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CHANGES IN THE SEX- AND AGE-RATIO IN POPULATIONS OF PIONEER DIOECIOUS WOODY SPECIES (*JUNIPERUS, POPULUS, SALIX*) IN CONNECTION WITH THE COURSE OF VEGETATION SUCCESSION IN ABANDONED FARMLANDS

ABSTRACT: It has been found that a succession leads from therophyte communities through herb-grasslands to juniper-aspen brushwoods and pine woods, and lasts about 60–70 years. Eight phases of development of vegetation and of juniper populations were distinguished and synchronized. The sex structure and sex ratio in juniper populations were found to change under the influence of the factors occurring during the succession. An overcrowding in a juniper population, accompanied by a changed community structure, impedes the growth of individuals and delays by 10–15 years the starting of generative reproduction by the whole generation. A conclusion has been formulated concerning the role of dioecism in pioneer woody species in the process of colonization.

KEY WORDS: Abandoned-field (old farmland) vegetation, vegetation succession, population structure and dynamics, sex ratio, dioecious woody species populations: *Juniperus communis, Populus tremula, Salix aurita, S. rosmarinifolia, S. caprea.*

Contents

1. OBJECT AND AIM OF STUDY

In studies of the dynamics of vegetation, invasion by woody species is believed to play an important role in the course of succession, whereas the formation of brushwoods and woods in originally, or secondarily woodless habitats, is usually considered as the birth of a new quality. The distinct, consecutive phases of plant succession, commonly distinguished on this basis (cf. the review of studies in the paper by Bråkenhielm 1977, and Hard 1975), are understood not only as signs of physiognomical (structural) changes in a community, but also as an effect and a cause of further and greater changes in the biocenose and biotope. The understanding of the ecological role of woody species in the process of succession resulted mainly from the various investigations into the parallel transformation of vegetation and habitats, and studies of the durability and potential of woodland habitats. The undurableness, revealed and described on this occasion, even of centuries-long anthropogenic landscapes, and their being subject to invasion by trees (cf. e.g. Faliński 1966, 1977, Tüxen 1973, Hard 1975) became quite clear as a result of the populational approach to succession. This occurred relatively recently (Blackurn and Tueller 1970, Schmidt 1975, Tramer 1975, Bråkenhielm 1977, etc.), though certain trials of this kind can be found already in earlier papers (cf. Knapp 1974).

One of the more original attempts at describing and explaining the invasion by woody species through population studies has been made by the American investigators Blackburn and Tueller (1970) in Nevada State, in a community with *Artemisia nova* A. Nels, secondarily colonized by the pine, *Pinus monophylla* Torr. et Frem., and the juniper, *Juniperus osteosperma* (Torr.) Little. In the USA, pine-juniper sagebrush of this type have formed secondarily in an area of about 100 million acres (400000 km^2), in a way corresponding to the European juniper scrubs and juniper-aspen brushwoods. The history of their invasion has been reconstructed by American scientists who used the dendrochronological dating method. This made it possible to establish that the invasion began at least at the beginning of the 18th century.

In his investigations into the succession of vegetation in abandoned farmlands (old farmlands) and meadows the author of the present paper (Faliński – in press) tried to find the causes of the exceptional success of some woody and shrub species in colonizing new areas in a short time. Comparing data from the literature with his own findings, the author found that among the species colonizing abandoned farmlands, meadows and town ruins, as well as newly exposed areas, e.g., in the process of deglaciation, there occur representatives of the same, not numerous genera: *Salix*, *Populus*, *Betula*, *Alnus*, *Pinus*, *Juniperus*, Common to all of them, except juniper, is anemochory (1). A closer comparative analysis has revealed more biological and ecological properties common to the species of these genera. These are: (2) a strong tendency towards vegetative propagation in parallel with an effective generative reproduction, (3) anemogamy (except *Salix*), (4) dioecism (except *Alnus*, *Betula* and *Pinus*), (5) proandry – except *Pinus* and *Juniperus*. One must add to this list of properties: the tendency to mass and aggregate occurrence, short span of individual life with a relatively early beginning of generative reproduction, etc. Five main properties can most fully be seen in the species of the genus *Populus*.

In the relevant literature trials can be found at analyzing the role of only some of these factors, especially anemochory (Ciosek 1975, Czarnowski 1978).

The least clear, from ecological point of view, is the role of dioecism. Separate sexes, though not as common among plants as among animals, make it, at any rate, possible to speak of a sex structure of the populations of some species, including, for example, the pioneer woody species.

The sex structure of the populations of dioecious species is in essence characterized by two factors:

1. percentage of reproducing individuals relative to the total number of individuals in the population, or relative to the number of non-reproducing individuals (juvenile, old);
2. participation of males and females relative to the total number of reproducing individuals, or the males to females ratio. This ratio is most often referred to as the sex ratio, being expresses in the form of ♂ : ♀ = 1 : ..., that is to say the multiple of the number of males to females.

Most often, usually in stabilized populations, a sex ratio of ♂ : ♀ = 1 : 1 is observed, that is to say, equal proportions of males and females. However, nemerous cases have been known where the actual value of the ratio differed from the above (Vernet 1971, Freeman, Klikoff and Harper 1976, Harper 1977). The 1 : 1 ratio seems to be determined genetically (Rodkiewicz 1974, Harper 1977).

Searches for certain relationships between the sex structure of a population, and more precisely – between the sex ratio and the dynamics of vegetation, have been rare and concerned herbaceous species, e.g., *Rumex acetosa* L. (Zarzycki and Rychlewski 1972), *Asparagus acutifolius* (Vernet 1971). There has been a fairly large number of studies of the participation of male and female individuals in the populations of dioecious woody species. The studies dealt with, e.g., the aspen, *Populus tremula* L. (Langhammer after Białobok 1973), and the American aspen, *Populus tremuloides* Michx. (Pauley and Mennel 1957, Framer 1964, Muhle Larsen 1970), and some interesting data have been obtained relating to the sex dimorphism in the species of the genus *Populus* (Białobok 1973). For *Salix purpurea* it has been demonstrated experimentally (Zarzycki 1975) that density causes different survival rates of males and females. As in the case of herbaceous plant populations, the sex ratio was supposed to vary as a result of the action mainly of simple habitat factors, obviously apart from genetical factors. There is an extensive literature on this subject. However, from the reviews done by Freeman, Klikoff and Harper (1976), and by Zarzycki (unpublished) it may be presumed that in the action of these factors there is some syndynamics background. They could, therefore, be interpreted, at least in part, as being an effect of plant succession, or at least as being related to succession. This does not, of course, contradict the opinion held by some investigators that habitat factors exert an influence on the sex ratio.

The aim of the present paper is to describe and try to explain changes in the sex structure of the populations of pioneer dioecious woody species in connection with the course of plant succession in abandoned farmlands (old farmlands). It was, therefore, necessary to add to the results obtained from the research a description of plant succession, although this is to make the subject of a separate publication. For it is the author's intention to show in the present paper – at least approximately – changes in the properties of the populations of the main participants and originators of a succession, as a result of complex interactions.

Studying plant successsion on abandoned farmlands (old farmlands), even in oligotrophic habitats, is exceptionally rewarding, because as many as 5 dioecious woody species (*Juniperus communis* L., *Populus tremula* L., *Salix rosmarinifolia* L., *S. aurita* L., *S. caprea* L., and occasionally other willow species) take part in one sere. For the purpose of comparison, a discussion is provided of the data from the author's investigations into the sex structure of the populations of other willow species participating in seres in more fertile habitats.

2. STUDY SITES

The studies were carried out on abandoned farmlands located on the south-western outskirts of the Białowieża Primavel Forest, in the commune of Kleszczele, Białystok voivodship. The lands concerned form one of the largest complexes of this type (12000 ha) in the eastern region of Poland.

At present, the main causes of land abandonment in this region of Poland are the same as those in western Europe: demographic and social changes in the country (ageing of population, emigration of youth to towns, etc.), and changes in the agricultural policy of the government.

However, the history of the abandoned farmland complex on the outskirts of the Białowieża Primeval Forest is longer, as indicated by old maps, and names of places and topographic names. For instance, the name of the village of Starzyna means a village on former woodlands where cultivation was abandoned when the soil had been impoverished, and where the wood has returned spontaneously (Hedemann 1934, Kondratiuk 1974).

The main part of the wastelands arose during the last 30 years on poorer lands (land classes IV and V), usually dry and sandy, or water-logged. However, abandoned farmlands can be found here in areas where cultivation was stopped over 60 years ago, i.e., during World War I. In a triangle delimited by the roads Kleszczele-Jelonka–(Hajnówka), Kleszczele–Suchowolce–(Bielsk Podl.), and a field road Suchowolce–Jelonka all phases of spontaneous overgrowing of abandoned fields by vegetation can be seen. The previous ownership relations, indicated by the chessboard of farmlands, can be seen locally in the form of very narrow (5–20 m) and very long (1–2 km) field-patches. Due to the discontinuity of the abandoned lands, this chessboard in the area in question gave rise to a peculiar landscape. It can be compared to a striped cloth. In this landscape there are alternate stripes of sand grasslands, juniper scrub, juniper-aspen brushwood and a few farmlands.

The area of the present abandoned lands near Kleszczele was without woods already in the 16th century (Wiśniewski 1964). The woods that had existed there before represented part of the Bielsk Primeval Forest which does not exist now. Here farmlands arose after the cutting down of the previous fresh pine forests, Peucedano-Pinetum typicum, Peucedano-Pinetum pulsatilletosum, dry pine forests, Cladonio-Pinetum (the range of Piaski), and in places hygrophilous pine forests Peucedano-Pinetum typicum var. with Molinia coerulea and Molinio-Pinetum (vicinity of the range of Wielki Ług). Fragments could probably be found here also of meso-oligotrophic pine-oak forests, Pino-Quercetum, and thermophilous oak forests, Potentillo albae-Quercetum.

Kleszczele, the oldest settlement in the area (civic rights before 1522; Kondratiuk 1974) has developed in the best habitats of this region, i.e., in the place of mesotrophic mixed oak-linden-hornbeam forests, *Tilio-Carpinetum.* Lands immediately bordering on the former town continue to be utilized as farmlands The original potential of the habitats has not undergone basic changes, in spite of the extensive agriculture that lasted for many centuries (Faliński 1972). Only locally can examples of a far advanced soil degradation be shown. This applies particularly to dry and damp habitats.

The area we are interested in is covered with deposits of the Riss glaciation in middle Poland during the Mazovian-Podlasian stadial. These are primarily sands, gravels and glacial boulders. The central part of the area is covered with Holocene sands, forming not very distinct ridges running NW-SE.

The commonest soils are podsols formed of poorly clayey sands. In the lower portions of a profile, usually below 1 m or 1.20 m, a layer of loose sand can sometimes be found. In a soil profile, even in soils that have not been utilized for a long time, the arable layer is clearly marked down to the depth of 13 (19) cm. The content of humus in a horizon varies between 0.62 and 3.36%. The soils are acid (4.0–4.4 in pH), the soil pH varying slightly from horizon to horizon over the profile. This applies to soils originally associated with pine forest, Peucedano-Pinetum, habitats. The supposed habitats of the former thermophilous oak forests are weakly acid, or neutral, the pH value changing towards the deeper part of the profile (from 5.1 to 5.9 at the depth below 1 m).

Changes in soil properties in the course of plant succession will be the subject of a separate paper, where the results of soil analyses will be published.

3. METHODS

In the years 1972–1978 studies of the sex- and age-structure in populations of pioneer tree and shrub species were carried out, in a series of permanent plots, as a part of researches into the vegetation dynamics on abandoned farmlands. Only samples of willow populations (*Salix aurita, S. caprea*) had to be taken from larger areas. All individuals, a total of 100 (except. *S. aurita* – 50), encountered within an abandoned farmland, homogeneous environmentally and as regards its age, were examined.

The basic study plot was 1000 m^2 in area and rectangular in shape (25 x 40 or 20 x 40 and only in rare cases was it more elongate). The width of the site depended on the former field stretches (chessboard of fields) and sequence of cultivation abandonment in them. This areal pattern has been "preserved" well by the later spontaneous vegetation. Each site was homogenous in respect of habitat diversity and developmental phases of spontaneous vegetation. The investigations were carried out at 40 permanent sites, that is to say, on a total of 4 ha. Studies with a wider scope, only partially presented in this paper, have also been carried out at two larger sites: in a 0.6 ha area on a dune, and in a transition zone of heathland and sedge bog 0.4 ha in area. A map showing location of the permanent sites was published earlier (Faliński 1977).

The programme of the basic investigations included: sample abundance (ind. · 0.1 ha^{-1}), sexing of individuals, measurement of shrub height and breadth (the latter being made twice across), estimation of the number of cone-berries on female individuals on the scale < 100, 100–1000, > 1000.

Between May and August sexing of juniper individuals was easy, and it was still possible even in October and November, that is to say, as long as the male inflorescences remained on the male scrubs. For willow trees, and especially for the aspen, this period was very short, and observation had to be carried out in the spring (end of April, beginning of May). On account of the efficiency of field work, sexing is best done, even in the case of the juniper, at the time of maximum flowering, i.e., in the period immediately preceding spring, or in early spring.

Sexed individuals were marked with coloured bands on their trunks or branches: red – females, yellow – males, white – individuals not yet flowering (juvenile), or those that do not flower any more (senile). After being sexed in the following years, the originally juvenile individuals received an additional band – red or yellow – above the white one. On sites of large areas, to be used for wider-scope research work, juniper individuals were additionally marked with permanent aluminium plates with sequence numbers and coloured ribbons. In the sketches, the distribution of marked trees and scrubs on the sites to be used for further investigations is shown on the scale of 1 : 100.

To determine the age structure of populations in 11 plots, at all juniper individuals, in 2 plots all aspens were cut down and used for obtaining sections from the main trunk. For shrub willow species (*S. rosmarinifolia*, *S. aurita*), where possible, from each individual 3 sections were obtained from the thickest branches immediately above ground.

Age was determined by counting the annual rings in microscope preparations (except the aspen) in J solution in KJ (Lugol's solution), after a previous softening of the material in 60% alcohol. A trial to count the annual rings under a binocular dissecting microscope failed, because of locally high densities of the rings, as well as because of decayed wood occurring concentrically, parallel to the annual rings. Under the dissecting microscope decayed wood rings could be counted as additional rings of wood. Because of this, inherent in the assessment of age in the aspen, for which microscopic sections could not be made due to the considerable thickness of the wood, and the assessment was needs limited to the counting of annual rings under a dissecting microscope, may be an error.

The main results of field and laboratory studies have been presented in the form of sex- and heihgt-pyramids, sex- and age-pyramids and diagrams. The pyramids have been supplemented with numerical descriptions of the populations.

Names of vascular plants according to Szafer, Kulczyński and Pawłowski (1976), bryophytes according to Szafran (1957, 1961), lichens according to Nowak and Tobolewski (1975).

4. SUMMARY OF RESULTS

1. For 60 years the plant succession in the abandoned farmlands under study, where the juniper and other pioneer woody species (*Populus tremula*, *Salix caprea*, *S. aurita*, *S. rosmarinifolia*, *Pinus sylvestris*) occur, has been a regeneration succession (Fig. 1).

