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EFFECT OF TEMPERATURE, RELATIVE HUMIDITY AND LIGHT ON CONIDIAL GERMINATION OF OAK POWDERY MILDEW (*MICROSPHAERA ALPHITOIDES* GRIFF. ET MAUBL.) UNDER CONTROLLED CONDITIONS

P. PAP[1], B. RANKOVIĆ[2] and S. MAŠIREVIĆ[3]

[1] *Institute of Lowland Forestry and Environment, University of Novi Sad,* 21000 Novi Sad, Serbia
[2] *University of Kragujevac, Faculty of Science,* 34000 Kragujevac, Serbia
[3] *University of Novi Sad, Faculty of Agriculture,* 21000 Novi Sad, Serbia

Abstract - The influence of temperature, humidity and light on the conidial germination and germ tube elongation of oak powdery mildew (*Microsphaera alphitoides* Griff. et Maubl.) was studied in controlled conditions. The maximal germ tube length was attained at 25°C, whereas at lower and higher than optimal temperatures, germ tube growth was significantly lower. Germ tubes begin to develop at all values of relative humidity (10-100%), reaching the maximum length at 90%. The development of germ tubes was the most intense in full light and the lowest in total darkness. The artificial infection of floating leaves showed that an increasing age had an inhibitory effect on the mycelium development and spore formation. Since conidia play a crucial role in powdery mildew epidemiology, it is of particular importance to elucidate the influence of environmental factors in the complex relations that exist between the plant and its pathogen.

Key words: Oak powdery mildew, conidial germination, environmental factors

INTRODUCTION

Oak powdery mildew caused by the fungus *Microsphaera alphitoides* (Griff. et Maubl.) is certainly the most important common oak leaf disease in Europe. According to professional and scientific literature, this fungus is very harmful because of its direct effect on plants (nutrient uptake from leaf tissue), and indirect harmful effect since its epiphytic mycelium reduces assimilation by covering the leaf surface. During the vegetation period, the fungus forms several micro cycles of conidial stage, so its infectious potential on the leaves increases exponentially. In favorable conditions, new conidia are formed from a mature conidium in 3-4 days (Butin, 1989). Because of its harmful effects, this fungus was and still is the subject of interest and intensive study from various aspects. A less studied aspect is the part of its life cycle from the time of conidial maturity to hyphal penetration into host leaf tissue. This period is crucial for further development of the fungus and thereby infection of the host plant. During an interval of favorable conditions, which in nature do not last very long, conidia germinate and form germ tubes that infect the leaf tissue by developing secondary hyphae. In addition to external conditions, a critical factor in infection is the susceptible phenological stage, i.e. the presence of young leaves (Edwards and Ayres, 1982; Thomas et al., 2002; Marçais et al., 2009; Desprez-Loustau et al., 2010; Glavaš, 2011).

The aim of this study was to examine the importance of basic environmental factors such as temperature, relative humidity and light, on the germination of oak powdery mildew conidia and, based on the obtained results, to clarify their roles and place in the epidemiology of this pathogen. The objective of the study was also to assess the importance of leaf age as a factor of passive resistance of plants to powdery mildew infestation.

MATERIALS AND METHODS

The sources of conidia were heavily infected one-year-old common oak (*Q. robur*) seedlings from naturally regenerated stands in the area of Ravni Srem (Serbia). The fact that conidia germinate well in various smooth substrates (Ranković, 2002) was used in the experiment. The spores from the leaves were applied directly on dry microscope slides and a leaf fragment of about 1 cm^2 was placed over the mass of conidia. The microscope slides were carefully placed in open Petri dishes, which were then placed into a climate chamber (Fig. 1). The conidia were incubated under different conditions of temperature, relative humidity and light for 24 h.

Fig. 1. Incubation of conidia in the climate chamber.

The influence of temperature on germ tube development was tested at 5, 10, 15, 20, 25, 30 and 35°C. Incubation of conidia developed in full light, and relative humidity was set at 90%.

The conidia were exposed to the influence of relative humidity in a wide range of values (10-100%) with intervals of 10%. Under these conditions, conidia were incubated at the optimum temperature of 25°C in full light.

