# The biology of Pleurospermum austriacum (L.) Hoffm. in a relict locality of the Kashubian Lake District

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#### ABSTRACT

A local lowland population of the mountain species, *Pleurospermum austriacum* was studied. The population's spatial structure was of a cluster type. The population size, density and age-structure revealed spatial diversity and variability in time. The main reason for the instability of these traits was the changeable occurrence of generative individuals in the respective years. The reproductive tactics of the studied monocarpic perennial are characterized and its chances of survival in this locality are evaluated.

Key words: Pleurospermum austriacum, reproduction tactics, age-structure of population

#### INTRODUCTION

Pleurospermum austriacum is an European species which grows mainly in the mountains and on a few, mainly isolated and relict, lowland localities (Szafer 1930, Meusel et al. 1978). In Poland this is a rare plant (Środoń 1970), which has been included on the list of rare and endangered plant species of this country (Jasiewicz 1981). In Pomerania, about 26 of its localities, which create a relict distribution island, formed in the late glacial after the recession of the last glaciation (Czubiński 1950, Środoń 1970), are known.

For this study, a locality of this species in the Radunia River Gorge Nature Reserve in the Kashubian Lake District (Fig. 1) was chosen. *P. austriacum* grows here on steep slopes of the river valley in the company

of several other mountain species. This is an exceptionally abundant, for a lowland locality, populaton with a clustery spatial structure. The environmental conditions in which it is found (Table 1) are similar to the conditions prevalent over most of the species' stands in Pomerania (see Herbichowa and Herbich 1982, Markowski and Chojnacki 1982, Piotrowska and Stasiak 1982).

Selected traits of the population structure and reproduction were studied and the chances of *P. austriacum* surviving in this locality evaluated.

# **METHODS**

The study was conducted in 1970-1972 and in 1980 on 4 permanent plots encompassing the largest clusters of the local population (Table 1).

Flowering and fruiting were studied in 1971 and 1972. Five developmental stages were distinguished: flower bud, flowering unripe fruit, ripe fruit and

Table 1
General description of the permanent plots

	Plot	Α	В	C	D		
Number of forest section		96	96	95	82		
Plot area		48 m <sup>2</sup>	36 m <sup>2</sup>	48 m <sup>2</sup>	40 m <sup>2</sup>		
Exposure		SEE	W		NW		
Slope inclination		35°	45°	40°	30°		
Soil	type	brown soil					
	pН	7.0	6.5	7.0	5.5		
Plant	association	Stellario-Carpinetum					
community	subassociation	typicum	deschampsietosum	typicum	deschampsietosum		

fruit shedding. The number of individuals in each stage was determined every 5-8 days. The phenological spectra and calendar of flowering and fruiting were drawn up according to the principles accepted by Falińska (1972, 1973).

Germination was tested in a Jacobsen germination apparatus and on damp filter paper in Petri dishes. Under natural conditions, mericarps were sown at a depth of 1 cm on  $15 \times 15$  cm plots from which the herb layer and litter had been removed. The experiments were conducted in replicate. In Spetember 1970, 100 mericarps, collected several days earlier, were sown per plot over 4 plots, 4 other plots were left as controls. In April 1972, mericarps collected in September 1971 were sown. They had been stored indoors and about 3 weeks prior to sowing, part of them had been placed in a freezer  $(-4^{\circ}C)$ . Fifty mericarps which had not been frozen were sown

on 4 plots, on the next 4, 50 frost-treated mericarps were planted: 8 plots remained as controls.

The age structure of the population was studied in 1972 and 1980, using the age state method worked out by Rabotnov and Uranov (see Smirnova et al. 1976, Gatsuk et al. 1980). Five age-stages in the ontogeny of *P. austriacum* were determined: seedlings, juveniles, immatures, virginiles, reproductives. The number of plants in each group on the permanent plots was determined, next the age-state spectra were plotted.

