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## An investigation of forest succession in Bieszczady Mountains using a computer model

*Ihor Kozak<sup>1,2</sup>, Vladimir Menszutkin<sup>1</sup>*

<sup>1</sup>International Centre of Ecology, Polish Academy of Sciences  
1 Konopnickiej St., 05-092 Dziekanów Leśny, Poland

<sup>2</sup>Institute of Ecology of the Carpathians  
National Academy of Sciences of Ukraine  
4 Kozelnytska St., 79026 Lviv, Ukraine

### ■ Abstract

The study presents the results of investigation on beech, fir and spruce forest succession in Bieszczady Mountains using the FORKOME\* model. The model was verified in the field trials in 1998–1999 in the forests with dominating beech (*Fagus silvatica* L.), fir (*Abies alba* Mill.) and spruce (*Picea abies* L.) in the forest district Procisne.

For the natural beech forest the model assumes cyclic changes in the number and biomass of beech and fir in a single simulation run and Monte Carlo realisations. The cutting out of trees does not change the general tendency of the dynamics of beech and fir stands. Under the logging management only the time of this dynamics varies.

The fir stand of an average age of 72 years is the stage of succession for regeneration of the beech forest. The model assumes that after 100 years of simulation for the number of trees and 200 years for the biomass this fir stand will change into

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\* FOrest KOzak MEEnshutkin



the beech stand. The model also assumes the acceleration of beech succession in the variant with cutting out all the trees after 20 years of the model time as compared with the control variant.

The model confirmed a short-term growth of the man-made spruce forest in the Bieszczady Mountains. The transformation of the man-made spruce forest into beech forest followed by the cyclic changes in the biomass and number of trees of the beech forest and the fir forest was simulated.

## ■ Key words

beech, fir, spruce, forest, dynamics, computer model, Bieszczady Mountains

## ■ Introduction

Since the 1960s and 1970s the progressive mathematisation of the field of ecology has been developed. As a result different models of forest dynamics were constructed (Waggoner and Stephens 1970, Sullivan and Clutter 1972, Suzuki and Unemura 1974, Mitchell 1975, Horn 1975, Solomon 1977, Shugart and West 1977).

The forest gap model approach has proved to be useful in many respects (Shugart 1984). Since the early eighties many gap models, especially by Shugart and his collaborators, have been developed for different forest types (Szwagrzyk 1994). The first models (Botkin et al. 1972) were rather simple. The subsequent research led to more complicated models. These models included detailed information such as soil processes (Pastor and Post 1985), phytosociological concepts (Kienast 1987), explicit modelling of tree crown structure (Leemans and Prentice 1989), detailed treatment of ecophysiological (Friend et al. 1993) and biophysical processes (Bonan and van Cleve 1992, Martin 1992) and intraspecific competition (Pawłowski 1996).

The increasing complexity of forest gap models may have helped to make detailed and presumably more accurate projections of forest succession. An ecological model of forest stand applicable in environmental conditions prevailing in Polish forest stands has been developed (Brzeziecki 1991, 1999).

The main aim of the present study is to investigate the succession dynamics of beech, fir and spruce forest in the Bieszczady Mountains under different cutting conditions using the FORKOME model.

## ■ Materials and method

Permanent research plots are situated on the north slope of Kosowiec mountain at the altitude of 750-900 m a.s.l. (Stuposiany Forest District) and inclination 14-18°. Brown soils over the Carpathian flish are characteristic of the plot. The average age of the beech stand is 92, that of fir stand 72 and spruce stand – 40 years.

In the FORKOME model we investigated the forest dynamics on small plots of 28 m × 28 m in size (Menshutkin and Kozak 1997; Kozak and Menshutkin 1999). Shugart and West (1979) and Shugart (1984) used 0.08 ha plots. The model was based upon the main



