

VEGETATION DYNAMICS AND SEX STRUCTURE OF THE POPULATIONS OF PIONEER DIOECIOUS WOODY PLANTS

Janusz B. FALIŃSKI

Geobotanical Station, 17.230 Białowieża, Poland

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Introduction

The incursion of trees and shrubs in the course of succession is frequently so impetuous that it has often been referred to as 'invasion' (e.g. Blackburn & Tueller 1970, Bråkenhielm 1977, Tüxen 1973, Hard 1975, Meisel 1978, Faliński 1980, in press).

Studies on vegetation succession lead to the question – what the causes are of the exceptional success attained by certain tree and shrub species in the establishment on new territories (Faliński 1980).

Data from the literature and the author's own observations indicate that the list of species invading old fields and meadows and city ruins as well as recently denuded areas, for instance in the process of deglaciation, includes representatives of the same few genera: *Salix*, *Populus*, *Betula*, *Alnus*, *Pinus* and *Juniperus*. What are the common features uniting these species?

With the exception of *Juniperus* all these species are anemochorous. Further comparative analysis revealed further biological and ecological features of the species of the above-mentioned genera (Fig. 1). These are: a strong tendency to vegetative propagation, together with effective generative multiplication, anemogamy, that is wind-pollination, with the exception of *Salix*, dioecism, with the exception of *Alnus Betula* and *Pinus* which are monoecious and monosexual, and proanthia, that is flowering before development of foliage, with the exception of *Pinus* and *Juniperus*. To the list of these characteristics should be added: a tendency to mass occurrence and agglomeration, low nutritional requirements, and a short individual life span with relatively early maturation for generative reproduction. The five main characteristics first enu-

merated are mostly fully represented in *Populus* (Fig. 1). In the pertinent literature attempts may be found to analyse the role of some of the factors mentioned, for instance anemochory. From the ecological point of view the role of dioecism, which is rather common among pioneer species, is the most obscure (Faliński 1980).

Dioecism (in plants not as common as in animals) allows to consider a sex structure of some populations, for instance in the pioneer woody species. The sex structure of the dioecious species populations is characterized by two indices:

1. Participation of reproducing individuals in a population in comparison to all individuals, or to not-reproducing individuals (juveniles, seniles).
2. Participation of male or female individuals in the total number of reproducing individuals, i.e. the ratio of male individuals to female ones, or sex ratio; it is usually shown as a formula $\sigma : \varphi = 1 : \dots$

In stable populations the sex ratio is mostly 1 : 1. However, deviations are well known (Freeman, Klikoff & Harper 1976, Harper 1978, Vernet 1971).

	Anemochory	Strong tendency to vegetative propagation	Anemogamy	Dioecism	Proanthia	Σ
POPULUS	● ● ●	● ● ●	● ● ● ●	● ● ● ●	● ● ● ●	5
SALIX	● ● ●	● ● ●	entomogamy	● ● ● ●	● ● ●	4
JUNIPERUS	ornithochory barochory	● ● ●	● ● ● ●	● ● ● ●	evergreen	3
BETULA	● ●	●	● ● ● ●	} monoecious and monosexual	● ●	4
ALNUS	● ●	● ●	● ● ● ●		● ●	4
PINUS	●	●	● ● ● ●		evergreen	4

Fig. 1. Biological characteristics of the woody pioneer plants (after Faliński, 1980).

The search for relationships between the sex structure of the population and vegetation dynamics or vegetation differentiation was rarely attempted and then only for herbaceous plants (Vernet, 1971, Zarzycki & Rychlewski 1972, Falińska 1979).

Investigations on the proportion of male and female individuals in populations of dioecious woody species are rather numerous. They dealt, for instance, with *Populus tremula* L. (Langhammer quoted by Bialobok 1973), *Populus tremuloides* Michx (Muhle Larsen, 1970, Pauley & Mennel 1957, Frammer 1964), *Salix viminalis* (Rabotnov, 1958) and *Acer negundo* (Freeman, Klikoff & Harper 1976).

Similarly, as in herbaceous plant populations, the variability of the sex ratio in populations of woody plants was considered mainly to be the result of a simple habitat or for instance of competition (Zarzycki 1975), and genetic conditioning. The reviews of Freeman, Klikoff & Harper (1976) and Zarzycki (not published) suggest that these factors operate on a *syndynamic* basis. They might, perhaps at least partly, be interpreted as the effect of

vegetation succession or at least connected with succession. This does not rule out, that some of the investigators, are of the opinion that there is an influence of habitat conditions on the sex ratio.

The present paper is an attempt to present the changes in sex structure of pioneer tree and shrub populations with reference to regeneration succession on old farmland and old meadows in the Białowieża Primeval Forest region (Faliński 1966, 1972, 1977).

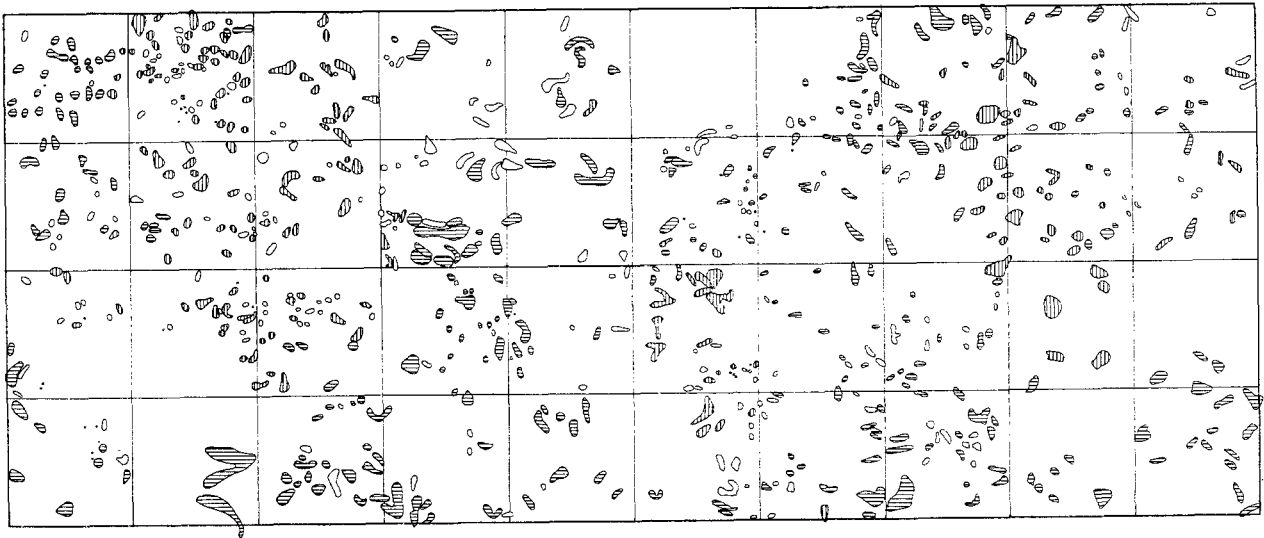
This process is an exceptionally rewarding object for research, because in one succession series, e.g. an oligotrophic pine forest habitat – *Peucedano-Pinetum typicum* – as many as 5 dioecious woody species are found (*Juniperus communis* L., *Populus tremula* L., *Salix rosmarinifolia* L., *S. aurita* L., *S. caprea* L.); sporadically other willow species are found. Monoecious species (*Pinus silvestris*, *Betula pendula*) appear in later stages. Similarly, in the early stages of vegetation development on old fields, meadows, clearings and forest edges in *Alnus glutinosa* bog forest, and mixed forests, *Salix pentandra*, *S. cinerea*, *S. aurita*,



Fig. 2. The main study object : old farmland at oligotrophic pine forest habitat, colonised by juniper. 6 succession phase. (photo J. Hereźniak).

