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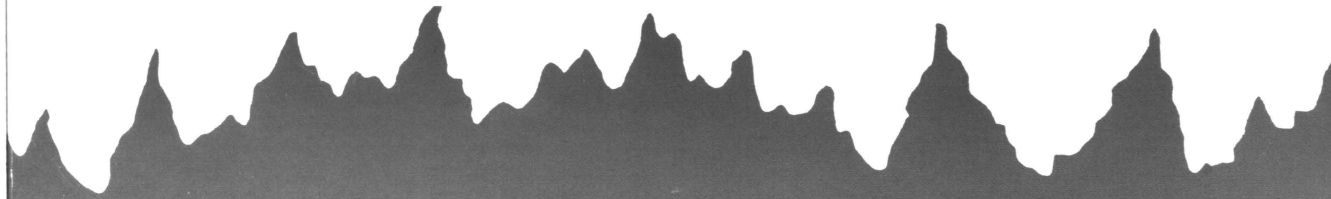

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AIM AND SCOPE - TAVOITTEET JA TARKOITUS

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Simulations on the occurrence of dead trees in natural pine stands

Seppo Kellomäki, Taneli Kolström, Esko Valtonen & Hannu Väisänen

TIIVISTELMÄ: EKOLOGISEEN MALLIIN PERUSTUVIA LASKELMIA KUOLLEIDEN PUIDEN ESIINTYMISESTÄ LUONTAISESTI KEHITTYVISSÄ MÄNNIKÖISSÄ

Kellomäki, S., Kolström T., Valtonen, E. & Väisänen, H. 1989. Simulations on the occurrence of dead trees in natural pine stands. Tiivistelmä: Ekologiseen malliin perustuvia laskelmia kuolleiden puiden esiintymisestä luontaisesti kehittyvissä männiköissä. Silva Fennica 23(3): 203–214.

The study aimed at recognizing the phases of forest succession where dead trees most probably occur. The model simulations showed that the increasing occurrence of dead trees culminated after the canopy closure. Thereafter the occurrence of dead trees decreased representing a pattern where high frequency of dead trees was followed by low frequency of dead trees, the intervals between the peaks in the number of dead trees being in southern Finland about 15–30 years. Around this long-term variation there was a short-term variation, the interval between the peaks in the number of dead trees being 2–4 years. This pattern was associated with the exhausting and release of resources controlled by the growth and death of trees.

Mallilaskelmiin perustuva tarkastelu osoitti kuolleiden puiden määrän kasvavan luontaisissa männiköissä, kunnes puusto sulkeutui ja kuolleiden puiden määrä alkoi vähetä. Tämä kulminoituva trendi selitti pääosan kuolleiden puiden esiintymisestä. Kuolleiden puiden esiintymisessä oli myös jaksollisuutta, jossa kuolleiden puiden suurta frekvenssiä seurasi pieni frekvenssi. Spektrianalyysissä selvimpinä erottuivat 2–4 ja 15–30 vuoden jaksot. Jaksollisuus oli yhteydessä kasvutilan loppumisen ja vapautumisen jaksottaiseen vaihteluun, jota puiden kasvaminen ja kuoleminen säätelivät.

Keywords: mortality, succession, *Pinus sylvestris*, time series.
ODC 238.8+174.7 *Pinus sylvestris* + 562.22

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1. Introduction

The effects of air impurities on the boreal forest ecosystem are still poorly understood, as indicated by contradicting estimates of the future development of the forest ecosystem. For example, Hari and Raunemaa (1983) expect that the productivity of boreal forests will increase in the near future due to nitrogen deposit. In the long run the enhanced growth rate, however, accelerates the detrimental effects of air impurities, giving rise to decreasing productivity and excess tree death compared to the conditions not affected by air impurities (Katainen et al. 1983, Nilsson 1987). One of the basic problems in studying the tree death under the influence of air impurities is to make distinction between the natural tree death due to succession of tree stand, the natural variation of environmental factors and the tree death induced by air impurities (Materna 1983).

The natural succession of a tree stand is determined by the life span of trees, i.e. the birth, growth and death of trees as controlled by the prevailing environment. In early succession the death of trees is closely related to the exhausting of resources due to *competition* (Mäkelä and Hari 1986). This is especially true at the canopy closure. In the late succession the aging of trees with increasing occurrence of insect and fungus attacks will also accelerate the tree death (Kulman 1971). Thus, the tree death at the late succession could be more related to the *life cycle* of trees than to the resource availability as in the early succession (Waring & Schlesinger 1985). The death induced by insect and fungus attack can also be regarded as a *random process,* since the outbreak of insect and fungus diseases is quite unpredictable like windblow and destruction by snow (Monserud 1976).

