ABSTRACT: Parasitic plants species of the genus Orobanche produce a very high number of small dust-like seeds. The seed shape of Orobanche sp. is ellipsoid to globose, ca. 0.3 × 0.4 mm. Orobanche picridis F.W. Schultz is a sub-Mediterranean-sub-Atlantic species. It has the NE range limit in Poland and Ukraine. The species is seriously endangered in Poland and neighbouring countries. O. picridis occurs only in southern Poland (34 localities). It prefers habitats on chalky rendzina, especially S-facing. It colonizes abandoned fallows and wastelands, field margins, initial xerothermic grasslands. They are mostly ecotone communities, in semi-ruderal xerothermic pioneer communities belonging to the Dauco-Picridetum (Artemisietea vulgaris class). The aim of this study was to determine potential and real seed productivity in Orobanche picridis and correlations between the characteristics of the shoots. Research hypothesis is to show that the studied traits of shoots show the highest correlation with the production of seeds.

The paper presents investigations into potential and real seed productivity of Orobanche picridis for the first time. Investigations were conducted in 2010 at three most abundant localities of O. picridis in southern Poland in the Wyszy Małopolska upland (S Poland) - Wesołówka (Przedgórze Iłżeckie foreland), Pińczów, and Pęczelice (Niecka Nidziańska basin). Research into the number of seeds produced per fruit and per shoot is discussed. Strict correlations between seed productivity and shoot features, i.e. shoot height, inflorescence length, number of fruits and corolla tube length were observed. The number of seeds in a single ovary in O. picridis varied and ranged from 457 to 3 246. The mean number of seeds per shoot is 55 172 based on the data collected at the three sites and ranges between 8 911 and 151 050. Seed productivity depends significantly on the size of a plant, that is on the shoot height, correlation coefficient r = 0.7, inflorescence length, r = 0.6, number of flowers and fruits per plant, r = 0.6, and on the flower size, r = 0.5.

KEY WORDS: Orobanche picridis, Orobanchaceae, shoot features, seed production, seed variability, Poland

1. INTRODUCTION

Parasitic plants comprise ca. 4 500 species worldwide (1% of all flowering plants) belonging to 20 families and 280 genera; 390 of them are holoparasites and others are hemiparasites (Heide-Jørgensen 2008). Holoparasites of the genus Orobanche (Orobanchaceae) are some of the most critical and difficult genera to determine in the world flora, especially when dry. Seed morphology is an alternative method to distinguish genera. Seeds have been examined by light
microscopy (Joel 1987a) or very effectively by electron microscopy. However, only scanning electron microscopy reveals structures invisible using other equipment and different or similar taxa have been identified by SEM studies (Abu Sbaih and Jury 1994, Musselman and Mann 1976, Joel 1987b, 1988, Plaza et al. 2004, Domina and Colombo 2005, Halamski and Piwowarczyk 2008).

The greatest number of seeds is produced by ruderal plants, orchids, parasites and light-seeded species. Record numbers of propagules are produced by spore plants and fungi. In the plant world, species producing the greatest number of very small, dust-like seeds (Harper 1977) are mostly representatives of the families Orobanchaceae, Burmanniaceae, Corsiaceae, Orchidaceae, Triuridaceae, Peterosavieae, Ericaceae, Gentianaceae, Polygalaceae, Rubiaceae, Buddlejaceae and Gesneriaceae (Eriksson and Kainulainen 2011).