The influence of light on germ tube dynamics and growth was tested in three different variants. In the first variant, the tests were performed in full light (9 fluorescent lamps of 40W with light intensity of 12000 lux); in the second variant, the light and dark periods were alternated (with a photoperiod of 4 h), and the third test was performed in total darkness. In all three cases, conidia were incubated at 25°C and at 90% of relative air humidity.

The conidial germination dynamics and germ tube lengths were determined microscopically after 4, 8, 12 and 24 h after the onset of incubation, using Quick Photo Camera 2.3. The experiments were conducted in three replicates for each treatment. In each replicate, germ tube lengths of 30 conidia were measured to obtain their average lengths. The samples of conidia were selected at random in the visual field of a microscope. The results were statistically analyzed using ANOVA and Duncan's test with a significance threshold of P=0.05 (STATISTICA 10).

Artificial infections of floating leaves of different ages were carried out by applying a suspension of conidia on the leaf surface. The concentration of conidia in the suspension was adjusted to 250-300 spores per 1 mm^3. In glass jars 20 cm in diameter a suspension of conidia in the form of fine mist was applied to adaxial and abaxial leaf surfaces. Leaves aged 7-10 days were light green, thin and soft, semi-expanded. Fully developed, but still thin and mesophilic leaves were aged 10-15 days, while the leaves aged 20 and more days were dark green and leathery (Fig. 2). The surface of epiphytic mycelium was determined at 12 h intervals during the five-day experiment (120 h) and its surface was measured using computer software APS Assess 2.0.

Fig. 2. The floating leaf method (7-10 day-old leaves)

RESULTS

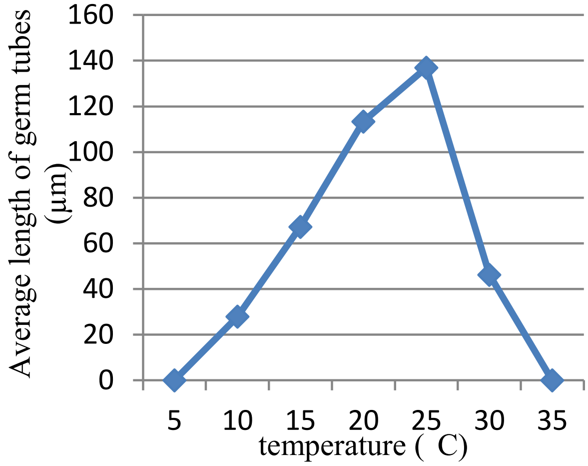
Influence of temperature on conidial germination and germ tube length

The highest average length of germ tubes was recorded at 25°C at all of the stated time intervals (Table 1). At temperatures lower and higher than optimal, germ tubes growth was significantly lower, while at 5°C and at 35°C the conidia did not germinate. Conidia formed germ tubes at a wide range of temperatures (10-30°C), exhibiting the eurivalent character to this environmental factor (Graph 1). Therefore, temperature is not a restricting factor in the germination of conidia, as powdery mildew occurs in temperate zones with prevailing favorable temperature conditions for its occurrence and spreading.

Table 1. Influence of temperature on *M. alphitoides* conidial germination and germ tube length (relative humidity 90%, photoperiod 24 h).

Temperature (°C)	Time intervals from the beginning of conidium incubation			
	4h	8h	12h	24h
	Average length of germ tubes (μm)			
5	0	0	0	0
10	0	10.1	20.6	27.9
15	13.9	30.2	43.6	67.2
20	16.0	44.7	67.1	113.3
25	16.9	48.9	74.4	136.9
30	11.8	27.1	42.7	46.2
35	0	0	0	0

Temperature (°C)	Average length of germ tubes (μm)
35	0.0 a
5	0.0 a
10	27.9 b
30	46.2 c
15	67.2 d
20	113.3 e
25	136.9 f
F=1289.83 p=0.00*	



Graph 1. Average length of *M. alphitoides* germ tubes at different temperatures after 24 h incubation according to the results of Duncan's test.

