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GENECOLOGICAL ASPECTS OF AIR POLLUTION EFFECTS ON NORTHERN FORESTS

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Natural forest tree populations are adapted to their natural environment. Forest tree species under northern conditions are at the edge of their range where the short growing season and the low winter temperatures are the two main factors limiting their ecological niche. Effects of air pollution on the ecological niche, designated as the environmental conditions that permit a population to survive permanently, are discussed according to G. E. Hutchinson's concept of the ecological niche. Air pollution as an additional stress factor influences the ecological niche either by the direct influence as an additional dimension of the ecological niche or by interactions with the other dimensions. These interactions are especially important for low level long term effects of air pollution which can result in reduced resistance to low winter temperature or, due to reduction of netassimilation, reduced capability to survive the long period of winter dormancy. These effects influence the boundary of the ecological niche and reduce the area of the biotope of the respective species.

Within the remaining biotope genetic changes in forest tree species take place. Due to individual differences in exposure and susceptibility of trees to air pollution, higher and therefore more exposed trees as well as more susceptible trees will be reduced in reproduction or even be eliminated. This causes genetic changes in the tree populations.

INTRODUCTION

This lecture shall give an introduction to the symposium on "Air Pollutants as Additional Stress Factors under Northern Conditions" with special emphasis on genecology.

The title of this lecture consists of three topics: forests as they have evolved under natural northern conditions during the last 6000 years since the ice age, anthropogenous air pollution influence during the last and for the future tree generations, and genecology.

Using the concept of genecology we follow HESLOP-HARRISON (1964) who describes genecology as a synthetic discipline, which combines ideas and methods of genetics, taxonomy and physiology. Air pollution here means low pollution dosage (GUDERIAN and KÜPPERS 1980a), which can influence the reproduction of forest tree populations. Of course medium and high pollution dosage influences the reproduction as well. It is trivial for instance that a population killed by high pollution dosage does not reproduce. The effect of low pollution dosage on reproduction however is not a question of yes or no, it is a question of more or less and there is a severe interaction with other stress factors, especially in northern forests. This makes pollution effects very difficult to detect and to quantify. For this reason and because of the very sharp increase of pollutant emission since the fifties of this century, which, in connection with the high stack policy, leads to increasing areas of remote forests exposed to low pollution dosage, we want to concentrate on northern forests.

Northern forests are mainly characterized by two natural factors, which limit tree growth and reproduction: short growing season which limits total net photosynthesis and seed production, and low winter temperature which is a stress factor mainly due to water stress (winter drought).

THE CONCEPT OF THE ECOLOGICAL NICHE

For discussing the problems of interactions between the natural stress factors and additional stress by air pollution under northern conditions we want to use G. E. Hutchinsons concept of the ecological niche (HUTCHINSON 1958), which STERN and ROCHE (1974) introduced into forestry. The ecological niche is defined as "The environmental conditions that permit a population to survive permanently".

Concerning the environmental factor "low winter temperature" the ecological niche is limited by the extreme value at which the population still can survive. We call this the first dimension of our ecological niche, which graphically can be demonstrated by the line x_1', x_1'' on the x_1-axis of the system of co-ordinates in figure 1.

The second main limiting factor for tree growth and reproduction is the number of days of the growing season. For graphic reasons (figure 1) instead of the number of days of the growing season subsequently the number of days of the winter dormancy is chosen to describe this dimension x_2 of the ecological niche. It is demonstrated by a line x_2', x_2'' on the x_2-axis. Together with the first dimension x_1 it forms a rectangle which describes the ecological niche according to these two factors.

We now add air pollution as the third dimension x_3. If we had no pollution, the ecological niche would not be restricted in the direction x_3. Air pollution however limits growth and reproduction of a population as demonstrated by the line x_3', x_3'' on the x_3-axis. Hence, theoretically the ecological niche concerning these three dimensions is represented by a space in a system of co-ordinates. Real ecological niches are represented by respective spaces within the space of figure 1, depending on interactions between the dimensions.

Of course, there are many additional factors (dimensions) to be taken into account such as soil conditons, water supply, pathogens etc.. The pollution dimension itself can be divided into several dimensions with regard to different pollution components, an example of which will be discussed later.

