THE DYNAMICS OF *LISTERA OVATA* POPULATIONS ON MINERAL ISLANDS IN THE BIEBRZA NATIONAL PARK

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(Received: December 6, 2001. Accepted: March 15, 2002)

ABSTRACT

Observations of two isolated populations of *Listera ovata* (Oparzelisko and Zabudnik) were conducted for 7 years in the Biebrza National Park. The studied populations differed in size, proportion of flowering individuals and effectiveness of reproduction. High number of juvenile individuals in OPA population was noted under conditions more favourable for germination (gaps in vegetation and higher moisture of soil). On the other hand, vegetative reproduction is important in the dynamics of ZAB population. The natural fruiting rate of *L. ovata* is relatively high (up to 90%) and does not seem to be pollinator limited. Some costs of reproduction especially in terms of leaf size were observed. The dormancy is important in the population dynamics. In some years even one third of the population may be dormant. *L. ovata* produces enough seeds and offspring to maintain or even increase population sizes. These facts, connected with the longevity of individuals, indicate that populations of *L. ovata* in the Biebrza National Park are not threatened with extinction in the nearest future.

KEY WORDS: autogamy, cost of reproduction, dormancy, flowering, fruiting, orchids, recruitment.

INTRODUCTION

The Orchidaceae is one of the largest families of flowering plants, estimated as 20 000 species (Atwood 1986), and many new ones are being discovered and described each year. The demographic data, especially from long-term studies, are still scarce in comparison to the size of this family. Studies by Tamm (1972, 1991) and Kull (1995, 1998) are exceptional. This type of study is crucial for the understanding of mechanisms of the population dynamics of a given species and affects orchid conservation strategies (Ackerman 1987, 1998). It is well known that populations of some orchid species fluctuate greatly in numbers from year to year, while others remain fairly constant (Wells 1967; Inghe and Tamm 1988; Tamm 1991; Jones 1998). One of the most important factors affecting population dynamics in orchid species is their life history, for example the phenomenon of dormancy which complicates all types of population analyses.

The effective conservation of orchids is in large part dependent upon an understanding of the reproductive habits and the environmental conditions necessary for the maintenance of the population of a given species. In terrestrial orchids the number of flowering plants may vary enormously from year to year, probably in response to external factors, such as changing weather conditions or management measures (Tamm 1991; Willems and Bik 1991). In most orchid species fruit set under natural condi-

tions is predominantly pollinator dependent. A recent review of fruit set in the Orchidaceae by Neiland and Wilcock (1998) reported (1) a positive association between orchid rarity and lack of nectar reward to pollinators, and (2) that the provision of nectar as a reward to pollinators doubled on average the probability of fruit set. Understanding this type of causal relationship between pollinator visit, fruit set, and rarity is important for orchid conservation. Little is known about influencing factors, which site will be preferred or favourable for orchid establishment, growth and flowering. However, it is clear that successful establishment of orchid seedlings requires the presence of an appropriate fungal symbiont in soil.

Populations of rare species can be, by definition, considered as of the island type, characterised by low abundance and limited range of occurrence. In the Biebrza National Park (NE Poland) populations of *Listera ovata* are of the island type not only because of the rarity of the species, but also because they are environmentally isolated due to their occurrence on mineral elevations surrounded by peat bogs.

Listera ovata is a shade-tolerant forest herb (Tamm 1972). It is a long-lived species with an average half-life of 80 years (Hutchings 1989). *L. ovata* is common throughout Poland. The geographic range of the species covers all of Europe and reaches Eastern Siberia in Asia. Many different kinds of insects are known to visit *L. ovata* flowers, but ichneumonid wasps are the most commonly reported pollinators (Ackerman and Mesler 1979). Although appa-

rently all twayblades secrete nectar onto the surface of the labellum, not all species are odoriferous. Van der Pijl and Dodson (1966) report that *L. ovata* is scentless. The yellow-green flowers are on a loose flowering stalk. Fruits of this species contained on average ca. 1240 seeds per capsule (Willems and Melser 1998). Tamm (1972) noted that "a few of the new individuals may originate from seedlings, but according to the observations, the normal propagation is vegetative".