Modelling of tree death in studies of forest succession and growth and yield are based on one or several reasons listed above. For example, Walters (1969), Monserud (1976) and Buford and Hafley (1985) apply models which are based on the random tree death given the dying probability of a tree as a member of the whole tree stand or its subpopulation specified in terms diameter distribution or tree position (see also Hamilton & Edwards 1976). Valen (1975) applies the same approach, but the probability of trees to die increases as a function of tree age in accordance with the life cycle of a tree. The self-thinning models based on the -3/2-power law (Yoda et al. 1963) are the most popular way to describe the effects of competition on the tree mortality (e.g. Lonsdale & Watkinson 1983, Hara 1985, Oker-Blom et al. 1988). This approach implies the exhaust of the resources being the reason of tree death, but it does not specify the competition process in terms of resources. Mäkelä and Hari (1986) determine the tree death induced by the competition more explicitly, and relate the tree death to the availability of light and, thus, the availability of carbohydrates for growth.

In growth and yield studies trees are quite often assumed to die at a constant rate, thus, implicating the preference to model the tree death as a random process (Hamilton & Edwards 1976). However, there is evidence that the death rate of tree could vary according to the phase of the stand development. For example, the study by Sirén (1955) on the development of *Picea abies* stand on raw humus sites in northern Finland shows that the tree death during the succession could be cycle in time step of decades or longer as derivable on the basis of the life span of trees and the availability of the resources. The similar pattern is also recognized by Sprugel (1976) for *Abies balsamifera* in eastern United states and Hett and Loucks (1976) for *Tsuga canadensis* indicating the wave pattern in the regeneration of tree stands. The possible variability in death rate could make it particularly difficult to make the distinction between different causes of tree death.

The death pattern related to the life span of trees is probably magnified by the resource competition as implied by the models related to the self-thinning law, since the death of a tree or trees releases resources for the remaining trees improving their survival. This does not eliminate the role of life span and the pure random factors being inducing tree death. We assume that this justifies one to describe the total pattern of tree mortality as a process related to the factors derivable from the competition, life span of trees and pure random phenomena.

This study aims at recognizing the patterns of tree death as related to the successional dynamics of the forest ecosystem and the occurrence of dead trees in a tree stand at different phases of the stand development assuming that the life span of trees and the resource availability are the main factors controlling the death rate. The study is based on a computer model, which allows the biological properties of trees and the climatic conditions to affect the death rate.

This study is supported by a grant (No. 387/422/86) from the Ministry of Environment as a part a nation-wide project to recognize the effects of acid deposition on the terrestrial and aquatic ecosystem. We also acknowledge the help given by Mr. Matti Häkkinen, Mr. Mika Smolander and Mr. Timo Pukkala in different phases of the analysis and in compiling the manuscript. Prof. Pekka Kilkki, Dr. Annikki Mäkelä and Dr. Risto Sievänen have read the manuscript several times. We acknowledge this support which has made the manuscript more readable in many respects.

2. Methods

21. Outlines

We applied the simulation model developed by Aber and Melillo (1982), tailoring it for the boreal conditions within the 60th and 70th latitudes in Finland. It incorporates four submodels representing the birth, growth and death of trees and decomposition of litter and humus in soil compartments on an area of 100 m² (Fig 1). Tree growth is based on optimal growth of individual trees modified by the temperature conditions and the availability of light, water and nutrients. The regeneration and death of trees depend also on the state of the tree stand and the environment. In the present computation the birth procedure was excluded out of the consideration and, hence, out of the model description, since the survival (death) of a particular tree cohort was followed in the computations. The results are presented as mean values of several simulations representing the same stand. All the computations represent pure, even-aged Scots pine (*Pinus sylvestris*) stands growing on sites of *Myrtillus* type being of the medium fertility in Finnish conditions.

22. Tree growth

Actual and potential growth

The modelling of the tree growth is based on the radial growth and the allometric relations between stem diameter and the biomass of different tree organs. The *actual radial growth* (1.3 m above ground level) of a tree (Y) is a product of the potential radial growth (Y_O) (1.3 m above ground level) and growth multipliers, which depend on the temperature conditions (T) and the availability of light (I), water (W), and nitrogen (N) as follows

$$Y = Y_O \cdot Y_I \cdot Y_T \cdot Y_W \cdot Y_N. \qquad (1)$$

The multipliers Y_I, Y_T and Y_W have values within the range [0,1], and Y_N varies within [0,2]. The growth multipliers affect the radial growth of the breast height diameter, which is used for the incorporation of the environmental effects on the other components of tree biomass (foliage, branches and roots) with the help of ordinary allometric relations (see for example Ogawa & Kira 1977) between stem diameter and the biomass of different tree organs. The models for the allometric relations are not described here, but their parameters are given in Table 1. with the reference to the study utilized in the estimation of the parameters.

