ECO-GENE, a Model for Simulation Studies on the Spatial and Temporal Dynamics of Genetic Structures of Tree Populations

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Abstract

For a comprehensive evaluation of human influences on the genetic system, the simulation model ECO-GENE was developed. The model combines population genetic and population dynamic processes with forest growth models. The dynamics of genetic structures (single locus and multilocus genotypes up to 200 loci) can be simulated. Spatial and temporal genetic dynamics are included in the model. Overlapping or separated generations can be created and different modes of mating systems can be implemented. The model can be run with empirical and fictitious input data. The simulated genetic structures can be directly analysed with established genetic analysis programmes. An example demonstrates the use of the model for validation of interactions among components of the mating system. Another example demonstrates the applicability of the model in decision-making for seed sampling strategies. The genetic differences between the adult trees and the harvested seeds and the danger of genetic drift regarding to different seed sampling strategies are investigated by use of the genetic distance and the reproductively effective population size.

Key words: Simulation model, population genetics, genetic structure, silviculture, reproductively effective population size, genetic system, sustainability, forest management, Scots pine, oak.

FDC: 165.3; 165.5; 174.7 *Pinus sylvestris.*

Introduction

During the last decades in population genetics of forest tree species considerable progress has been made towards understanding single processes of the genetic system, especially by improving the methods for assessing variation at single loci since the KLAUS STERN Memorial Workshop (MICKSCHE, 1976) and by fostering population genetics experiments and theory (ADAMS et al., 1992; GREGORIUS, 1985). Research on genetic conservation in tree species and on effects of air pollutants on the genetic structure of trees resulted in a rich body of literature, mostly dealing with certain special factors and processes (BARADAT et al., 1995; KIM and HATTEMER, 1994; SCHOLZ et al., 1989). These reductionistic approaches generated a wealth of knowledge which to a large extent explains many aspects of the genetic system. Yet, understanding of singular aspects needs not imply understanding of the whole.

If we really want to understand the complex interactions and feed back mechanisms between the various component processes and if we want to be able to predict the possible reaction of the system to natural or anthropogenic influences, we need an approach which integrates the components of the genetic system. As an example we regard directional selection and gene flow. Considering directional selection alone would suggest endangering genetic variation. Directional selection and gene flow between populations represent a negative feedback system that can stabilise genetic variation. The integrated approach must thus enable us to combine empirical knowledge on component processes with knowledge on the operations joining these components in order to model reality.

Effects of air pollutants on forest tree populations were the challenge for developing such a model. The possible impact on single population genetic processes was investigated intensively. Various authors observed viability selection (BERGMANN and SCHOLZ, 1985; MÜLLER-STARCK, 1985a), fertility selection (VENNE et al., 1989), genetic drift (ZIEGENHAGEN et al., 1995) and mutations (BAKHTIYAROVA et al., 1995). An overview is given by SCHOLZ and BERGMANN (1995).

Also silviculture activities can influence different population genetic processes (SAVOLAINEN and KARKKÄINEN, 1992). Differences in flowering phenology and annual variation in fertility caused genetic differences among harvested seed subpopulations (GREGORIUS et al., 1986). The type of regeneration can affect the genetic diversity of a stand (GÖMÖRY, 1992). CHOI (1993), HOSIUS (1993) and BERGMANN and RUETZ (1991) found genetic differences among the remaining and the harvested part of a population. Also, stand structure and density can influence the mating system especially the frequency of selfs (SMITH et al., 1988; FARRIS and MITTON, 1984).

The predictive capacity of operable models is required especially with respect to the possible effects of global climate change on the genetic structure of tree populations as discussed by HATTEMER and GREGORIUS (1990), LEDIG and KITZMILLER (1992) and NAMKOONG (1994) and the needs for adaptability (SCHOLZ, 1993).

For meeting such needs we developed a model with the following general tasks:

1. Analysing complex population genetic interactions for better *understanding of complexity;*
2. *Testing of hypotheses* on the genetic system of tree populations;
3. Analysing the *effects of human influence* on the genetic system of tree populations;
4. *Deriving of recommendations* for sustainable management of genetic resources.