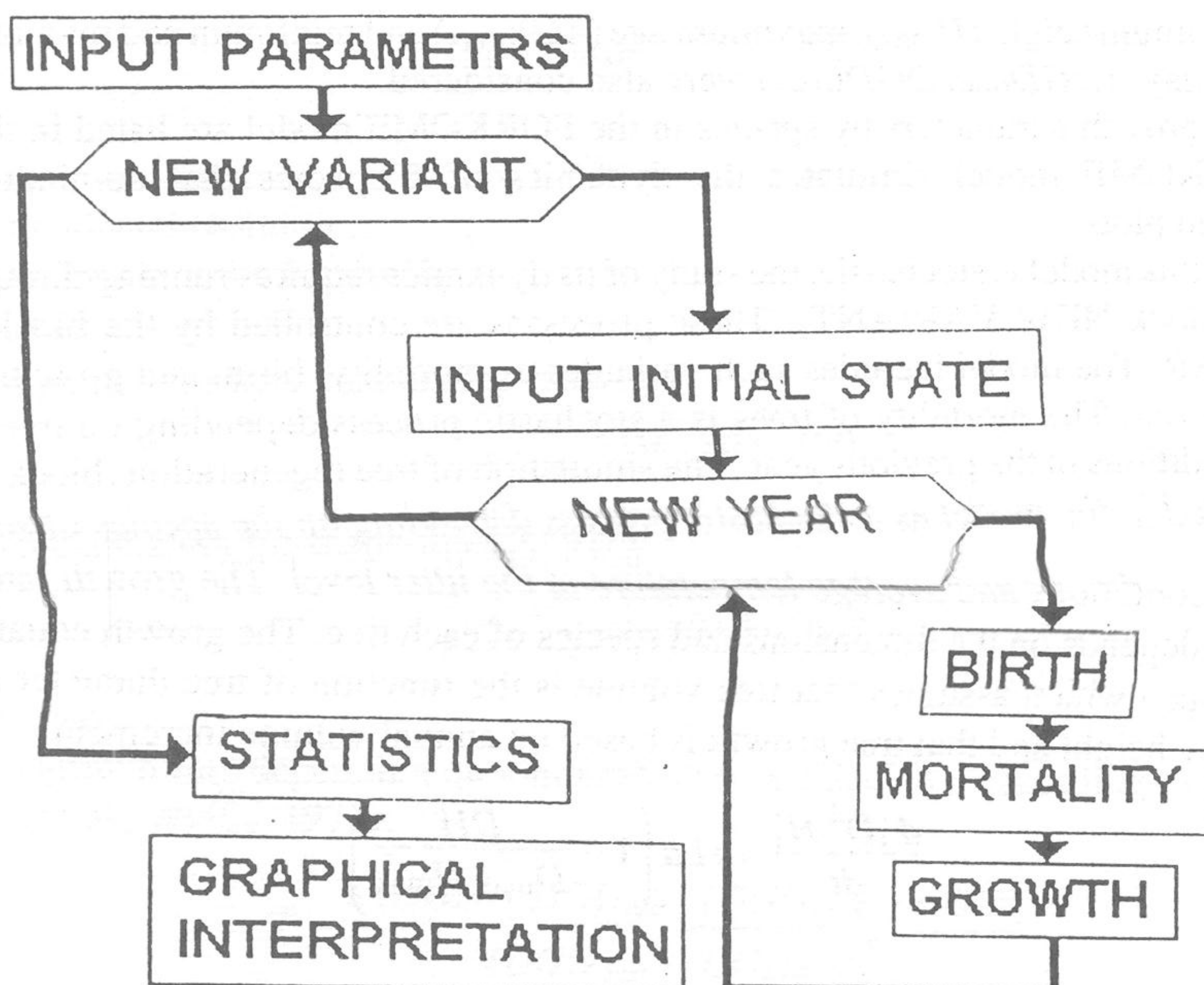


FIG. 1. Diagram of the FORKOME model algorithm

assumption, that the dynamics of the whole forest stand is a sum of processes taking place within a small unit of the size comparable to canopy gaps. In such gaps the forest dynamics was simulated.

The FORKOME model was constructed on the basis of a FORET model (Shugart and West, 1977) with authors' modifications considering, for example, temperature or other elements.

In the FORKOME model different modules (blocks) were distinguished (Fig. 1). The block "INPUT PARAMETERS" represents the estimation of tree and stand parameters such as maximum tree diameter ( $D_{\max}$ ) at a standard height of 130 cm above the ground

TABLE  
Basic growth parameters for the main tree species in the Bieszczady Mountains used in the FORKOME model

Tree species	$H_{\max}$ [cm]	$D_{\max}$ [cm]	Age [years]	$B_2$	$B_3$	$G$	$DGD$ min	$DGD$ max
<i>Fagus sylvatica</i> L.	4500	150	300	58.26	0.194	290	4650	12 700
<i>Abies alba</i> Miller	6000	150	400	78.26	0.261	200	3855	12 684
<i>Picea abies</i> (L.) Karsten	5500	150	400	71.60	0.239	370	882	3 960
<i>Betula pendula</i> Roth	3200	100	100	61.40	0.307	500	0	3 840
<i>Pinus sylvestris</i> L.	4500	150	400	58.3	0.194	330	270	2 500



level. Maximum height ( $H_{\max}$ ), maximum age ( $AGE_{\max}$ ) and minimum and maximum sums of degree-days ( $DGD_{\min}$ ,  $DGD_{\max}$ ) were also considered.

Basic growth parameters by species in the FORKOME model are listed in the Table. The FORKOME model simulates the dynamics of 5 species that dominate on the investigated plots.

Since this model is stochastic, the study of its dynamics requires running through many variants (block NEW VARIANT). These processes are controlled by the block entitled NEW YEAR. The model includes such variables as mortality, birth, and growth for each year of the run. The mortality of trees is a stochastic process depending on tree age and growth conditions in the previous year. The simulation of tree regeneration (block BIRTH) is represented in the model as a stochastic process depending on the species of seedlings, soil surface conditions and average temperature at the litter level. The growth rate (block GROWTH) depends on the dimensions and species of each tree. The growth equation has been developed which assumes that tree volume is the function of tree diameter squared times the tree height and that tree growth is based on annual volume increment:

$$\frac{d[D^2 H]}{dt} = rLa \left( 1 - \frac{DH}{D_{\max} H_{\max}} \right)$$

where:

- $r$  – growth rate parameter,
- $La$  – tree leaf area ( $m^2/m^2$ ),
- $D$  – diameter at breast height (cm),
- $H$  – tree height (cm),
- $D_{\max}$  – maximum diameter (cm),
- $H_{\max}$  – maximum height (cm).

Since the height is the function of the diameter the basic equation was simplified:

$$H = 130 + b_2 D - b_3 D^2$$

where:

$b_2$  and  $b_3$  – parameters quantifying tree form, and the constant 130 (in cm) is the breast height.

If a tree has the maximum height when it has the maximum diameter ( $dH/dD = 0$  and  $H = H_{\max}$  when  $D = D_{\max}$ ) it is possible to calculate the parameters  $b_2$  and  $b_3$ :

$$b_2 = 2 \left( \frac{H_{\max} - 130}{D_{\max}} \right)$$

and

$$b_3 = \left( \frac{H_{\max} - 130}{D_{\max}^2} \right)$$

The growth rate depends on the most important ecological agents such as light, temperature and nutrients, as well as other elements.

The light that reaches a given tree is calculated by attenuating the incidental radiation by the sum of leaf areas taller than the tree:



$$Q(h) = Q_{\max} E^{-0,25LA(h)}$$

where:

$La(h)$  – distribution of the leaf area as the height function,

$Q_{\max}$  – incidental radiation,

$Q(h)$  – radiation at the height ( $h$ ),

-0.25 – constant

The equation for light-demanding trees

$$r = 1 - e^{-1.136 [Q(h) - 0.08]}$$

and the equation for shade-tolerant trees

$$r = 1 - e^{-4.64 [Q(h) - 0.05]}$$

were used.

The growth rate depending on temperature was calculated according to the equation (Botkin, Janak, Wallis, 1972):

$$T = \frac{4 (DGD - DGD_{\min}) (DGD_{\max} - DGD)}{(DGD_{\max} - DGD_{\min})^2}$$

where:

$T$  – growth reduction due to temperature effects,

$DGD$  – base heat sum for a site,

$DGD_{\min}$  – minimum degree-day value where the species is known to occur,

$DGD_{\max}$  – maximum degree-day value where the species is known to occur.