The *potential radial growth* [mm] of a tree (Y_O) is the radial growth not limited by temperature conditions and the availability of light, water and nitrogen. This situation could hold for solitary trees, but growth measurements for the whole life span of such trees are not available for trees growing on forest land. Therefore we assumed that the values of the potential radial growth equal to values of the empirical measurements (Y_E) on the radial growth [mm] of stand-grown trees multiplied by the maximum values of the growth multipliers Y_I, Y_T, Y_W and Y_N, i.e.

$$Y_O = Y_E \cdot Y_{Imax} \cdot Y_{Tmax} \cdot Y_{Wmax} \cdot Y_{Nmax}. \qquad (2)$$

Since $Y_{Imax} = 1$, $Y_{Tmax} = 1$, $Y_{Wmax} = 1$ and

$Y_{Wmax} = 2$, the potential radial growth can be written as a function of the stem diameter (1.3 m above ground level) as follows

$$Y_O = 2 \cdot Y_E, \text{ where } Y_E = G \cdot D \cdot e^{DGRO \cdot D} \tag{3}$$

The values of the parameters G and DGRO were estimated based on the values of the mean radial growth (Y_E) obtained from the growth and yield tables for the natural Scots pine stands on *Myrtillus* sites (Koivisto 1959, Table 12 by Koivisto) (Table 1).

Growth multipliers

The effect of *light* on potential growth indicates a between-tree competition for light, since light received by a particular tree will be attenuated when passing through the crowns of trees taller than this particular tree. The relative light (fraction of that above the canopy) was computed as follows (Table 1)

$$AL = e^{-SL/SLA}, \tag{4}$$

where AL is the relative light [0...1], SL the amount of foliage passed by light [kg/ha] and SLA a parameter [ha/kg]. The growth multiplier (Y_I) introducing the between-tree competition into the model (1) was computed as follows (Table 1)

$$Y_I = A1 \cdot (1 - e^{A2(AL-A3)}), \tag{5}$$

where A1, A2 and A3 are parameters [dimensionless]. The values of the parameters match the shape of the photosynthetic-light response curve for any shade-intolerant tree species like for Scots pine (Larcher 1983, pp. 41-43).

The dependence of growth on *temperature* was described with the help of the growth multiplier (Y_T) which is a function of the effective temperature sum (threshold 5°C) as follows (Botkin et al. 1972) (Table 1)

$$Y_T = \frac{4 \cdot (DMAX-X) \cdot (X-DMIN)}{(DMAX-DMIN)^2} \tag{6}$$

where DMIN is the minimum value of the temperature sum [d.d.] and DMAX the maximum value of the temperature sum [d.d.] making it possible for a particular tree species to survive and X the temperature sum [d.d.]. The maximum and minimum values of the temperature sum were estimated on the basis of the geographical spreading of Scots pine (Sarvas 1964), the minimum and maximum values of the temperature sum determining the area possible for Scots pine to survive. Thus, the range of temperature sum 650-1300 d.d characterizing the Finnish territory represents a suboptimal area for Scots pine growth ($Y_T < 0.6$) in our computations.

