Structure and dynamics of silver fir (*Abies alba* Mill.) population in forest communities of the Świętokrzyski National Park. II. Population dynamics

MARIA MAZUR*

Department of Botany, Institute of Biology, The Kielce High Pedagogical School, Rewolucji
Październikowej 33, 25-518 Kielce, Poland

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Abstract

The paper presents the dynamics of silver fir population, and forecasts the changes in its size. The studies were conducted within the area of fir decline, in a fir forest and Carpathian beechwood. Changes in the size of following groups were illustrated in diagrammatic life-tables: i.e. seedlings, new growth, up-growth, and trees. The direction and rate of expected changes in the population was inferred from the matrix model. The studies showed that the population was in a regression phase. Population growth rate λ amounted to 0.83.

Key words: *Abies alba*, reproduction, mortality, life-tables, matrix model

INTRODUCTION

The paper aims to apply matrix algebra and diagrammatic life-tables (Begon and Mortimer 1981) in the analysis of dynamics of fir population, and in the prognosis of the direction and rate of changes in its size. It is a part of wider studies on the regeneration of fir population and its further fate in the forest communities of the Świętokrzyski National Park (Mazur 1989). The quantitative relations between seedlings, new growth and up-growth individuals, as alive and dead trees are analysed. This has enabled to answer the question whether a large number of dead trees can be replaced by a new fir generation.

* Present address: School of Biological Sciences, Macquarie University, NSW 2109, Australia

Matrix algebra has been applied in the models for population dynamics of: annuals (Law et al. 1977, Leverich and Levin 1979), biennials (Caswell and Werner 1978), herb perennials (Sarukhan and Gadgil 1974, Fetcher and Shaver 1983), shrubs and trees (Bosch 1971, Hartshorn 1975, Enright and Ogden 1984, Piñero et al. 1984, Huenneke and Marks 1987).

The matrix model is one of those where "realism of the model is partly sacrificed in order to obtain the benefit of the mathematical formulation" (Jeffers 1978), as it assumes stable reproduction and mortality rates. In a consequence, it gives only a limited forecast for future and is usually applied to illustrate current population behaviour.

In the studies on population dynamics reproduction and mortality are comprised in static or dynamic life-tables (Silvertown 1982). There are also diagrammatic life-tables that concern some elements of the former (Begon and Mortimer 1981). For trees static tables have been mainly applied (Hett and Loucks 1971, Van Valen 1975), although e.g. Hett (1971), Guittet and Laberche (1974) give dynamic tables for the first decade of *Acer saccharum* and *Pinus sylvestris* lives.

METHODS

The studies were conducted in 1979-1984 in three forest phytocoenoses: one representing silver fir forest *Abietetum polonicum* (Dziub. 1928) Br.-Bl., Vlieg 1939, the other two — Carpathian beechwood *Dentario glandulosae-Fagetum* Klika 1927. Fir individuals in the fir forest were considered coenopopulation A, in the Carpathian beechwood — coenopopulations B and C. Those were the grounds for the description of a local fir population (L) in Świętokrzyski National Park.

The description of the study areas, and methods applied to assess the age and other fir properties were presented in the part I (Mazur 1989). Hence below, only methods concerning reproduction and mortality, as well as basic assumptions of the model are given.

The reproduction was determined from the number of seedlings and juvenile individuals (new growth and up-growth). Real reproduction rates were calculated as seedling numbers, while cumulative reproduction rates as the number of juvenile individuals per one fir tree. In order to assess mortality, dead seedlings (for one study year) and new-growth individuals (for 3 study years) were noted and mapped. Their survival was expressed as per cent of seedlings surviving within the transects against their initial number. Both mortality and survival were comprised in static life-tables (conventional and diagrammatic). The tables were based upon population age structure, and

numbers of new growth, up-growth and trees. It was assumed that the number of individuals in age classes and mentioned above groups (new growth, up-growth and trees) reflect survivorship of individuals in a population.

