FOREST GENETICS 1(2):97–104, 1994

IMPACT OF GLOBAL CHANGE ON POLLINATION PROCESSES AND ON THE GENETIC DIVERSITY OF FOREST TREE POPULATIONS

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Received February 4, 1994; accepted September 30, 1994

ABSTRACT

Several mechanisms are considered by which both pollution and climate change are likely to affect pollination processes, altering the genetic structure of forest tree populations. Stand density, distance of pollen dispersal, asynchrony and sexual asymmetry in reproductive efficiency among different genotypes could all be altered, resulting in rearranged mating systems. Patterns of resource allocation, which are related to paternal reproductive success, could be modified. The anthropogenic change could interact with male gametophytic selection and with early zygotic selection, either as a direct stress or by reducing pollen load. Mechanisms of self-incompatibility could also be modified. This could strongly affect both adaptedness and adaptability to further changes of forest tree populations.

Key words: global change, pollen, mating system, paternal success, male gametophytic selection.

INTRODUCTION

Several effects of human activities increasingly influence the environment on a global scale; we generally refer to them as global change. Although this concept encompasses many processes, from land use change and habitat fragmentation to the depletion of the ozone layer, the scope of the present paper will be limited to the effects of two of its major components, pollution and the projected climate change.

Pollution now constitutes a serious threat both to man and to ecosystems in many parts of the world (BRESSER & SALOMONS 1990; LINDBERG *et al.* 1990) and the relevance of long range, transboundary pollution has become clear. The combined effects of several pollution agents on plants and on other components of the ecosystems are pointed out as an important determinant of the forest decline observed in several regions of Europe and of North America (SCHULZE *et al.* 1989; TRESHOW & ANDERSON 1989).

A rise in the atmospheric concentration of CO_2 and other polyatomic gases was observed during the past century (SCHNEIDER 1989). These "greenhouse gases" are expected to determine an increase of the global temperature, eventually resulting in sensible climate changes worldwide (GOODES & PALUTIKOF 1992). A global temperature increase of about 2.5 °C is expected, associated at northern mid latitudes with stronger precipitations during the winter, but reduced soil moisture during the summer (IPCC 1990). Plants will be affected directly by the increased availability of CO_2 and even more by the shift of climatic conditions (SHUGART *et al.* 1986).

Environmental changes due both to pollution and to the greenhouse effect differ from common natural disturbances in that they are unidirectional and relatively fast. Their effects on biological diversity are currently the subject of much research; changes in species distribution and in ecosystem composition in response to climate change are in particular forecast (BOLIN *et al.* 1986; SHANDS & HOFFMAN 1987; PETERS & LOVEJOY 1992; SMITH *et al.* 1992). The effect of air pollution on species diversity of ecosystems is also investigated (BARRETT & BUSH 1991).

The impact of anthropogenic changes on genetic diversity of plants, in particular, deserves great attention, since diversity constitutes the basis both for physiological performances at the individual level and for adaptability to a changing environment at the population level.

The genetic structure of a population is affected by environmental constraints in three different ways. The death of least fit individuals results in the loss of unfavoured allelic combinations and even alleles altogether (MÜLLER-STARCK 1985a, 1989); secondly, the effect on the vegetative vigor of plants variously reflects on reproductive processes, e.g. altering stand density, plant resource allocation, pistil and pollen formation; thirdly, the biology of reproduction is affected directly by environmental factors acting on pollen, ovules, zygotes and seeds.

Pollen is particularly exposed to the environment, due to its temporary independence of the sporophyte; moreover, in the last few years both reproduction biologists and geneticists have recognized the preeminent role of pollen in determining plant reproductive success (MULCAHY 1979; BERTIN 1988; STANTON *et al.* 1992) and in shaping the mating system and consequently the genetic structure of plant populations (BROWN *et al.* 1985).

We will focus our attention on the effect of anthropogenic changes on the processes of pollen formation, pollen dispersal and fertilization, and on the consequences for genetic diversity of plant populations. These effects will greatly depend upon both species' life history characteristics and the kind of disturbance considered. The present paper is therefore intended only to outline the possible mechanisms of these processes and to stress the need for further investigation.

GENE FLOW AND MATING SYSTEM DETERMINANTS

Two different processes interact during reproduction in determining the genetic structure of populations: gene flow and selection acting on reproductive structures, either sporophytic or gametophytic.

