Host-parasite relationships during the germination phase in *Orobanche crenata* and *O. minor*

Vztahy mezi hostitelem a parazitem během klíčení u *Orobanche crenata* a *O. minor*

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Končalová M. N. et Kropáč Z. (1997): Host-parasite relationships during the germination phase in *Orobanche crenata* and *O. minor*. – Preslia, Praha, 68(1996):329–339.

A fast laboratory method for testing the germination of *Orobanche crenata* Forsk. and *O. minor* Smith was elaborated by using agar media containing root exudates from host and/or provocative plants. Ecophysiological conditions suitable for germination of both *Orobanche* species were found. The method proved useful also for studying the dynamics of the first ontogenetic stages of both *Orobanche* species; their germination, growth of procaulome and its attachment to the host plant were described. The terminology of the first stages of broomrapes' development is discussed.

Keywords: *Orobanche crenata, O. minor,* parasitic plants, host plants, provocative plants, trap crops, germination, root exudates, infestation

Introduction

Weedy broomrapes (*Orobanche* sp.) seriously damage various agricultural crops, especially in warm regions of the globe. In spite of intensive research on the biology of broomrapes and their control (Musselman et al. 1979, Pieterse 1979, Parker et al. 1984, Borg 1986, Weber et Forstreuter 1987, 1991, Teryokhin 1988) many theoretical as well as practical problems remain unsolved. In Egypt, *Orobanche crenata* Forsk. is a real menace for the cultures of *Vicia faba* L. (ICARDA 1985). During the studies on this dangerous weedy parasite, a need for a fast method testing *Orobanche* seed germination under different conditions emerged. The time of infestation by the parasite during the ontogenetic development of faba beans also remains unclear. The present study attempts at filling these gaps in our knowledge.

In addition, the seeds of *Orobanche minor* were tested for comparison. This species, a parasite of the red clover, is considered a quarantine weed in the Czech Republic (Kropáč 1973).

Material and methods

Plant species used

Plant species used in the experiments are listed in Table 1. Seeds of all species were harvested in 1984 and stored at room temperature under dry and dark conditions. The

This study was carried out during 1984–1986 as a part of the research program "Weedy *Orobanche* species and their control" under the cooperation between the Botanical Institute, Czechoslovak Academy of Sciences, Průhonice, Czechoslovakia, and the Botany Laboratory, National Research Centre, Cairo, Egypt.

Table 1. – Plant species used in the experiment (see Methods for details). H – host, TH – typical host, AH – atypical host, P – provocative plant.

Species	Place of origin	Typical host plant
A. Parasitic plants:		
Orobanche crenata	Egypt (surroundings of Cairo)	*Vicia faba*
O. minor	Czech Republic (eastern Bohemia)	*Trifolium pratense*
B. Host and/or provocative plants:		for *Orobanche*:
TH *Vicia faba* subsp. *faba*		*crenata*
cv. Giza 1	Egypt, Cairo-Giza	
cv. Giza 2	Egypt, Cairo-Giza	
cv. Giza 4	Egypt, Cairo-Giza	
P *Zea mays*	Egypt	*crenata*
P *Linum usitatissimum*	Egypt	*crenata, minor*
P *Medicago sativa*		*minor*
cv. Pálava	Czech Republic	
cv. Europa	Czech Republic	
TH *Trifolium pratense* subsp. *pratense*	Czech Republic	*minor*
AH *T. hybridum*	Czech Republic	*minor*
AH *T. repens*	Czech Republic	*minor*
AH *T. incarnatum*	Czech Republic	*minor*

spectrum of cultivated plants was chosen in order to cover (i) typical host plants (TH), i.e. those on which the ontogenesis of certain *Orobanche* species is fully completed, (ii) atypical host plants (AH) inducing only underground development of *Orobanche* up to the stage of tubercles, and (iii) provocative plants (P), i.e. those inducing only germination of *Orobanche* seeds (see Kropáč 1973 for further details on the terminology used in the present paper).