For the block nutrient a polynomial function was used (Weinstein, et al. 1982):

$$GMF = a + b [RNA] + c [RNA]^2$$

where:

$a, b, c$  – constants estimated by the regression of field data,

$RNA$  – relative nutrient availability,

$GMF$  – the growth-modifying factor of the growth rate of trees under nutrient limitation.

In this case

$$RNA = 1 - \frac{B}{B_{\max}}$$

and

$$B = 0.1193 \sum_{i=1} D_i^{2.393}$$

where:

$B$  – actual tree biomass,

$B_{\max}$  – maximum tree biomass.



The probability of tree mortality was calculated. If  $D^{t+1} - D^t < 0.1$  cm then  $Pn = 0.368$  or

$$Pn = 1 - \left( 1 - \frac{4.605}{AGE_{\max}} \right)^n$$

The equations are open to the modification, which takes into account the influence of other agents on tree growth.

After the realisation of all variants of the model block "STATISTICS" was applied for statistical analysis of the obtained results. In the simplest case the analysis consisted of the calculation of the mean and standard deviation values, whereas in more complex cases serial- and cross-correlation functions were calculated.

The interface of the FORKOME model (Fig. 2) has different pictures for SINGLE SIMULATION RUN: "PARAMETERS", "INITIAL STATE", "SHOW GRAPHICS", and "PRINT GRAPHICS". After having pressed the left button of the mouse in the position of each tree in the picture, information about the age, height and diameter of the tree can be obtained. The right button of the mouse allows cutting out the tree.

The statistics "MONTE-CARLO REALIZATION" can simulate as much as 200 runs under the same starting and management conditions. It was accepted that 30-40 simulations were sufficient to estimate statistical parameters of the model in each variant.

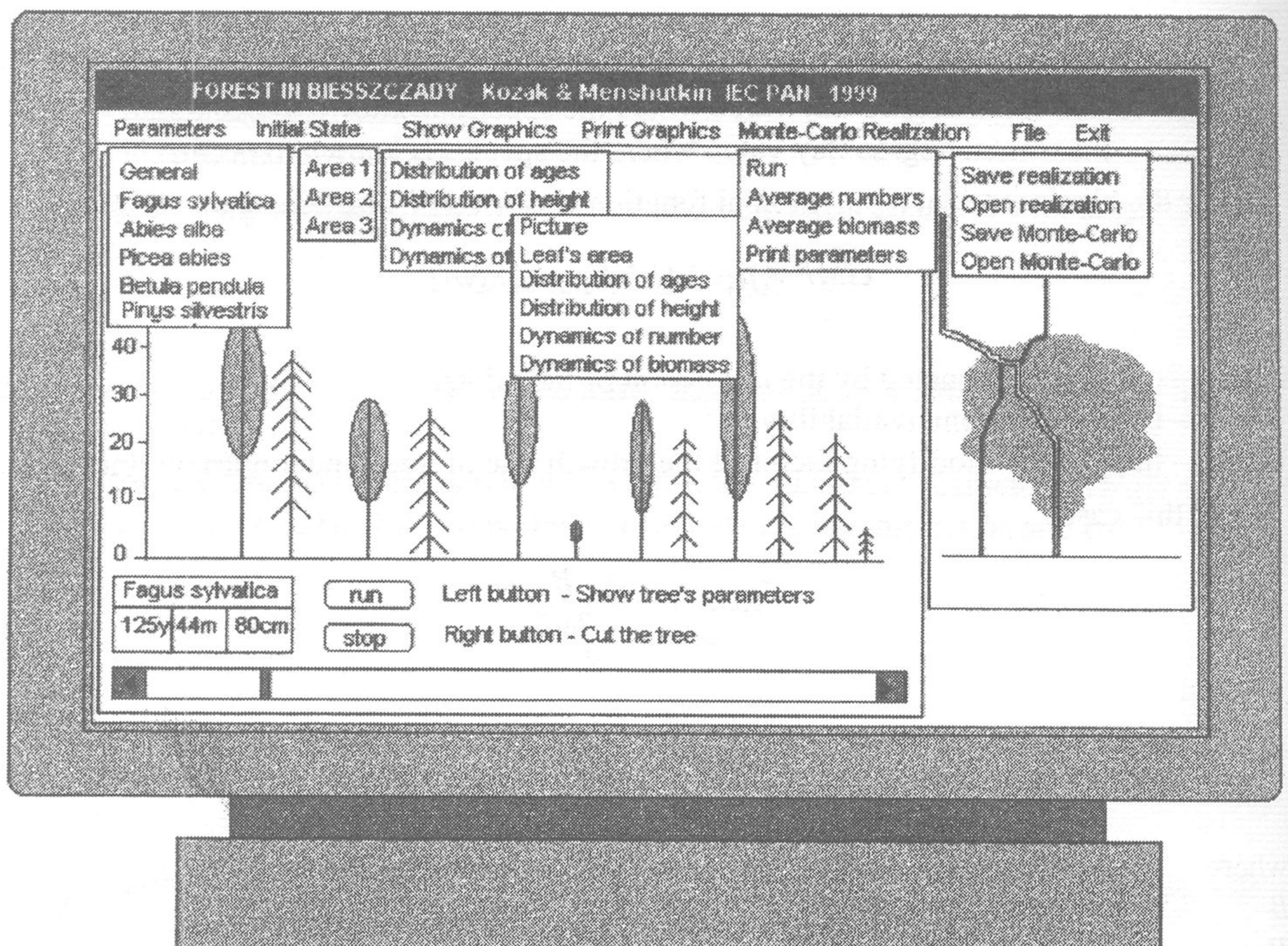


FIG. 2. Interface of the FORKOME model



The position of each tree in the forest is projected along a diagonal of research plots. The year 1999 was regarded as the first year of the model time. In the study time is used as the model time.