Description of the Model

The following description gives an overview about general properties, the integrated population genetic processes, parameter sets, input data and output. For more details a demo version of the model and a user's manual will be available in the following internet homepage:

http://www.rrz.uni-hamburg.de/OekoGenetik/welcome.htm

General properties

- The model combines population genetic (dynamic of allele and genotype frequencies) and population dynamic processes (dynamic of the number of individuals in different age classes) with forest growth models. This implies the involvement of stochastic and deterministic factors.

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- The model is structured in modules representing subsystems or component systems. Therefore variable combinations of different processes can be simulated. This is important for sensitivity studies on the effect of specific factors on the behaviour of the integrated system.
- The dynamics of single locus and multilocus genotypes can be simulated (up to 200 loci).
- Spatial and temporal genetic dynamics are included in the model.
- Overlapping or separated generations can be created.
- Different modes of mating systems can be implemented.
- The model can be run with empirical and fictitious input data (genetic, spatial, age structure of stand).
- The output data of the simulations can be directly analysed with established genetic analysis programmes GSED (GILLET, 1994) and BIOSYS (SWOFFORD and SELANDER (1981)).
- The model ECO-GENE is programmed with VISUAL BASIC™ as a user friendly WINDOWS application.

Most of the models existing so far can only regard single locus structures or are restricted to effects of single processes. Moreover, in many cases it is not possible to use empirical data of multilocus genotypes as input for the simulations. However, in a more complex modelling approach, some aspects of the mating system (different modes of pollen and seed dispersal, and spatial distribution of parents) are already regarded (GÖMÖRY, 1995).

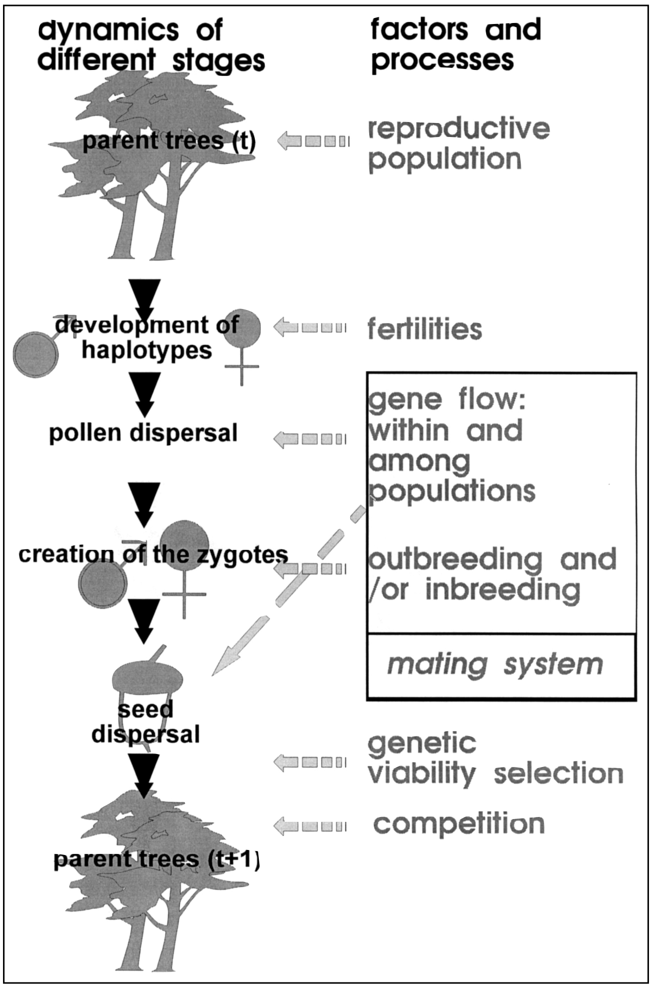


Figure 1. — Overview of the integrated population genetic factors and processes and their corresponding ontogenetic stages.

Integrated population genetic processes and factors

Figure 1 shows the processes and the corresponding ontogenetic stages integrated in the model. The graph presents the genetic system as discrete generations. For simulations with overlapping generations the model works with different stages simultaneously.

Reproductive population

The total number of fructifying trees, their male and/or female fertility and their spatial isolation affect the reproductively effective population size N_r (ASKEW, 1988; KANG and NAMKOONG, 1988; XIE et al., 1994). The effective population size is negatively correlated to the extent of genetic drift as demonstrated by the model application.

