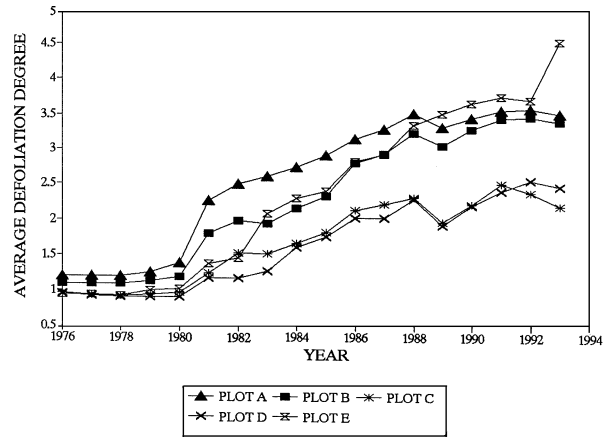
4. Weighted crowding of crowns. This index is calculated in a similar way as the preceding index, but the value of each overlap is multiplied by the ratio of the heights of the neighbouring and the target trees. The influence of tall neighbours therefore has a greater weight than that of low neighbours.

These indices were calculated for all trees in a square of 42 m × 42 m in the centre of the plot. The trees in a 4-m wide belt on the edge were not included as 'target' trees, but only as neighbours influencing target trees. This procedure was used to avoid any edge effect.

Many indices of neighbourhood competition have been developed (see Rejmánek & Messina 1990; Randall & Rejmánek 1993). We selected the index with regard to the type of vegetation; for example, the angular competition index, proved useful for woody weed competition in *Pinus ponderosa* plantations (Rejmánek & Messina 1990) would be difficult to apply in dense stands with widely overlapping crowns. These indices were correlated (Spearman Rank Correlation) with the defoliation degree of the respective target tree in 1976 and 1993 and with the change in defoliation degree during 1976-1993, 1976-1980, and 1980-1981. The period 1976-1980 is representative of the state prior to the start of massive health deterioration; during the winter 1980-1981, the most severe deterioration of the forest was observed (Fig. 2).

The defoliation degree is an ordinal variable. Nevertheless, the variable is roughly a linear transformation of the percentage of foliage present and, consequently, size of increase in defoliation degree corresponds roughly to the amount of foliage lost and can be used as a variable in statistical analyses. Nevertheless, the results could be confirmed by the fact that the possible loss of foliage is highest for the healthy trees i.e. the tree with defoliation degree 4 cannot lose more than 30 % of its foliage.

Individual trees are not entirely independent; each tree is once considered as a target tree, and usually once

Fig. 2. Changes between 1976 and 1993 in average defoliation degree of trees in five plots which were alive in 1976.

or even more often as a neighbour, influencing other trees. So the significance of the Spearman coefficient may be slightly overestimated.

Spatial pattern

The spatial pattern of individuals within the square was evaluated using the index of Clark & Evans (1954):

$$R = 2\bar{r}\sqrt{\rho} \qquad (1)$$

where $\bar{r}$ is the mean value of an individual-to-neighbour distance over all individuals and ρ is density. Values greater than 1 indicate regularity, values smaller than one clumping. There is no reason why we should *a priori* expect a random spatial pattern of individuals; the null hypothesis of randomness has no logical priority. Consequently, we do not use the Clark-Evans index for testing a null hypothesis of randomness, but as a descriptive index: changes in the type of pattern are of basic interest. Changes in spatial pattern resulting in an increase in R are referred to in the text as changes toward regularity, regardless whether the original and final values are smaller or greater than 1. To avoid the edge effect, the inner square of 42 m × 42 m was used for estimating density and only distances to those trees were considered; however, if an individual had a closer neighbour in the edge belt than in the inner square, the distance to this neighbour was used. This is why, in a few cases, the value of the Clark-Evans index changed over time although no trees died in the inner square during that time. The spatial pattern was calculated for all live trees, and for trees that died after the observa-

tions had started (i.e. 1976), for all the years. However, the values are not displayed in the figures if the index has been calculated for less than five trees. Whereas the significance of departure from random pattern is of little ecological interest, the significance of changes in the pattern is highly important. We compared the state in 1976 and 1993 by the Monte Carlo procedure. In each plot the 'random mortality' was simulated by removing randomly selected subsets of trees from the population. The size of the subset equates to the number of trees that died during the period. The Clark-Evans index was then calculated for the remaining trees. Repeating this procedure 500 times, we obtained the expected distribution of the index under the null hypothesis of random mortality and used the distribution to estimate the significance of the real value (see, e.g. Sokal & Rohlf 1981, p. 791; sampled randomization test).

