DECLINES IN POPULATIONS OF *SALIX CAPREA* L. DURING FOREST REGENERATION AFTER STRONG HERBIVORE PRESSURE

JANUSZ BOGDAN FALIŃSKI

Białowieża Geobotanical Station, Warsaw University
17-230 Białowieża, Poland

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ABSTRACT

Communities of broadleaved forest subject to strong pressure from large herbivores underwent degeneration. The relief of this pressure led to regeneration of the community, in which an important role was played by the sallow *Salix caprea* and other light-seeded pioneer species of tree (*Populus tremula, Betula pendula* and *B. pubescens*).

Regeneration involving *Salix caprea* proceeded following the conservatorial protection of the degenerate stands in a reserve and later in Białowieża National Park. The emergence and development of the population of *Salix caprea* proceeded following the invasion of spruce, which coincided with the period of enhanced animal pressure on broadleaved forest. *Salix caprea* filled all the gaps in the tree stand arising as a result of the destruction of trees and undergrowth by herbivores (in the years 1892-1915). It also appeared en masse on old, at that time unforested, clearings and felled areas.

In these places, *Salix caprea* created very abundant populations, with particular trees being in good condition, with a habit typical of forest trees and attaining considerable heights. The majority of trees were 50-60 years old at the time of death, although individuals reached 74 years of age. The process of extinction of the sallow population – observed over 19 years on permanent plots and fixed trees – proceeded very quickly, especially in the first decade of observation. It led to the almost complete disappearance of sallow for the forest communities of Białowieża National Park. The death of individual trees is preceded by impairment of their health and reduced annual increments in the 4-9 last years of life.

The extinction of the population is associated with the loss of its primary phenological differentiation and with a change in the sex structure of the population from a prevalence of female trees to a near even distribution of the two sexes.

The development of the populations of permanent constituents of the forest (*Carpinus betulus, Tilia cordata, Acer platanoides* and *Ulmus glabra*) under the canopy of light-seeded trees, and the non-creation of a new generation of pioneer species points to the imminent end of the process of regeneration in the forest communities of Białowieża National Park.

KEY WORDS: Forest dynamics; pioneer woody species; population decline; population development; forest community degeneration; forest community regeneration; herbivore impact; *Salix caprea*; Białowieża Forest.

INTRODUCTION. SUBJECT AND AIM OF RESEARCH

1. Degeneration and regeneration of forest communities and the role in these processes of pioneer tree species with light seeds

Degeneration and regeneration are processes linked with each other. **Degeneration** defines the process of deformation of community structure, as well as the perturbations in its functioning within all or part of a phytocoenosis. It is mainly caused by the action of external natural or anthropogenic factors. Today the main factors responsible for the degeneration of forest communities are the exploitation of timber, the introduction of alien species of tree, the construction of roads, penetration by tourists, the encouragement of game animals and contamination of the environment. In the past, in contrast, the most important factors were fire management, uncontrolled cutting of trees, fires, cattle grazing, woody charcoal production and potash making (Faliński 1966, 1986a).

These factors lead to long-term changes in the structure and dynamics of forest communities which affect not only the tree stand, but all layers of the forest community including the synusiae of cryptogamous plants. Changes may even extend to soil properties. Frequent symptoms of such changes are the simplification of the vertical structure of the stand, changes in the quantitaive relationships between the species making up the different layers and even the disappearance of some stenotopic species. The degree or advancement of community degeneration is well displayed in the encroachment of native non-forest species and those of foreign origin. Some of the latter have taken up permanent residence in disturbed forest communities, attaining the status of neophytes over time (see for example Faliński 1966, 1968b, 1968c, 1986a, 1991, Kornaś and Medwecka-Kornaś 1968, Kornaś 1983, Sukopp 1972, Lohmeyer and Sukopp 1992).

The invasion of tree species with light seeds like birches, aspens, willows and alders, as well as hornbeams, only becomes effective when the basic factors responsible for degeneration recede. The coming-to-dominance of these species marks the beginning of the process of regeneration in forest communities (see later). However, this remark does not refer in full to the behaviour of the spruce, pine and juniper in degenerate forest communities on fertile habitat. For these species, as the ones most resistant to browsing, may spread as the much-damaged broadleaved species retreat.

Disturbances to the structure and dynamics of forest communities, including the slowing of natural regeneration of stands under the influence of extensive forms of management, are as old as human activity in the forest itself. However, they were perceived later than the processes of deforestation and the liquidation of forest formations from the landscape. An awareness of the internal transformation of forests first appeared in the 18th and 19th centuries in France, Germany and Poland, although it goes back much further in a form restricted to the minds of those closely associated with natural management, in the Mediterranean area, where cutting and permanent grazing had already brought about permanent changes in the structure and dynamics of forests by the classical era. In this case, the majority of society was convinced that the low branching forest was a natural phenomenon.

The changes brought about by zoogenic pressure, especially as the combined effect of excessive populations of game animals and the grazing of livestock, were very clearly seen in the hunting forests of princes and monarchs (e.g. in France, Bavaria, Tirol, Silesia and Mazury), of which at least parts arose naturally, only to later take on the functions of game parks.

In the search for the mechanisms and sequences of events making up the processes of degeneration and regeneration, the forest communities of Białowieża Primeval Forest and National Park have attained the status of models. For occurring here in a defined order were all the former anthropo- and zoogenic factors (Faliński 1966, 1986a, Zaręba 1958, 1968), of which the forest was later freed following the establishment of the Park.

Within the boundaries of the present Białowieża National Park, the main factor in the degeneration of forest communities in the not-too-distant past was the maintenance of excessive populations of game animals (including the non-native fallow deer *Dama dama*) as the grazing of cattle.

The presence of large herbivores and their various forms of impact (grazing, debarking, rooting, wallowing, refuges in the reproductive period) may be considered within forest ecosystems as permanent internal biotic/biocoenotic factors. The excessive numbers and concentrations of animals in a small space is only becoming a factor in degeneration (Table 1).

Between 1892 and 1915, the effective transformation of Białowieża Forest into a hunting park for the Russian Tsars brought about the following changes in the first period:

(1) complete destruction of the lower layers of the forest, especially the undergrowth;
(2) the debarking of broadleaved trees;
(3) the prevention of the natural regeneration of hornbeam, linden and oak, as well as of ash and maple;
(4) the rapid appearance of spruce in place of the above species, and its spread under the canopy formed by old broadleaved trees.

In the course of more than 50-70 years under the influence of excessive numbers of game animals, spruce became the absolute dominant in the forests of Białowieża, although the scientific and literary descriptions of the Białowieża Forest in the 19th century still mentioned it among other species, putting oak and pine in first place for the forests of the area. It should be stressed that the processes of forest devastation brought about by game animals were not associated with the exploitation of timber, and neither were the later processes of the spontaneous rebuilding of stands within the area of the present Park.

Changes in the overall picture of the forest, as well as in the structure and dynamics of forest communities, were observed by many researchers at the end of the period of enhanced pressure from game animals (see in Table 1 fragments of the original observations of Wróblewski, 1927). These changes were of such an order, and of such permanence, that they became a source of much speculation encouraging long-term research some 20-40 years after the disappearance of the main causative factors (Włoczewski 1972, Karpiński 1949, Adamczewski 1950, Matuszkiewicz W. 1952). The main subject of interest was the decline of some species of tree, such as lime, the invasion of spruce and the far-reaching simplifi-

TABLE 1. Effect of impact of large herbivores on forest community structure and species composition in Białowieża Forest, observed by K. Wróblewski (1927, p. 95 and 96).

Description of the effects of animal pressure on the forest communities in Białowieża Forest prior to World War I.

Source: K. Wróblewski, 1927. Żubr Puszczy Białowieskiej [The Bison of Białowieża Forest] – Wydawnictwo Polskie, Poznań, 232 pp. + tables; [text, pages 95 and 96].

"BATTLE FOR FOOD

The division of the ruminants living in the primeval forest ["*Puszcza*"] into grazers and browsers is based on the relations between these animals and the forest, as well as their mutual relations with one another. This property has not passed unnoticed in the Białowieża Forest. Looking at its physiognomy, we note that it is now an organism in a highly pathological state, degenerate and dying. Speaking of this is a series of facts. As has already been mentioned, many species from the forest undergrowth have disappeared from the "*Puszcza*" without trace. Old trees are not replaced by a new generation and young spruce dominates over all other species of tree. In places with pine, oak or hornbeams, in high and low places, in coniferous, broadleaved and alder forests – everywhere young spruces are growing. In many places the species creates a young scrub, while in others its is more scattered, but in either case it tends to replace other species in the forest.

Further on – by rivers, on meadows and in marshes, where willows and different kinds of osier usually grow in abundance, today they have all disappeared. Their remains can sometimes be found among the high sedges, but they are little half-dead, stunted shrubs only able to show live shoots near the roots, or leaves hidden in thick grass. It is clear to see that the little tree has tried again and agin to come back to life, but every time some alien force has suppressed its efforts.

Disappearing in this way are all the species of willow growing in the "*Puszcza*" (*Salix pentandra, Salix fragilis, Salix repens, Salix cinerea, Salix aurita* and others). Disappearing in this way are many shrubs which still grew abundantly in the "*Puszcza*" until recently. Today you can no longer meet with *Ribes alpinum* – alpine currant, *Ribes nigrum* – blackcurrant, *Ribes rubrum* – redcurrant, *Rubus saxatilis* – stone bramble, *Rubus ideus* – raspberry, *Rubus fruticosus* – blackberry, *Viburnum opulus* – guelder rose, *Spirea ulmaria* meadowsweet, *Rhamnus Cathartcica* – buckthorn, *Rhamnus frangulá* – alder buckthorn, *Prunus padus* – bird cherry or *Hedera helix* – ivy."

cation of the structure of forest communities. These phenomena made it difficult to identify the types of forest habitat and of forest community, as well as to interpret the dynamic trends affecting them.

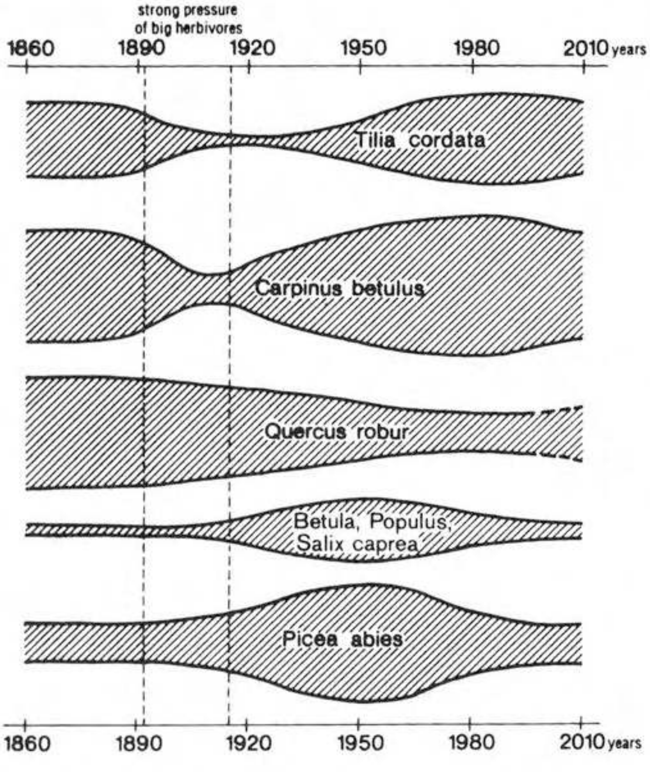


Fig. 1. Changes in species structure of deciduous forest stand (*Tilio-Carpinetum*) in Białowieża National Park. Note temporary increase of spruce and pioneer tree (incl. *Salix caprea)* participation due to strong game pressure as well as prognosis for stand regeneration under strict conservation (moderate herbivore pressure).
Source: J.B. Faliński (1986a, modified).

Regeneration – as the process of rebuilding of deformed communities via forces and agents within those communities - appeared dramatically in the National Park following the disappearance of the main factor preventing it – the excessive numbers of game animals – as a consequence of the disappearance of virtually all of them during World War I (Fig. 1). It ultimately emerged that the invasion of spruce as a result of the destruction of the undergrowth, and the complete regeneration of broadleaved trees (hornbeam, linden and oak) together constituted but a short-lived phenomenon in the history of the forest, for the self-thinning of the species had already begun after 50-60 years. In the meantime, a new generation of broadleaved trees had developed under the spruce canopy. Together with the old oaks and linden still standing these created a stand with a characteristic two-layered structure (Fig. 2). In places the oldest generation of trees had already been replaced. In respect of this, the stands in question stand out in aerial photographs in either having a complex large/fine/grainy texture or only a fine-grained texture. The intensity of the impact of animals in the past is attested to by the lack in these stands of trees in the middle age class (80-100 years old). This is particularly the case for linden (Faliński 1986a, see also Paczoski 1928, 1930, Włoczewski 1972, Zaręba 1958, 1968).