The importance of gene flow in shaping the genetic structure of populations is now generally acknowledged. Relevant amounts of gene flow due to pollen dispersal are observed in most plant species, both wind- and insect-pollinated. SMITH *et al.* (1990), in a survey of 17 lodgepole pine (*Pinus contorta*) stands of different density, measured even in the most disperse stands an airborne-pollen density almost 50% of that in pure stands, due to migration from surrounding populations. This is consistent with the results of paternity analyses: the proportion of offspring identified as having pollen parents outside the local population (mostly for long-distance dispersal) was 36 and 43% in two stands of *Pseudotsuga menziesii*, a wind-pollinated species, and respectively 30 and 50% in *Platypodium elegans* and *Gleditsia triacanthos*, two insect-pollinated species (ADAMS 1992).

High rates of gene flow prevent local genetic differentiation, but also low levels of migration, with little effect on the frequencies of common alleles, continuously introduce new alleles and genotypes, thus counterbalancing genetic drift and fixation; WRIGHT (1948) has shown that for the island model if $4Nm >> 1$ (where N is the effective population size and m is the rate of gene flow) then genetic drift will play a minor role. An important function could therefore be played by even small amounts of long--distance dispersal, very effective in increasing neighborhood size and often underestimated. As a result, life history characteristics which enhance gene flow are associated with high species genetic diversity (HAMRICK *et al.* 1981) and with high intrapopulation diversity (HAMRICK 1987).

Migration in plants is due to the movement of both seeds and pollen; although pollen has only half the genetic information carried by seeds, the patterns of pollination which result in a species' mating system are of utmost importance in perennial outcrossers such as many gymnosperms and woody angiosperms (GOVINDARAJU 1988).

The mating system of plants departs under many respects from the purely random model expected for Hardy-Weinberg equilibrium. Several mechanisms of positive and negative assortative mating are present: the outcrossing rate is reduced not only by the actual amount of selfing, but also by the spatial structuration of the population into neighborhoods of genetically related individuals, resulting in an "effective selfing" (RITLAND 1984); moreover, different genotypes show different patterns of resource allocation (in terms not only of investment in reproductive structures, but also of balance among pollen and ovule production) and there is often at least a partial incompatibility of their flowering timing. By altering these determinants of mating systems, global change could affect in the end plant genetic diversity.

Amount of selfing and neighborhood size are affected by the distance of pollen dispersal. According to WRIGHT (1976) in anemophilous species this is unrelated to wind speed, but determined by air turbulence, which is expected to be increased by a climate warming (IPCC 1990). On the other hand, prolonged precipitation negatively affects pollen dispersal; as precipitation is expected to increase in mid latitudes during the winter, species which flower during this period (e.g. *Corylus avellana, Alnus* spp., *Populus alba, Fraxinus oxycarpa*) will be negatively affected.

Both outcrossing rate and neighborhood size are however more variable in self-compatible entomophilous species, and greatly depend on pollinator activity and behaviour (BROWN *et al.* 1989). The synchrony between anthesis and life cycles of pollinating animals could be disrupted by changes in climate as well as by pollution (SMITH 1981). On the other hand, at high latitudes and altitudes a climatic warming could hasten pollinator activity. This would result not only in higher outcrossing rates, but also in increased seed sets, as in cold and damp conditions reproduction is sometimes pollination-limited (CAMPBELL 1987). The consequent increase of the effective population size is the primary condition for a shift northward and upward of specific natural ranges (PETERS & LOVEJOY 1992).

The timing of male and female activities of different genotypes (nicking) is under a combination of genetic and environmental control, and temperature plays a major role in it. EL-KASSABY and DAVIDSON (1991) observed an increased frequency of heterozygotes in seeds from plants subjected to an overhead spray cooling treatment; this was partly attributed to an increased outcrossing rate, as the treatment shortened the pollination period and crossing was therefore possible among previously asynchronous clones. A warming, on the contrary, would presumably prolong the pollination season, resulting in an opposite effect. Warm and dry conditions are also known to reduce the duration of pollen discharge of individual plants (FRANKEL & GALUN 1977), thus exalting asynchrony.

Temperature changes could also interact with sexual asymmetry in reproductive efficiency of different genotypes. Paternal and maternal reproductive success of monoecious plants (as number of offspring sired through either pollen or ovules) is generally unbalanced in each plant, different among genotypes and variable in time under the effect of the environment (MÜLLER-STARCK & ZIEHE 1984). This sexually asymmetrical fertility will promote outcrossing and heterozygosity if male and female fertilities are negatively correlated within the same plant, as genotypes producing many ovules will release little pollen and will therefore most likely cross with genotypes producing much pollen instead (ZIEHE 1985). SCHOEN and STEWART (1987) pointed out that if male and female fertilities are correlated within years, the opposite mechanism will lead to heterozygote frequencies below Hardy-Weinberg expectations. In response to environmental changes, however, a shift in resource allocation from female to male function in sensitive plants is expected and often observed. This seems to support the hypothesis of an increase in outcrossing and heterozygosity under negative association.