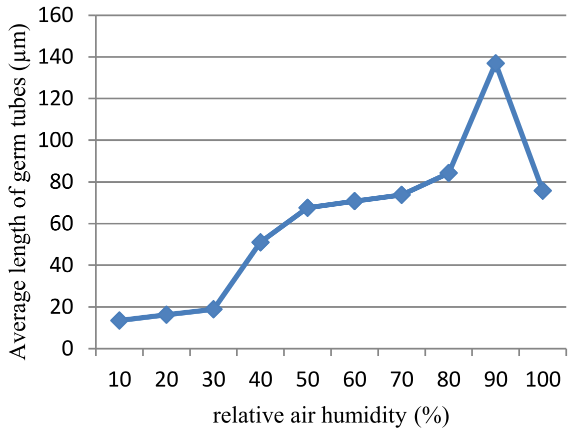
Influence of relative humidity on conidial germination and germ tube length

The occurrence of germ tubes was observed at all values of relative air humidity (Table 2, Graph 2). Germ tube lengths increased with increasing relative humidity up to a maximum 90%. At 100% relative humidity (conidia immersed in a drop of water), germ tube length was significantly lower than the maximal recorded value. The conidia formed germ tubes with appressoria even at a relative humidity of 10%, but their growth was stopped after 8 h incubation. This shows that powdery mildew is largely independent in terms of moisture, especially in the early stages of conidial germination. Thanks to a high water content, conidia start their germination even in very dry environmental conditions with a low content of wa-

Table 2. Influence of relative air humidity on *M. alphitoides* conidial germination and germ tube length (25°C, photoperiod 24 h).

Relative humidity (%)	Time intervals from the beginning of incubation of conidia			
	4 h	8 h	12 h	24 h
	Average length of germ tubes (μm)			
10	7.8	13.5	growth stopped	growth stopped
20	13.3	16.3	22.5	growth stopped
30	14.1	18.9	37.0	growth stopped
40	12.9	21.2	38.3	51.0
50	13.8	29.7	37.6	67.6
60	14.7	25.8	39.8	70.8
70	15.6	31.5	44.6	73.8
80	14.0	32.2	48.9	84.3
90	16.9	48.9	74.4	136.9
100	15.0	28.8	39.9	75.8

Relative humidity (%)	Average length of germ tubes μm)
10	13.5 a
20	22.5 b
30	37.0 c
40	51.0 d
50	67.6 e
60	70.8 ef
70	73.8 f
100	75.8 f
80	84.3 g
90	136.9 h
F=196.12 p=0.00*	



Graph 2. Average length of *M. alphitoides* germ tubes at different air humidity values after 24 h incubation, according to the results of Duncan's test

ter vapor (<30%), or in conditions that are rarely or almost never found in nature. High relative humidity (80-90%) had the most favorable effect on germ tube growth, while conidial germination in a drop of water was slowed down (Figs. 3 and 4).

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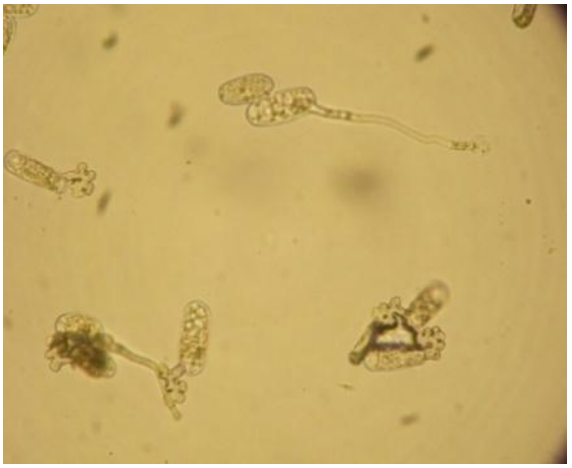

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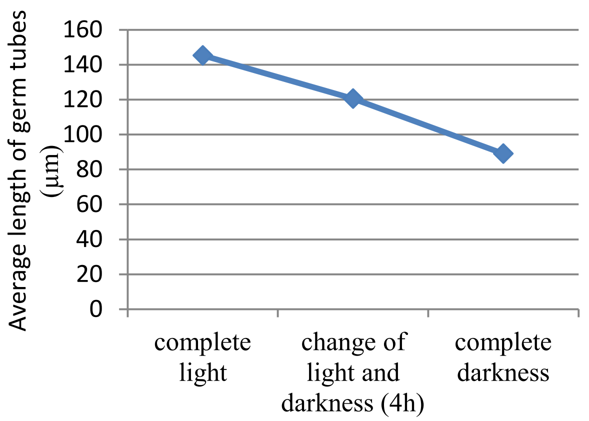
Figs. 3 and 4. Powdery mildew germ tubes and appressoria

Table 3. Influence of light on *M. alphitoides* conidial germination and germ tube length (25°C, relative humidity 90%).