The Clark & Evans index characterizes the spatial pattern by a single value. This is a simplification, useful for displaying changes during years; however, a single value could not describe the two characteristics of spatial pattern: grain and intensity. Hence we used K-function analysis to describe the pattern of mapped data (Cressie 1991, p. 615, see also Haase 1995). The function is defined as

$$K(h) = n(h)/\lambda \qquad (2)$$

where λ is tree density and $n(h)$ is average number of extra trees within a distance h of an arbitrary tree. In reality, the estimates of K are badly influenced by the edge effect, and various corrections are necessary. We used the estimator with variable-width edge correction $\hat{K}_3(h)$ according to Cressie (1991, p. 616). If the trees are distributed randomly then $K(h) = \pi \cdot h^2$. If trees are clumped at a spatial scale h, $K(h)$ tends to be greater than $\pi \cdot h$, under regularity, $K(h)$ tends to be less than $\pi \cdot h$. This is used for construction of the L-function:

$$L(h) = \sqrt{\{k(h)/\pi\} - h} \qquad (3)$$

Positive values of $L(h)$ indicate clumping, negative values regularity. The graph of $L(h)$ vs. h gives a good description of spatial point pattern. In this way, $L(h)$ compares the real number of extra trees within a distance h of a tree with the number expected under randomness. Clearly, if the number of extra trees is higher than expected the trees are clumped. For all plots, the $L(h)$ function was calculated for the years 1976, 1985, and 1993. The significance of changes in spatial pattern was tested by randomization tests. The 95 % envelopes for the $L(h)$ function were calculated for the null hypothesis that the mortality of trees was random (given number

of trees was randomly selected and removed from the population), similarly as for the Clark-Evans index. Similar envelopes were generated by Kenkel (1988). 99 randomizations were carried out, the 3rd and the 97th value for each h was taken as envelope. The hypotheses tested in this way were: the trees having died between 1976 and 1985 (between 1976 and 1993) are a random subset of all trees, independent of tree location.

Results

General trend

In 1976 the average height, average DBH and average tree age decreased with elevation (Table 1). Although some dead trees were always present in the plots (see Vacek & Lepš 1987), the mortality prior to the start of heavy air pollution was relatively low (estimated 1 % or less per year for trees 50-140 yr old; Vacek & Lepš 1991). Obviously, the mortality varied with time and no trees died during the period 1976-1980.

Regarding average tree height (Table 1), the growth of the trees might seem relatively fast. For example, the average height of trees increased during 1976-1991 from 10.8 m to 14.4 m, this increase is caused simply by the fact that the smaller trees died. If the average height is calculated only for trees that survived the whole period, we obtain a value of 13.7 m in plot A in 1976; this means that average increase in height was 0.7 m for 15 years. The same is true for other characteristics and other plots. The younger trees were usually the smaller ones. Consequently, mortality of those trees led to increase of the average age, usually more than 15 years between 1976 and 1991; this phenomenon is most pronounced in plot A.