Female and male fertilities

The fertilities are defined by the number of pollen and ovules produced by a tree. Their influence on the reproductively effective population size was already mentioned. The normalised relation of the female and male fertility defines the sex function of the individual (ROSS, 1984). For cosexual tree species the sex function is distributed continuously. The sex function is correlated with the frequency of self-fertilization.

Pollen dispersal

Pollen dispersal is an important part of the gene flow system within and among populations. Gene flow conserves genetic variation but can also introduce a migration load. Spatially limited gene flow affects the frequency of self-fertilization and, when applying to seed dispersal as well, creates family structures.

Outbreeding/inbreeding

Many tree species are cosexual and self-compatible. Therefore self-pollination leads to inbreeding. But also mating among relatives influences the degree of inbreeding. Inbreeding influences the genotypic structure of the population (excess of homozygots in comparison to panmixia structure), influences the quantity of genetic drift in small populations and can increase mortality in all stages due to inbreeding depression. In many cases mating systems of tree populations are not merely mixtures of random outcrossing and self-pollination but may rather involve all degrees of random mating, mating among neighbours and self-fertilization.

Seed dispersal

Seeds distribution establishes the diplophase component of the gene flow system. Usually seed dispersal is more limited than pollen dispersal and has a major effect on creating family structures. The 2 components of the gene flow system, pollen and seed dispersal, have large impacts on a population's capacity to maintain genetic polymorphisms (see NAMKOONG and GREGORIUS, 1985).

Genetic viability selection and competition

Usually each adult tree produces a tremendous number of seeds. For example in German beech stands often more than 2,000,000 seeds per ha are produced. In an old beech stand (150 years) only 200 adult trees remain. In case of one fructification period per 200 years, an extreme reduction in population size (99.99%) would occur. In reality there is abundant fructification every 5 years. Thus the reduction in population size is 40 times higher in this case.

One part of this reduction is totally independent from the genotype and occurs by chance or uniform resource limitation. Viability selection and competition cause another part of reduction. This reduction depends on the genotypes of the offspring. Here genetic viability selection causes the so-called hard selection which is forced by environmental factors and the competition causes soft selection which results from intraspecific factors.

Parameters and processes

The population genetic processes are programmed as modules corresponding to subsystems. By combining different modules the user can define the complexity of the genetic system.

The following *table 1* lists the steps of an ECO-GENE simulation and characterises the necessary parameters.

Table 1. — Steps of an ECO-GENE simulation and necessary parameters.

Steps	Necessary data/parameters
1. Reading the input data or generation of input data ↓	• spatial position of the trees • age • genotype
2. Specification of parameter sets ↓	• time scale (years) • growth function • competition • forest management • mating system • wind direction • genotype-environment interaction
3. Calculation of the potential annual increment ↓	
4. Analysing the situation of competition ↓	• overlapping of the crowns • differences in height • differences in vitality
5. Annual increment ↓	Correction of the potential annual increment by: • situation of competition • environmental variation • genetic effects
6. Fructification ↓	• different female and male fertilities • temporal differentiation in fertility • different pollen and seed dispersal • selection against selfs • generating of offspring genotypes
7. Thinning/ harvesting ↓	• height • vitality • overlapping of the crowns
8. Output of simulation results ↓	• map of the stand • genetic structure of different subpopulations • frequency of selfs, reproductively effective population size • spatial genetic structure • distribution of age, height, d.b.h., vitalities, growth • forest growth statistics • GSED input files
9. Continuation with step 1, 2 or 3	

Stochastic Elements in the Model

The model works with 3 different probability density functions:

$$y = f(x) = \begin{cases} 1/(b-a) \; for\, a < x < b \\ 0 \qquad for\, x \leq a \; or\, x \geq b \end{cases}$$

Rectangular distributions

a to *b* is the area of the distribution and *a* and *b* are parameters of the model.

application:

- temporal distribution in fertility (start and duration of pollen release, start and duration of fertility of ovules);
- wind directions.