Salix rosmarinifolia

X-955



Juniperus communis

X-80 (fragm)

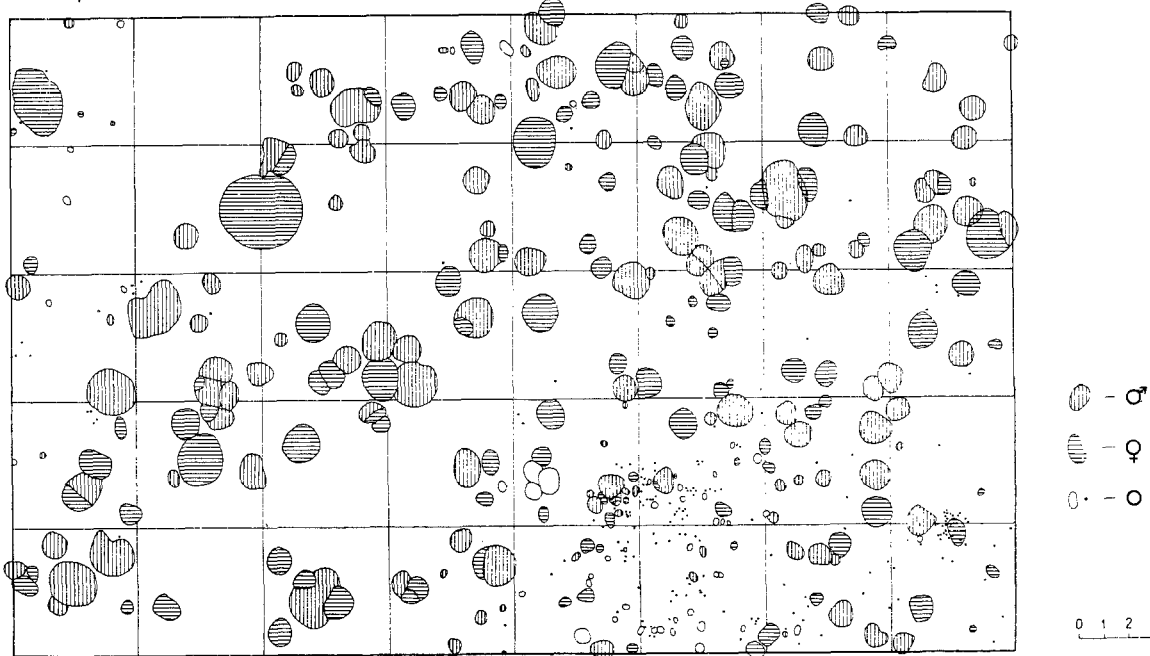


Fig. 3. Example maps of spatial sex structure of pioneer dioecious scrub species populations. Each permanent plot measures 1000 m².

S. rosmarinifolia, *S. starkeana*, *S. myrsinifolia*, *S. caprea* and their numerous hybrids appear. (Figs 2, 3 and 4).

Materials and methods

The basic investigations were performed in habitats on

poor soil, primarily overgrown with pine forest of the *Peucedano-Pinetum typicum* and additionally on: *Cladonio-Pinetum*, *Carici elongatae-Alnetum*, *Circaeo-Alnetum*, *Tilio-Carpinetum* and *Pino-Quercetum* habitats (Figs 2, 3, 4). Studies on permanent plots made it possible to distinguish the main phases of vegetation development and unite

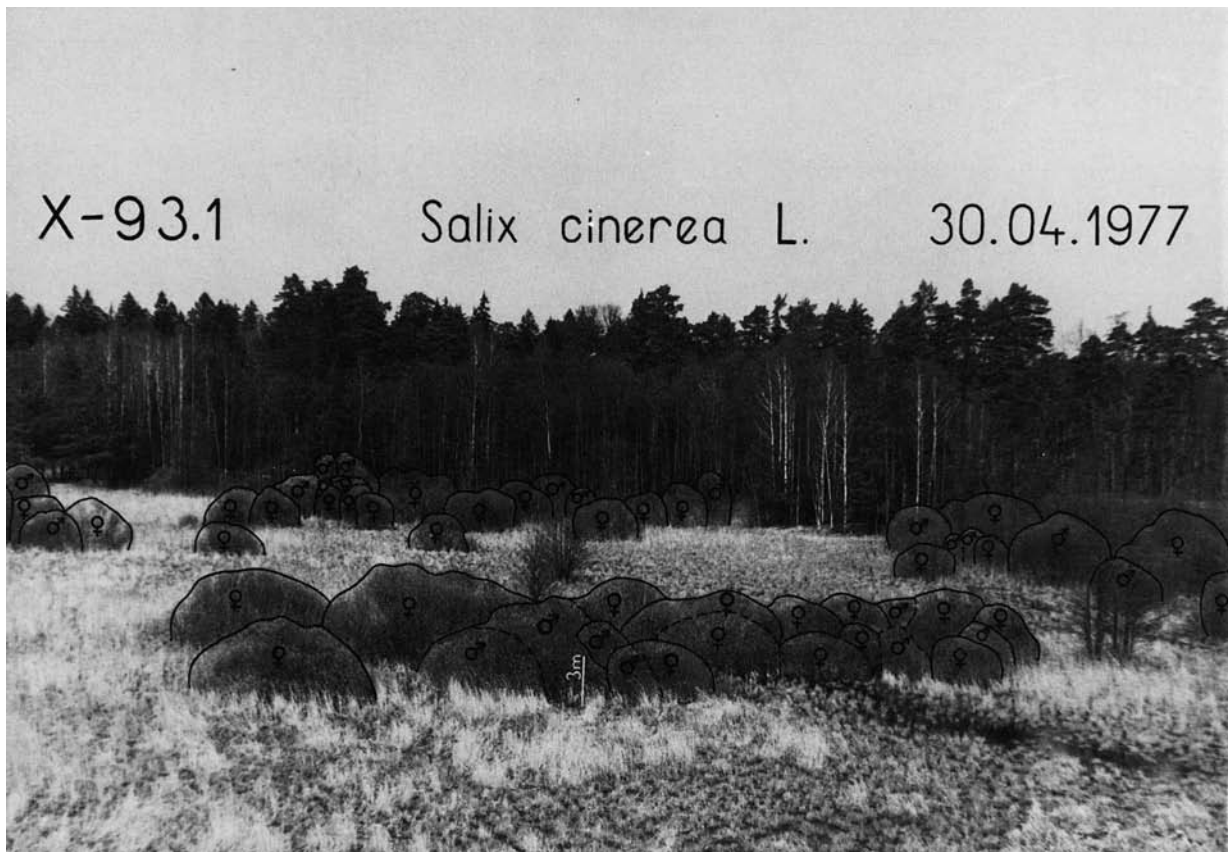


Fig. 4. Sex structure of the *Salix cinerea* population in the valley of the river Leśna. (photo J.B. Faliński).

them into one succession series. The duration of the particular phases and *absolute* dating were based on the knowledge of the age of *Juniperus communis* and other tree and shrub populations. In other habitats dating was based on determinations of the age of *Salix*. The data were verified by interviews with the local people, forest service and analysis of cadastre maps. The scheme of vegetation succession on oligotrophic pine forest habitats is presented in Fig. 5.

Analysis of changes in the population structure of pioneer tree and shrub species in connection with vegetation succession was based on samples of populations of these species collected on the above mentioned permanent plots. The basic experimental plot was 1000 m² in size. Analyses are based on sex and age pyramids and pyramids of sex and size (Figs 6–10). The age of the individuals was dated by dendro-chronological methods, and by counting the year rings. The population age was determined by the age of the oldest individuals in it. The age of the

studied populations was within the range of 5 to 55 yr. Changes in the size structure, sex structure and changes in population density, as well as vegetation succession, have been followed simultaneously for several years on twin permanent plots (Table 1).

Results

1. Regeneration vegetation succession in pine forest, *Peucedano-Pinetum-typicum*, habitats from fresh fallow land to the phase of *Juniperus Populus tremula* brushwood takes place over about 70 yr. Its course is anthropogenically retarded by extensive sheep grazing (in early phases) and plunder felling, mainly of *Pinus* (in the final phases). beginning of propagation phase,
2. Synchronisation of vegetation development (vegetation succession) and development of the main species involved in this process, i.e. *Juniperus*, are shown in Fig. 14.

