Equilibrium and non-equilibrium concepts in forest genetic modelling: population- and individually-based approaches

K. Kramer* and D. C. van der Werf

Alterra. Wageningen University and Research Centre. P.O. Box 47. 6700 AA Wageningen. The Netherlands

Abstract

The environment is changing and so are forests, in their functioning, in species composition, and in the species' genetic composition. Many empirical and process-based models exist to support forest management. However, most of these models do not consider the impact of environmental changes and forest management on genetic diversity nor on the rate of adaptation of critical plant processes. How genetic diversity and rates of adaptation depend on management actions is a crucial next step in model development.

Modelling approaches of genetic and demographic processes that operate in forests are categorized here in two classes. One approach assumes equilibrium conditions in phenotype and tree density, and analyses the characteristics of the demography and the genetic system of the species that determine the rate at which that equilibrium is attained. The other modelling approach does not assume equilibrium conditions and describes both the ecological —and genetic processes to analyse how environmental changes result in selection pressures on functional traits of trees and the consequences of that selection for tree— and ecosystem functioning. The equilibrium approach allows analysing the recovery rate after a perturbation in stable environments, *i.e.* towards the same pre-perturbation stable state. The non-equilibrium approach allows, in addition to the equilibrium approach, analysing consequences of ongoing environmental changes and forest management, *i.e.* non-stationary environments, on tree functioning, species composition, and genetic composition of the trees in forest ecosystem.

In this paper we describe these two modelling approaches and discuss advantages and disadvantages of them and current knowledge gaps.

Key words: forest genetic models; population-genetic; individually-based genetic models; equilibrium and non-equilibrium paradigms; environmental change.

Resumen

Concepto de equilibrio y no-equilibrio en los modelos genéticos forestales: los enfoques de la población y de arbol individual

El ambiente está cambiando así como los bosques, en su funcionamiento, en la composición de especies, y en la composición genética de la especie. Existen muchos modelos empíricos y basados en procesos para apoyar al manejo forestal. Sin embargo, la mayoría de estos modelos no tienen en cuenta el impacto de los cambios ambientales y la gestión forestal sobre la diversidad genética ni sobre la tasa de adaptación a los procesos críticos de la planta. Cómo la diversidad genética y la tasa de adaptación dependerá de las acciones de gestión es un paso futuro decisivo en el desarrollo de los modelos.

Los enfoques de modelización de los procesos genéticos y demográficos que operan en los bosques se clasifican en dos clases. Un enfoque asume las condiciones de equilibrio en el fenotipo y la densidad de árboles, y analiza las características de la demografía y el sistema genético de las especies que determinan la velocidad a la que se alcanza ese equilibrio. El otro enfoque de modelización no asume las condiciones de equilibrio y describe tanto los procesos ecológicos y genéticos para analizar cómo los cambios ambientales influyen en la presión de selección en características funcionales de los árboles y en las consecuencias de esta selección para el árbol y el funcionamiento de los ecosistemas. El enfoque de equilibrio permite analizar la tasa de recuperación después de una perturbación en un entorno estable, es decir, hacia el mismo estado que antes de la perturbación estable. El enfoque de no-equilibrio permite, además del enfoque de equilibrio, el análisis de las consecuencias de los actuales cambios del medio ambiente y la

* Corresponding author: koen.kramer@wur.nl

ordenación forestal, es decir, ambientes no estacionarios, en el funcionamiento de árboles, la composición de especies, y la composición genética de los árboles en el ecosistema forestal.

En este trabajo se describen estos dos métodos de modelización y se discuten las ventajas y desventajas de ellos y las lagunas actuales de conocimientos.

Palabras clave: modelos genéticos forestales; población; modelos genéticos de árbol individual; paradigmas de equilibrio y no-equilibrio; cambio climático.

Introduction

Changes in the environment and in society put forest managers to new challenges. In the environment, not only the climate is changing but also inputs of nitrogen (Solberg *et al.,* 2009) and air pollution to a forest (Woo, 2009; Geburek, 2000). In society, the change is that not only timber is demanded but also a wide array of non-wood goods and services. Non-wood goods and services range from mushroom and berry picking (Huttunen, 2009) to carbon sequestration (Matala *et al.,* 2009) and improving water holding capacity (Bouten, 1995); places where biodiversity is maintained (Mitchell *et al.,* 2009); and areas that are accessible for recreation and leisure by the public (Champ *et al.,* 2009). Forests are changing as a consequence of these changes in the environment and societal demands, in species composition and in functioning, such as growth and productivity; capture and recycling of resources; and in genetic composition. Ultimately, the ability of forests to adapt to changing conditions depends on the genetic diversity present in the forest (Geburek *et al.,* 2005). Although much practical knowledge and scientific insight on adaptive management are obtained over the last decades in the disciplines of silviculture, eco(physio)logy, and genetics, this knowledge is still largely unconnected. In particular, few models are operational to integrate ecological, genetic and silvicultural knowledge in a manner that future assessments can be made of the adaptive potential of forest in the face of climate change and land use change and the role of forest management to maintain genetic diversity and guide adaptation in a desired direction (Kramer *et al.,* 2008).

Two paradigmatic alternatives exist for the modeling of demographic and genetic processes: equilibrium and non-equilibrium approaches (Hengeveld *et al.*, 1999; Walter *et al.*, 2000). Population-genetic modeling abides to the equilibrium paradigm and individually-based genetic modeling to the non-equilibrium paradigm. With population-genetic modeling we mean in the following that such a model contains parameters that defined at the population level, *e.g.* the carrying capacity of an area. With individually-based genetic modeling we mean that the model does not include population-level parameters but that all parameters are defined at the individual level (DeAngelis *et al.,* 1992). In the following we first describe concepts of equilibrium and non-equilibrium modeling paradigms are outlined below. Secondly, we describe the consequences of these approaches for modeling demographic and genetic processes. Finally, we discuss advantages, disadvantages, and knowledge gaps for both approaches. Thus, in analogy of the paper by Gracia *et al.* (2010) in this Special Issue, are the objectives of this paper: (*I*) to identify the conceptual approaches and structural differences of forest genetic models, and (*II*) to discuss advantages and disadvantages of both approaches, and (*III*) to identify key knowledge gaps associated by each of the modelling approaches. Modelling details of either the equilibrium approach or the non-equilibrium approach are obtained from the models METAPOP (Corre *et al.*, 1997; Le Corre *et al.*, 2003) (Austerlitz *et al.*, 2000) and ForGEM (Kramer *et al.*, 2008; Kramer *et al.*, 2010), respectively. The emphasis is on the non-equilibrium approach as that is a new development in process-based modelling of forest dynamics (Kramer *et al.*, 2008). It is not attempted to present an overview of existing forest genetic models and to classify them in one of these approaches.