As highly specialized parasitic plants, species of the genus Orobanche produce a very high number of small seeds. The Orobanchaceae with dust seeds probably evolved in the Mid-Tertiary, exploiting spatially abundant host plants, the dominants of grassland and herbaceous communities (Eriksson and Kainulainen 2011). Parasitism is a secondary trait (reduced morphology, leaf and stem reduction, chlorophyll loss, sturdy development of reproductive organs). A range of morphological and physiological adaptations are observed in obligatory parasites. High seed mortality is compensated for their high productivity. Species whose life strategy relies on a developed ability to disperse and colonize easily dominate in early stages of succession or in systems that are often disturbed: a high number of seeds dispersing easily but with a small quantity of storage substances. Species of this group (r-selection) invest energy in high reproductive effort and the production of highly numerous propagules (MacArthur and Wilson 1967, Pianka 1970). Seeds of the genus Orobanche are extremely small, (rarely exceeding 400 μm), with a wide variety of shapes and seed coat. The seed coat is reticulated with polygonal cells (Plaza et al. 2004). Seeds are usually oval but they are also irregularly shaped due to varied conditions of seed growth and maturation, and the location in the ovary in relation to other seeds (Teryokhin 1997). Humans, machinery, water or wind can easily disperse these seeds (Buschmann et al. 2005). Small seeds of this type do not contain endosperm almost at all. In Orchidaceae further seed development depends on establishing symbiosis with a suitable mycorrhizal fungus. In parasitic species, i.e. in Orobanche, the development depends on the immediate proximity of a seed to the host’s root (3–5 mm) and seeds have to be stimulated to germinate by compounds (e.g., strigol, sorgolactone, orobanchol, alectrol) exuded by the roots of the host. Orobanche seeds do not have a developed germ cell and germinate only when in contact with the root of the host plant. A high number of seeds makes the likelihood of germination success greater (Black et al. 2008).

Data on potential and real seed productivity of the species of the family Orobanchaceae are scarce in the world literature and they are often very broad-based and discontinuous, usually investigating the same economically important species (e.g. Sukachev 1900, Salisbury 1942, Ponce de Leon et al. 1974, Hosamini et al. 1971, Kabulov et al. 1981, Sauernborn 1991, Quasem and Kasravi 1995, Quasem 1998, Teryokhin 1965, 1968, 1997, Buschmann 2004). Information on seed productivity in Orobanche picridis can be found only in a study by Salisbury (1942) but it is very general.

The aim of this study was to determine potential and real seed productivity in Orobanche picridis, as well as correlations between the characteristics of shoots: shoot height, number of fruits/flowers, the length of the inflorescence and the corolla tube. The aim of research is to demonstrate that the shoots of the studied traits show the highest correlation with the production of seeds.

Orobanche picridis F.W. Schultz is a sub-Mediterranean-sub-Atlantic species. It has the NE range limit in Poland and Ukraine (Piwowarczyk 2012). The species is endangered in Poland (Zarzycki 2001, Piwowarczyk in press) and neighbouring countries, i.e. Germany, the Czech Republic, Slovakia (Korneck et al. 1996, Feráková et al. 2001, Procházka 2001).

In Poland it has been reported from 34 localities. It mostly occurs in Poland in the south in the Wyżyna Śląsko-Krakowska up-
The productivity of seeds of Orobanche picridis

The productivity of seeds of Orobanche picridis in the land, Wyżyna Małopolska upland, the Lublin region and the Pogórze Przemyskie foreland. It parasitizes only Picris hieracioides. The occurrence optimum is recorded in calcareous wastelands, field margins, semiruderal grasslands, mostly in the community Dauco-Picridetum hieracioidis (Artemisietea vulgaris class), at an altitude from 140 to 435 m. The number of individuals at the sites varies considerably (from a few to over a thousand shoots) and can change each year; individuals may not occur every year (Piwowarczyk 2012a, b, 2013, Piwowarczyk et al. 2011).

The seed shape of Orobanche picridis is ellipsoid to globose, ca. 0.3 x 0.4 mm. The surface is reticulate-foveolate, lustrous to matt, dark brown to black (Bojňanský and Fargaso-vá 2007).

2. STUDY AREA

Three most abundant localities of Orobanche picridis in southern Poland in the Wyżyna Małopolska upland were investigated (Fig. 1). These are:

- Góry Pińczowskie Mts (GP): between Skowronno and Pińczów (Niecka Nidziańska basin), GPS: 50°32'08.3"N, 20°30'55.6"E, 245 m. Habitat: ecotone zone of xerothermic grasslands and fallows, wastelands on slopes, S-facing. Plant communities: Dauco-Picridetum hieracioidis (Artemisietea vulgaris class), with admixture species belonging to Festuco-Brometea class (Cirsio-Brachypodion pinnati), Arrhenatherion elatioris (Molinio-Arrhenatheretea class), Trifolio-Geranieta sanguinei class. Population size <400 shoots, on chalky rendzinas, pH=7.9, host: Picris hieracioides (Piwowarczyk 2012a, b, 2013).
- Ostra Góra (OG) ecological site, S of Pęczelice (Niecka Nidziańska basin), GPS: 50°26'34"N, 20°47'05"E, 239 m. Habitat: S-facing wastelands and field margins. Plant communities: Dauco-Picridetum hieracioidis (Artemisietea vulgaris class), with admixture species belonging to Festuco-Brometea class (Cirsio-Brachypodion pinnati), Arrhenatherion elatioris (Molinio-Arrhenatheretea class), Trifolio-Geranieta sanguinei class. Population size <100 shoots, on chalky rendzinas, pH=7.9, host: Picris hieracioides (Piwowarczyk 2012a, b, 2013).