The general trend of the health deterioration in the course of the last 18 yr can be characterized by changes in average defoliation degree in a plot. The average value for all the trees that lived in 1976 reflects both the increasing defoliation and death of the trees (a dead tree has defoliation degree 5) and increases steadily (Fig. 2). During the first five years (1976-1980), defoliation increased very slowly. The defoliation degree of the two upper plots was slightly higher than that of the rest; this need not have direct connection with air pollution and may be caused by environmental stress near the timberline (Jeník & Lokvenc 1962). The fast deterioration started in the winter of 1980/1981; during that winter, many trees died and the defoliation of some others increased. Perhaps, the catastrophic changes in the winter of 1980/1981 were (besides the air pollution) triggered by an extreme climatic event in the winter of 1978/1979, when a sudden fall of air temperature
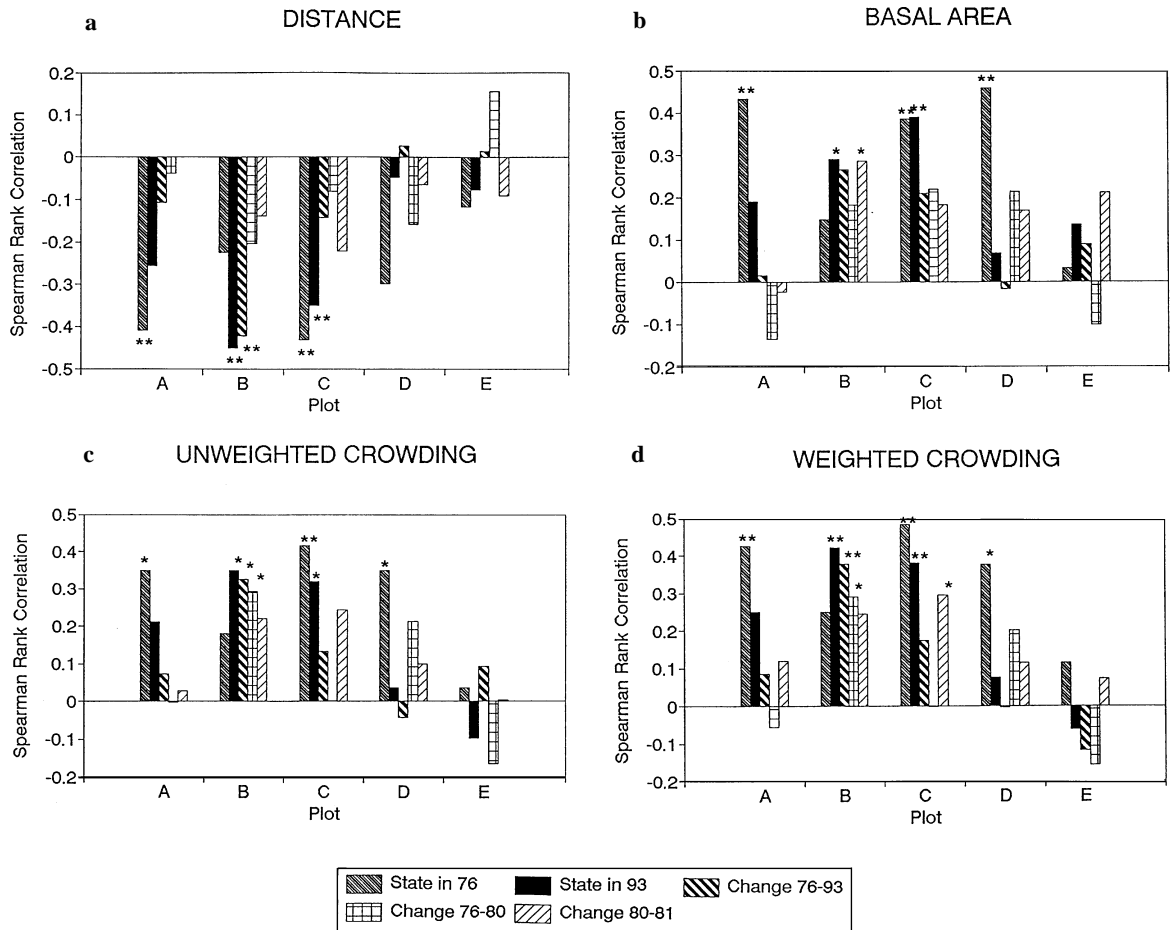
occurred from ca. +10 °C to below − 20 °C within 15 hours. The rate of deterioration increased with increasing elevation. After 1981 the rate of deterioration was relatively constant until 1988, with the defoliation degree increasing with altitude. The only exception is plot E, at the lowest altitude, where forest decline was speeded up by an outbreak of the barkbeetle (*Ips typographus*). During 1988-1989 the health state of trees in all the plots (with the exception of plot E) improved and the situation seems to have been stabilized. The average defoliation of live trees shows a similar trend; there is some improvement of the state of live trees after 1981, mainly due to dying off of trees with high defoliation degrees.