The process of regeneration progressed relatively rapidly in fertile, moderately moist and fresh habitats, i.e. in oak-linden-hornbeam forest (*Tilio-Carpinetum stachyetosum, T-C. typicum*). In contrast, in the poor and dry habitats proper to *Tilio-Carpinetum calamagrostietosum* and *Pino-Quercetum*, the process of regeneration is held up by the lack of regeneration of oak and the more difficult access to these habitats for hornbeam and linden (Włoczewski 1972, Faliński 1986a, 1991).

Other factors in the delayed completion of the regeneration process in the *Tilio-Carpinetum* community are: the spread of aspen, birches and sallow over large areas and their lengthy persistence in the forest stand in spite of the fact that their roles have in principal been fulfilled (Figs. 2 and 3). A product from these trees is a decomposition-resistant litter layer beneath them and the effect of the delayed breakdown of aspen litter is the secondary hydrophobia of the upper soil layers (Faliński, Canullo and Biały 1988). However, recent years have witnessed marked dieback and fall amongst the

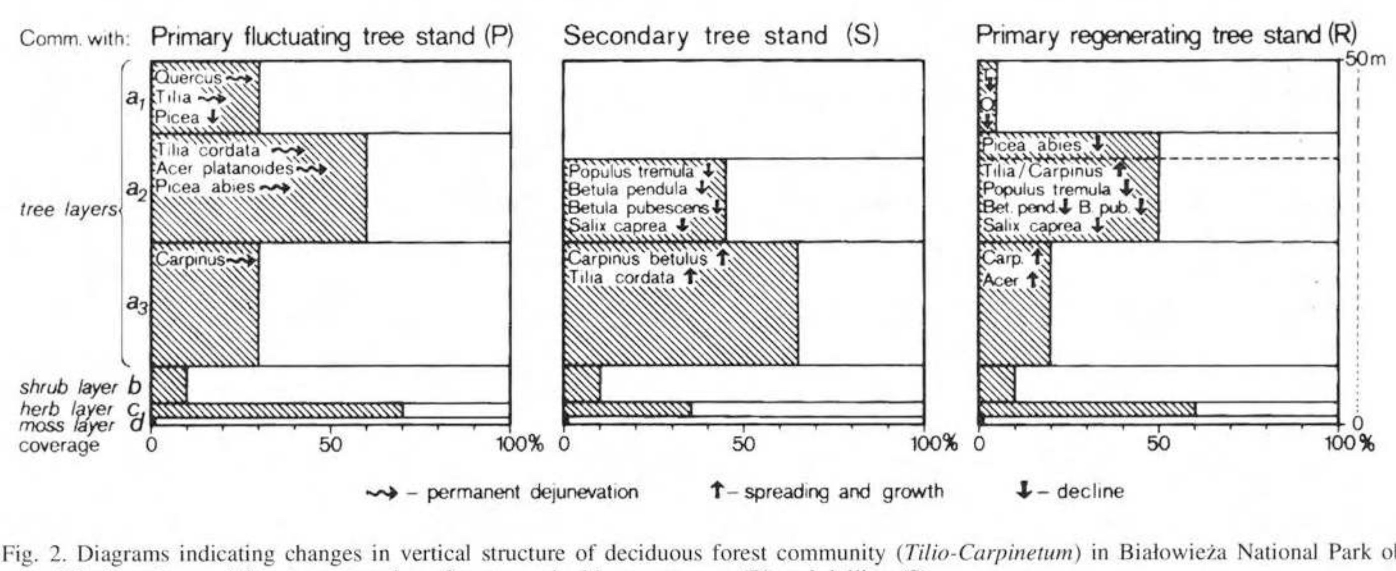


Fig. 2. Diagrams indicating changes in vertical structure of deciduous forest community (*Tilio-Carpinetum*) in Białowieża National Park observed during advanced forest regeneration after strong herbivore pressure (R) and dolling (S).
Source: J. B. Faliński, R. Canullo & K. Biały (1988).

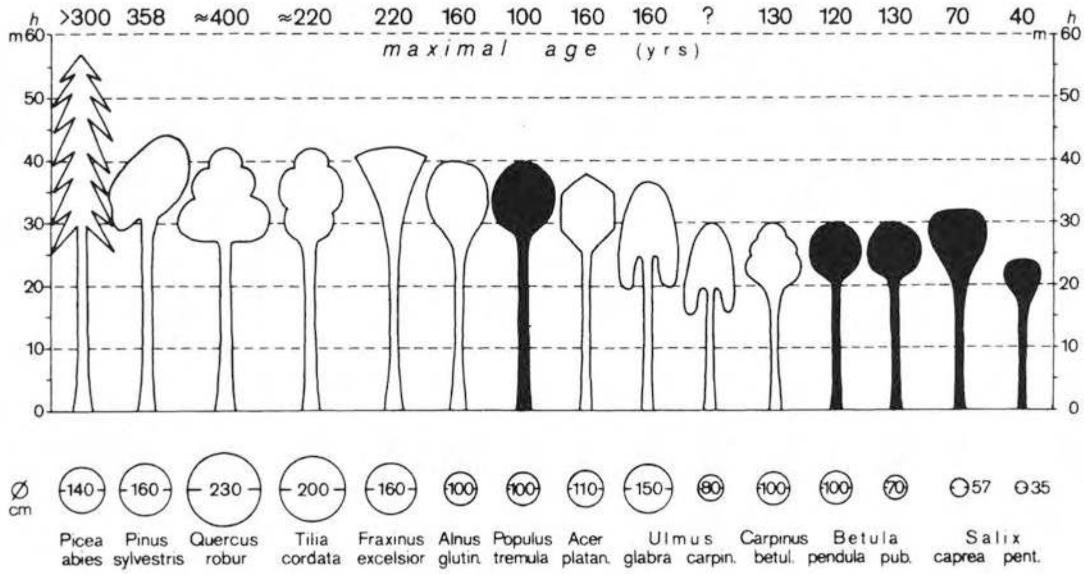


Fig. 3. Maximal ages and dimensions of pioneer and final forest tree species in the Białowieża Forest.
Source: J. B. Faliński (1977), supplemented.

pioneer tree species of *Tilio-Carpinetum* stands. This is occurring both within tree stands, in the immediate vicinity of forest roads and at the forest edge (Photos 1-6).

In contrast, the important factors accelerating regeneration are: the very abundant generative regeneration of hornbeam and maple, the vegetative spreading and the vegetative reproduction of linden, which appeared following the removal of excessive pressure from game animals and which still plays an important role (Faliński 1986a, 1991, 1996, Faliński and Pawlaczyk 1991, Pawlaczyk 1991). It is manifested in the growth among older linden of consecutive generations of offshoots from which at least one is capable of replacing the mother plant and in this way of maintaining the species in the same place for many generations.

The communities undergoing regeneration continue to display a simplified horizontal and vertical structure for long periods of time. The exchange of species in the herb layer is linked with a certain rise in their numbers from year to year (Faliński 1986a, 1991). These changes find their expression in the seasonal rhythms of the communities departing to some extent from the behaviour of destroyed or stable forest communities (Faliński, Canullo and Biały 1988, Faliński 1986a, 1991).

2. Biological and ecological features of willows

The literature devoted to the dynamics of forest communities is lacking in significant data on the behaviour of *Salix caprea*, even though much has been said about other pioneer species from the genera *Populus* and *Betula* – especially where their roles in the succession and regeneration of boreal forests is concerned. In effect *Salix caprea* is most often found and described in keys, monographs and guides as a small tree usually with a large number of trunks (e.g. Skvorcov 1968, Meikle 1984, Neumann 1981, Chmelař and Meusel 1979, 1986, Lautenschlager 1983, Parfenov and Mazan 1986, Martini and Paiero 1988, Hörandl 1992, Głowacki 1987).

Data on *Salix caprea* as a tall tree have been repeated many times in the literature following Białowieża Forest sources.

There has recently been a growth of interest in the sallow or goat willow, *Salix caprea*, on account of the rapid increase in its mass and the possibilities for using it as a home-grown source of alternative energy (e.g. Ericsson 1981c).

In connection with this, data have been gathered and checked in relation to the biology of the species, and hence germination conditions (Simak 1980), the rooting of seedlings, generative and vegetative reproduction (Popcov and Buč 1957, Suszka 1990), and the use of grafting in cultivation (Krössman 1964, Bärtels 1982). The goat willow is one of several species known for its high tolerance to the action in the environment of fluorine (Kisser and Lehnert 1960, Kluczyński 1975) and sulphur dioxide (Lattke 1969, Pelz 1956).

The stems and bark of sallow form a permanent component of the diets of European bison, red deer, moose and roe deer (Borowski and Kossak 1972, 1975; see also Klötzli 1965 in relation to the diet of roedeer). A total of 17 mammal species use the species as food (Turček 1967). Browsing and debarking by animals modify the fabric of the whole plant, its crown, apical shoots and trunk, often leading to the more frequent occurrence of the species as a shrub in the forest than as a tall tree (Faliński 1986a, 1991). All beekeeping manuals emphasize the significance of sallow as a species favouring the production of honey.

Furthermore, shrubby species of *Salix*, besides their long-known application in the reconstruction of river courses and channels, are researched from the point of view of their use in the treatment of wastewaters.

Relatively well-known are the biology and ecological role of two species of willow growing as riverside trees, namely *Salix fragilis* and *Salix alba*, in relation to the structuring of forest communities and the scrub of streamside habitats (e.g. Moor 1958, Seibert 1962, Philippi 1984, Matuszkiewicz J. 1976, Faliński 1990 and literature cited therein), as well as where their use in the reinforcement of the banks of rivers and canals is concerned (e.g. Krause 1985, Olsson et al. – undated, Ericsson 1981a, 1981b).

characteristics: / genera:	broad tolerance vs. climate and soil 1	heliophyly 2	active growth in youth 3	early flowering and fruiting 4	proanthy 5	dioecy 6	anemogamy (anemophyly) 7	abounding and ± yearly fruiting 8	anemochory 9	strong tendency to vegetative propagation 10	morpholog. plasticity vs. abiotic and zoogenic factors 11	Number of characteristics; intensity	Degree of pioneerity
POPULUS	● ●	● ●	●●●	● ●	●●●	●●●	●●●	●●●	●●●	●●●	●	11 *1-3*	I
SALIX	●●●	●●●	●●●	●●●	● ●	●●●	entomogamy	●●●	●●●	●●●	●●●	10 *0; 2-3*	II
JUNIPERUS	● ●	●●●	●	●●●	evergreen	●●●	●●●	● ●	ornithochory; barochory	●	● ●	9 *0-3*	V
BETULA	●●●	●●●	●●●	● ●	●	monoecy of species: monoecious individuals; nonsexuality of flowers and inflorescens	●●●	●●●	● ●	●	●	10 *0-3*	III
ALNUS	●	●	● ●	● ●	● ●		●●●	●●●	● ●	● ●	● ●	10 *0-3*	IV
PINUS	● ●	● ●	●	●	evergreen		●●●	● ●	●	●	● ●	9 *0-3*	VI
Number of genera: *Intensity:*	6 *1-3*	6 *1-3*	6 *1-3*	6 *1-3*	4 *0-3*	3 *0; 3*	5 *0; 3*	6 *2-3*	5 *0-3*	6 *1-3*	6 *1-3*		

Fig. 4. Biological features of willow species (*Salix*) and other woody pioneer species.
Source: J. B. Faliński (1980a, 1980b), augmented.

Since a dozen or so year, work has been ongoing on the sex structure of the populations of various willow species (Faliński 1980a, 1980b, 1986a, 1986b, 1990), ecological determinism and the strict selectivity of individuals of the two sexes in relation to habitat/environmental conditions (e.g. Faliński 1980a, 1980b, Alliende 1989, Alliende and Harper 1989, Iacobelli and Jefferies 1991, Crawford and Balfour 1990, Alström-Rapaport and Gullberg 1995).

A very interesting problem is presented by the preferences of herbivores in relation to the different species of willow, and even individuals of the two sexes (e.g. Faliński 1986a, Elmquist et al. 1988).

Obviously, the issue of the derivation of the genus *Salix* also remains lively (as well as the *Salicaceae* family and the proper entomogamy of all its species).

As a representative of the genus *Salix*, the great sallow or groat willow *Salix caprea* embodies not only the most important biological and ecological properties of the majority of species of this very well-represented genus, but also – away from entomogamy – shows all the properties of the tree species considered to be pioneers (Fig. 4; Iversen 1973, Faliński 1991, 1996, Rameau et al. 1989). The following is an attempt to define pioneer species (after Faliński 1990):

The term pioneer species is used to define those which have certain particular biological and ecological properties, such that:

- they use extreme environmental conditions in carrying on their life functions;
- they have an ability to adapt to extreme conditions;
- they have an ability to convert extreme conditions to those optimal for the lives of single organisms, populations and ultimately whole biocoenoses;
- they overtake other species in the processes of conquering and colonizing new areas;
- they determine the course of the initial phases of primary or secondary succession as well as regeneration, but they usually disappear as ecosystems attain full stability.