# RESULTS

# THE POPULATION NUMBER AND DENSITY

The numbers and densities of *P. austriacum* individuals in the plots were highly variable (Table 2). In 1972, 8 and 16 times more individuals

Table 2

Number of *Pleurospermum austriacum* individuals and their density in plots

Year	Plot	Total		Reproductives		Seedlings		
		number	per 1m <sup>2</sup>	number	per 1m <sup>2</sup>	number	per 1m <sup>2</sup>	
	A	32	0.7	8	0.2	7	0.1	
1972	В	34	0.9	6	0.2	7	0.2	
15.72	C	248	5.2	8	0.2	2	0.04	
	D	538	13.4	10	0.2	122	3.0	
	A	139	2.9	1	0.02	93	1.9	
1980	В	154	4.2	0	0.0	55	1.5	
	C	703	14.6	3	0.06	303	6.3	
	D	265	6.6	0	0.0	28	0.7	

were noted on plots C and D, respectively, than on plots A and B. The density per m<sup>2</sup> was also higher by 7 and 15 times.

In 1980 the differences between the population numbers and densities of the plots were smaller. On plots A and B, which 8 years previously had been distinguished for their low density, a 4-fold increase in population number had taken place. Also, the number of individuals on plot C increased 3-fold, while on plot D, where the density had been the greatest in 1972, it decreased by a factor of two. These data point to the lability of the discussed traits in different sites of the local population.

# FLOWERING AND FRUITING

P. austriacum is a monocarpic perennial which propagates itself exclusively through generative reproduction. Its short, vertical rhizome annually forms

several basal leaves, and, in the last year of its life, forms an above-ground shoot with an inflorescence. The flower bud phase begins from the emergence of the first umbels from the leaf sheaths. The flower phase starts with the emergence of the stamens from under the petals. After the petals are shed,

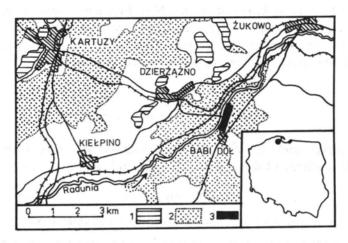


Fig. 1. Location of the investigated *Pleurospermum austriacum* population. 1 — lakes, 2 — forests, 3 — the locality of the species

the unripe fruit phase begins and along with the change of fruit color from green through yellowish-white to light brown, the ripe fruit phase starts. The onset of the fruit shedding phase is marked by the splitting of the schizocarp into mericarps.

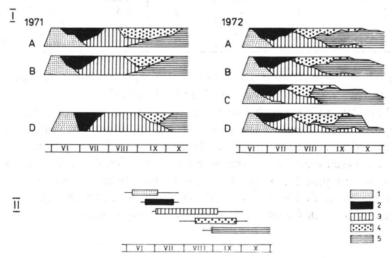


Fig. 2. Phenological spectra (I) and a calendar of flowering and fruiting (II) of *Pleurospermum austriacum*. A, B, C and D—plots: 1—flower bud phase, 2—flower phase, 3—unripe fruit phase, 4—ripe fruit phase, 5—fruit shedding phase

The flower bud phase usually began at the end of May and lasted one month on average, at most (plot D in 1971) over 6 weeks (Fig. 2). Flowering usually began in mid-June, although it was sometimes late by one (plots B and D in 1972) or two weeks (plot D in 1971). The flowering phase lasted 3-5 weeks.

The unripe fruit phase began in late June or early July, only on plot D in 1972 did it start 3 weeks later (Fig. 2). Its duration was very changeable (2-3.5 months). The reason for such a wide span was mainly the delayed development of fruit on lateral umbels, caused by accidental injury to terminal umbels. The change of fruit color in 1972 began at the turn of July and August, almost simultaneously on all of the plots, while in 1971 it was late by 2 weeks (plot A), 4 weeks (plot B) and 6 weeks (plot D). The ripe fruit phase lasted an average of 5 weeks.