This paper presents the results from a 7-year study of demography of two *Listera ovata* populations. The objective of this work was describing the dynamics of two populations studied. The study addresses the following questions: 1) are populations developing in different environmental conditions variable, 2) what is the level of sexual and asexual reproduction and their importance in population dynamics, 3) is the phenomenon of dormancy significant in population dynamics, 4) what factors influence population development in a limited area.

MATERIAL AND METHODS

The study of *Listera ovata* populations was carried out in the Biebrza National Park (NE Poland). Among the widespread peat bogs there are mineral elevations of different size, shape, origin and type of vegetation cover. The islands are formed on fields of inland dunes in the shape of classical ridges or fused parabolic forms (Żurek 1975). There are a few hundred islands in the Biebrza river valley, but *L. ovata* has been reported only on few of them. Two of the mineral islands: Zabudnik (ZAB) and Oparzelisko (OPA) were chosen for the study (Fig. 1). Zabudnik is

a dune on the subpeaty surface covered by fluvial soils, in the zone of peat bog eolians and river forms. This island is about 1.2 m above peat level and its total area is 5500 m². There is only a small piece of the oak-linden-hornbeam forest community in this place, and the remaining area is covered by shrubs and reed grass patches. Oparzelisko is a remnant of the river meanders connected with the oldholocene Biebrza and consecutively eolited. This mineral elevation is less than 1 m above peat level and is about 5000 m² large. The stand is built of birch trees, 15-20 years old. The herb layer is typical for a hornbeam forest.

The observations were conducted on permanent plots for 7 years (1995-2001) in ZAB population and for 6 years (1996-2001) in OPA population. The size of permanent plot in ZAB was 1000 m² and 220 m² in OPA. Plants were labelled with markers and the position of individual plants was mapped (Fig. 1). Using this method, it was possible to return to the same plant, or location if the plant was absent, in subsequent years. The main observations were made in June each year when flowers were fully open. The following parameters were recorded for each plant: (1) the state of a plant (flowering, non-flowering), (2) height of a plant, (3) length and width of the largest leaf, (4) height of flowering stem and length of inflorescence, (5) the number of flowers on inflorescence, (6) the number of fruits. The study area was searched for new plants at each recording. Plants with two small leaves (with leaves not longer than 3 cm) were interpreted as juveniles. My description of the population dynamics of *L. ovata* takes the common approach and terminology adopted by other orchid researchers, in which life history stages: flowering, vegetative and absent (or dormant) are used rather than ages. This approach is necessitated by the slow development of orchid see-

Fig. 1. Localities of *Listera ovata* populations and the distribution of individuals in the permanent plots in years of their maximum abundance aboveground – 1998 in OPA, 1999 in ZAB.

dlings, and because mature plants may be strictly subterranean for several years. An experiment aimed at investigating self-pollination was carried out in 2001. Five inflorescences were covered with cotton net to evaluate seed production without pollinators (autogamy). These inflorescences were covered before any flowers were open and the cotton net remained in place until fruiting time.

RESULTS

Populations size and spatial pattern

The number of plants (present above-ground and dormant) in the permanent plot in ZAB population was stable and varied from 80 (1996) to 98 (1999) (Fig. 2). In OPA population fluctuations were greater, the number of plants varied from 119 (1996) to 225 (2001) (Fig. 2). The total number of plants growing on mineral islands was not more than twice greater than the number of individuals on permanent plots. In ZAB mature individuals dominated each

year, while in OPA a high proportion of juveniles was recorded. In OPA many new individuals (not observed earlier) appeared from 1996 to 1999, while in ZAB only four new individuals were noted in 1999. During the observation period from 2% to 6.4% of individuals died yearly in OPA population. In ZAB mortality was not observed at this time (Fig. 2).

Individuals of *L. ovata* were often aggregated (Fig. 1). The average density of plants was stable in both populations. The density of plants in OPA population varied from 6.7/10 m² to 8.2/10 m² (excluding 1996 – 4.7/10 m²) and was about ten times greater than in ZAB population (ca. 0.8/10 m² in each year of observation).

The role of generative and vegetative reproduction in population dynamics

The role of sexual reproduction in population dynamics is different in the two populations studied (Fig. 2). In OPA population the proportion of juvenile individuals ranged from 19.2% (1996) to 41.4% (1997). New juvenile indivi-

Fig. 2. Dynamics of *Listera ovata* populations in the Biebrza National Park. Total population is the sum both above-ground and dormant plants.