Equilibrium and non-equilibrium modeling approaches

The equilibrium paradigm (Hengeveld *et al.*, 1999; Walter *et al.*, 2000), considers organisms living in a stationary and environmentally homogeneous local population. Spatial differences in the environment are accounted for by a meta-population structure which is composed of a number of such locally homogeneous populations. It is assumed that the climate is stationary relative to the rate of recovery. Hence following perturbations, demographic and genetic adjustments either

lead to the return to the previous equilibrium state in population size and distribution of phenotypic values, or to new equilibrium values if the environment attains another stationary state. The population size is thereby assumed to be controlled by density dependent factors leading to a numerical equilibrium. The population is assumed to be able to «foresee» either the old pre-disturbance or a new future optimum phenotype towards it must evolve, which leads to an equilibrium of phenotypic values in the population.

The nonequilibrium- or autecological paradigm approaches (Hengeveld *et al.*, 1999; Walter *et al.*, 2000) on the other hand, recognizes that nature is variable in space and time at all scales and that stochastically occurring disturbances drive that variability. This approach looks how individual organisms cope with a non-stationary environment that is unknown to them from one moment to the next, and from one site to the other. Hence, the adaptive response of the species is ever lagging behind to changes in both the climate and biotic factors. A tree species constantly «tracks» environmental conditions to which it is adapted and adapts. The demographic response of the species is milarly as the adaptive response the consequence of the environment which the organism can perceive. Thus, neither an equilibrium in population size nor in equilibrium phenotypes is assumed in this approach.

See (Kramer, 2007; Kramer *et al.*, 2005) for a more detailed discussion of equilibrium and non-equilibrium concepts in environmental modelling.

Genetic and demographic processes operational in forest genetic models

Forest genetic models include a genetic map representing the location of loci and genetic markers at the chromosomes of the species. This can either be based on bi-parental inheritance, to simulate inheritance of genetic information from the cell-nucleus, or based on uni-parental inheritance to simulate inheritance of genetic information from chloroplasts and mitochondria in the cytoplast. Such a representation of the genetic map can thereby represent observed nuclear- and cytoplasmic genetic markers obtained from sequencing of the genome of the species of interest. This allows simulating the dynamics of these genetic markers observed in a forest. See the Appendix A for an overview of genetic statistics that can be derived as model output based on the simulated genetic markers.

To connect genetic information to an observed or theoretical phenotype, one or more loci and one or more alleles are considered in these models. For quantitative genetic traits, multiple loci with multiple alleles are considered to be able to represent a broad range of values of the phenotype. To initialize a genetic model, the number of loci and alleles per locus need to be set, as well as initial allele frequencies and allelic effects for the traits under selection. Usually neutral traits are considered, which are not under selection, as detailed genetic information is often missing. An impact analysis of environmental change of forest management then provides an upper estimate of the genetic diversity maintained in the forest. However, no assessment of a rate of adaptation can be made. If adaptive traits are considered, an allelic effect needs to be assigned to each allele and for all loci considered, as well as possible interactions between alleles and between loci (Falconer *et al.,* 1996). In the most complicated genetic system also loci are considered that affect the phenotypic value of multiple traits.

The genetic processes included in mechanistic forest genetic models are immigration, emigration, selection, and mutation (Hartl *et al.,* 1997). *Mutation* is only relevant when simulating over a very large number of generations or for very large populations. As we focus on forest genetic models as tool for forest management, mutation is not considered here.

Immigration and emigration refers for forest stands to gene flow by dispersal of pollen and seeds toward and from the stand. Forest genetic models describe gene flow in considerable detail either between individual trees, between and among patches, or over the landscape, depending on the spatial scale of the model. The use of genetic markers made it possible to do a parental analysis both to determine which tree fathered a seed collected from a mother tree, to assess pollen dispersal, and to determine from which mother tree the seed originated from which a seedling established, to assess seed dispersal. Using the distance between father and mother tree and between mother tree and seedling, elaborate statistical dispersal kernels are calibrated for both short distance dispersal and long distance dispersal. For the dispersal of seeds, dispersal kernels are developed dispersal by wind, birds, mammals and other dispersal strategies.

A Weibull distribution is such a dispersal kernel to simulate the decline of the amount pollen with distance. This is a generic and flexible distribution to describe this process (Kotz *et al.*, 2000):

$$D = b \cdot c \cdot \left(b \cdot x\right)^{c-1} \cdot e^{-\left(b \cdot x\right)^c} \qquad [1]$$

where: *b:* slope parameter, *c:* shape parameter, *x:* distance to the father tree.

For individually-based genetic models, the probability that gametes of a mother tree, M_i, and father tree, F_j, meet is simulated by the fraction pollen of F_j that arrives at the position of M_i, relative to the contribution to all other known and unknown potential father trees. The amount of pollen of any father tree arriving at the position of a mother tree depends on: 1) the amount of pollen produced by the father tree; 2) the distance between the mother and father trees; 3) the overlap in flowering phenology between the father and mother trees; and the wind direction relative to the orientation between the father and the mother tree. The overlap in flowering phenology between father and mother trees determines which portion of the pollen emitted by the father tree can actually pollinate a given flowering mother tree. Thus, the fraction of F_j pollen arriving at position M_i can be described as follows:

$$P\left(M_i x F_j\right) = $$

$$= \frac{Y_0\left(F_j\right) \cdot D\left(M_i, F_j\right) \cdot t\left(M_i, F_j\right)}{\sum_k \left(Y_0\left(F_k\right) \cdot D\left(M_i, F_k\right) \cdot t\left(M_i, F_k\right)\right) + E_{M_i}} \qquad [2]$$