3. Subject and aim of research

The subject of the research is the behaviour, in the process of regeneration of forest communities, of the great sallow or goat willow (*Salix caprea*), as one of the pioneer species which persists longest in the forest (apart from aspen and the two species of birch). In certain circumstances, these species become for long periods (60-70 years or more) fully-fledged components of the forest stand from the point of view of abundance, size and spread – on a par with hornbeam, linden and maple. Locally, these species have been able to limit the invasion of spruce, or else to accelerate its replacement in places where it appeared commonly.

The behaviour of the sallow is all the more interesting in that it occurs abundantly and for long periods in climax forest communities which in this region are undoubtedly those of oak-linden-hornbeam forest (*Tilio-Carpinetum*). Outside Białowieża Forest (Faliński 1991) the phenomenon of the mass and long-term persistence of sallow in forests has not been described in references.

With that, it is characteristic that the long-term persistence of sallow in a tree stand, the attainment of considerable sizes and habits typical for constant components of a tree stand, and at last the abundant flowering and fruiting, do not lead to the emergence of consecutive generations in local populations of the species (in the National Park). The mass occurrence of sallow and other pioneer species in this Park was thus basically a one-off phenomenon, in spite of the fact that the species always appears universally and abundantly in disturbed tree stands or cuts in managed forests in the vicinity.

Admittedly, *Salix caprea* has appeared repeatedly in the National Park, but only once and this only in small numbers. The appearance of sallow in natural forest communities in whose stands large areas were blown down by winter gales at the beginning of the years 1982 and 1984.

The main aim of the research presented here is to determine the degree to which sallow corresponds to the concept of a pioneer species (see above), as well as to determine the biological and ecological features which are of significance in the

Photos: 1-6. Sallow *Salix caprea* during secondary succession and forest regeneration. (Photo: J. B. Faliński)

1. Pair of ♀ and ♂ sallow trees in the farmland of Białowieża. ♂ tree damaged by last frost.

2. Sallows and birches on the abandoned farmland since 1974. Experimental garden in Białowieża (1996).

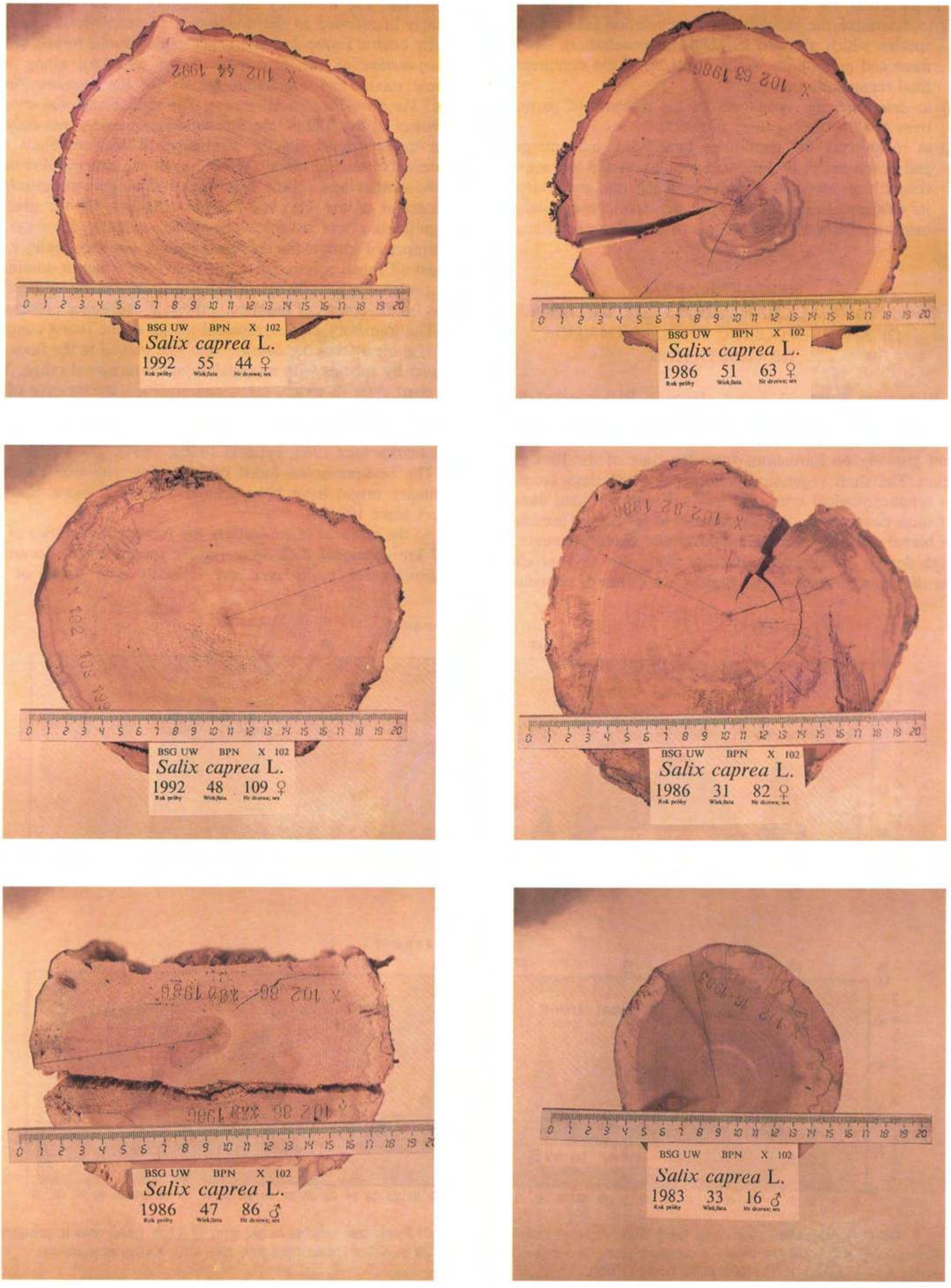
3. "Safe place for germination" at the foot of sallow with maple *Acer platanoides*. Experimental garden.

4. One from the living sallows in the broadleaved forest, Białowieża National Park. Permanent plot X-87.

5. Uprooted tree of sallow in the broadleaved forest, Białowieża National Park. Permanent plot X-87.

6. Decomposed sallow trunk in the broadleaved forest, Białowieża National Park. Permanent plot X-87.

Photos: 7-12. Yearly rings of six *Salix caprea* trees. Białowieża National Park. Permanent plot X-102. Explanations on the photos: year of wood simple; minimal age (yrs.); No. and sex of tree. (Photo: J. B. Faliński)



process of regeneration in the communities of fertile broad-leaved forest.

In particular, the work aimed:

1) to determine the individual and population features of the species which allowed its abundant penetration, development and persistence in the forest up to the community's final regeneration phase;
2) to determine the symptoms of the dieback of particular trees and the direct causes of death;
3) to reconstruct the conditions underlying the emergence and development of a pioneer population and to trace – by research on associated processes – the rate and causes of its disappearance, together with the development and ultimate termination of the process of forest regeneration.

RESEARCH AREA: GEOBOTANICAL CHARACTERISTICS AND DEGREE OF ANTHROPOGENIC TRANSFORMATION OF VEGETATION

Białowieża Primeval Forest (Puszcza Białowieska) today covers some 1300 km^2 on the Poland/Belarus border. It represents types of forest appropriate to the boreo-nemoral zone and growing on formations from the time of the Riss glaciation. The short vegetation period (mean 185 days according to synphenological criteria) combines with the long duration of snow cover (mean 92 days a year) to favour the occurrence of boreal elements in the plant cover and fauna. However, the high degree of climatic variability from year to year allows for the co-occurrence in the Białowieża Forest of elements of more varied biogeographical character. It is thus possible to talk of transitional biogeographic characteristics of this forest complex. The transitory biogeographical nature of the Puszcza is manifested in the dominance of geophyte-rich, essentially central European, multi-species deciduous forests (*Tilio-Carpinetum* of the *Carpinion betuli* alliance), along with some mixed and coniferous forests (of the *Dicrano-Pinion* and *Vaccinio-Piceion* alliances). The unique regional characteristics of the Białowieża forests are emphasized not only by the co-occurrence in the landscape of thermophilous oak forests (*Potentillo albae-Quercetum* of the order *Quercetalia pubescentis*) and spruce bog forests (*Sphagno girgensohnii-Piceetum* of the *Vaccinio-Piceion* alliance). Of the greatest significance here are three phenomena resulting from the occurrence of spruce: the universal presence of the species in almost all forest communities, the ease with which it dominates in favourable circumstances in all habitats and the influence it has on the course of the most important ecological processes.

The transitory biogeographical nature of the forest complex is also clear from the considerable role played in the flora and fauna by species with a boreal-montane or boreal range. This is most clear in spruce forest communities, irrespective of the participation of suboceanic or central European elements which dominate in deciduous forest complexes (Faliński and Matuszkiewicz 1963, Faliński 1986a, 1994).

The best-preserved forest communities with tree stands of primary origin have been protected in Białowieża National Park since 1921.

At the moment of protection, the forest communities of the 47 km^2 National Park were largely spontaneously-occurring, multi-species, multi-layer and variously-aged stands of pri-

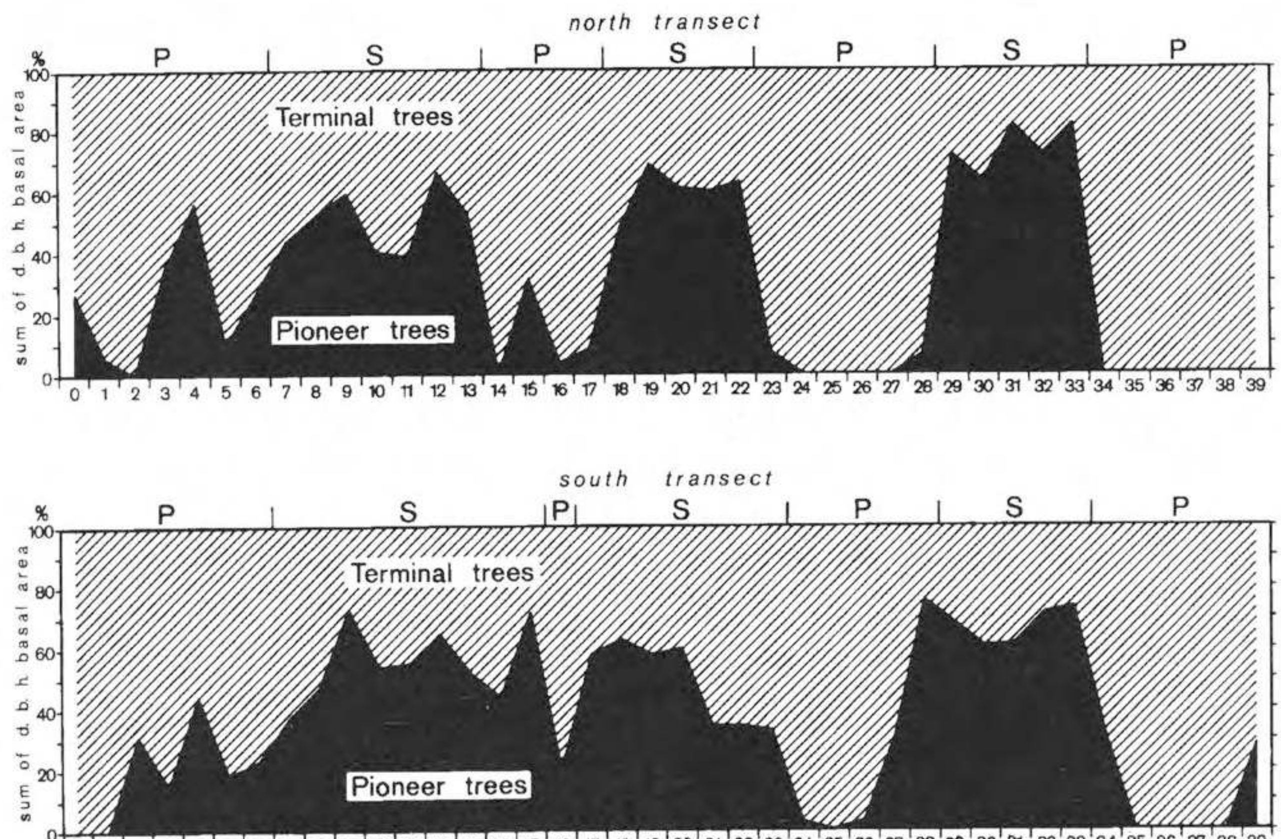


Fig. 5. Relative proportion of pioneer (incl. *Salix caprea*) and final (terminal) forest tree species in the sum of d.b.h. basal area in primary (P) and secondary (S) stands of *Tilio-Carpinetum* along two transects, 800 m × 20 m either (permanent plot 150, with Kulisy population). Source: J. B. Faliński, R. Canullo & K. Biały (1988).