Fig. 3. Frequency of *Listera ovata* plants that flowered between 0 and 7 times during the study period.

Fig. 4. The number of years between flowering events for individuals of *Listera ovata*.

duals (not observed in previous years) constituted from 3.7% (1999) to 32% (1997) of individuals present above-ground. In the last two years no new individuals were noted. In ZAB population juvenile individuals were present only during the last three years of observations, and their proportion ranged from 2.5% to 4.8% (Fig. 2). It should be emphasised that the level of recruitment assessed on the basis of the number of juvenile individuals is an overestimation because this number may include not only those which appeared in a given year, but also juveniles from the previous years. They can remain in this stage for a few years (five individuals in OPA population remained in juvenile stage throughout the study period). Most often juvenile individuals emerged at small distances from flowering and fruiting plants (Fig. 1).

A plant was considered to be vegetatively reproduced when at a given spot two or more shoots appeared, whereas only one shoot was recorded in a previous year. Vegetative reproduction plays a minor role in the populations dyna-

mics of *L. ovata* in OPA. Only one shoot originated by vegetative reproduction was observed during seven years. In ZAB population vegetative propagation shaped at higher level. Plants of this origin were noted in this population from 1998 to 2001, and their proportions in consecutive years were: 7.5%, 16.5%, 15.2%, and 13.2%.

Flowering

Most of individuals in OPA have never flowered (64%) or have flowered only once (16%) (Fig. 3). In ZAB population, frequency of flowering was greater, and participation of individuals, which did not flower during six years, was almost twice lower than in OPA (Fig. 3). Among plants flowering two or more times, the majority flowered in consecutive years (Fig. 4). Nineteen plants (16%) in OPA flowered once, eighteen (15%) flowered 2-3 times, the remaining six flowered during four or six years. One plant was in flower during seven consecutive years. In ZAB population one-year flowering was observed in nine (10.8%) plants, and the probability of flowering 2-5 times was similar (10-12 plants in each case), and one plant in this population flowered during six consecutive years.

The proportion of flowering individuals varied considerably from year to year and was significantly greater in ZAB population than in OPA population in each year of observations (Fig. 5). ZAB population consisted of 20.5%-48.8% flowering plants, while OPA population of 7.7%-24%.

The average length of inflorescence ranged from 14.8±5.5 cm to 20.3±4.9 cm in OPA population (no statistically significant differences between years) and from 14.1±6.1 cm to 19.3±5.4 cm in ZAB population (significant differences between years were observed; $F=7.098$; $df=176$; $p<0.001$). Two populations differed in this parameter in 1999 only ($F=8.546$; $df=59$; $p<0.01$).

The average number of flowers per inflorescence over the observation period varied in the same range in both populations (Fig. 6). There was significant positive correlation between the inflorescence length and the number of flowers per inflorescence; $r=0.77$ ($p<0.05$), and $r=0.63$ ($p<0.05$) for OPA and ZAB population, respectively.

Fruiting

The mean number of fruits per spike varied substantially from year to year. Greater values of this parameter were noted in OPA population (Fig. 6). In OPA population no differences between years were found, while in ZAB the differences were statistically significant ($F=4.718$;

Fig. 5. Proportion of flowering individuals and proportion of fruits in comparison to number of flowers in two *Listera ovata* populations.

Fig. 6. Annual mean number of flowers and fruits per flowering individual (± 1 standard error) in two *Listera ovata* populations.

Fig. 7. The mean size (± 1 standard error) of flowering and non-flowering individuals of *Listera ovata* in two populations studied.

df=153; $p<0.01$). Two populations differed in these properties in four of six years of observations. The number of fruits per inflorescence was positively correlated with the number of flowers per inflorescence ($r=0.86$ in OPA and $r=0.68$ in ZAB).

The overall fruit set was high and ranged in the study period from 66.8% to 89.8% in OPA population and from 27.1% to 80.5% in ZAB population (Fig. 5). Inflorescences, which were covered during the flowering season, did not produce any fruits.