Generalized, an ecological niche with n environmental factors can be described by a hyperspace in an n-dimensional system of co-ordinates. This theoretical approach facilitates the understanding of pollution effects on ecosystems and the integration of the very different objectives to be presented to this symposium.

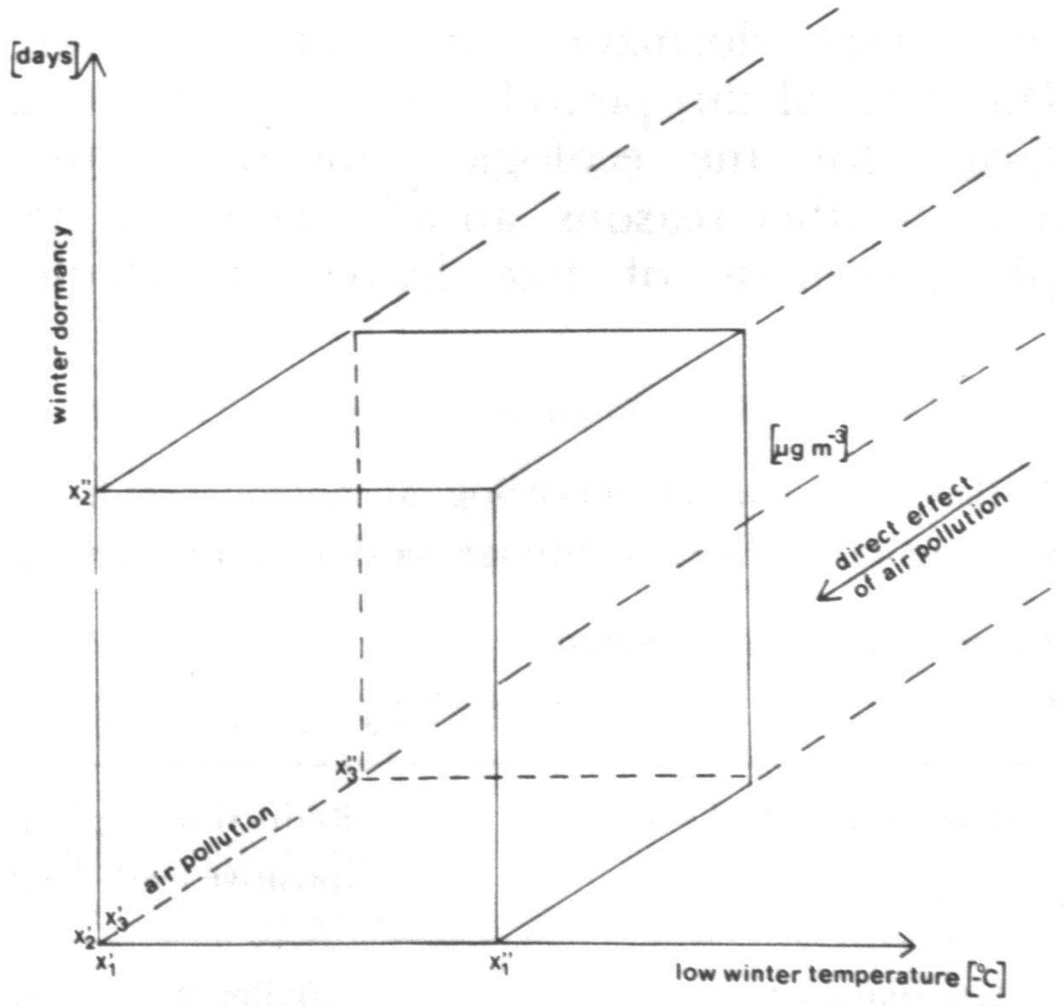

Fig. 1 The ecological niche of a population according to the ecological factors low winter temperature (x_1) winter dormancy (x_2) and air pollution (x_3) · x_1'', x_2'' and x_3'' are the limiting values concerning the respective ecological factor. The parallelepiped represents the niche when no interactions occur. (after Stern and Tigerstedt, 1974).