Light regime	Time intervals from the beginning of conidial incubation			
	4h	8h	12h	24h
	Average length of germ tubes (μm)			
photoperiod 24 h	16.9	48.9	74.4	136.9
alteration of light and dark periods with 4 h photoperiods	17.8	50.8	73.7	120.6
total darkness	17.0	47.3	68.7	89.1

Light regime	Average length of germ tubes (μm)
total darkness	89.1 a
alteration of light and dark periods (4h)	120.6 b
full light	136.9 c
F=180.42 p=0.00*	



Graph 3. Average length of *M. alphitoides* germ tubes at different light values after 24 h incubation, according to the results of Duncan's test.

Influence of light on conidial germination and germ tube length

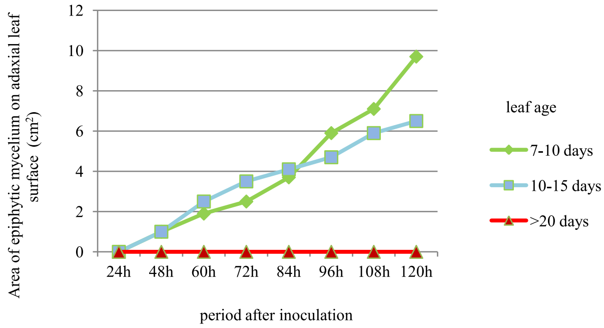
The increase in germ tubes was significantly higher in full light than in dark conditions. The influence of the alteration of light and dark periods made the transition between these variants (Table 3). In the first 12 h, germ tubes in all treatments had approximately the same growth trend. At the end of the experiment, germ tube lengths showed different relations between the tested variants. During the time interval from 12-24 h, the rate of germ tube growth increased significantly in full light compared to the other tested variants (Table 3, Graph 3). Therefore, light is a very important environmental factor that had a stimulating effect on the development and growth of germ tubes.

Fig. 5. Mycelium on 7-10 day-old leaf.

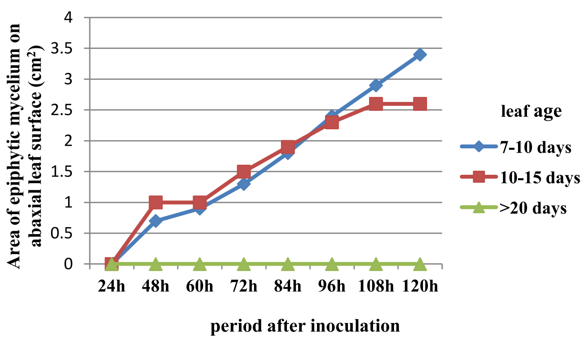
Fig. 6. Mycelium on 10-15 day-old leaf.

Development and sporulation of the fungus on the floating leaf

The infection was accomplished only on young leaves below 15 days of age (Graphs 4 and 5). The appearance of mycelium was observed 48 h after inoculation and already after 2.5 days (60 h) sporulation or appearance of conidia occurred on the conidiophores. Thus, under optimal controlled conditions, a new generation of conidia was formed in less than 3 days. Mycelium developed gradually, taking a relatively limited area, both on the upper and the lower



Graph 4. Development of *M. alphitoides* mycelium on the adaxial side of the inoculated floating leaves (25°C, relative humidity 90%, light intensity 12000 lux).



Graph 5. Development of *M. alphitoides* mycelium on the abaxial side of the inoculated floating leaves (25°C, relative humidity 90%, light intensity 12000 lux).

sides of young leaves. At the end of observations, on the upper side of 7-10 day-old leaves, the mycelia reached the maximum value of 9.7 cm^2, while on 10-15 day-old leaves, the area of mycelia was 6.5 cm^2 (Graph 4, Figs. 5 and 6).