In 1971 the fruit shedding phase started at the beginning of September on plots A and B but not until the beginning of October on plot D. In 1972 it began on all of the plots in the second half of August (Fig. 2). It lasted several months. At the end of October, withered shoots with partially un-shed mericarps remained, some of them to mid-December.

#### GENERATIVE INDIVIDUALS AND THEIR FERTILITY

In 1971 and 1980, very few generative individuals were found, both on the studied plots (Tables 2, 3) and outside of them. In 1972, however, more of them appeared (Table 2). Up to 10 flowering plants per plot were found then, although not all of them bore fruit, this due to, e.g., the fracturing of the tall and brittle stems, drying up or gnawing by animals.

The P. austriacum inflorescences were most often large and branched into

Number of maricarps produced by individual plants Year Plot total mean A . B \_ C D A 519.5  $\mathbf{B}$ 387.5 C 421.5 D 94.5

Table 3

Production of generative diaspores by *Pleurospermum austriacum* 

a few or several umbels. The terminal umbels were the most highly developed, containing from 18 to 36 umbellets, and usually fruit developed only on them. The flowers on the lateral umbels mainly functioned as pollen-producers, and only in the case when the terminal umbel was destroyed did they develop fruit. As a result, the number of fruits was many times less than that of flowers.

The number of mericarps was counted during two growing seasons on a total of 31 individuals. In 1971, when only 3 plants bore fruit, the individual production ranged from 20 to 490 mericarps (Table 3). In 1972, when more generative individuals appeared, the individual production of mericarps on plots A, B and C was greater and numbered from 209 to 972 (an average of 450.4). A significantly lower production of diaspores was noted on plot D, where the individuals formed from 28 to 211 (on average 94.5) mericarps (Table 3). Their inflorescences were smaller, and the percentage of formed fruits was significantly lower than on plots A, B and C.

The different individual fertility of *P. austriacum* together with the variable number of generative individuals (reproductives) appearing each year are the reason that the annual supply of diaspores to the soil fluctuates considerably. In the years under study, the number of diaspores per 1 m<sup>2</sup> ranged from 0 to 86.5.

#### THE GERMINATION OF SEEDS AND APPEARANCE OF SEEDLINGS

Under laboratory conditions seeds did not germinate, and after several weeks they became infected with fungi and died.

The seeds sown on the plots in the autumn of 1970 did not germinate before winter as well as in the following year; seedlings did not appear until the spring of 1972. From the 100 seeds on each of the 4 plots, the following numbers of seedlings appeared: 46, 52, 60 and 70, and 3 seedlings on 4 control plots. Thus, the mean germination capacity equalled about 56%. The seeds sown in the spring of 1972 also did not germinate to the end of the growing season. The seedlings did not appear until the spring of 1973. On the plots on which 50 seeds which had been frost-treated had been planted, 17, 19, 24 and 28 seedlings appeared, while on the plots sown with seeds which had not been so treated, 17, 26, 28 and 29 seedlings germinated. No seedlings appeared on the control plots. The average germination capacity was 44% for the seeds which had been frost-treated and 50% for those which had not.

The germination capacity of the seeds in both experiments was similar. The time period between the formation of seeds and their germination was about 1.5 years, regardless of the conditions under which they had been stored and time they had remained in the soil.

Observations were carried out in 1972 and 1980 on the natural appearance of seedlings on the plots (Table 2). They appeared in the second half of May, from 2 to 303 per plot, which made up about 0.8 to 66.9% of the total number of individuals. The variable ratio of the number of seedlings to fruiting individuals (0.2-101) also indicates unstable natality.