Stand density has been strongly reduced in extreme cases of forest decline and is expected to be affected by global warming. This could result in increased levels of inbreeding, as each plant would be reached by a decreasing amount of pollen from other individuals. The relationship between stand density and mating systems is however controversial and probably depends on specific or local characteristics (HAMRICK 1989; MITTON 1992).

MORGANTE *et al.* (1991), for example, compared two *Picea abies* populations with markedly different stand densities. They did not observe significant differences in multi-locus estimates of outcrossing rates; on the other hand, single locus estimate discrepancies suggested higher population substructuring associated with low density, resulting in an excess of homozygotes.

RESOURCE ALLOCATION

Sexual selection is the differential production or siring of offsprings by individuals of one sex as a result of mate selection (BERTIN 1988); it is due to differential patterns of resource allocation (different pollen production among individuals) as well as to incompatibility mechanisms (sporophytic incompatibility, gametophytic partial incompatibility involved in male gametophytic selection and in early zygotic selection).

The amount of pollen produced widely changes among genotypes (ADAMS 1982). This different investment in reproductive structures reflects in differential paternal success (SCHOEN & STEWART 1986, 1987): under certain assumptions (lack of pollen selection, wide pollen dispersal) the number of seeds sired by a paternal plant is positively correlated to the amount of pollen produced.

In general, resource allocation to reproductive organs is reduced in stressed plants, particularly in perennial species (BARRETT & BUSH 1991), and an increase in pollen production is observed only in the terminal phase preceding plant death. Pollution in particular is reported to inhibit flower formation (SMITH 1981).

From an evolutionary standpoint, this is probably the principal effect of the reduction in plant productivity induced by anthropogenic changes, on which most research has focused: if the reproductive output of a plant is resource-limited, any vegetative disadvantage will result in reproductive damage as well, allowing for selection even in the absence of lethal stresses.

OWENS and BLAKE (1985) reviewed the direct effects of environmental factors on pollen formation and development; contrasting effects on pollen production of drought, plant warming and fertilization as could result from pollution are reported, depending on the species considered and on the timing of treatment. Pollen formation and development are negatively affected in conifers by extreme temperatures, in particular low temperatures (ANDERSSON 1980, ALAMI *et al.* 1988, GIANNINI 1988) which can also result in floral abnormalities (ANDERSSON *et al.* 1969). On the other hand, most temperate forest trees have a winter cold requirement for pollen development, different among populations in accord with local climate. Increased temperatures could therefore have opposite effects in different environments.

The effect of environmental factors on paternal success is under genetic control; there is a strong year x genotype interaction in pollen production (SCHMIDTLING 1983) and the comparative paternal success of different clones therefore changes both over years and among sites (MÜLLER-STARCK 1985b). BROWN *et al.* (1989), however, questioned the significance of these genetically-based differences in reproductive success, usually observed in seed orchards: natural populations are expected to be tuned to the local environment and consequently to be much more homogeneous in their response.

Vegetative vigor of the paternal plant reflects not only on the amount of pollen produced, but also on its size and composition, which in turn could affect pollen performances and fertilization (STEPHENSON *et al.* 1992); YOUNG and STANTON (1990) for example observed that pollen success in fertilization was related to the nutrient conditions in which paternal plants were grown. This view is consistent with the observation that pollen from individuals damaged by air pollution shows decreased viability and germination (BELLANI *et al.* 1988).

MALE GAMETOPHYTIC SELECTION

Even greater consequences of anthropogenic changes on the genetic structure of populations could arise in Angiosperms from male gametophytic selection (MULCAHY 1979).

Pollen grains are already subject to competition for resources and to selection within the anther (MULCAHY *et al.* 1992), but they are at this stage sheltered from any selective pressure from outside.

At germination both pollen germinability and the rate of the pollen tube growth through the style are controlled predominantly by expressed gametophytic genes (ZAMIR 1983); at the same time they are affected by environmental conditions (i.e. by the outer environment buffered by the stigma and by the maternal tissues themselves). In the presence of a sufficient number of pollen grains on the stigmatic surface, the race for fertilization provides the occasion for effective selection, all the more effective as in haploid pollen single alleles are exposed (OTTAVIANO & MULCAHY 1989).