Normal distribution

$$y = f(x) = f(x|\mu,\sigma) = \frac{1}{\sigma \bullet \sqrt{2\Pi}} \bullet e^{-1/2[(x-\mu)/\sigma]^2}$$

$$(-\infty < x < \infty, \; -\infty < \mu < \infty, \qquad \sigma > 0)$$

σ = standard deviation, μ = expectation => both are parameters of the model.

application:

- environmental variation of annual increment (expectation μ in each year given by growth function and standard deviation σ constant);
- genetical variation of annual increment (expectation μ for each individual normally distributed and constant for the whole life; standard deviation σ constant);
- different female and male fertilities (constant expectation μ = number of pollen grains per unit crown surface and number of ovules per unit crown surface; constant standard deviation σ). According to experimental results one can assume different types of distributions. We decided to assume normal distribution according to data from SCHMIDTLING (1983) and MÜLLER-STARCK (1985b). Compared to asymmetric distributions symmetric distributions would cause overestimation of N_r.

Exponential distribution

$$y = f(w) = b \bullet e^{-b \bullet w}$$

b = parameter of the model;

w = distance, age.

application:

- pollen and seed dispersal;
- generation of age structure in a natural stand.

Deterministic Elements in the Model

One examples for the deterministic elements of the model is provided by the growth functions. These are regression functions of the German yield tables. For example beech of the yield class I:

$$y = f(x) = \begin{cases} -0{,}0013x^2 + 0{,}445x \; for\, x < 342 \\ 0 \qquad for\, x \geq 342 \end{cases}$$

x = age

y = height

According to the age of an individual the model calculates the potential increment by use of the regression function. Then the programe reduces the potential increment regarding to stochastic environmental and stochastic genetic effects and according to the competition conditions.

For more technical details see the manual of the programme in the internet.

Validation

By definition, a model is an abstraction of a defined reality. Thus, a model employs a number of hypotheses on the function of the real system. In many cases these hypotheses are derived from prior experimental investigations. Before a model can be used for deriving recommendations on the management of the real system the accordance between simulation and reality must be tested. As long as there are no critical differences between simulation and reality, the integrated hypotheses are acceptable and the model is regarded as ”valid“. Validation comprises characterisation of system state (spatial genetic structure, age structure, etc.) and mode of operation (mating system, selection, etc.) yielding the response. Usually it is impossible to validate all these variables. Therefore it is essential to identify the most important variables of the model. These are the elements with the greatest effect on the simulation output. For the operational simulation model ECO-GENE, the mating system is an essential component.

The mating system of a tree population shapes the genetic structure of the seeds and creates the genetic basis for the next tree generation. If the modelled mating system of ECO-GENE is in accordance with the real mating system of the respective tree population only slight differences between the simulated and the experimentally analysed genetic structure of single tree progenies should occur. This was tested for 3 single tree progenies of a Scots pine stand and for 5 single tree progenies of an oak stand in the arboretum of our institute.

The following experimental data serve as input for the simulations:

- Genotypes at 5 isozyme gene loci of almost all adult trees in the pine stand (162 Scots pine = 90%) and genotypes at 8 isozyme gene loci of all adult oaks (16 oaks = 100%);
- exact spatial position of the trees in the stand (see *figure 2* for the pine stand).

Another important system variable is defined by characteristics of the pollen dispersal (see *figure 3*). For the present simulations, the distribution function was chosen in accordance with empirical results of STERN (1972) and MÜLLER-STARCK (1976 and 1977).

The empirically investigated allele frequencies at 5 gene loci of 3 single tree progenies (65, 89, 130 seeds analysed) in a pine stand (see *Figure 2*) and the empirically investigated allele frequencies at 8 gene loci of 5 single tree progenies (112 to 120 seeds analysed) in an oak stand were compared to the simulated allele frequencies in these progenies. The simulations were repeated 50 times with the same parameter set for each single tree progeny.

During these simulations the “surviving probability of selfs” and the parameter “b” of the pollen dispersal function (see *Figure 3*) was varied across a wide range. Gene pool distance between simulated and empirical allele frequencies was at its smallest for more widely distributed pollen (b = 0.01 see *Figure 3*). The gene pool distances decrease with decreasing surviving probability of the selfs. For *b* = 0.01 and for a surviving probability of 20%, there was the best agreement between simulation and reality.

