WORKING PAPER

SOME QUESTIONS RELATING TO THE AGE DYNAMICS OF BOREAL FORESTS

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Foreword

This manuscript is a result of discussions prior to and during the workshops "Impacts of Change in Climate and Atmospheric Chemistry on Northern Forest Ecosystems and Their Boundaries" (August 1987) and "Global Vegetation Change" (April 1988) and is an initial step in the development of a synthesis between realistic (e.g. biological-detail-rich) computer oriented models of forest and more mathematically, tractable, but simpler forest models. The work is focused on the boreal forests of the world (an important carbon reservoir and an important reserve of softwood timber). The boreal forests are also potentially strong impact systems under current scenarios of CO_2-induced climate warming.

One purpose of building a model is to get an understanding of what may happen to the climate if, for example, all of the boreal belt were to disappear, or if its functional efficiency were to double. Could such a disappearance occur simultaneously with changes in the tropical forests? How would this change the exchange between atmosphere and the earth surface? The authors try to describe a forest (or vegetation as a whole) as a boundary layer between fast atmospheric processes and slow processes in soil and underground water systems, and consider the geometry of canopies and roots as a function of extremes corresponding to a stable equilibrium of soil and underground water systems.

The authors hope to consider these and similar problems during their continuing cooperation.

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H.H. Shugart and M.Ya. Antonovsky

1. INTRODUCTION

Present discussions of the dynamics of the biosphere and of global ecology come at a time when there is renewed interest in time- and space-scales in ecological systems. An appreciation of scales is a prerequisite to unifying the dynamics of the atmospheric and oceanographic process with the dynamics of the terrestrial surface. Of particular importance is a knowledge of the patterns of dominance (in the sense of a controlling pattern) of particular phenomena at particular scales. The categorization of certain phenomena as being important to understanding the space and time scale in a particular ecosystem has been the topic of reviews for several different ecosystems (Delcourt et al., 1983; O'Neill et al., 1985). A focus on expressing relevant mathematical developments in a manner that can provide insight into the ways ecoystems are structured would be a useful addition to these discussions.

We are particularly concerned with the ecological modeling of the world's boreal forest belt and we would posit several reasons for this concern.

2. ENVIRONMENTAL CONTROLS OF STAND DYNAMICS IN BOREAL FOREST ECOSYSTEMS

The boreal forests of the world are a major repository of the world's terrestrial organic carbon (Bolin, 1986). Moreover, the amplitude in the annual sinusoidal dynamics of atmospheric carbon dioxide is greatest in the northern boreal latitudes, and at these latitudes, there is a strong correlation between the dynamics of atmospheric carbon dioxide and the seasonal dynamics of the "greenness" (Goward et al., 1985) of the earth (Tucker et al., 1986). The association at higher northern latitudes of dynamics of atmospheric carbon dioxide and the dynamics of an index of the productivity of the vegetation (Tucker et al., 1986) is correlational, but a possible causal relation (with the dynamics of the forests at these latitudes driving the atmospheric carbon concentrations) appears to be consistent with the present-day understanding of ecological processes in these ecosystems (Fung and Tucker, 198?b). Along with its familiar role in plant photosynthesis, CO_2 is a "greenhouse" gas that has an active role in governing the heat budget of the earth (Flohn, 1980, Manabe and Stouffer, 1980; Budyko, 1982). Thus, the possibility that the boreal forests of earth may be actively participating in the dynamics of an important atmospheric trace gas is of considerable significance.

Current predictions of the climatic response to elevated CO_2 concentrations in the atmosphere, motivated by the recorded increase in atmospheric CO_2 reported first at Mauna Loa Observatory in Hawaii (Bacastow and Keeling, 1983) and subsequently at all latitudes, are based on a range of large, physically-based climate models (called general circulation models or "GCM's"; e.g., Manabe and Stouffer, 1980; Hansen et al., 1984; Washington and Meehl, 1984). While the GCM's vary as to certain underlying assumptions, resolution and other features, they converge in their prediction of a global warming with increased atmospheric CO_2. The degree of this warming is most pronounced at the higher latitudes (Dickinson, 1986). Thus, the effect of changes in the atmospheric concentration of CO_2 would seem to be strongly directed to the boreal forests of the world (Bolin, 1977; Shugart et al., 1986).