Root exudates

Seeds of host and provocative plants were sterilized in 1 % $KMnO_4$ for 5 minutes, then washed in distilled water and allowed to germinate on moist filter paper in Petri dishes at room temperature (20°C) under permanent light or normal daylight. After five days, the seedlings were transferred onto plastic nets fastened on the top of glass tubes (250 ml volume) which were filled to the top with distilled water. Attention was paid that all roots of the seedlings were submerged. Five seedlings of faba bean or corn, 30 seedlings of flax, or 100 seedlings of the remaining species were used for each tube. A presumption was taken that the concentration of root exudate in the water would increase with the duration of root submergence.

To obtain the root exudates from plants in various stages of their ontogenetic development, two weeks old plants of *Vicia faba* cv. Giza 1 and cv. Giza 4 were transferred in 700 ml glass tubes filled with Hoagland 3 nutrient solution. Three plants per tube (3 tubes for each variety) were cultivated under permanent aeration until the blooming stage. Because of low evaporation of the nutrient solution due to the parafine lid, there was no need to add either water or the nutrient solution.

Table 2. – Germination of *Orobanche crenata* after 5 days of cultivation. Values in % of germinated seeds.

Root exudate	Days of moist pretreatment of *Orobanche* seeds								
	0–8	9	10	11	12	13	14	15	16–18
Vicia faba cv. Giza 1	0	0	0	3	10	5	0	0	0
Linum usitatissimum	0	5	13	8	8	10	0	1	0

Germination of Orobanche seeds

Fully developed seeds were separated from debris of inflorescences. Hundred seeds for each sample were counted and each seed was picked by a plastic needle attracting it by electrostatic power. To remove substances inhibiting *Orobanche* seed germination, the seeds were wrapped in filter paper and exposed to a moist pretreatment (conditioning) by distilled water at room temperature (20°C) using the ascendent paper chromatography method. The period of conditioning lasted 0, 1, 2, ... to 18 days for individual variants.

Cultivation media for the germination of *Orobanche* seed were prepared by dissolving Difco-Agar in different root exudates to obtain 1% agar solution. To test the germination, the samples of 100 pretreated seeds were sown on the surface of 10 ml 1% agar media (in Petri dishes 4 cm in diameter) and incubated at 20°C in darkness.

To identify which part of the root is attacked by the parasite, seedlings of typical or atypical host plant were incubated in Petri dishes (9 cm in diameter) on 1% agar in Hoagland nutrient solution together with pretreated *Orobanche* seeds.

The *Orobanche* seed was considered as germinating if the threadlike procaulome reached at least the length of the seed itself (according to Bischof et Koch 1973). Photodocumentation of germinating *Orobanche* seeds was made on living plants in Petri dishes using both down-through and upper illuminations.

The experiments were carried out from 1 February to 15 May 1985 and from 1 June to 15 July 1986. Almost 150 experimental variants were used in order to identify the best period of *Orobanche* seeds pretreatment and find optimal conditions for seed germination of both *Orobanche* species studied. Because of the time-consuming separation and counting of *Orobanche* seeds, only two replicates were used for each variant, i.e. the results were based on the response of 200 *Orobanche* seeds.

Results

Pretreatment (conditioning) of Orobanche seeds

The root exudates resulting from three-day cultivation of host or provocative plant were used in this part of the study. Experiments with different duration (0,1,2,3,...18 days) of *Orobanche* seed pretreatment showed that no germination occurred in either *Orobanche* species if moist pretreatment was shorter than 9 days. For *Orobanche crenata* the best results were obtained with seeds washed for 10–14 days. The exudate from roots of *Linum usitatissimum* was used as a stimulating agent in cultivation media (Table 2). For *Orobanche minor*, the highest seed germination (30 %) was obtained after 12 days of

Table 3. – Germination of *Orobanche* seed (in %) in media with root exudates obtained after 6 days of cultivation of the host or provoking plant.