3. MATERIALS AND METHODS

Investigations were conducted in 2010 at three most abundant localities of Orobanche picridis in southern Poland in the Wyżyna Małopolska upland. These are: Wesołówka (WE), Pińczów (GP), and Pęczelice (OG).
A total of 90 shoots, 30 per each locality, were examined. Specimen size differentiation in local populations was examined and the following characters were studied: shoot height, number of fruits/flowers, the length of the inflorescence and the corolla tube in the middle part of the inflorescence. A fruit (an ovate-cylindrical capsule) was collected from each specimen to count the number of seeds. A total of 90 ovaries were examined. Ovaries were sampled in the final stage of maturation before their opening in July and August and were collected into paper bags which were then left to dry in natural conditions. Metric features of each shoot were recorded on the bags. Data were examined using Statistica 7.1. Microscopic observations were carried out with a stereo microscope NIKON SMZ800 and a biological microscope NIKON Eclipse 50i.

4. RESULTS

The number of seeds in a single ovary in *Orobanche picridis* varied and ranged from 457 to 3 246. The greatest number of seeds was recorded in specimens at the site in WE (992–3 052) and in OG (853–3 246), and the smallest number at the site in GP (457–2 517). The mean number of seeds in a single ovary in specimens was 2 188 in WE, 1 788 in OG, and 1 353 in GP. The mean number of seeds per fruit at the three sites was 1 776 (Fig. 2).

The total potential number of seeds produced by a single plant was calculated based on the number of fruits on shoots from which single fruits were collected to count the seeds. Total potential seed productivity ranges from 13 665 to 142 824 in specimens in OG, from 11 904 to 151 050 in specimens in WE, and from 8 911 to 100 408 in specimens in GP (Fig. 3). The greatest differentiation of seed productivity is observed for specimens at the site in OG, smaller in WE and the smallest in GP. Based on mean values, the greatest total potential seed productivity is recorded in specimens at the site in WE (71 351), smaller in specimens at the site in OG (58 366), and the smallest in specimens at the site in GP (35 798). The mean number of seeds per specimen is 55 172 based on the data collected at the three sites and ranges between 8 911 and 151 050.

Shoot, inflorescence and flower length was measured, and the number of fruits per shoot were counted for each specimen from which a flower was collected. Shoot height in *O. picridis* ranges from 18 to 55 cm in WE, mean 38 cm; from 18 to 41 cm in GP, mean 30 cm; from 20 to 51 cm in OG, mean 31 cm. Shoot height ranged from 18 to 55 cm in total at the three sites, mean 33 cm (Fig. 4).

Inflorescence length ranged from 5 to 25 cm in WE, mean 15 cm; from 5 to 19 in GP, mean 11; from 6 to 24 in OG, mean 14. Inflorescence length ranged from 5 to 25 in total at the three sites, mean 13 cm (Fig. 5).

Between 10 and 50 fruits per shoot occurred in WE, mean 30, 13–44 in GP, mean 25, and 11–52 in OG, mean 29. The number of fruits produced per shoot at the three sites was 10–52, mean 29 (Fig. 6).

Flower length was 1.2–2.1 cm in WE, mean 1.7 cm; 1.3–1.9 in GP, mean 1.6; 1.1–1.9

![Fig. 2](image-url) Differences between the number of seeds per fruit of *Orobanche picridis* tested by t test. WE – Wesołówka, GP – Pińczów, OG – Pęczelice.

![Fig. 3](image-url) Differences between the number of seeds per shoot of *Orobanche picridis* tested by t test. WE – Wesołówka, GP – Pińczów, OG – Pęczelice.
The productivity of seeds of *Orobanche picridis*

in OG, mean 1.5. Flower length was 1.1–2.1 at the three sites, mean 1.6 cm (Fig. 7).