Due to the large overlap between sporophyte- and pollen-expressed genes (MASCARENHAS 1990), this male gametophytic selection is expected to affect the vegetative response of the offspring to the same environmental pressure (OTTAVIANO *et al.* 1988; MULCAHY *et al.* 1988). If the environmental pressure keeps constant, selection will lead to an increased mean fitness, i.e. to a reduction of genetic load and of population genetic diversity; due to the peculiarities of male gametophytic selection, the pace of adaptation is expected to be particularly fast.

Several components of global change are reported to affect plant genetic diversity through male gametophytic selection.

Both high (HERRERO & JOHNSON 1980) and low temperatures (ZAMIR & GADISH 1987) applied to pollen resulted in enhanced resistance in the offspring. Cold treatment was particularly effective when applied during pollen function, much less so during pollen formation (ZAMIR 1983). Overlapping gene expression between pollen and the sporophyte was also demonstrated for copper tolerance: pollen from plants selected for metal resistance performed better in a polluted medium (SEARCY & MULCAHY 1985a) and a more metal tolerant progeny was produced by pollen from copper treated plants (SEARCY & MULCAHY 1985b).

It is still unclear, on the contrary, whether air pollution can result in male gametophytic selection.

Pollen of many species is known to be highly sensitive to air pollutants, in concentrations lower than required for foliar injury (COX 1987). WOLTERS and MARTENS (1987) summarized the effects of several agents both on pollen germinability and on pollen tube growth. They stressed however the great dependence of results not only upon species and pollution agent considered, but also upon experimental conditions. Pollen resulted in particular less sensitive to air pollution in *in vivo* experiments, probably due to the buffering capacity of the stigmatic surface (COX 1984).

It should also be noted that pollen performances (germinability and pollen tube growth) are not always good predictors of genetically-based siring ability (STEPHENSON *et al.* 1988).

The sensitivity to ozone of pollen and of foliar tissues was demonstrated to be correlated among varieties of several crop species (FEDER & SULLIVAN 1969); no such correlation was found however in *Pinus strobus* (BENOIT *et al.* 1982). VENNE *et al.* (1989) observed in poplar clones a genetically-based difference in the effect of *in vivo* O_3 fumigation on reproduction, but it was related only to maternal genotype.

Sterility resulting in different provenances of *Lepidium virginicum* L. from *in vivo* SO_2 fumigations was observed to be inversely related to ambient air SO_2 concentrations experienced in the place of origin (MURDY 1979), suggesting the evolution of tolerance by the reproductive system in natural populations.

COX (1989) obtained contrasting results: of four species analyzed, only *Pinus strobus* showed a significant difference in pollen response to acidity among provenances and this was probably related to adaptation to local edaphic conditions.

VENNE *et al.* (1989), based on the differential effects of in vitro SO_2 fumigation on pollen germination and pollen tube growth in different Scots pine genotypes, predicted large consequences of air pollution for differential male reproductive success.

It is however unclear whether male gametophytic selection does occur in conifers. The number of pollen grains per ovule is normally not greater than five. Moreover, first-pollination primacy was demonstrated experimentally in Douglas-fir (OWENS & SIMPSON 1982); the second pollination was less effective than the first pollination even with a delay of just five minutes (WEBBER & YEH 1987). Under these conditions, random factors are likely to predominate on competition among pollen grains for fertilization.

On the other hand, early zygotic selection is likely to occur in conifers. Most conifers have several archegonia per ovule; if several pollen grains are sucked with the pollination drop, they fertilize different archegonia to produce embryos with different genotypes. Early zygotic selection results in only one of them to survive; the causes of abortion are unknown, but temperature at pollination was suggested as one possible determinant (OWENS & MOLDER 1980); the process is supposed to favour heterozygotes. As already mentioned, EL-KASSABY and DAVIDSON (1991) observed an increased seed heterozygosity when the pollination period was reduced by an overhead cooling treatment. They suggested that this could have determined greater pollen loads per ovule; this would have resulted in enhanced early zygotic selection, since under normal conditions the number of pollen grains per ovule is positively related to the number of fertilization events (CROOK & FRIEDMAN 1992).

Both male gametophytic selection and early zygotic selection could therefore be reduced by pollution, were this to induce low pollen germinability and therefore reduce pollen load.

The interaction between stylar genotype and either pollen or paternal genotype results in negative ("self--incompatibility") or positive assortative mating ("self-advantage"). The intensity of this interaction is reported to be affected by environmental factors. It was suggested, for example, that self-incompatibility could be removed by CO_2 (WOLTERS & MARTENS 1987) and affected by temperature (STEPHENSON *et al.* 1992).