## ■ Results

The model assumes the dynamics of the biomasses of beech and fir in the natural beech forest in one realisation run (Fig. 3a). The cutting of beech trees after the first year (Fig. 3b) and after 20 years (Fig. 3c) of the model time did not change this dynamics. Cutting out beech trees after the first year resulted in a long-term dominance of fir.

Cutting out all the trees after the first year and after 20 years did not change the dynamics of beech and fir biomasses, either. Depending on the cutting conditions only the time in the transformation of the beech stand into the fir stand differed.

In the Monte Carlo realisation (30 simulations on the average) the model also assumes a decrease in the beech biomass in the control plots from  $400 \text{ t ha}^{-1}$  after the first year to  $140 \text{ t ha}^{-1}$  after 65 years. After reaching the minimum biomass the model assumes the tendency of the beech to increase the biomass to  $196 \pm 7.3 \text{ t ha}^{-1}$  after 130 years. The model also assumes an increase in the fir biomass from  $50 \pm 1.1 \text{ t ha}^{-1}$  in the first year to  $195 \pm 4.1 \text{ t ha}^{-1}$  in 280 years. Between 150-280 years there is fir dominance and after that time – beech dominance. In different variants of tree cutting, the Monte Carlo realisation assumes a long-term dominance of fir.

The model also assumes cyclic changes in the number of trees: beech dominated for 180 years and then fir dominated for 250 years of the model time. This transformation of the beech stand into the fir stand repeated two times in a single simulation run. Cutting out beech trees after the first year caused the dominance of fir for 120 years and the later cutting of beech trees, after the 20 years of the model time – for 150 years.

The Monte Carlo realisation assumes the dominance in the number of beech trees for 190 years. After 190-240 years fir began to dominate and after that time beech dominated for 560 years followed by fir dominance. The model assumes more domination stages of the fir when cutting the beech trees.

The fir stand with the average age of 72 years is, as the stage of forest succession, on the way to beech regeneration. The model assumes that after 120 years for the tree number (Fig. 4a), and after 200 years for biomass (Fig. 4b) this stage will change into the beech stand. In the variant with the cutting of all the trees after 20 years of the model time, the succession towards the beech stage, as compared with the control variants will be quicker.

The FORKOME model also confirms a short-term growth of the spruce. On the controlled plots the model assumes a decrease in the number of spruce trees and beech natural regeneration.

In the process of beech natural regeneration, the biomass of trees was reduced from  $82 \text{ t ha}^{-1}$  after the first year to 0 after 20 years (Fig. 5a). In the following period of time the model assumes beech dominance for 100 years.

In the variant with the cutting of all trees after the first year of the model time, the model assumes similar dominance of the beech and fir biomasses for 90 years (Fig. 5 b).

Figure 6 illustrates beech regeneration in the man-made spruce stand. After the first year of the model time, the spruce plot included 48 spruces, as well as 5 birches, 2 beeches



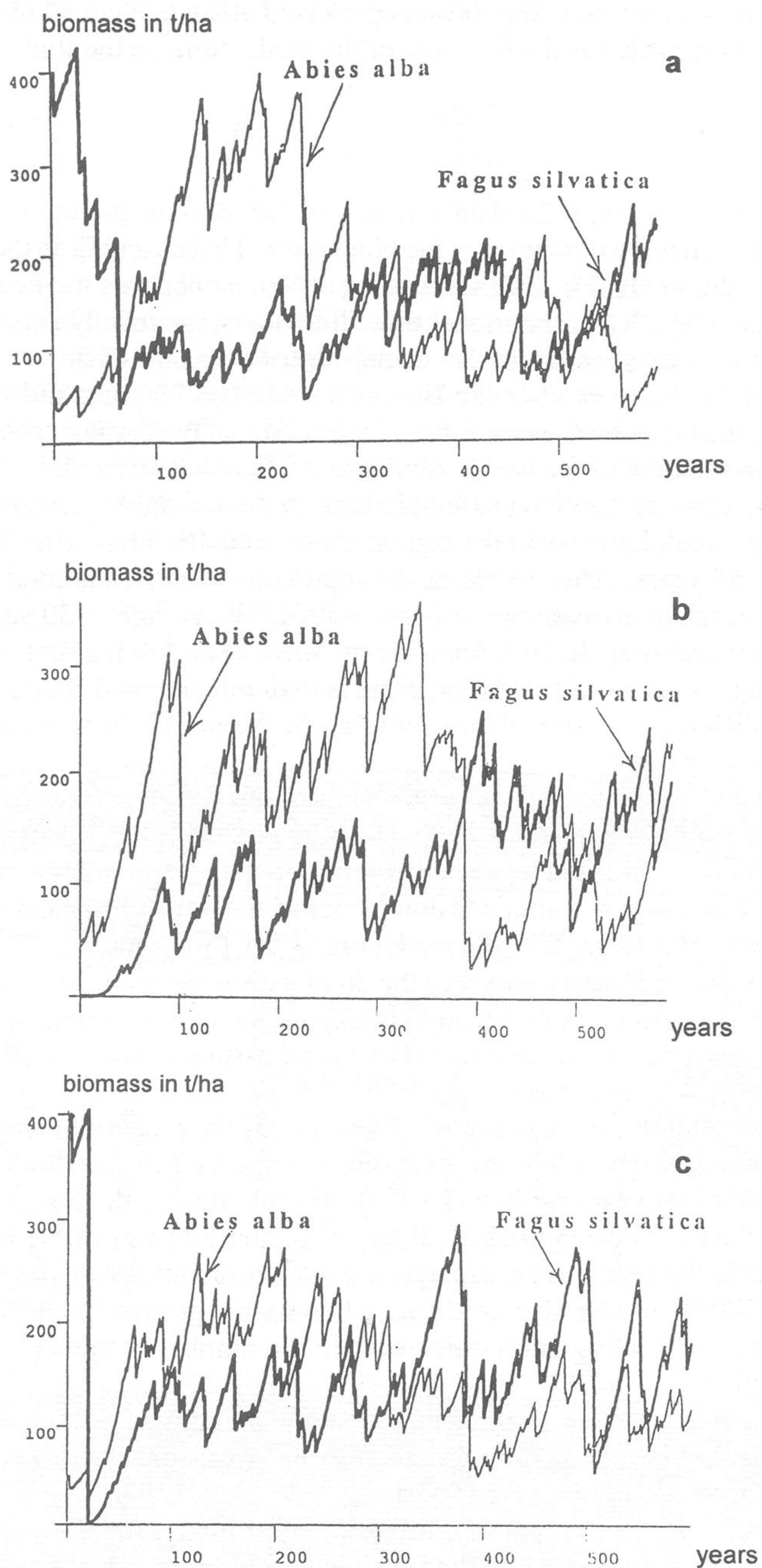


FIG. 3. Tree biomass in the beech stand; a – control, b – cutting out the beech trees after the first year of the model time, c – cutting out beech the trees after the 20 years of the model time