Following assumption were made for the model:

- Time interval within which the changes in fir population size were considered was 70 years.
- Seeds were produced by trees 70 or more years old (after Tyszkiewicz 1952).
- Fir mast years occurred every 5th year, hence during the analysed time interval there would be 14 such years (after Krysztofik 1964 and Suszka 1983).
- Dead trees accounted for 5% trees in the natural forest stand (Faliński 1986).
- Up-growth individuals had the chance to reach canopy only when a gap was formed. This was conditioned by the fir up-growth number and its proportion against that of beech up-growth, fairly common in the undergrowth of the analysed phytocoenoses. From the estimated fir and beech covers it was inferred that 2/3 gaps in the forest stand were available to fir.
- The number of free microsites equaled to the number of dead standing fir trees (mainly fir trees died).
- Constant environmental conditions.

The population was considered as a cohort, hence changes in the population size were analysed on the assumption of stable reproduction and mortality rates within the interval considered.

The model for population dynamics was based on the results of the field studies and reference data. The first included:

- The number of fir seedlings that occurred only once, after the mast year.
- The number of new-growth and up-growth individuals, and those of dead and alive fir trees:
 - age of up-growth individuals and trees,
 - the cover of beech and fir up-growth,
 - approximate number of cones per fir tree in the mast year.

From the Research Workshop of the National Park the data on the average number of seeds in one fir cone was obtained (unpublished data). The number of seeds and seedlings, determined for one mast year were re-calculated for 14 mast years.

Survival rates for seeds, seedlings, new growth and up-growth were calculated as the ratio of the number of individuals in a given group to the number of individuals in a younger group, while that for trees — as the number of dead to the number of alive individuals. Fecundity rate was an average seed number produced by a tree in a given time interval.

RESULTS

REPRODUCTION

In the course of 6-year studies seedlings emerged only once. Cumulative fir reproduction (c. 108 juvenile individuals per one tree) was twice as big as the real one. It indicated the presence of new growth and up-growth individuals, abundant in the local population and originating from many mast years. Intrapopulation variation was reflected in higher reproduction, both cumulative and real, in the beechwood B population (large fir proportion in the ground layer and undergrowth) (Table 1).

Table 1

Reproductive rates of fir coenopopulations in fir forest (A), Carpathian beechwood (B and C) and in the local fir population (L)

Coeno- popu- lation	Average number of individuals per ha				Reproduction rates	
	seed- lings	new growth	up- -growth	trees (alive)	real	cumulative
A	13 667	16 450	630	279	48.99	61.22
B	10 233	15 700	1 123	68	150.48	247.40
C	700	7 450	623	44	15.91	183.48
L	8 200	13 200	792	130	63.08	107.63

MORTALITY

Seedling survival to a next season amounted to 24% in the local fir population. New growth individuals survived fourfold better (Tables 2 and 3). The mortality in different age classes, expressed as death risk (q_x), oscillated between 0.39 and 0.96. The highest mortality was experienced by less than 20-year-old individuals. The period of intense mortality differed between coenopopulations: in the fir forest it was typical of age class up to 20 years, in the beechwood B — up to 40 years and the beechwood C — up to 80 years (Table 4).

The mortality analysed for groups of individuals in the local population was the highest for a new growth (0.94). Also high up-growth mortality in the Carpathian beechwood, as compared to that in the fir forest, should be mentioned (Table 5).

Table 2

Survival of fir seedlings to the next season in fir coenopopulations of fir forest (A), Carpathian beechwood (B and C) and the local fir population (L)

Coenopopulation	Study area	Number of seedlings on a transect (100 m ²)		Seedling survival (%)
		1983	1984	
A	1	181	39	24.2
	2	289	67	
	3	30	15	
B	1	113	34	21.8
	2	109	5	
	3	85	28	
C	1	17	6	33.3
	2	3	1	
	3	1	—	
L		Σ 828	Σ 195	23.5

1-3 — study areas: 1 — with a large proportion of fir new growth, 2 — with a large proportion of fir up-growth, 3 — with a small proportion of fir new growth and up-growth.