Vegetation development phases and their duration in years

0	1	2	3	4	5	6	7	8	9	
Segetal community <i>Teesdaleo - Arnoseridetum</i>	Pioneer phase of <i>Koelerion glaucae</i> with segetal species	Perennial grasses, herbs and lichens communities: <i>Koelerion Corniculario - Cladonietum</i> , etc.	and lichens <i>glaucae</i> , etc.	Complex, herbs communities: <i>Koelerion, Cornic.-Cladonietum, Sperg. Corynephorum... Juniperus</i> brush comm.	<i>Juniperus - Populus tremula</i> brushwood	<i>Juniperus communis - Populus tremula</i> community	Spontaneous pine forest <i>Peucedano-Pinetum</i>	earlier phase	later phase	earlier phase
	1-2	2-5	5-12	8-15	12-18	15-25	25-45	40-70	> 70	

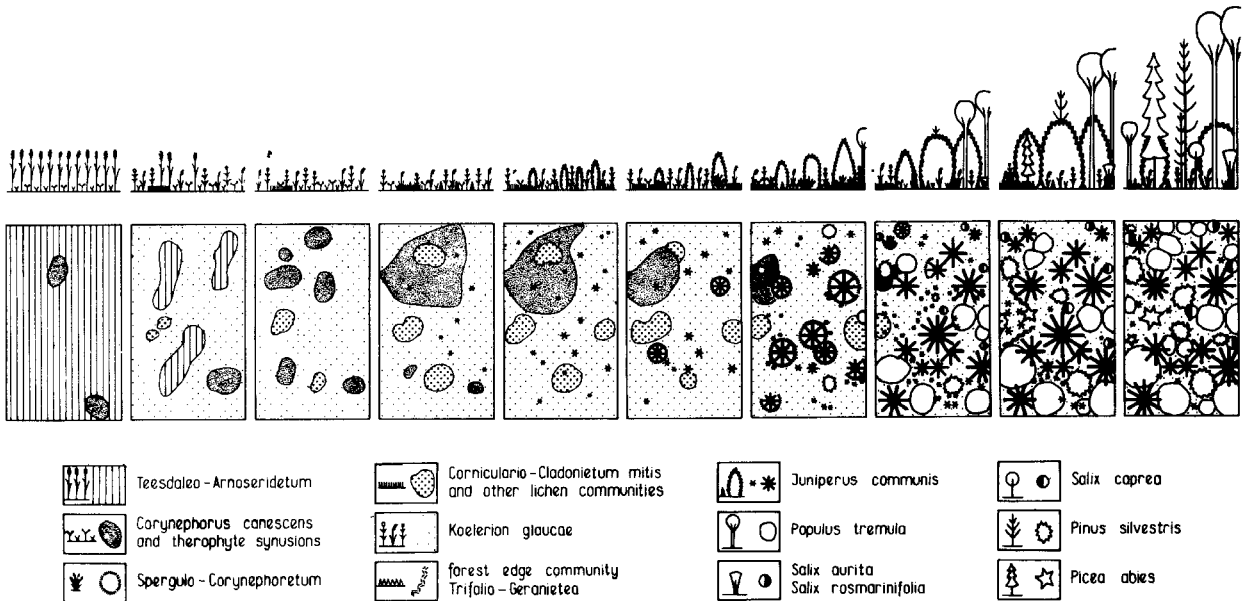


Fig. 5. Scheme of the course of plant succession in old farmland.

The succession process is described in 8 development phases which may be combined into 3 stages. The initial stage comprises: therophyte communities, lichen and sandy grassland communities; the optimal stage includes: a complex of grassland and *Juniperus* brush; the terminal stage brings juniper-aspen brushwood. To the particular developmental stages correspond the following phases of the *Juniperus* population:

- *initial succession stage*: invasion and colonisation phases,
- *optimal succession stage*: - stabilisation phase and beginning of propagation phase,
- *terminal stage* - phase of intensive propagation, overcondensation and regression of population. This stage is at the same time the initial stage for *Pinus* forest development (Figs. 5 and 14).

3. The main phases of *Juniperus communis* population development can be followed in the particular sex and age pyramids of the oldest populations (Fig. 6) and by com-

parison of pyramids for populations of various ages which arose and developed under analogous habitat conditions (Fig. 7).

In the first case, beginning from the vertex, traces of the following phases can be reconstructed (Fig. 6):

- age 55-45 yr (1922-1931) colonization
- 45-30 yr (1932-1947) stabilization
- 29-12 yr (1948-1964) stabilization and propagation
- 12- 3 yr (1965-1974) overcondensation and regression

4. Comparison of *Juniperus communis* populations participating in the successive phases of vegetation succession on fields, as well as direct observations for several years on permanent plots (Table 1), reveals changes in the sex structure of these populations. These changes are characterised not only by a differing contribution by generatively reproducing individuals, but also by changes in sex ratio (Fig. 7).

Younger *Juniperus communis* populations in old fields with a small proportion of reproducing individuals

Table 1. Changes of density and sex structure in the juniper population on the oldfield (examples).

Phase of vegetation and population development	Number of permanent plot	Sex, sex indices	Individuals/ 0.1 ha in year				
			1975	1976	1977	1978	1979
4 Perennial grasses, herbs and lichens communities – with sex determ. juniperus	66.13	♂	8	9	33	45	62
		♀	7	10	20	28	36
		○	181	214	193	181	175
		Σ	196	233	246	254	273
		$\frac{\delta + \text{♀}}{\Sigma} \cdot 100\%$	7.7	8.2	21.5	28.7	35.9
		♂ : ♀	*	*	1:0.6	1:0.6	1:0.6
5 Complexity of herbs and lichens communities with juniperus brush community – earlier phase	66.17	♂	* *	18	29	33	35
		♀		15	24	29	32
		○		44	31	25	28
		Σ		77	84	87	95
		$\frac{\delta + \text{♀}}{\Sigma} \cdot 100\%$		42.9	63.1	71.3	70.1
		♂ : ♀	1:0.8	1:0.8	1:0.9	1:0.9	
6 Complexity of herbs and lichens communities with juniperus brush community – optimal phase	66.1	♂	83	80	88	96	109
		♀	80	85	88	97	105
		○	77	91	104	91	94
		Σ	240	256	280	284	308
		$\frac{\delta + \text{♀}}{\Sigma} \cdot 100\%$	67.9	64.4	62.9	67.9	69.4
		♂ : ♀	1:1.0	1:1.1	1:1.0	1:1.0	

* calculation non rational ** no data

○ 'neutral' = non flowering individuals (juvenile or senile)

exhibit a certain preponderance of male individuals. This is the consequence, among other things, of the earlier maturity for reproduction of male- as compared with female individuals. The above – mentioned preponderance is no longer noted in stabilized populations $\delta : \text{♀} = 1 : 1$), and in older populations a gradual prevalence of female individuals is observed. Thus reliable sex ratio changes lie within the limits of $\delta : \text{♀} = 1 : 0,4$ to $1 : 1,15$.

5. The relatively late appearance in the succession process of the *Populus* and *Salix* species (phase 6) allows analysis of their population sex structure only in the terminal stage of vegetation development. This corresponds to the phase of overcondensation and recession of the *Juniperus* vegetation.

Populations of all three *Salix* species (Fig. 8) present at that time consist exclusively of individuals reproducing

generatively. The rare juvenile individuals are mostly of vegetative origin. The youngest flowering individuals were 5 years (*S. rosmarinifolia*) and 7 years (*S. aurita*) old. In both cases they were female (Fig. 8).

The samples sizes allow only approximate determinations of the sex ratio:

for *Salix rosmarinifolia* $\delta : \text{♀} = 1 : 3.2$ at population age 21 yr

for *Salix aurita* $\delta : \text{♀} = 1 : 4.3$ at population age 32 yr

for *Salix caprea* $\delta : \text{♀} = 1 : 2.0$ at population age ca 20 yr.