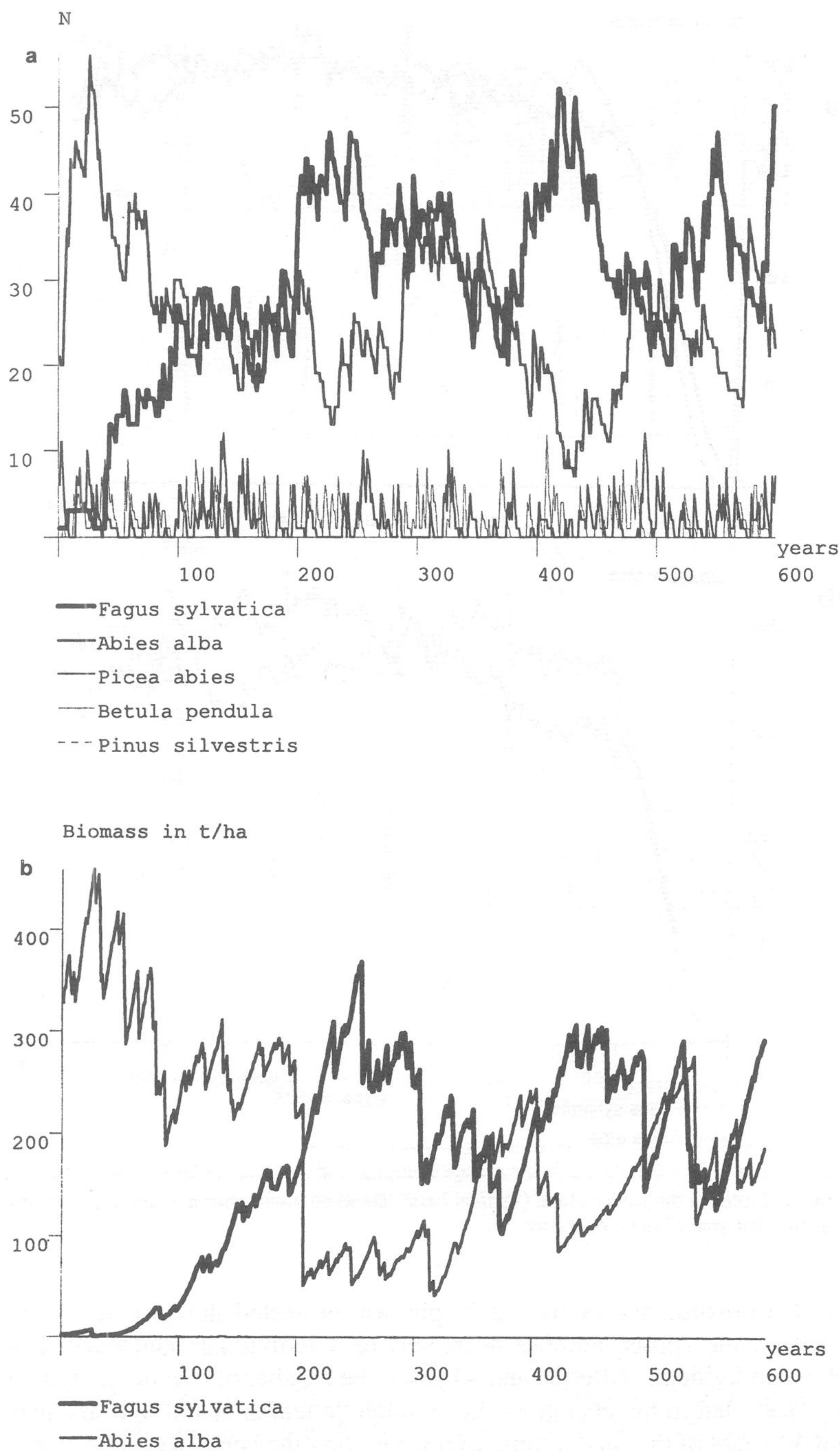


FIG. 4. Number and biomass of trees in the fir stand a – number of trees , b – biomass of trees