These large-scale forest/environment interactions are a motivation to a better understanding of the environmental processes controlling the structure and function of boreal forest ecosystems. One hypothesis is that the structure and function of taiga forests are predominantly controlled by soil thermal and moisture regimes promoted by local topography and the successional buildup of a thick forest floor organic mat. This hypothesis was developed by researchers working in the uplands of interior Alaska (Viereck, 1975; Van Cleve, and Viereck, 1981; Van Cleeve and Dyrness, 1983a; Viereck and Van Cleve, 1984; Van Cleve et al., 1986) where slow growing, nutrient conservative black spruce (Picea mariana) stands occupy the least productive, cold, wet, north-facing sites and fast growing, nutrient dynamic white spruce (Picea glauca) and hardwood (Populus temuloides, Betula papyrifera) stands grow on productive, warmer, drier, south-facing slopes. The low soil temperatures and high moisture contents found on permafrost-dominated Picea mariana sites are thought to act as a negative feedback that promotes moss growth and inhibits decomposition rates so that over time the forest floor becomes the principal reservoir of biomass and nutrients.

Historically, the complex unravelling of these sorts of ecological interactions was evident in the early work of A.S. Watt (1925) on beech forests and elaborated in his now-classic paper on pattern and process in plant communities (Watt, 1947). When one inspects Tansely's (1935) original definition of the ecosystem

> "These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom." ... "Actually, the systems we isolate mentally are not only included as parts of the larger ones, but they also overlap, interlock and interact with one another,"

one finds that the same concepts that one sees in hierarchy theory were explicit in the original definition of the ecosystem. Of course, the Watt/Tansely ecosystem paradigm has been introduced as a major ecosystem construct in ecological studies in the United States. One conspicuous example of the introduction of these concepts was Whittaker's (1953) review which used the Watt pattern-and-process paradigm to redefine the "climax concept" that was (and still is) an important construct in American ecology. These same ideas are found in ecosystem concepts developed by Bormann and Likens (1979a, 1979b) in their "shifting-mosaic steady-state concept" of the ecosystem as well as in what has been called a "quasi-equilibrium landscape" (Shugart, 1984).

3. NON-EQUILIBRIUM DYNAMICS OF ECOLOGICAL SYSTEMS

In ecosystems that are dominated by sessile organisms, the temporal dynamics at the scale of the individual organism are almost by necessity non-equilibrium dynamics. This is most apparent in forest systems where the spatial scale of the individual organisms (the canopy trees) is relatively large. The space below a canopy tree has reduced light levels and a considerably altered microclimate due to the influence of the tree. These conditions determine the species of trees that can survive beneath the canopy tree. Upon the death of the canopy tree, the shading is eliminated and the environment is changed. In cases in which the canopy tree dies violently (e.g. broken by strong winds), the changes in the microenvironment are extremely abrupt. The death of the canopy tree initiates a scramble for dominance among the smaller trees that were persisting in the environment created by the canopy tree and seedlings that establish themselves in the high-light environment. Eventually, one of the trees becomes the canopy dominant. The establishment of a new canopy dominant represents the closure of the death/birth/death cycle that can be thought of as the typical small-scale behavior of a forest.

In ecosystems other than forests but still dominated by sessile organisms, one would expect the same sorts of dynamics. This nonequilibrium behavior at fine spatial scales has been noted in a diverse array of ecosystems including coral reefs (Connel, 1978; Huston, 1979; Pearson, 1981; Colgan, 1983), fouling communities Karlson, 1978, Kay, 1980), rocky inter-tidal communities (Sousa, 1979; Paine and Levin, 1981, Taylor and Littler, 1982; Dethier, 1984) and a wide range of heathlands (Christensen, 1985).