The average relative crown height (the ratio of crown height to total tree height) has decreased during the years (this means that the height of crown bottom increased as the lowest branches died off). In 1976, prior to the massive damage, the relative crown height was highest in plots near the timberline, where the trees are relativel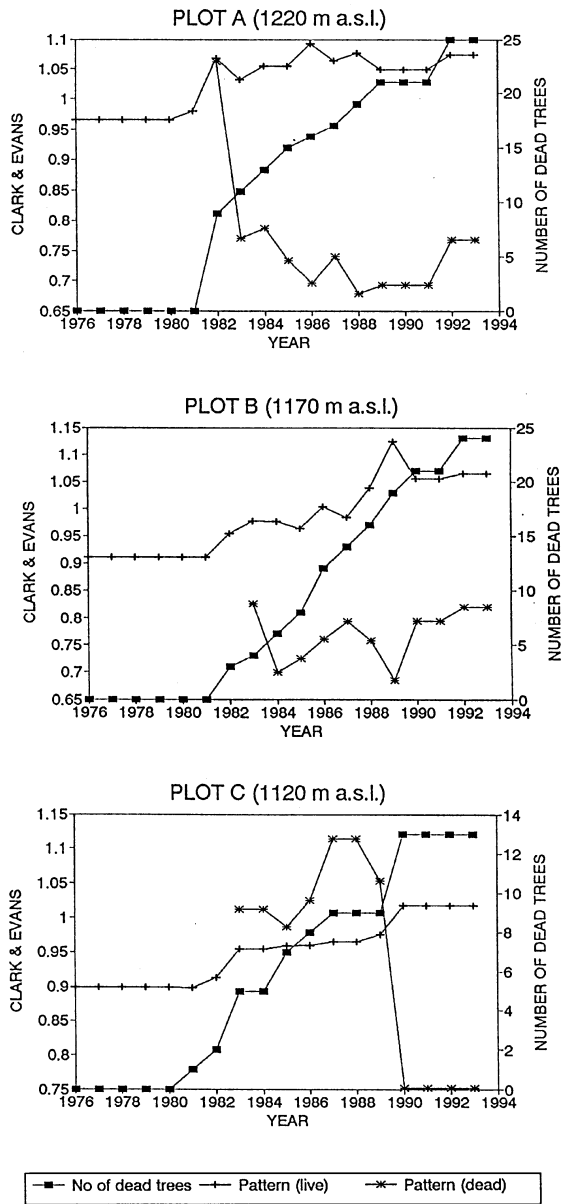y low and do not form a closed canopy, and lowest in a closed-canopy forest formed by high trees. This rule also generally holds in the damaged forest.

Influence of neighbours

The influence of neighbours on a target tree was evaluated by correlating the state of the tree (or the magnitude of its change) with indices of neighbourhood influence, i.e. Distance to the neighbour, Basal area of trees within 4 m from the target tree, Unweighted crowding and Weighted crowding. The Spearman rank correlation coefficient was used. Some interesting patterns were observed (Fig. 3a-d). In all plots (except E), both the defoliation degree and its increase are positively correlated with the indices of neighbours' influence (note that distance to the neighbour is a negative measure of neighbourhood influence); this means that the closer the neighbour the higher the defoliation. In most of the plots (A, C, D) the defoliation in 1976 was significantly positively correlated with most indices of neighbour-
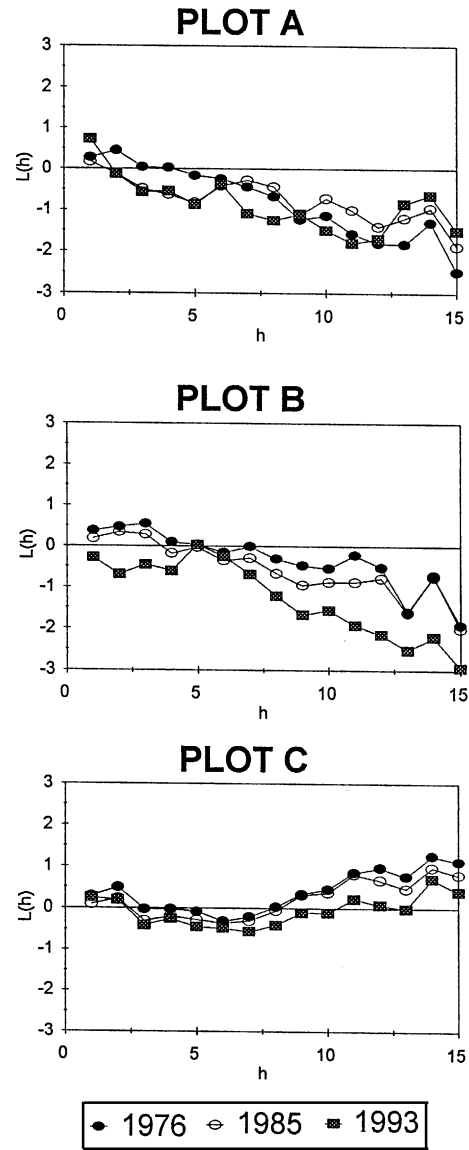