The correlation between the number of seeds and respective features was analyzed using the above data. Seed productivity depends significantly on the size of a plant, that is on the shoot height, correlation coefficient $r = 0.7$ (Fig. 8), inflorescence length, $r = 0.6$ (Fig. 9), number of flowers and fruits per plant, $r = 0.6$ (Fig. 10), and on the flower size, $r = 0.5$ (Fig. 11).

As well as typical “large” seeds, “small” seeds, as if not fully developed, were observed in ovaries. The percentage contribution of smaller seeds in a single ovary was estimated and it ranged between 5 and 70% in total at the three localities, mean 13%. No evident corre-

5. DISCUSSION

Research on seed productivity of species of the genus *Orobanche* to date is broad-based and discontinuous. Seed productivity is briefly noted in a study by Sukachev (1900), who reports that *O. cumana* produces 1 200–1 500 seeds per fruit and a single plant can produce up to 48 000–60 000 seeds over one season. Studies by Teryokhin (1997) comprising several *Orobanche* species (*O. cernua, O. crenata, O. aegyptiaca, O. mutelii, O. ramosa*) parasitizing wild hosts have shown that 1 000–1 500 seeds can be found in one seed capsule and one plant can therefore produce between 45 000 and 150 000 seeds. This is much higher than seed productivity of *Orobanche* species parasitizing cultivated plants and indicates variability in real seed productivity. *O. crenata* parasitizing faba beans produces from 40 000 seeds per shoot, mean 150 000, maximum 450 000 (Ponce de Leon et al. 1974). Seed productivity in *O. aegyptiaca* is 1 500–2 000 per fruit and 150 000–200 000 per shoot (Kabulov et al. 1981). High variability of seed productivity in *O. cernua* parasitizing different hosts (wild and cultivated plants) has been demonstrated in studies by Teryokhin (1997) and Hosamini et al. (1971). Other studies have shown that a single fruit of *O. ramosa* can produce between 700 and 4 000 seeds. Every plant can produce 35 000 – 500 000 durable and very small seeds (200 000 seeds per gram), leading to a dramatic increase of the *Orobanche* seed bank in the soil (Sauerborn 1991, Quasem 1998, Quasem and Kasravi 1995, Buschmann 2004). In important studies on seed productivity, Salisbury (1942) or Teryokhin (1965, 1968), demonstrated that *Orobanche* species could produce up to 1000 seeds per fruit and up to 350 000 per shoot. By comparison, the number of seeds per single fruit in other genera of the family Orobanchaceae...
can reach 5,500 in *Cistanche flava*, 20,000 in *Diphelypaea coccinea*, and even up to 70,000 in *Aeginetia indica* (Ter yok hin 1965, 1968, Ling 1955 after Kuijt 1969). Such high productivity of small seeds can be compared only to that of the species of the family Orchidaceae (Salisbury 1942, Alexander et al. 2010).

Present investigations into *Orobanche picridis* productivity show that the species produces between 10 and 52 fruits per shoots, mean 28. *O. picridis* has a very high reproductive potential. Seed productivity per fruit ranges from 457 to 3,246 seeds per fruit. The mean number is 1,776 seeds in a single fruit from the three localities. The mean number of seeds per shoot is 55,172 and ranges between 8,911 and 151,050. Salisbury (1942) reports that *O. picridis* an average can produce 4,164 seeds per capsule and up to 94,000–116,000 (very large specimens: 350,000) per single shoot. The difference in the results can be caused by the location of the examined populations at the NE range limit and habitat conditions.

The correlation between individual characters and the number of seeds was also analyzed. Seed productivity is significantly dependent on the plant size: shoot height, correlation coefficient $r = 0.7$ (Fig. 8), inflorescence length, $r = 0.6$ (Fig. 9), number of flowers and therefore the number of fruits on a plant, $r = 0.6$ (Fig. 10), and the flower size, $r = 0.5$ (Fig. 11).