The ecosystems that are both historically and currently the most studied in this regard are forests. For this reason it is worthwhile to elaborate the details of the death/birth/death process in forests. In forests, the non-equilibrium dynamics are quasi-periodic with the period corresponding to the potential longevity of the individual organisms. This "cycle" can be modified by a variety of factors. One important consideration is the manner of death of the dominant tree. Some trees typically die violently or catastrophically and the attendant alterations of environmental conditions at the forest floor (and thus the effect on the regeneration of potential replacements) are very abrupt. Typically these abrupt changes are associated with exogenous disturbances but there are some species of trees that are "suicidal" in that mature trees flower but once and die to release canopy space to the progeny (Foster, 1977). Some trees tend to "waste-away" before they die so that the changes in the microenvironment that they control are more continuous. Some trees tend to snap at the crown when torn down by winds; others are heaved over at the roots exposing mineral soil. All of these modes of death (and others) influence the stochastic regeneration success of the trees that form the next generation.

It is an open question as to whether mode of death or mode of regeneration is the strongest determinant of pattern diversity in forests. Both are attributes of the various tree species and may be strongly interrelated. One aspect of the mortality of canopy trees and the associated opening in the forest canopy ("gap formation") is the size of the gap that is created. Several authors (van be Pijl, 1972; Whitmore, 1975; Grubb, 1977; Bazzaz and Pickett, 1980) have discussed species attributes that are important in differentiating the gap-size-related regeneration success of various trees. The complexity of the regeneration process in trees and its apparently stochastic nature makes it very difficult to hope to predict the success of an individual tree seedling even if one could determine the attendant environmental factors. Most current reviewers recognize this and tend to discuss regeneration in trees from a pragmatic view that the factors influencing the establishment of seedlings can be usefully grouped in broad classes (Kozlowski, 1971a, 1971b; van der Pijl, 1972; Grubb, 1977; Denslow, 1980).

Since the time scales of the replacement cycle in forests in relatively long, tools for a better understanding of these difficult-to-measure phenomena are mathematical models of forests. Our current research interest is to develop a fusion of the simulation-based stand dynamics models ("Gap models") and more analytically tractable demographic models of tree populations. These two approaches will be discussed below.

Gap Models.

Gap models are a subset of a class of forest succession models called individual-tree models (Munro, 1974) because the models follow the growth and fate of individual trees. The first model of this genre was the JABOWA model developed by Botkin et al. (1972); a similar modeling approach has been applied to several forests in different parts of the world (see Chapter 4 of Shugart, 1984, for a review of several of these applications, also see Kercher and Axelrod, 1984).

Gap models simulate succession by calculating the year to year changes in diameter of each tree on small plots. The plot size is determined by the size of the canopy of a single large individual. Forest succession dynamics are estimated by the average behavior of 50 to 100 of these plots. The growth of each tree is determined by the average competitive influence of the neighboring trees on a plot. Due to the small size of plots, gap formation events (the removal of canopy trees through mortality) strongly affect the resource availability on a plot which in turn affects tree growth.

The exact location of each tree is not used to compute competition in these models. Tree diameters are used to determine tree height, and then simulated leaf area profiles are computed to devise competition relationships due to shading. These models are spatial in that competition is computed in the vertical dimension. There is an implicit assumption that within a plot of a certain size the horizontal spatial patterns of the individual plants do not affect the degree of competitive stress acting on an individual to any significant degree beyond that accounted for by the plant's height (i.e., tree biomass and lead area are considered to be homogenously distributed across the horizontal dimension of the simulated plot).

The regeneration of seedlings on a plot and their subsequent growth is based on the silvicultural characteristics of each species, including site requirements for germination, sprouting potential, shade tolerance, growth potential, longevity, and sensitivity to environmental factors (water and nutrients). Under optimal growth conditions, the growth of a tree is assumed to occur at a rate that will produce an individual of maximum recorded age and diameter. This curvilinear function grows a tree to two-thirds of this maximum diameter at one half of its age under optimal conditions. Modifications reducing this optimal growth are imposed on each tree based on the availability of light and, depending on the specific model, other resources. In most gap models, tree growth slows as the simulated plot biomass approaches some maximum potential biomass observed for stands of the given forest type. Growth is further reduced as climate stochastically varies. Death of an individual tree's death is a stochastic process. The probability of an individual tree's death in a given year is inversely related to individual's growth and the longevity of its species.