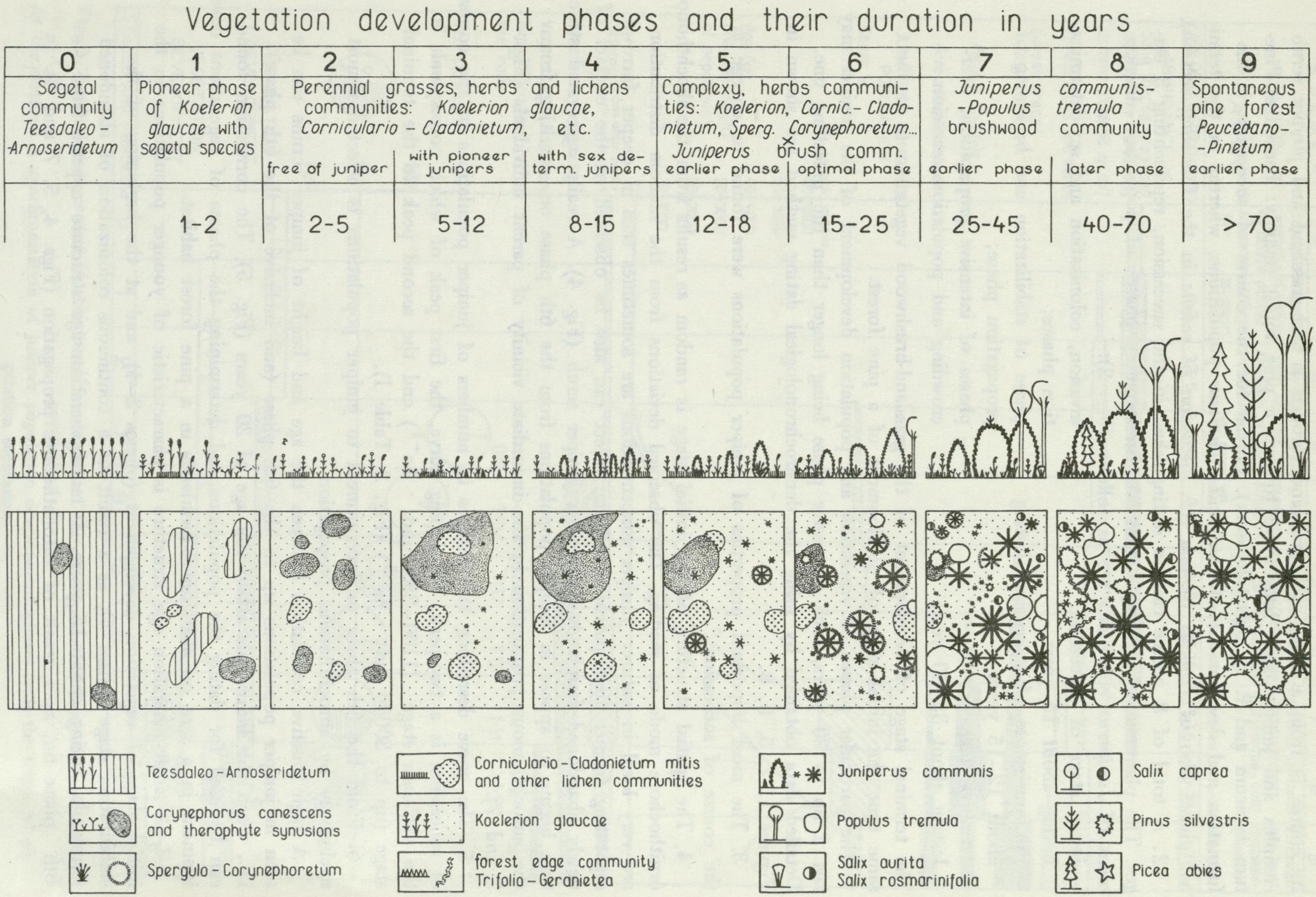

Fig. 1. A diagrammatic representation of the course of vegetation succession in abandoned farmlands

Its course is from a loose sand grassland through a herb-grassland and juniper scrub complex and juniper-aspen brushwood towards a pine forest (mainly: Peucedano-Pinetum typicum and P. P. pulsatilletosum). Crucial for the course of succession is the formation and development of *Juniperus communis* populations, whereas in the terminal phases also of *Populus tremula* (cf. discussion of results in the following section).

2. A total of 8 phases can be distinguished in the succession, representing 3 stages. The plant succession stages and the corresponding phases of population development of *Juniperus communis* are as follows (Fig. 2):

– initial stage of succession, lasting about 15 years	– invasion, colonization and sex-determination phases;
– optimum stage of succession, lasting about 12–15 years	– phase of stabilization and beginning of propagation phase;
– terminal stage, lasting about 35–40 years	– phases of intensive propagation, overcrowding and population recession.

The terminal stage of development of the grassland-brushwood vegetation is at the same time the initial stage of development of a pine forest.

The particular phases of vegetation and population development of the juniper may last 2 up to 30 years, each successive phase being longer than the preceding one. Detailed data obtained by using the dendrochronological dating method are shown in Figures 1, 2, 5, 6, 8.

3. The most important properties of juniper populations were found to change in the course of succession.

4. The spatial structure of the initial stage is random as results from the allochthonous, ornithochore mode of seeding. The observed deviations from the random distribution are very local in nature. Juniper concentrations are sometimes seen in deeper furrows separating former field patches, and the effect can also be observed of the contact of newly abandoned farmlands with older juniper scrub (Fig. 4). A really aggregated structure begins to appear in juniper populations from the 6th phase on, resulting from the autochthonous propagation in the immediate vicinity of parent individuals (Figs. 3 and 7).

5. The curve describing the changes in numbers of juniper populations in the course of succession is a two-peak, left-sloping curve, the first peak of which corresponds to the optimum stage (1100–2500 ind. $\cdot$ ha^{-1}) and the second peak to the terminal stage (up to 30000 ind. $\cdot$ ha^{-1}) (Fig. 2, Table I).

6. From the 6th phase on, recruitment to juniper populations is effected almost exclusively by autochthonous propagation.

A high positive correlation between the age and height of juniper scrubs can be seen in juniper populations up to the 6th phase (and inclusive of the 6th phase), i.e., when the individuals attain the age of 20 years (Fig. 5). The correlation found can be used for dating the populations and determining the phases of vegetations development in a sere on abandoned farmlands in a pine forest habitat.

7. A single-generation age structure is characteristic of younger populations in the initial stage of vegetation development (phases 2–4), and at the beginning of the stabilization stage (phase 5), as a result of a continuous colonization of abandoned farmlands, lasting about 15 years. A multi-generation age structure appears from the 6th phase on, as a result of autochthonous propagation (Figs. 4, 5, 7 and 8). In

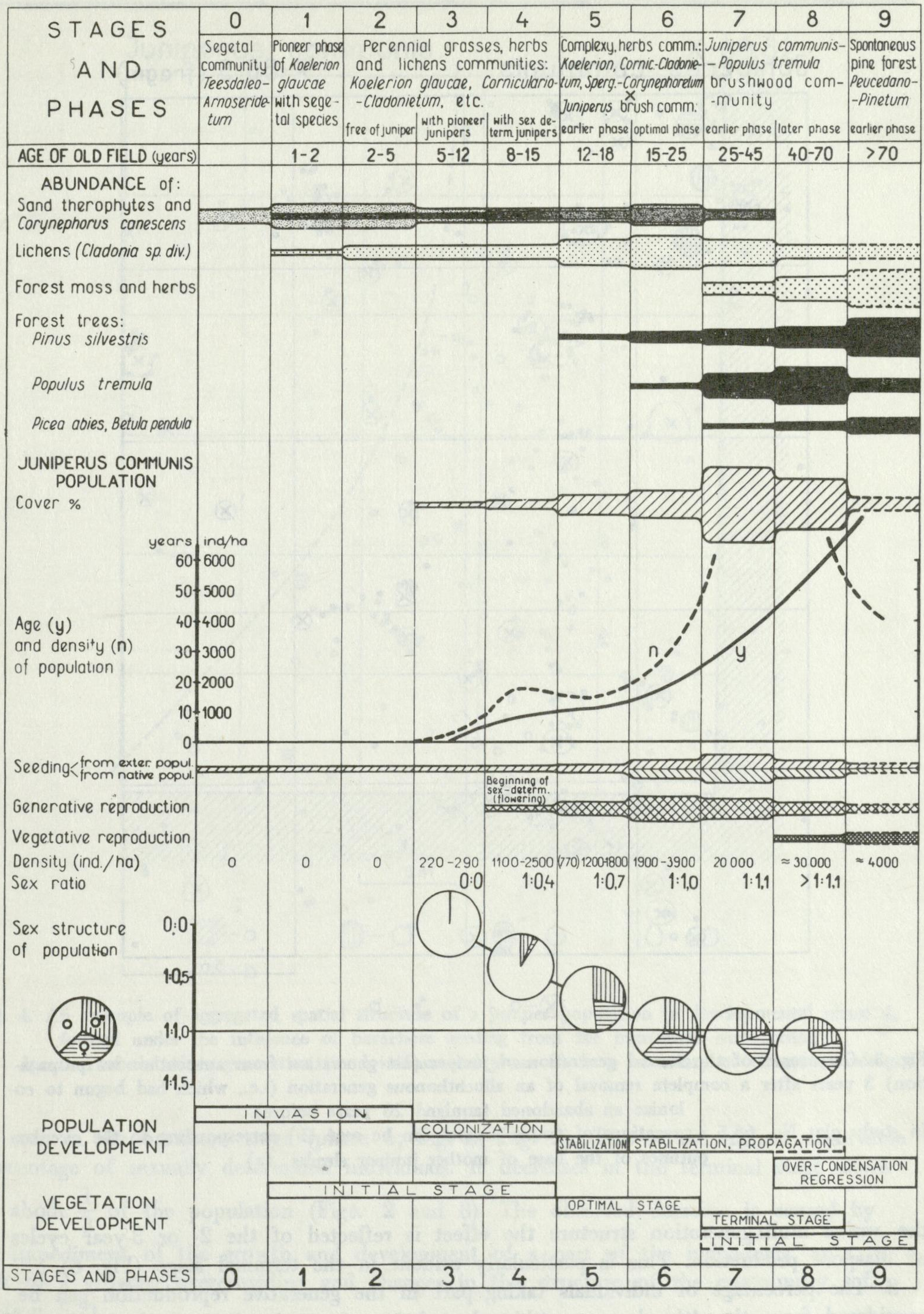

Fig. 2 Vegetation succession in abandoned farmlands and the development of *Juniperus communis* populations
At the bottom: a synchronization of juniper population development phases with the stages of vegetation succession

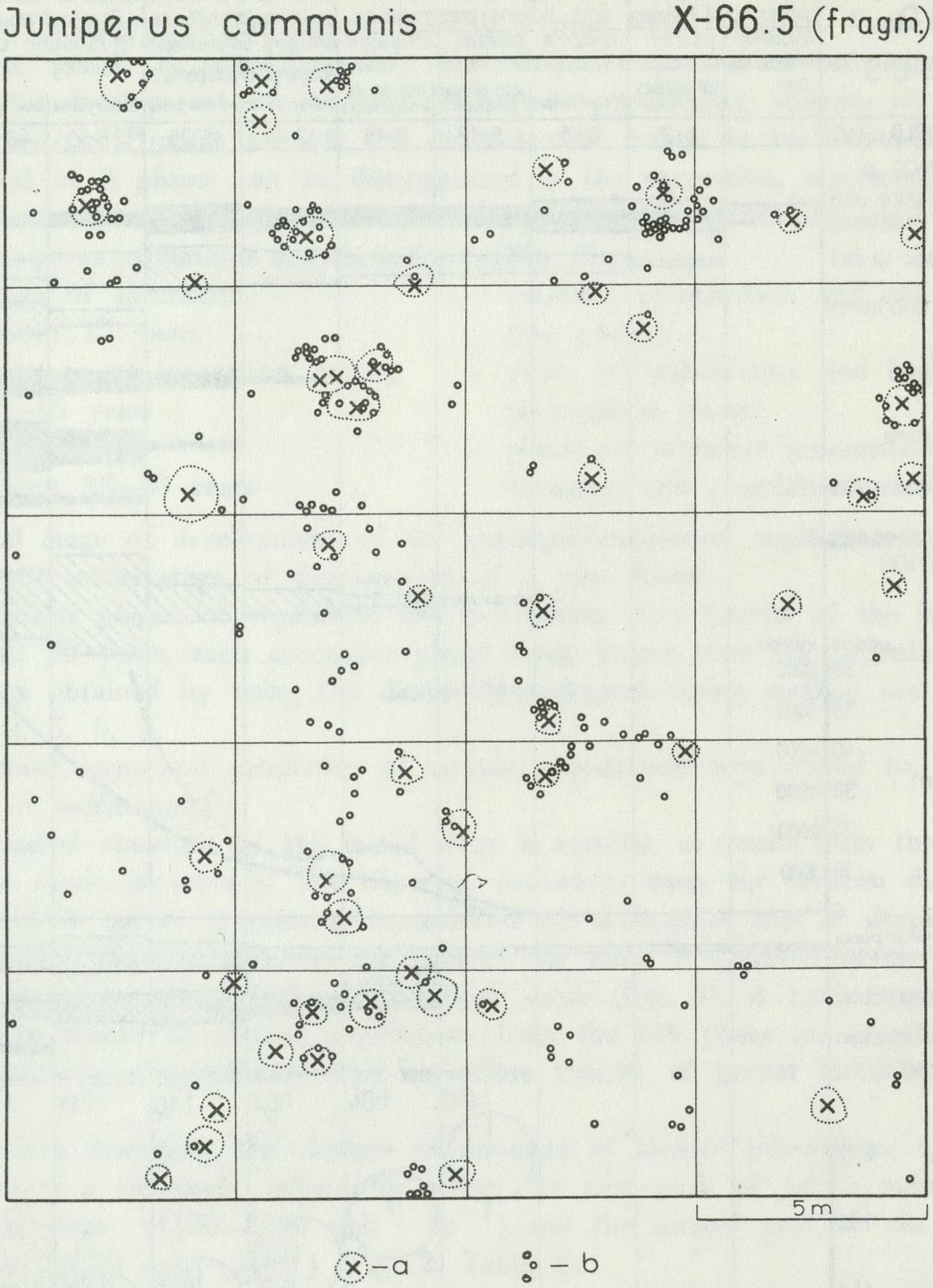

Fig. 3. Occurrence of the second generation of juniper (1st generation from autochthonous propagation) 3 years after a complete removal of an allochthonous generation (i.e., which had begun to colonize an abandoned farmland 20 years before)

In study plot No. 66.5 aggregations of young juniper can be seen (b) corresponding to the circular outlines of the base of mother juniper shrubs (a)

the varied multi-generation structure the effect is reflected of the 2- or 3-year cycles of diaspore production. This is particularly evident in the terminal stage (Fig. 6).