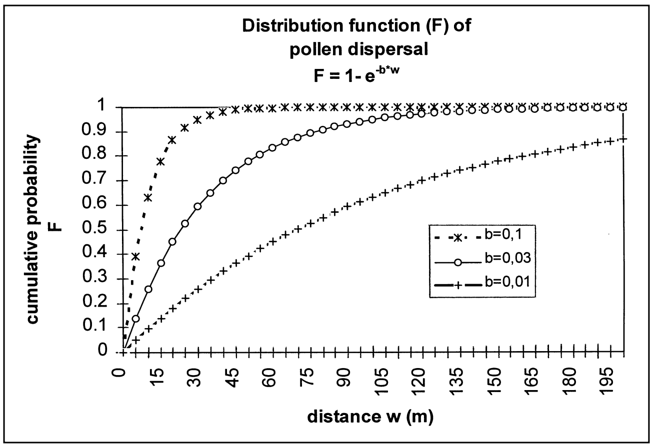


Figure 3. — Distribution function of pollen dispersal. The variable b (see formula in the graph) is an important parameter for the simulations. It defines the distribution distance according to an exponential distribution function.

For these optimised parameter sets, *figure 4* shows the similarity between simulated and empirical allele frequencies

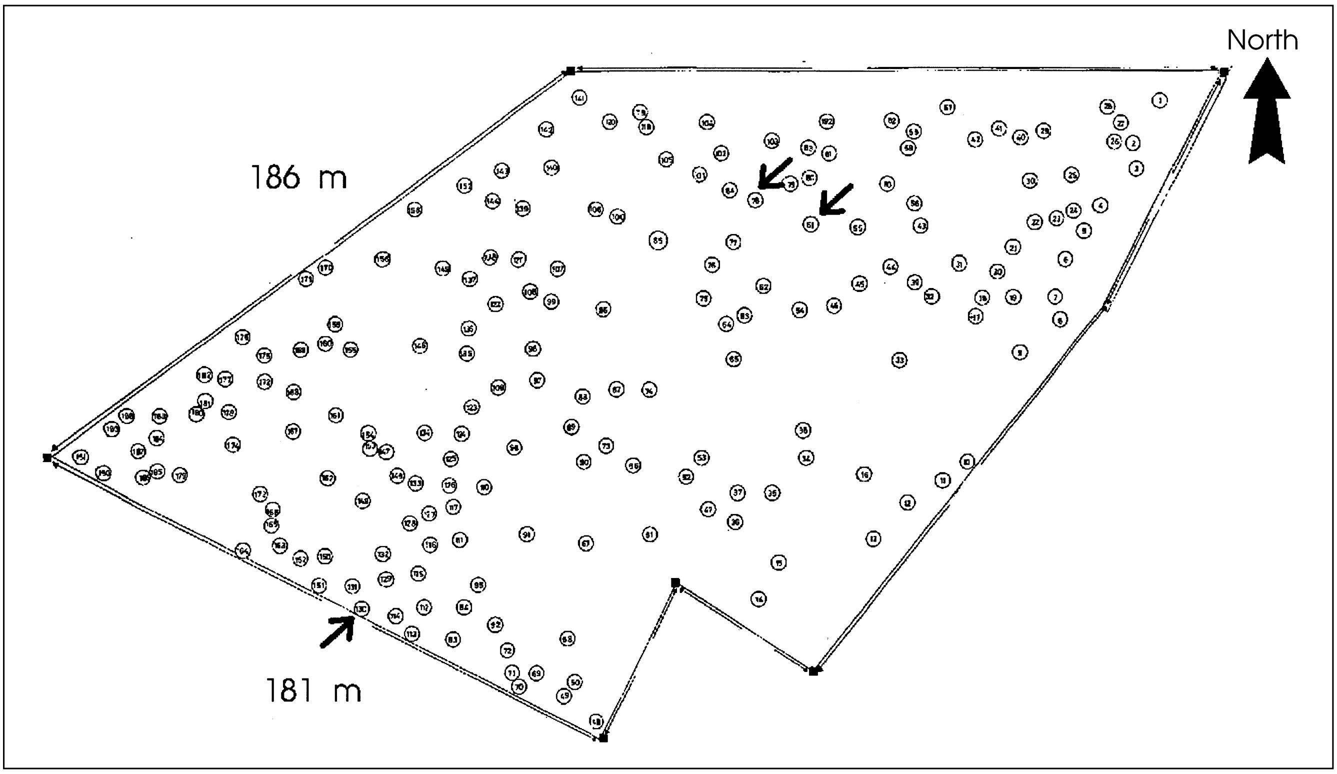


Figure 2. — Spatial position of all trees in the Scots pine stand (Quickborn). Each single circle represents a tree. Three trees are marked by arrows. From these trees the empirical genetic structure of the progenies was compared to the simulated genetic structure.