	O. crenata	*O. minor*
Vicia faba cv. Giza 1	66	95
Vicia faba cv. Giza 2	25	37
Vicia faba cv. Giza 4	22	92
Trifolium hybridum	23	45
Trifolium repens	2	3
Trifolium incarnatum	1	0
Linum usitatissimum	13	15
Zea mays	1	8

Table 4. – Germination of *Orobanche crenata* seeds influenced by various amounts of root exudates.

	Quantity of fresh root (mg) used for exudate (10 ml)	Seed germination (%)
Vicia faba cv. Giza 1	12	15
	18	30
	31	47
	46	51
	62	55
Vicia faba cv. Giza 2	17	12
	24	16

moist pretreatment. The exudate from roots of *Trifolium hybridum* was used as a stimulating agent in this case.

Germination of Orobanche seeds

No germination occurred without root exudate of either host or provoking plant. The most effective root exudates stimulating seed germination in both *Orobanche* species were obtained after six days of cultivation of the host or the provoking plant (Table 3).

Under suitable ecophysiological conditions (temperature 20°C or little higher, well pretreated seeds and sufficient amount of an active substance from the root exudate of the host or provoking plant) the germination of *Orobanche* seeds started the second day after sowing. The maximum of germinated seeds was achieved during the first 7 days.

Under the experimental conditions used in the present paper, the root exudates from *Medicago sativa* (both cultivars) did not provoke *Orobanche* seed germination.

Three cultivars of *Vicia faba* were used to prove their assumed different influence on the germination of *Orobanche* seed. In the field experiments carried out in Egypt, the cultivars Giza 1 and Giza 4 were found as very sensitive to broomrape infestation if compared with Giza 2 which seemed to be more resistant (E. A. Hassan, personal communication). In our experiments (cultivation in glass tubes in nutrient solution), the root systems of Giza 1 and Giza 4 were twice as large as those of Giza 2 after the same period of cultivation. Table 4 demonstrates the relationship between the germination of *Orobanche* seeds and the quantity of roots producing the stimulating exudates.