Fig. 3. Values of Spearman's rank correlation coefficient between four indices of neighbourhood competition and the defoliation degree in 1976 and 1993, and changes during three periods for plots A-E in a *Picea abies* forest. Significance levels: * = $P < 0.05$; ** = $P < 0.01$.
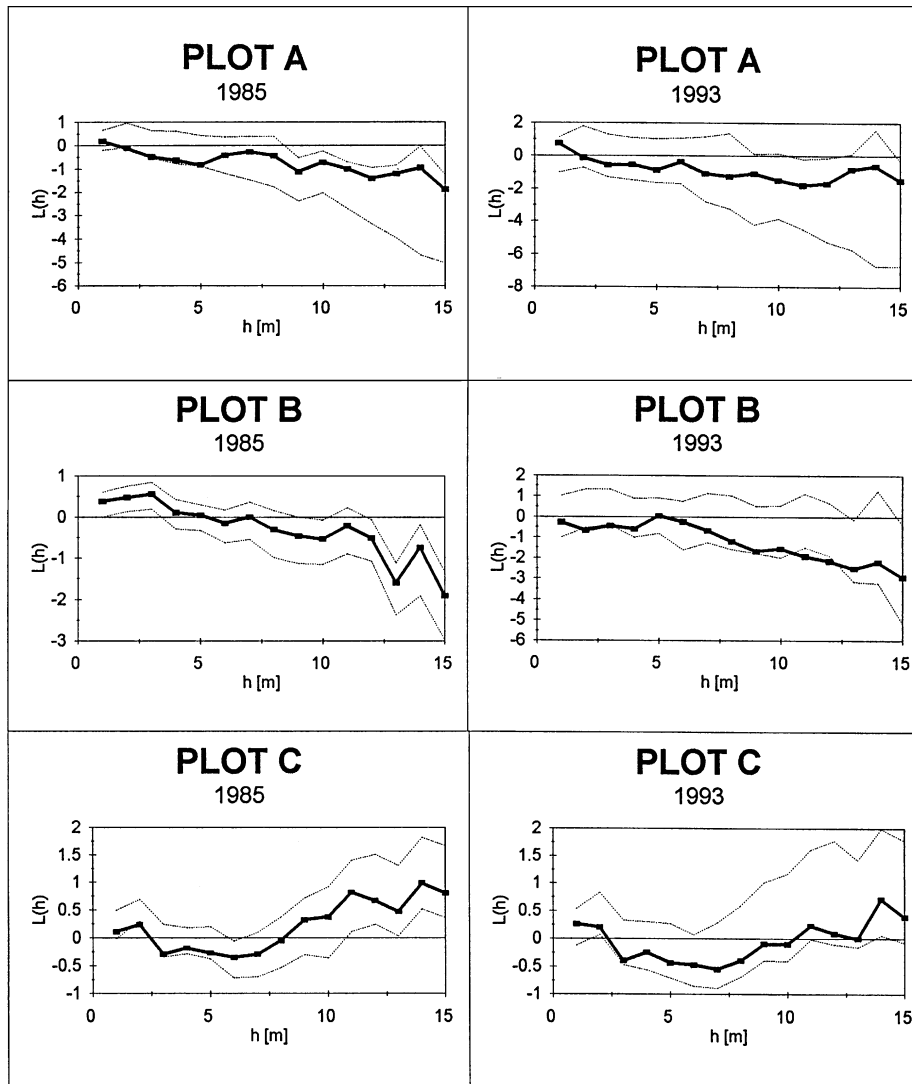
Fig. 4. Changes in spatial pattern (expressed as Clark-Evans index) of live and dead trees in plots A-C and numbers of dead trees in each plot. Only trees alive in 1976 are considered. Values of the index based on less than five trees are not displayed. Number of dead trees in each plot is given for the inner 42 m × 42 m square.