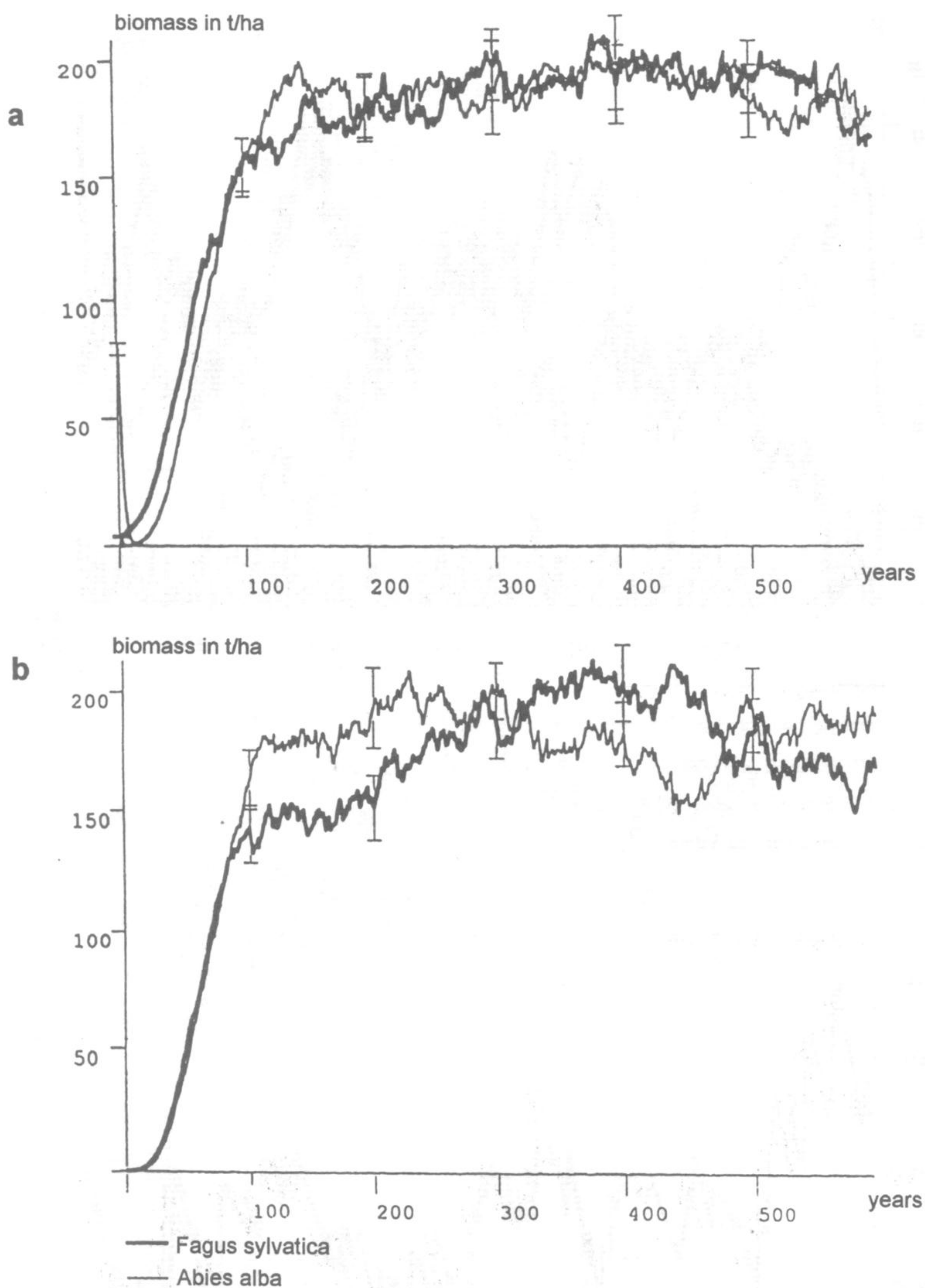


FIG. 5. Biomass of trees in the spruce stand (vertical bars – standard deviation); a – control, b – cutting out the trees after the first year of the model time

and 1 pine. The position of each tree on the plot was projected along a diagonal of this plot. After 10 years, the spruce number decreased to 4 individuals and the beech number increased to 6 individuals. After 20 and 40 years, the number of beeches and firs increased.

This process led to the change in the cumulative leaf area and light intensity after 1, 10, 20 and 40 years of the model time. In regenerating the beech forest the distribution of the cumulative leaf area in the variant without cutting out spruce trees was less compact than in the variant with tree cutting.