in the 3 pine progenies for 1 simulation run. The x-value of each point represents the empirical allele frequency and the y-value represents the corresponding simulated allele frequency. In case of total similarity all points are located on a line. The average gene pool distance D_g (GREGORIUS, 1974) between the simulated and experimental allele frequencies was 5% ± 3.5% for the progenies of the 5 oaks and 6% ± 4% for the progenies of the 3 pines.

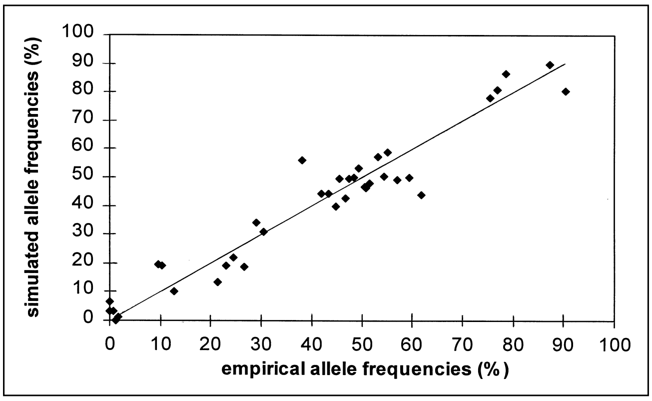


Figure 4. — Comparison of empirical and simulated allele frequencies in the seeds of 3 trees of a *Pinus silvestris* stand.

Conclusion for the model validation

The good agreement found between the empirical observed and the pertinent simulations for the parameter set of the mating system indicate that the model assumptions on the components of the mating system and their interrelations are realistic. This agreement is important for the following application of the model.

Example for the Application of the Model

Today more than 50% of all stands in Germany are artificially regenerated. In all these cases, the harvested seeds or seedlings, respectively, form the genetic basis for the next generation. The sampling strategy, the stand structure and the mating system of the tree population determine the genetic structure of the harvested material and, thus, define the genetic similarity of harvested seeds and adult trees. With decreasing number of harvested seed trees the risk of genetic drift increases. For quantification of this risk, the reproductively effective population size N_r (CROW and KIMURA, 1970; GREGORIUS, 1991; KANG and NAMKOONG, 1988; XIE et al., 1994) is an important parameter. The measure N_r does not only take into account the absolute number of reproducing (sampled) trees but also the relative gametic input (fitness):

$$1 \le N_r = \frac{1}{\sum w_i^2} \le N_{abs}$$

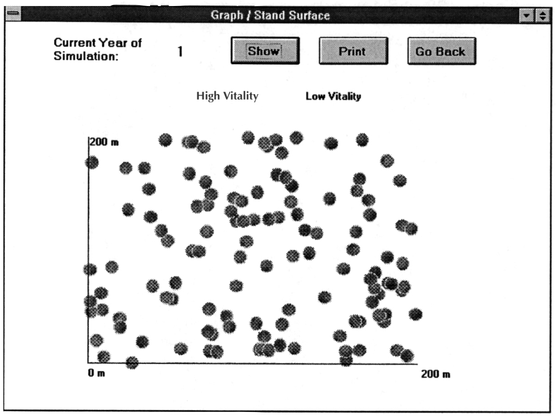
w_i = proportion of gametes of individual i among all successful gametes;

N_{abs} = number of all fructifying individuals;

w_i depends on the genotype, age and environmental conditions (SCHMIDTLING, 1983). It is very difficult to estimate the important parameter N_r by experimental investigations. So far, only in seed orchards the measure of fitness w_i could experimentally be estimated (MÜLLER-STARCK, 1985b; XIE et al., 1994). Within the ECO-GENE simulations, however, data required for calculation of the reproductively effective population size N_r (number of successful gametes) are computed.

As an example we simulated the effect of different stand structure, different mating system and different number of sampled seed trees on the reproductively effective population size. Two fictitious stands and 5 different scenarios were chosen. The 2 stands have the same genetic structure but different spatial distributions of their 120 trees (see *Figure 5*). The differences among the 5 scenarios are listed in *table 2*.