INTERACTIONS BETWEEN THE THREE DIMENSIONS

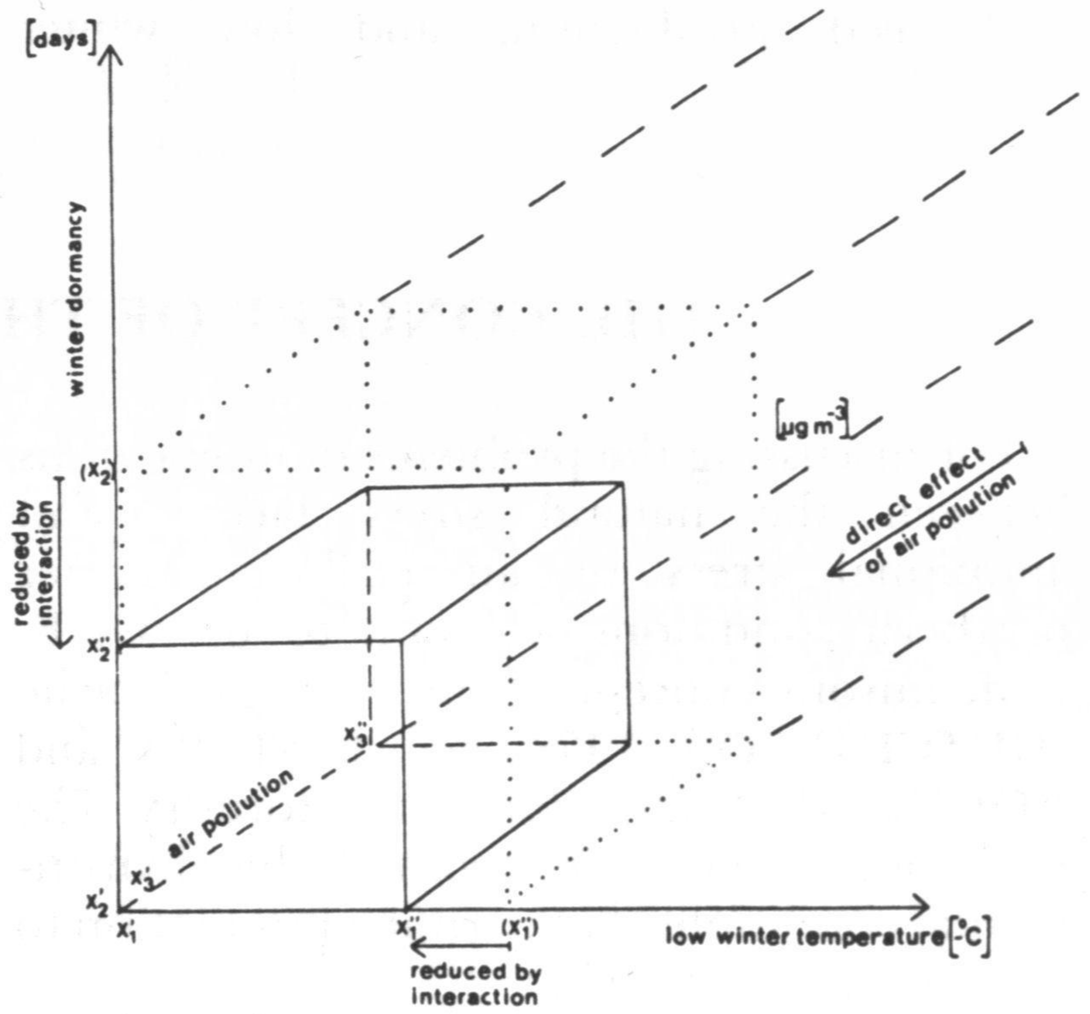

Fig. 2 The ecological niche of a population as shown in Fig. 1 (dotted lines), reduced by interactions between the natural ecological factors x_1, x_2 and air pollution x_3. The small parallelepiped represents the reduced ecological niche. (after Stern and Tigerstedt, 1974, modified).