with: $Y_0(F_j)$: amount of pollen of father tree F_j at distance $= 0$; and $t(M_i, F_j)$: overlap in flowering phenology; and E_{Mi}: the amount of external pollen arriving at mother tree M_i. Figure 1 presents and example of the
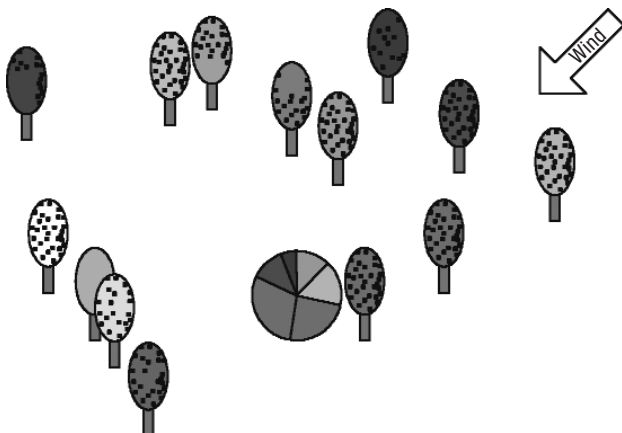
Figure 1. Example of the fraction of pollen arriving at a target mother tree (in red) from different father trees (the other trees). This fraction depends on the distance to father trees, flowering overlap between father trees and the target mother tree, and the wind direction. In this example self-pollination is possible.
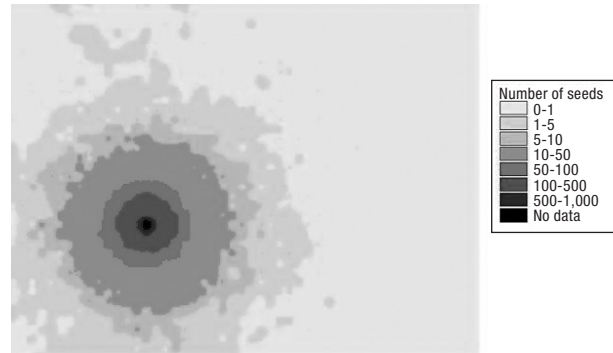
Figure 2. Example of dispersal of seeds (# m^{-2}) around a mother tree.

fraction of pollen arriving at a target mother tree from different father trees.

For seed dispersal also a Weibull distribution can be fitted or a simpler single parameter exponential function. Figure 2 presents and example of the number of seeds around an individual mother tree.

For population-genetic modeling of gene flow by dispersal of pollen and seeds the modeling approach is the same, however, gene flow is in that case not determined for individual trees but for subpopulations of trees that are spatially distributed over a landscape.

Selection in forest genetic models refers to the loss of genetic diversity due to differential selection pressure at one or more stages of the tree's life cycle. This is done either as a result of differences in the genetic composition of trees or population of trees for particular traits, or directly related to differences in the tree's fitness depending on the whole tree's phenotypic value. In the former approach the following the stages of the life cycle considered to be under selection: male and female fertility in production of gametes; fecundity; and viability of seedlings and trees resulting in differential mortality. In the latter approach an optimal phenotypic value is assumed for particular environmental conditions.

Equilibrium-based, population-genetic modelling

Equilibrium-based, population-genetic models assume an optimal phenotypic value in a stationary environment to simulate selection. This concept can be formalized as (Eqn. [3], Fig. 3):

$$F(Z) = \exp\left(-\frac{\left(Z - Z_{opt}\right)^2}{2\omega^2}\right) \qquad [3]$$
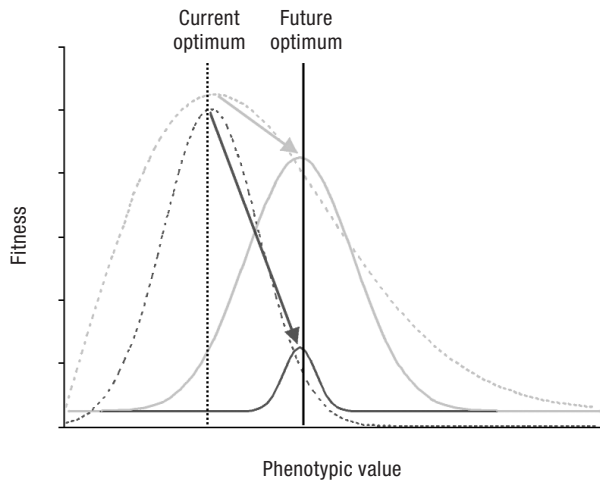
Figure 3. Example of fitness functions (Eqn. [3]) for two phenotypes (indicted in red and blue) and the change thereof if the environment changes in the future. Both the optimum and the shape of these fitness functions need to be known to run a population-genetic model.

with: Z_{opt} the optimal phenotype in a population in equilibrium with prevailing environmental conditions, and $1/\omega^2$ the intensity of selection determining the rate at which the optimal value is attained. Usually only one abstract phenotypic trait is considered so that the individual's fitness depends on that compound trait. In case multiple abstract traits are considered, a multiplicative model can be used to attain the overall fitness of individual i ($F_i(Z_1,Z_2) = F_i(Z_1)*F_i(Z_2)$) for phenotypic value Z_1 for trait 1, and Z_2 for trait 2).

A new optimal phenotypic value for one or more traits is considered if the environment changes (Fig. 3). The environment is subsequently assumed to be stationary for a sufficiently long period to equilibrate the distribution of phenotypic values in the population around the new optimal phenotypic value. In the case of future climate change such information is not available, but can be estimated from clines along either altitudinal or latitudinal gradients that mimic expected climatic gradients.

These population-genetic models also assume equilibrium to simulate demographic dynamics by setting a maximal tree density or carrying capacity for an area (Eqn. [4]):

$$N_{t+1} = N_t + r \cdot N \cdot \left(\frac{K - N_t}{K} \right) \qquad [4]$$

with: N_t: the actual number of individuals in a (sub-)population at time t, r the per capita growth rate, and K the carrying capacity.

The carrying capacity is an equilibrium value as the population can only increase if the population size is less than the carrying capacity, whereas if the population size exceeds the carrying capacity, population size declines. This equilibrium is also maintained in METAPOP by adjusting female fecundity such that it is maximal at $N = 1$ and zero at $N \geq K$. The per capita growth rate determines the maximal rate at which the population returns to the equilibrium value in case of deviation between actual and equilibrium population size. In a multi-species simulation, each species is assigned a carrying capacity and a per capita growth rate.

In case of environmental change, is the carrying capacity enhanced or decreased depending on the expected impact of the environmental change on the species. For in stance, in case of climate change the carrying capacity can be considered to depend on the temperature sum that determines the upper and lower limit of the geographic distribution of a species. The carrying capacity then attains a zero value at the temperature sum characterizing the upper and lower limit, and attains an observed maximum in the centre of the species' distribution.