8. The percentage of individuals taking part in the generative reproduction can be considered from the 4th phase on (this phase being conventionally named the "sex determination phase"), that is to say, from the initiation of flowering and fruit-bearing. An increase in the percentage of "determined" individuals to $\frac{2}{3}$ of the population can

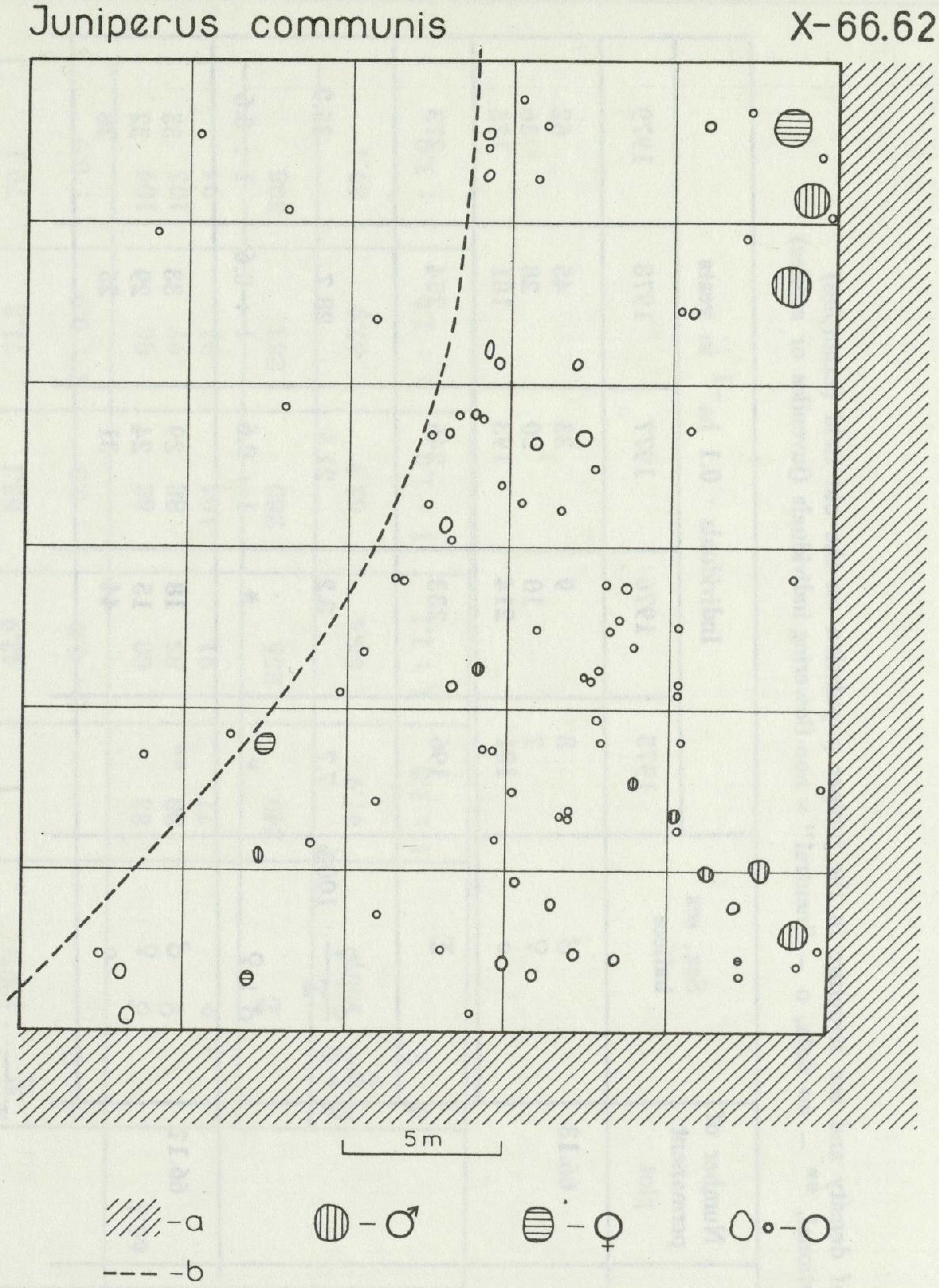

Fig. 4. An example of aggregated spatial structure of a juniper population in developmental phase 4, formed under the influence of barachore seeding from the immediate surrounding
a – location of the older generation (in developmental phase 6), b – boundary of effective seeding

be seen in the optimum stage (phase 6; Fig. 6, Fig. 2). This is the highest observable percentage of sexually determined individuals. It decreases in the terminal stage down to about $\frac{1}{3}$ of the population (Figs. 2 and 8). The observed decrease is caused by an impediment of the growth and development of a part of the individuals, as a result of a growing overcrowding and changes in the structure of the community (cf. section 5.2).

9. The sex ratio of the youngest populations, typical of the initial stage of vegetation development, can be established when the sex of at least 10% of the popula-

Table I. Changes of density and sex structure in the juniper population on the old field (examples)
* – calculation non-rational, ** – no data, o – "neutral" = non-flowering individuals (juveniles or seniles)

Phase of vegetation and population development	Number of permanent plot	Sex, sex indices	Individuals · 0.1 ha^{-1} in years				
			1975	1976	1977	1978	1979
4 Communities of perennial grasses, herbs and lichens – with determined sex of juniper	66.13	♂	8	9	33	45	62
		♀	7	10	20	28	36
		o	181	214	193	181	175
		Σ	196	233	246	254	273
		$\frac{\text{♂} + \text{♀}}{\Sigma} \cdot 100\%$	7.7	8.2	21.5	28.7	35.9
		♂ : ♀	*	*	1 : 0.6	1 : 0.6	1 : 0.6
5 Complexes of herb and lichen communities with juniper brush community – earlier phase	66.17	♂	**	18	29	33	35
		♀		15	24	29	32
		o		44	31	25	28

		Σ		77	84	87	95
		$\frac{♂ + ♀}{\Sigma} \cdot 100\%$		42.9	63.1	71.3	70.1
		♂ : ♀		1 : 0.8	1 : 0.8	1 : 0.9	1 : 0.9
6 Complexes of herb and lichen communities with juniper brush community – optimal phase	66.1	♂	83	80	88	96	109
		♀	80	85	88	97	105
		o	77	91	104	91	94
		Σ	240	256	280	284	308
		$\frac{♂ + ♀}{\Sigma} \cdot 100\%$	67.9	64.4	62.9	67.9	69.4
		♂ : ♀	1 : 1.0	1 : 1.1	1 : 1.0	1 : 1.0	1 : 1.0

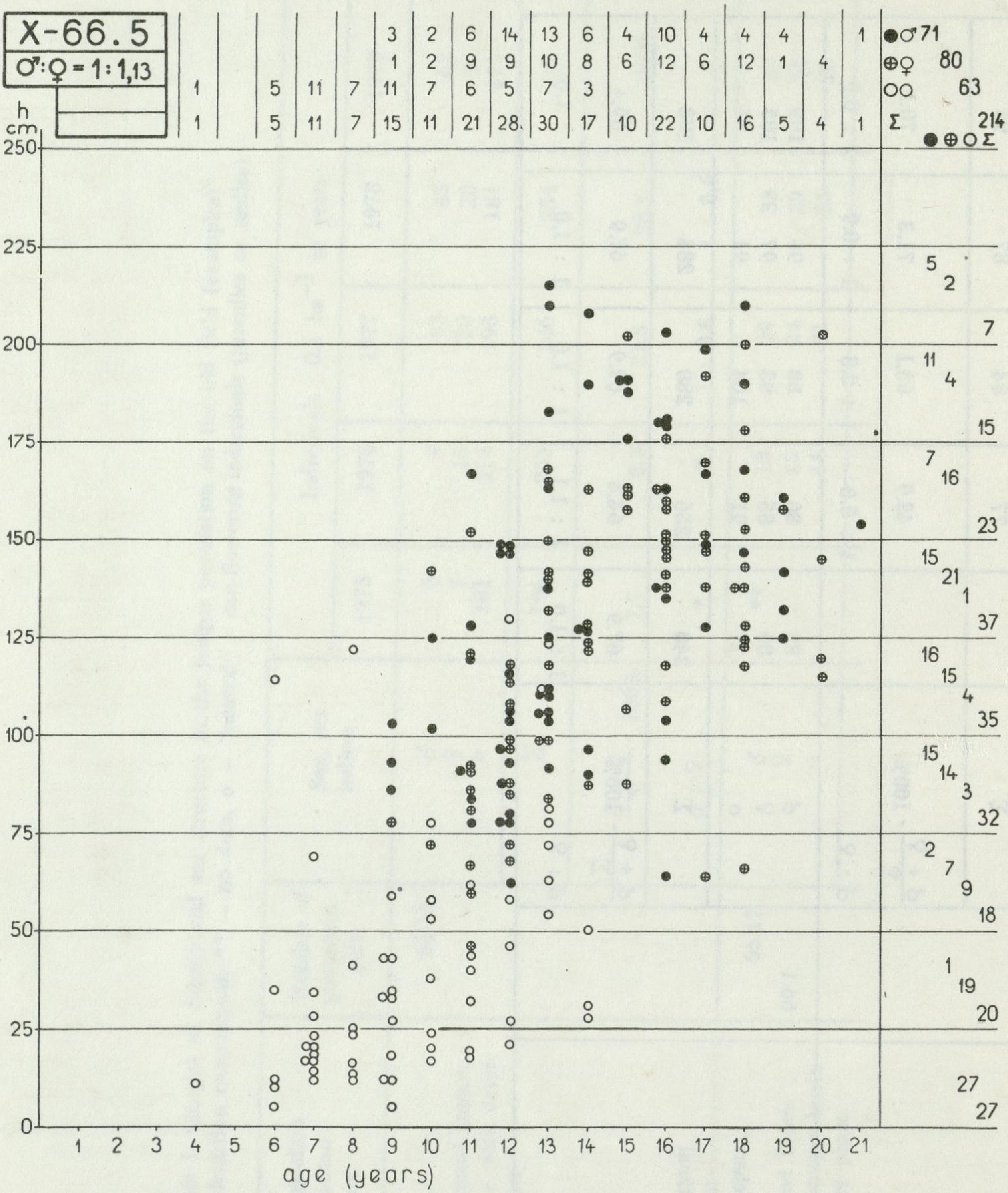

Fig. 5. Correlation between the age and size of a *Juniperus communis* shrub
A sample from a population in the stabilized stage from a site 1000 m^2 in area. Study plot X–66.5

tion has been determined. For phase 4 it was estimated at ♂ : ♀ = 1 : 0.4, with a tendency to change (Table I, Fig. 6) towards ♂ : ♀ = 1 : 1. This value of the ratio is attained at the optimum stage (phase 6), whereas at the terminal stage it comes up to ♂ : ♀ = 1 : 1.15. Changes in the sex ratio of a *Juniperus communis* population developing in the course of a plant succession on abandoned farmlands

Fig. 6. Age- and sex-, and age- and size-pyramids from a *Juniperus communis* population in sex determination phase (phase 4), the younger stabilization phase (phase 5) and the older stabilization phase (phase 6)
X–66.21, etc. – designations of the study series and plots

can be defined as changes leading from a male predominance through a state of sex equilibrium to a slight predominance of females.

10. In the *Juniperus communis* populations under observation, the sex ratio depended on the generative reproduction. Contrary to the circulating opinions, vegetative propagation occurs in the juniper only exceptionally, only at the terminal stage. It is usually forced by overcrowding, or destruction of the main stems, or a limited growth of the latter, e.g., due to being covered by eolic deposits.

11. If the spatial structure of a juniper population is loose, the individuals begin to reproduce themselves at the age of 6–7 years (phases 4–6), after attaining the height of 0.5 m, males usually starting a year earlier. During the terminal stage (phases 7 and 8), the calendar age at which the generative reproduction begins is delayed and is spread over the age range of 10 to 20, and even 26 years (Figs. 9 and 10). This phenomenon is caused by population overcrowding and community structure changes. These are discussed in more detail in the following section.

Table II. Estimated individual and population diaspore production of *Juniperus communis* in different succession phases

Succession phases	Population age (years)	Density (♀ ind. ha^{-1})	Total diaspore production		Mean individual diaspore production		Maximum individual diaspore production	
			number · ha^{-1}	weight (kg · ha^{-1})	number	weight (g)	number	weight (g)
4	9	80	290	0.014	3.6	0.17	13	0.48
5	14	140	62310	2.589	445.1	18.50	3140	132.28
6	21	780	867810	51.861	1112.6	66.50	22625	996.87
8	55	5460	1466556	91.564	286.6	16.77	1619	93.93

12. Diaspore production by an individual is at its highest at the optimum stage (Table II), and drops during the terminal stage, as a result of overcrowding and community structure changes. The total production of a population increases from the initial stage (phase 4) on and continues to increase until the terminal stage (phase 7), as a result of the increasing numbers (Table II).

13. Preliminary data on the sex ratio in other dioecious woody species (Figs. 11, 12 and 13) permit the statement that their ratio undergoes similar changes in the course of succession.

14. In the light of the research carried out so far, changes in the sex ratio of the populations of pioneer dioecious woody species can be defined as changes leading on to a sex equilibrium, where two ways seem to be possible (Fig 14):

a. from male predominance to a state near equilibrium (*Juniperus communis*, *Salix pentandra* L., *Populus tremula*);

b. from female predominance towards an increased proportion of females, but without a possibility to attain the level of ♂ : ♀ = 1 : 1 (*Salix caprea*, *S. cinerea* L., and perhaps *S. rosmarinifolia* and *S. aurita*).

5. DISCUSSION OF RESULTS

5.1. VEGETATION SUCCESSION

As has been pointed in the introduction, the farmlands concerned and the later wastelands arose in habitats that had once been occupied by pine forests and mixed oak-pine forests. The description that follows is restricted to the presentation of the development of vegetation in the commonest habitats, i.e., mesophilous pine forests, Peucedano-Pinetum typicum. The environmental conditions prevailing in those forests have also been dealt with in the introduction.

A direct floristic-phytosociological analysis makes it possible to distinguish 8 consecutive phases of vegetation development in abandoned farmlands. Their duration and the absolute dating were based on the known ages of the populations of *Juniper communis*, and for the later phases additionally also of *Salix aurita*, *S. rosmarinifolia* and *Populus tremula.* These data have been checked against interviews with the local people and persons employed in the forest services, and against the information obtained from an analysis of cadastral surveys. A general diagram of plant succession in the abandoned farmlands during a period of 60 years has been presented in Figure 1.

Phase 0 is a segetal community. Crops of rye, oats, potato, yellow lupine (*Lupinus polyphylus* Ldl.) and buckwheat (*Fagopyrum sagittatum* Gilib.) are accompanied by a weed association poor in species, the Teesdaleo-Arnoseridetum (Mak., 1929) R. Tx. 1937. More frequent in it are: *Rumex acetosella* L., *Scleranthus annuus* L., *Convolvulus arvensis* L., *Viola arvensis* Murr., *Sinapsis arvensis* L., *Arabidopsis thaliana* (L.) Heynh., *Festuca rubra* L., *Antemis arvensis* L., *Stachys annua* L., *Galeopsis ladanum* L.

Filago arvensis L., *Veronica verna* L., *V. dillenii* Cr., *Myosotis micrantha* Pall., *Teesdalea nudicalis* (L.) RDr., and especially *Arnoseris minima* Schweig. et Koerte, like other species of extremely oligotrophic, acidophilic, usually fairly dry habitats, occur at present in the crops in rather small numbers. This is probably due to the treatment with commercial fertilizers and pesticides.

On the whole, the group of sand therophytes is less numerous in the segetal communities than in the adjacent abandoned farmlands.

Phase 1 is the pioneer phase of the sand herb-grassland in a new fallow. Duration 1–2 years. The vegetation of all the consecutive developmental phases in the above-mentioned habitats, starting from fallows through herb-grasslands to brushwoods and younger stages of a pine forest, can jointly be described as one constantly containing 10 herbaceous perennials among which typical psammophytes predominate. These are: *Jasione montana* L., *Helichrysum arenarium* (L.) Moench, *Artemisia campestris* L., *Hypericum perforatum* L. (along with *H. humifusum* L.), *Solidago virga-aurea* L., *Hypochoeris radicata* L., *Rumex acetosella* L., *Hieracium pilosella* L., *Knautia arvensis* (L.) Coult., *Achillea millefolium* L. They are also accompanied by *Corynephorus canescens* (L.) P. B., which, however, retreats somewhat earlier. The main community that begins to form in the fallow phase is in its nature a sand herb-grassland, the optimum of which occurs in phases 4–6 (cf. above). Taxonomically, it can be placed in the class Sedo-Scleranthetea Br.-Bl. 1955, and the order Festuco-Sedetalia R. Tx. 1951.

Our community no doubt represents a type of inland sand grassland, continental in nature. It belongs to the alliance Koelerion glaucae Klika 1935, or Heliochrysion arenariae s. l. R. Tx. et Prsg 1951. For the time being, a complete identification with Festuco-Koelerietum glaucae Klika 1931, the only association described for this alliance, is impossible. In phase 1 and in the phases that follow, the perennial psammophytes are accompanied by therophytes such as *Filago minima* (Sm.) Fr., *Gnapholium silvaticum* L. and *Scleranthus annuus* L. Only in this phase the typical field weeds still continue to occur, such as: *Galeopsis ladanum* L., *Stachys annua* L., *Digitaria ischaemum* (Scherb) Muehlenb, *Spergula arvensis* L., *Gypsohila muralis* L.