# THE AGE-STRUCTURE OF THE POPULATION

Five age-states have been determined in the ontogeny of P. austriacum:

- 1. Seedlings (Fig. 3) 1 year-old individuals with cotyledons retained until the end of July and one juvenile leaf with its blade from 1.1 to 1.4 cm long, divided into three sessile segments set on a petiole 1 to 5 cm in length; stock and persistent leaf bases lacking; underground parts (root and hypocotyl) are thread-like without transverse fissures.
- 2. Juveniles (Fig. 3) cotyledons lacking; one or more juvenile leaves with 3.5-12.0 cm long petiole and leaf blades divided into three sessile or nearly sessile segments 0.7-2.5 cm long; individual segments are cut to 2/3 of their

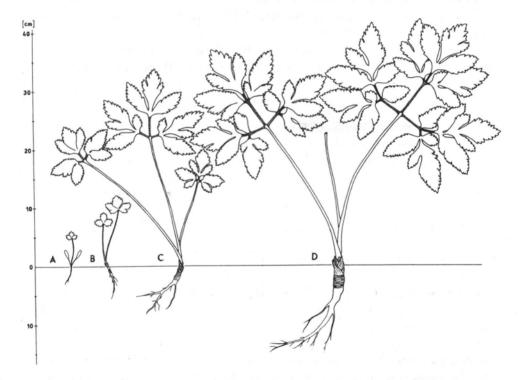


Fig. 3. The habitus of plants in the age-states of the pre-reproductive period of *Pleurospermum austriacum* ontogeny. A — seedling, B — juvenile, C — immature, D — virginile (mature vegetative plant). Petiolules of the primary leaf segments — dotted, and those of the secondary leaf segments — blackened

width; the root-stock is whitish in color, thin fusiform, 0.15-0.4 cm thick, with marked transverse fissures; present are rudiments of persistent leaf bases.

- 3. Immatures (Fig. 3) two to three leaves on petioles 14-35 cm in length; leaf blades 4-19 cm long, divided into three segments set on distinct petiolules (Fig. 3 dotted parts), all of the segments, or at least the apical ones, are lobed to the midrib into secondry segments; the latter are sessile, simple or lobed at most to half of their width, stocks are fusiform, 0.6-1.5 cm in diameter, light brown with distinct transverse fissures.
- 4. Virginiles or, in other words, vegetatively mature (Fig. 3) two to three leaves with petioles 25-35 cm long and blades usually 17-20 cm in length, 2-ternate; secondary segments on distinct petiolules (Fig. 3 blackened fragments), on at least the apical leaves have third degree segments; stocks are thick fusiform, 1.0-2.0 cm thick, dark brown with transverse fissures and persistent leaf bases.
- 5. Reproductives present is an above-ground, leafy stem, 50-200 cm long terminating in an inflorescence. It is consisted of several to over a dozen compound umbels, of which the terminal umbel is the largest and attains over 29 cm in diameter. The plant dies after fruiting only once.

The age-state spectra drawn in the form of piramids (Fig. 4) on the basis of data from 1972 and 1980 (Table 4) represent three types

Table 4

Number of *Pleurospermum austriacum* individuals in age-state groups

Year	Plot	S	j	im	v	g
	Α	7	5	2	10	8
1972	В	7	7	2	12	6
	C	2	66	73	99	8
	D	122	230	122	54	10
	Α	93	26	10	9	1
1980	В	55	54	20	25	-
	C	303	244	87	66	3
	D	28	73	119	45	-

Explanation: s — seedlings, j — juveniles, im — immatures, v — virginiles, g — reproductives

of distributions. The unequivocal identification of a definite, basic model structure was sometimes hindered by the irregular indentations and projections of the piramids' steps.

Spectra A1 and B1 from 1972 are similar, and in their general outline, represent a bell type distribution, in spite of the relatively small participation