Table 3

Survival of fir new growth in coenopopulations in fir forest (A), Carpathian beechwood (B and C) and in the local fir population (L) (as per cent of initial number of individuals)

Coenopopulation	Study area	Number of individuals on a transect (100 m ²)	Dead individuals (%)			Survival during following years (%)			Cumulative survival in 3 years (%)
			1981	1982	1983	1981	1982	1983	
A	1	280	13	7	7				84.6
	2	160	8	13	11	94.7	94.7	95.3	
	3	53	7	7	5				
B	1	355	7	8	4				93.3
	2	156	6	5	6	97.4	97.6	98.2	
	3	39	1	0	0				
C	1	222	3	3	2				96.4
	2	104	1	1	1	98.8	98.8	98.8	
	3	10	0	0	1				
L		Σ 1379	Σ 44	Σ 44	Σ 37	96.8	96.8	97.3	90.9

1-3 — study areas: 1 — with a large proportion of fir new growth, 2 — with a large proportion of fir up-growth, 3 — with a small proportion of fir new growth and up-growth.

Table 4

Life tables of fir coenopopulations in fir forest (A), Carpathian beechwood forest (B and C) and of the local fir population (L), based on age structure

Coeno-population	x	a_x	l_x	d_x	q_x	$\log_{10} l_x$
A	3-20	16 553	10 000	9 736	0.9736	4.0000
	21-40	437	264	192	0.7272	2.4216
	41-60	119	72	—	—	1.8573
	61-80	190	115	79	0.6869	2.0607
	81-100	60	36	—	—	1.7782
B	3-20	16 575	10 000	9 242	0.9242	4.0000
	21-40	1 256	758	690	0.9103	2.8797
	41-60	112	68	54	0.7941	1.8325
	61-80	24	14	—	—	1.1461
	81-100	48	29	24	0.8276	1.4624
	101-140	8	5	—	—	0.6990
C	3-20	6 652	10 000	8 089	0.8089	4.0000
	21-40	1 271	1 911	1 683	0.8807	3.2813
	41-60	152	228	175	0.7675	2.3579
	61-80	35	53	47	0.8867	1.7243
	81-100	4	6	3	0.5000	0.7782
	101-140	2	3	—	—	0.4771
L	3-20	13 110	10 000	9 570	0.9570	4.0000
	21-40	564	430	327	0.7605	2.6335
	41-60	135	103	40	0.3883	2.0128
	61-80	83	63	35	0.5555	1.7993
	81-100	37	28	25	0.8928	1.4472
	101-140	4	3	—	—	0.4771

x — age interval, a_x — number of survivors at start of age interval x (data collected from field), l_x — proportion of individuals surviving to start of age interval x ($l_1 = 10\,000$), d_x — number of individuals dying during age interval x to $x+1$ ($d_x = l_x - l_{x+1}$), q_x — mortality rate during age interval x to $x+1$ ($q_x = d_x / l_x$), $\log_{10} l_x$ — survival rate as logarithm of l_x .

MODEL FOR POPULATION DYNAMICS CALCULATED RATES

In the local fir population (1 ha) 75 trees produced seeds, i.e. 58% of the total number of 130 (Table 6). If one assumed that each individual produced 40 cones on average, with 100 seeds in each, then tree fecundity amounted to 4000 while total seed number produced in one mast year equaled:

$$4000 \times 75 = 300000,$$

hence seed production for 70 years (14 mast years) amounted to:

$$300000 \times 14 = 4200000.$$

Table 5

Life tables of fir coenopopulations in fir forest (A), Carpathian beechwood and of the local fir population (L), based on numbers of new growth, up-growth and trees