Non-equilibrium, individually-based genetic modelling

Individually-based models do not include equilibrium assumptions as attractor points neither for the optimal fitness value of a phenotype nor for the maximum tree density a population that a species can attain in a particular environment. Although also in individually-based models a stationary distribution of both phenotypic values and tree density can be attained in a constant environment, neither a target value is required as input to the models (Z_{opt}, and K in Eqns [1] and [2]), nor a parameter that determines the rate at which the target state is reached if the actual state deviates from the target state (ω and r in Eqns. [3] and [4], respectively).

In case of ForGEM, is selection pressure on an individual tree the consequence of the effects of meteorological drivers on ecophysiological processes like photosynthesis, respiration and the uptake of resources to determine net primary production. Carbon uptake by an individual tree from the atmosphere is limited by intercepted light by the leaves in canopy, and of water and nutrients (N, P) uptake by the roots from the soil. The probability that a sapling or adult tree dies depends on

the five-year averaged stem diameter increment, with increasing probability of mortality with decreasing growth. In addition, can seedlings die because of adverse conditions such as late spring frost. Male and female fecundity is determined by the number of flowers per metre square of canopy surface and the number of seeds per flower. Thus, male and female fecundity are related to the tree's carbon balance as the canopy growth depends on the uptake of resources. Male and female reproductive success depends on gene flow by dispersal of pollen and seeds as is described in the general section on mechanistic forest genetic models. The dynamics of numbers of a tree species in a patch is in ForGEM solely based on the number of seeds arriving at a patch and competition for resources by seedlings, saplings and adult trees. Although there is a maximum tree density as a consequence of maximal canopy diameter that a tree can attain, this upper limit is not a target function towards the population must develop because of the model equations prescribe that. See Figure 4 for a schematic overview of the life —and annual cycle that is described in the model ForGEM. Appendix B presents the principle state and empirical equations used in ForGEM.

The link between genotype and phenotype in ForGEM is that a multi-locus and multi-allelic genetic system can be assigned to any model parameter of the ecophysiological processes related to uptake and distribution of resources over plant components. Allelic effects are
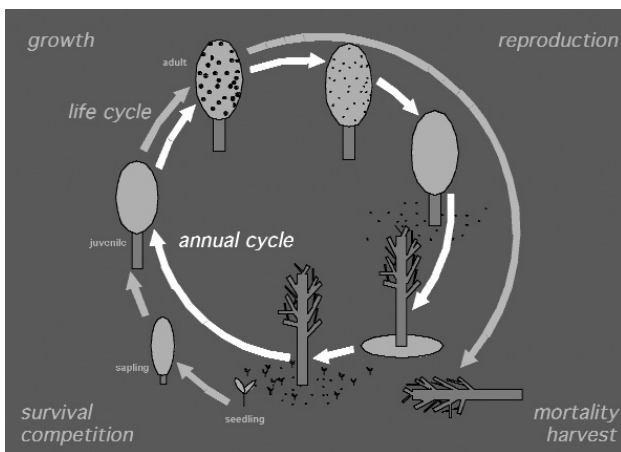
Figure 4. Life cycle and annual cycle simulated by the individual-based genetic model ForGEM. Detailed eco(physio)logical and genetic information on all stadia of the life- and annual cycle of a tree species is required to run an individually-based genetic forest model. However, no additional ecological or genetic information is required to apply the model in changed environmental conditions.

then assigned to these alleles in such a manner that each individual tree attains a tree specific parameter value (*i.e.* phenotypic value) with an initial genetic and environmental variance.

The average phenotypic value of a population, $\bar{F}$, can be obtained from the following formula (Falconer, 1996) valid for a two allele system (Eqn. [5]):

$$\overline{F} = \sum_{i=1}^{n} a_i \left(p_i - q_i \right) + 2 \sum_{i=1}^{n} d_i p_i q_i \qquad [5]$$

where: n is the total number of loci determining the trait; a_i is the allelic dose; p_i and q_i are the allelic frequencies; d_i measures the degree of dominance of locus i.

The allelic effects of the alleles of a locus are assumed opposite in sign and of the same magnitude, and are expressed as deviance from the population mean.

For a randomly mating population in equilibrium (neither linkage nor epistasis), the observed phenotypic variance, V_P, is the sum of the additive and dominance genetic variance and the environmental variance, V_E (Falconer, 1996) (Eqn. [6]).

$$V_P = 2 \sum_{i=1}^{n} p_i q_i \left[a_i + d_i \left(p_i - q_i \right) \right]^2 + 2 \sum_{i=1}^{n} \left(d_i p_i q_i \right)^2 + V_E \quad [6]$$

V_E can be assessed from the observed phenotypic variance (V_P) once the narrow-sense heritability (ratio of additive genetic variance to total variance) of the trait is known ($V_E = (1 - h^2_{ns}) \cdot V_P$). A reasonable value for h^2 must otherwise be assumed, *e.g.* based on observations from related species.

Thus, the allelic effect, *a,* for model parameters in Eqns. [4] and [5] is determined given: (1) initial allele frequencies (initially assume to be in equilibrium); (2) environmental and genetic variance as determined by the heritability of the trait; and (3) the mean and variance of the phenotypic trait (*i.e.* model parameter) as observed in the population. Though this approach is a complicated system to relate the whole tree phenotypic fitness to the genetic composition for each trait, no additional genetic or ecophysiological information is required to assess effects climate change, land use change, forest management or other disturbances on forest functioning, species composition, genetic diversity and rate of adaptation of functional traits.