So far our ecological niche did not consider interactions between the dimensions. Such interactions may be negligible when high dosage of pollutants with severe acute injuries occurs, so that the pollution dimension of our niche is much more important than the other dimensions. Such conditions are to be found in the industrial regions of Central Europe, e.g. in the Ruhr District, Saxonia, and Upper Silesia. However, the further north the location and the higher the elevation of forests is, the more important are interactions between the natural ecological factors and the air pollution influence. What are these interactions alike?

It has often been reported, that in areas with low pollution, winter injuries in forest plants can occur, which cannot be explained by temperature conditions or pollution influence alone. (WENTZEL 1965, HUTTUNEN 1975, MATERNA 1979). However, forest plants, exposed to low pollution concentrations are more sensitive to low temperature KELLER 1978). This means that the ecological niche concerning the factor low winter temperature is reduced by air pollution (figure 2).

The ecological niche is also influenced by interactions between duration of the period of winter dormancy and air pollution. Duration of this period as such is a limiting factor for the ecological niche because, among other reasons, an adequate total net photosynthesis of tree leaves or needles during the growing season is necessary for a sufficient carbon balance of the tree. Air pollution affects this balance. It is well known, that air pollutants reduce photosynthesis of trees already at concentrations where no symptoms are visible. Up to 40 % reduction of diameter growth without visible symptoms have been reported (GRIESS 1980). TRANQUILLINI (1980) describes the physiological and ecological consequences for trees at the timber line, suffering from low growth increment as a result of low rates of photosynthesis (table 1). The resultant effects in table 1 indicate that reduction of dry matter production by air pollution reduces the ecological niche with regard to the dimension of winter dormancy (figure 2). The resultant smaller space of the niche in figure 2 is a theoretical niche in which real niches are represented by the respective spaces with form and size depending on the real conditions.

Table 1 Physiological and ecological consequences from low growth increment of trees at timberline, as a result of organic matter deficiency through weak photosynthetic productivity (from Tranquillini, 1979).

Reduced growth increment of:	Resultant effect
Shoot length and leaves	Reduction in photosynthetic productivity of the tree (positive feed–back)
Stem diameter	Smaller storage capacity for water and organic reserves, poor transport of water and assimilates
Roots	Deficient mineral nutrition and water supply
Seed	Restricted dispersal of regeneration

Of course, there are interactions between air pollution and the dimensions of other ecological factors as well. How complex their interactions are, shows the following example. The reduction of frost hardiness by air pollution can cause higher susceptibility to pests, which for its part can already be increased by pollution too (HEAGLE 1973).

INTERACTIONS BETWEEN DIFFERENT POLLUTANT COMPONENTS

We already mentioned the interaction of different components of air pollutants which, for example, are to be seen as synergistic effects. These, however, are dependant on the concentration of each of the components. An investigation by v.d. Eerden (pers. communication) shows that the lower the concentrations are, the higher are their synergistic effects (figure 3). For example exposing a sample of a plant species to 1000 μg/m³ only SO_2 leads to adverse effects after 0.06 days compared with almost the same time for getting adverse effects when applying 1000 μ g/m³ SO_2 and 1000 μ g/m³ NO_2 simultaneously. However, doing such experiment only with 100 μ g/m³ SO_2 and in combination with 100 μ g/m³ NO_2 respectively reveals, that in this case the time for getting adverse effects differs by a factor of about 100. This shows that the lower the concentration, the higher are the synergistic effects and it demonstrates that synergistic effects as well as interactions of air pollution with natural stress factors have to be investigated by low pollution dosage experiments with conditions as close to the polluted ecosystem as possible.