Mycelium was less developed on the abaxial leaf surface. At the end of the observation period, mycelia covered 3.4 cm^2 of 7-10 day-old leaves, and 2.6 cm^2 of 10-15 day-old leaves (Graph 5).

Artificial infections of floating leaves showed that leaf resistance to powdery mildew increases with leaf age. The most sensitive were the young leaves aged 7-10 days. A higher degree of resistance was shown by 10-15 day-old leaves, while infection was completely absent on the leaves aged 20 days or more. The upper (adaxial) leaf surface was more sensitive to the infection, which confirmed the epiphyllous character of this fungus.

DISCUSSION

Oak powdery mildew occupies a special place in the complex of biotic and abiotic factors that threaten the common oak and its regeneration. It is also well known that the influence of climatic conditions is very important in the epidemiology of this pathogen. The available literature is mostly focused on the general assessment of environmental conditions, without detailed studies of their influence on the fungus development cycle from its maturity and release of conidia to the moment of infection. One of the few works in which the impact of these factors on oak powdery mildew conidial germination is considered is that of Hewitt in 1974. He examined the correlation between the effects of temperature and relative humidity on germ tube length and found that the optimum for their growth was at 25°C and 96% relative humidity. Germ tube elongation was also recorded at low values of relative humidity of only 32% in the temperature range 15-25°C. The results of our research into environmental conditions are in accordance with the data presented by Hewitt (1974). From these results, it can be concluded that a combination of favorable temperature and optimal humidity is of great importance in the epidemiology of the pathogen.

The data on the influence of temperature on oak powdery mildew conidial germination are few and usually presented as parts of general research. According to Škorić (1926), the optimal growth of the fungus requires the temperature of 26-28°C, which is slightly higher than the values determined in our experiments. Karadžić and Milijašević (2005) reported that oak powdery mildew conidia germinated most intensively in the range of 20-30°C and relative humidity of 76-96%. Croatian authors (Vajda, 1948; Glavaš, 2011) have pointed out that powdery mildew growth and spread requires moderate temperature, favorable relative humidity, plenty of light and young oak leaves. Therefore, temperature is very important, but only in combination with other environmental factors, including the leaf development stage.

Relative humidity is not a limiting factor in the germination of conidia, especially in the early stages of their germination. In our experiment, conidial germination took place in very dry air. According to Josifović (1964), the conidia of fungi from the order Erysiphales can germinate and cause infection in a relatively dry atmosphere, or in air with a low percentage of relative humidity. This feature gives oak powdery mildew the opportunity to occur on a large scale in areas with hot, dry summers. Conidia formed in dry conditions are even more infectious and remain vital for a longer time than those formed in wet conditions (Hammarlund, 1925; Škorić, 1926; Yarwood, 1978). However, it was also found and confirmed that high relative humidity had a positive effect on the germination of conidia (Hewitt, 1974; Sivapalan, 1993, 1994; Karadžić and Milijašević, 2005), which was also confirmed by the results of our experiments. Increased humidity is more favorable and even necessary for the emergence and spread of oak powdery mildew (Vajda, 1948; Glavaš, 2011). Many authors emphasize the adverse effects of saturated moisture, i.e. drops of water, on the germination of conidia of different powdery mildews (Nour, 1959; Zaracovitis 1966; Uchiyama et al. 1978; Yarwood, 1978; Mishina and Talieva, 1987; Chellemi and Marois, 1991). Our findings show that oak powdery mildew conidia germinated very well when they were immersed in drops of water (100% relative humidity), although the germ tube length was significantly shorter than the maximum recorded value. Similar results were obtained by Hewitt (1974) and Sivapalan (1993, 1994). Hewitt (1974) reports that the average lengths of germ tubes in the drops of water were by about 25% shorter than the values recorded at the optimum for conidial germination (96%). Based on the analysis of the impact of water on the germination of conidia of 50 different powdery mildew species, Sivapalan (1993) classified oak powdery mildew in the group of pathogens whose conidia can germinate well in a drop of water. However, the average length of germ tubes of conidia immersed in water were about 60% shorter compared to those of conidia germinated on the water surface. The above-mentioned author believes that in natural conditions, fine rain or mist in the form of tiny water droplets deposited on the surface of the leaves create favorable conditions for conidial germination. According to Perera and Wheeler (1975), conidia can descend down the drops of water, or stay within air bubbles, while they normally germinate by taking advantage of high relative humidity. On the other hand, frequent rain, especially heavy rain showers, have an adverse effect on the development of powdery mildew because the conidia are washed down to the ground where they are destroyed, and the rain also removes the mycelia from the infected plants, thus slowing down the parasite development (Josifović 1964; Merchan and Kranz, 1986; Karadžić and Milijašević, 2005).