Sex manifested in *Populus tremula*, in contrast to *Juniperus* and *Salix*, by a sudden flowering of a large part of the population at the same time (Fig. 9). In comparable samples from 1000 m² plots with about 400

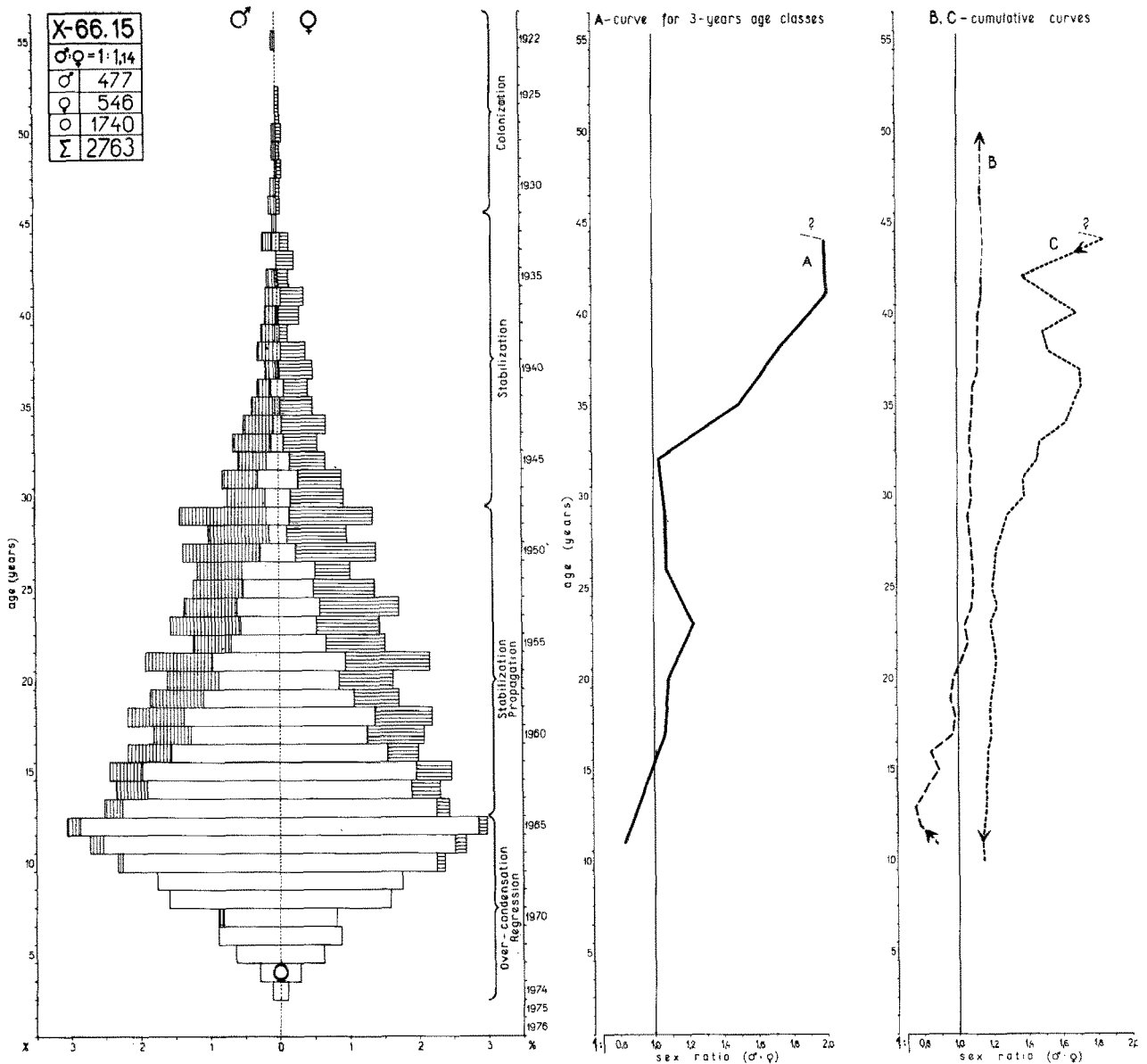


Fig. 6. Sex and age pyramid in the oldest population of *Juniperus communis* (55 yr old) in the phase of increasing propagation and over-crowding, i.e. in terms of plant succession in the older phase of juniper-aspen communities. Within the range of the pyramid: reconstruction of main phases of the development of the population. Next: an analysis of the sex structure of the pyramid (the margin edge) classes are omitted due to low numbers;

A- changes of the sex ratio in consecutive 3 yr age classes;

B- cumulative curve of the sex ratio coefficient with consecutive (successive) addition of the increasingly reproducing individuals from the bottom to the top of the pyramid, e.g. 10 years old, 10 + 11, 10 + 11 + 12 etc./;

C- cumulative curve of the sex ratio coefficient with successive addition of increasingly reproductive individuals from the top of the pyramid to the bottom (e.g. 44 yr old, 44 + 43, 44 + 43 + 42, etc.).

individuals a marked prevalence of male individuals appears immediately. The sex ratio reaches the value $\sigma : q = 1 : 0.01$, thus one female individual per 100 male

ones or more. This ratio in pioneer populations of *P. tremula* may change only slightly with time, where female individuals start to reproduce.

The *P. tremula* populations examined so far in 11 samples can be decidedly classified as 'male'. Attainment of the theoretical ♂:♀ = 1 : 1 ratio in older populations, found for instance in the forest populations of Norway, is only possible after a large proportion of male individuals die out. It cannot be ruled out, however, that in some regions on old farmland 'female' populations may still be found (Fig. 10).

Thus, over a larger area we would be dealing with a 'patchy' population space structure with regards to sex ratio index.

6. The changes in sex structure, particularly those in sex ratio connected with succession, observed in the succession series on pine forest habitats in *Juniperus communis* and *Populus tremula* populations were also observed in the populations of several *Salix* species involved in vegetation regeneration in other habitats (Fig. 11).

It was obvious that both increase of the density and changes of the plant community structure in the final vegetation succession stage on an old farmland, are the main factors responsible for changes of the sex structure and the size structure in older populations of *Juniperus communis* (Figs. 12 and 13; for a more detailed description see Discussion).

Discussion

At present the action of at least 3 factors responsible for the changes in the sex structure of the pioneer populations of woody species in the course of succession can be considered. In the order of their occurrence in the course of succession they are: (1) The state of the habitat in old farmland in the initial stage of succession, or rather: in

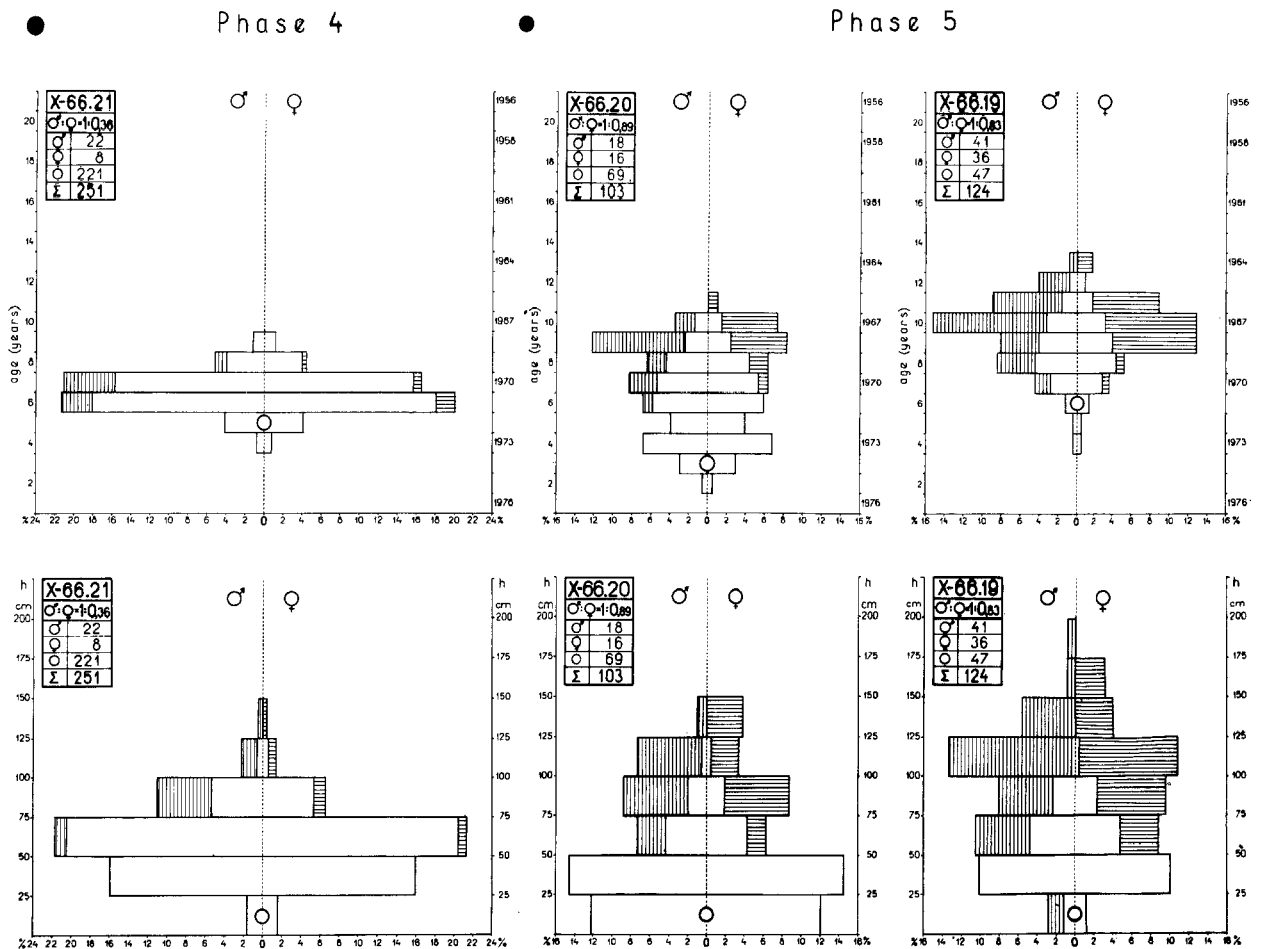


Fig. 7. Pyramids of sex and age and sex and size sampled taken from the population of *Juniperus communis* at the phase of colonization (phase 4), the younger phase of stabilization (phase 5) and the older phase of stabilization (phase 6).