Size of plants

The height of flowering plants showed a great variability in both populations (Fig. 7). In OPA population no statistical differences between years were noted. In ZAB population the mean values of this parameter differed significantly between the years ($F=14.418$; $df=221$, $p<0.0001$).

The two analysed populations differed in the height of flowering plants in 1997 ($F=6.830$; $df=54$; $p<0.05$) and in 2000 ($F=3.983$; $df=90$; $p<0.05$).

The differences in the height of non-flowering plants were greater than in flowering ones, both between populations ($F=22.043$ - 109.048 ; $df=145$ - 216 ; $p<0.001$) and years (OPA: $F=6.559$; $df=740$; $p<0.001$; ZAB: $F=8.312$; $df=289$; $p<0.0001$) (Fig. 7). The height of the former group of plants ranged from 4.5 ± 3.1 cm (1995) to 6.7 ± 2.7 cm (2001), from 7.3 ± 3.7 cm (2001) to 11.3 ± 4.1 cm (1998) in OPA and ZAB population, respectively.

Flowering plants had greater leaves than non-flowering ones (Fig. 7). There were no significant differences between years in leaves size of flowering plants in OPA, but in ZAB both length and width was different in consecutive years ($F=6.963$; $df=220$; $p<0.0001$ and $F=2.897$; $df=284$; $p<0.05$, respectively). The two observed populations differed

Fig. 8. The leaf size (length and width) of *Listera ovata* individuals before and after flowering. 0=year of flowering. Values are means ± 1 standard error.

red statistically in 1999 (length of leaves of flowering plants: $F=5.263$; $df=65$; $p<0.05$) and in 2000 (width of leaves of flowering plants: $F=4.703$; $df=88$; $p<0.05$).

The size of leaves of non-flowering plants showed, in most cases, statistically significant differences, both between populations and years. In OPA population the leaves of non-flowering plants were smaller than in ZAB population (Fig. 7).

Cost of reproduction

The size of leaves increased in a significant way in the year leading to the flowering event and then decreased dramatically in two consecutive years after flowering in case of individuals, which flowered once during the observation period (Fig. 8). In the third and fourth year after flowering, the size of leaves (both length and width) remained the same as in the second year after flowering. The study period was too short to estimate the time of comple-

te recovery of leaf size. No significant differences in height of shoots and size of leaves were noted within the group of plants that flowered during two or more consecutive years. On the other hand, changes in inflorescence length and in number of flowers per inflorescence were observed (Fig. 9). The values of both parameters decreased slightly in the second year of flowering, and then increased in consecutive years.

Dormancy

Not all individuals of *Listera ovata* appeared every year above the ground. The observed phenomenon of dormancy indicates its great importance for the population dynamics (Fig. 2). Among the 83 labelled individuals, 35 (41.7%) were dormant at least once during 6 years in ZAB population. The period of dormancy lasted usually one year. In ZAB twenty individuals (23.8%) went dormant only once during six years of observation, ten others (11.9%) twice or thrice, but not in subsequent years. Five plants (6%) were not evidenced above the ground for four years. In OPA population dormancy was more often recorded. Among 119 individuals, 78 (65%) were dormant at least once. Fifty one (42.5%) were dormant once or twice, and twenty others (16.7%) were absent during three or four years. Only one individual in this population appeared above ground after 5-year dormancy. The influence of dormancy on population dynamics was differentiated (Fig. 2). From 7.1% to 16.8% individuals in ZAB population, and from 9.1% to 33.9% in OPA were absent above ground. Significant differences in frequency of dormancy for flowering and non-flowering plants were noted. Non-flowering individuals more often accede to dormancy (on average 20.2% in OPA and 11.7% in ZAB during study period) than flowering (12.9% and 7.7%, respectively). Most of the plants (38 out of 48 in ZAB and 118 out of 122 in OPA) were still absent or in vegetative state after dormancy. The probability of flowering decreased after dormancy in OPA: from among 8 flowering individuals before dormancy, only one started flowering after dormancy. In ZAB, 8 from among 11 plants were still in flowers after dormancy.

Fig. 9. The length of inflorescence and number of flowers per inflorescence for individuals of *Listera ovata* that flowered in successive years. Values are means and ± 1 standard error.