See Figure 5 for an example of the spatial distribution of a genotype in a simulated forest stand of about 2 ha based on gene flow by pollen and seed dispersal. Figure 6 presents the spatial distribution of a phenotypic value, *i.e.* the date of bud burst, based on the link between genotype and phenotype described above.
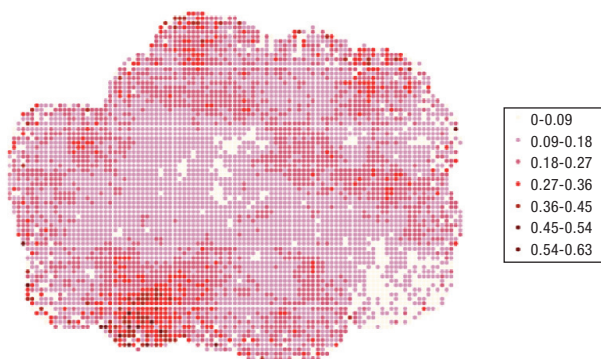
Figure 5. Example of spatial distribution of a genotype in a simulated forest stant. The dots indicated frequency of most common genotype among seeds per pixel. Pixel size is 2 × 2 m, the entire area is about 2 hectares.
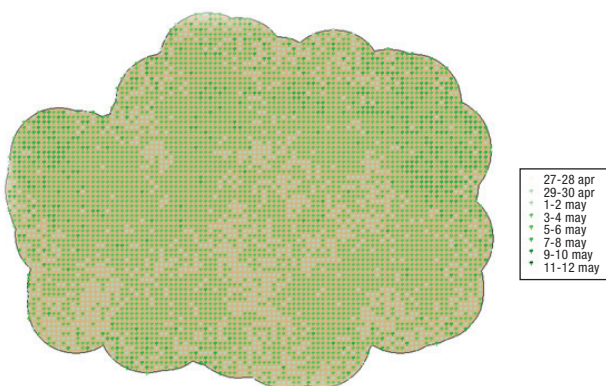
Figure 6. Example of spatial distribution of a phenotypic value, *i.e.* date of bud burst, among seedlings per pixel. Pixel size is 2 × 2 m, the entire area is about 2 hectares.

Discussion

In other fields of environmental modelling are the paradigms of equilibrium and non-equilibrium modelling regularly reviewed (Austin, 1999; Boyce, 1998; Briske *et al.*, 2003; Dietze *et al.*, 2008; Gladwin *et al.*, 1995; Hengeveld, 1997; Hengeveld *et al.*, 1999; Lomolino, 2000; O'Connor, 2002; Rushton *et al.*, 2004; Simberloff, 1980; Sunderlin, 1995; Walter *et al.*, 2000; Wu *et al.*, 1995). However, these alternative concepts have not received much attention neither in forest growth models nor in forest genetic modelling. Understanding of the underlying concepts of models is of great importance both for model developers and model users (see Gracia *et al.,* 2010, in this Special Issue). The advantages and disadvantages and current gaps of knowledge need to be clearly described. This is done here from both the modeller's perspective and the user's perspective.

Model developers

The advantage of the equilibrium approach in forest genetic models is the power with which past evolutionary dynamics can be analyzed in spatially structured populations with known optimum phenotypes and equilibrium tree densities. In population-genetic models there is a close coincidence in the representation of observed and modelled nuclear and cytoplasmic markers which allows to evaluate and test the importance of particular features of the genetic system such as dominance, epistacy and pleiotropy on the rate of adaptation over hundreds to thousands of generations.

The disadvantage of the equilibrium approach is that future optimal phenotypes and maximum tree densities are unknown. Such information may be represented by clinal variation from populations along altitudinal or latitudinal gradients mimicking variation among future climatic gradients. However, this requires intensive sampling of subpopulations along these gradients to determine the distribution of phenotypic values as well as extensive genetic research to relate variation in phenotypic values with observed variation in genetic markers.

Usually a whole-tree phenotypic value with a single fitness value is considered. These values therefore represent compound or integrated traits which cannot be measured on a population of trees. As indicated above, multiple traits can be considered and their fitness value determined using a multiplicative model. However, multiplication of fitness values, which are by definition less or equal to unity, results in a leptokurtic whole-tree fitness curve (Fig. 1). The selection coefficients per trait therefore need to be re-calibrated depending on the number of traits considered to obtain the same whole-tree fitness function. It would require an experimental design to obtain per trait fitness values because clinal variation provides only whole-tree fitness functions and not fitness functions per trait.

The advantage of the individually-based genetic approach is that no additional information on genetic, demographic, or eco(physio)logical information of future populations is required depending on future scenarios on climate change, land use, and forest management. The basic assumption is that the future can be induced from currently known genetic and eco(physio)logical processes. If that assumption is reasonable, both the effects of stationary and non-stationary changes in the environment on genetic diversity and adaptive rates of important plant functional traits can be assessed using these models (Kramer, 2007).

The disadvantage of the individually-based approach is that the number of loci, number of alleles, allelic effects, and interaction between alleles, loci, and traits are currently largely unknown. Extensive genetic and ecophysiological research is required to obtain that, though is can be expected that such information can be used generically for a species, and is potentially representative for a larger number of related tree species, *e.g.* within a genus or family.

The choice of the proper traits for the simulation is therefore very important in individually-based genetic models. Two types of adaptive phenotypic traits are considered in individually-based model: phenotypic plastic traits that attain different values under different environmental conditions, *e.g.* bud burst, and conservative traits that have the same values under different environmental conditions, *e.g.* the critical temperature sum required for bud burst. Phenotypic plastic traits are considered processes in ForGEM and need their own set of equations. The parameters of these equations are then assumed to be conservative traits. ForGEM is particularly suitable to evaluate the effects of environmental changes on conservative traits for which trade-offs can be assumed. The latter means that both the gains and the costs of change of the trait are modelled. *E.g.* selection towards a lower critical temperature sum for bud burst enlarges the growing season and thereby the annual carbon gain, but increases the probability of late frost damage which counteracts the beneficial effects. Traits without a cost function, like critical frost damage temperature or critical soil water potential for cavitation, cannot be reliably simulated with ForGEM. The model will simply change these traits to values at which no damage occurs, at a rate of adaptation proportional to the genetic diversity available in the population.

Model users

For model users such as forest managers, it is important to be able to put specialized and technical forest genetic models and modelling results to their practical needs. Society demands today from forest managers not only a reliable supply of timber of sufficient quality and amount, but a wide array of goods and services. Guidelines of forest management to optimize the genetic diversity of a stand for a sustainable yield must therefore be embedded in guidelines for the management of other forest functions (Geburek *et al.*, 2005).

At the same time, environmental changes in the climate, land use, nitrogen deposition, pollution etc. occur resulting in a situation that forest stands, and species distributions are not in equilibrium anymore with prevailing abiotic conditions. This situation demands that forests should be managed in a way that is can adapt, in a genetic sense and can adjust, in an ecological sense, to such changes. For this, we need to learn from the past and use current knowledge to assess the future (Mátyás, 1997; Mátyás, 1994). The equilibrium and non-equilibrium modelling approaches are, however, not equally suitable for these tasks. As a rule of thumb for model users, it can be said that population-genetic models on the one hand are excellent tools to analyse the past based on currently observed patterns in genetic and demographic composition of the forest. However, because of the lack of information on future patterns, they are unreliable tools to apply under future conditions. Individually-based genetic models on the other hand, are excellent tools to induce the future based on currently observed genetic, demographic and eco(physio)logical processes. However, because of lack of detailed information on past environments, particularly on the climate and disturbances, they are unreliable tools to analyse historic patterns to explain current patterns. Together, provide both approaches insight on the past levels of genetic diversity, structural diversity and species diversity that required for forests to adapt and adjust to future conditions, and the genetic and ecological processes that determine the future of the species.