Phases 2, 3 and 4 are represented by a sand herb-grassland with lichen communities. Duration 2–15 years. Phase 2 begins with the invasion by *Thymus serpyllum* L. and *Astragalus arenarius* L., which, like the 10 species enumerated at the beginning, will persist until the brushwood phases (7–8). The next species to appear are *Poa compressa* L. and *Pteridum aquilinum* (L.) Kuhn. The final formation of a Koelerion glaucae type of grassland, lichen communities, Corniculario-Cladonietum mitis Krieger 1937, and other small-space communities or synusiae of cryptogams (e.g., with *Stereocaulon condensatum* Hoffm., with *Polytrichum piliferum* Schreb., with *Racomitrium canescens* Brid.) takes place in phase 4 and the phases that follow it.

The formation of the Corniculario-Cladonietum is preceded by a gradual entrance of a considerable number of lichen species, especially those of the genus *Cladonia*. In phase 2, there already appear *C. cornutoradiata* (Coem.) Vain., *C. chlorophaea* (Flk.) Spreng., *C. fimbriata* (L.) Fr. emend. Vain., *C. glauca* Flk., *C. minor* (Hag) Vain., and *C. mitis* Sandst. In phases 3 and 4, the entrance is observed of: *C. furcata* (Huds.) Schrad., *C. pleurota* (Flk.) Schaer., *C. degenerans* (Flk.) Spreng., *C. verticillata* Hoffm., *C. bacillaris* Nyl., as well as representatives of other genera such as: *Cornicularia aculeata* (Schreb.) Ach., *Bacomyces roseus* Pers., and already in phases 5 and 6: *Stereocaulon condensatum* Hoffm. and *S. incrustatum* Flk., *Lecidea granulosa* (Ehrh.) Ach, and *L. uliginosa* (Schard.) Ach. In phase 3, *Gnaphalium silvaticum*, a fallow therophyte, retreats, and there appear the first juniper seedlings in considerable numbers. In phase 4, individuals that have attained the age of 6–9 years and have grown above the sward begin to flower. At the end of phase 4, the ratio of the area occupied by the sand grassland of the alliance Koelerion glaucae and the communities of lichens, primarily Corniculario-Cladonietum mitis, is established, assuming the value of about 4 : 1 or 5 : 1.

Phases 5 and 6 are represented by a sand herb-grassland and lichen communities in a complex with juniper scrub. Duration 12–25 years.

The basic changes in this picture are brought about by an increase in numbers of the juniper, and particularly the growth in height and breadth of the juniper shrubs. At that time the following can be observed: an increase in the projection cover per grassland area in the vicinity of the shrubs, permanent shading of the ground, needle accumulation, xeric relations in the soil, because of an almost complete interception of precipitation by the needles. The joint action of these new factors leads to the formation of specific ecological niches under the canopy of larger juniper shrubs. The existence of different conditions in the vicinity of larger juniper shrubs is manifested by an aggregation in those places of typical sand therophytes, such as *Teesdalea nudicaulis* (L.) R. Br., *Cerastium semidecandrum* L., *Myosotis stricta* Lk., and above all *Spergula vernalis* Willd. They are accompanied by *Corynephorus canescens* (L.) P. B. This concentration forms a ring-like edge around a juniper shrub (Fig. 7). If juniper shrubs grow close together, the rings unite. More or less 15 years

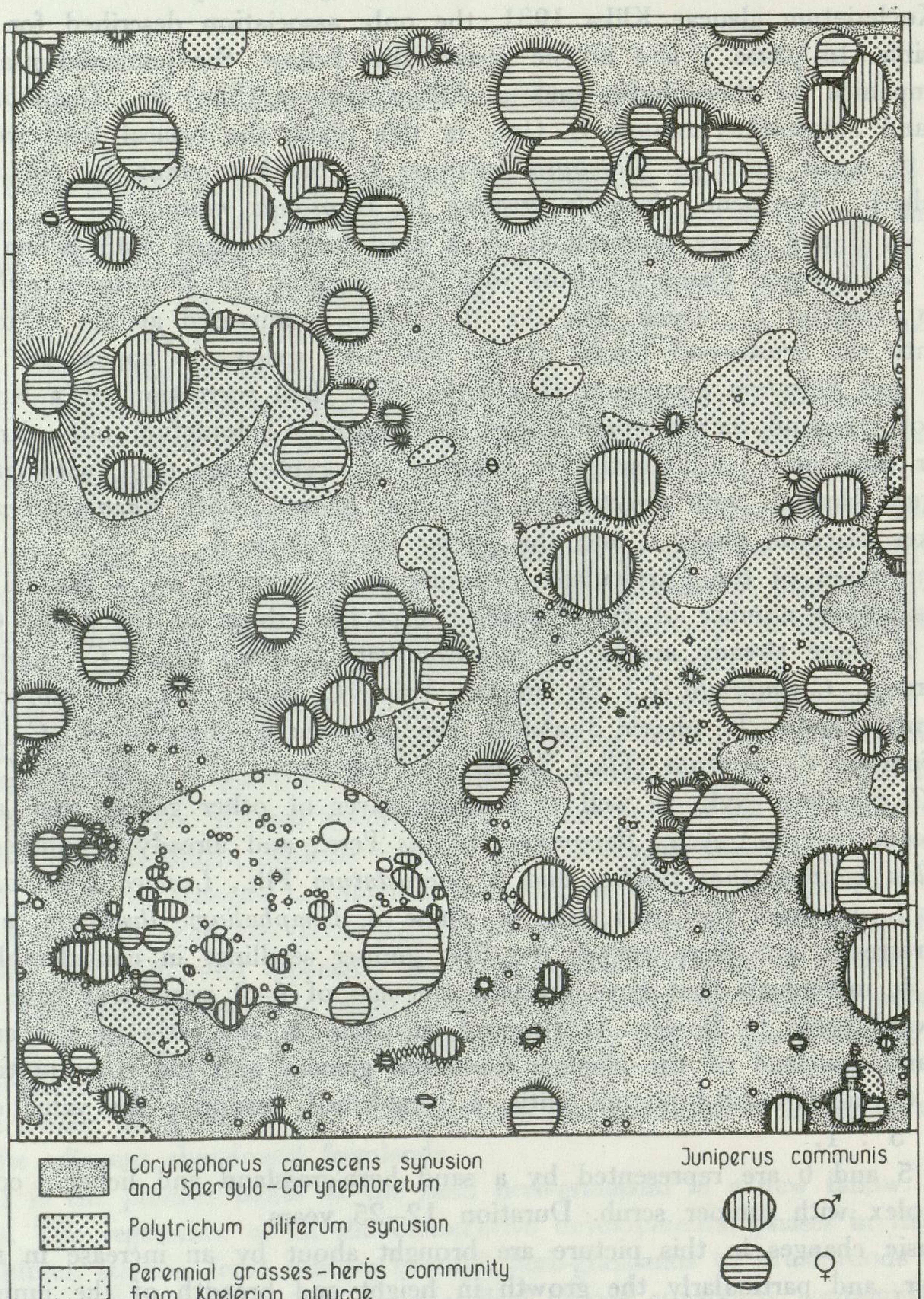

Fig. 7. An example of interaction between a juniper population and a sand grassland in phase 6 of succession

Formation of circular "cutouts" in the grassland under the canopy of juniper shrubs, due to the accumulation of needles and the specific microclimatic conditions that prevail there. In the cutouts at the base of the parent individuals the autochthonous generation settles

after the abandonment of farmlands, within the compact sward a short-lived community forms rather typical of the early succession phases. Taxonomically, it can be identified with Spergulo-Corynephoretum R. Tx. (1937) 1955. As the juniper shrubs grow in size, the therophyte rings become, as it were, pushed away, whereas near the base of each shrub there forms a new ring consisting of liverwort synusiae and several of the original *Cladonia* species. Already in phase 6, the spatially well diversified complex consisting of several lichen communities and grassland communities, of different composition and genesis, becomes disturbed by the appearance of several permanent species which attain their optimum in the brushwood phases. These are: ***Peucedanum oreoselinum*** (L.) Moench, and the shrubs: ***Cytisus ruthenicus*** Fish and ***C. ratisbonensis*** Schaeff, ***Lycopodium clavatum*** L. In this phase also, there occurs a growth in numbers of the juniper derived from local seeding. At the end of phase 6, single pine and aspen trees grow above the sward, but do not yet form aggregations.

Phase 7 is the beginning of the formation of juniper-aspen brushwoods. It lasts 25–45 years. With the increasing compactness of juniper shrubs the proportion of grassland communities clearly diminishes. However, in this phase there still persits ***Corynephorus canescens.*** Under the canopy of the aspen, juniper and *Cytisus* typical therophytes can no longer occur. In the small gaps among the shrubs there appear typical verge perennials: ***Vincetoxicum officinale*** Much., ***Stellaria graminea*** L., ***Galium mollugo*** L., ***G. verum*** L., and the shrub ***Genista tinctoria*** L. More and more frequent become the willows: ***Salix aurita, S. rosmarinifolia, S. caprea,*** and less frequent ***S. nigricans*** Sm. Lichen communities typical of open country disappear completely, whereas under the canopy of trees and shrubs a lichen-moss layer forms with the following typical forest species: ***Pleurozium schreberi*** Mitt., ***Dicranum undulatum*** Ehrh., ***Cladonia silvatica*** (L.) Hoffm.

Phase 8 is represented by juniper-aspen brushwoods. It lasts 40–70 years. The aspen which becomes more and more numerous and taller, accompanied by the pine, single birches and the spruce, begin to form the treestand. In the shrub layer, ***Pirus communis*** L. and ***Frangula alnus*** Mill. appear, and in the ground vegetation typical components of coniferous forests begin to be present, among which more numerous is ***Melampyrum pratense*** L., while the following occur singly and in dispersion: ***Vaccinium myrtillus*** L., ***Pirola secunda*** L., ***P. rotundifolia*** L., ***Lycopodium complanatum*** L., ***Majanthemum bifolium*** (L.) F. W. Schm. and ***Hylocomium splendens*** (Hedw.) Br. Juniper-aspen scrubs, aged about 60–70 years (as counted from the abandonment of the farmland), already attain in places a stratification similar to that of a forest community (treestand, undergrowth, herb layer, lichen-moss layer). A transient nature of the community under consideration towards a pine forest of the type Peucedano-Pinetum (phase 9) is indicated only by the proportions of the developing layers (poor thickness of the stand, overdevelopment of the shrub layer, patchy nature of the ground vegetation layer).

5.2. DEVELOPMENT OF A *JUNIPERUS COMMUNIS* POPULATION

0–4. The invasion, colonization and sex "determination" phases. Pioneer *Juniperus communis* individuals become conspicuous only at the end of phase 2 and in phase 3, i.e., on a land that has not been used for at least 5 years. In phase 3 the density does not exceed 220–290 individuals $\cdot$ ha^{-1}, whereas in the next phase is shows an about 5-fold increase, attaining the first maximum of population abundance (from 1100 to 2500 ind. $\cdot$ ha^{-1}).

A continuous increase in numbers by seeding from outside (Table I) results in a diversity of age and height of a population, which can be seen in the pyramids presented (study plot 66.21 in Fig. 6), although only 2 classes show a clear dominance: aged 6 and 7 years. The oldest individuals are 9 years old.

In phase 4 the oldest individuals of *Juniperus* which rise above the sward begin to flower, males at the age of 6–7 years, females usually a year later. The first diaspores are few in number, and their ripening which is spread over more than 2 years ends at the beginning of the next phase. However, the number of individuals participating in reproduction does not exceed 10%.

In phase 4 the value of the sex ratio, an important index, can be determined for the first time. The numerical ratio ♂ : ♀ is 1 : 0.4 (Fig. 6, study plot 66.21) and indicates a predominance of males. Later changes of the sex ratio proceed towards ♂ : ♀ = 1 : 0.6 (Table I, study plot 66.13). In spite of an increase in the percentage of females, males continue to dominate among individuals with "determined" sex.

5–6. Stabilization and propagation phases. In the next phase the density of a population is established, but then more than a half of the individuals begin to flower. The individual age varying between 2 and 13 years, with a maximum at the age of 9 or 10 years. The tallest individuals attain the height of 2 m. In this phase the first examples of sex dimorphism can be seen: among column-shaped individuals males predominate.

The stabilizing numbers of the population, though not yet very high, permit the determination, already in this phase, of the sex ratio. The value of ♂ : ♀ is 1 : 0.8 or 1 : 0.9 (Table I, study plot 66.17; Fig. 6 — study plots 66.20 and 66.19).

In phases 5 and 6, a further differentiation of age, and an increase in the absolute number of reproducing individuals bring about a change in the sex ratio. In all populations aged 20–21 years the ratio is established at 1 : 1, often even with a small predominance of females. This indicates a gradual increase in the proportion of females. On the average only $\frac{1}{3}$ of the individuals of a population do not reproduce generatively (Table I). All individuals aged above 13–14 years, and over 1 m (1.25 m) tall have already revealed their sex. At the same time the lower age limit of reproducing individuals rose (to 8–9 years). In the sex- and age- and sex- and height-pyramids (samples 66.3, 66.2 and 66.5 in Figure 6) two changes can be seen: an increase in height of the pyramids (a gradual passing of individuals to higher classes), as a result of population maturation, and a slight disturbance in the pyramid asymmetry, due to an increase in the percentage of females, especially in the older classes. However, males continue to dominate in the youngest age classes. The pyramids presented in Figure 6 make it possible to observe this phenomenon, as a continuous process, from the sex determination phase (phase 4). In juniper populations attaining the age of 20 years the first juvenile individuals can be seen in the immediate vicinity of older individuals bearing large numbers of fruits. Their presence almost exclusively in the vicinity of females, and the lack of such aggregations in an earlier phase of juniper scrubs, permit the assumption that they are derived from individuals which had made their home in the abandoned farmlands 15 years before. This is confirmed by a simple calculation: 2 years for the ripening of the cone-berries after their setting, 2–3 years for their germination. Sufficiently efficacious seeding could only be ensured by individuals producing larger numbers of fruits, i.e., those aged at least 12–15 years (Table II).

Direct evidence to prove an autochthonous origin of this group of the youngest juniper individuals has been supplied by the experiment carried out in the permanent plot no. 66.5. In 1975, all juniper individuals (214) growing on this plot (0.1 ha) were cut down. The oldest males were 21 years old; the oldest females – 20 years. Junipers occurred on this site again in 1979. They formed circular aggregations the size of which corresponded to the range of the base of each of the juniper shrubs that had been cut down (Fig. 3).

The size and age of the individuals indicate that they come from the seeding by shrubs that had been cut down later. The close occurrence of 2 and more individuals together, often with remnants of the cone-berries still connected by twigs, proved that they originated from a barochore seeding. Thus the origin of the youngest group of individuals was autochthonous.

It must be pointed that the factor favouring the settling of young individuals in the vicinity of large parent individuals in phase 6 of population development was primarily the loosening of the initially compact sward, due to the effect of large juniper shrubs, and the formation on its place of open therophyte communities.

7–8. The overcrowding and population regression phases. A further growth in numbers, and more precisely an increased density per unit area is accomplished probably not so much due to the seeding from outside, for which a compact sward is closed, as to the propagation of the older individuals of the population. Maximum density, up to 30000 individuals $\cdot$ ha^{-1}, is attained by populations aged over 50–55 years, that is to say, on lands not utilized for at least 60 years. Such populations can only be found in juniper-aspen brushwoods, that is, thick brushwoods which gradually pass on into a forest (cf. subsection 5.1). A good picture of the age and sex structure of such a population is provided by the pyramid for a sample from study plot 66.15 (Fig. 8).

5.3. AN ANALYSIS AND INTERPRETATION OF THE PYRAMID OF THE OLDEST POPULATION OF *JUNIPERUS COMMUNIS*

The sex- and age-pyramid of *Juniperus communis* from sample 66.15 consists of "two cones": a bigger and a smaller, connected by their bases. The sample includes 2763 individuals aged from 3 to 55 years (Fig. 8). Individuals with determined sex represent 37%. So 63% of juvenile and senile individuals do not participate in the generative reproduction. Females predominate among the individuals reproducing themselves generalively. The sex ratio is ♂ : ♀ = 1 : 1.14. The youngest reproducing individuals of the first juvenile individuals can be seen in the immediate surroundings of older individuals bearing large numbers of fruits. Their presence almost exclusively in the vicinity of females, and the lack of such aggregations in an earlier phase of juniper scrubs, permit the assumption that they are derived from individuals which had made their home in the abandoned farmlands 15 years before. This is confirmed by a simple calculation: 2 years for the ripening of the cone-berries after their setting, 2–3 years for their germination. Sufficiently efficacious seeding could only be ensured by individuals producing larger numbers of fruits, i.e., those aged at least 12–15 years (Table II).