This is consistent with the view of GREGORIUS (1989b) that gametophytic incompatibility is often relative and as such coincides with male gametophytic selection. It could be involved in the preservation of polymorphism: when one allele is favoured both on heterozygous and on the opposite homozygous pistils, increasing selfing results in endangered polymorphism, but the effect is counteracted by high pollination densities. It is therefore apparent the importance of pollen load; as above outlined, this could be variously affected by anthropogenic changes (e.g. through their effect on stand density, on pollen production and on pollen viability).

CONCLUSIONS

Pollution and climate change are likely to affect pollination processes in several ways, altering both gene flow and selection. This will result in contrasting effects on the adaptedness of plant populations to a changed environment and on their adaptability to further changes (GREGORIUS 1989a). Reduced gene flow among populations and enhanced selection would result in a greater mean population fitness (lower genetic load). This is thought to constitute the mechanism of adaptation to air pollution (BRADSHAW & MCNEILLY 1991). On the other hand, this reduction of genetic diversity would reduce the plasticity of the population in a changing environment. As climate change seems to be unpredictable on a local scale, the conservation of diversity will probably be a crucial factor.

The effects on endangered species require a particular attention: increased gene flow could be either beneficial (avoiding genetic drift) or detrimental (by interspecific hybridization and outbreeding depression) depending on specific conditions (ELLSTRAND 1992).

Much research has been done in the last two decades on pollination and its significance for population genetics. As it results from this outline, however, many questions still need to be answered and many mechanisms to be quantified. Moreover, several results obtained on herbs or crop species still have to be tested on conifers and forest trees in general.

REFERENCES

ADAMS, W. T., 1982: Clonal variation in pollen-related characteristics of Douglas-fir. *Can. J. For. Res.* **12**:-403–408.

ADAMS, W. T., 1992: Gene dispersal within forest tree populations. *New Forests* **6**:217–240.

Alami, S., Souvre, A. & Albertini L., 1988: The effects of stresses (cold or/and darkness) on pollen viability of two varieties of grain-*Sorghum*. *In:* Sexual Reproduction in Higher Plants. (eds. Cresti, M., Gori, P. & Pacini, E.). p. 259–264. Springer-Verlag, Berlin.

Andersson, E., 1980: Temperature-conditioned irregularities in pollen mother cells of *Picea abies* (L.) Karst. *Hereditas* **92**:27–35.

Andersson, E., Ekberg, I. & Eriksson, G., 1969: A summary of meiotic investigations in conifers. *Studia Forestalia Suecica* **70**:1–19.

Barrett, S. C. H. & Bush, E. J., 1991: Population processes in plants and the evaluation of resistance to gaseous air pollutants. *In*: Ecological Genetics and Air Pollution. (Taylor, G. E., Pitelka, L. F. & Clegg, M. T., eds.). p. 137–165. Springer-Verlag, New York.

Bellani, L. M., Paoletti, E. & Cenni E., 1988: Air pollution effects on pollen germination of forest species. *In:* Sexual Reproduction in Higher Plants. (Cresti, M., Gori, P. & Pacini, E. eds.). p. 265–270. Springer-Verlag, Berlin.

Benoit, L. F., Skelly, J. M., Moore, L. D. & Dochinger, L. S., 1982: The influence of ozone on *Pinus strobus* L.. *Can J. For. Res.* **13**:184–187.

Bertin, R. I., 1988: Paternity in plants. *In:* Plant Reproductive Ecology. (Doust, J. L. & Doust, L. L., eds.). p. 30–59. Oxford University Press, New York.

Bolin, B., Doos, B. R., Jager, J. & Warrick, R. A. (eds.), 1986: The Greenhouse Effect, Climatic Change, and Ecosystems. J. Wiley and Sons, Chichester, 541 pp.

Bradshaw, A. D. & McNeilly, T., 1991: Evolution in relation to environmental stress. *In:* Ecological Genetics and Air Pollution. (Taylor, G. E., Pitelka, L. F. & Clegg, M. T., eds.). p. 11–31. Springer-Verlag, New York.

Bresser, A. H. M. & Salomons, W. (eds.), 1990: Acidic Precipitation. Vol.5: International Overview and Assessment. Springer-Verlag, Berlin. 444 pp.

Brown, A. H. D., Barrett, S. C. H. & Moran, G. F., 1985: Mating system estimation in forest trees: models, methods and meanings. *In:* Population Genetics in Forestry. (Gregorius, H.-R., ed.). p. 32–49. Springer-Verlag, Berlin.