Input data set = “Random”


Current Year of Simulation: 1

Input data set = “Cluster”

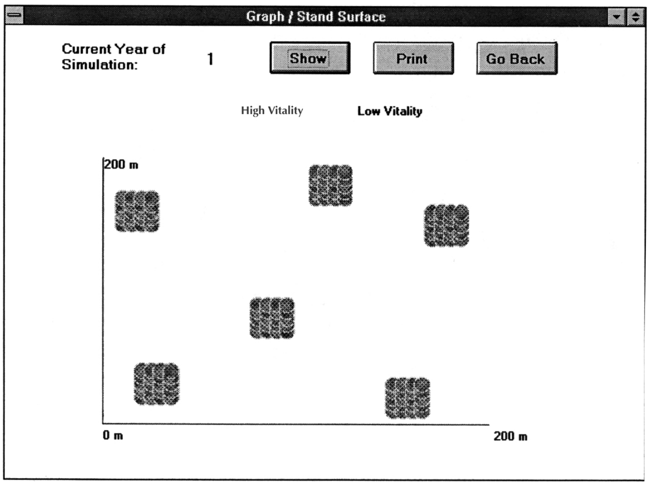

Current Year of Simulation: 1

Figure 5. — Different spatial structure of the 2 fictitious stands with random and clustered distribution of the trees.

Results of the simulations

For each of the 5 scenarios the simulations were done with both fictitious stands. All simulations were repeated 20 times (200 simulations in total). *Figure 6* shows the reproductively effective population sizes N_r of the 5 scenarios and the variation between the repetitions.

The results can be summarised as follows:

- In the 5 scenarios only 10% to 33% of the theoretical maximum of N_r =120 was realised.
- In all scenarios the reproductively effective population size N_r of the stand with the clustered structure (Cluster) is higher than in the stand with even structure (Random).
- In comparison to equal fertilities (sim1) the incorporation of variation in male and female fertilities (sim2) reduces N_r by 6.8% (Cluster) and 3% (Random). In this case the male and female fertilities varied according to a normal distribution (standard deviation = 50% of the mean).

Table 2. — Characters of 5 ECO-GENE scenarios, varying in number of sampled trees, wind directions, fertility and flowering phenology of the trees (the underlined characters are varied).

Name	Characters
sim1	• 20 seed trees • random wind directions • no variation in fertilities • no variation in flowering phenology
sim2	• 20 seed trees • random wind directions • variation in fertilities • no variation in flowering phenology
sim3	• 20 seed trees • random wind directions • variation in fertilities • variation in flowering phenology
sim4	• 20 seed trees • only one wind directions • variation in fertilities • variation in flowering phenology
sim5	• 10 seed trees • only one wind direction • variation in fertilities • variation in flowering phenology

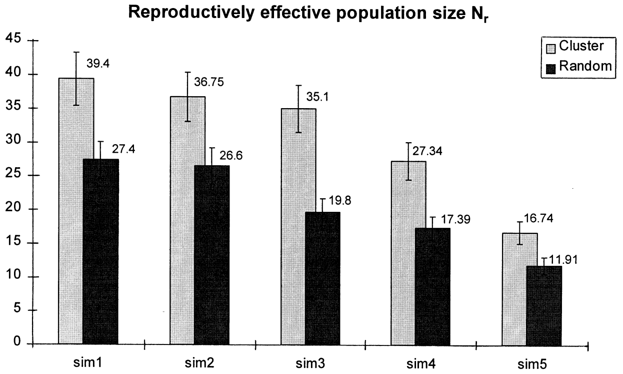


Figure 6. — Reproductively effective population size N_r in 5 scenarios with the 2 different stand structures "Random" and "Cluster".

- The introduced variation in flowering phenology (sim3) additionally reduced the effective population size N_r by 4.5% (Cluster) and 26% (Random). The start of pollen release and ovule maturation varied randomly among the trees from 1 to 14 days and the duration of pollen shedding and ovule fertility varied randomly from 3 to 7 days.
- In case of only one wind direction (sim4), N_r decreases drastically. For the randomly distributed stand an additional reduction of 22% and for the clustered stand a reduction of 27% occurs.
- The reduction of the number of seed trees from 20 to 10 (sim5) also reduces the reproductively effective population size (39% for the clustered stand and 32% for the even stand).