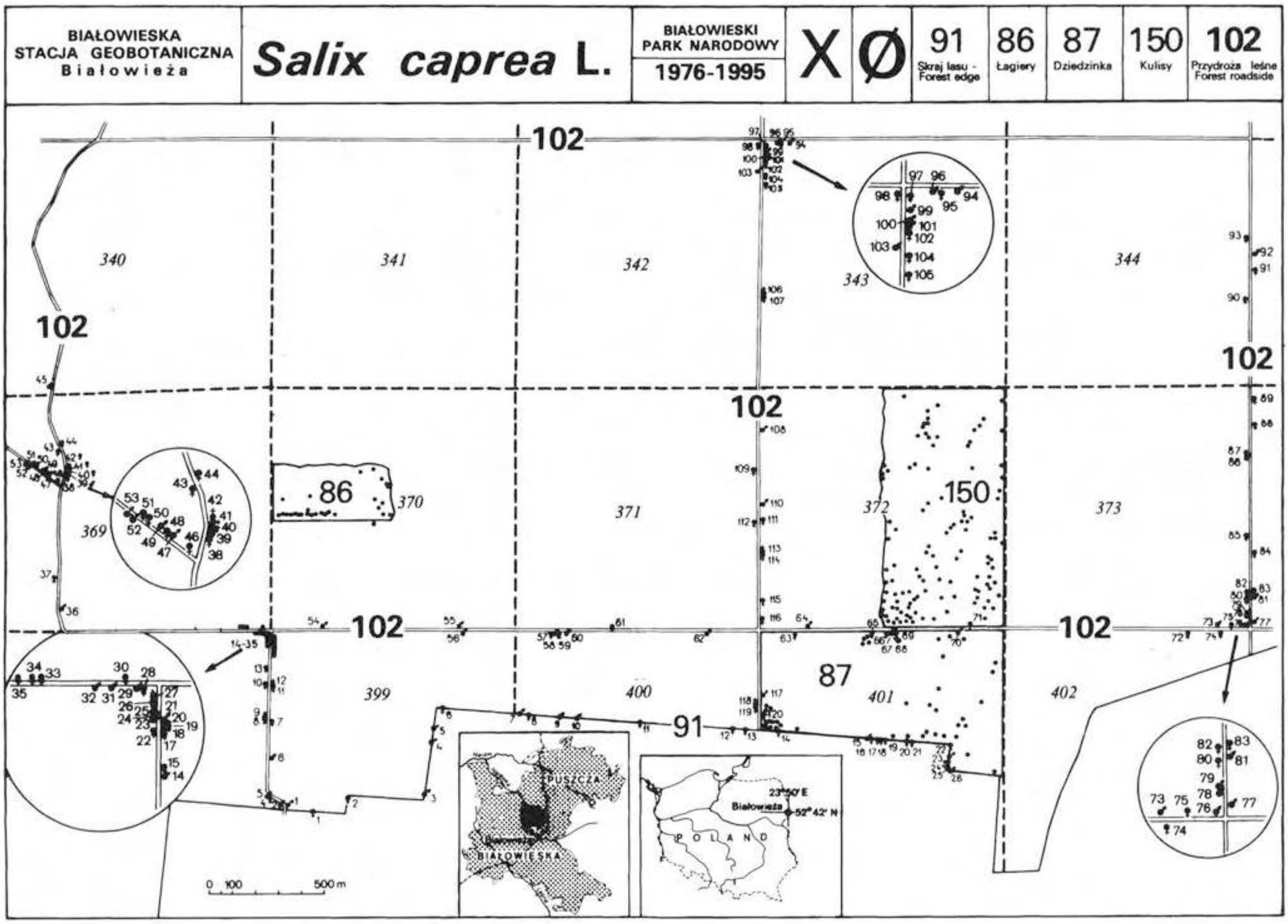


Fig. 6. *Salix caprea* in Southern part of Białowieża National Park. Five permament plots subject to multi-year study (1976-1995) on population decline during forest regeneration.
Source: orig.

mary origin. As a whole these were more than 200 years old, especially in oak-linden-hornbeam forest, with many individual trees being between 300 and 400 years old (Fig. 2). They occurred in a contiguous area in which the only holes were constituted by small clearings and overgrown cuts from 1910 (Paczoski 1930, Zaręba 1958, Faliński, Canullo and Biały 1988; Figs. 5 and 6). Visible in the stands were gaps following plundering cuts which had been filled by aggregations of light-seeded species like birches, aspen and willows. Still numerous are trees with holes cut for bees, charcoal piles from the 18th and 19th centuries and extensive cemetery mounds from the 10th-13th centuries. To this day, the network of tracks is made up of old hunters' trails and newer paths running between forestry divisions. The current density of such roads is c. 0.75 km/km^2 (Faliński 1961).

As mentioned above, the most visible effect of human activity was the damage done by game animals stocked by long-lasting rearing programmes at densities beyond the support capacity of the food base.

MATERIALS AND METHODS

Field research was carried out in the years 1976-1995. It involved tracing the progress of all the indiviuals of *Salix caprea* which had been marked previously. The groups of trees in each of the five permanent plots (see Table 2, Fig. 6) were treated as separate populations. The permanent plots had been designated in Białowieża National Park in the habitat of mesoeutrophic forest (*Tilio-Carpinetum*). The plots included all individual sallow trees occurring in given conditions modified previously by human activity and were as follows:

Plot 102 Roadside (with 122 sallow trees at the beginning of the study). Area by an earth road running through the largest contiguous expanse of forest of the oak-linden-hornbeam phytocoenosis occupying the whole of the southern part of Białowieża National Park. With the exception of the two oldest sections (the palace road and the bypass road), the roads run along the boundaries of forest compartments, often along embankments.

Under observation were all the trees occurring directly by roads with a total length of 19 km on both sides of the drainage ditches. The greatest collection of sallow trees was found near the crossroads (Fig. 6). The crowns of the sallows were found fully or partly over the road, creating a characteristic "tunnel" with other roadside trees (*Quercus robur, Tilia cordata, Carpinus betulus, Picea abies, Populus tremula, Betula pendula* and *B. pubescens*).

Plot 150 Kulisy (with 114 sallow trees). A system of old cut areas in forest compartment 372 formed from 3 belts with widths of about 107m (or 0.1 versts) and a length of about 1066 m (1 verst). On these the tree stands which had been en-

TABLE 2. Observation calendar for *Salix caprea* trees on the permanent plots in Białowieża National Park in the period 1976-1995.

Number and name of permanent plot	**102** **Forest roadside**		**150** **Kulisy**		**87** **Dziedzinka**		**86** **Łagiery**		**91** **Forest edge**	
Location of plot with observed trees.	in oak-linden- -hornbeam forest		old cut area in oak-linden- -hornbeam forest		old cut area in oak-linden- -hornbeam forest		old pastoral clearing		edge of oak-linden- -hornbeam forest and farmland	
Total number of observed trees:	n	%	n	%	*n*	%	n	%	*n*	%
at beginng ♂	48	*39.3*	51	*43.0*	13	*31.7*	16	*48.5*	20	*34.6*
♀	74	*60.7*	63	*57.0*	28	*68.3*	17	*51.5*	30	*65.4*
Total:	**122**	***100.0***	**114**	***100.0***	**41**	***100.0***	**33**	***100.0***	**50**	***100.0***
at end ♂	12	*46.2*	0	.	0	.	0	.	1	.
♀	14	*53.8*	1	.	1	.	1	.	1	.
Total:	**26**	***100.0***	**1**	.	**1**	.	**1**	.	**2**	.
Observation years:										
1976	*1, 2, 3, 9;* ! ø		*1, 2, 3;* !, ø		*1, 2, 3;* ! ø		.		*1, 2, 3, 10;* ! ø □	
1977	!		.		.		.		*10;* ! □	
1978	!		.		.		*1, 2, 3;* ø		*10;* ! □	
1979	!		.		.		.		*10;* ! □	
1980	*1,2,3,4,7,8,9;* ! ● □		.		.		.		.	
1981	!		.		.		.		.	
1982	!		.		.		.		.	
1983	*1, 2, 3, 4, 7, 8;* ! ●		*4*		*4*		.		.	
1984	!		.		.		.		.	
1985	!		.		.		.		.	
1986	*1, 2, 3, 4, 7, 8;* !		.		.		.		.	
1987	!		.		.		.		.	
1988	!		.		.		.		.	
1989	*1, 2, 3, 4, 7, 8;* ! ●		.		.		.		.	
1990	!		.		.		.		.	
1991	!		*4*		*4*		.		*4*	
1992	*1, 2, 3, 4, 7, 8;* ! ●		*4*		*4*		.		.	
1993	!		.		.		.		.	
1994	!		.		.		.		.	
1995	*1,2,3,4,5,6,7,8;* ! ●		*4*		*4*		*4*		*4*	
Observation subject:	I n d i v i d u a l a n d p o p u l a t i o n f e a t u r e s									
	1. Nr. of indiv. *2.* Individ. size *3.* Sex ratio *4.* Mortality *5.* Growth of yearly rings *6.* Age *7.* Dieback *8.* Death causes *9.* Phenological differentiation in population		*1.* Nr. of indiv. *2.* Individ. size *3.* Sex ratio *4.* Mortality		*1.* Nr. of indiv. *2.* Individ, size *3.* Sex ratio *4.* Mortality		*1.* Nr. of indiv. *2.* Individ size *3.* Sex ratio *4.* Mortality		*1.* Nr. of indiv. *2.* Individ size *3.* Sex ratio *4.* Mortality *10.* Seasonal development of tree	

Observation methods and technics:
ø - measurement of tree dimensions; mapping; ! - conservation of identification number and photo-repers; ● - collect of tree section; □ - repeated photography.

tirely cut are separated by bands of primary forest. This primary forest was to ensure the regeneration of the forest on clearings by way of side seeding (Paczoski 1930, Zaręba 1958, 1968). The stands were cut around 1910, i.e. before the establishment of the National Park. Sallows here are mainly found in the secondary stand arising spontaneously and with a prevalence of old aspens and birches, under which a later generation of permanent forest components (*Carpinus betulus, Tilia cordata, Ulmus glabra* and *Acer platanoides*) grew up. However they also penetrated the primary stand (Fig. 5; Faliński, Canullo and Biały 1988).

Plot 87 Dziedzinka (with 41 sallow trees). A stand in forest compartment 401 changed by plundering takes of the most valuable specimens, but still with many old trees standing (*Quercus robur, Tilia cordata* and *Picea abies*). Sallow trees are mainly concentrated beside roads and cuts delimiting forest compartments, and in the vicinity of the southern boundary of the forest (Photos 4-6).

Plot 86 Łagiery (with 33 sallow trees). An old clearing in forest compartment 370, on which local inhabitants took shelter during wartime (Paczoski 1930, Zaręba 1958). Evidence of grazing is provided by the abundant presence of *Rumex obtusifolius* and other non-forest plants, and signs of long-term habitation include old apple trees among the pioneer *Salix caprea, Populus tremula, Betula pendula* and *B. pubescens*. As time passed, light-seeded pioneer tree species were ousted and replaced by permanent forest constituents (*Carpinus betulus, Acer platanoides, Tilia cordata* etc.). *Salix caprea* specimens are most abundant along the southern and eastern boundaries of the clearing from the primary forest side (Fig. 6).

Plot 91 Forest edge (with 26 sallow trees). This runs for 4 km along the northern boundary of the Białowieża Clearing, which emerged as an agricultural/settlement complex at the beginning of the 17th century, before developing up to the mid 20th century (Faliński 1966, 1968a) to cover an area of about 14 km^2. At the time the research began, the cultivated fields and meadows extended to the forest edge. However, the abandonment of the fields and their designation as buffer zone for the National Park allowed for the gradual development of secondary brushwood in the vicinity of the old forest.

The permanent marking of trees involved the affixing of a metal plate with a printed number to the trunk, at a height of about 2m from the ground. The number was also painted directly onto the bark of the tree, and its sex indicated using coloured paint on the trunk - with yellow representing males and red females.

The total of 336 studied trees included 135 males and 201 females. Young, non-flowering trees of unknown gender were not present at the time the research was first undertaken. All trees which could be found in the described conditions were alive. The only ones omitted occurred singly deep in the forest and beyond the designated permanent plots. Sallows were completely absent at the time from near-road areas in the northern half of the Park, i.e. in the area to the north of the orlowski road, irrespective of the forest community bordering on the road. The occurrence of sallow was linked exclusively with oak-linden-hornbeam habitats (*Tilio-Carpinetum*).

All the trees found and marked were measured for height and breast height diameter at the beginning of the study (1976, or 1978 on the Łagiery plot) and marked on a distribution map (Fig. 6). The number of trunks was also counted in the case of trees branching from the base. The gender of trees, their condition and habit were all determined in the flowering period.

Trees along roads (in permanent plot 102) were observed repeatedly, first after 4 years and then every 3 years – giving a total of 7 checks over 19 years if the initial monitoring is included. These occurred independently of the preservation of markings and the updating of the plan. Research on plots 150, 87, 86 and 91 was confined to the mortality of trees after 15 and 19 years, or 16 and 19 years, or else 17 and 19 years.