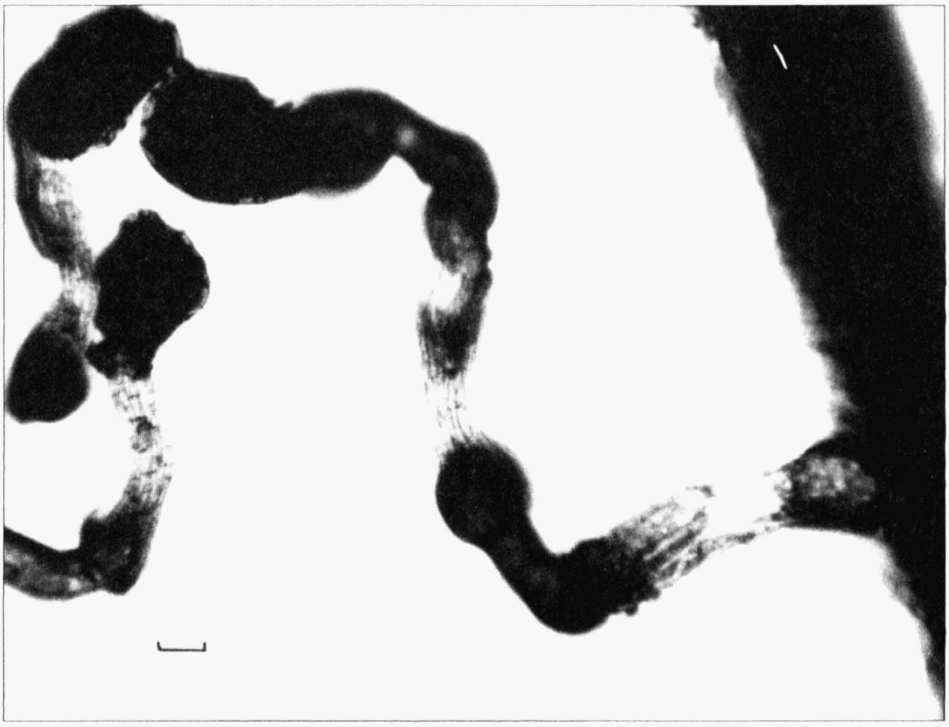

Fig. 1. – *Orobanche crenata* Forsk. attacking its typical host plant *Vicia faba* L., nine days after germination. The bar corresponds to 10^{-1} mm.

The experiments with root exudates from plants of *Vicia faba* in different ontogenetic stages of development showed that the provoking effect of the root exudate did not depend on the ontogenetic stage of the host plant.

Dynamics of the early stages of Orobanche development

The first ontogenetic stages of *Orobanche crenata* and *O. minor* were studied directly on agar plates by binocular magnifying glass (27 ×). Under the optimum conditions, both *Orobanche* species started to germinate 36–48 hours after sowing and reached the maxima of germinated seeds usually during the first week. The procaulome reached the maximum length (3 mm for *Orobanche crenata* and 2 mm for *O. minor*) in two weeks (Fig. 1). The screw-like movement of the procaulome was observed from the 7th day following the germination (Fig. 2).

Dynamics of infestation

The process of infestation was studied on agar plates where seedlings of host plants and parasite procaulomes were grown together at room temperature (20°C). Injured roots were not attacked at all. *Orobanche* procaulomes attacked only healthy fast growing roots. The maximum distance between *Orobanche* seed and host root was equal to the maximum length of procaulome, i.e. 3 mm for *O. crenata* and 2 mm for *O. minor*. The

Fig. 2. – Screw-like growth of the procaulome of *Orobanche crenata*. The bar corresponds to 10^{-1} mm.

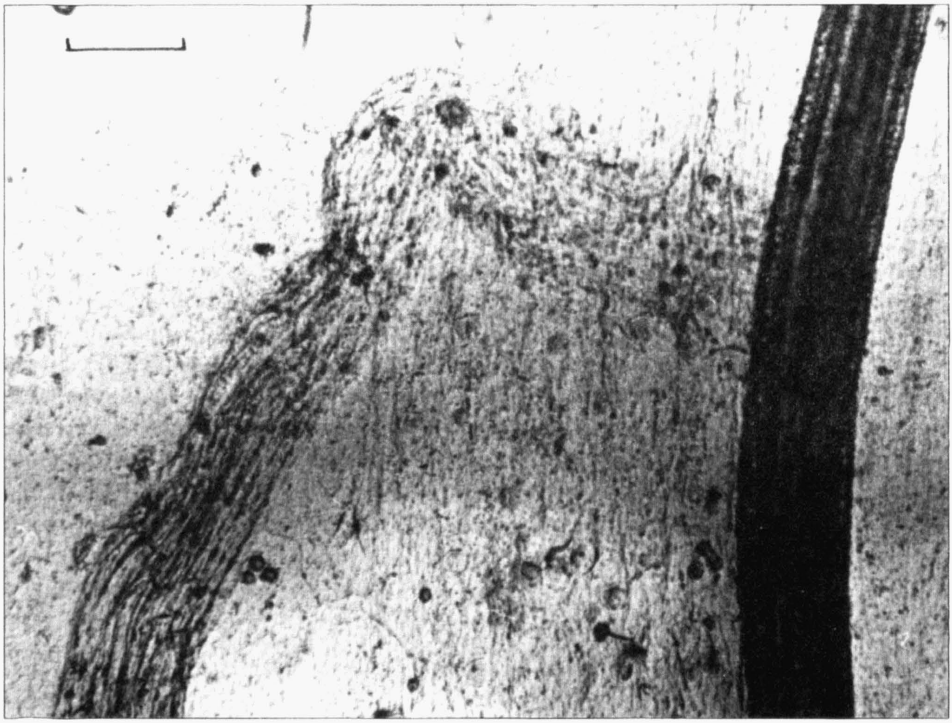

Fig. 3. – Procaulome of *Orobanche crenata* penetrating to vascular tissues of an atypical host plant *Trifolium hybridum* L. The bar corresponds to 10^{-1} mm.