Acknowledgements

References

AUSTERLITZ F., MARIETTE S., MACHON N., GOUYON P.-H., GODELLE B., 2000. Effects of colonization processes on genetic diversity: differences between annual plants and tree species. Genetics 1309-1321.

AUSTIN M.P., 1999. A silent clash of paradigms: some inconsistencies in community ecology. Oikos 86, 170-178.

BOUTEN W., 1995. Soil water dynamics of the solling spruce stand, calculated with the FORHYD simulation package. Ecological Modelling 83, 67-75.

BOYCE M.S., 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin 26, 391-398.

BRISKE D.D., FUHLENDORF S.D., SMEINS F.E., 2003. Vegetation dynamics on rangelands: a critique of the current paradigm. J Appl Ecol 40, 601-614.

CHAMP J.G., WILLIAMS D.R., KNOTEK K., 2009. Wildland fire and organic discourse: negotiating place and leisure identity in a changing wildland urban interface. Leisure Sciences: An Interdisciplinary Journal, 31 237-254.

CORRE V.L., MACHON N., PETIT R.J., KREMER A., 1997. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. Genet Res Camb 66, 117-125.

DEANGELIS D.L., GROSS L.J., 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. Chapman & Hall Publishers 525 pp.

DIETZE M.C., CLARK J.S., 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. Ecological Monographs 78, 331-347.

FALCONER D.S., MACKAY, T.F.C., 1996. Introduction to quantitative genetics. Addison Wesley Longman Ldt, Edinbrough. 464 pp.

FALCONER D.S., MACKAY T.F.C., 1996. Introduction to quantitative genetics, 4th ed. Adison Wesley Longman Group Ltd.

GEBUREK T., 2000. Effects of environmental pollution on the genetics of forest trees. In: Forest conservation genetics. Principles and practice (Young A., Boshier D., Boyle T., eds). CABI, Oxon, United Kindom.

GEBUREK T., TUROK J., 2005. Conservation and management of forest genetic resources in Europe. Arbora Publishers, Zvolen.

GLADWIN T.N., KENNELLY J.J., KRAUSE T.-S., 1995. Shifting paradigms for sustainable development: implications for management theory and research. Academy of Management Review 20, 874-907.

GRACIA C., FONTES L., BONTEMPS J.-.D. *et al.,* 2010. Models for forest management in a changing environment. Forest Systems.

GREGORIUS H.-R., 1978. The concept of genetic diversity and its formal relationship to heterozygozity and genetic distance. Math Biosc 41, 253-271.

GREGORIUS H.R., 1977. The genotype*environment-to-phenotype relationship. Theoretical and Applied Genetics 49, 165-176.

GREGORIUS H.R., 1986. Measurements of genetical differentiation among subpopulations. Theoretical and Applied Genetics 71, 826-834.

GREGORIUS H.R., 1987. The relationship between the concepts of genetic diversity and differentiation. Theoretical and Applied Genetics 74, 397-401.

GREGORIUS H.R., 1988. The meaning of genetic variation within and between subpopulations. Theoretical and Applied Genetics 76, 947-951.

HANSSEN A., 2002. Hessisches ministerium fuer umwelt, landwirtschaft und forsten. Hannover, Muenden. 142 pp.

HARTL D.L., CLARK A.G., 1997. Principles of Population Genetics. Sinauer Associates, Inc., Sunderland, Massachusetts, 542 pp.

HATTEMER H.H., 1991. Measuring genetic variation. In: Genetic variation in european populations of forest trees (Muller-Starck G.Z.M., ed). JD Sauerlander's Verlag, Frankfurt am Main. pp. 2-20.

HENGEVELD R., 1997. Guest editorial: impact of biogeography on a population-biological paradigm shift. Journal of Biogeography 24, 541-547.

HENGEVELD R., WALTER G.H., 1999. The two coexisting ecological paradigms. Acta Biotheoretica 47, 141-170.

HUTTUNEN S., 2009. Ecological modernisation and discourses on rural non-wood bioenergy production in Finland from 1980 to 2005. Journal of Rural Studies 25, 239-247.

KOTZ S., BALAKRISHNAN N., JOHNSON N.L., 2000. Continuous multivariate distributions. Models and applications. Wiley Press, Vol. 1. 752 pp.

KRAMER K., 2007. In Climate change and forest genetic diversity: implications for sustainable forest management in Europe (Koskela J., Buck A., Teissier du Cros E., eds). IPGRI. Workdocument for Ministerial Conference on the Protection of Forests in Europe, April 2007, Poland, Paris, 15-16 March, 2006.

KRAMER K., BRINKMAN A.G., KUITERS A.T., VERDONSCHOT P.F.M., 2005. Alterra-report 1277. p. 80.

KRAMER K., BUITEVELD J., FORSTREUTER M. *et al.,* 2008. Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. Ecological Modelling 216, 333-353.

KRAMER K., DEGEN B., BUSCHBOM J., HICKLER T., THUILLER W., SYKES M.T., WINTER W.D., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – Range, abundance, genetic diversity and adaptive response. Forest Ecology and Management 259, 2213-2222.

KRAMER K., BAVECO H., BIJLSMA R.J.,CLERKX A.P.P.M., DAM J., VAN GOETHEM J., GROEN T.A., GROOT BRUINDERINK G.W.T.A., JORRITSMA I.T.M., KALKHOVEN, KUITERS A.T.,LAMMERTSMA D., PRINS R.A., SANDERS M., WEGMAN R., VAN WIEREN S.E., WIJDEVEN S., VAN DER WIJNGAART R., 2001. Alterra Report 216. Wageningen, The Netherlands. 168 pp.

LARSEN A.B., 1996. Genetic structure of populations of beech (*Fagus sylvatica* L.) in Denmark. Scandinavian Journal of Forest Research 11, 220-232.

LE CORRE V., KREMER A., 2003. Comparative dynamics of genetic variability of an adaptive trait and its underlying genes in a subdivided population. Genetics 1205-1219.

LOMOLINO M.V., 2000. A call for a new paradigm of island biogeography. Global Ecology and Biogeography 9, 1-6.