Coeno-population	x	a_x	l_x	d_x	q_x	$\log_{10} l_x$
A	new growth	16 450	1 000	962	0.9620	3.0000
	up-growth	630	38	21	0.5526	1.5798
	trees	279	17	—	—	1.2304
B	new growth	15 700	1 000	928	0.9280	3.0000
	up-growth	1 123	72	68	0.9444	1.8573
	trees	168	4	—	—	0.6021
C	new growth	7 450	1 000	916	0.9160	3.0000
	up-growth	623	84	78	0.9286	1.9243
	trees	44	6	—	—	0.7782
L	new growth	13 200	1 000	940	0.9400	3.0000
	up-growth	792	60	50	0.8333	1.7782
	trees	130	10	—	—	1.0000

x — a group of individuals, a_x — number of individuals in a group (data collected from field), l_x — proportion of individuals reaching the next group ($l_1 = 1000$), d_x — number of individuals dying in a group ($d_x = l_x - l_{x+1}$), q_x — mortality rate during passing from one to another group ($q_x = d_x / l_x$), $\log_{10} l_x$ — rate of survival as logarithm of l_x .

Table 6

Some characteristics of fir coenopopulations in fir forest (A), Carpathian beechwood (B and C) and of the local fir population (L)

Coeno-population	Average number of trees per ha		Proportion of fir trees (alive) 70 and more years old (%)	Average age of alive up-growth (years)	Average density of seedlings per ha, after seed year
	alive	dead			
A	279	201	49	26.0 ± 1.8	13 667
B	68	40	100	28.9 ± 1.9	10 233
C	44	39	50	37.6 ± 2.0	700
L	130	93	58	31.0 ± 1.9	8 200

In further calculations all alive fir trees were considered, hence the fecundity of average tree for 70 years was:

$$4200000 : 130 = 32308.$$

The seedling number after one mast year was 8200 per 1 ha, on average (Table 6), hence after 14 years — 114800.

The survival rates for seeds, seedlings and new growth were obtained respectively from the ratios of: seedlings to seeds, new growth to seedlings, and up-growth to new growth, as in following equations:

$$114800 : 4200000 = 0.02733,$$

$$13200 : 114800 = 0.11498,$$

$$792 : 13200 = 0.06.$$

Tree mortality rate equaled to 0.72. Acting on the assumption that 5% of dead trees in a population was a constant phenomenon (i.e. 11 dead fir trees of the total number of 223) modified tree mortality rate amounted to:

$$93 - 11 = 82,$$

$$82 : 130 = 63077,$$

hence tree survival rate equaled to 0.36923.

The survival rate for up-growth was calculated from the ratio of potential gap number (dead tree number) to the number of up-growth individuals. From the mortality rate it was inferred that within 1 ha there were 82 gaps, among which 2/3 (55) were available to fir. Within the analysed period (70 yrs) up-growth, on average 31-year-old, would appear twice. Hence, up-growth survival rate would be:

$$55 : (792 \times 2) = 0.3472.$$

DIAGRAMMATIC LIFE-TABLES AND MATRIX MODEL

Model description

The model for fir population dynamics is presented in diagrammatic life-tables and by matrix algebra. It has been constructed for the local population and for three coenopopulations separately.

Diagrammatic life-tables concern demographic phenomena for the analysed 70 years. They show reproduction and survival in consecutive groups of individuals, hence stress inner population dynamics (Fig. 1). On the other hand matrix model gives general situation that can be followed throughout time, based on the 70-year data. The model indicates the direction and rate of changes in the population size, and presents the prognosis of its further fate.

The presented matrices are square, with 5 columns and 5 rows. Fecundity and survival rates in the population are matrix elements ($\bar{A}$). The numbers of seeds, seedlings, new growth, up-growth and trees in time to are the elements of column vector ($\bar{v}_0$) (Table 7). The numbers of individuals in consecutive, groups after interval of 70 years, i.e. in time t_1 are the elements of vector $\bar{v}_1$, obtained through multiplication of matrix by $\bar{v}_0$. From the matrices dominant latent roots have been calculated which in ecology are interpreted as estimates of a population growth rate after age distribution becomes stable.