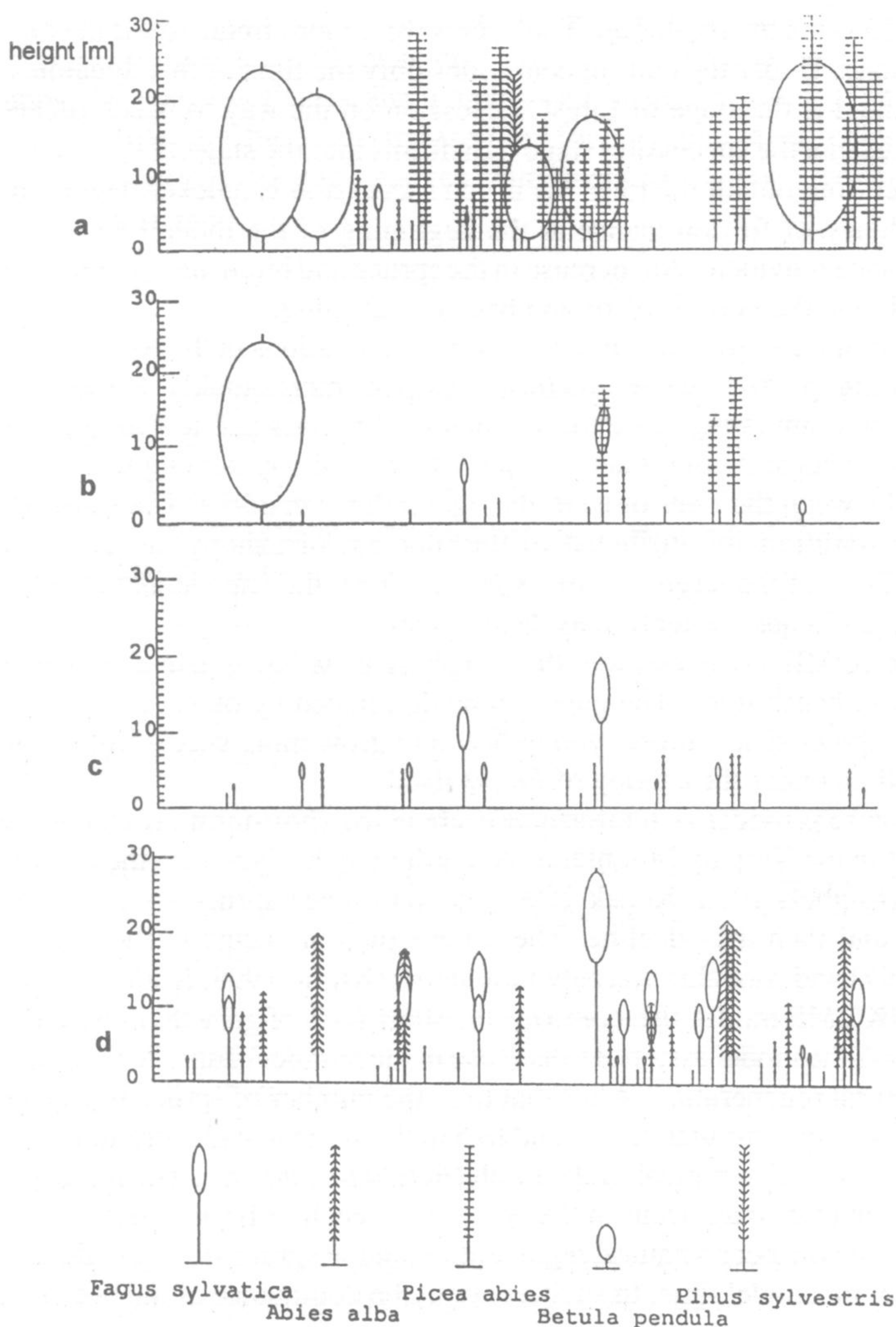


FIG. 6. Beech regeneration which replace the man-made spruce stand; a – after the 1<sup>st</sup> year, b – after 10 years, c – after 20 years, d – after 40 years of the model time

## ■ Discussion

The model confirms the cyclic nature of stand development trends. Such cycles were already described in the literature (Shugart 1984). The FORKOME model assumes the cyclic changes in tree number and biomass. This tendency of cyclic changes was also confirmed for the variants with cutting out only beech trees and with cutting all trees after



the first and 20 years of simulation. The cycles were more frequent for the number of trees than the biomass. Under the cutting conditions only the time of this dynamics varies.

The fir stand is the stage of forest succession on the way to beech regeneration. The model assumes that the succession stage transforms into the stage of the beech stand. In the variant with cutting out all the trees the beech succession is quicker than in the control.

The tendency of fir dominance at the beginning of the modelling time followed by beech dominance is evident. An increase in the spruce and birch number up to 12 individuals is also probable in the periods of fir and beech weakening.

Beech and fir trees grow in similar ecological conditions in the Bieszczady Mountains. When the old canopy trees die the smallest trees grow more quickly. In the gap formed after the death of the dominating large trees, when the biomass and leaf area are insignificant, the regeneration stage predominates. The next stage of gap development is related to the competition between the trees of a similar age in the overstorey. The starting point of this stage can be traditionally attributed to the moment of canopy closure resulting in the dominance of one of the large-size tree species. Then, the gap enters the initial peak stage (in terms of the biomass) affecting its development.

The FORKOME model assumes the gap phase in which regeneration occurs following the death of old beech trees. The gaps can be dominated by other species, such as fir and birch, whose lighter shade allows young beech to grow more successfully, and even more successfully than under the canopy of *Fagus* itself.

The literature provides rich information about the short-term growth of the man-made spruce forests in the Karpaty Mountains. According to the data from the Ukrainian Karpaty Mountains (Holubets 1978, Kozak 1990) the man-made spruce stands grow quickly for 35-40 years, and then they decline. The same situation occurs in the Polish Bieszczady (Jaworski 1997) and Slovakia Karpaty mountains (Klimo 1998, Kodric 1998).

The FORKOME model also confirms the short-term of growth of the spruce stand. On the control plots the model assumes a decrease in the number of spruce trees during 20 years and beech natural regeneration. After that time the number of spruce trees increased to 12 individuals in a single simulation run and to 5 in the statistical elaboration and it may often decrease to 1. It was also typical of the birch (*Betula pendula* L.). The increased number of spruce and birch trees may occur in the periods of beech or fir weakening.

To accelerate the beech natural regeneration all the spruce trees should be cut out after the first year of the model time. In such a variant the dominance of the beech is accelerated by 20 years.

The model confirms that the spruce stand declines and allows to analyse the changes using different data, for example, changes of increment, spruce mortality, temperature and light on the soil surface, etc.

A single simulation run ensures more detailed analysis of changes within the simulation. Noteworthy are the investigations concerning the changes of tree age and height or the distribution of leaf area indices and light intensity in the course of succession.

The Monte Carlo method also assumes cyclic changes. The amplitude of these changes is not as high as in a single simulation run. But in the Monte Carlo method it is possible to analyse the tendency of the changes in tree biomass and number. The Monte Carlo method also assumes the cyclic change of the beech stand into the fir stand.

The FORKOME model presented in this study is based on a gap-phase theory of a natural forest. The structure of our model is open and modular, enabling its easy



development and modification. The important feature of the FORKOME model is its possibility to assess the impact of the changing environmental conditions on forest growth and functioning the question that is also emphasised in the literature (Bernadzki 1993, Brzeziecki 1999). Generally, the model may be used for quantitative estimates of the effects of various factors (cutting, climate changes, introductions of new tree species) on the dynamics of the forest stand.

## ■ Conclusions

- ☐ The FORKOME model assumes the dynamics of the beech forest in the Bieszczady Mountains.
- ☐ Cutting out the trees does not change the general tendency of cyclic changes in beech and fir biomasses and tree number. Only the time of the transformation of the beech stand into the fir stand is different.
- ☐ The fir stand is the stage leading to beech regeneration and it changes into the forest with beech dominance after 100 years of simulation.
- ☐ The model confirms the short-term growth of the man-made spruce forest in the Bieszczady Mountains.
- ☐ The changes in tree number are more frequent than the changes in tree biomass.
- ☐ Cutting out spruce trees after the first year of the model results in the dominance of the beech and then in cyclic changes in the biomass and number of beech and fir trees.
- ☐ The beech regeneration, which replaces the spruce stand, is more intensive in the variant with cutting out the trees after the first year of the model time than in the variant without cutting.