MATALA J., KARKKAINEN L., HARKONEN K., KELLOMAKI S., NUUTINEN T., 2009. Carbon sequestration in the growing stock of trees in Finland under different cutting and climate scenarios. European Journal of Forest Research, 128, 493-504.

MÁTYÁS C., 1994. Modelling climate change effects with provenance test data. Tree Physiology, 14, 797-804.

MÁTYÁS C., 1997. Perspectives of forest genetics and tree breeding in a changing world. Wien, 160 p pp.

MITCHELL R.J., DUNCAN S.L., 2009. Range of variability in southern coastal plain forests: its historical, contemporary, and future role in sustaining biodiversity. Ecology and Society, 14, art.

O'CONNOR R.J., 2002. The conceptual basis of species distribution modelling: time for a paradigm shift? In: Predicting species occurrences: issues of accuracy and scale (Scott J.M., Heglund P.J., Haufler J., Morrison M., Raphael M., Wall B., Samson F., eds). Island Press, Covelo, California.

RUSHTON S.P., ORMEROD S.J., KERBY G., 2004. New paradigms for modelling species distributions? J Appl Ecol 41, 193-200.

SIMBERLOFF D.S., 1980. A succession of paradigms in ecology: essentialism to materialism and probabilism. Synthese 43.

SOLBERG S., DOBBERTIN M., REINDS G.J. *et al.,* 2009. Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: a stand growth approach. Forest Ecology and Management 258, 1735-1750.

SUNDERLIN W.D., 1995. Global environmental change, sociology, and paradigm isolation. Global Environmental Change Human and Policy Dimensions 5, 211-220.

WALTER G.H., HENGEVELD R., 2000. The structure of the two ecological paradigms. Acta Biotheoretica 48, 15-46.

WOO S.Y., 2009. Forest decline of the world: a linkage with air pollution and global warming. African Journal of Biotechnology 8, 7409-7414

WU J., LOUCKS O.L., 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70, 439-466.

Appendix A. Statistics as output of genetic models

In this section an overview of common population-genetic statistics is presented as output of genetic models. The population statistics, within and among populations, include diversity measures, differentiation measures between populations, heterozygozity and fixation, and F-statistics. The statistics described in this section are obtained from Hanssen (2000) and Hattemer (1991). Details on the use and interpretation can be found there and in (Gregorius, 1977, 1978, 1986, 1987, 1988)

Diversity measures

Genetic variety

The genetic variety can be measured as the number of different alleles or different genotypes in population (Gregorius, 1977; Gregorius *et al.,* 1985).

Genetic diversity

The genetic diversity characterizes the heterogeneity of the distribution of genetic variants in a population of a sample therefrom (Hattemer, 1991). It can thus be measured the allelic diversity of the *k*-th locus or genotype diversity of a deme.

$$v_k = \frac{1}{\sum_{i=1}^{n_k} \left(p_i^k \right)^2}, \qquad 1 \le v_k \le n \qquad [\text{A.1}]$$

where: *n* number different genetic types (alleles, genotypes); *p* frequency of i-th genetic type; *v* equals unity if there is only 1 genetic type, and equals *n* if every all genetic types are equally frequent (Gregorius, 1978).

Mean effective number of alleles

In case of allele diversity, v_k can be considered as the effective number of alleles for locus *k* if n_k alleles occus with frequencies p_i^k ($i = 1,\dots n_k$) (Hattemer, 1991). Thus, the mean effective number of alleles is the harmonic mean of v_k at *m* loci.

$$\bar{v} = m \cdot \frac{1}{\sum_{k=1}^{m} \frac{1}{v_k}}, \qquad 1 \le v \le \frac{1}{n} \sum_{k=1}^{n} n_k \qquad [\text{A.2}]$$

Hypothetical gametic multi-locus diversity

The diversity of the gametic output of populations is a special case of diversity and characterizes the adap-

tive potential of sexually reproducing populations (Gregorius 1978). It is hypothetical in the sense that the absence of fertility selection is assumed as well as the independence of the distributions of alleles at different loci (*i.e.* no linking) (Hattemer, 1991).

$$v_{gam} = \prod_{k=1}^{m} v_k, \qquad 1 \le v \le \prod_{k=1}^{m} n_k \qquad [A.3]$$

where: *m* the number of unlinked loci; v_k the allelic diversity for the *k*-th locus; v_{gam} is thus a measure for effective number of the multiloci gametes that can be produced in a population (Gregorius, 1978).

Actual heterozygosity

$$H_a = \sum_{i \ne j} P_{ij} \qquad [A.4]$$

where: P_{ij} the frequency of genotype with alleles *i* and *j*, with $i \ne j$; H_a indicates the fraction of observed heterozygotes in the population.

Fixation index

The fixation index indicates for the locus considered the surplus or deficit of heterozygotes compared to Hardy-Weinberg-equilibrium.

$$F = \frac{H_e - H_a}{H_e}, \qquad [A.5]$$

where: H_e the expected heterozygosity based on Hardy-Weinberg-equilibrium.

Differentiation measures

Genetic distance between demes

The differentiation between two demes is characterized by counting the number of genetic variants which the demes do not share. Thus, the allelic differentiation between demes *X* and *Y* represents the genetic distance between the demes (Gregorius, 1974; Gregorius and Roberts, 1986).

$$d_{xy} = \frac{1}{2} \cdot \sum_{i=1}^{n} |x_i - y_j|, \qquad 0 \le d_{xy} \le 1 \qquad [A.6]$$

where: x_i and y_j genetic frequencies (of alleles at a given locus or of a genotype) of deme *X* and *Y*.

If the genetic distance equals zero, then both populations have the same alleles or genotypes with the same frequency. d_{xy} equals unity if both populations have no alleles or genotypes in common (Gregorius, 1974, 1978, 1984). Note that the genetic distance is a symmetrical statistic ($d_{xy} = d_{yx}$) and that the distance between population *X* and *Y* cannot exceed the sum of their distances to a third population *Z* ($d_{xy} \le d_{xz} + d_{yz}$) (Hattemer, 1991).

Genetic differentiation among demes

This statistic represents the genetic distance between a deme and its complement, *i.e.* the union of all other demes (Gregorius, 1985).

$$D_j = \frac{1}{2} \cdot \sum_{i=1}^{n} \left| p_i^{(j)} - \overline{p}^{(j)} \right|, \qquad 0 \le D_j \le 1 \qquad [A.7]$$

where: $p_i^{(j)}$ frequency of allele or genotype *i* in deme *j*; and $\bar{p}_i^{(j)}$ average allele or genotype frequency in the complement of deme *j*.