Table 7

Matrix model of dynamics of the local fir population (L), fir coenopopulations in fir forest (A) and Carpathian beechwood (B and C)

$$\begin{array}{l}
 \bar{A} \\
 \begin{bmatrix} 0 & 0 & 0 & 0 & 32308 \\ 0.02733 & 0 & 0 & 0 & 0 \\ 0 & 0.11498 & 0 & 0 & 0 \\ 0 & 0 & 0.06 & 0 & 0 \\ 0 & 0 & 0 & 0.03472 & 0.36923 \end{bmatrix} \times \begin{bmatrix} \bar{v}_0 \\ 4200000 \\ 114800 \\ 13200 \\ 792 \\ 130 \end{bmatrix} = \begin{bmatrix} \bar{v}_1 \\ 4200040 \\ 114786 \\ 13200 \\ 792 \\ 75 \end{bmatrix} \\
 L \\
 \begin{bmatrix} 0 & 0 & 0 & 0 & 27496 \\ 0.02494 & 0 & 0 & 0 & 0 \\ 0 & 0.08597 & 0 & 0 & 0 \\ 0 & 0 & 0.03830 & 0 & 0 \\ 0 & 0 & 0 & 0.07433 & 0.36559 \end{bmatrix} \times \begin{bmatrix} 7671384 \\ 191338 \\ 16450 \\ 630 \\ 279 \end{bmatrix} = \begin{bmatrix} 7671384 \\ 191324 \\ 16449 \\ 630 \\ 149 \end{bmatrix} \\
 A \\
 \begin{bmatrix} 0 & 0 & 0 & 0 & 56000 \\ 0.03762 & 0 & 0 & 0 & 0 \\ 0 & 0.10958 & 0 & 0 & 0 \\ 0 & 0 & 0.07153 & 0 & 0 \\ 0 & 0 & 0 & 0.01434 & 0.48529 \end{bmatrix} \times \begin{bmatrix} 3808000 \\ 143267 \\ 15700 \\ 1123 \\ 68 \end{bmatrix} = \begin{bmatrix} 3808000 \\ 143257 \\ 15699 \\ 1123 \\ 49 \end{bmatrix} \\
 B \\
 \begin{bmatrix} 0 & 0 & 0 & 0 & 2800 \\ 0.00795 & 0 & 0 & 0 & 0 \\ 0 & 0.76020 & 0 & 0 & 0 \\ 0 & 0 & 0.08362 & 0 & 0 \\ 0 & 0 & 0 & 0.0142 & 0.20455 \end{bmatrix} \times \begin{bmatrix} 1232000 \\ 9800 \\ 7450 \\ 623 \\ 44 \end{bmatrix} = \begin{bmatrix} 1232000 \\ 9794 \\ 7450 \\ 623 \\ 18 \end{bmatrix} \\
 C
 \end{array}$$

$\bar{A}$ — matrix, listing group survival rates (seeds, seedlings, new growth, up-growth, trees) and fecundity rate; $\bar{v}$ — vector, listing sizes of groups, mentioned above at present ($\bar{v}_0$), and after 70 years ($\bar{v}_1$); λ — population growth rate.

$\lambda_L = 0.83$, $\lambda_A = 0.78$, $\lambda_B = 0.88$, $\lambda_C = 0.77$.

Fig. 1. Diagrammatic life table of the local fir population (L). Time interval $t_0 - t_1 = 70$ years. Group size (number of individuals) — in rectangles, survival rates — in arrows, and fecundity rate — in a diamond

Model interpretation

Survival of individuals from seeds to juvenile phases (up-growth included), expressed as a survival rate, for the local population equaled 0.03-0.11. Tree survival was much higher, 0.37 in the assumed time interval (Fig. 1). The coenopopulations differed with respect to the survival of individuals in consecutive groups. In the beechwood coenopopulation C (small fir proportion in the ground layer and undergrowth) tree survival was lower (c.0.20) than in the other two. In the beechwood coenopopulation B and in the fir forest coenopopulation survival of seeds, seedlings, new growth and up-growth were similar to those of the local population (Table 7). Also tree survival did not differ (0.36-0.48).