The *water* available for growth was des-

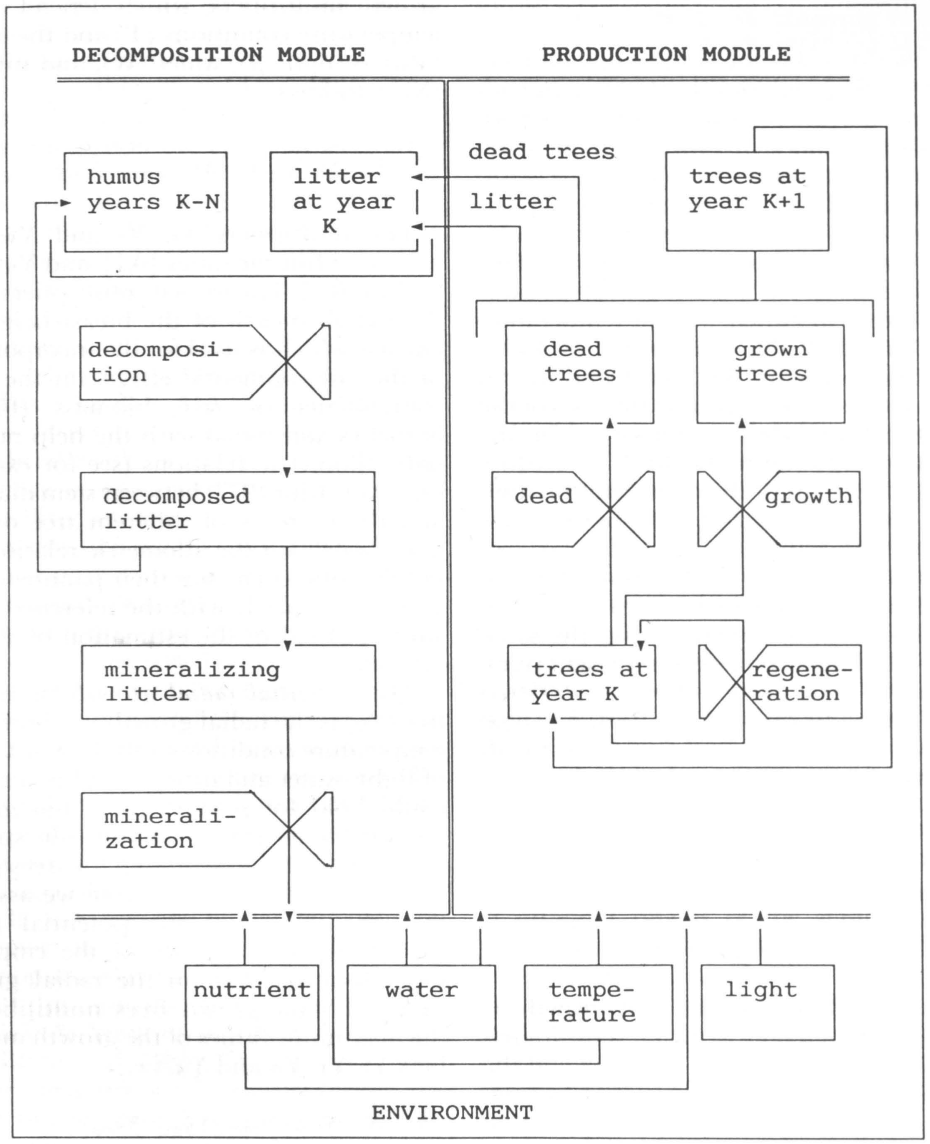

Fig. 1. General description of the Fornite model (Aber &Melillo 1982).

Table 1. The parameters of the applied simulation model. The decimal numbers in parenthesis in the column Explanation refer to the proper equations. The other numbers in the same column indicate the reference given below the Table. The alphabet f indicates the factor being the function of the dimension in question.

Parameter	Value	Explanation	Parameter	Value	Explanation
G	0.372	Parameter for Y_0 (2) (1)	TC	3	Nitrogen in foliage litter
B2	1.2	Dependence of tree height on	SA	0.022	Stem mass f($D_{1\cdot3}$)
B3	0.19	$D_{1\cdot3}$	SB	0.9403	(2)
LFWT	634.7	Unit mass of foliage (2,3,4)	BA	0.042	Branch mass f($D_{1\cdot3}$)
DMIN	650	Temperature sum (5)	BB	2.158	(2)
DMAX	4000	- " -	RA	0.0081	Root mass f($D_{1\cdot3}$)
WMIN	150	Evapotranspiration (6)	RB	2.8242	(2)
WMAX	600	- " -	SLTA	0.80	Width of crown f($D_{1\cdot3}$)
RTST	0.3	Root/Shoot ratio (2,3)	SLTB	0.119	(3)
DIMX	80	Maximum $D_{1\cdot3}$	N1	2.94	Parameter for Y_N (8)
AINC	0.01	Lower limit of growth of $D_{1\cdot3}$	N2	-.00204	- " -
AGMX	400	Maximum age (9)	N3	217.52	- " -
SAPN	40	Pot. number of new seedlings	N4	-1.2	Parameter for Y_N (7)
LMAX	0.4	Lower limit for rel. light	N5	1.3	- " -
A1	0.99	Parameter for Y_I (4)	DGRO	-0.1069	Parameter for Y_0 (2) (1)
A2	-5.1	- " -	SLA	15500	Attenuation of light (3)
A3	0.0286	- " -			

Sources: (1) Koivisto 1959, (2) Mälkönen 1974, (3) Jakobsons 1970 cribed with the help of evapotranspiration, which affects growth through the growth multiplier (Y_W) as given in Equation (7) (Botkin et al. 1972) (Table 1),

$$Y_W = \frac{4 \cdot (\mathrm{WMAX}-\mathrm{X}) \cdot (\mathrm{X}-\mathrm{WMIN})}{(\mathrm{WMAX}-\mathrm{WMIN})^2} \qquad (7)$$

where WMAX is the maximum value of the evapotranspiration [mm], WMIN the minimum value of evapotranspiration [mm] making it possible for a particular tree species to survive, and X the evapotranspiration [mm]. The values of the parameters were estimated as those for temperature.