Gap model dynamics are based on information concerning the demography and growth of trees during the lifespan of species. The models have a capability to predict the sequence of replacement of species through time and other dynamics on the scale of the average tree generation time (Figure 1). At this scale, the success of a tree at growing into the canopy is more related to the opportunity for inseeding into a plot and the relative growth rate compared to other seedlings than it is related to the distribution of distances from other competing individuals.

The relationship of the height of the individual to the distribution of heights of competitors is assumed to be sufficient to determine the level of competitive stress experienced by an individual in relation to other trees on the plot. This implies that the distance of a tree to its competitors has no significant influence on the amount of light and other resources available to a given tree. In terms of implementing these models, these assumptions lead to a requirement that the dynamics of a large number of plots be averaged to better estimate the mean rate of success of canopy invasion of each species.

Because regeneration, growth and death are modeled on a pre-tree basis and the silvics of individuals vary among species, gap models are particularly useful tools for exploring the dynamics of mixed-aged and mixed-species forests. The models have been tested and validated against independent data (Shugart, 1984, Chapter 4). For these reasons, gap models can also be used to explore theories about patterns in forest dynamics at time scales that are sufficiently long to prohibit direct data collection. Such applications have been instrumental in developing a theoretical basis for understanding the coupled effects of tree death and regeneration in forest systems (Shugart, 1984).

One gap model that has been used in a large number of applications in complex, mixed-species, mixed-aged forests is the FORET model, a derivative of the JABOWA model (Botkin et al., 1972). The JABOWA/FORET modeling approach has been the central topic of two books on the dynamics of natural forests (Bormann and Likens, 1979a; Shugart, 1984). The FORET model and other analogous models have been modified and applied to simulate the dynamics of a wide range of forests: mixed hardwood forests of Australia (Shugart and Noble, 1981); upland forest of Southern Arkansas (Shugart, 1984); eastern Canadian mixed species forest (El-Bayoumi et al., 1984); the arid western coniferous forest (Kercher and Axelrod, 1984); a western coniferous forest (Reed and Clark, 1979); and northern hardwood forests (Botkin et al., 1972; Aber et al., 1978, 1979; Pastor and Post, 1985).

4. DEMOGRAPHICAL MODEL

This type of forest model represents the classic approach to the investigation and prognosis demand of forest dynamics. It would appear to us that the analytical possibilities of this modeling technique are not completely revealed. The basis of any demographical forest model consists of some set of dynamical equations for tree numbers of definite subgroups inside a whole population and for some individual tree variables - masses, lead and root surface, diameter, etc. The subdivision into subgroups is dictated by the task under consideration and can be very detailed. It is usual in classical mathematical ecology to describe the basic demographical processes - birth, migration, growth and death - by means of definite functions which are derived from theoretical ideas and empirical data. The potential complexity and diversity of dynamical and parameter behavior that the corresponding equations demonstrate are unlimited. For example, modeling techniques can describe systems with many stationary states, oscillations, hysteresis, wave phenomena, stochastic (even chaotic) and adaptive behavior.

We are certain that the basic dynamical effects shown by gap models in various concrete applications (multi-stationary state phenomena, the sorting out of some tree species, when appropriate conditions vary, etc.) may be achieved inside dynamical forest models with rather simple growth, birth and death functions and their dependence upon ecological parameters in the right parts of equations. Dynamical models give a smooth trajectory; the corresponding trajectory for the gap-model is obtained by means of an averaging procedure applied to individual gap trajectories. So, it would appear to us that the difference between the two modeling approaches is not very large. The gap-model is applied to average tree positions inside the gap and determines the fate of each tree by means of the Monte-Carlo mechanism. Dynamical equations are applied to average tree positions in large (potentially infinite) territories to determine the fate of definite groups of trees by means of viability functions. One can match the two types of models comparing one tree in the gap with one group from a large territory and averaging the Monte-Carlo variability to get a determinate variability function. A possible and rather interesting task of this type has not yet been comprehensively undertaken.