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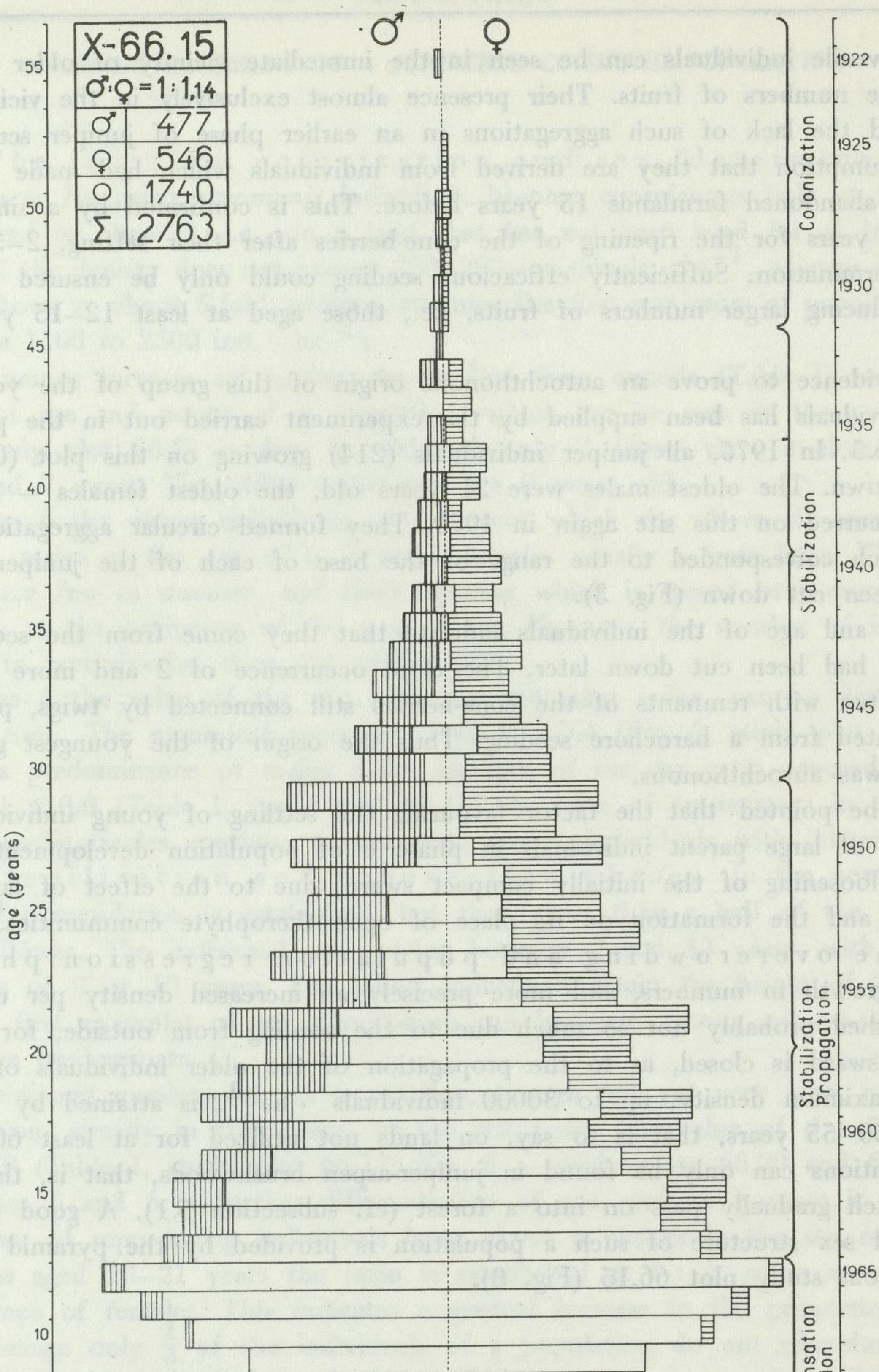
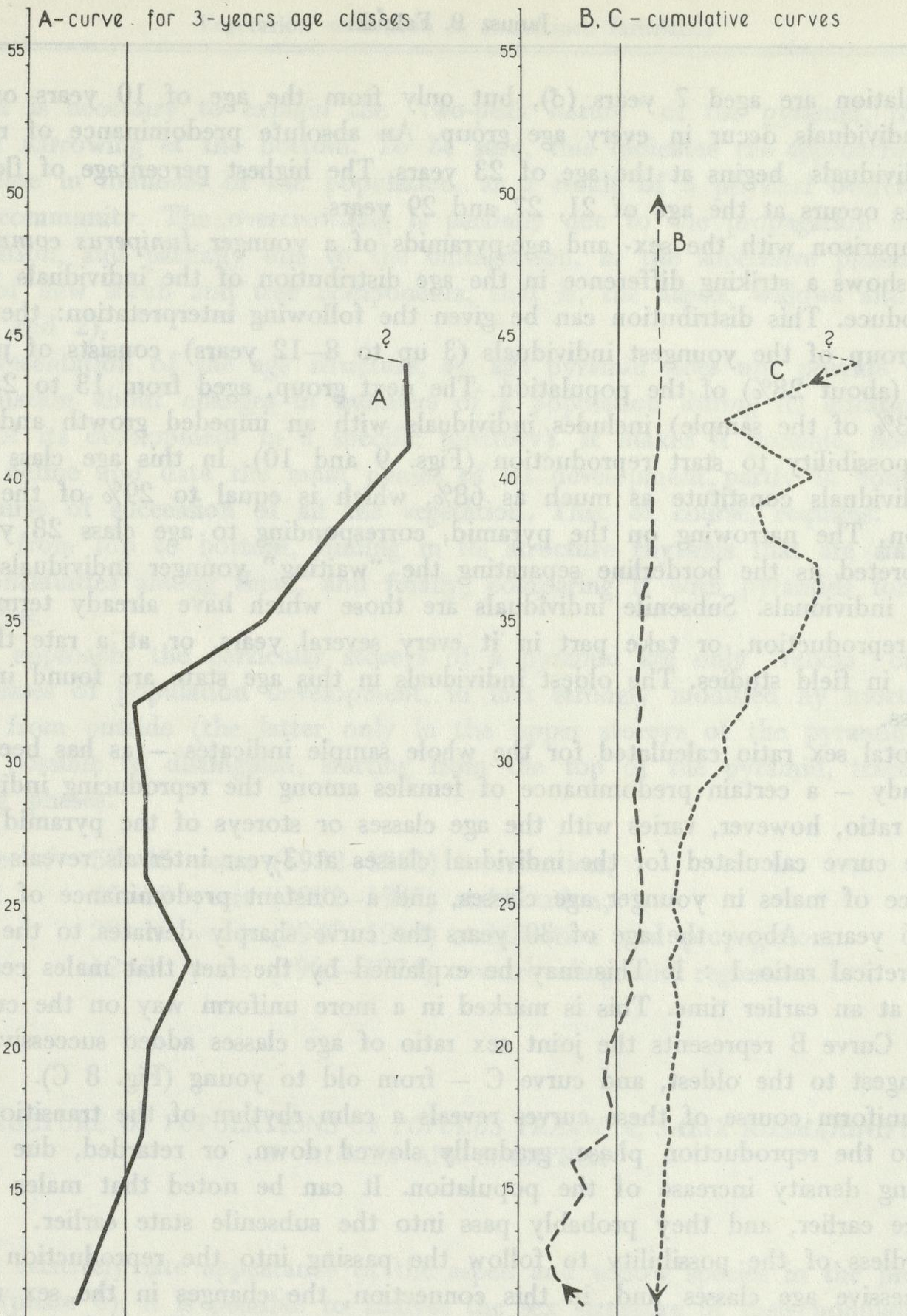


Fig. 8. A sex- and age-pyramid in the oldest population of *Juniperus communis* (55 years) in the phase of niper-aspen

In the field of the pyramid: a reconstruction of the main phases of population development. Near it: an bers); A — changes in the sex-ratio in the consecutive 3 years'age classes; B — a cumulative sex-ratio curve mid base to top, e.g., aged 10 years, 10 + 11, 10 + 11 + 12, etc.); C — a cumulative sex-ratio cur- 44 years, + 43, 44 +



increased propagation and overcrowding, corresponding with the older phase of vegetation succession in ju-
brushwood (phase 8)
analysis of the sex structure of the pyramid (the extreme classes have been left out because of flow num-
obtained by successive additions of reproducing individuals in ascending order according to age (from pyra-
ve obtained by successive adding of reproducing individuals in descending order according to age (e.g.,
43 + 42, etc.)

the population are aged 7 years (♂), but only from the age of 10 years on do flowering individuals occur in every age group. An absolute predominance of reproducing individuals begins at the age of 23 years. The highest percentage of flowering individuals occurs at the age of 21, 27 and 29 years.

A comparison with the sex- and age-pyramids of a younger *Juniperus communis* population shows a striking difference in the age distribution of the individuals which do not reproduce. This distribution can be given the following interpretation: the most numerous group of the youngest individuals (3 up to 8–12 years) consists of juvenile individuals (about 28%) of the population. The next group, aged from 13 to 23 years (about 43% of the sample) includes individuals with an impeded growth and waiting for the possibility to start reproduction (Figs. 9 and 10). In this age class the "waiting" individuals constitute as much as 68%, which is equal to 29% of the whole population. The narrowing on the pyramid, corresponding to age class 28 years, may be interpreted as the borderline separating the "waiting" younger individuals from the subsenile individuals. Subsenile individuals are those which have already terminated generative reproduction, or take part in it every several years, or at a rate that can not be noted in field studies. The oldest individuals in this age state are found in the 45-year class.

The total sex ratio calculated for the whole sample indicates – as has been mentioned already – a certain predominance of females among the reproducing individuals. The sex ratio, however, varies with the age classes or storeys of the pyramid. In Figure 8 A, the curve calculated for the individual classes at 3-year intervals reveals a clear dominance of males in younger age classes, and a constant predominance of females above 16 years. Above the age of 30 years the curve sharply deviates to the right, from the theoretical ratio 1 : 1. This may be explained by the fact that males cease to reproduce at an earlier time. This is marked in a more uniform way on the cumulative curve B. Curve B represents the joint sex ratio of age classes added successively, from the youngest to the oldest, and curve C – from old to young (Fig. 8 C).

The uniform course of these curves reveals a calm rhythm of the transition of individuals to the reproduction phase, gradually slowed down, or retarded, due to the progressing density increase of the population. It can be noted that males begin to reproduce earlier, and they probably pass into the subsenile state earlier.

Regardless of the possibility to follow the passing into the reproduction phase of the successive age classes and, in this connection, the changes in the sex ratio, two other phenomena can be read from the pyramid considered. First of all, over the period of 12 to 33 years a several-year rhythm can be seen: a 3-year rhythm (12, 15, 18, etc.) in the lower part of the pyramid, and a 2-year rhythm in the middle. The rhythm corresponds to periodical increments of the size of the population. This probably is the resultant of individual, many-year rhythms of reproduction, typical of woody species. It would thus depend mainly on the autochthonous propagation, so it would be difficult to suppose that the 12–33 years' interval of the pyramid contains a record of the history of an increased (increasing) seeding from outside, as new *Juniperus communis* populations matured in the vicinity, on newly abandoned farmlands. The existing observations seem to indicate that middle-aged populations (phase 6) are in essence already closed to autochthonous propagation, because of the strong thickness of the sand grassland. At the bases of juniper shrubs in a loosened sward diaspores derived from mother individuals no doubt take priority (Figs. 3 and 7).

Finally, it is necessary to explain the "two-peak nature" of the pyramid, that is, its complete narrowing at the bottom. To be sure, this indicates the approaching end of the increase in numbers of the population, as a result of a physical overcrowding in a plant community. The overcrowding is partially due to the propagation in a juniper population, and partially due to the immigration, in the successive phases of succession, of new shrub and tree components, that is, the aspen, willows and pine (cf. Figs. 1 and 2).

As a representation of the age structure, an age pyramid does not provide any direct information about changes in numbers of a population during its duration (as a function of its development in a specific territory). It makes it possible, however, to indirectly define and date the main phases of its development, partly in connection with the course of succession of all the vegetation. This, of course, requires: "reading" the pyramid from top to bottom, finding in its structure rhythms that are similar, or certain discontinuities among them, and finally, comparing it with pyramids for younger populations.

With this approach, the particular storeys of a pyramid are only "relicts" of the successive phases of population development, in fact strongly modified by mortality and seeding from outside (the latter only in the upper storeys of the pyramid). However, it is possible to distinguish, starting from the top of the pyramid, traces of the following phases:

at the age of 55–45 years (1922–1931) colonization,
45–30 years (1932–1947) stabilization,
29–12 years (1947–1964) stabilization and propagation,
12–3 years (1965–1974) overcrowding and regression.

5.4. SEX STRUCTURE OF POPULATIONS OF *POPULUS TREMULA, SALIX ROSMARINIFOLIA, S. AURITA* AND *S. CAPREA*

Due to the relatively late appearance of the aspen and willow species in the process of succession (phase 6), it is possible to analyse the sex structure of their populations only in the terminal stage of vegetation development. This corresponds with the phase of overcrowding and regression of *Juniperus communis* populations (Figs. 1 and 2).

Populations of all the three willow species consist almost exclusively of individuals that already reproduce themselves generatively. The juvenile individuals, few in number, are as a rule of vegetative origin. The youngest individuals of *S. rosmarinifolia* were 5 years old, of *S. aurita* – 7 years. In both cases they were females (Fig. 11).

The small number of "counted" samples permit the determination of only an approximate sex ratio for:

Salix rosmarinifolia – ♂ : ♀ = 1 : 3.2, with a population age of 21 years,
Salix aurita – ♂ : ♀ = 1 : 4.3, with a population age of 32 years,
Salix caprea – ♂ : ♀ = 1 : 2.0, with a population age of about 20 years.

The value of the sex ratio can be interpreted, very cautiously, using data collected for populations of these species in different areas.