infestation occurred during the second week of *Orobanche* seed germination (day 9–13). *Orobanche crenata* was observed to infest *Vicia faba* cv. Giza 1, *Trifolium incarnatum*, *T. hybridum*, and *T. repens*, whereas *O. minor* infested *Trifolium pratense*, *T. repens*, and *T. incarnatum*. In each case, the infestation occurred in the area of root hairs of the host plant. Individual cells from the top of the procaulome grew in the form of small tentacles around root hairs and gradually penetrated through the root epidermis and primary cortex and reached vascular tissues of the host root (Fig. 3). This process lasted for another 6–7 days.

The procaulomes older than 14 days lost their screw-like movement and were not able to penetrate into the root tissues of the host plant. Under the stable moisture conditions, those *Orobanche* procaulomes which did not succeed to reach the host plant root remained without any visible change for more than 30 days (with the observed maximum of 35 days). After then the colourless procaulome turned brownish-yellow and the germinated *Orobanche* plant died.

Discussion

High fecundity of a single plant and enormously large soil seed bank persisting for many years is the main problem in the control of weedy broomrapes (Kadry et Tewfic 1956, Hiron 1973, etc.). As control measures aiming at the reduction of broomrape population in crop stands mostly failed, effort was taken to elaborate preventative measures before the populations start to expand (see Ramaiah 1987 for a review). The studies are thus focused on the stimulating effect of chemical substances on broomrapes' seed germination (Kukula et Masri 1984) with the aim to elaborate the methods of reducing the seed reserves in the soil (Sauerborn et Saxena 1986). Various methods for the investigation of germination and early development of *Orobanche* were described (Kadry et Tewfic 1956, Hiron 1973, Bischof et Koch 1973, Linke et Vogt 1987). Field experiments as well as traditional pot cultures or cultures in special transparent boxes are rather space-demanding and long-term before the results are available. Water solutions of substances provoking *Orobanche* seed germination were often used in laboratory methods using sand or blotting paper as a base. Later on, Aalders et Pieters (1986) cultivated host plants in glass tubes filled with agar media and seeds of the parasite. However, our method using Petri dishes with solid agar media as a base for soluble provoking substances seems to be indispensable for accurate quantification of these substances and/or germinated *Orobanche* seeds. This method is also suitable for direct and continuous observations of the first stages of *Orobanche* development by means of magnifying device which may be complemented with camera.

To check the suitability of our method for testing the germination of *Orobanche* seed under different conditions, the experiments were performed in many different variants. Despite of the limitation due to the low number of replicates, we believe that the results demonstrate the usefulness of the method not only for this purpose but also for direct observation of the parasite's behaviour during its first ontogenetic stages.

For successful germination, *Orobanche* seed needs (a) after-ripening, i.e. breaking of dormancy, (b) pre-treatment (i.e. conditioning), and (c) biochemical stimulation. All these aspects must be taken into account when conducting laboratory experiments. Only limited data are available for the period of dormancy: Hiron (1973) succeeded to germinate six

weeks old seeds of *O. crenata*. In the present paper, the seeds used in the first experiments with *O. minor* were at least six months old and those used in experiments with *O. crenata* and in the summer part of all experiments were even older; both species were able to germinate provided the other two conditions were met.

The 9–14 day pretreatment period corresponds to the current knowledge (cf. Linke 1987). If the conditioning lasted too long, secondary dormancy could be induced, e.g. the so-called "wet dormancy" described for *Striga hermontica* (Pieterse et al. 1984).