## ■ References

- Bonan, G.B., van Cleve, K. 1992. Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests. *Can. J. For. Res.*, 22, p. 629-639.
- Botkin, D. B., Janak, F. J., Wallis, J. R. 1972. Some ecological consequences of computer model of forest growth. *J. Ecol.*, V. 60, p. 649-873.
- Bernadzki, E. 1993. Obecne problemy planowania hodowlanego. *Prace IBL. Ser. B.15*: 134-140.
- Brzeziecki, B. 1991. Ecological growth Model of the Forest: some methodical and calibration problems. *Sylwan* 9, p. 5-15.
- Brzeziecki, B. 1999. Ekologiczny model drzewostanu. Zasady konstrukcji, parametryzacja, przykłady zastosowań. Warsaw: 115.
- Friend, A.D., Shugart, H.H., Running, S.W. 1993. A physiology-based gap model of forest dynamics. *Ecology* 74, p. 792-797.



- Holubets, M. A.** 1978. Spruce forests of the Ukrainian Carpathians. Naukova dumka, Kiev, 280 pp.
- Horn, H.S.** 1975. Forest succession. *Sci. Am.* 232, p. 90-98.
- Jaworski, A.** 1997. Carpathian forests of primeval character and their importance in shaping the pro-ecological model of forest management in mountains. *Sylvan* 4, p. 33-47.
- Kienast, F.** 1987. FORECE – A forest succession model for southern central Europe. Oak Ridge National Laboratory, Oak Ridge, TN, ORNL/TM 10575, 69 pp.
- Klimo, E.** 1998. Stress conditions of a man-made Norway spruce pure stand established outside its natural range in the region of the Drahanska Uplands. *Ecologie* 29, p. 97-300.
- Kodrik, M.** 1998. Investigation of fine roots of *Picea abies* ecosystem in the Northern Slovakia. *Ekologia Bratislava*. 17, 4, p. 358-363.
- Kozak, I.** 1990. Anthropogenic transformation of forests in the mountain part of Prut river basin. *Lesovedenie*. 3, p. 3-10.
- Kozak, I., Menszutkin, V.** 1999. Computer simulation of forests Ecosystem Dynamics. *Biology Bulletin*. Volume 26, No 6, p. 586-592.
- Leemans, R. and Prentice, I.C.** 1989. FORSKA, a general forests succession model. Institute of Ecological Botany, Uppsala, 70 pp.
- Martin, Ph.** 1992. EXE: A climatically sensitive model to study climate change and CO<sub>2</sub> enrichment effects on forests. *Aust. J. Bot.*, 40, p. 717-735.
- Menszutkin, V., Kozak, I.** 1997. An Investigation of a mixed beech forest dynamics in Ukrainian Carpathians using a computer model. In: Perzanowski K., Augustyn M. (eds): Selected ecological problems of Polish-Ukrainian Carpathians. Bieszczady, p. 23-29.
- Mitchell, K. J.** 1975. Stand description and growth simulation from low-level stereophotos of tree crowns. *J. For.* 73, p. 12-16.
- Pastor, J., Post, W.M.** 1985. Development of a linked forest productivity-soil process model. U.S. Dept. of Energy, ORNL/TM-9519.
- Pawłowski, W. J.** 1996. Computer simulation of growth of a spruce stand using the PICEAT model // *Ekol. Pol.* V. 44 No 3-4, p. 333-349.
- Shugart, H. H.** 1984. Theory of forests dynamics. Springer Verlag, NY 278 pp.
- Shugart, H. H., West, D. C.** 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Environ. Manag.* 5, p. 161-179.
- Shugart, H. H., West, D. C.** 1979. Size and pattern of simulated forest stands. *For. Sci.* 25: 120-122.
- Solomon, D.S.** 1974. A growth model of natural and silviculturally treated stands of even-aged northern hardwoods. U.S.D.A. Forest Service Tech. Report. NE. 36, 30 pp.
- Sullivan, A. D., Clutter, J. L.** 1972. A simultaneous growth and yield model for loblolly pine. *For. Sci.* 18, p. 76-86.
- Suzuki, T., Umemura, T.** 1974. Forest transition as a stochastic process. *V. J. Jpn. For. Soc.* 56, p. 195-204.
- Szwagrzyk, J.** 1994. Simulation models of forest dynamics based upon the concept of tree stand regeneration in gaps. *Wiadomości Ekologiczne*. T. XL. 2, p. 57-95.



- Waggoner, P. E., Stephens, G.R. 1970. Transition probabilities for a forest. *Nature* 225: 1160-1161.
- Weinstein, D.A., Shugart H. H., and West D.C. 1982. The long-term nutrient retention properties of forest ecosystems: A simulation investigation. ORNL/ TM-8472. ORNL, Oak Ridge, Tennessee. 145 pp.

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#### ■ **Streszczenie (Summary)**

##### **Badania dynamiki lasów w Bieszczadach za pomocą modelowania komputerowego**

W pracy przedstawiono wyniki modelowania dynamiki bukowego, jodłowego i świerkowego lasu w Bieszczadach z wykorzystaniem modeli FORKOME\*. Model zweryfikowano po terenowych badaniach z lat 1998-1999 w lasach z dominacją buka (*Fagus silvatica* L.), jodły (*Abies alba* Mill.) i świerka (*Picea abies* L.) w leśnictwie Procisne, Nadleśnictwie Stuposiany.

Dla lasu bukowego model prognozuje cykliczne zmiany między bukiem a jodłą, tak dla liczebności jak i dla biomasy drzew. Wyrąb drzew nie zmienia tej ogólnej tendencji do wspomnianych cyklicznych zmian.

Jodłowy drzewostan w średnim wieku 72 lat jest w stadium sukcesji na drodze do odnowienia lasu bukowego. Model pozwala prognozować, że po 100 latach czasu modelowego dla liczebności i po 200 latach dla biomasy, las jodłowy zmieni się na las bukowy. W wariantcie wyrąbania wszystkich drzew w 20. roku czasu modelowego model prognozuje – w porównaniu do wariantu kontrolnego – przyspieszenie bukowego stadium sukcesji.

Model prognozuje krótkotrwały wzrost sztucznie wprowadzonego świerka w Bieszczadach. Symulowano jego zamianę na las bukowy i następną cykliczną zmienność między bukiem a jodłą.

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