In general, in younger populations of *Salix caprea*, *S. aurita* and *S. rosmarinifolia*

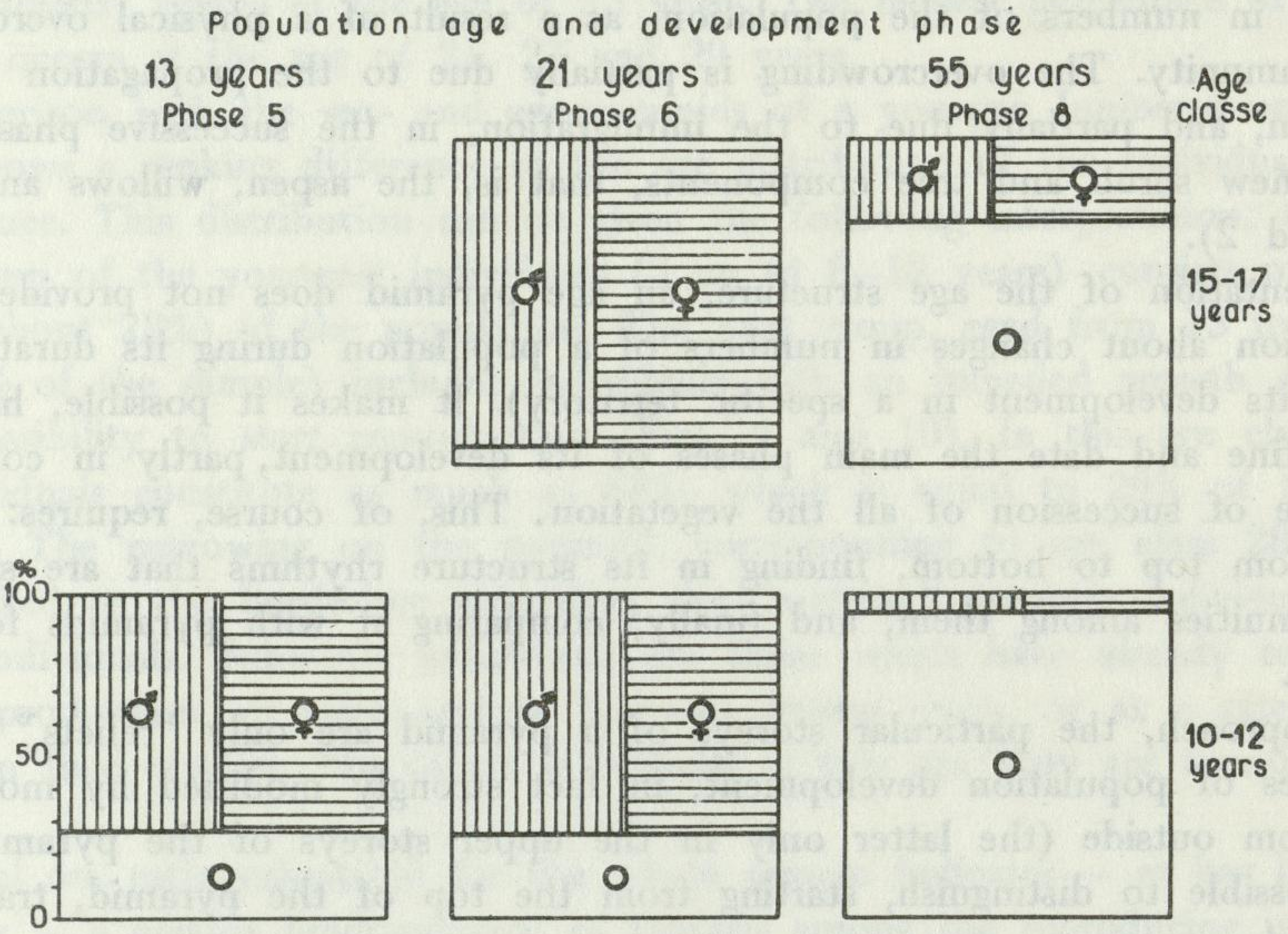


Fig. 9. A comparison of the sex structure of analogous age classes (10–12 and 15–17 years) in younger (13 years), older (21 years) and the oldest (55 years) populations of *Juniperus communis*, corresponding to the successive population development phases and vegetation succession phases The data have been taken from surface samples Nos. 66.12, 19, 21, 2, 3, 5, 15 (cf. Figs. 6, 8)

there exists an absolute dominance of females, and with advancing age of the population the sex ratio changes towards ♂ : ♀ = 1 : 1, but it never attains this value.

By contrast to the juniper and willows, in the aspen, *Populus tremula*, sex is revealed rapidly by a large proportion of a population simultaneously entering the flowering phase. In samples from comparable sites 0.1 ha in area, and with 400 individuals, a clear predominance of males can at once be seen (Fig 12). The sex ratio attains the value of ♂ : ♀ = 1 : 0.01, that is, there are 100 and more males per each female. In pioneer populations of *Populus tremula* this ratio may change only slightly with time when females start taking part in reproduction.

The *Populus tremula* populations known so far from 11 samples are distinguishable as "male" (Figs. 12 and 13). So the attainment in old populations of the theoretic ratio ♂ : ♀ = 1 : 1, known, e.g., from forest pppulations in Norway is only possible by a recession (death) of a large number of males. However, the possibility cannot be ruled out that in certain areas on the abandoned farmlands under study "female" populations may still appear (cf. sample 66.38 in Fig. 13).

We should thus be dealing with a patchiness in the spatial structure of a population in respect of the sex ratio.

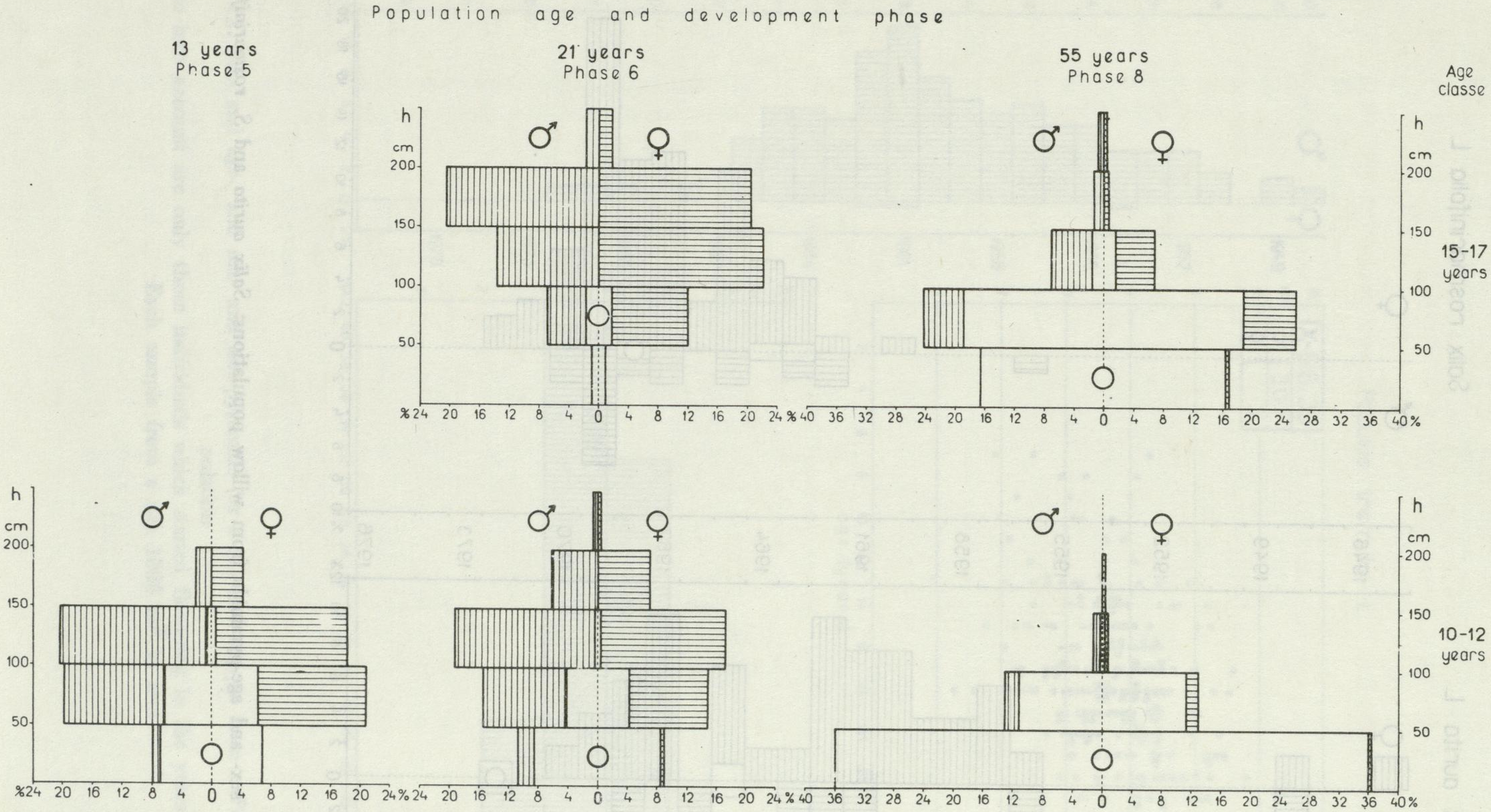


Fig. 10. Structure of sex and of the size of individuals in analogous age classes in younger, older and the oldest *Juniperus communis* populations. A detailed analysis of the material presented in Figure 9

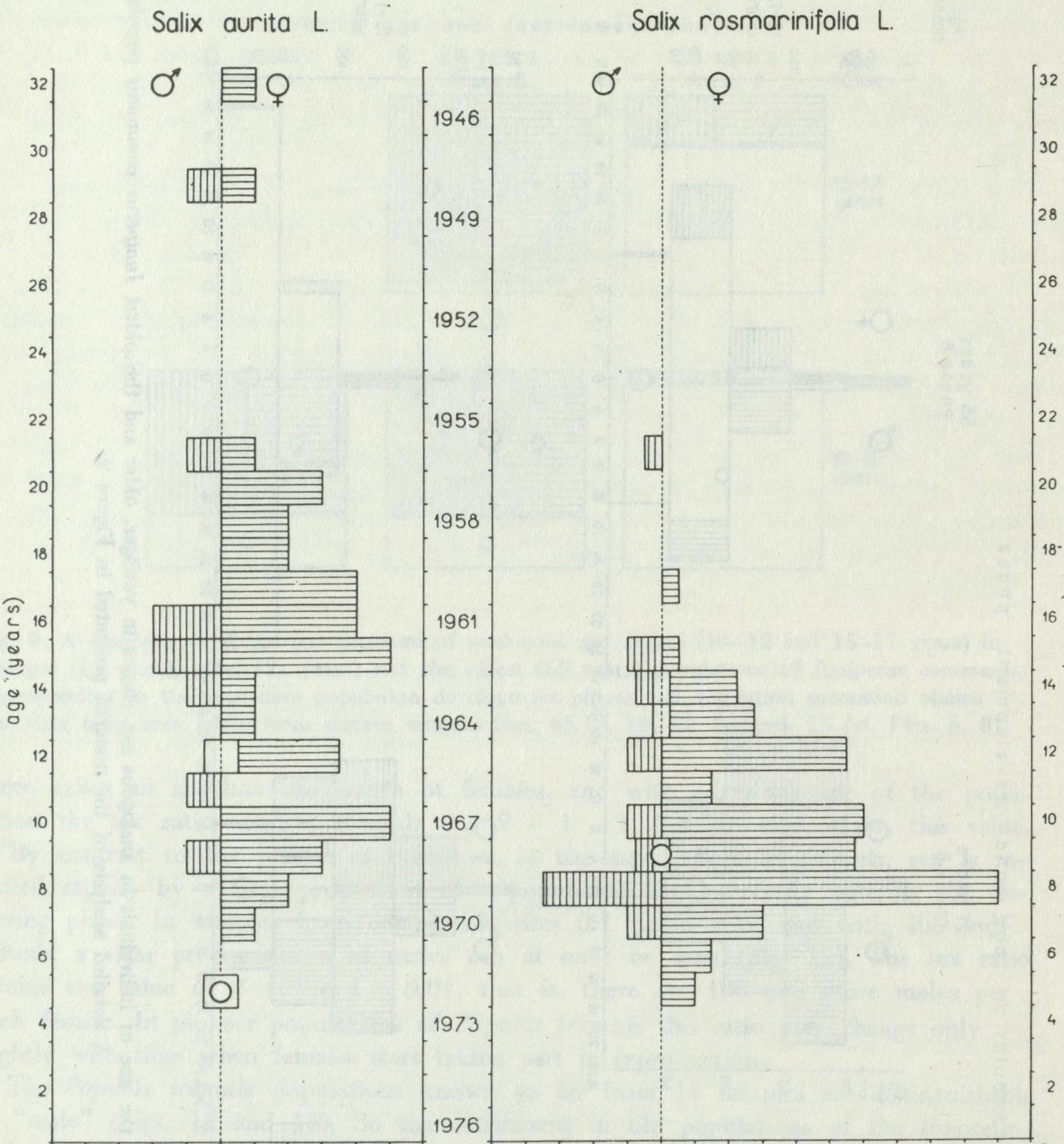


Fig. 11. Example sex- and age-pyramids from willow populations: *Salix aurita* and *S. rosmarinifolia*

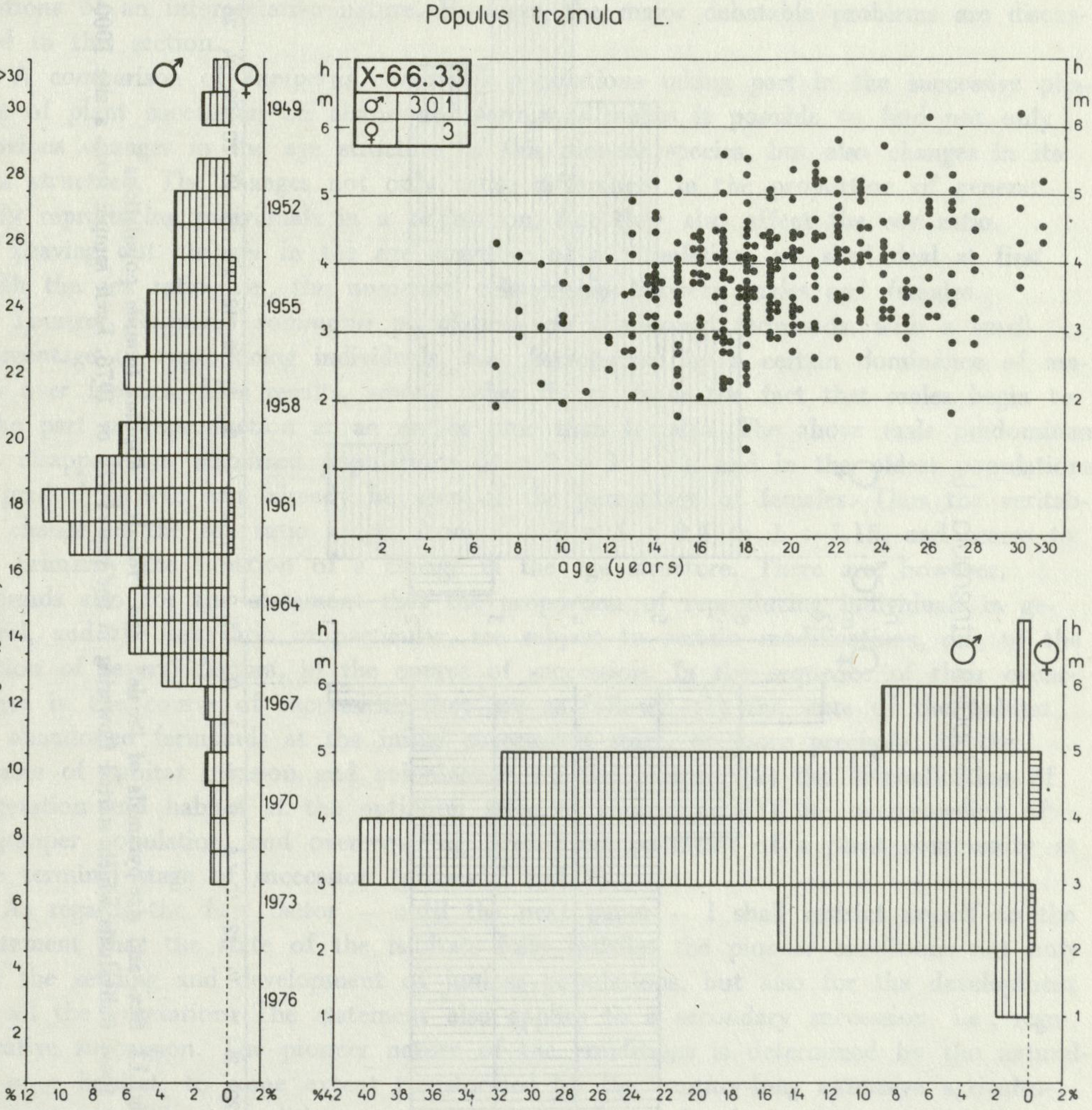


Fig. 12. Sex- and age-, and sex- and size-pyramids for a selected sample from a *Populus tremula* population

Taken into account are only those individuals which started flowering in the years 1977 and 1978. Each sample from a site 1000 m^2 in area

Fig. 13. Sex- and size-pyramids of "male" and "female" *Populus tremula* populations
Taken into account are only those individuals which started flowering in the years 1977 or 1978. Each sample from a site 1000 m^2 in area

6. GENERAL DISCUSSION

On account of the nature of the phenomenon, the relationships between the structure and dynamics of pioneer species populations, and plant succession have been presented in a descriptive form. It was also necessary to give some incidental explanations of an interpretative nature. However, the major debatable problems are discussed in this section.