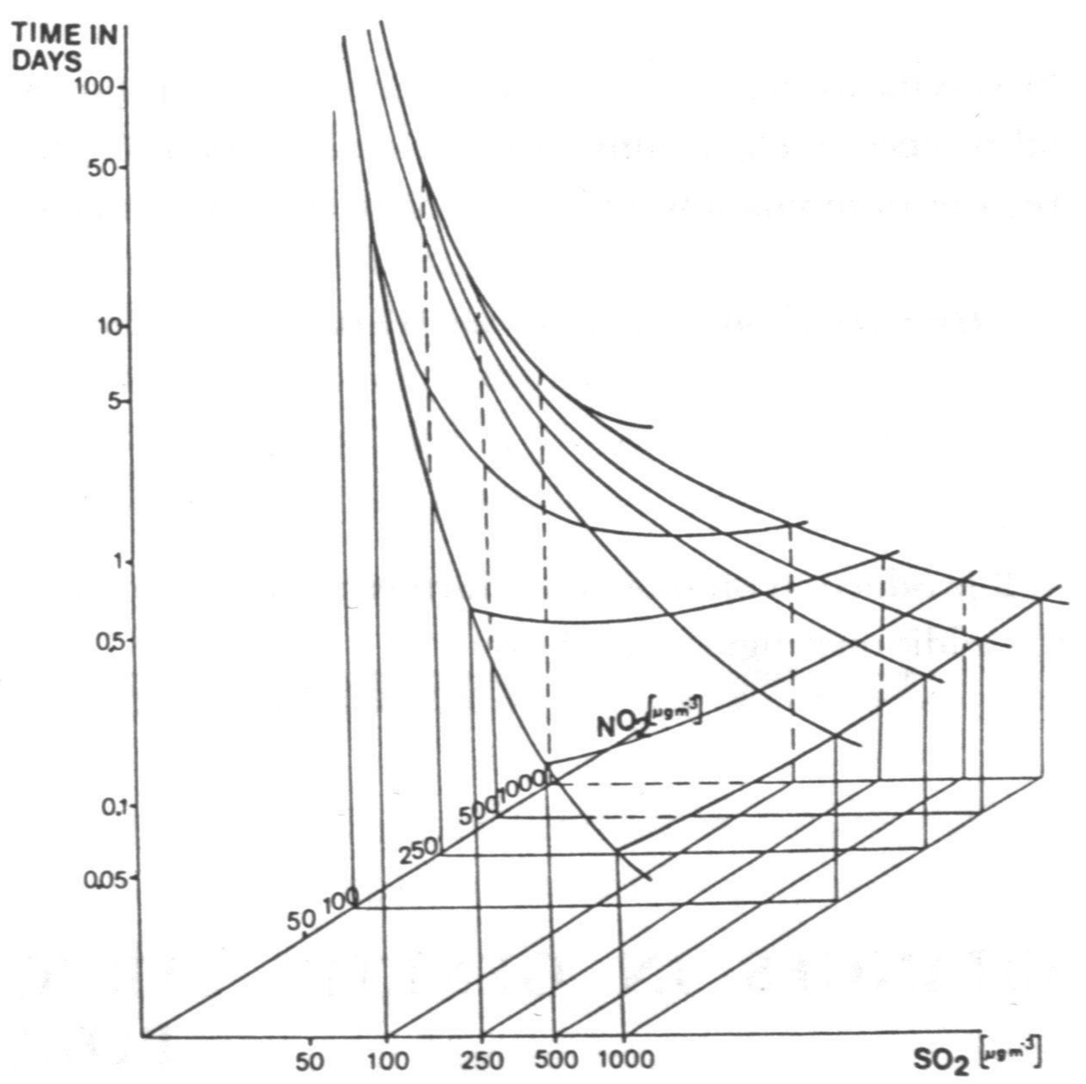

Fig. 3 Estimate of non-adverse-effect-level for SO_2 – NO_2 combination, based on literature data and own results (from v.d. Erden, unpublished)

CONSEQUENCES FOR REAL BIOTOPES

Many of the biotopes which fulfilled the conditions for ecological niches for many forest tree generations before air pollution came about, have already changed to conifer (fir, spruce, pine) deserts. This has mainly been caused by high and medium dosage pollution. We have to discuss the question whether low dosage pollution continues the desertification process also in other regions. This means we have to concentrate on the interactions of air pollution and natural stress factors. Hence mainly northern biotopes or biotopes at higher elevations or poor sites have to be regarded. But also the dramatic fir dying (SCHÜTT 1977) and spruce dying (SCHÜTT 1981) at good conifer sites should be regarded with this respect. Effects of air pollutants on soil conditions (ULRICH et al.

Table 2. Air quality standards for sulphur dioxide and hydrogen fluoride for the protection of forests (IUFRO S2. 09–00, 1979).