Optimum temperature for *Orobanche* seed germination lies between 18–23°C (Kasasian 1973, Linke 1987). By using the same range we obtained very rapid germination of *Orobanche* seed, i.e. during 2–4 days. Many authors refer to the necessity of darkness for germination, although small numbers of germinated seeds can be also obtained under some light (Hiron 1973).

Plants with stimulating effect on germination of the parasite may be sown as so-called "trap crops" (Ramaiah 1987) in various crop rotation. In our experiments, flax (*Linum usitatissimum)* was confirmed as a very effective provocative plant, representing thus potential "trap crop" for both *Orobanche* species. Corn (*Zea mays*) stimulated seed germination of *O. crenata* and *O. minor* to much lesser extent than flax. Under our experimental conditions, lucerne (*Medicago sativa)* did not stimulate seed germination of *O. minor* at all. Although the range of hosts and/or provocative plants has been relatively well known for each *Orobanche* species (see the thorough review by Parker 1986), some regional alterations or shifts may be observed. This phenomenon was demonstrated earlier by Kropáč (1973). Parker (1986) summarized very broad range of hosts with *Orobanche minor*, some of them probably locally acting as provocative plants, and discussed the complicated problems involved including taxonomic ones (see also Musselman 1986).

Besides, there are various cultivars of typical host plants with different susceptibility to the infestation, and the use of those more resistant thus represents an alternative way of broomrape control. Faba bean cv. Giza 2 seemed to be more resistant against broomrape infestation during field experiments than cv. Giza 1 or cv. Giza 4 (E. A. Hassan, personal communication 1984). In our experiments the smaller size of the host's root system from faba bean cv. Giza 2 probably caused the lesser broomrapes germination compared to the cv. Giza 1 and Giza 4. Therefore the lower rate of infestation of *Vicia faba* cv. Giza 2 under the field conditions could be explained by smaller size and slower development of root system of this cultivar in comparison with cv. Giza 1 and possibly cv. Giza 4.

The interactions in the host-parasite system are rather complicated (Cubero 1983, Aalders et Pieters 1986, Borg 1986a, Ramaiah 1987, Linke 1987, Teryokhin 1988). Borg (1986b) recommended to distinguish at least three types of resistance (true resistance, tolerance, and avoidance) and pointed out to the problems caused by the variability of both the host and the parasite. According to this classification, faba bean cv. Giza 2 may exhibit avoidance rather than true resistance. However, Nassib et Hussein (1989) referred to faba bean cv. Giza 402 as true resistant.

Our experiments also indicate that the provoking effect of root exudates is independent of the ontogenetic stage of the host plant. Aalders et Pieters (1986) and Linke (1987) came to the same conclusion with provoking plants. This information is very important for control by means of sowing various trap crops.

The maximum length of procaulome is species-dependent, ranging from 2 to 4 mm for *Orobanche* species (Linke 1987) which corresponds to our observation. According to

Borg (1986a) the diameter which can be overcome by procaulome when attaching the host root is 3–4 mm. Kadry et Tewfic (1956) stated for *O. crenata* the common distance 2.5 mm, less frequently 3 mm.

The screw-like movement of the procaulome is of the chemotropic nature. Whitney (1979) showed the influence of the exudate concentration on the development of procaulome, especially the effect on its length, screwing and positive chemotropic response, which corresponds with our observations. On the contrary Teryokhin (1988) takes the straigth chemotropic growth of the procaulome for granted and its screw-like movement considered as doubtful.