The growth multiplier for *nitrogen* (Y_N) is a function of the nitrogen concentration of foliage as given in Equation (8) (Table 1)

$$Y_N = (\mathrm{N4}+\mathrm{N5} \cdot \mathrm{CONN})/1.7, \qquad (8)$$

where N4 and N5 are parameters and CONN is the nitrogen concentration of leaves and needles [% of dry weight] given in Equation (9) as a function of the available nitrogen (ammonium and nitrate)

$$\mathrm{CONN} = \mathrm{N1} \cdot (1-10^{\mathrm{N2} \cdot (-170+4000 \cdot (\mathrm{AVAILN}+\mathrm{N3}))}), \qquad (9)$$

where N1 [dimensionless], N2 [ha/kg] and N3 [kg/ha] are parameters and AVAILN the amount of nitrogen available for growth [kg/ha] (Mitchell & Chandler 1939, Aber et al. 1978, 1982). The values of the parameters are the same as those used by Aber and Melillo (1982) for pines comparable with Scots pine.

23. Decomposition

The nitrogen availability is a function of the nitrogen *deposition* and *decomposition* and *mineralization* of litter and humus. Deposited nitrogen is added to the nitrogen mineralized from humus and mineral soil (humus in mineral soil), the total sum of these components being equal to the nitrogen available for the tree growth. Decomposing litter is treated in cohorts representing each type of litter, i.e. stems, branches, twigs, foliage and roots. The *decomposition rate* of litter (K) [dimensionless] is dependent on the lignin (L) and nitrogen (N) concentration [%] (foliage, twigs, fine roots) or on its size (woody litter) as follows

$$\mathrm{K} = 0.79 - 0.3 \cdot (\mathrm{L}/\mathrm{N}) \qquad (10)$$

or

$$\mathrm{K} = 0.13 - 0.014 \cdot \mathrm{DIAM} \qquad (11)$$

where DIAM is the mean diameter [mm] of the size class of a particular type of woody litter [the dimension of the parameter 0.014 being mm^{-1}].

A part of the nitrogen released in decomposition is immobilized in decomposition processes. Non-woody litter immobilizes nitrogen as a function of its nitrogen and lignin content. Woody litter does not immobilize nitrogen until only 20 % of its initial weight remains. Thereafter litter is transfered to a new cohort of well-decayed wood, which decomposes and immobilizes nitrogen in linear relation to its lignin and nitrogen content.

The *mineralization* will onset, if the nitrogen concentration of any type of litter exceeds 2 % of the dry weight. At this moment of the remaining weight of litter and nitrogen is transfered to the humus layer (F and H layers). Nitrogen mineralization from humus is proportional to weight loss (9.6 % per year). This is multiplied by the decomposition multiplier (MCMLT) [dimensionless], which increases decomposition under canopies of low leaf area as follows

$$\mathrm{MCMLT} = 1 + 1.5 \cdot ((1 - \mathrm{LFWT}/2.8))^{0.5} \qquad (12)$$

where LFWT equals to the total foliage weight of the canopy [t/ha], the dimension of the parameter 2.8 being [ha/t]. This function simulates the response of decomposition rate to the disturbances like tree death which enhances the decomposition rate through the improvement of environmental conditions for decomposition (e.g. improvement of temperature conditions and water supply).

24. Death of trees

The model for the tree death is based on the effects of the environmental factors combined with the life span of trees and pure random factors. In the case of seedlings (height < 1.3 m), the survival of the seedlings is a function of the available nitrogen, evapotranspiration, temperature sum, prevailing light conditions on the forest floor and the shade tolerance of the tree species (Table 1). The survival of the taller trees (height > 1.3 m) is expressed as a probability of death, which is a function of the radial growth and the maximum age of the tree species, the function of the radial growth introducing the effects of the growth multipliers into the death process (see Equation 1). If the amount of the radial growth is greater than 0.01 mm/a, the probability of death (C), is

$$\mathrm{C} = 4/\mathrm{AGMX}, \qquad (13)$$

where AGMX is the maximum age of a tree species [a]. Thus, the radial growth > 0.01 mm results in the constant death rate equal to 0.01. If the radial growth is smaller than 0.01 mm/a, the probability of the death is 0.37, which is common in cases of the suboptimal supply of resources. If the age of a tree is equal to the maximum age, the tree will die (Table 1).

25. Simulations

The computations represent conditions in southern and northern Finland so that the values of the temperature sum (threshold 5 °C) 1300 d.d (southern Finland) and 900 d.d. (northern Finland) were combined with the values of 300 mm (dry) and 400 mm (moist) of the evapotranspiration. The nitrogen input was assumed to be 10 kg/ha/a as it was the case of the nitrogen mineralization from the mineral soil. The initial stand in the computations was a pure Scots pine stand with a density of 9600 stems of equal size per hectare and the diameter of 1.0 cm at the breast height not considering the time to achieve this height. For each combination of temperature sum and evapotranspiration the number of dead trees is given as a function of time elapsed since the onset of the simulation. The simulations were extended over 200 years in southern and 500 years in northern Finland. The results are given as mean values of eleven separate simulations, since the submodel for the tree death will result in a variable output in each separate model run (see Equation (13)) and the manner how the environment affects the growth and death of trees.