DISCUSSION

Two *Listera ovata* populations differed in their properties, especially in type and effectiveness of reproduction. In OPA population reproduction from seeds has an important effect on population dynamics, while in ZAB vegetative propagation seems to be more significant. These differences may be caused by different abiotic and biotic conditions on mineral islands. Although twayblade is more shade-tolerant than other orchid species and is able to thrive beneath a relatively dense canopy (Tamm 1972, 1991), the light seems to be an important factor influencing flowering. Both flowering frequency and proportion of flowering individuals were greater in ZAB population, where light conditions were more suitable. Flowering and survivorship of *Isotria medeoloides* and *Orchis militaris* were also positively correlated with light (Mehroff 1989; Farrell 1991). Flowering is also determined by weather conditions such as the precipitation, drought and frosts in the spring (Case 1987; Firmage and Cole 1988; Wells and Cox 1991; Willems and Bik 1991; Wells et al. 1998). In 2001 in ZAB population the proportion of flowering individuals was the lowest during observation period, probably due the drought in previous year, frost in May and fire in early spring. Fruit set in ZAB population in this year was 2-3 times lower than in previous years. Flowering does not only depend on external factors, but is also determined by the condition of a plant (Wells and Cox 1991; Willems and Bik 1991; Wells et al. 1998; Willems and Dorland 2000). Plant size was the main determinant of flowering behaviour of the *Cyclopogon cranichoides* individuals (Calvo 1990). The passage of an individual plant from the vegetative to reproductive stage is associated with reaching a certain size. Flowering plants of *L. ovata* had larger leaves than non-flowering, and the size of leaves increased significantly before flowering.

The natural fruiting rate of *L. ovata* is relatively high, given the fact that fruit set in outcrossing orchids is generally low and limited by pollinator availability under natural conditions (Gregg 1989; Waite et al. 1991; Whigham and O'Neill 1991; Willems and Lahtinen 1997; Neiland and Wilcock 1998). Almost 100% of flowering plants produced fruits (excluding damaged plants), and most often from over 70% to almost 90% flowers developed fruits in *L. ovata* populations studied. High pollinator's activity and the fact that under certain circumstances this species may be autogamous (Darwin 1895, after Ackerman and Mesler 1979) may explain this fact. In my experiment, inflorescences covered by cotton net did not produce any fruits, demonstrating that *L. ovata* is not an autogamous species. Ackerman and Mesler (1979) described high pollination efficiency of *L. cordata* from several localities, with 61% to 78% of flowers setting fruit. The differential fruiting success may be related to the attractiveness of the spikes. The longer spikes with more flowers would be more attractive than the shorter ones. Murren and Ellison (1996) also found that fruit set was more frequent on multiflowered racemes than on racemes with fewer flowers.

Flowering and fruiting in a given year affect future growth and reproduction of terrestrial orchid species (Snow and Whigham 1989; Primack and Hall 1990; Primack and Stacy 1998). For example, the high cost of reproduction was clearly demonstrated in a lower growth and flowering rate in *Cypripedium acaule* (Primack and Hall

1990). It was evident in the present study that flowering of *L. ovata* plants in a given year resulted in decrease of leaf size in the next years. This negative effect of flowering on future size was only observed in the group of plants, which flowered only once during the study period. In plants flowering in two or more consecutive years no costs of reproduction were noted. The flower stalks of *L. ovata* did not display a decrease in the average length and size of leaves with increasing plant age. Thus, the question whether there are any costs of reproduction in *L. ovata* is still open. The physiological explanation for the costs of reproduction is that limiting resources used in present reproduction are not available for future use by the individual (Primack and Hall 1990).

Mortality in *L. ovata*, did not occur in every year, and the number of plants dying in any one year was not highly variable. Mortality was high, however, in 1998 and 1999, following a period of high recruitment. This suggests that juvenile plants are more likely to die than older, well-established plants. Similar results were reported by Wells and Cox (1991) in *Ophrys apifera* and Tremblay (1997) in *Lepanthes caritensis*.