Finally it could be helpful to clear up the rather confusing and dissent terminology of the first stages of *Orobanche* development. Already the pioneer monograph by Koch (1887) stated that the embryo of broomrape seed represented an undifferentiated globe of cells lacking cotyledons and primary root. Germination is morphologically manifested by expanding embryo cells out of the testa. This threadlike organ was first called "procaulome" by the Czech botanist in 1892 (see Velenovský 1907 for detail). Several other names were used later on by various authors, e.g. "radicle" (Chabrolin 1939 and others), "germ tube" (Krenner 1958), "germ-tube-like organ" (Abou-Raya et al. 1973) or "filiform germ" (Teryokhin 1988). We follow the oldest term procaulome (cf. Aber 1984), although the other terms are used simultaneously by various authors. When the procaulome reaches the root of the host plant its apex attaches to the root of the host and a part of the procaulome ("endophyte") gradually penetrates to the host's vascular tissues. New histological data have been revealed recently by using the scanning electron microscope (Aber 1984), and especially the processes of procaulome differentiation into the outer and inner part were described. After the connection with host vessels, the procaulome changes into the primary haustorium, sometimes called also "sucker". The attachement of the procaulome is usually termed "holdfast stage" or "appressorium" and the part of the procaulome remaining outside gives rise to a tubercle. The tubercle subsequently grows and produces numerous tentacles in the form of root-like organs. These tentacles attack neighbouring host's roots on which they may form secondary haustoria and secondary tubercles. This stage was termed by Kropáč (1973) as "underground clusters" or by others as "tubercles" with crown-like appearance. After this, bud stage follows soon, i.e. the buds are produced by the tubercles subsequently forming the emergent stem and the inflorescence, representing thus the shoot (above-ground) stage of the parasite's development. This description relates only to the case of a full parasite's development with typical host plants. With atypical host plants, the broomrape reaches only the stage of underground tubercles or clusters. With provocative plants, parasite's seed germination takes place and then only the stage of procaulome is reached.

Acknowledgements

Thanks are due to Mrs. H. Janovská, Institute of Botany, Průhonice, for technical assistance in separating and counting *Orobanche* seeds.

Souhrn

Byla vypracována laboratorní metoda pro testování klíčení plevelných druhů záraz (*Orobanche crenata* Forsk. a *Orobanche minor* Smith). Vzorky zárazových semen byly předem vypírány metodou vzestupné

papírové chromatografie (optimální doba předpůsobení pro *O. crenata* byla 9 dní, pro *O. minor* 12 dní). Nakličování bylo prováděno na agarových plotnách s přidáním stimulujících kořenových výměšků rostlin hostitelských nebo provokačních. Nejméně šestidenní a starší kultury hostitelských rostlin (bez ohledu na stupeň jejich ontogenetického vývoje) poskytovaly při daném uspořádání pokusů dostatečně koncentrované kořenové výměšky v kultivačním mediu, které byly schopny stimulovat maximální počet vyklíčených semen záraz (66 % u *O. crenata*, 95 % u *O. minor*). Z testovaných provokačních rostlin měl len největší schopnost stimulace klíčení zárazových semen, naproti tomu s kořenovými výměšky vojtěšky se nám nepodařilo semena záraz naklíčit. V našich experimentálních podmínkách klíčící záraza napadala kořen hostitelské rostliny vždy v oblasti kořenového vlášení.

Popsaná metoda je vhodná nejen k rychlému zjišťování vlivu různých substancí na klíčení záraz, ale také umožňuje průběžné sledování, případně fotodokumentaci počátečních vývojových stádií parazita. V optimálních podmínkách dochází ke klíčení záraz během dvou dnů, prokaulom *O. crenata* dosahuje maximální délky 3 mm, prokaulom *O. minor* 2 mm. Chemotropické pohyby prokaulomu se objevují druhý týden po vyklíčení. V této době také dochází k jeho spojení s hostitelskou rostlinou. Pokud k němu nedojde, zárodek odumírá nejpozději za 35 dní od počátku klíčení.

Vzhledem k tomu, že různí autoři používají pro jednotlivé vývojové fáze záraz různé názvy, je v závěru práce uveden i terminologický přehled.

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Received 11 December 1995
Accepted 30 September 1996