A comparison of *Juniperus communis* populations taking part in the successive phases of plant succession on abandoned farmlands makes it possible to find not only obvious changes in the age structure of this pioneer species, but also changes in its sex structure. The changes not only cause differences in the proportion of generatively reproducing individuals in a population, but they also affect the sex ratio.

Leaving out changes in the age structure of a population, we shall deal at first with the sex ratio, i.e., the numerical relationship between males and females.

Younger *Juniperus communis* populations on abandoned farmlands, with a small percentage of reproducing individuals, are characterized by a certain dominance of males over females. This results, among other things, from the fact that males begin to take part in reproduction at an earlier time than females. The above male predominance disappears in stabilized populations (♂ : ♀ = 1 : 1), and in the oldest populations a gradual growth can already be seen of the percentage of females. Thus the veritable change in the sex ratio ranges from ♂ : ♀ = 1 : 0.4 to 1 : 1.15, and seems to be primarily the function of a change in the age structure. There are, however, grounds also for the statement that the proportion of reproducing individuals in general, and the sex ratio in particular, are subject to certain modifications, due to the action of several factors, in the course of succession. In the sequence of their occurrence in the course of succession, they are as follows: (1) the state of the habitat in abandoned farmlands at the initial successsion stage, or more precisely: in the phases of habitat invasion and colonization by the juniper, (2) the diversification of vegetation and habitat at the optimum stage of succession, (3) the overcrowding of a juniper population, and overcrowding (strong compactness) of a plant community at the terminal stage of succession (phases 7 and 8).

As regards the first factor – until the next paper – I shall restrict myself to the statement that the state of the habitats fully satisfies the pioneer conditions not only for the settling and development of juniper populations, but also for the development of all the vegetation. The statement also applies to a secondary succession, i.e , regenerative succession. The pioneer nature of the conditions is determined by the naturally poor habitat, to some extent transformed by the century-long extensive agricultural economy. These conditions not only cause a delay in the spontaneous development of vegetation, and wasteland colonization by the juniper, but they may also act selectively at the time of germination of the diaspores of this shrub. Unfortunately, there are no grounds for considerations concerning the mechanism and causes of such a selection, although the properties of similar abandoned farmland soils have been known well (Strzelecki and Sobczak 1972). We can, therefore, assume that the selection affects to a larger extent the diaspores and seedlings of the future females. Assuming that the males of this species are more resistant to extreme conditions already in the germination phase and at the juvenile stage, we would have a situation similar to that known from *Salix cinerea*. In the Białowieża Primeval Forest, in peat bogs, periodically water-logged, in river valleys, male individuals (polycormones) usually occupy deeper depressions in the terrain, so they can endure stagnant water for a longer time than can the females (Faliński – in press). The same probably applies to *Salix pentandra*. The transformation of the habitats in the course of succession leads on to, among other things, a shallowing, and even complete decline of the small depressions, creating conditions, favouring the appearance of females. A similarity can be seen here also to the different occurrence of the males and females of *Salix caprea* which is a large tree. This long-trunk tree appears especially in the regenerative phases of a mixed oak-linden-hornbeam forest, also along roads passing through such a forest (Faliński – in press). In the vicinity of changed or deformed stands males aggregate, though only exceptionally is the percentage of this sex equal to that of the females.

Our observations concerning the aggregation of males under more extreme conditions, peculiar, mainly though not exclusively, to pioneer habitats agree with the findings reported by Freeman, Klikoff and Harper (1976), as well as those by Putwain and Harper (1972). According to the former investigators, the males of species such as *Acer negundo* L. var. *interior* (Britt) Sarg., *Ephedra viridis* Coville, *Thalictrum fendleri* Engelm., *Atriplex confertifolia* (Torr. et Fern.) S. Wats., *Distichlis spicata* (L.). Greene var. *stricta* (Torr.) Beetle were found to concentrate in drier or saltier habitats. I agree with Putwain and Harper (1972), and with Zarzycki (unpublished) that we can even speak about different ecological niches of the males and females.

A mildening of the extreme conditions in the course of succession, in connection, for instance, with the accumulation of organic matter in the soil, development of soil processes and diversification of the structure of plant communities does not only mean changes in the living conditions of a population. It may also favour changes in the numerical ratios in a population, between the males and females, or the sex ratio.

Transformations and a spatial diversification of the vegetation and habitat, as a result of a plant succession in abandoned farmlands in which the juniper, among other plant species, takes part (cf. subsection 5.1. and Fig. 7), bring about, in the wake of changes in the density and spatial structure of the population of this shrub species, also some changes in the sex structure of the population. Namely, with the replacement of the random type of spatial structure by an aggregated structure, there appear a local tendency among the females to from concentrations. This applies to the generation of females which appear, due to the propagation of pioneer individuals, in habitats that had already been colonized by vegetation. A phenomenon like this was observed by the author on dune sands previously fixed by turf, the juniper and introduced *Salix acutifolia* (plot 80 in the range of Piaski; Faliński – unpublished observations).

Let us also consider sex structure changes in a juniper population in connection with a rapid increase in density, characteristic of the terminal phases of succession. Special proof of the effect of density on the sex structure, and size structure of a *Juniperus communis* population is provided by the analysis of analogous age classes in different-aged populations, thereby in different phases of plant succession (Figs. 9 and 10). The object of analysis was the age classes 10–12 years and 15–17 years (in populations aged 13 years only 10–12 years), 21 years and 55 years. In populations aged 13 and 21 years, in the stabilization phase (phases 5 and 6) and with a density of 3900 ind. · ha^{-1} (on the average 1 ind. per 3 m^2), the individuals occur loosely in the grassland community. In the oldest population, where the density of the juniper alone is up to 30000 ind · ha^{-1} (1 ind. per 0.3 m^2), that is, almost 10 times as high, there also occur other tree and shrub species (*Populus tremula, Pinus silvestris, Betula verrucosa, Salix caprea, S. aurita, S. rosmarinifolia, Cytisus rathenicus,* etc.). This situation corresponds to the older phase of the juniper-aspen brushwoods.

In the 10–12 years age class, in both the 13 years old and 21 years old populations over 70% of the individuals already participate in the generative reproduction, whereas in the oldest population the proportion of reproducing individuals is below 10%. The differences are only slightly smaller in the age class 15–17 years. In populations without overcrowding virtually all individuals at this age are already reproducing themselves (Figs. 6 and 10). The height pyramids worked out for these classes in uneven-aged populations show a clear growth impediment in individuals of an older overcrowded population. The greater majority of individuals in overcrowded populations do not attain the stature of 1 m, while in the "loose" populations more than half of the individuals of the same age have already attained the height class of 1–2 m.

The effect of population density on the sex- and size-structure may thus be defined as an impediment of growth and retardation of the beginning of reproduction, and a reduction in the individual production of diaspores. It must be noted, however, that the above mode of action of an overcrowding affects the younger generation, that is, juniper individuals derived from an autochthonous propagation. Maybe, the cause of the low resistance to overcrowding of these generations is a lower genotype and phenotype variation (lower diversity). The change of the sex ratio towards a female dominance seems to be a combined effect of the ageing of a population and changes in its living conditions during the terminal stage of succession.

7. CONCLUSIONS

1. The growth of a juniper population on abandoned farmlands proceeds gradually under more and more diversified phytocoenotic and synecologic conditions. This diversification is only reduced of the terminal stage of succession. A complete series of transitory communities with a pioneer therophyte community and the end forest community of the type Peucedano-Pinetum represent one sere. The course of the succession sere is most dependent on the development of the juniper population and populations of other pioneer dioecious tree species, but the dynamics and structure of the population of the first species is, at least in three phases of succession, modified by this succession. An analysis of the material presented allows for the conclusion that all properties of a population, and the sex structure as the most important of them, are modified by succession.

2 In the light of the studies carried out so far it seems that a sex equilibrium (sex ratio ♂ : ♀ = 1 : 1) in the populations of various pioneer tree species in the course of succession can be attained in two ways: from a male predominance, or from a female predominance (Fig. 14).

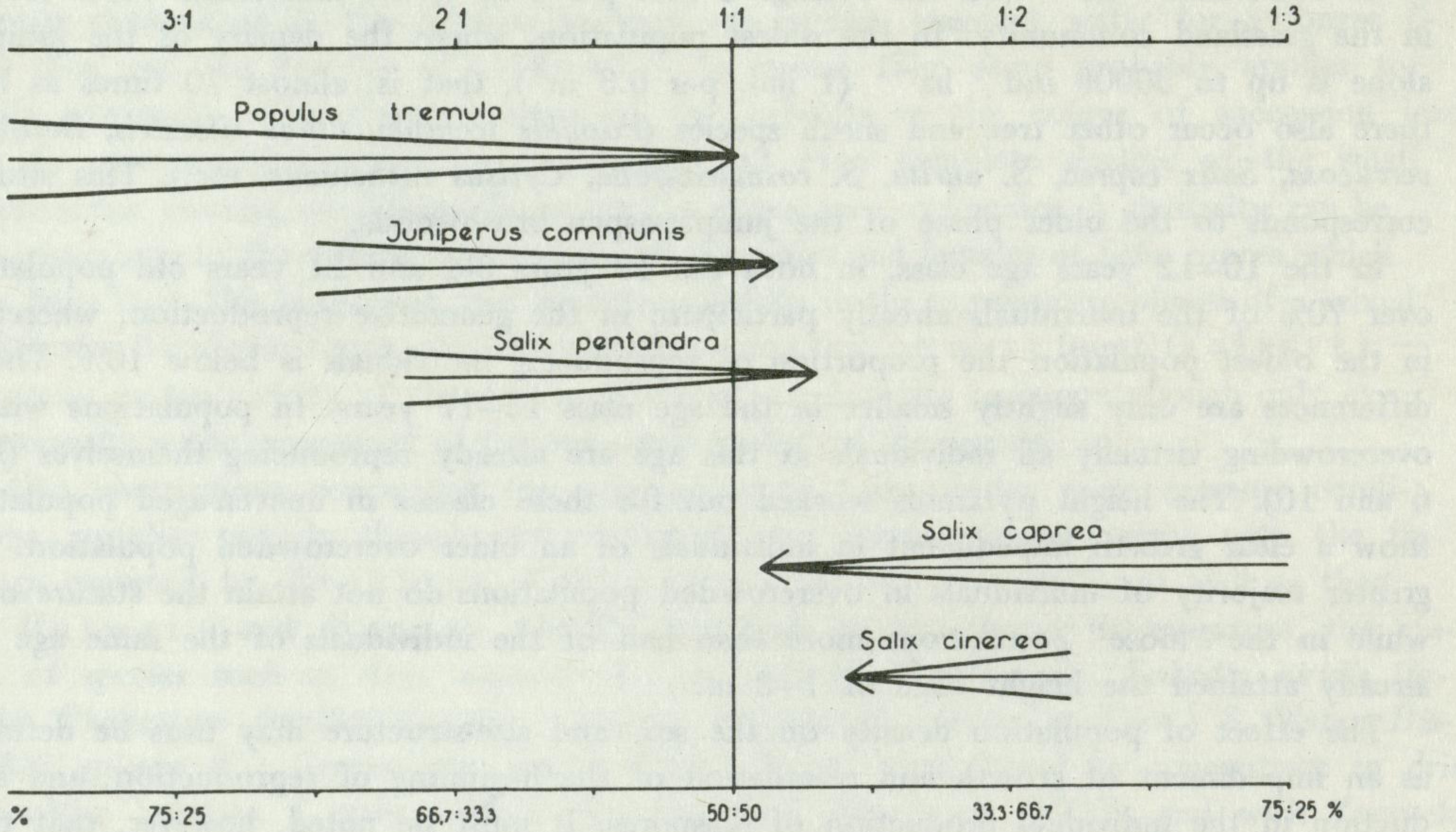


Fig. 14. Probable sex-ratio changes in the pioneer populations of woody species in the course of vegetation succession

3. The important role of dioecious tree species in the early phases of succession suggests that their success in the colonization of new habitats is based on the possibility of using a colonization tactics and a strategy of reproduction which are exceptional among plants. This possibility is determined by the partially different ecological requirements of the males and females, an earlier beginning of reproduction by the males, and probably an earlier settling of the males in pioneer habitats, or at least their greater ability to adapt to extreme conditions.

4. In order to more fully understand the relationship between the dynamics and structure of the vegetation, and the dynamics and structure of a population in the course of succession, it will be useful to take into account changes in the habitat. It seems also necessary to consider the populations of pioneer tree species in the aspect of reproductiveness and mortality. However, this requires specially devised, long-term studies.

5. As a complex ecological process, plant succession can to a considerable degree be described and explained by an analysis of population phenomena.

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8. SUMMARY

A regenerative succession occurring on abandoned farmlands that had once been torn from a forest and leading to the return of the forest is a rewarding object for study, because of the great dynamics of the phenomenon. It is, therefore, possible to trace within a relatively short time the main phases of this process and define the typical interactions observable in the relationship vegetation-a plant population. One of the main biological properties of the pioneer tree species is dioecism. It is found in most tree and shrub species which take part in the plant succession an abandoned farmlands (*Juniperus communis, Populus tremula, Salix aurita, S. rosmarinifolia, S. caprea,* etc.) and in abandoned meadows (locally 11 *Salix* species).

Changes in the sex-, age- and size-structure in populations of these pioneer tree and shrub species have been studied on lands successively abandoned since the end of World War I. The lands concerned are located on the south-western outskirts of the Białowieża Primeval Forest. The successive stages of the abandonment of cultivation are documented by the occurrence side by side of spontaneous plant communities in various phases of succession in almost identical habitat conditions. The basic investigations have been carried out in poor habitats previously occupied by a pine forest of the type Peucedano-Pinetum typicum. Investigations carried out at permanent plots have made it possible to identify the main phases of plant succession and join them together into one sere (Figs. 1 and 2). The duration of the particular phases and the absolute dating were based on the knowledge of the age of the populations of *Juniperus communis* and of other tree and shrub species.

The analysis of changes in the population structure of pioneer tree and shrub species in connection with vegetational succession was based on samples from the populations of those species, collected from the above-mentioned permanent plots. The basic material was mainly the sex- and age-, and sex- and size-pyramids (Figs. 6, 8, 11–13). Individual age was determined by the dendrochronological method based on the counting of annual rings in trunk sections. The age of a population was defined by the age of the oldest individuals present in it. The age of the populations studied was in the range of 5 to 55 years. Changes in the size- and sex-structure, and in the density of populations have simultaneously been followed for several years on permanent twin sites (Table I).

The process of succession over a period of 60 years is defined in terms of 8 developmental phases which can be joined together to represent 3 stages: the initial stage: therophyte communities, lichen and sand grassland communities, the optimum stage: a complex of grassland and juniper scrub, the terminal stage: juniper-aspen brushwoods. The particular stages of vegetation development and the corresponding phases of development of a juniper population (Fig. 2) are as follows:

initial stage – phases of invasion, colonization and sex determination,
optimum stage – phase of stabilization and beginning of propagation phase,
terminal stage – phase of intensive propagation, overcrowding and recession of populations.

The last named stage is at the same time the initial stage in the development of a pine forest (Figs. 1 and 2).