Observations made at this time included also checks on the state of health of the tree, classed as living, dying or dead. Noted at the same time were such phenomena as limited flowering, the drying-out of branches, the breaking-off of tops or crowns, the breaking of trunks below the crown or at the base and the uprooting of trees with roots. None of these phenomena (even the uprooting of trees) were universally associated with the immediate death of the tree. Cases were also reported of the creation of offshoots around fallen trees and the survival of trees in a secondary position (leaning, supported by other trees etc.). After the recording of actual death, attempts were made to obtain cores from trees with a view to determining tree age, rate of growth and onset of dieback on the basis of annual rings. Polishing of the surface of the core was followed by measurements of annual increments carried out three times with the aid of a BIOTRONIC increment-meter furnished with a stationary video camera and a special monitor. Final analysis was carried out on diagrams and tables drawn up on the basis of the appropriate computer program from the same firm. Measurements and analyses were carried out for cores from 47 trees, and hence for almost half of the 96 trees whose lives ended during the 19-year study. It was not possible to obtain appropriate cores from the remaining trees on account of the high degree of decomposition of the wood or else the disintegration of the trunk following a fall (Photos 5-6 and 7-12).

On the basis of the measurements described, and with account taken of the results of all direct observations, a special diagram was drawn up depicting the life history of each of the 47 trees (establishment, development, dieback, death and cause of death; Fig. 15). Using dendrochronological curves of growth increments, the years of establishment and death were determined, along with the period of limited increments in girth and the age of some trees whose deaths could have occurred in the period between observations. The remaining material is presented in Table 2 as well as in Figures 6-14. These relate to the entire studied population.

In addition, the phenological differentiation of the roadside trees (in plot 102) were studied in 1976 and 1980 using one-off photographic registration.

With the same aim in mind, the seasonal development of 26 selected trees (9 male and 17 female) occurring at the edge of the forest (plot 91) was observed at intervals of 5 days in the spring and autumn between 1976 and 1979. The degree of development was measured in spring by reference to the opening of leaf buds, flowering, fruiting, the fall of aments, and foliage, and in autumn by reference to yellowing and the shedding of leaves. As with phenological differentiation, the roadside population was also monitored for its development using a Practica LLC camera with Pancolor 1.8/50 objective to take whole-crown photographs, as well as a ZENIT-ES Foto-SNIPER with a TAIR PhS 4.5 300 mm teleobjective to take photographs of parts of crowns. The procedure in these cases was as described previously (Faliński 1977, p. 82).

Data from these studies are used here in a limited, but significant proportion. Research on the emergence and development of the younger populations of *Salix caprea* and their behaviour in the process of secondary succession will be the subjects of separate reports.

The basic results of the research presented in this work are derived from many observations and analyses of the annual growth increments of trees in the best-represented and most-acessible Roadside population (plot 102). On account of the similar abundances, efforts were made to maximize the use of data on the Kulisy population (plot 150). The results of the observations made on the three remaining populations were treated as supplementary only on account of their low abundance (less than 50 trees).

RESULTS

1. The state and structure of the 5 populations. Habits and state of health of individuals of *Salix caprea* in the first year of study (1976).

Population abundance and tree habits (Table 2, Fig. 7). All five studied populations consisted entirely of adult, flowering individuals. The Roadside population (plot 102) had 122 trees, of which 48 were male and 74 female. Corresponding data for the 4 other populations are contained in Table 2. Trees occurring in the vicinity of roads in closed stands of *Tilio-Carpinetum* (plot 102) differed from those in the remaining populations in their tall, well-shaped single trunks. In this population only 2 trees had 2 trunks, while 3 branched at a height of 1 m above the ground and 1 had 5 trunks (total 5% of all trees).

In the remaining populations in which trees developed freely without restraint imposed by other, older trees, the fraction of trees with 2 or more (up to 7) trunks was rather greater. In turn, in the Kulisy population which arose earlier under the

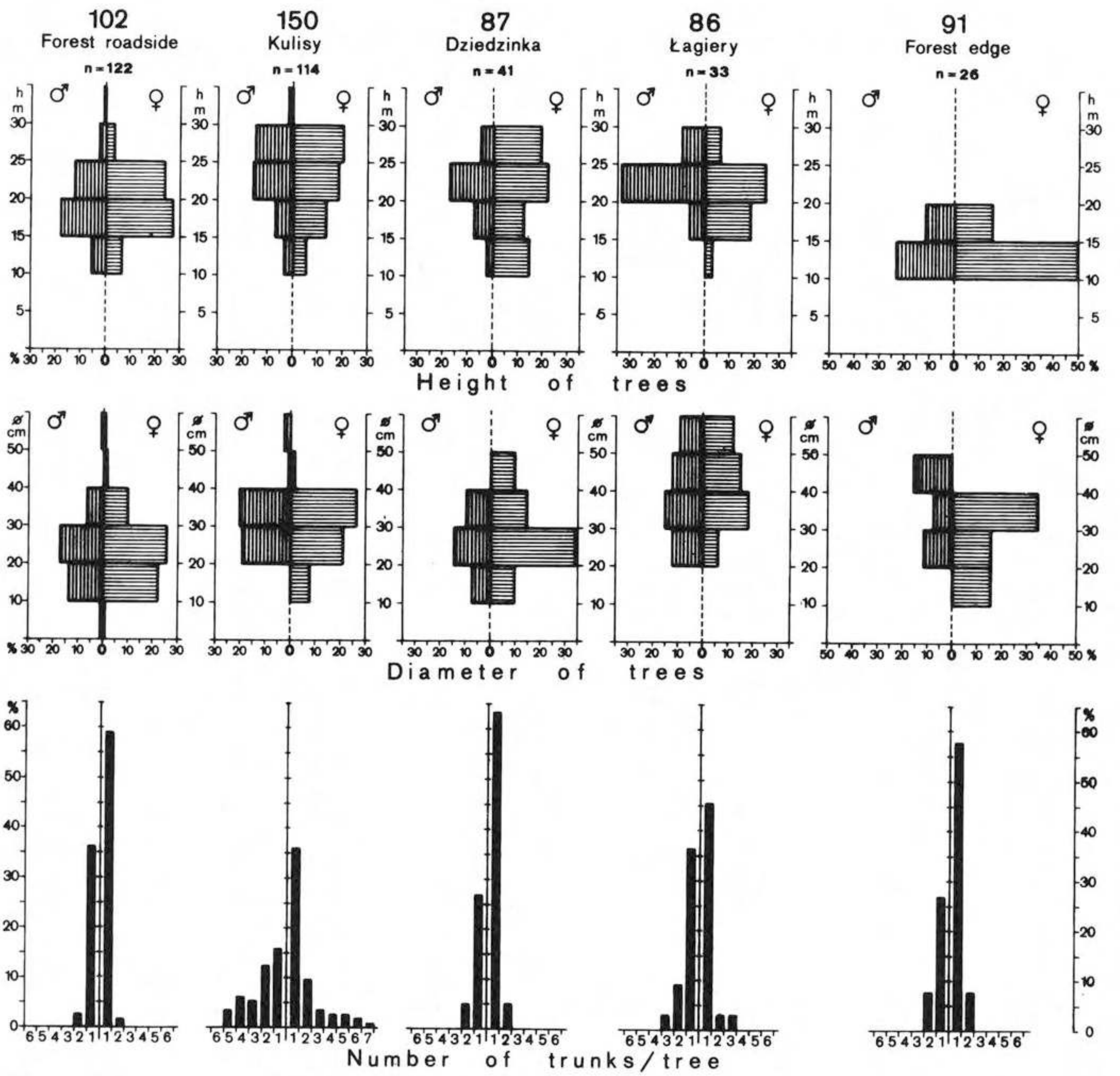
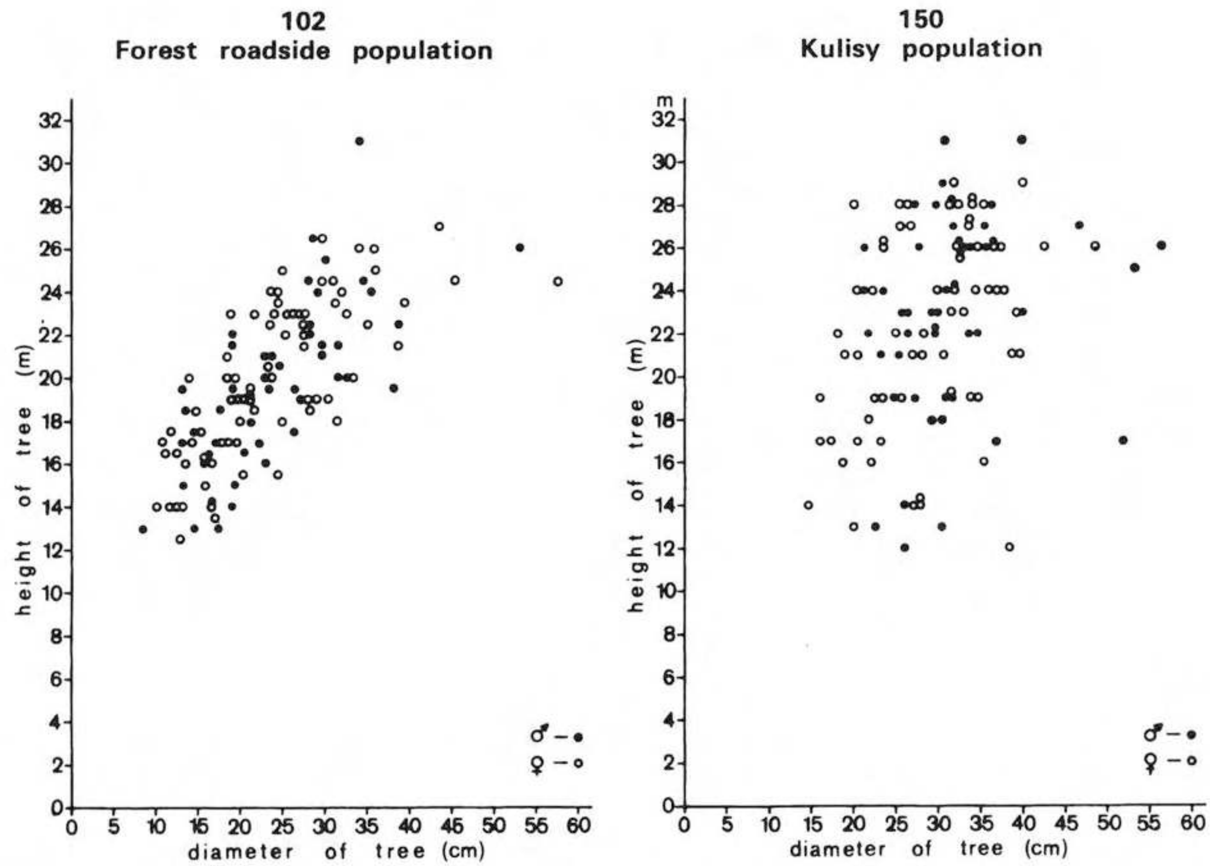


Fig. 7. Individual size and sex structure in the 5 *Salix caprea* populations.
Data from beginning of observation period.
Source: orig.



sex	n	Correlation coefficient	Stnd. Error of Est.
♂	48	0.716**	2.729
♀	74	0.741**	2.487
♂+♀	122	0.728**	2.575

significant correlation $^{**}P<0.01$

sex	n	Correlation coefficient	Stnd. Error of Est.
♂	49	0.207°	4.510
♀	65	0.395*	4.307
♂+♀	114	0.322*	4.381

significant correlation $^{**}P<0.05$; ° - not significant

Fig. 8. Correlation between tree height and diameter in two *Salix caprea* populations.
Dependent variable: height of tree.
Source: orig.

influence of herbivores, almost half of the total number of trees (49%) had between 2 and 7 trunks (Fig. 7 below).

Gender percentage (table 2). **Sex ratio of the population**. All five populations consisted solely of mature individuals whose gender could therefore be determined. Female specimens prevailed (accounting for 52% in the Łagiery clearing population, about 61% in the Roadside population and up to 68% in the previously-cut forest of the Dziedzinka plot; see Table 2).

The sex ratios showing this predominance of females were:
1:1.1 for the Łagiery population (plot 86);
1:1.2 for the Kulisy population (plot 150);
1:1.5 for the Roadside population (plot 102);
1:1.9 for the Forest edge population (plot 91);
1:2.2 for the Dziedzinka population (plot 87).

Size structure of individuals in the population (Figs. 7 and 8). **Sexual dimorphism**. The heights of individuals measured in the first year of observation were between 3.5 and 32 m, while trunks had diameters of between 10 and 61.5 cm. The greatest maximal and average heights were reached by *Salix caprea* trees in the two most abundant populations (Roadside and Kulisy). These populations showed the closest positive correlation between height and diameter (only the diameter of the thickest trunk, Fig. 8). Sexual dimorphism was poorly marked where the features "height of tree", "trunk diameter" and "tree habit" were concerned. However, reference may be made to the cases of the two most abundant populations in which male trees were on average larger and thicker than females, while the females of the Kulisy population are also more often and more markedly branched at the base.