Fig. 5. The *K*-function analysis expressed as *L(h)* for particular plots in 1976, 1985 and 1993. See text for explanation of *L(h)*.

hood influence. The neighbourhood competition seems to be the most important cause of foliage loss under normal conditions (in the other two plots the correlation is similar, but not significant). The state and the changes in 1993 show a similar pattern; the suppressed trees are those suffering most from air pollution. Nevertheless, the correlations are usually loose. For the magnitude of change this can be explained by the fact that the trees

with a higher defoliation degree at the beginning of the period under consideration were those competitively suppressed; obviously, those trees cannot loose as much of their foliage as the healthy trees. This suggests that, in reality, the relationship is stronger than that suggested by the low correlation coefficients. In all cases, however, the trees were in the best state when they did not have close neighbours. For example, the relationship between weighted crowding and defoliation in plot C was fitted by a third order polynomial using Generalized Linear Models in S-plus (Anon. 1995), defoliation modelled as a Poisson variable. The relationship is loose, the quad-

Fig. 6. The *K*-function analysis for plots A, B, and C. The solid line shows the *L(h)* function for a particular year, the dotted lines are the 95 % envelopes under the hypothesis of random mortality between 1976 and 1985 and between 1976 and 1993 respectively. The changes in plots D and E were not significant.

ratic and cubic terms are insignificant, and nothing suggests that there might be some optimum distance caused by sheltering. In plot E, the health state of the trees is influenced most strongly by barkbeetles and is not predictable on the basis of neighbour configurations.

Of the indices, Weighted crowding shows the highest number of significant correlations; consequently, it may be considered as the best predictor of all indices used. Unlike the other indices, it also uses the information about the target tree – the undercanopy trees are lower than their neighbours and, consequently, the index of neighbourhood influence is high. Generally, we may conclude that undercanopy and suppressed trees which are in the worst state of health normally will suffer most from air-pollution induced stress.

Spatial pattern

In 1976, the spatial pattern of trees was close to random, with a slight tendency to aggregation in all but plot E. In plot E, where the mortality was caused mainly by a barkbeetle outbreak, the value of the Clark-Evans index for live trees decreased significantly ($P < 0.05$). On the other hand, in all plots out of the reach of the local barkbeetle outbreak, the value of the Clark-Evans index for live trees increased (i.e. pattern changed toward regularity; Fig. 4). The changes are most conspicuous in plot C but the changes are not statistically significant in any of the plots, although the significance values are low enough to be suggestive ($P = 0.086$ for plot B, $P = 0.074$ for C, one-sided test). We decided to combine

the probabilities from this test using the procedure of Sokal & Rohlf (1981, p. 779), and obtained the resulting value of $-2 \Sigma \ln P = 15.3$. If all the null hypotheses were true, this quantity is distributed as χ^2 with eight degrees of freedom (number of tests $\times$ 2), the corresponding $P = 0.054$. Although this value is > 0.05, it is sufficiently low to allow interpretation of the changes as an increase in regularity. The increase in regularity is usually ascribed to mortality due to neighbourhood competition (Lepš & Kindlmann 1987). In most of the plots, the dead trees were clumped, and their degree of aggregation was usually higher than that of live trees. Their values of the Clark-Evans index fluctuate more widely than those of the live trees – this is caused by a lower number of individuals encountered – but these changes seem entirely random.

The *K*-function analysis (Fig. 5) shows that there were some clumps in plots A, B, C, D at a scale of 1 - 4 m. At scales over 6 m, there was some regularity in all plots but C. The lowermost plot (E), developed differently from the other plots because the mortality was influenced by bark beetle infestation. In all the other plots the *L(h)* values had been decreasing from 1976 to 1993 at a scale of 2 - 5 m. In plots A, B and C the decrease was significant in one of the time intervals studied (either 1976-1985 or 1976-1993; Fig. 6) at scales of 2-3 m. At the scale of 1 m the values are unstable, as the number of (both expected and observed) neighbours closer than 1 m is low and, consequently, the sampling error large. At larger scales, there is no general pattern in the plots. The decrease of *L(h)* at smaller scales concords with the hypothesis that trees with close neighbours have a higher mortality than the others. The results show, that this factor is most conspicuous for neighbours closer than 3 m.