the phases of invasion and colonization of the habitat by *Juniperus*; (2) differentiation of vegetation and habitat in the optimal stage of succession; and (3) overcondensation of the *Juniperus* population and of the plant community (covering) in the terminal succession stage (phases 7 and 8).

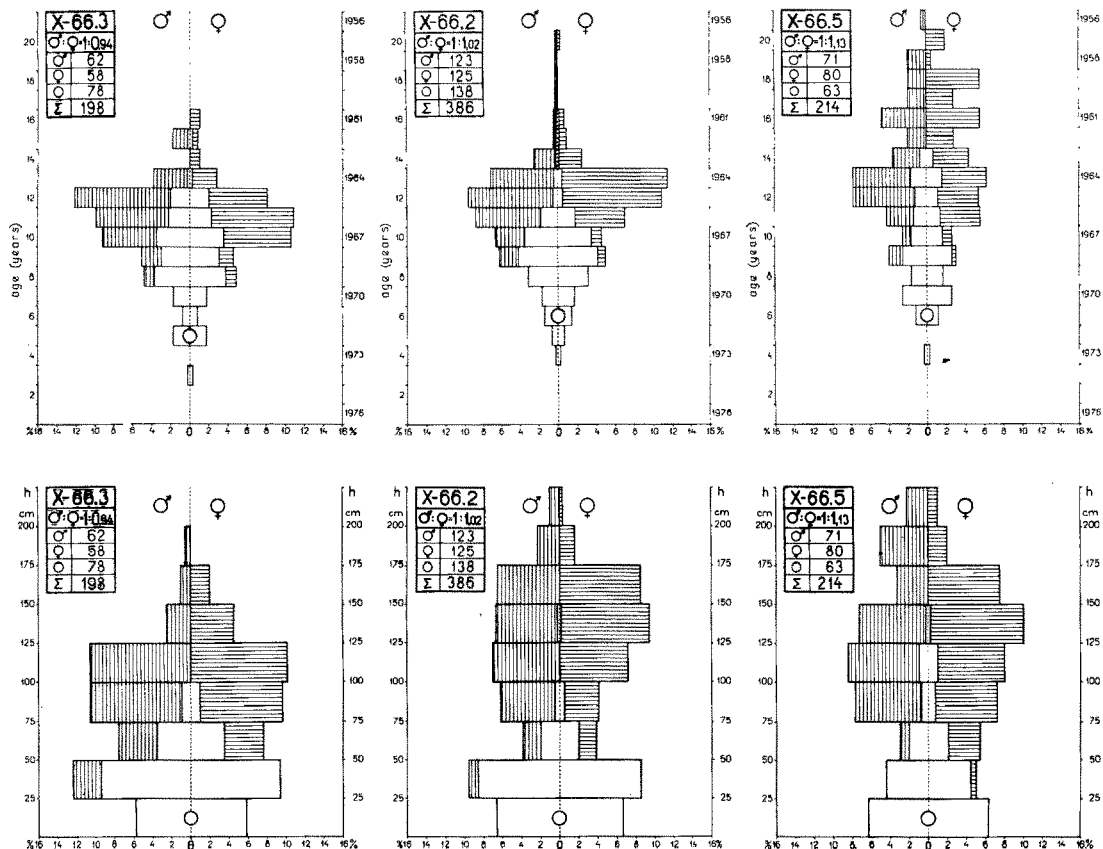
The pioneer conditions are determined by the naturally poor habitat, which is secondarily still further impoverished, and to some extent transformed by extensive agricultural management for many centuries. These conditions do not only retard the spontaneous development of vegetation and colonisation of old fields by *Juniperus*, but may also act selectively at the moment of germination of diaspores of this shrub. The mechanism and causes of such selection, are not yet known, although the characteristics of old farm soils are by now well known (Strzelecki & Sobczak 1972). We can, therefore, only presume

that this selection would reach the diaspores and seedlings to a greater extent from which female individuals will develop.

This leads to the further assumption that the male individuals in pioneer species are more resistant to extreme conditions already during the germination and in the juvenile phase. Such is the situation, for instance, for the shrub *Salix cinerea*. In the Białowieża Primeval Forest, under conditions of periodical flooding on low peatfields in the river valley, the male clones occupy the deeper troughs (unpublished observations). Thus they tolerate a longer water stagnation than female individuals do. The same counts for *Salix pentandra*.

The transformation of the habitats in the course of succession leads, among other things, to a shallowing or even complete levelling of small hollows, which creates conditions favourable for the appearance of female

Phase 6



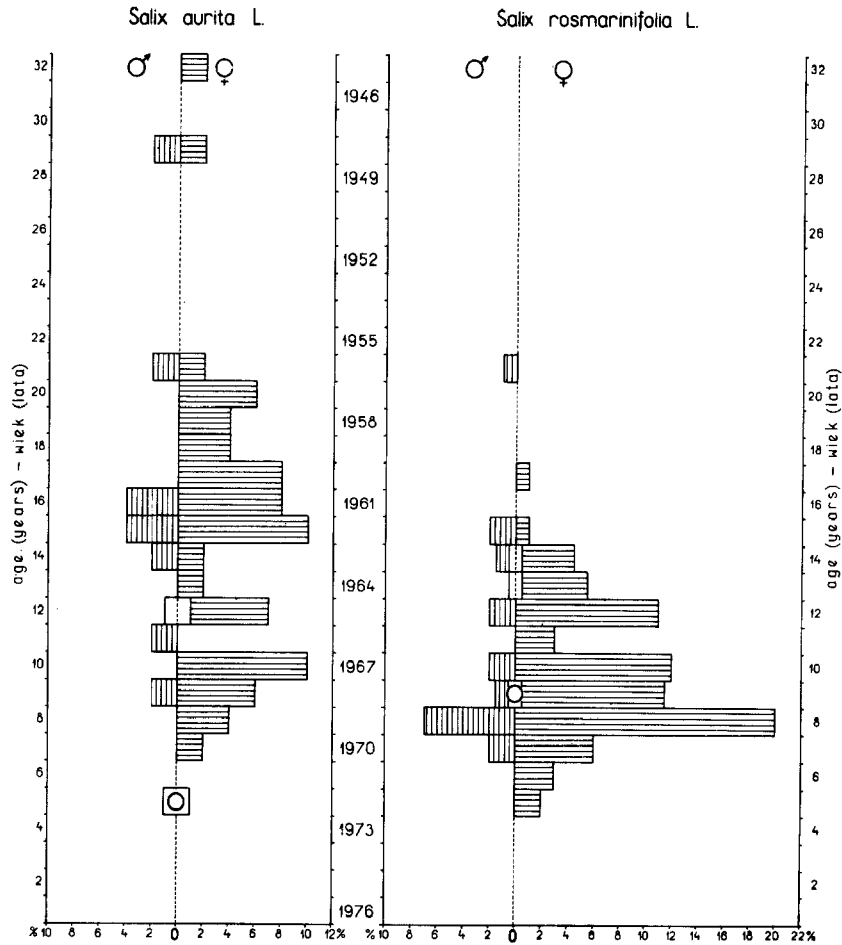


Fig. 8. Examples of the sex and age pyramids from populations of *Salix aurita* and *S. rosmarinifolia*.

individuals. A certain analogy may be also found here in the occurrence of male and female individuals of the large tree *Salix caprea*. This species appears as a high-growing tree particularly in the regenerative phases of mixed forest of the *Tilio-Carpinetum* type, e.g. along roads through the forest. In the neighbourhood of the changed or denaturated stands this willow species is relatively more frequently represented by male individuals, although exceptionally the contribution of male and female sexes may be equal (unpublished observations).