Brown, A. H. D., Burdon, J. J. & Jarosz, A. M., 1989: Isozyme analysis of plant mating systems. *In:* Isozymes in Plant Biology. (Soltis, D. E. & Soltis, P. S., eds.). p. 73–86. Chapman and Hall, London.

Campbell, D. R., 1987: Interpopulational variation in fruit production: the role of pollination-limitation in the Olimpic Mountains. *Amer. J. Bot.* **74**(2):269–273.

Cox, R. M., 1984: Sensitivity of forest plant reproduction to long range transported air pollutants: *in vitro* and *in vivo* sensitivity of *Oenothera parviflora* pollen to simulated acid rain. *New Phytol.* **97**:63–70.

Cox, R. M., 1987: The response of plant reproductive processes to acidic rain and other air pollutants. *In:* Effects of Atmospheric Pollutants on Forests, Wetlands and Agricoltural Ecosystems. (Hutchinson, T. C. & Meema, K. M., eds.). p. 154–170. Springer-Verlag, Berlin.

Cox, R. M., 1989: Natural variation in sensitivity of reproductive processes in some boreal forest trees to acidity. *In:* Genetic Effects of Air Pollutants in Forest Tree Populations. (Scholz, F., Gregorius, H.-R. & Rudin, D., eds.). p. 77–88. Springer-Verlag, Berlin.

Crook, R. W. & Friedman, W. E. 1992: Effects of pollen tube number and archegonium number on reproduction in Douglas-fir: significance for seed orchard management. *Can. J. For. Res.* **22**:1483–1488.

El-Kassaby, Y. A. & Davidson, R., 1991: Impact of pollination environment manipulation on the apparent outcrossing rate in a Douglas-fir seed orchard. *Heredity* **66**:55–59.

Ellstrand, N. C., 1992: Gene flow by pollen: implications for plant conservation genetics. *Oikos* **63**:77–86.

Feder, W. A. & Sullivan, F., 1969: Differential susceptibility of pollen grains to ozone injury. *Phytopath.* **59**:339 (abstr)

Frankel, R. & Galun, E., 1977: Pollination Mechanisms, Reproduction and Plant Breeding. p. 281. Springer-Verlag, Berlin.

Giannini, R., 1988: Produzione di polline e meccanismi pollinici. *In:* Scritti di Selvicoltura in Onore di A. De Philippis. p. 89–115. Coppini, Firenze.

Goodess, C. M. & Palutikof, J. P., 1992: The development of regional climate scenarios and the ecological impact of greenhouse gas warming. *Adv. in Ecol. Res.* **22**:33–62.

Govindaraju, D. R., 1988: A note on the relationhip between outcrossing rate and gene flow in plants. *Heredity* **61**:401–404.

Gregorius, H.-R., 1989a: The importance of genetic multiplicity for tolerance of atmospheric pollution. In: Genetic Effects of Air Pollutants in Forest Tree Populations. (Scholz, F., Gregorius, H.-R. & Rudin, D., eds.). p. 163–172. Springer-Verlag, Berlin.

Gregorius, H.-R., 1989b: Characterization and Analysis of Mating Systems. Ekopan Verlag, Witzenhausen. 158 pp.

Hamrick, J. L., 1987: Gene flow and distribution of genetic variation in plant populations. *In:* Differentiation Patterns in Higher Plants. (Urbańska, K. M., ed.). p. 53–67. Academic Press, London.

Hamrick, J. L., 1989: Isozymes and the analysis of genetic structure in plant populations. *In:* Isozymes in Plant Biology. (Soltis, D.E. & Soltis, P.S., eds.). p. 87–105. Chapman and Hall, London.

Hamrick, J. L., Mitton, J. B. & Linhart, Y. B., 1981: Levels of genetic variation in trees: influence of life history characteristics. *In:* Isozymes of North-American Forest Trees and Forest Insects. (Conkle, M.T., ed.). Pacific SW For. Range Sta. Tech. Report No.48. p. 35–41.

Herrero, M. P. & Johnson, R. R., 1980: High temperature stress and pollen viability in maize. *Crop Sci.* **20**:796–800.

Intergovernmental Panel on Climate Change (IPCC), 1990: Climate Change – The IPCC Scientific Assessment. (Houghton, J. T., Jenkins, G. J. & Ephrraums, J. J., eds.). p. 365. Cambridge University Press, Cambridge.

LINDBERG, S. E., PAGE, A. L. & NORTON, S. A. (EDS.), 1990: Acidic Precipitation. Vol.3: Sources, Deposition, and Canopy Interactions. 332 pp. Springer-Verlag, Berlin.

MASCARENHAS, J. P., 1990: Gene activity during pollen development. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **41**:317–338.