After a simulation ECO-GENE calculates the gene pool distance D_g between the genetic structure of the set of all adult trees and the harvested seeds. *Figure 7* shows the observed negative correlation between the reproductively effective population size N_r and D_g. As expected, the gene pool distance increases with decreasing N_r. This demonstrates the increasing risk of genetic drift.

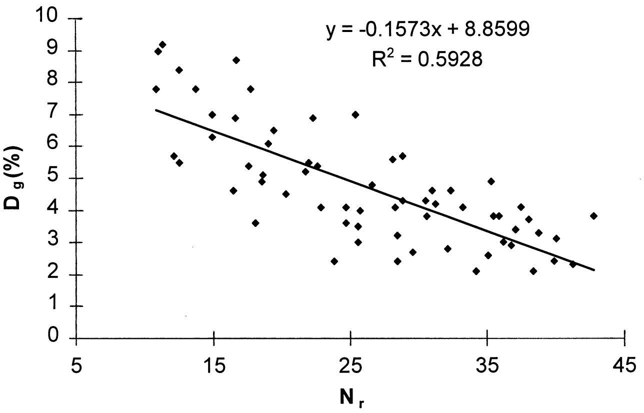


Figure 7. — Correlation between reproductively effective population size N_r and gene pool Distance D_g (between the genetic structure of the set of all adult trees and the genetic structure of the simulated seeds).

Conclusions of the simulations

The simulations clearly demonstrate the effect of the stand structure, variation of fertilities and flowering phenology, the number of seed trees and limitation of wind directions on the reproductively effective population size. The general results show a good agreement to simulations of XIE et al. (1994). If the adult trees are arranged in a clustered structure, N_r is higher. This result is important for the establishment of mixed stands. It suggests that rare tree species should be introduced as blocks to increase the reproductively effective population size. In stands with only one main wind direction during the pollination the number of chosen seed trees should be increased. According to *figure 7* the gene pool distance D_g between the genetic structure of harvested seeds and the set of all adult trees seems to be very small when N_r is higher than 50. If the levels of variation in fertility and flowering phenology does not exceed the simulated values and if the stand has at least the simulated density, 30 randomly distributed seed trees seem to be enough to get N_r higher than 50. Gene flow between populations, is not yet included in these simulations. If there is gene flow between populations the risk of genetic drift decreases additionally but the genetic distance between the adult trees and the seeds can increase. We need more simulations with other parameter sets to estimate the risk of genetic drift for very rare alleles.

Application of ECO-GENE

This paper presents the general structure and one example for application. ECO-GENE, however is a generic model which allows simulation of many ecological genetic aspects in different fields such as evolutionary biology, assessing man made impacts on the genetic system including silviculture, preservation of gene resources, breeding, risk assessment of genetically modified organisms (GMO's) etc..

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Investigations on the Correlation Pattern in Even-Aged Stands of Larch

IV. Relationships between Neighbourhood Correlations and Means of Different Entries1)

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Summary

For a dynamic description of spatial neighbourhood correlation patterns of stands of larch and an analysis of temporal changes and time trends of such patterns during stand development extensive data sets from a field trial (trial no. 1) with 27 entries of *Larix decidua* Mill. (*Larix europaea* DC.), *Larix kaempferi* (Lamb.) Carr. (*Larix leptolepis* (Sieb. et Zucc.) Sieb. ex Gord.), and *Larix* x *eurolepis* Henry have been used. Single tree measurements of this trial were available for 7 stages of stand development (ages: 11, 13, 18, 19, 42, 49 and 50 years).

Additionally, for a static description of spatial neighbourhood correlation patterns of stands of larch extensive data sets from 9 field trials (trials nos. 2 to 10) with a varying number (8 to 23) of entries have been used which provide an analysis of the correlations between neighbours at only one point in time. These trials are slightly different in their ages (7 to 11 years).

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1) Dedicated to Prof. Dr. W. Langner on his 90th birthday.

Note: This paper is dedicated to Prof. Dr. W. Langner although he himself serves as a co-author. This publication is a result of common research between the senior author and Prof. Dr. W. Langner who prepared the extensive data sets from some of his trials with larch as an empirical basis for these correlation studies.

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