Our findings concerning the agglomeration of a greater number of male individuals when conditions tend to be extreme, for instance conditions of drought or high salinity, which are specific mainly, though not exclusively, for pioneer habitats, agree with the reports of Freeman, Klikoff & Harper (1976) and also of Putwain & Harper (1972). I am of the same opinion as Putwain & Harper

(1972) and Zarzycki (unpublished) that in these cases one may even speak of separate ecological niches of male and female individuals.

The gradual decrease of extreme conditions in the course of the succession, caused for instance by accumulation of organic-matter in the soil, progress of soil processes and differentiation of the structure of plant communities does not only mean a change in the conditions under which the population lives. It may also favour changes in the numerical proportions of male and female individuals in the populations, that is the sex ratio.

Let us now consider in detail the changes in sex structure of *Juniperus* populations in connection with the drastic increase in density, characteristic for the end phases of succession. Special evidence of the influence of density on the sex structure and population size structure of *Juniperus communis* is supplied by analysis of analogous age classes

Populus tremula L.

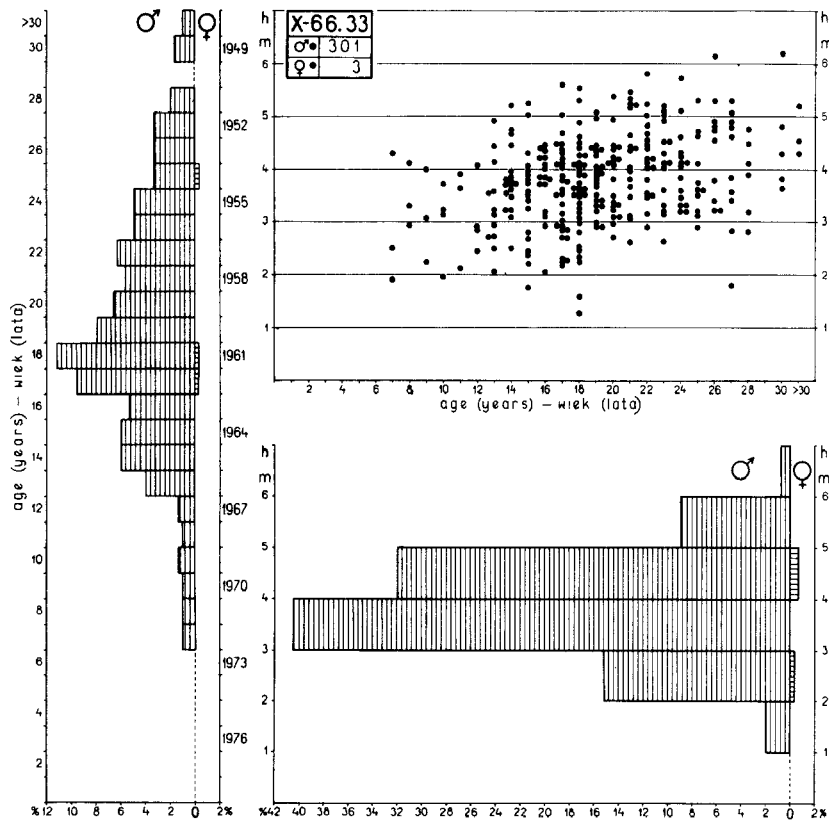


Fig. 9. Pyramids of sex-and-age and sex-and-size for chosen samples from the population *Populus tremula*. Only those individuals which flowered during 1977 and 1978 in the area of 1000 sq. m. were chosen.

Populus tremula L.

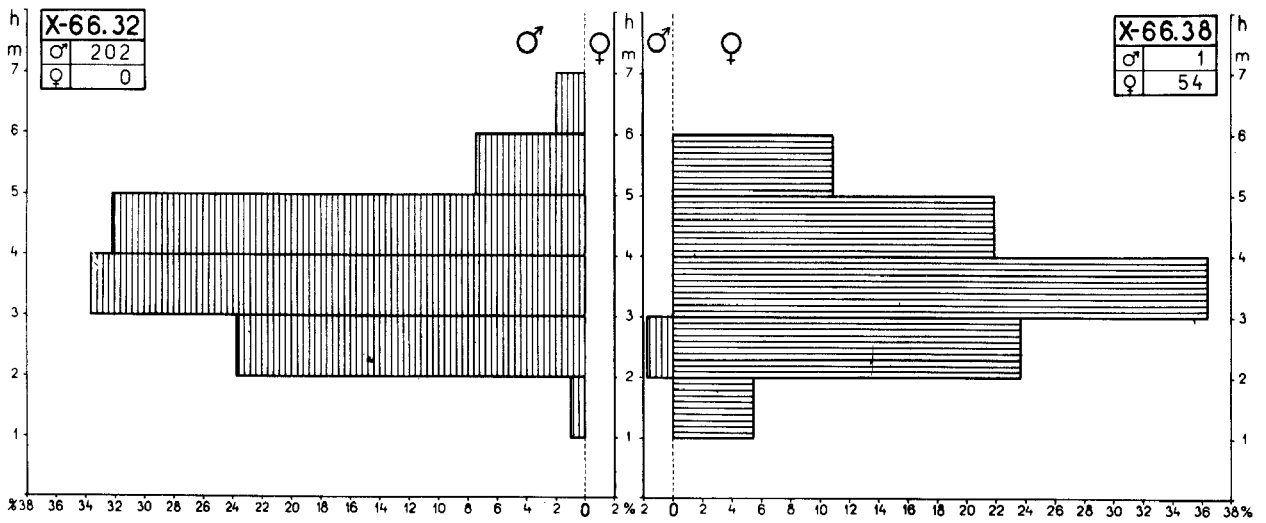


Fig. 10. Sex and size pyramids of 'male' and 'female' populations of *Populus tremula*. Only those individuals which were flowering during 1977 or 1978 were taken into account. Each sample was taken from an area of 1000 sq. m.