MITTON, J. B., 1992: The dynamic mating system of conifers. *New Forests* **6**:197–216.

MORGANTE, M., VENDRAMIN, G. G. & ROSSI, P., 1991: Effects of stand density on outcrossing rate in two Norway spruce (*Picea abies*) populations. *Can. J. Bot.* **69**(12):2704-2708.

MULCAHY, D. L., 1979: The rise of the Angiosperms: a genecological factor. *Science* **206**:20–23.

MULCAHY, D. L., MULCAHY, G. B., POPP, R., FONG, N., PALLAIS, N., KALINOWSKY, A. & MARIEN J. N., 1988: Pollen selection for stress tolerance or the advantage of selecting before pollination. *In:* Sexual Reproduction in Higher Plants. (Cresti, M., Gori, P. & Pacini, E. eds.). p. 43–50. Springer-Verlag, Berlin.

MULCAHY, D. L., MULCAHY, G. B. & SEARCY, K. B., 1992: Evolutionary genetics of pollen competition. *In:* Ecology and Evolution of Plant Reproduction. (Wyatt, R., ed.). p. 25–36. Chapman and Hall, New York.

MÜLLER-STARCK, G., 1985a: Genetic differences between "tolerant" and "sensitive" beeches (*Fagus sylvatica* L.) in an environmentally stressed adult forest stand. *Silvae Genetica* **34**:241–247.

MÜLLER-STARCK, G., 1985b: Reproductive success of genotypes of Pinus sylvestris in different environments. *In:* Population Genetics in Forestry. (Gregorius, H.-R., ed.). p. 118–133. Springer-Verlag, Berlin.

MÜLLER-STARCK, G., 1989: Genetic implications of environmental stress in adult forest stands of *Fagus sylvatica* L. *In*: Genetic Effects of Air Pollutants in Forest Tree Populations. (Scholz, F., Gregorius, H.-R. & Rudin, D., eds.). p. 127–142. Springer-Verlag, Berlin.

MÜLLER-STARCK, G. & ZIEHE, M., 1984: Reproductive systems in conifer seed orchards. 3. Female and male fitnesses of individual clones realized in seeds of *Pinus sylvestris* L. *Theor. Appl. Genet.* **69**:173–177.

MURDY, W. H., 1979: Effect of SO_2 on sexual reproduction of *Lipidium virginicum* L. originating from regions with different SO_2 concentrations. *Bot. Gaz.* **140**(3):299–303.

OTTAVIANO, E. & MULCAHY, D. L., 1989: Genetics of Angiosperm pollen. *Advances in Genetics* **26**:1–64.

OTTAVIANO, E., SARI GORLA, M., FROVA, C. & PÉ, E., 1988: Male gametophytic selection in higher plants. *In:* Sexual Reproduction in Higher Plants. (Cresti, M., Gori, P. & Pacini, E. eds.). p. 35–42. Springer-Verlag, Berlin.

OWENS, J. N. & BLAKE, M. D., 1985: Forest Tree Seed Production. Information Report PI-X-53 Petawawa National Forestry Institute. 153 pp.

OWENS, J. N. & MOLDER, M., 1980: Sexual reproduction in western red cedar (*Thuja plicata*). *Can. J. Bot.* **58**:-1376–1393.

OWENS, J. N. & SIMPSON, S. J., 1982: Further observations on the pollination mechanism and seed production of Douglas-fir. *Can. J. For. Res.* **12**:431–434.

PETERS, R. L. & LOVEJOY, T. E., 1992: Global Warming and Biological Diversity. Yale Univ. Press, New Haven. 386 pp.

RITLAND, K., 1984: The effective proportion of self-fertilization with consanguineous matings in inbred populations. *Genetics* **106**:139–152.

SCHMIDTLING, R. C., 1983: Genetic variation in fruitfulness in a loblolly pine (*Pinus taeda* L.) seed orchard. *Silvae Genetica* **32**:76–80.

SCHNEIDER, S. H., 1989: The greenhouse effect: science and policy. *Science* **243**:771–781.

SCHOEN, D. J. & STEWART, S. C., 1986: Variation in male reproductive investment and male reproductive success in white spruce. *Evolution* **40**(6):1109–1120.

SCHOEN, D. J. & STEWART, S. C., 1987: Variation in male fertilities and pairwise mating probabilities in *Picea glauca*. *Genetics* **116**:141–152.

SCHULZE, E.D., LANGE, O. L. & OREN, R. (EDS.), 1989: Forest Decline and Air Pollution. Springer-Verlag, Berlin. 475 pp.