Population growth rate (λ) equaled 0.83. The direction of changes in coenopopulation sizes was the same, but their rate was lower in the coenopopulation B ($\lambda = 0.88$) than in the fir forest and the beechwood C ($\lambda = 0.78$ and 0.77 , respectively), (Table 7).

The matrix data enabled to construct survivorship curves of the local population, comprising all developmental fir phases. It was concave (Fig. 1).

DISCUSSION

The process of forest regeneration is one of the fundamental problems of forest ecology, especially of applied ecology. Natural forest regeneration comprises seed production by mother forest stand, self-seeding and development of a new tree generation.

Fir produces seeds abundantly every few years (Suszka 1983). Seedlings appear in large number after mast years, whereas in between they emerge only occasionally. Seedlings survive 2-3, even 4 years. Hence they experience mortality for at least 2 years. A decrease in the population size takes place mainly in the phases of seedlings and juvenile individuals (new growth and up-growth), a rule in many species, also trees, producing a great deal of offspring. Due to a slow fir growth and its shade-tolerance in early developmental phases, the juvenile mortality can be prolonged and last even 70 years.

The presence in a population of juvenile individuals with retarded growth and development is known as Oskar syndrome (Grime 1979). Thus, seedling, not seed, bank is formed — according to Silvertown (1982) — a specific reproductive mechanism that gathers individuals ready to colonize the sites in a phytocoenose as soon as they become free.

Adult trees constitute only few per cent of individuals that appear after fir mast years. The studies have showed that from among 114800 seedlings per 1 ha only 130 individuals reach tree layer. Such a proportion is characteristic of a population if one cohort derived from the seed of one mast year is

concerned. Under the conditions of actual phytocoenose the probability of an individual reaching the tree layer is determined by the number of gaps formed by falling trees. Moreover only the part of these gaps can be re-colonized by fir. Hence, from among the same 114800 seedlings only 27 individuals may reach tree layer. This number is relatively high due to the presence of many dead trees, i.e. potential free microsites.

Individual survival in consecutive groups, presented as a survivorship curve (Fig. 2), is characteristic of a population with a high death risk at juvenile stages (Odum 1977). Similar, concave survivorship curves have been observed for many forest trees, e.g. *Abies balsamea* and *Tsuga canadensis* (Hett and Loucks 1976), *Acer pensylvanicum* (Hibbs 1979), *Araucaria* sp. (Gray 1975) and some neotropical species (Sarukhan 1980). Watkinson (1986) associates this phenomenon with a high plant fecundity.

Fig. 2. Survivorship curves for the local fir population (L), based on its diagrammatic life table

The matrix model has been applied to determine mainly the direction and rate of changes in the fir population size in the National Park. Population finite rate of increase equals 0.83, i.e. the population size will decrease by 17% when the age structure becomes stable.

The reduction of population size will be faster in the fir forest and the beechwood on the northern slopes of the Łysogóry, where the finite rates of increase are 0.78 and 0.77, respectively. The fir regression will be slower in the beechwood with many juvenile fir individuals on the southern slopes of the ridge ($\lambda = 0.88$).

According to Enright and Ogden (1984) the value of the infinite rate of increase for long-lived forest species equals nearly unity, which is characteristic of stable populations, e.g. 1.002 for *Pentaclethra macroloba* (Hartshorn 1975), 1.0399 for *Astrocaryum mexicanum* (Piñero et al. 1984), and 1.0 for

Alnus incana ssp. *rugosa* (Huenneke and Marks 1987). The value calculated for alpine forest (Usher 1966) was 1.204, while that for *Sequoia sempervirens* ranged from 0.8322 to 1.2346 (erronously calculated by Bosch (1971), corrected by Namkoong and Roberds (1974)).