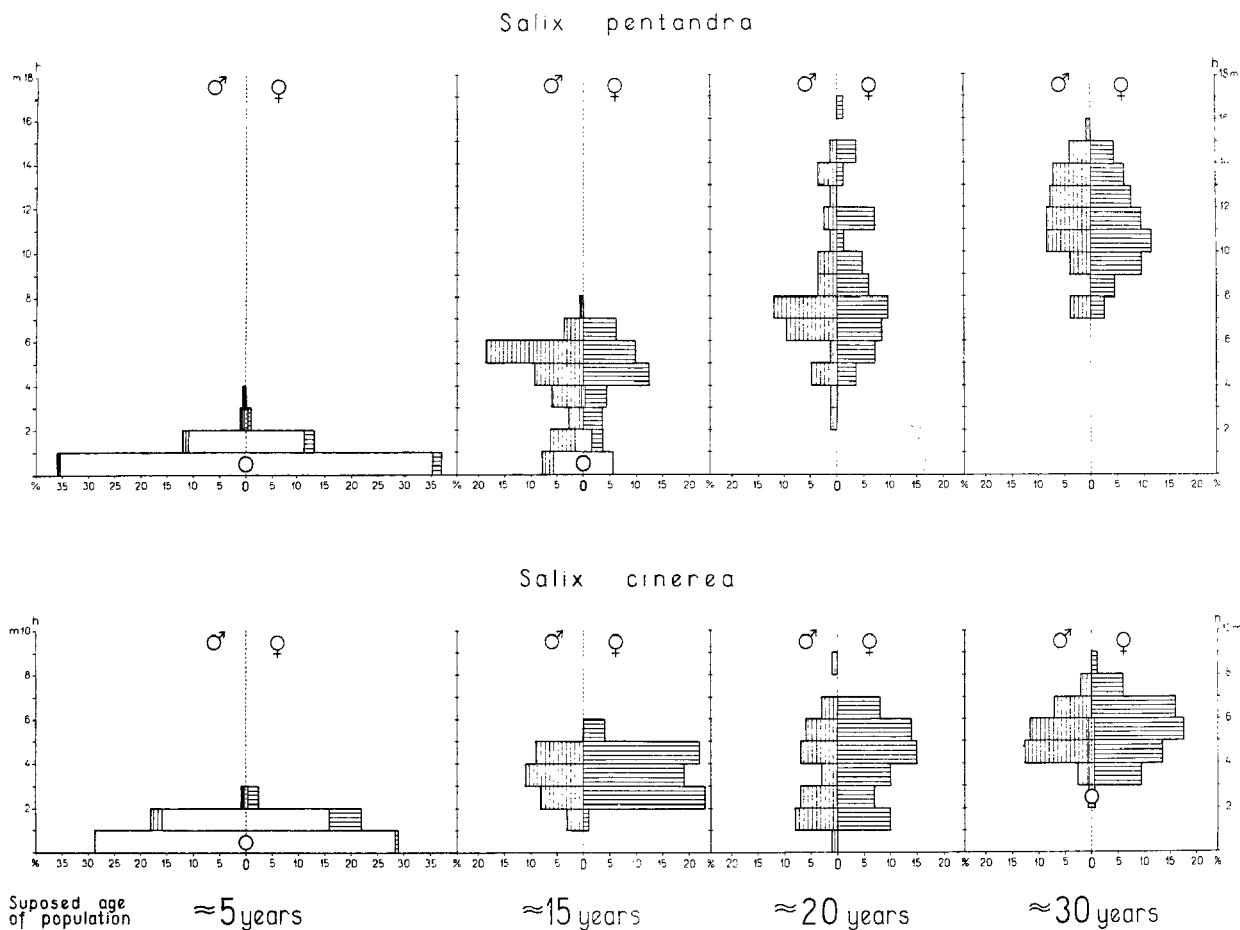


Fig. 11. Pyramids of sex and size from populations of *Salix pentandra* and *Salix cinerea*.

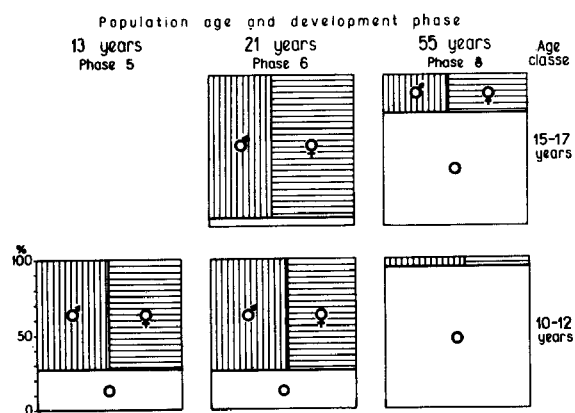


Fig. 12. Comparison of the sex structure of analogous age classes (10-12 yr) and (15-17 yr) of the younger (13 yr old/older and the oldest/55 yr old) populations of *Juniperus communis*, corresponding to the successive phases of the development of the population and phases of the plant succession. Data are taken from the surface samples no.: 66.12, 19, 21, 2, 3, 5, 15.

in different-aged populations, occurring in various phases of vegetation succession (Figs. 12 and 13). Age classes of 10-12 and 15-17 yr were subjected to analysis in populations aged 13, 21 and 55 yr. Individuals in the populations 13 and 21 yr old in the phase of stabilisation (phases 5 and 6) with a density of up to 3900 ind./ha. are dispersed over the stand. In the oldest population with a density of *Juniperus* alone up to 30 000 ind./ha. that is almost 10 times higher, other tree and shrub species are present: *Populus tremula*, *Pinus silvestris*, *Betula pendula*, *Salix caprea*, *S. aurita*, *S. rosmarinifolia*, *Cytisus ruthenicus*. This situation corresponds to the older phase of juniper-aspen brushwood.

In the 10-12 yr age class, both in the 13 - and 21 - yr population, more than 70 % of the individuals participate in generative reproduction (Fig. 13). On the other hand, in the oldest population the contribution of reproductive individuals in the same class does not reach 10 %. These differences diminish slightly in the 15-17 yr class. In not

Population age and development phase

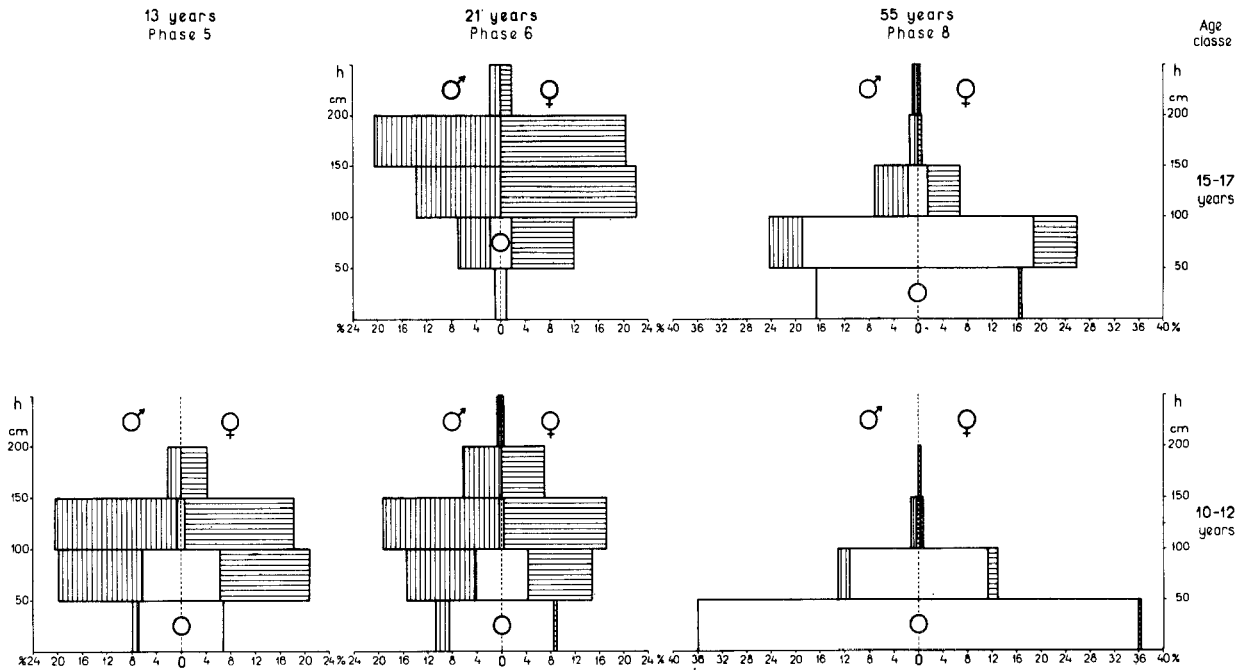


Fig. 13. Sex structure and individual size structure in analogous age classes from the younger, older and the oldest populations of *Juniperus communis*. Detailed analysis of the material is shown in Fig. 12.

overcondensed populations practically all individuals of this age reproduce (see Fig. 7). The height pyramids elaborated for these population classes at various ages demonstrate a distinct growth inhibition of individuals in the older overcondensed population (Figs. 6ABC and 14). The majority of individuals in the overcondensed population does not reach a height of 1 m, whereas in not so dense populations more than one half of the individuals of the same age belong to the height class 1–2 m.

The influence of density on the sex size structure may, therefore, be defined as inhibition of growth of individuals and retardation of the whole age class in reaching the phase of reproduction.