In the first year of observation the trees showed themselves to be in good condition, with well-developed trunks and crowns (without many breaks) and a good state of health (as witnessed by abundant flowering and fruiting). In the Roadside population (plot 102, Fig. 9), only 3 trees were of more limited health (with some branches dying and weaker flowering). In addition, 8 dry trees grew by roads. It was not possible to define the years in which these died, so they were omitted from the marking procedure and from further research. In the remaining populations, the fractions of trees of less good health or else showing dieback were higher (from 6% in the very abundant Kulisy population to 12% in the smaller populations).

2. Mortality in the population. Causes of death among particular trees (Figs. 9 and 10).

Mortality was high in all the studied populations of *Salix caprea* trees, affecting between 79 and 99% of observed trees in the different populations over the 19 years of the study. That said, the lowest mortality was in the Roadside population and the highest in the Kulisy population. In relation to this, at the end of the period of observation, the Roadside population retained 26 living trees or trees affected by dieback (Fig. 9), while the other populations had 1 to 9 trees strongly affected by dieback and in the form of stumps.

Data from the Roadside area showed that the main direct cause of the deaths of 46% of the total of 96 trees dying in the 19 years was the breaking of the trunk at the base of the crown or below it. About 20% of trees died after being uprooted (Fig. 10). Both causes of death occurred similarly in male and female trees. However, in the case of the rarer cause of death from gradual dieback, there was a preponderance of cases affecting male trees (about 30% of all the trees studied).

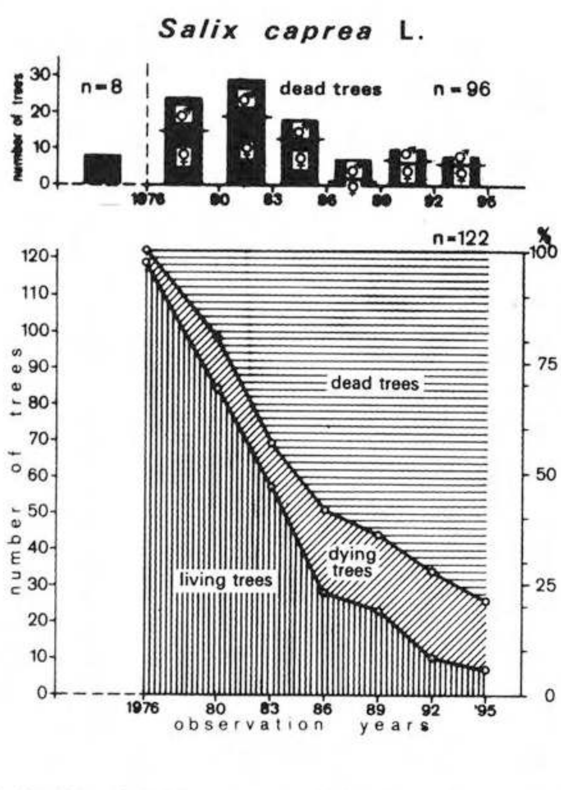


Fig. 9. Decline of *Salix caprea* population over 19 years from 122 trees at beginning of observation (1976) to 26 trees at end (1995). Above: total mortality between consecutive observations. Below: present population longevity. Data from roadside forest population. Source: orig.

3. The course of extinction (Figs. 9 and 11). **Changes in the sex ratio** (Fig. 12).

The rate of extinction in the roadside population was observed regularly and was higher in the first half of the study period (Figs. 9 and 11). Extinction had affected more than half of all individuals over 10 years. The years 1976-1986 saw 7 trees die each year on average, albeit with the highest mortality rate being noted for the period 1980-1983, when an average of 10 trees died each year. The rate of extinction of female trees was higher throughout than that of male trees, but groups of male and female individuals considered separately showed similar trends to the whole population. The effect of the uneven rate of extinction of trees of the two sexes was to change the sex ratio from a predominance of males to a state of near-balance between the sexes (Fig. 12).

4. The proportion of trees undergoing dieback in the population (Figs. 9 and 11).

The progress of the process of extinction of trees was associated over the 19 years of study with absolute and relative rises in the proportions of trees undergoing steady dieback. At the beginning of the observation period, such trees represented 2.5% of the total, but by the mid-point some 45% of trees were affected, and by the end some 73% (Figs. 9 and 11).

Dieback manifested itself in the death of parts of branches and even part of the crown, in limited flowering, in the drying-out of some aments prior to their development and in the shedding of female aments prior to the maturation of fruits.

These behaviours were also reflected in limitations on the increase in the girth of the trunks, as shown from cores obtained after the death of trees (Fig. 15). Among the 47 cores obtained, this phenomenon was observable in 15 out of 17 males and in 28 out of 30 females. More than 91% of the trees studied from this point of view were therefore affected, and the degree of limitation to growth in girth was such that some years recorded only 1/15 of the maximal growth achieved in favourable years.

The period of limited growth in girth generally outstripped limitations to the healthiness of trees, and hence steady dieback was observed directly in particular trees. The period of limited growth in girth (radial growth) even lasted for 16 years in some trees, although 5-10 years prior to death was more usual (Photos 7-12).

5. Survivorship of trees. Age of dying trees (age at the moment of death; Figs. 13, 14 and 15).

Information on the age at death is available for the same number of trees (47; Figs. 13 and 15). The oldest tree was at least 74 years old, but was female specimen (see Fig. 14; also tree no. 114 on Fig. 15). The oldest male individual was at least 58 years old (see tree no. 39 on Fig. 15). However, the mean ages of male and female trees at the moment of death did not differ significantly and amounted to 48 and 51 years respectively. More than half of the sallow trees in the Roadside population reached ages of more than 50 (maximum in 50-60 class; Fig. 13).

The ages of particular trees calculated on the basis of the number of annual growth increments is in fact the minimal age, which may very likely be extended by between 2 and 5 years (c. 3 years on average). The year the tree began to grow must therefore be put back accordingly (Fig. 15). The reason for this phenomenon reflects a property of soft-wooded trees (of which *Salix caprea* is one). These species do not lay down clear annual rings, especially in their first years of development. Furthermore, the preservation state of wood often makes it difficult to read the growth rings from the last years of life, i.e. in the dying phase.

Account should also be taken of the fact that a certain number of the earliest and oldest trees had already disappeared prior to the onset of long-term observations in 1976. Such trees could have been destroyed in an early phase of development by the last herbivores seeking whatever food they could

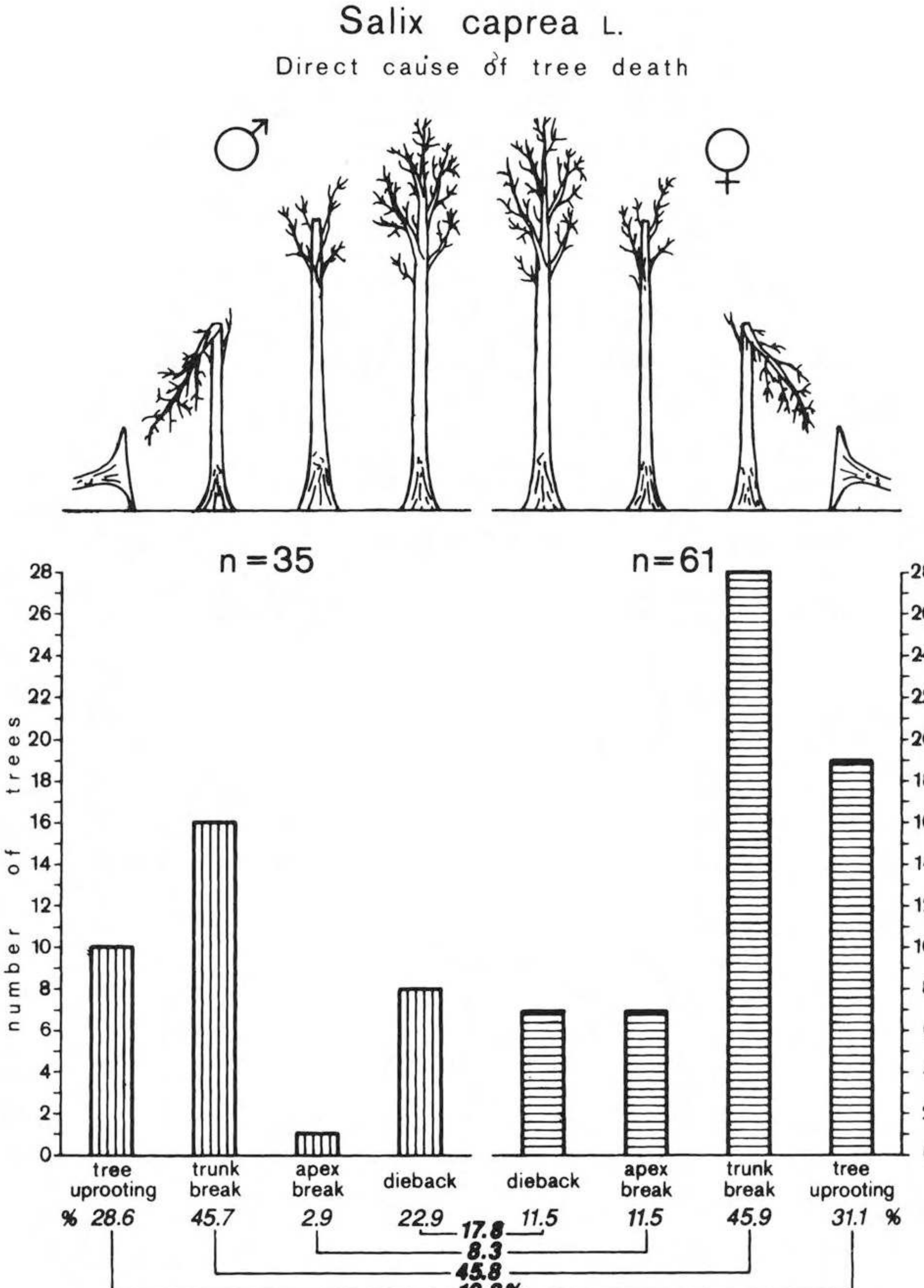


Fig. 10. Direct causes of death of sallow *Salix caprea* in roadside population situated near forest roads running across deciduous forest *Tilio-Carpinetum* community in Białowieża National Park over 19 years.
Source: J. B. Faliński (1990) augmented.

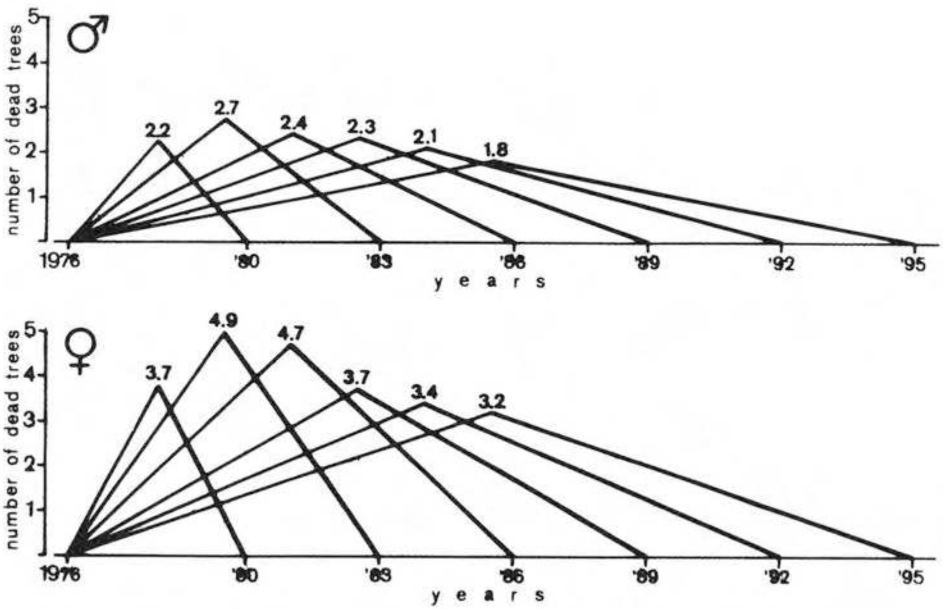


Fig. 11. Changes in intensity of decline of roadside population of *Salix caprea*. Mean number of dead trees/year over diverse time intervals. Source: orig.