The value of the rate of increase of fir population is undoubtedly affected by dying of adult trees. In the population as much as 40% of dead trees were observed (Mazur 1989). All changes in the population size seem small if such a high proportion of dead trees is concerned. However, dead trees may create gaps which can be partly reoccupied by numerous juvenile fir individuals.

On the other hand, dying of fir trees, caused by unfavourable exogeneous agents (Sierpiński 1977, Bernadzki 1983), is followed by changes in the environment adverse to fir regeneration. Open, unshaded sites are often colonized by blackberry and other species which signify loss of balance in a forest phytocoenose. The lack of sub-canopy trees in the population may hamper the colonization of free sites by fir. Besides, due to natural rotation juvenile fir individuals do not well the canopy of nature trees, hence, the probability that fir will occupy all newly formed gaps is rather low if the mortality rate is maintained. It may result in the change in fir proportion in forest stands of the Park, from co-dominant or dominant to the mere admixture.

From the expected decrease in the population size it may be inferred that fir forests tend to develop into mixed or deciduous forests. Many authors indicate that mixed forest stands, with beech, spruce or other species, are the best for natural fir regeneration (Bernadzki 1967, Jaworski 1973, 1979).

The fir population dynamics can be affected by competition with other tree species. Habitat contamination (fir being a sensitive species (Krysztofik 1963, Sierpiński 1977, Zawada 1978, Zawada and Widera 1980)) and other unpredictable agents can be also very important.

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Struktura i dynamika populacji jodły pospolitej (Abies alba Mill.) w zbiorowiskach leśnych Świętokrzyskiego Parku Narodowego. II. Dynamika populacji

Streszczenie

Przedstawione opracowanie jest częścią szerszych studiów, których celem było poznanie możliwości odnawiania się populacji jodły w Świętokrzyskim Parku Narodowym. Problem zrodził się w związku z zamieraniem drzew jodły, notowanym w ostatnim czasie w lasach Parku. W opracowaniu przedstawiono ocenę dynamiki liczebności populacji jodły. Badania prowadzono w fitocenozach leśnych boru jodłowego i buczyny karpackiej, w latach 1979-1984. Rozrodczość populacji wyrażono w postaci wskaźników rozrodczości rzeczywistej i skumulowanej. Śmiertelność i przeżywalność ujęto w tabele życia, opracowane dla kolejnych klas wieku oraz grup osobników (nalot, podrost, drzewa). Opracowano tzw. graficzne tabele życia i model macierzowy dynamiki populacji.

Wskaźniki rozrodczości rzeczywistej i skumulowanej wynoszą 62 i 108, co oznacza, że na jedno drzewo przypadają 62 siewki i 108 osobników juvenilnych (nalot i podrost) (tab. 1). Największą śmiertelnością charakteryzują się wczesne fazy rozwojowe (rys. 1). Przeżywalność w tych grupach (0.03-0.11) jest kilkakrotnie mniejsza niż wśród drzew (0.37). Krzywa przeżywalności jest wklęsła (rys. 2). Przewidywane zmiany liczebności populacji mają charakter regresji. Wskaźnik wzrostu populacji wynosi $\lambda = 0.83$, co świadczy o tym, że liczebność będzie się zmniejszać o 17% po ustabilizowaniu się struktury wieku populacji (tab. 7). Proces ten będzie postępować, jeżeli czynniki odpowiedzialne za wymieranie drzew, jakie ma miejsce w ostatnich 10-15 latach, będą się utrzymywać. Bardziej prawdopodobne jest jednak, że zmiany doprowadzą do mniejszego udziału jodły w drzewostanach Świętokrzyskiego Parku Narodowego, gdzie jodła będzie pełnić rolę domieszki, a nie gatunku dominującego.