3. Analysis of simulation output

Dead trees appeared in the model stands already at the early succession both in southern and northern Finland (Fig. 2). In particular, in southern Finland most trees died during the first 50 years. The death of trees started and attenuated slower in northern than in southern Finland. The death rate was greater in humid and warm conditions than in dry and cold conditions where the death of trees was prolonged. It was apparent that dead trees could occur during a prolonged period in dry and cold conditions, whereas in humid and warm conditions most trees die within a relatively short period.

The general pattern of the occurrence of dead trees resembled an attenuating wave with the peak number of dead trees just after the canopy closure. A time series analysis was applied to this time series in order to recognize, if there could exist any systematic short-term variation around this

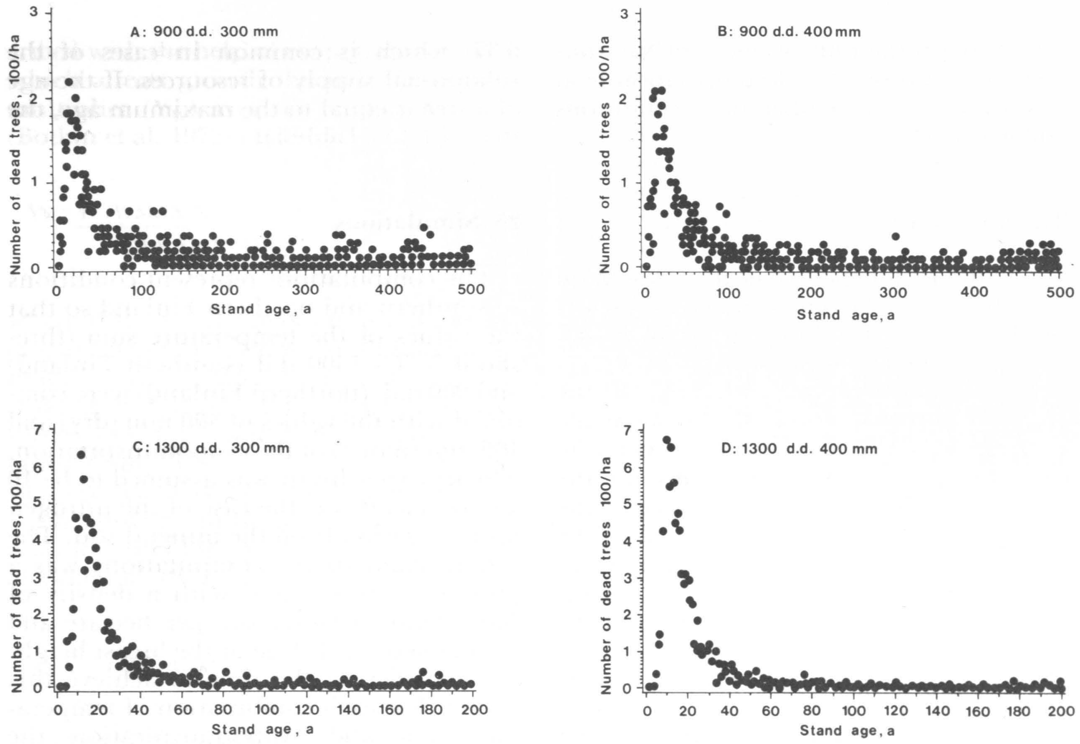

Fig. 2. Occurrence of dead trees during the succession as a function of climatic conditions. A: 900 d.d., 300 mm. B: 900 d.d., 400 mm. C: 1300 d.d., 300 mm. D: 1300 d.d., 400 mm.

pattern in the occurrence of dead trees. For this purpose the time series was differenced once

$$z_t = y_t - y_{t-1}. \tag{14}$$

Thereafter the values of z_t were analyzed using the power spectrum as described shortly by Box and Jenkins (1970, pp. 36–45) and more completely by Jenkins and Watts (1968). The power spectrum of z_t was estimated using the FTFREQ subroutine in the IMSL Library (The IMSL Library, Volume 1 1984). In FTFREQ, the estimates are first computed by

$$PS(I) = \frac{2}{\pi} \cdot \left(\frac{ACV(0)}{2} + \sum_{j=1}^{M-1} ACV(j) \cdot \cos((I-1) \cdot j \cdot \pi/M) + ACV(M) \cdot \cos((I-1) \cdot \pi)/2\right) \tag{15}$$

and then smoothed using a Hamming window.

In Equation (15) ACV(j) is autocovariance of the series at lag j, M number of observations and I = 1...M. In order to compare the results of each scenario, the spectrum was normalized by dividing it by the variance. The resulting function g(i) = PS(i)/var(z) is called the spectral density function. The spectral density function for each scenario is shown in Fig. 3, where the inverse value of the frequency gives in years the length of a possible cycle.