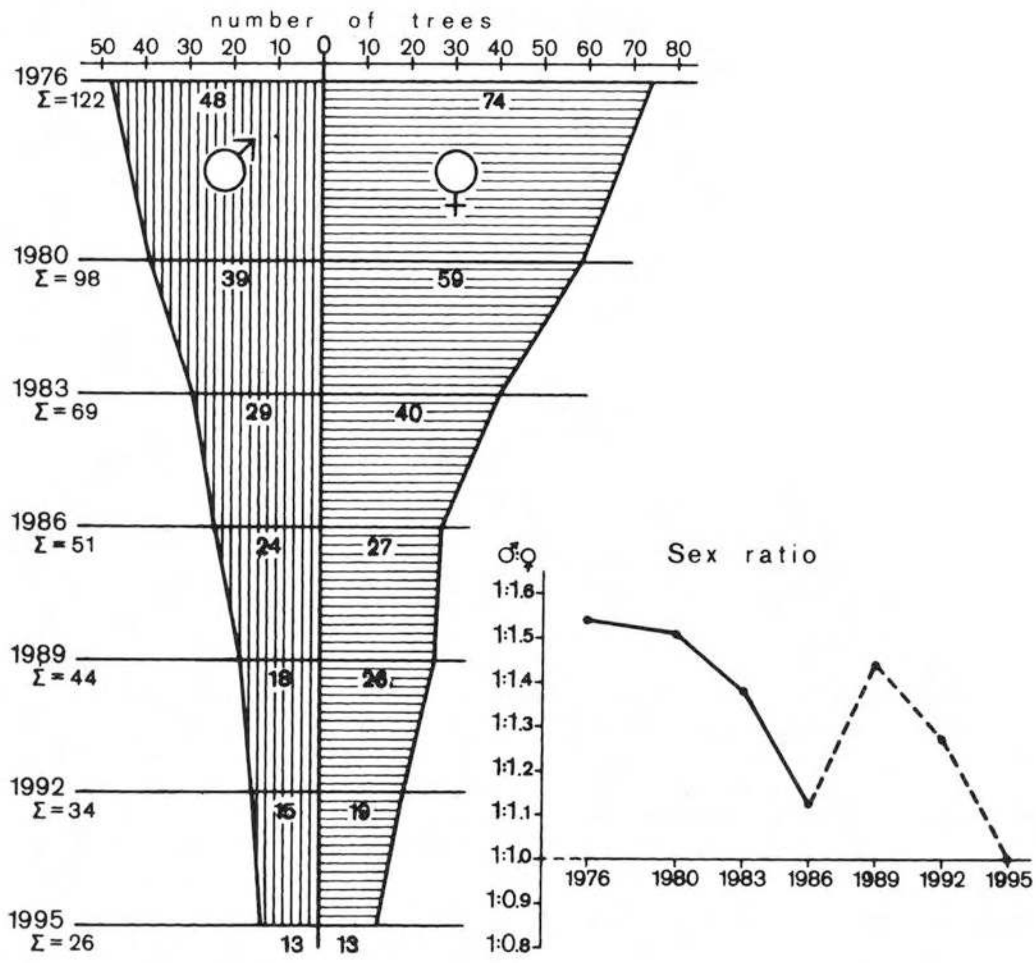


Fig. 12. Changes in sex structure in roadside *Salix caprea* population as a result of tree death.
Changes in secondary sex ratio (1976... 1986) only possible to interpret in the presence of large numbers of individuals (50).
Source: orig.

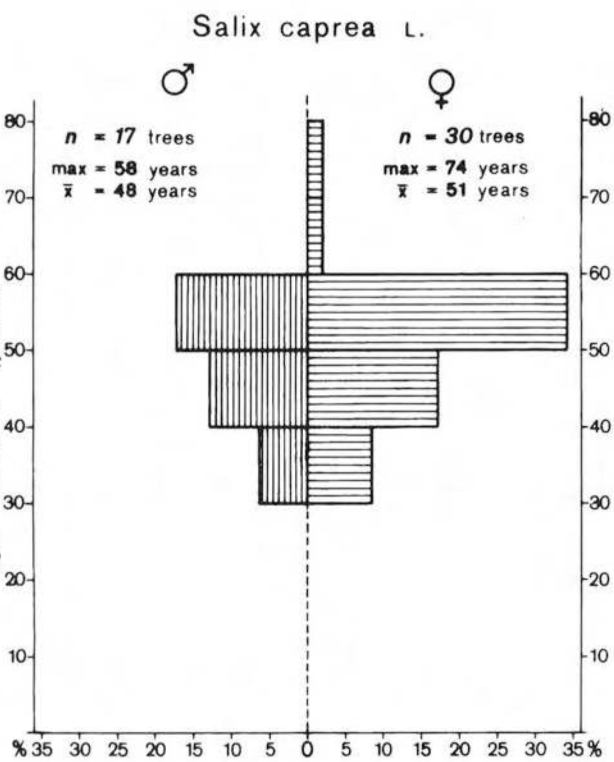


Fig. 13. Individual age of *Salix caprea* trees (and) in year of death. Data from roadside population collected between 1976 and 1995 (see also Fig. 15).
Source: orig.

find in the devastated forest. After all, sallow (bark and stems) has always been a favourite food of all herbivores, including European bison.

In the light of this, the present and now-declining Roadside population must have arisen and developed in conditions of zero or very limited zoogenic pressure. The appearance of sallow and other light-seeded trees must have been preceded by an invasion of spruce, which is not readily taken by animals and which therefore easily occupied all free space beneath the devastated broadleaved trees and shrubs (compare with observations from the time by K. Wróblewski – Table 1).

Speaking for the development and growth of sallow in conditions of zero or later limited pressure from animals is the habit of trees from the Roadside population, which are almost exclusively tall trees.

DISCUSSION

1. The time of emergence and conditions of development of the pioneer population of sallow.

Combining the results of direct, long-term observations of the process of the disappearance of *Salix caprea* populations from the forest with reconstructed dendrochronological data, it is possible to establish the time and conditions of the emergence and development of the population of sallow *Salix caprea* in forest of primary origin but subjected for about 22 years to very strong herbivore pressure (Figs. 1 and 15). This pressure increased from year to year before disappearing abruptly during the First World War, when uncontrolled shooting removed virtually all the larger herbivores, both native (red deer, roe deer, moose, wild boar and bison) and introduced (fallow deer). The regeneration of the oak-linden-hornbeam community (*Tilio-Carpinetum*) – subjected previously

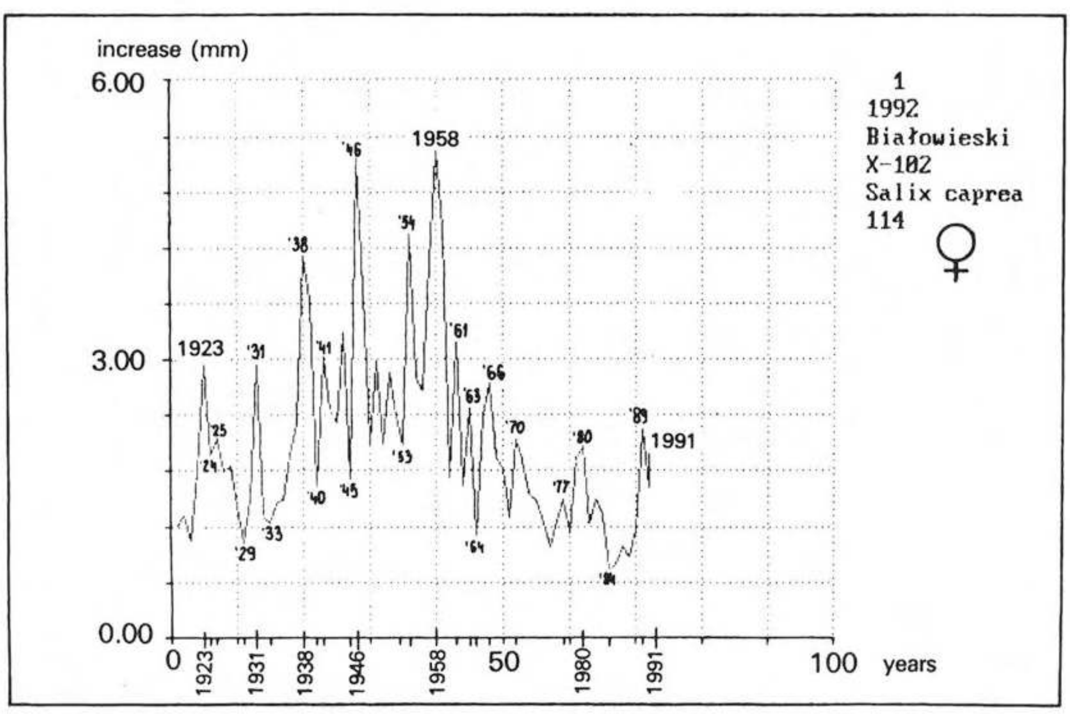


Fig. 14. Course of yearly growth of oldest sallow *Salix caprea* in roadside population: tree: No. 114 :74 years; 1918-1992 (see also Fig. 15).
Source: orig.

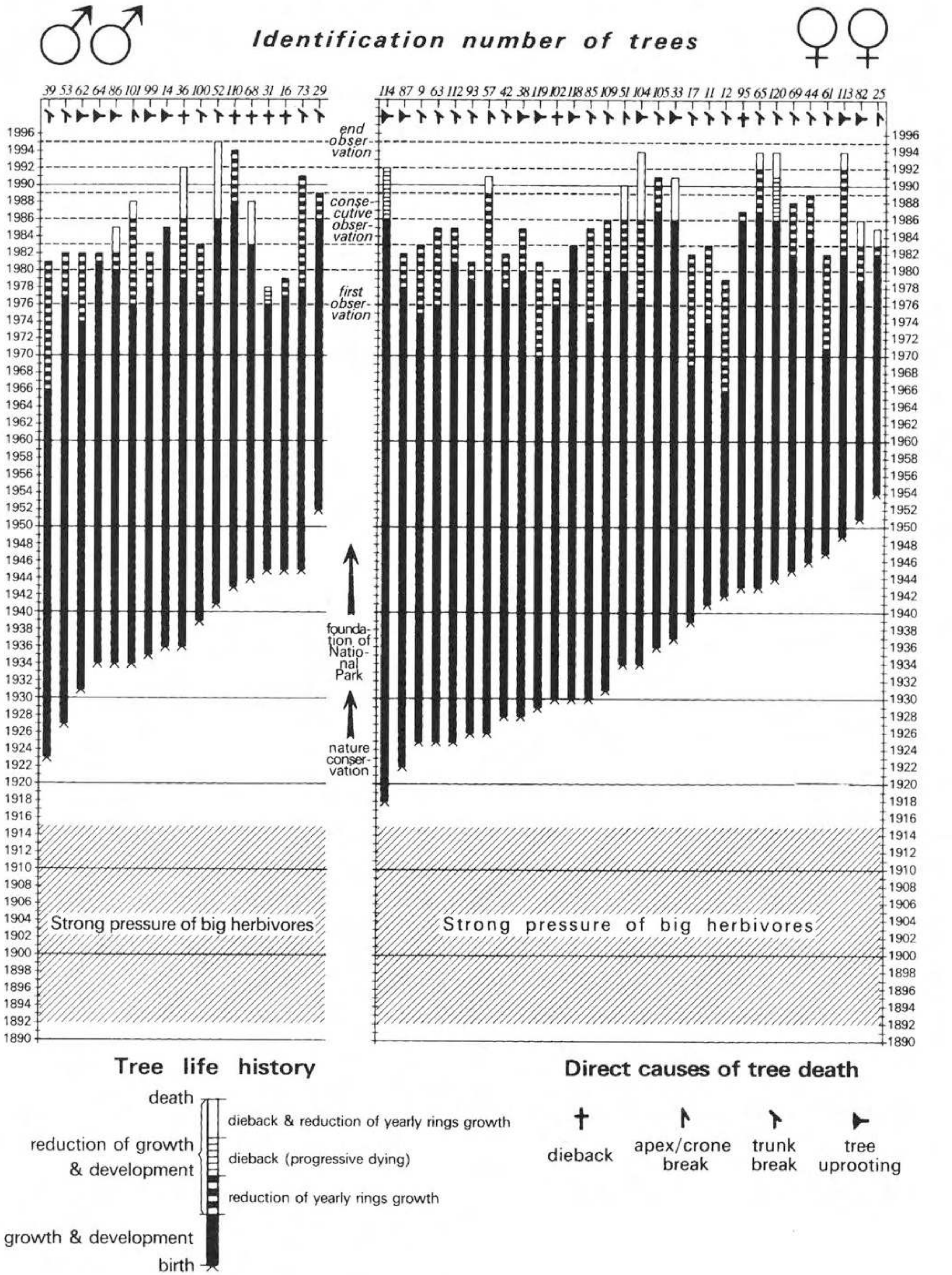


Fig. 15. *Salix caprea* life history with causes of death of 17 male and 30 female trees during forest regeneration. Data from permanent observations and yearly ring analysis in roadside population.
Source: orig.

to herbivore pressure, was then able to progress for a while in the absence of such pressure and then during the time that such animals made their first attempts at reintroduction (e.g. red deer in 1936; Pucek 1968). This coincided with the first protection of this part of the Białowieża Forest in a Forestry Reserve and then (from 1932) in the National Park.