SEARCY, K. B. & MULCAHY, D. L., 1985A: The parallel expression of metal tolerance in pollen and sporophytes of *Silene dioica* (L.) CLAIRV., *S. alba* (MILL.) KRAUSE and *Mimulus guttatus* DC. *Theor. Appl. Gen.* **69**:597–602.

SEARCY, K. B. & MULCAHY, D. L., 1985B: Pollen selection and the gametophytic expression of metal tolerance in *Silene dioica* (*Cariophyllaceae*) and *Mimulus guttatus* (*Scrophulariaceae*). *Amer. J. Bot.* **72**(11):1700–1706.

SHANDS, W. E. & HOFFMAN, J. S. (EDS.), 1987: The Greenhouse Effect, Climate Change, and U.S. Forests. Conserv. Found. Washington, D.C., 304 pp.

SHUGART, H. H., ANTONOVSKY, M. YA., JARVIS, P. G. & SANDFORD, A. P., 1986: CO_2, climatic change and forest ecosystems. *In:* The Greenhouse Effect, Climatic Change, and Ecosystems. (Bolin, B., Doos, B. R., Jager, J. & Warrick, R. A., eds.). p. 475–521. J. Wiley and Sons, Chichester.

SMITH C. C., HAMRICK J. L. & KRAMER C. L., 1990: The advantage of mast years for wind pollination. The *American Naturalist* **136**(2):154–166.

SMITH, W. H., 1981: Air Pollution and Forests. Springer--Verlag. Berlin 379 pp.

SMITH, T. M., SHUGART, H. H., BONAN, G. B. & SMITH, J. B., 1992: Modeling the potential response of vegetation to global climate change. *Adv. in Ecol. Res.* **22**:93–116.

STANTON, M. L., ASHMAN, T.-L. & GALLOWAY, L. F., 1992: Estimating male fitness of plants in natural populations. *In:* Ecology and Evolution of Plant Reproduction. (Wyatt, R., ed.). p. 62-90. Chapman and Hall, New York.

STEPHENSON, A. G., LAU, T.-C., QUESADA, M. & WINSOR, J. A., 1992: Factors that affect pollen performance. *In:* Ecology and Evolution of Plant Reproduction. (Wyatt, R., ed.). p. 119-136. Chapman and Hall, New York.

STEPHENSON, A. G., WINSOR, J. A. & SCHLICHTING, C. D., 1988: Evidence for nonrandom fertilization in the common zucchini, *Cucurbita pepo*. *In:* Sexual Reproduction in Higher Plants. (Cresti, M., Gori, P. & Pacini, E., eds.). p. 333-338. Springer-Verlag, Berlin.

TRESHOW, M. & ANDERSON, F. K., 1989: Plant Stress from Air Pollution. J. Wiley and Sons, Chichester, 283 pp.

VENNE, H., SCHOLZ, F. & VORNWEG, A., 1989: Effects of air pollutants on reproductive processes of poplar (*Populus* spp.) and Scots pine (*Pinus sylvestris* L.). *In:* Genetic Effects of Air Pollutants in Forest Tree Populations. (Scholz, F., Gregorius, H.-R. & Rudin, D., eds.). p. 89-103. Springer-Verlag, Berlin.

WEBBER, J. E. & YEH, F. C. H., 1987: Test of the first-on, first-in pollination hypothesis in coastal Douglas-fir. Can. J. For. Res., **17**:63-68.

WOLTERS, J. H. B. & MARTENS, M. J. M., 1987: Effects of air pollutants on pollen. *Bot. Rev.* **53**:372–414.

WRIGHT, S., 1948: On the roles of directed and random changes in gene frequency in the genetics of populations. *Evolution* **2**:279–295.

WRIGHT, J. W., 1976: Introduction to Forest Genetics. Academic Press, New York, 463 pp.

YOUNG, H. J. & STANTON, M. L., 1990: Influence of environmental quality on pollen competitive ability in wild radish. *Science* **248**:1631–1633.

ZAMIR, D., 1983: Pollen gene expression and selection: applications in plant breeding. *In:* Isozymes in Plant Genetics and Breeding, Part A. (Tanksley, S. D. & Orton, T. J., eds.). p. 313–330. Elsevier Science Publishers, Amsterdam.

ZAMIR, D. & GADISH, I., 1987: Pollen selection for low temperature adaptation in tomato. *Theor. Appl. Gen.* **74**:545–548.

ZIEHE, M., 1985: Polymorphic equilibria under inbreeding effects and selection on components of reproduction. *In:* Population Genetics in Forestry. (Gregorius, H.-R., ed.). p. 92–106.