The following properties of a juniper population have been found to change in the course of succession:

Spatial structure: from a random structure at the initial stage to an aggregated structure at the optimum stage and the terminal stage (Fig. 2);

Population size: a rise of the two-peak left-slanting curve, with the first peak corresponding to the optimum stage, and the other to the terminal stage (Fig. 2, Table I);

Age structure: from a single-generation structure at the initial stage to a multi-generation structure from the optimum stage on; in a diversified multi-generation structure the effect is reflected of a 2-year, or a 3-year cycle in diaspore production – during the terminal stage (Fig. 8);

Sex structure: percentage of determined individuals (= those taking part in the generative reproduction): an increase in the percentage of determined individuals to 2/3 of a population during the optimum stage, then a decrease down to about 1/3 during the terminal stage (Figs. 2, 6 and 8, Table I);

Sex structure – sex ratio: from ♂ : ♀ = 1 : 0.4 at the initial stage through ♂ : ♀ = 1 : 1 at the optimum stage to ♂ : ♀ = 1 : 1.15 at the terminal stage (from a male predominance, through an equilibrium to a female predominance) (Fig. 2, Table I);

Types of reproduction: generative throughout all course of succession; vegetative exceptionally, only when forced by overcrowding or destruction of the main shoots – only during the terminal stage;

Recruitment: replacement of seeding from outside, peculiar to the initial stage, by autochthonous propagation during the optimum and the terminal stages (Fig 2);

Diaspore production: total of a population: a continual increase from the end of the initial stage till the terminal stage;

Diaspore production – individual: an increase from the end of the initial stage till the optimum stage, and a decrease during the terminal stage (Table II);

Calendar age of individuals starting to participate in the generative reproduction: during the optimum stage of succession – at the age of 8–9 years, during the terminal stage – delayed and spread over the age range from 10–20 (26) years (Figs. 6, 8, 10).

Changes in the structure of a juniper population, and particularly changes in the sex-, and size-structure are caused mainly by three factors. The effects of these in the course of plant succession are manifested in the following sequence:

1. the state of the habitat in abandoned farmlands at the initial stage,
2. diversification of vegetation and habitat during the optimum stage of succession,
3. overcrowding of a population and a high compactness of the plant community at the terminal stage of succession (Figs. 8, 9 and 10).

On the basis of the results from studies carried out so far, a model has been presented of the probable directions of changes in the sex ratio in populations of dioecious tree species in the course of plant succession (Fig. 14).

The important role of dioecious tree species in the early phases of succession suggests the conclusion that their success in the colonization of new habitats is based on the possibility of using a specific, exeptional among plants, colonization tactics and reproduction strategy. This possibility results from the partially different ecological requirements of the males and females, an earlier beginning of reproduction by the males, and probably an earlier settement of males in pioneer habitats, or at least their greater ability to adapt themselves to extreme conditions.

9. POLISH SUMMARY

Sukcesja regeneracyjną na gruntach porolnych, a więc niegdyś lasowi wydartych i prowadząca do powrotu lasu, jest wdzięcznym obiektem badań ze względu na wielką dynamikę zjawiska. Możliwe jest zatem prześledzenie w stosunkowo krótkim czasie głównych faz tego procesu i określenie typowych interakcji roślinność-populacja roślinna. Jedną z głównych właściwości biologicznych drzewiastych gatunków pionierskich jest dwupienność. Występuje ona u większości gatunków drzew i krzewów, które biorą udział w sukcesji roślinności na nieużytkach porolnych (*Juniperus communis, Populus tremula, Salix aurita, S. rosmarinifolia, S. caprea* itd.) i połąkowych (lokalnie 11 gatunków *Salix*).

Zmiany struktury płciowej, wiekowej i struktury wielkości w populacjach tych pionierskich gatunków drzew i krzewów były badane na gruntach systematycznie porzucanych od I wojny światowej. Leżą one na południowo-zachodnich peryferiach Puszczy Białowieskiej. Kolejne etapy zaniechania uprawy rolnej udokumentowane są przez egzystujące obok siebie w niemal identycznych warunkach siedliskowych spontaniczne zbiorowiska roślinne w różnych fazach sukcesji. Podstawowe badania wykonano na ubogich siedliskach zajętych pierwotnie przez bór sosnowy typu *Peucedano-Pinetum typicum*. Poprzez badania na stałych powierzchniach udało się ustalić zasadnicze fazy rozwoju roślinności, połączyć je w jedną serię sukcesyjną (rys. 1, 2). Czas trwania określonych faz i bezwzględne datowanie oparto na znajomości wieku populacji *Juniperus communis* i innych gatunków drzew i krzewów.

Analiza zmian struktury pionierskich gatunków drzew i krzewów w związku z sukcesją roślinności opierała się na próbach z populacji tych gatunków zebranych ze wspomnianych stałych powierzchni. Podstawą materiałową były głównie piramidy płci i wieku oraz piramidy płci i wielkości (rys. 6, 8, 11–13). Wiek osobników datowano metodą dendrochronologiczną przez liczenie pierścieni przyrostów

rocznych na wyrzynkach z pnia. Wiek populacji określano wiekiem jej najstarszych osobników. Wiek zbadanych populacji mieścił się w granicach od 5 do 55 lat. Zmiany struktury wielkości, struktury płciowej i zmiany zagęszczenia w populacji są równocześnie śledzone od kilku lat na bliźniaczych stałych powierzchniach (tab. I).

Proces sukcesji w ciągu 60 lat opisuje 8 faz rozwojowych, dających się połączyć w 3 stadia: stadium inicjalne – zbiorowiska terofitów, zbiorowiska porostów i muraw piaskowych, stadium optymalne – kompleks murawy i jałowczyska, stadium terminalne – zapusty jałowcowo-osikowe. Poszczególnym stadiom rozwoju roślinności odpowiadają następujące fazy populacji jałowca (rys. 2):

- stadium inicjalnemu sukcesji – fazy inwazji, kolonizacji i determinacji płci,
- stadium optymalnemu sukcesji – faza stabilizacji i początek fazy propagacji,
- stadium terminalnemu – faza intensywnej propagacji, przegęszczenia i ustępowania populacji.

Stadium to jest jednocześnie stadium inicjalnym w rozwoju boru sosnowego (rys. 1, 2).

Stwierdzono, że w toku sukcesji ulegają zmianom następujące właściwości populacji jałowca:

Struktura przestrzenna: ze struktury losowej w stadium inicjalnym do struktury skupiskowej w stadiach optymalnym i terminalnym (rys. 2).

Liczebność: wzrost typu krzywej dwuszczytowej lewoskośnej z pierwszym szczytem w stadium optymalnym i drugim w stadium terminalnym (rys. 2, tab. I).

Struktura wiekowa: z jednopokoleniowej w stadium inicjalnym na wielopokoleniową począwszy od stadium optymalnego; w zróżnicowanej strukturze wielopokoleniowej zaznaczają się skutki 2- lub 3-letniej cykliczności w produkcji diaspor – w stadium terminalnym (rys. 8).

Struktura płciowa: udział osobników zdeterminowanych (= biorących udział w reprodukcji generatywnej) – wzrost względnego udziału osobników zdeterminowanych do 2/3 składu populacji w stadium optymalnym, następnie spadek do ok. 1/3 w stadium terminalnym (rys. 2, 6, 8, tab. I).

Struktura płciowa: sex ratio – od ♂ : ♀ = 1 : 0,4 w stadium inicjalnym przez ♂ : ♀ = 1 : 1 w stadium optymalnym do ♂ : ♀ = 1 : 1,15 w stadium terminalnym (od przewagi osobników męskich przez równowagę do przewagi osobników żeńskich) (rys. 2, tab. I).

Typy reprodukcji: generatywna w całej serii sukcesji, wegetatywna wyjątkowo, tylko wymuszona przez przegęszczenie lub zniszczenie pędów osiowych – tylko w stadium terminalnym.

Zasilanie liczebności: zastąpienie obsiewu z zewnątrz właściwego dla stadium inicjalnego przez propagację autochtoniczną w stadium optymalnym i terminalnym (rys. 2).

Produkcja diaspor – całkowita populacji: stały przyrost od końca stadium inicjalnego do stadium terminalnego.

Produkcja diaspor – osobnicza: przyrost od końca stadium inicjalnego do stadium optymalnego i spadek w stadium terminalnym (tab. II).

Wiek kalendarzowy przystępowania osobników do reprodukcji generatywnej: w stadium optymalnym sukcesji w wieku 8–9 lat, w stadium terminalnym opóźniony i rozłożony na okres od 10 do 20 (26) lat (rys. 6, 8, 10).

Zmiany struktury populacji jałowca, a zwłaszcza zmiany w strukturze płciowej i strukturze wielkości, spowodowane są głównie przez 3 czynniki. Ich działanie w toku sukcesji roślinności ujawnia się w następującej kolejności:

1. stan siedliska na nieużytkach porolnych w stadium inicjalnym,
2. różnicowanie się roślinności i siedliska w optymalnym stadium sukcesji,
3. przegęszczenie populacji jałowca i silne zwarcie zbiorowiska roślinnego w terminalnym stadium sukcesji (rys. 8–10).

Na podstawie wyników dotychczasowych badań przedstawiono model przypuszczalnych kierunków zmian sex ratio w populacjach dwupiennych gatunków drzewiastych w toku sukcesji roślinności (rys. 14).

Wyjątkowa rola dwupiennych gatunków drzewiastych we wczesnych fazach sukcesji nasuwa wniosek, że ich powodzenie w zasiedlaniu nowych stanowisk opiera się na możliwości zastosowania szczególnej u roślin taktyki kolonizacji i strategii reprodukcji. Możliwość ta jest pochodną częściowo odmiennych wymagań ekologicznych osobników męskich i żeńskich, wcześniejszym przystępowaniem do reprodukcji osobników męskich, a także prawdopodobnie wcześniejszym osiedlaniem się osobników męskich na siedliskach pionierskich lub przynajmniej większą zdolnością przystosowania się do skrajnych warunków.

10. REFERENCES

1. Białobok S. 1973 – Zagadnienia genetyczne i hodowla. Topole [Genetic problems and cultivation. Poplars] – Państwowe Wydawnictwo Naukowe, Warszawa–Poznań, 12: 315–369.
2. Blackburn W.H, Tueller P.T. 1970 – Pinyon and juniper invasion in black sagebrush communities in East-Central Nevada – Ecology, 51: 841–848.
3. Bråkenhielm S. 1977 – Vegetation dynamics of afforested farmland in a district of Southeastern Sweden – Acta Phytogeogr. Suecica, 63: 1–106.
4. Ciosek M. 1975 – Przejawy regeneracji lasu na gruntach porolnych na Polanie Białowieskiej w Puszczy Białowieskiej [Symtoms of forest regeneration of previously cultivated areas on the Białowieża Clearing, Białowieża Primeval Forest] – Phytocenosis, 4: 117–136.
5. Czarnowski M. S. 1978 – Zarys ekologii roślin lądowych [Ecology of terrestrial plants] – Państwowe Wydawnictwo Naukowe, Warszawa, 458 pp.
6. Falińska K. 1979 – Modification of plant populations in forest ecosystems and their ecotones – Pol. ecol. Stud. 5 (1): 89–150.
7. Faliński J. B. 1966 – Antropogeniczna roślinność Puszczy Białowieskiej jako wynik synantropizacji naturalnego kompleksu leśnego [Vegetation anthropogene de la Grande Forêt de Białowieża comm' un résultat de la syntanthropisation du territoire silvestre naturel] – Diss. Univ. Vars. 13: 1–256.
8. Faliński J. B. 1972 – Potencjalna roślinność naturalna Wysoczyzny Bielskiej [Potential natural vegetation of the Bielsk Plateau] – Mater. Zakł. Fitosoc. stos. UW, Warszawa–Białowieża, 24: 1–23.
9. Faliński J.B. 1977 – Research on vegetation and plant population dynamics conducted by Białowieża Geobotanical Station of the Warsaw University in the Białowieża Primeval Forest and in the environ (1952–1977) – Phytocenosis, 6: 1–132.
10. Faliński J.B. (in press) – Właściwości biologiczne i ekologiczne pionierskich gatunków drzew i krzewów [Biological and ecological properties of pioneer woody species] – Wiad. ekol.
11. Farmer R.E. 1964 – Sex ratio and sex related characteristics in Eastern Cottonwood – Silvae Genet. 13: 597–599.
12. Freeman D. C., Klikoff L. G., Harper K. T. 1976 – Differential resource utilization by the sexes of dioecious plants – Science, N. Y. 193: 597–599.
13. Hard G. 1975 – Vegetationsdynamik und Verwaldungsprozesse auf den Brachfächen Mitteleuropas – Erde, 106: 243–276.
14. Harper J. L. 1977 – Population biology of plants – Academic Press, London–New York–San Francisco, 892 pp.
15. Hedemann O. 1934 – Dawne puszcze i wody [Ancient primeval forests and waters] – Księgarnia Św. Wojciecha, Wilno, 187 pp.
16. Knapp R. (Ed.) 1974 – Vegetation dynamics. Handbook of vegetation science – Dr. W. Junk Publishers, The Hague, 8: 364 pp.
17. Kondratiuk M. 1974 – Nazwy miejscowe południowo-wschodniej Białostocczyzny [Locality names of south-eastern Białystok region] – Monogr. Slav. 29: 1–304.
18. Meisel K. 1978 – Vegetationsentwicklung auf Brachflachen (In: Ref. v. 3 Symposion (13–17. 9. 1976) Synanthrope Flore und Vegetation) – Acta bot. slov. A, 3: 311–318.
19. Muhle Larsen C. 1970 – Recent advances in poplar breeding – Interv. Rev. of Forestry Res., Academic Press, New York–London, 3: 1–67.
20. Nowak J., Tobolewski Z. 1975 – Porosty polskie [Polish lichens] – Państwowe Wydawnictwo Naukowe, Warszawa–Kraków, 1177 pp.
21. Pauley S. S., Mennel G. T. 1957 – Sex ratio and hermaphroditism in a natural population of qualing aspen (*Populus tremuloides*) – Minn. For. Not. 55: 33–103.
22. Putwain P. D., Harper I. L. 1972 – Studies in the dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosa* and *R. acetosella* – J. Ecol. 60: 113–129.
23. Schmidt W. 1975 – Vegetationsentwicklung auf Brachland – Ergebnisse eines fünf jährigen Sukzessionsversuches (In: Ber. d. Inten. Symposien d. Intern. Vereinigung für Vegetationskunde Sukzessions-Forschung) – 1978: 407–427.

24. Strzelecki W., Sobczak R. 1972 – Zalesienie nieużytków i gruntów trudnych do odnowienia [Afforestation of the old lands and the soils difficult for regeneration] – Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 352 pp.

25. Szafer W., Kulczyński S., Pawłowski B. 1976 – Rośliny polskie [Polish plants] – Państwowe Wydawnictwo Naukowe, Warszawa, 1020 pp.

26. Szafran B. 1957 – Mchy [Mosses] – Państwowe Wydawnictwo Naukowe, Warszawa, I: 449 pp.

27. Szafran B. 1961 – Mchy [Mosses] – Państwowe Wydawnictwo Naukowe, Warszawa, II: 407 pp.

28. Tramer E.J. 1975 – The regulation of plant species diversity on an early successional old-field – Ecology, 65: 905–915.

29. Tüxen R. 1973 – Zum Briken – Anflug im Naturschutzpark Lüneburger Heide. Eine pflanzensoziologische Betrachtung – Mitt. florsoz. Arbeitsgem. NT 15/16, Todeumaun-Göttingen, NF, 15/16: 203–209.

30. Vernet P. 1971 – La proportion des sexes chez *Asparagus acutifolius* L. – Bull. Soc. Fr. 118: 345–358.

31. Wiśniewski J. B. 1964 – Rozwój osadnictwa na pograniczu polsko-rusko-litewskim od końca XIV w. do połowy. XVII w. [Colonization development of the Polish-Ruthenian-Lithuanian borderland from end of XIV to the early part of XVII century] – Balto-Slavica, 1: 115–135.

32. Zarzycki K. 1975 – Competition between male and female plants of *Salix purpurea* L. in single and both sex cultures in different densities (In: Abstr. of the papers presented at the XII Intern. Bot. Congress, July 3–10, 1975) – Leningrad, 175–175.

33. Zarzycki K., Rychlewski L. 1972 – Sex ratios in Polish natural populations and in seedling samples of *Rumex acetosa* L. and *R. thyrisiflorus* Fing. – Acta Biol. Crac., Ser. Bot. 15: 135–151.