Discussion

Two outcomes of neighbours interference with a target tree were considered: a negative one, usually interpreted as competition, and a positive one, which may be called sheltering (the assumed mechanism is the keeping of a favourable microclimate within a continuous canopy; Wolak 1981). We may expect that competitive interactions are always present and become quite strong when the neighbours are very close to each other. Then, if there is some positive effect of neighbours (sheltering), it will exceed the competitive influence at some distance between neighbours. In this case, we can expect that some optimum distance between neighbours can be found, at which competition is weak and the target tree is still protected by its neighbours. We have found no such optimum in our data. Instead,

the rate of foliage loss was positively correlated with intensity of competition. This is in good agreement with Quednau (1989), who proved 'negative contagion' by completely different methods (other statistical methods used for data from remote sensing) in extremely damaged stands in Frankenwald. Our results do not exclude the possibility of a sheltering effect; we expect that the increased rate of foliage loss may be more pronounced at openings larger than those encountered in this study – despite the fast decline in our plots, there are hardly any trees there that might be considered as solitary.

In this study, the neighbour configuration was not manipulated. Consequently, the results have to be interpreted with caution. In manipulative studies (e.g. Rejmánek & Messina 1990; Randall & Rejmánek 1993) the interpretation is straightforward, as it is clear that the target tree is the influenced partner. In non-manipulative studies, the interaction of the target tree with its neighbours is two-sided, and the results can be confounded by some third variable, usually reflecting the heterogeneity of the plot (see, for example, Šrůtek & Lepš 1994). However, the result of such interaction would be a positive correlation between the performance of a target tree and neighbourhood competition indices. So, if this exists in our plots, the effect of competition is even stronger than suggested by values of correlation obtained in this study.

It might be questioned to what extent the described changes are caused by air pollution and how this influence interferes with natural stand development and influence of climatic events. Unfortunately, we do not have an unpolluted control as no unpolluted control exists at a comparable elevation within at least 100 km from the study area. All stands were in a mature phase of development in 1976, and with regard to the density, age and size of particular trees no natural self-thinning was to be expected. From 1980 on, the start of a massive forest decline was observed in all mountainous spruce forests on the Czech-German and Czech-Polish border, more or less simultaneously across the whole area. Consequently, the process could hardly be the result of certain internal dynamics of the forest stand. Our stands happened to be situated in a less damaged part of the Krkonoše Mts.; in some other parts whole stands died off completely. It seems that in the plots at lower altitudes, decline of the tree layer speeded up seedling regeneration and sapling growth. Near the tree-line regeneration is much slower (Vacek 1990). It is generally difficult to separate the influence of anthropogenic stress (e.g. air pollution) from the influence of climate fluctuations and internal stand dynamics (e.g. Peart et al. 1992; Cook & Zedaker 1992; Johnson et al. 1992) in the absence of experiments or, at least, without comparable unstressed stands. However, the temporal and spatial

coincidence of forest decline with increased air pollution is, at least in Central Europe, so striking that there is little doubt about the role of air pollution (Kubíková 1991; Balcar et al. 1994), even though the understanding of mechanisms is far from complete (Loehle 1988; Schulze 1989; Johnson et al. 1992). The effect of air pollution is modified by the climate and each tree is also influenced by its biotic neighbourhood. A striking similarity was found between spatial dependence of mortality in our case and that described by Kenkel (1988) in an unpolluted self-thinning Jack-pine stand. In both cases, the K-function analysis has shown the largest increase in regularity at a scale of about 3 (2 - 5) m, indicating roughly the radius of mean 'area of influence' of an individual. In accordance, we found that in 1976 (i.e. before the start of the process) live trees were more regularly spaced than all the trees (live and dead) in our plots (Vacek & Lepš 1987). Evidence is available from various stands (Laessle 1965; Tagawa 1965; Prach 1981) for similar increases in regularity, or for increasing regularity with tree size (Szwagrzyk 1990). This supports the hypothesis that local density promotes mortality (Peet & Christensen 1987). A similar effect was found by Quednau (1989) in severely damaged stands in Germany. Very probably the competition among neighbouring trees, which has pronounced effects on the mortality during self-thinning in natural stands, also increases the rate of defoliation and mortality caused by other stress factors. On the other hand, in a study by LeBlanc (1990), the growth of dominant and codominant red spruce was unrelated to the basal area of neighbouring trees.

In conclusion, defoliation rate and tree mortality was higher in trees with close and large neighbours; as a consequence, the spatial pattern changed toward regularity at a scale of 2 - 5 m; at larger scales, no consistent changes were found.

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