The values of the spectrum density vary substantially within the frequency range of 0.25-0.5. This equals to the interval of 2-4 years in cycling indicating that there is substantial short-term variation in the death of trees. In southern Finland there is an additional peak within the frequency range of about 0.03-0.08. This represents the interval of about 15-30 years in cycling. Hence, the variation in the occurrence of dead trees was smaller in dry and cold than in humid and warm conditions where the variation was a mixture of short- and long-term cycling in the occurrence of dead trees.

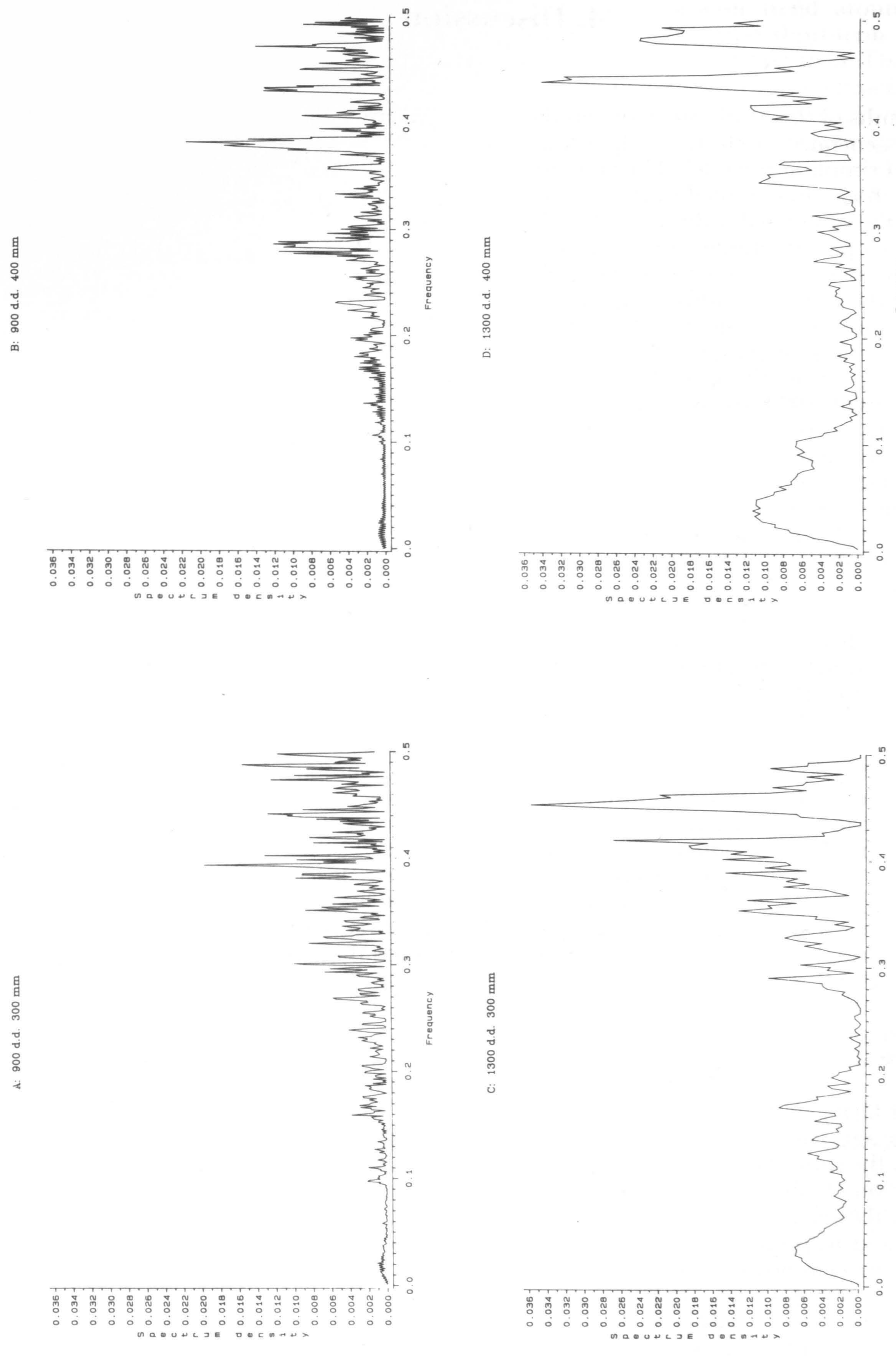

Fig. 3. Results of the spectral analysis of the time series in the occurrence of dead trees. A: Northern Finland (temperature sum 900 d.d., evapotranspiration 300 mm). B: northern Finland (temperature sum 900 d.d., evapotranspiration 400 mm). C: Southern Finland (temperature sum 1300 d.d., evapotranspiration 300 mm). D: Southern Finland (temperature sum 1300 mm, evapotranspiration 400 mm).