We see some advantages of dynamical models as compared to gap-models which have a simulative nature. Firstly, they give the possibility of analytical investigation of simple, preliminary models aimed at qualitative system analysis. This level of forest dynamics investigation enables one to discover some basic properties of the system. For example, Antonovsky and Korzukhin (1986), described the basic dynamical effects of an even-aged forest stand by means of two dynamical variables (tree number and individual tree biomass). This model may help to make estimations of climatically induced shifts in the general system characteristics (total biomass, average diameter, tree number, etc.). Another example is a phytophaque interaction with an uneven-aged one-species tree population (Antonovsky, Kuznetsov, Clark (1987).

Although both models are extremely schematic, they seem to be among the simplest models allowing complete qualitative analysis of a system in which the predator differentially attacks various age classes of the prey.

The main qualitative implications from the present paper can be formulated in the following, to some extent metaphorical, form:

1. The pest feeding the young trees destabilizes the forest ecosystem more than a pest feeding upon old trees. Based upon this implication, we could try to explain the well-known fact that in real ecosystems, pests more frequently feed upon old trees than on young trees. it seems possible that systems in which the pest feeds on young trees may be less stable and more vulnerable to external impacts than systems with the pest feeding on old trees. Perhaps this has led to the elimination of such systems by evolution.
2. An invasion of a small number of pests into an existing stationary forest ecosystem could result in intensive oscillations of its age structure.
3. The oscillations could be either damping or periodic.
4. Slow changes of environmental parameters are able to induce a vulnerability of the forest to previously unimportant pests.

Let us now outline possible directions for extending the model. It seems natural to take into account the following factors:

1. more than two age classes for the specified trees;
2. coexistence of more than one tree species affected by the pest;
3. introduction of more than one pest species having various interspecies relations;
4. the role of variables like foliage area which are important for the description of defoliation effect of the pest;
5. feedback relations between vegetation, landscape and microclimate.

Secondly, comparatively low computer expenses for solution of the dynamical equations give the possibility of an exact parameter definition even for realistic, not simplified models. It is well-known that many biological and ecological parameters are hardly measured in field conditions. so the task arises of their identification by means of comparing model and real behavior (trajectories). For example, this approach was undertaken in quantitative modeling of post-fire succession in West Siberia (Korzukhin, Sedyh, Ter-Mikhaelian, 1987, 1988; Antonovski, Ter-Mikhaelian, 1987; Antonovski, Korzukhin, 1986b).

The dynamical equations were essentially nonlinear, and viability functions were constructed with the help of the developed theory of tree competition. Age dynamics of two-species (cedar + birch) uneven-aged stand was considered over a 200-year period after catastrophic fire occurrence. Six important parameters of the system - two seeds immigration intensities and four inter- and intra-specific competition coefficients were determined by means of the usual technique of least square minimizing. Wave-like age dynamics, typical for boreal forest post-catastrophic successions, were analyzed from the mathematical and ecological points of view. These dynamics are quite similar to one-gap dynamics during a one-life tree cycle (Shugart, 1984).

In spite of the roughness of the model (Antonovski, Ter-Mikhailian, 1987), in our opinion the main assumptions to be corrected are assuming a single succession line over the entire area and assuming that all stands are of equal size), so we are not going to insist on the quantitative exactness of parameter estimations. Nevertheless, the following conclusions seems to be non-controversial:

1. Boreal forests are not in a stable state (in the sense of stability of age structures) but there is a stable fire regime, i.e., fire years in which a small part of the territory is burned alternating with major fire years occurring irregularly; this conclusion arises firstly from the nonmonotonous shapes of the age structures and secondly from convergence of the dynamics of that part of the territory burned per year with the pattern described above; thereafter a stable pattern is maintained.
2. The probabilities of burning increase with the age of the forest. Other alternative patterns of the probability vector result in patterns of distribution of fractions of area burned per year different to the observed ones.
3. The deterministic mechanism of auto-coordination of the forest is insufficient to explain the phenomenon of major fires (because such big differences in values of burning probabilities between stages is hardly probable); so there should be a combination of auto-coordination and fluctuations of climatic parameters that affect forest dynamics. Simultaneously this fact indicates the direction of future investigations: to take as a starting point a vector of burning probabilities of the type obtained in our model (i.e. with values increasing with forest age) and to add random fluctuations of climatic parameters in accordance to their statistical distributions constructed with the help of long-term observations.