Sulphur dioxide in micrograms per cubicmeter of air		
annual average	*average of 24 hrs*	*97,5 percentile of 30 minutes values in period of vegetation*
50	*100*	*150 microgr.*
(full production on most sites; the average of 24 hours may be exceeded 12 times during a period of six month)		
25	*50*	*75 microgr.*
(necessary to maintain full production and environmental protection e.g. against erosion, avalanches, in higher regions of mountains, in boreal zones, extreme sites etc.)		
Hydrogen fluoride in microgram per cubicmeter of air		
0,3		*0,9*
(full production on most sites; further research necessary for additional figures as above)		

1979) have to be included.

Of course, there is already a great amount of knowledge which has been considered when the IUFRO-Recommendations "Air Quality Standards for the Protection of Forests" were approved (table 2). Two categories of values for different biotopes were approved, one for optimal sites and one with lower values for higher regions of mountains, boreal zones, extreme sites etc.. There is, however, still insufficient knowledge for HF-values for the second category, values for other pollutants, values that consider interactions between different pollutants, and values which consider the influence of air pollutants on soils. And there is still the discussion whether the values for the second category of sites are still too high. This demonstrates the urgent need for intensive research work on interactions between natural ecologicial factors and air pollution for stopping conifer desertification, which of course only reveals processes which started much earlier and at a lower pollution dosage when pollution effects are still latent (KELLER 1977). An example of such processes are genetic changes in forest tree populations which shall be discussed in more detail.

CHANGES IN GENETIC STRUCTURE OF POPULATIONS BY AIR POLLUTION

For discussing genetic changes in forest tree populations under pollution influence we want to start with the concept of fitness. Fitness is defined by the proportionate contribution of offsprings of a tree to the next generation. Fitness is influenced by two main characters, the viability and the fertility. Viability is mainly based on resistance against abiotic and biotic stress factors, fertility results from pollen production, flowering, fruit and seed development etc. . It is well known that viability is influenced by air reported PELZ 1963, ROQUES et al. 1980). Not all trees of a population are influenced in all trees of a population are influenced in their fitness to the same extent, thus we have to discuss the variation of air pollution influence on a population at the individual tree level. We have to differentiate between individual variation in exposure of trees to air pollution and individual variation in plant response to air pollution.

INDIVIDUAL VARIATION OF PLANT EXPOSURE IN POLLUTED FOREST TREE POPULATIONS

To affect plant metabolism pollutants have to enter the leaves or needles, (other plant organs are not regarded in this respect). The amount of gaseous pollutant that enters plant leaves depends on pollutant concentration c [$\mu g \cdot m^{-3}$] (the leaf assumed as a perfect sink

with c = 0) and deposition velocity v [$m \cdot s^{-1}$]. The flux into the leaves is denoted as $F = v \cdot c$ [$\mu g \cdot m^{-2} \cdot s^{-1}$]. For theoretical (UNSWORTH 1979) and experimental reasons, which are discussed more detailed by SCHOLZ (1981), the deposition velocity, without regarding influences by the gas and the leaves, depends on the wind velocity u [$m \cdot s^{-1}$] the leaves are exposed to. In the crown region of a forest stand wind velocity increases with height (BAUMGARTNER 1961) e.g. the annual mean in a spruce stand from 0.04 $m \cdot s^{-1}$ in the lower crown region up to 1.04 $m \cdot s^{-1}$ just above the crown (MAYER 1976). Consequently higher trees in a stand should be more exposed and take up more pollutants and be more injured than smaller trees. Experimental results which confirm these considerations are discussed by SCHOLZ (1981).

INDIVIDUAL VARIATION OF PLANT RESPONSE IN POLLUTED FOREST TREE POPULATIONS

Assuming we had no differences in exposure of trees to pollution in a stand we would still get individual variation of response because of the individual sensitivity of trees. ROHMEDER and VON SCHÖNBORN (1965) showed for Norway spruce that environmental and genetic factors are responsible for this variation. The proportion of environmental and genetic components was quantified by SCHOLZ et al. (1979) regarding the variation of response to HF under experimental conditions. Under those conditions 60 % of phenotypic variation based on genetic factors.