The substructure of the complement has no influence of *D*, as different complement can yield the same $\bar{p}_i^{(j)}$. Thus, identical *D's* do not necessarily indicate the demes with an identical genetic structure. However, *vice versa* demes with an identical genetic structure do possess an identical genetic structure (Hattemer, 1991).

Average genetic differentiation

The average genetic differentiation among *m* demes is the weighted mean of D_j.

$$\delta = \sum_{j=1}^{m} D_j \cdot c_j, \qquad 0 \le \delta \le 1 \qquad [A.8]$$

where: *m* number of populations; c_j relative size of deme *j* (Gregorius 1984, 1988).

δ attains zero if all demes have the same genetic structure, and reaches unity if all demes considers in pairs have no gene in common (Hattemer, 1991).

Differentiation within a population

The concept of differentiation can also be applied within a population by considering each individual in that population a deme. The number of identical individuals can be counted and expressed relative to the number of other genetic types.

$$\delta_T = \frac{N}{N-1} \cdot \left(1 - \sum_{i=1}^{n} p_i^2\right) = \frac{N}{N-1} \cdot \left(1 - \frac{1}{v}\right), \quad [A.9]$$

$$0 \le \delta_T \le 1$$

where: N the sample size; p_i frequency of genetic type (allele or genotype).

δ_T indicates the total genetic difference between all individuals of a population. δ_T equals zero if all individuals of the population are of the same genotype, and δ_T equals unity if all individuals are different (Gregorius 1987, 1988). δ_T represents the probability that two individuals samples from the sample population without replacement represent the same variant (Hattemer, 1991).

Note that all differentiation measures range between zero and unity, whereas the genetic diversity measures range between unity and the number of genetic types, n (Gregorius 1987).

F-statistics

F-statistics measure the degree of deviation of genotypic frequencies from those expected under random mating in structured populations (Falconer, 1996), [Weir and Cockerham, 1984; ref in (Larsen, 1996)].

F_{IS} : Inbreeding coefficient of an individual relative to its on subpopulation. Measures inbreeding due to non-random mating in a sub-population. Within population fixation index.

F_{ST} : Average inbreeding of the subpopulation relative to the whole population, or correlation between two randomly chosen alleles in a sub-population relative to the alleles in the whole population. Measures inbreeding due to correlation among alleles cause by their occurrence in the same sub-population. Between populations fixation index.

F_{IT} : Inbreeding coefficient of an individual relative to the whole population, or correlation between gametes for the total population. Measures the extend of inbreeding in the entire population (for neutral alleles). Total fixation index.

Note that:

— In a random mating population: $F_{IS} = 0$ and $F_{IT} = F_{ST}$.

— If all populations are genetically identical: $F_{ST} = 0$ and $F_{IS} = F_{IT}$.

Appendix B.   Principal equations in ForGEM

In this appendix an overview is presented of the principal state and empirical equations used in ForGEM. See (Kramer, 2001, Kramer *et al.*, 2008) for details and references.

State variables

$$\frac{dN_x}{dt} = NNew_x - NMrt_x \qquad [B.1]$$

$$\frac{dW_y}{dt} = f_y \cdot NPP - T_y \qquad [B.2]$$

$$\frac{dS_z}{dt} = RS_z \qquad [B.3]$$

with: N: number (# ha^{-1}); W: weight (kg tree^{-1}), S: structural feature; *x:* seeds, seedlings, trees; *y:* foliage, branches, heartwood, sapwood, coarse roots, fine roots, reserves; *z:* height, stem volume, dbh; *R:* rate of change; *T:* turnover; NPP: net primary production;

New: new individual seed, seedling or tree in the population; Mrt: mortality of individual or cohort in case of seeds and seedlings.

Empirical equations are used for both allocation (f_y, Eqn. [B.2]) and the rate of change of structural features (Eqn. [B.3]). Empirical coefficients of these equations are indicated as C_n, with n a numeric identifier.

Allocation

$$\ln\left(\frac{Wfl}{Wst}\right) = C1 + C2 \cdot \ln(Wsh) + \quad [B.4]$$
$$+ C3 \cdot \ln(Wsh)^2 + C4 \cdot \ln(Wsh)^3$$

$$\ln\left(\frac{Wbr}{Wst}\right) = C5 + C6 \cdot \ln(Wsh) + \quad [B.5]$$
$$+ C7 \cdot \ln(Wsh)^2 + C8 \cdot \ln(Wsh)^3$$

$$\Rightarrow \frac{Wst}{Wsh} = \frac{1}{1 + \ln\left(\dfrac{Wfl}{Wst}\right) + \ln\left(\dfrac{Wbr}{Wst}\right)} \qquad \text{[B.6]}$$

with: *fl* – foliage; *br* – branches *st* – stem (= heartwood +sapwood).

The fraction of NPP allocated to the plant components (f_y in Eqn. [B2]) are derived such that the tree strives for partitioning ratios between plant organs, *y*, as indicated by Eqns [B.4]-[B.6]. A fixed fraction of NPP is allocated to the roots.

Volume

$$\frac{dV}{dt} = \frac{f_{st}}{\rho_{st}} \cdot NPP \qquad \text{[B.7]}$$

with: f_{st} - allocation of NPP to stem, ρ_{st} - wood density

Height

$$H = H_{max} \cdot \left(1 - e^{C7 \cdot t}\right)^{C8} \qquad \text{[B.8]}$$

$$\Rightarrow \frac{dH}{dt} = C7 \cdot C8 \cdot H \cdot \left(\frac{e^{C7 \cdot t}}{1 - e^{C7 \cdot t}}\right) \qquad \text{[B.9]}$$

with: *H* – tree height (m), *t* - the tree age (yr).

Diameter

$$V = D^{C1} \cdot H^{C2} \cdot e^{C3} \qquad \text{[B.10]}$$

$$\Rightarrow \frac{dD}{dt} = \frac{D}{C_1} x \left\{ \frac{1}{V} \cdot \frac{dV}{dt} - \frac{C_1}{H} \cdot \frac{dH}{dt} \right\} \qquad \text{[B.11]}$$

with: *V* – volume (dm³ stem⁻¹); *D* – stem diameter at breast height (cm). *e* is the exponent of the natural logarithm.