In Antonovski, Glebov, Korzukhin (1987) an attempt was made to model in qualitative terms the dynamics of an entire forest and bog ecosystem which includes abiotic and biotic components. The former was the thickness of the peat deposit and the latter was the fraction of hygrophytes in the total phytomass. The dynamics of these two variables modeled by formalizing the associated ecological mechanism, was the main line of this research.

The proposed model describes simultaneously the process mechanism for an ecosystem and its regional setting because it is referenced to basic types of ecological conditions to be found in the chosen area.

The bog-formation proceeds in two qualitatively different phases. The first is exogenetic in that the system develops under the impact of exogenous forced watering which reduces aeration. The characteristic time of climatically dictated bogging-debogging fluctuations ranges from several to 200 years. The horizontal bogging rates are as high as meters per year.

The second phase is endogenetic in which the gradual bogging fluctuates relatively little at a horizontal rate of centimeters per year. For this reason, the bogging is irreversible with usual climatic variations (against whose background exogenesis occurs) but is reversible over large time spans during which the bog ecosystems are influenced by the specifics of mire development, i.e., when regional aspects become important. The peat deposit and the impermeable horizon may be said to be the "memory" making the system stable. The exogenous watering effect may be reduced with peat accumulation preserved. This phase covers the remaining part of the hydromorphic series in the exogenetic succession of marshy forest → forested bog → open bog → lake-and-bog complex.

APPENDIX

Among the huge set of models described above we will now give more detailed information on the basic model FORET.

The structure of the inner stream of data and the structure of organization of interrelation of modules of model FORET show that the imitation of successional progress of regeneration of forest stand is essentially a realization of computer procedure of the system of equations. In the model FORET, the yearly increase in the diameter of a tree is defined by the expression (for notation see Shugart, 1984)

$$\Delta_t D_i = BIOM(t) \cdot DINT_i(t) \cdot SMGF_i(t) \cdot I_j(t) \cdot \Delta D_i(t)\,. \tag{*}$$

This system of equations is completed by the equations of functional dependence of values of the seeking variable from other variables of the system and also by the constraints that we put on values of variables of the system, for example, zero increase in diameter in the case of a cold winter.

The simulation of successional processes in the model is realized by using the results of studies of the life cycle of a tree: birth, growth and death. The reconstruction of a gap in a forest stand is supported by module PLOTIN (Shugart, 1984). By the end of a simulation of one life cycle, the existence of gaps is determined. If such a gap exists, then the model starts up again with module PLOTIN until all gaps are filled.

The feature of the given system of equations is the time dependence of a number of equations in this system. The set of equations is subdivided into two sub sets having the numbers $N_1(t-1)$ and $N_2(t-1)$ i.e, $(N(t-1) = N_1(t-1) + N_2(t-1)$. The first subset consists of equations whose solution up to time t do not involve disturbance of the condition of intersection of the lower bound of the interval of the permissible value of $\delta D(t)$; the second subset contains all cases in which such a disturbance has taken place. Each of these two subsets is, in turn, subdivided on j mutually non-intersecting subsets of equations, the solution of which are defined by a set of values of parameters characterized for each subset. In our case this corresponds to a subdivision of the modelled forest stand into separate species. So we have

$$N(t-1) = \sum_{j=1}^{N_{SPEC}} N_{1j}(t-1) + \sum_{j=1}^{N_{SPEC}} N_{2j}(t-1)$$