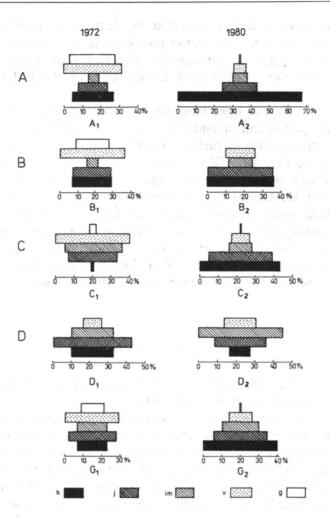


Fig. 4. Age piramids of the *Pleurospermum austriacum* population. A, B, C and D — symbols of permanent plots;  $A_1$ ,  $A_2$ , ....  $D_2$  — spectra from individual plots in two years,  $G_1$  and  $G_2$  — summary spectra from the four plots; s — seedlings, j — juveniles, im — immatures, v — virginiles, g — reproductives

of immatures (Fig. 4). They refer to plots on which the population number was relatively small. However, spectrum D1, also of the bell type, refers to the cluster with the highest density of individuals. It differs from the first two in, among others' its higher percentage of juveniles and immatures and lower participation of virginiles and reproductives. The fourth spectrum (C1) seems to be of the urn type due to the few seedlings and relatively small number of juveniles and immatures.

After eight years, the age distribution of the population changed signicantly on all of the plots (Fig. 4). On plots A and B the distribution,

initially close to the bell type, assumed the form of a large base piramid. On plot C, the urn type distribution also became transformed into a large base piramid. Changes in the opposite direction took place on plot D, where the distribution initially close to the bell type changed into the urn type.

The predominance of large base piramid and bell distributions indicates that the local population is under the present conditions capable of self-restoration and, in spite of periodic lacks of members of some of the age groups (compare Fig. 4B2, D2), does not exhibit symptoms of regression. The cases of lack or negligible participation of seedlings or reproductives, as well as the identations and pojections of the piramids which signify the unequalized group numbers, are caused by the irregular renewal.

The presented picture of the age structure of the local population is confirmed by two synthetic spectra from 1972 and 1980 created on the basis of data from four plots (Fig. 4G1, G2). The first represents the bell type distribution, the second a large base piramid distribution.

### DISCUSSION

Pleurospermum austriacum does not propagate vegetatively, and it attains its ability to reproduce generatively after a several year long period of development. The transition of a plant into the generative phase seems to depend on appropriately low temperatures acting on wintering, organs. This would explain the very small appearance in some years, and much higher in others, of flowering individuals. Vernalization has shown to be an indispensable condition for the onset of the generative phase of many monocarpic perennials, among others, in the related Pastinaca sativa (Baskin and Baskin 1979). Only those individuals which had attained a certain size reacted to it, while others of the same age, but smaller, remained in the vegetative state until the following year (Baskin and Baskin 1979). P. austriacum individuals also bloom only after attaining the appropriate size and specified morphological traits.

The studied reproductives formed from 20 to 972 mericarps, which clearly differs them from plants from Sweden, which formed on average about 6600 mericarps (Horn af Rantzien 1946). It does not seem that the significantly smaller amount of diaspores formed in the studied area is related to *P. austriacum* biology or rythm of flowering and fruiting. It forms here highly developed inflorescences with a huge number of flowers. They are promiscuous, hence accessible to a variety of pollinators, who regularly visit the inflorescences. Flowering and fruiting occurred in rather stable periods, this pertains to, in particular, the periods of the highest

intensity of the phases. The duration of some of the phases was significantly prolonged only when small lateral umbels developed in leaf-axils after the destruction or injury of the inflorescences.

The number of fruits developed by *P. austriacum*, as by other umbellifers (Håkansson 1923, Chojnacki 1985), is regulated by the amount and distribution of nutrients in the inflorescence. Ripe fruit develops only from the flowers of the terminal umbel, which develop first. Fruit can develop on the lateral umbels only if the terminal umbel has been destroyed.