Conclusions

It was found that in the course of the succession the *Juniperus* populations change as to the following characteristics: (Fig. 14):

Spatial structure: From random structure in the initial stage to agglomeration structure in the optimal and terminal stages;

- Abundance:** Type of growth: two-peak left-biassed curve with first peak at optimal stage and second one at terminal stage (Fig. 14);
 - Age structure:** From one-generation initial stage to a multigeneration one beginning at the optimal stage. In the differentiated multi-generation structure the consequences of a 2- or 3 yr cycle in diaspore production are visible (Figs. 6 and 7).
 - Sex structure:**
 - participation of identified individuals/involved in generative reproduction/
 - sex ratio
- A relative increase of the participation of identified individuals up to $\frac{2}{3}$ of the population composition in the optimal stage, falling to about $\frac{1}{3}$ in the terminal stage (Figs. 14);
- from $\delta : \varphi = 1 : 0.4$ in initial stage through $\delta : \varphi = 1 : 1$ in optimal stage to $\delta : \varphi = 1 : 1.1$ in terminal stage; / from prevalence of male individuals, via equilibrium to prevalence of female ones (Fig. 14, Table 1);

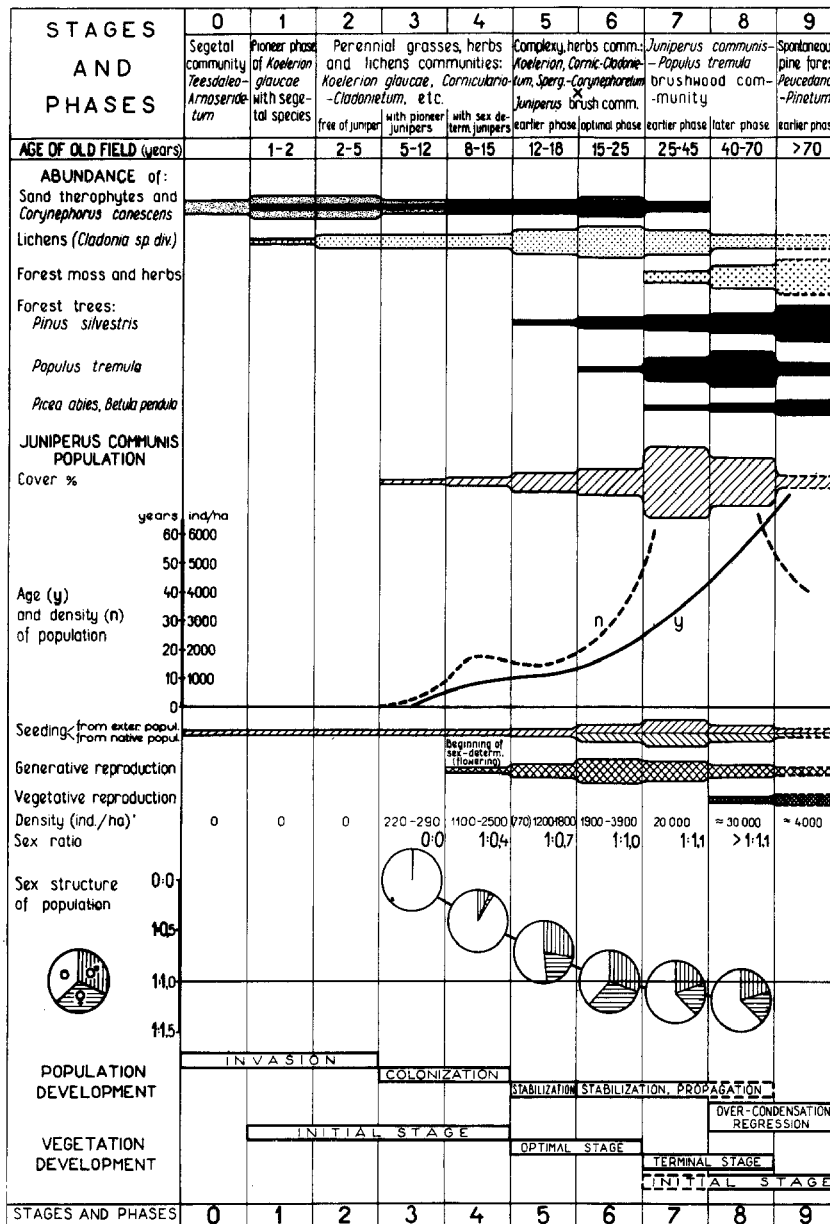


Fig. 14. Plant succession in old fields and development of the population of *Juniperus communis*. At the bottom: The synchronisation of the phases of juniper population development with the phases of vegetation succession.

Types of reproduction: Generative in the whole succession series; exceptionally vegetative, only when imposed by overcondensation or destruction of erect shoots – only in terminal stage,

Population growth: Substitution of seeding from outside, specific for initial stage, by

autochthonous propagation in optimal and terminal stages (Fig. 14);

Diaspore production:

– total of population

– individual

Continuous increase from the end of the initial stage to the terminal stage;

increase to end of initial stage and decrease in the terminal stage;

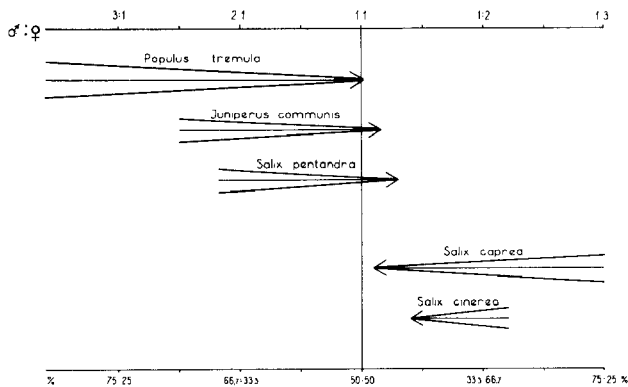


Fig. 15. Supposed sex ratio changes in the populations of pioneer woody species in the vegetation succession.

Calendar age of individuals at the moment of starting generative reproduction

In the optimal stage of succession at the age of 8-9 yr, in terminal stage retarded and occurring over a period from 10 to 20 (26) yr (Figs. 6 and 14).

In view of the changes in sex ratio in the population in connection with vegetation dynamics, at least two groups can be distinguished among the pioneer woody species (Fig. 15):

(1) *Juniperus communis*, *Salix pentandra* and eventually *Populus tremula* in which the sex ratio changes from prevalence of male individuals in the early phases of population and vegetation development to an equilibrium in the phase of stabilisation and to a greater or smaller numerical dominance of female individuals in the latest phases;

(2) *Salix caprea*, *S. aurita*, *S. cinerea* and *S. rosmarinifolia*, and their hybrids, the populations of which are characterized by a constant prevalence of female individuals, but the sex ratio of which in the early phases of population and vegetation development reveals a higher contribution of male individuals.

A possible confirmation of the hypothesis of 'patchiness' of the spatial population structure of *Populus tremula* could lead to the distinction of a third group of species. Otherwise the sex structure of the population of this pioneer tree would have to be considered on a much larger scale. Then, however, elimination of additional factors affecting the sex structure of the exceptional role of dioecious woody species in the early phases of succession suggests that their success in colonisation of new habitats is based on the ability to apply colonization tactics and a reproductive strategy exceptional in plants. This possibility

derives partly from the different ecological requirements of male and female individuals, an earlier initiation of reproduction by male individuals, and also probably their earlier colonization of pioneer habitats or, at least, their higher adaptability to extreme conditions.

Summary

In connection with vegetation succession in old farmland and meadows, changes in the sex structure were analysed, particularly the sex ratio in populations, of *Juniperus communis*, *Populus tremula*, *Salix aurita*, *S. caprea*, *S. rosmarinifolia*, *S. pentandra* etc. Particular attention was given to the changes in the characteristics of *Juniperus communis* populations, associated with succession in old fields, leading from the segetal community *Teesdaleo-Arno-seridetum*, through the therophyte communities with *Corynephorus canescens*, lichens *Corniculario-Cladoniëtum mitis*, sand sward with the alliance *Koelerion glaucae* to *Juniperus-Populus* brushwood and *Peucedano-Pinetum typicum* forest. The particular succession phases over 70 yr and the phases of development of the pioneer populations of tree species were dated by the dendro-chronological methods.

It was found that in the course of the succession the sex structure, and in particular the sex ratio, changes in the populations of the above-mentioned species. Among the factors that affect the natural populations, the increase in density of the *Juniperus communis* population itself together with changes in the structure of the whole associated community played the most important role. This factor inhibits growth of juniper individuals very strongly and retards the beginning of the generative reproduction phase of a given population by 10-15 yr.

A hypothesis is advanced concerning the role of dioecism in pioneer tree species in the process of colonisation.

In view of the changes in sex ratio in the population in connection with vegetation dynamics, at least two groups can be distinguished among the pioneer woody species:

(1) *Juniperus communis* and *Salix pentandra* in which the sex ratio changes from prevalence of male individuals in the early phases of population (and vegetation) development to an equilibrium in the phase of stabilisation and to a greater or smaller numerical dominance of female individuals /in the latest phases;

(2) *Salix caprea*, *S. aurita*, *S. cinerea* and *Salix rosmarinifolia* and their hybrids, the populations of which are characterised by a constant prevalence of female indivi-

duals, but the sex ratio in the early phases of population (and vegetation) development reveals a higher contribution of male individuals.

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