Selection of excluded equations before starting computation at time t is realized with some probability p_{1j} for each subset and inclusion of equations of the second-type is realized with probability p_2. Moreover, from the logic of the program organization of the procedure for excluding equations from the system, it follows that the formal model for exclusion is:

$$\begin{aligned} N^-(t) = & \sum_{j=1}^{N_{SPEC}} p_{1j} N_{1j}(t-1) + \sum_{j=1}^{N_{SPEC}} p_{1j} N_{2j}(t-1) \\ & + p_2 \Big(\sum_{j=1}^{N_{SPEC}} N_{2j}(t-1) - \sum_{j=1}^{N_{SPEC}} p_{1j} N_{2j}(t-1) \Big) , \end{aligned}$$

where $N^-(t)$ is the number of excluding equations to the beginning of calculation for the moment of time t. Thus, up to time t, there exist $N(t)$ of equations:

$$N(t) = N(t-1) - N^-(t) + N^+(t) .$$

The formalization of function $N^+(t)$ is a complex independent problem. The best way to describe it as an algorithm is through BIRTH (Shugart, 1984). So the complete system of equations are (Trushin, 1986):

$$N(t) = \sum_{j=1}^{N_{SPEC}} q_{1j} N_{1j}(t-1) + q_2 \sum_{j=1}^{N_{SPEC}} q_{1j} N_{2j}(t-1) + N^+(t)$$

$$D_{ojt} = \begin{cases} 1.27 + 0.3 \cdot (1-\xi_1(t))^3 \\ 0.1 + 0.1 \cdot (1-\xi_2(t))^3 \end{cases} \quad \text{Choice of expression depends on } N^+(t)$$

$$D_{jt}(t) = D_{ojt} + \sum_{\tau-1}^{t-1} \Delta D_{jt}(\tau)$$

$$H_{jt}(t) = 137 + b_{2j} D_{jt}(t) - b_{3j} D_{jt}^2(t)$$

$$B_{jt}(t) = B_o D_{jt}^{B_1}(t)$$

$$\varphi_{1j}(t) = 1 - \frac{\sum_{j=1,t}^{N(t)} B_{jt}(t)}{SOILQ}$$

$$\varphi_{2j}(t) = 4 \cdot \frac{(DEGD(t) - DMIN_j)(DMAX_j - DEGD(t))}{(DMAX_j - DMIN)^2}$$

$$\varphi_{3j}(t) = 1 - \frac{FJ(t)}{D3_j}$$

$$A_{ji}(t) = A_0 D_{ji}^{A_1}(t)$$

$$Q_i(t) = Q_0 e^{-0.25 \cdot \sum_{j, D_k > D_i} A_{jk}(t)}$$

$$I_{ji}(t) = \begin{cases} 2.24(1 - e^{-1.136 \cdot (Q_i(t) - 0.08)}) & \text{for } j \text{ to light species} \\ 1 - e^{-4.64 \cdot (Q_i(t) - 0.05)} & \text{for } j \text{ to shadow species} \end{cases}$$

$$X_{ji}(t) = g_i D_{ji}(t) \frac{\dfrac{1 - D_{ji}(t) \cdot H_{ji}(t)}{D_{\max} \cdot H_{\max}}}{274 + 3b_{2j} D_{ji}(t) - 4b_{3j} D_{ji}^2(t)}$$

$$\Delta D_{ji}(t) = \begin{cases} \varphi_{1j} \cdot \varphi_{2j} \cdot \varphi_{3j} \cdot I_{jk} \cdot X_{ji}(t) \\ 0, \text{ under the complex of conditions } \Omega_{ji}(t) \end{cases}$$

The modelled value of growth at each moment of time is proportional to the function X_{ji}, defining the increase of tree diameter in optimal environmental conditions. The functions $\varphi_{1j}(t)$ and $I_{ji}(t)$ define the decrease in this optimal value of growth due to competition with other trees for soil nutrients and light energy. The functions $\varphi_{2j}(t)$ and $\varphi_{3j}(t)$ define the decrease of "real" growth as a consequence of changes in external factors such as air temperature and soil humidity.

As mentioned previously, the model FORET is devoted to simulation of the process of forming a mature forest stand in some physio-geographical setting through regeneration of the forest stand via filling up the forest gaps. It is clear from the system of equations how to include anthopogenic pollution and how to develop FORET in other directions.

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