4. Discussion

The results of this study are based on the material generated with the help of an ecological simulation model. The validation of the model was limited to the comparison of the simulated values of growth, standing crop and number of dead trees with those given in the growth and yield tables. In the primary stands (stand age $<$ 200 a) the values of growth and standing crop were within the range of 20 percent of the values given in the growth and yield tables (Ilvessalo 1920, Ilvessalo & Ilvessalo 1975). Death of trees in simulated primary stands corresponds to that of the growth and yield tables of Ilvessalo (1920) (Fig. 4). In the simulated stand there are, however, systematically more dead trees during the first 20 years than indicated by the growth and yield tables. The opposite relations hold for the stands at the age 20-60 years.

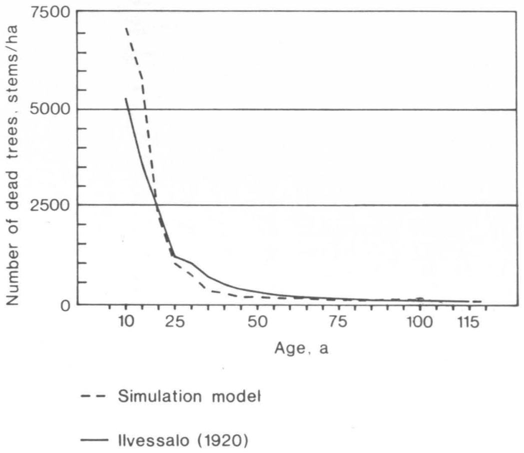

Fig. 4. The number of dead trees as a function of stand age according to simulation model and Ilvessalo (1920). The initial stand in simulation was 20 000 pines per hectare ($D_{1.3}$ = 1.0 cm).

This discrepancy can indicate a real deviation between the simulations and the empirical results or it can be the result due to the differences in the study layout. For example, the simulation output and the results by Ilvessalo (1920) given in Fig. 4 are not fully comparable, since the initial density of the stands belonging to Ilvessalo's material is not known. Therefore it is not possible to analyze, how the possible difference in the initial density of the model stand and the real stands affects the comparison. The initial stand density is known to be one of the determinants affecting the onset and the rate of self-thinning at the early development of the tree stand (e.g. Lonsdale & Watkinson 1983, Mäkelä & Hari 1986).

Another factor undermining the comparison is the age, which in the model output represents the time elapsed since the onset of simulation. At the onset the initial trees of the simulation were of one meter high. The height growth rate of the young pines (age $>$ 20 years) in dense, naturally regenerated stands is not known, but the mean height of one meter could represent the stem elongation at least during 10–15 years as derived on the basis of the stem elongation of planted Scots pines in sites of *Myrtillus* type (see Karjula et al. 1982). This correction will give the closer fit in older stands but result in increased deviation in younger stands. It remains, however, open how the age differences between the simulated stand and the real stand are affecting the validation of the model.

The growth of the trees is also affecting the mortality of trees giving an emphasis on how the growth functions and their parameters are affecting the simulation output. The parameters of Equation (3) were estimated on the basis of the growth and yield tables with a consequence that the effects of the natural removal on the radial growth were omitted in the estimation procedure. Therefore the radial growth of small suppressed trees is probably too small, since these trees represent trees most probable to die. The significance of this underestimation is probably very small in terms of stand growth, since the tall dominating trees represent the main part of the dry matter production.

The death pattern produced of the simulation scenarios are output of the same initial stand density applied in each scenario. The spacing had, however, effects on the results of the simulations. For example, wider spacing (e.g., 1000 and 4800 stem/ha) in northern Finland accelerated growth and development, but the differences between northern and southern Finland remained great representing the similar pattern as the narrow spacing (9600 stem/ha). Similarly, the parameter values of the growth and death procedures were the same in southern and northern Finland excluding genetic properties of the trees. Therefore the comparison between southern and northern Finland should be interpreted to show how a tree stand will grow and develop under a changing climatic pattern (temperature, humidity) as indicated by the mortality of the trees. Therefore, care should be taken when the results are interpreted with respect to stands representing varying initial structure and geographical distribution.

The total pattern of tree death was compiled by long-term trend around which there was substantial short-term variation in the occurrence of dead trees. This pattern can be described as an attenuating wave, where trees were dying from the very beginning of the growth and development of the tree stand, but in especially great numbers after canopy closure. The analysis of this time series gave some evidence that especially in southern Finland the periods of increased and decreased occurrence of dead trees could be cycling within periods of 15–30 years, around which there was short-term variation representing 2-4 years intervals between the peak number in the occurrance of dead trees. The cycling was controlled by the growth and death of trees, i.e. resources were exhausted by vigorous growth, thus resulting in an enhanced death of trees, which released extra resources for the remaining trees, etc. Coincidence of these two cycles could represent the tree death occurring at an expectionally high rate.

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