As far as we know, there are no exact data in the literature on the influence of light on oak powdery mildew conidial germination in controlled conditions. Our results indicate that light had a significant impact on the growth of germ tubes that reached the maximum value in full light. It is known that plants exposed to intense light are highly susceptible to parasitic fungi in the order Erysiphales. This phenomenon is explained by the fact that these are obligate parasites whose development requires organic matter exclusively from living cells, which are abundant in plants with more intensive assimilation under the influence of intense light (Josifović, 1964). According to Hammarlund (1925), the fungi of the order Erysiphales create a larger average number of conidia in the dark, but their germination capacity and germination energy are lower in comparison with the fungi that germinate in diffuse light or in direct sunlight. As for the influence of light on the development of oak powdery mildew, the opinions are undivided: light stimulates the emergence and spread of epiphytic mycelium on the leaves (Škorić, 1926; Vajda, 1948; Butin, 1989; Kelly, 2002; Jacobs, 2003; Giertych and Suszka, 2010; Glavaš, 2011). However, light has a beneficial effect on the host plant as well since it contributes to a more intensive assimilation, which allows the young leaves to develop to their full size more quickly and to form a protective layer of cuticle and wax coating in a shorter period of time. Conversely, in underexposed positions, plant ontogenetic development is slower, which increases their susceptibility to the pathogen. This was reported by Bobinac and Karadžić (1994) and Bobinac (1999, 2000), who studied the growth characteristics of common oak seedlings and juvenile plants depending on the amount of light in the regeneration areas of oak stands. In low light intensity prevailing in the ground layer (<5%), oak seedlings showed signs of devitalization already in mid August as a result of the constant presence of powdery mildew. In addition, at the beginning of the following growing season, there were no signs of new shoot growth in most of the study plants.

The effects of environmental factors are complexly interrelated. They act both on the genesis and spread of parasites and on the host plant itself and its susceptibility to the parasite. The complex of environmental factors is fully expressed when there are favorable conditions for pathogen emergence and spread and when plants are in a vulnerable stage of phenological development. In the case of common oak, it is the stage of new shoot and leaf formation.

The method of floating leaves showed that it was only young leaves before the time of full expansion that were sensitive to powdery mildew. The fungus' infectious potential on young leaves rapidly increases with the regeneration of conidial generations in short periods of time. Edwards and Ayres (1981) state that oak leaf resistance to powdery mildew is associated with the lignification of papillae that prevent the formation of secondary hyphae from the appressorium. According to these authors, large dome-shaped lignified papillae on the inner side of the epidermal cell wall almost completely prevent the penetration of the fungus into fully expanded mature leaves. The same authors confirm that fully developed sessile oak leaves are able to almost completely inhibit the development of secondary hyphae, and also significantly reduce the germination of spores (Edwards and Ayres, 1982).

Numerous authors point to the seasonal nature of oak resistance to powdery mildew, underlying the importance of abiotic factors as major determinants of the phenological adaptation of plants (Vajda, 1948; Edwards and Ayres, 1982; Butin, 1989; Bobinac, 1999; Thomas et al., 2002; Marçais et al., 2009; Desprez-Loustau et al., 2010; Glavaš, 2011). Our studies show that oak powdery mildew was mostly independent of environmental factors. The fungus can infect plants in a wide range of environmental conditions and their impact should always be considered in the light of the ontogenetic development of plants.

CONCLUSION

Our findings coincide largely with the results of other authors, so it can be concluded that natural conditions can be simulated in a climate chamber and reliable data can be obtained on the impact of various factors on the development of the fungus.

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