The appearance of sallow (*Salix caprea*) and other pioneer tree species (*Populus tremula, Betula pendula, B. pubescens* and *Alnus glutinosa*) in the process of regeneration must have occurred following the disappearance of herbivore pressure (Fig. 1). This results from data on the age structure of the Roadside population (Fig. 13), as well as from analysis of data on the year of establishment of particular trees, which show a first phase mainly in the years 1918-1934 (Fig. 15). This should probably be moved back by several (2-5) years, in the light of critical adjustment to data on the age of trees at death in the well-formed cross-sections obtained from single trees with preserved bark (see "Results" point 5).

One of the responses of trees, especially willows, to browsing at an early age is to create many trunks from the base. Such characteristics are possessed by almost half of the trees in the Kulisy population (see Fig. 7 and "Results", point 1). This population – or at least the greater part of it – arose earlier than the Roadside population, after 1910 on the Kulisy cut area (Figs. 5 and 6). Pointing to its earlier origin is the higher rate of mortality and rate of dieback, leading to its complete elimination before the end of the observation period (see Table 2).

2. The influence of the presence of pioneer species of tree on the course of the process of regeneration of forest communities.

The material collected allows for a precise description of the behaviour of sallow up to its gradual extinction as forest regeneration proceeds. Direct conclusions may also be drawn regarding the influence of this very abundant population on the course of the regeneration process. Above all, sallow and other light-seeded species limited the invasion of spruce in many areas, or else accelerated its self-thinning (Figs 2 and 5). In turn, in each case, the canopy of pioneer tree species provided a place for the permanent components of the forest: hornbeam, linden and elm (*Ulmus glabra*), and for their growth along with the growth of the pioneers. This was balanced by the creation of conditions for the filling of small gaps in the stand which arose gradually as the pioneer trees occurring initially in many large aggregations began gradually to die and fall (Fig. 6). This remark refers to a greater degree to the role of sallow on large clearings in the forest interior (Łagiery and Kulisy), where the long-term presence of this pioneer prevented the return of the stand's final constituent species.

3. The desintegration and colonization of rotting trees as a factor in the secondary differentation of the forest floor

Sallow trees dying back slowly first lose their branches and tops, later their boughs and crowns and finally break into transverse or longitudinal pieces which decompose quite quickly on the forest floor in a process conducted by cryptogamous plants, fungi and invertebrates. In spite of the considerable areas on which they grow, the synusia formed by these organisms differ quite clearly from the analogous groupings arising on the forest floor following the death and fall of trees of other species. They gather more on the broken fragments of pieces of wood, rather than on the fallen logs as in the case of linden, maple and hornbeam. In turn, the rapid progress of decomposition ensures that the synusia associated with sallow are less permanent than those working on the lying logs of other pioneer species like birch, or particularly aspen (Photos 5-6).

4. The decomposition of sallow litter

Similarly less permanent is the litter formed from sallow leaves. Its decomposition probably proceeds together with the rapid breakdown of the litter of linden and hornbeam (Dziadowiec 1987). Thus it is not retained on the forest floor for as long as the litter of aspen and is most probably not a source of secondary hydrophobia in the accumulation-humus layer of the soil (Faliński, Canullo and Biały 1988). Sallow litter is also a less rich source of nutrients, and particularly of phosphorus compounds, than the litter of alder (Marek 1965).

5. Other significant aspects of sallow in the forest.

In the past, abundantly-occurring sallow represented insects' earliest source of pollen and nectar – appearing long before those of other entomogamous trees (*Acer platanoides* and *Tilia cordata*). They may also have been used by honeybees still residing in numerous specially-excavated holes in pine, oaks, linden, etc. This despite the official liquidation of the practice in Białowieża Forest on the day before the forests became the hunting park of the Tsar (Karpiński 1948).

Apart from single observations, the literature on the regeneration of forest communities is lacking in data on the behaviour of sallow. This is a result of the destruction of the species by herbivores in the youthful phase of growth before entry into the stand, as well as of the removal of old trees in the course of the cultivation and exploitation of stands. In the Mediterranean area, where the role of anemogamic pioneer species of tree is in general significantly more limited (Pignatti 1982, Martini and Paiero 1988), single specimens of *Salix caprea* are found almost exclusively in the floors of the very numerous karstic gullies and by the edges of deep, dry gorges, within the range of beech and oak-hornbeam forests (e.g. on Promontorio del Gargano, Italy; Faliński and Pedrotti 1990, Faliński 1996 – in press).

CONCLUSIONS

1. The freeing of communities of mesoeutrophic broad-leaved forests (*Tilio-Carpinetum*) from strong, if short-lived, herbivore pressure, brought an end to the process of degeneration and activated the process of regeneration. In this process a fundamental role was played by light-seeded pioneer trees like *Salix caprea, Populus tremula, Betula pendula* and *B. pubescens*, as well as locally *Alnus glutinosa*.
2. The replacement and development of the populations of *Salix caprea* and other light-seeded species took place in conditions of very strong thinning of stands, destruction of the undergrowth and deformation of the ground cover layer, as well as limitation to the reproduction of broad-leaved trees. However, it happened after the dramatic invasion of spruce which accompanied the progressive degeneration of the community brought about by strong herbivore pressure.
3. *Salix caprea* and other light-seeded pioneer species in particular colonized gaps in the stand near crossroads and

there created aggregations of between 10-20 and several tens of trees. The emergence of the Roadside population happened in the years 1915-1934, and its further development took place in the period when the forest was brought under strict protection in a reserve and later in the National Park.

4. The freeing of the forest from strong grazing pressure also allowed for the development and increased abundance of populations of *Salix caprea* established earlier on cleared areas (the Łagiery clearing – X-86; the cut area Kulisy-X-150) and in forest heavily plundered by cutting of the most valuable trees (Dziedzinka X-87). The population on the forest edge (X-91) probably developed as a result of the fencing-off of the forest edge on the Białowieża Clearing side following the creation of the National Park.

5. The almost 20 years of observation (1976-1995) on permanent plots and marked individual trees coincided with the final phase of the retreat of willows and the extinction of all five of the studied populations. The 2 oldest populations (Kulisy and Łagiery) disappeared, along with 95% of the rather younger Roadside population. The process of the extinction progressed faster in the first period of the extinction than in the second. Its final completion is close, because there is a continued rise in the numerical prevalence of weakened trees in a state of dieback.

6. Sallow trees are dying out as the forest regenerates and most often when they attain ages of 50-60. However, some persist for as many as 74 years. The death of a tree is usually preceded by its gradual dieback, expressed through the breaking of branches and the top and the limitation of flowering and fruiting. It is also clear in cross sections of dead trunk as a reduction in annual growth increments over the 4-8 last years of life. In conditions in which the forest is relieved of most grazing pressure, sallow achieves a habit of the kind typical of forest trees (a height of 28 or even 32 m; a single tall and slender trunk ending in a small, compact crown and a well-developed bark). In contrast, sallow affected by browsing in the earlier years creates two or more (up to 7) trunks at the base.

7. The remaining live trees in the abundant roadside population were still (at the time the research began) characterized by well-marked phenological differentiation. This was manifested in the proportion of individuals of both sexes which developed early and late – in a manner analogous to that observed in populations of oak, ash, maple etc. A similar phenomenon also occurs in autumn in the season of the yellowing and shedding of leaves. Differences in the period of flowering of trees were of such an order that it might be treated as a manifestation of strategy safeguarding some individuals in the population from spring (or autumn) freezing. This phenological differentiation extends the process of pollination (with the possible genetic consequences). In consecutive years the phenological differentiation of the studied population was less and less visible considering the progressive dieback of an ever-greater number of individuals.

8. The constant decline in the populations combined with the more rapid extinction of females to give gradually increasing differences in the proportions of males and females. The sex structure in the Roadside population was characterized by a sex ratio of 1 male to 1.5 females. In the course of the 19 years this declined to approximately 1:1. In the first 10 years this fall proceeded steadily, but after the decline in numbers to 50 individuals the value of calculating consecutive sex ratios is questionable. Nevertheless, the continued trend towards the evening-out of the sex ratio is obvious. Also disappearing steadily in the course of the extinction is the sexual dimorphism in features like "size of tree", "diameter of trunk" and "number of trunks arising from the base".

9. The disappearance of old populations of *Salix caprea* was not associated with the appearance of young individuals. An exception is the Forest edge population, in which a few new individuals did appear, most probably as a result of changes in use, followed by the abandonment of fields and meadows adjacent to the forest.

10. The exceptionally high level of survivorship (continued good condition and longevity) of sallow *Salix caprea* and other light-seeded trees (*Populus tremula, Betula pendula* and *B. pubescens*) ensured the development under their canopy of a new generation of the permanent constituents of the forest (*Carpinus betulus, Tilia cordata, Acer platanoides* and *Ulmus glabra*). However there is a possibility of the transitory delaying of the sequence of species (e.g. the development of a second generation of permanent constituents), as well as of the reconstruction of the primary structure of the undergrowth and herb layer as a result of the slow decomposition of the accumulated leaf litter of light-seeded trees, particularly aspens.

11. The results of the present research confirm the previously-developed prognosis (Faliński 1986a, 1991) concerning the rapid completion (in the course of 20-30 years) of the process of regeneration of fragments of forest habitat in Białowieża National Park which had been subject to intensive if shortlived zoogenic pressure. The regeneration of forest communities destroyed or completely transformed by cutting or uncontrolled felling lasts about 30-50 years. Conservatorial protection of forests subjected previously to strong zoogenic and anthropogenic pressure favours the regeneration process.

12. The results of the research done confirm the validity of statements regarding the strongly-developed pioneer properties of willows, in particular the sallow *Salix caprea*. Marked in the process of forest regeneration are the roles of all 10 biological properties ascribed to willows (Fig. 4). There is no doubt that the longer-term persistence of sallow in forest communities is determined by its well-developed morphological plasticity in the face of the action of biocoenotic factors, including the impact of herbivores and the development of permanent constituents of the stand in the vicinity of, or beneath a canopy of, pioneer trees. In favourable conditions, the sallow reveals a physiological potential which allows it to attain a height, permanence and habit close to that attained by other pioneer species (aspen, birch and alder) and even a permanent constituent of the forest like hornbeam.

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WYMIERANIE POPULACJI *SALIX CAPREA* L. W TOKU REGENERACJI LEŚNEJ PO SILNEJ PRESJI ROŚLINOŻERCÓW

STRESZCZENIE

Zbiorowiska lasów liściastych poddane silnej presji wielkich roślinożerców ulegają degeneracji. Z chwilą ich uwolnienia od tej presji dochodzi do głosu regeneracja zbiorowiska. W regeneracji leśnej duża rola przypada wierzbie *Salix caprea* i innym pionierskim lekkonasiennym gatunkom drzew (*Populus tremula, Betula pendula, B. pubescens*).

Regeneracja z udziałem *Salix caprea* zachodziła po objęciu zdegenerowanych zbiorowisk leśnych ochroną konserwatorską w rezerwacie, a następnie w Białowieskim Parku Narodowym. Powstanie i rozwój populacji *Salix caprea* nastąpił po okresie inwazji świerka, który przypadł na okres wzmożonej presji zwierząt na las liściasty. *Salix caprea* wypełniła wszystkie luki w drzewostanie powstałe wskutek zniszczenia drzew i podrostu przez roślinożerców (w latach 1892-1915). Wystąpiła też masowo na starych, jeszcze nie opanowanych przez las, polanach i porębach.

Salix caprea utworzyła w tych miejscach bardzo liczne populacje, a poszczególne drzewa osiągnęły dobrą kondycję, pokrój typowy dla drzew leśnych i wysoki wiek. Większość drzew w chwili śmierci osiągnęła 50-60 lat, a pojedyncze drzewa do 74 lat. Proces wymierania populacji iwy, obserwowany w ciągu 19 lat na stałych powierzchniach i znakowanych drzewach, przebiegał bardzo szybko, zwłaszcza w pierwszym dziesięcioleciu obserwacji i doprowadził do niemal całkowitego wycofania się iwy ze zbiorowisk leśnych Białowieskiego Parku Narodowego. Śmierć poszczególnych drzew poprzedzona jest przez ograniczenie ich żywotności i rocznych przyrostów w ciągu 4-9 ostatnich lat życia.

Wraz z wymieraniem populacji zatraciło się stopniowo jej pierwotne zróżnicowanie fenologiczne i uległa zmianie struktura płciowa populacji; od przewagi drzew żeńskich do niemal równego udziału drzew obu płci.

Rozwój populacji trwałych składników lasu (*Carpinus betulus, Tilia cordata, Acer platanoides, Ulmus glabra*) pod okapem drzew lekkonasiennych i nie wykształcenie się nowego pokolenia gatunków pionierskich znamionuje rychłe zakończenie procesu regeneracji w zbiorowiskach leśnych Białowieskiego Parku Narodowego.

SŁOWA KLUCZOWE: dynamika lasu; pionierskie gatunki drzewiaste; wymieranie populacji; rozwój populacji; degeneracja zbiorowiska leśnego; regeneracja zbiorowiska leśnego; oddziaływanie roślinożerców na las; *Salix caprea*; Puszcza Białowieska.