*Orobanche picridis* in Europe prefers disturbed habitats, in early succession stages. These are mostly phytocoenoses of the association *Dauco-Picridetum hieracioidis*. Salisbury (1975) believes that early successional species, adjusted to the colonization of open sites, with low density, have smaller seeds than climax species. The persistence of the seed bank is strictly correlated not only with the seed mass but also with its ability to penetrate the soil (Thompson et al. 1993). Thus small seeds form persistent seed banks (Thompson and Grime 1979). Species of the genus *Orobanche* produce small-sized seeds, compact, glabrous or without hooks. The size, shape and number of seeds is an important factor in the species’ adaptation strategy to the environment (*r*-selection). Small seeds shaped to facilitate soil penetration are
The productivity of seeds of Orobanche picridis

The productivity of seeds of Orobanche picridis is long-lived and form a durable seed bank. For instance, seeds of O. ramosa can lie dormant in the soil for up to 13 years (Buschmann 2004). Germination is often caused by a disturbance in the environment which facilitates closer seed/host contact after the plant cover density decreases. Events such as soil disturbance encourage the occurrence of O. picridis and the species prefers newly abandoned fallows, field margins, grassland and field ecotones, and its abundant occurrence has been reported from sites rooted by boars.

Real seed productivity and seed vitality in Orobanche are always lower than potential. The difference between potential and real seed productivity is 70–90%. 10–25% seeds in almost every fruit is not sufficiently developed and the seeds cannot germinate (Teryokhin 1997). The present investigations into O. picridis also reveal a percentage of seeds not fully developed. The number of small seeds at the three sites ranged between 5 and 70, mean 13%. An evident correlation between the number of “small” seeds in a sample and, for example, the total number of seeds in an ovary, shoot height or the number of flowers, was not recorded. This diversity can depend on a variety of factors such as pollination and fertilization, nutrient supply from the host, climatic and soil conditions. Such observations were also conducted in orchids Platanthera praeclara. Seeds containing no embryos averaged 20% of the mean seeds per capsule (Alexander et al. 2010).

The above investigations show that there are clear differences between the minimal and maximal number of seeds in one fruit and the number of fruits and seeds on a single plant. Not all seeds germinate and minimum of seedlings are able to develop further despite high total seed productivity. This diversity is subject to a variety of factors such as nutrient supply from the host, pollination and fertilization, shoot morphology, climatic and soil conditions, and phytocoenoses in which a plant occurs. Damage caused by Phytomyza orobanchia (Diptera: Agromyzidae) also influences seed productivity in species of the genus Orobanche. Larvae of P. orobanchia mine in Orobanche shoots and capsules, feed on the seeds and also damage the stalks of the plant (Spencer...
1973). Considerable damage in the number of seeds and the shoot condition can also be caused by parasitic fungi, i.e. many species of the genus Fusarium, Ulocladium atrum, Rhizoctonia solani, Alternaria, Myrothecium verrucaria and Sclerotinia sp. They are increasingly used to biologically control invasive broomrape species (Zonno and Vurro 2002, Abouzeida et al. 2004, Andolfi et al. 2005). Plants with dust seeds have never become dominating in any community, with the odd exception of man-made agricultural systems infested by Orobanche or Striga (Eriksson and Kainulainen 2011).

Intraspecific and interspecific seed productivity varies and is subject to considerable changes. The results show that a variety of factors can influence a plant’s general condition and its later seed production. This causes the great majority of seeds does not germinate and wastes; its compensated for their high productivity. The number of seeds is one of the most important aspects of reproductive success in parasitic plants.

ACKNOWLEDGEMENTS: The author thanks Prof. Adam Zając for his helpful comments on the manuscript and Magdalena Smolarczyk for her assistance when counting seeds. This work was supported by the Polish State Committee for Scientific Research (KBN grant no. NN303357733 (2009) and NN303551939 (2010–2013).

6. REFERENCES


Teryokhin E.S. 1965 – O terminach "saprofit", "polusaprofit" i "poluparazit" (v sviazi s charakterom biologicheskix otnoshenij nekotorix pokrytosemennykh rastenij) [The terms saprophyte, hemisaprophyte, hemiparasite (due to the biology of some angiosperms)] – Bot. Zhurn. 50: 60–69 (in Russian).


Teryokhin E.S. 1997 – Weed Broomrapes – systematics, ontogenesis, biology, evolution – Auftieig-Verlag, Germany.


Received after revision May 2012