It is regarded that the reproductive capability of P. austriacum is limited by its very low, not exceeding 2%, germination capacity (Hegi 1926, Horn af Rantzien 1946). The negative results of tests of germination under laboratory conditions seemed to support this view, however, it is contradicted by the rather numerous appearance of seedlings on the studied plots. In addition, the number of seedlings did not exhibit a correlation with the number of mericarps formed in the preceding growing season. For example, on plot D in 1972, 122 seedlings were found although only 20 mericarps had been produced there the preceding year, and their inflow from the outside does not seem probable. Studies on germination under natural conditions have shown that the seeds germinate only after 1.5 years from their formation, and that their germination capacity equalls 50%. At the seed dispersal phase, the endospermous seeds of P. austriacum have a small, poorly developed globular embryo, and similarly as in Pastinaca sativa (Baskin and Baskin 1979), are at the morphological ripeness phase while attaining physiological ripeness only after a certain time (postripenning). The second condition for the germination of Pastinaca sativa seeds is stratification (Baskin and Baskin 1979). Although it has not been possible to unequivocally prove that it is necessary for P. austriacum, all of the mericarps from which seedlings had been obtained had spent one or two winters in the soil.

The habitat conditions, the species' distribution and distribution history testify about the role of vernalization and/or stratification in the life cycle of *P. austriacum*. In the mountains it is a hionophilous plant (Hadač et al. 1967), beyond the mountains it occurs in river and stream valleys, where locally the temperature can fall due to the streaming down of cold masses of air (Iversen 1954, Markowski and Chojnacki 1982). During the Pleistocene, the distribution of *P. austriacum* contracted during the interglacial periods of warmer climates and expanded during the colder periods (Hadač et al. 1967, Środoń 1970). At present, the western distribution limit coincides with the January isotherm — 2°C (Iversen 1954). This species does not grow in areas with distinct Atlantic climate influences (Czubiński 1950).

A synthetic picture of the state of the local population was attained by studying the age structure twice, in an eight year interval.

In the method used, the distinguished age groups include individuals at the same stage of developmet, but of an unknown, and not necessarily of the same, age. In *P. austriacum*, as in many other plants, it is not possible to determine age. In studies on the age structure, this lack does not seem to have any greater significance since the role played by an individual in the population depends more on its phase of development than on the number of years it has lived. For example, in *Pastinaca sativa*, the beginning of the generative period of ontogeny does not depend on its age, since the plants can bloom after 2, 3, 4 and more years of vegetative development (Baskin and Baskin 1979). The classification of individuals in the population according to their stage of development is done not on the basis of only one morphological trait, but on a combination of numerous ones. This makes it possible to avoid creating artificial and arbitrary groups, as e.g., in *Pastinaca sativa* on the basis of root-crown diameter (see Baskin and Baskin 1979).

Most of the age-state spectra were of the large base piramid and bell types, which indicates either a large increase in population number or its stabilization in clusters. The overall picture of the age structure of the local population in 1972 and 1980 obtained by summarizing the data from four plots, was also similar. The irregular indentations or projections of the piramid steps point to the unequalized number of individuals in the age groups. Situations such as these are usually explained by the past occurrence of unfavorable or favorable conditions for propagation and survival of progeny (Trojan 1975). In *P. austriacum* the reason is the differentiated appearance of fruiting individuals in previous years and the associated variable production of mericarps.

Only two spectra (C1 and D2) were similar to the urn type, which characterizes weakened and receeding populations. The weakening of the population on plot D is also signalized by the two-fold reduction of the number of individuals during eight years, the reduction in the number of individuals in all of the age groups and the significantly lower, in comparison with other plots, individual production of mericarps. On plot C, however, the urn type state was only temporary (compare spectra C1 and C2). In the case of *P. austriacum* the urn type distribution cannot then be generally considered to be a symptom of the dying-out of the population since its cause can also be the specific biology of the species.

A repeated study of the age structure showed that in only one case did a stabilized population (bell type) pass into the phase of population decline and dying out (urn type). On the remaining plots, the bell type distribution and one nearly urn type, changed into the large based piramid type. During the eight years which separated the observations, the sequence of distribution types was probably more diverse. Changes in the age structure

of *P. austriacum* seem to consist in the irregular seccession of different types of age distributions, and not in directional development leading from a young, dynamic population through a stabilized one, then to a receeding and finally disappearing in one place population.