Dormancy is commonly observed in orchids (Lesica and Steele 1994; Hutchings et al. 1998; Willems and Melser 1998; Shefferson et al. 2001). A three- to four- year dormancy is often set as the upper limit for orchid species (Hutchings 1987; Mehroff 1989; Calvo 1990; Gregg 1991). The dormancy is of great significance in the dynamics of *L. ovata* populations. In a given year even one third of the population may be dormant. Plants of the studied species may remain below-ground for even five years. Several plants in this study were documented as returning to a flowering condition after a dormant period. Dormancy was less likely to occur following the year in which a plant flowered than when it was vegetative or dormant. A return to flowering condition from a dormant period is reported by Calvo (1990) for *Cyclopogon cranichoides*, by Gregg (1991) for *Cleistes divaricata* and by Falb and Leopold (1993) for *Cypripedium candidum*, but is not reported by Mehroff (1989) for *Isotria medeoloides*. The ability to remain as an under-ground organ may be significant for survival of the plant in unfavourable seasons (Wells 1967) and for recovery of resources (Willems and Dorland 2000). Differences in site specific factors can have a great impact on probability of dormancy in populations (Shefferson et al. 2001). My results suggested some influence of environmental conditions on the occurrence of dormancy.

Different reproductive strategies were observed in two populations of *L. ovata*. Although more inflorescences in ZAB and similar numbers of fruits in both population were noted, the effectiveness of reproduction in OPA was higher. A high number of juvenile individuals characterised the OPA population, while in ZAB population only few juvenile individuals (not each year) were observed. On the other hand, vegetative reproduction was important in the dynamics of ZAB population. The conditions in ZAB are less favourable for germination, mainly because of the compactness of the vegetation and lack of safe sites for germination. In OPA there are gaps in the vegetation and the moisture of soil is higher, thus more juvenile individuals appeared there. The same results were obtained for *Cypripedium calceolus* populations, situated on these mineral islands (Brzosko and Werpachowski 1998; Brzosko 2002).

Similar observations have been reported for *Liparis loeselii* (Jones 1998) and *Cypripedium calceolus* (Kull 1998), where the percentage of seedlings in a population was strongly affected by the area of bare soil and litter covers.

For the survival of the population of *L. ovata*, situated on mineral islands, it is important to know that this long-lived species is not severely limited by natural pollination, as demonstrated for another orchid species. Due to their isolated position the survival of the *L. ovata* populations depends totally on the local seed production. *L. ovata* produces enough seeds and offspring (in sexual or vegetative way) to maintain or even increase populations sizes. On the other hand, mortality rate is relatively low and shaped at lower level than recruitment in the two populations studied. These facts connected with the longevity of individuals indicate that *L. ovata* populations from the Biebrza National Park are not threatened with extinction in the nearest future.

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DYNAMIKA POPULACJI *LISTERA OVATA* NA MINERALNYCH WYSPACH W BIEBRZAŃSKIM PARKU NARODOWYM

STRESZCZENIE

Obserwacjami objęto dwie populacje *Listera ovata* zlokalizowane na mineralnych wyspach w Biebrzańskim Parku Narodowym. Populacje różnią się m.in. wielkością, udziałem osobników kwitnących i efektywnością reprodukcji. W populacji OPA (gdzie obserwuje się warunki sprzyjające rekrutacji, tzn. obecność luk w roślinności i większą wilgotność gleby) stwierdzono wyższy udział osobników juwenilnych. Z kolei w populacji ZAB ważniejszą rolę w dynamice populacji odgrywa reprodukcja wegetatywna. Owocowanie kształtuje się na wysokim poziomie (do 90%) w obydwu populacjach i nie jest ograniczone brakiem czy aktywnością zapylaczy. Zmniejszanie się wielkości liści w następnych latach po kwitnieniu może świadczyć o tym, że osobniki *L. ovata* ponoszą koszty reprodukcji. Stwierdzono ponadto, że liczebność populacji jest w istotny sposób kształtowana przez zjawisko spoczynku roślin. W niektórych latach nawet jedna trzecia osobników może nie pojawić się nad powierzchnią ziemi. Liczba powstających w populacjach nasion i poziom rekrutacji wydają się być wystarczające do utrzymania, a nawet zwiększenia liczebności populacji. Fakt ten w połączeniu z długowiecznością osobników może wskazywać na to, że biebrzańskie populacje *L. ovata* nie są narażone na ekstynkcję w najbliższej przyszłości.

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