CONSEQUENCES FOR THE FITNESS OF TREES IN A STAND

We said that the fitness of a tree is based on viability and fertility. Both are influenced by air pollution. This influence is not equal for all trees of a stand, because higher trees are more exposed to air pollution than smaller trees and susceptible trees are more affected than more tolerant trees. Accordingly, higher trees in a polluted stand show more injury (PELZ and MATERNA 1964, WENTZEL 1964) and less fructification (PELZ 1963), which results in a reduction of fitness. Obviously the susceptible trees of a population are reduced in fitness too. This means that in polluted stands there must be a selection pressure against higher trees and susceptible trees as well, which causes a selection against tree height and susceptibility. As height growth and susceptibility are not correlated (SCHOLZ 1981), twofold or even more complex effects are to be expected.

GENECOLOGICAL CONSEQUENCES OF SELECTION PRESSURE BY AIR POLLUTION

We now regard processes which take place in an ecological niche as influenced by air pollution according to figure 2, where a population may still survive but is stressed by a selection pressure caused by air pollution which influences genotypic and genic diversity of populations. Reasons and consequences of a reduction of genotypic and genic diversity are discussed by GREGORIUS et al. (1979).

It is difficult to quantify the selection pressure in terms of genotypic changes of the population, because silvicultural management and other factors are changing genotypic structure, too. As our knowledge of effects of air pollution on the genetics of tree species is still rather poor, we want to regard a theoretical consideration with simplified assumptions. Let us say x is a trait against which air pollution is selecting, and σ^2_p is the phenotypic variance of this trait. By appropriate methods σ^2_P can be partitioned into the environmental component σ^2_E and the genotypic component σ^2_G which can be further partitioned into different genetic components of which the additive genetic variance component σ^2_A is of interest (FALCONER 1960). The quotient σ^2_A / σ^2_P is denoted as narrow sense heritability h^2 n.s., which indicates to what extent the variance of a trait is caused by genetic factors. Evidently the effect of selection against a trait is higher, the higher its heritability is. For our example the heritability of x be 0.2 and we assume those 50 % of the population to be excluded from reproduction by air pollution influences, for which x has high values (e.g. height or susceptibility). According to FINNEY (1956, cited after SHELBOURNE 1969) we have

$$\sigma^2_{A(i+1)} = \sigma^2_{Ai} \cdot (1 - \nu h^2).$$

The value for ν is derived from selection intensity (for 50 % $\nu = 0.6366$) and σ^2_A the additive genetic variance in the generation i, is 0.2. In the next generation (i+1) the additive genetic variance of x is narrowed from 0.2 to 0.1745, which is a reduction of 12,75 %. For generations this reduction continues while the population mean of x decreases. According to this consideration we may realize the effects of air pollution on height growth and other traits under selection pressure by air pollution. Such effects can occur even in stands with low pollution where no visible symptoms can be observed. With regard to the increasing areas of remote forests with long term low level pollution we have to intensify our investigations in these areas.

In polluted areas with high level air pollution genecological considerations led to practical consequences. Where forest tree populations are in danger to be extincted, e.g. populations of *Pseudotsuga macrocarpa, Pinus attenuata, P. coulteri, P. jeffreyi,* and *P. ponderosa* in the South Californian smog belt or populations of *Picea abies* in the Erzgebirge, 'evacuation' of these populations has been proposed (LIBBY et al. 1975) or is under way (MATERNA, pers. communication). GUDERIAN and KÜPPERS (1980b) pointed out the danger of gene impoverishment by air pollution for agricultural crops. This danger is also to be regarded for forest plants SCHOLZ, 1980).

CONSEQUENCES AND CONCLUSIONS

- Hutchinsons concept of the ecological niche serves as a good tool for understanding genecological effects of air pollution.
- Interactions between niche dimensions should be quantified for evaluation of latent injury by long term low level air pollution.
- Air pollution can change genetic structure and diversity of populations.
- For air quality standards possible effects on gene impoverishment should be regarded.
- This is especially important for marginal populations, for population with high specialization or under extreme conditions. This includes boreal and high mountain forests.

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