According to the classification system of age states (Rabotnov 1950), the local population of *P. austriacum* on all of the studied plots can be called normal, therefore capable of self-restoration and did not exhibit, with one exception (plot D) signs of regression. The lack in some years of reproductives and the absence or very small presence of seedlings should be treated, as already has been shown, as a passing phenomenon. Within the stand, but outside of the studied plots, also found are small clusters which exhibit traits of invasive populations, made up by the youngest individuals and not capable yet of self-maintenance. They are formed when in those places where the species has not; been present yet, solitary individuals, capable of attaining the generative phase and bear fruit, appear.

Appearance of new clusters and the disappearance of others indicate that the species translocates itself within the locality. As a result, the population does not decrease, although individual clusters can be impermanent. Such a situation reflects the phytocoenotic and habitat relationships. The oak-hornbeam forest on the valley slopes is a dynamically balanced community. An element of instability is introduced, however, by small but frequent landslides from the very steep slopes, which is of foremost importance for the maintenance of the species. Soils very rich in calcium carbonate form on the landslide sites; *P. austriacum* has high requirements for this compound. The species enters onto the landslide sites from the older parts of the forest, usually after a tree layer has been formed and the intially thick layer of shrubs has been thinned. The excessive growth of shrubs, e.g. in places where trees had been uprooted, is one of te major reasons for the species receding from some places. Plot D is an example.

In spite of the irregular self-renewal and impermanence of individual clusters, *P. austriacum* has a good chance of remaining in the studied locality. A necessary condition for this is, however, the maintenance of the natural state of the phytocoenosis and present dynamics of the valley slopes, subjected to erosion by the unregulated river having traits of the submontane stream. The nature reserve created here in 1972 increases the chances of survival of this species.

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# Biologia Pleurospermum austriacum (L.) Hoffm. na reliktowym stanowisku na Pojezierzu Kaszubskim

#### Streszczenie

Badano lokalną populację górskiego gatunku *Pleurospermum austriacum* na niżowym stanowisku reliktowym, oddalonym od zwartego zasięgu. Badania prowadzono w rezerwacie Jar rzeki Raduni na Pojezierzu Kaszubskim (rys. 1) na czterech stałych powierzchniach (tab. 1).

P. austriacum jest monokarpiczną byliną kłączową, która rozmnaża się wyłącznie generatywnie. Zmienny w poszczególnych latach pojaw osobników generatywnych sprawia, że badana populacja odnawia się nieregularnie, a jej liczebność podlega znacznym wahaniom (tab. 2). Przechodzenie osobników z fazy wegetatywnej w fazę generatywną wydaje się być uwarunkowane wernalizacją. Osobnicza produkcja rozłupek wynosi od 20 do 972 sztuk, średnio 333,1 (tab. 3). Nasiona kiełkują po 1,5 rocznym okresie spoczynku, a ich zdolność kiełkowania jest znacznie większa (około 50%) niż sądzono dotychczas (do 2%). Struktura wiekowa populacji wykazuje, że jest to populacja normalna, zdolna do samoutrzymywania się, chociaż niekiedy niepełnoczłonowa z powodu braku siewek lub osobników generatywnych (tab. 4). Na różnych powierzchniach i w różnych latach struktura wiekowa przyjmowała postaci trzech typów rozkładu: piramidy płaskiej, dzwonu i urny, które następowały po sobie w rozmaitej kolejności (ryc. 4), najczęściej niezgodnej z kierunkowym schematem rozwoju populacji. Przyczyna tego jest zmienne w poszczególnych latach natężenie reprodukcji.

Przy zachowaniu obecnych warunków środowiskowych lokalna populacja *P. austriacum* ma szanse na długotrwałe występowanie na badanym stanowisku. Zasadniczym czynnikiem kształtującym te warunki jest oddziaływanie nieregulowanej rzeki o cechach potoku podgórskiego.