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The root anatomy and mycorrhiza of *Epipactis pontica* TAUBENHEIM (*Orchidaceae*)

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Abstract: The adventitious roots of *Epipactis pontica* Taubenheim are monostellar. A single–layer rhisodermis is covered by root hairs throughout the lenght of roots. The primary cortex is formed by exo-, mezo- and endodermis. The single - layer endodermis comprises of thin walled permeable and thick walled impermeable cells. Central cylindres (actinostele) contain radial vascular bundles, from tetrarch to hexarch. The root anatomy of *Epipactis pontica* is similar to other species of the genus *Epipactis.* The rhisodermis is locally covered by a fungal hyphae cover which is the source of the hyphae for the root infection. The fungal hyphae infiltrate the root environment only at short distances. The anatomical index of endotrophic mycorrhiza (AIMen in %) expresses the relationship between the infected cells and all the cells of the primary cortex. It is used for the evaluation of the root and root hairs intensity of mycotrophy from the anatomical point of view. These three zones of the roots were evaluated: apical, middle and basal. The AIMen of the root hairs was 15.45% and for the primary cortex was 13.01%. The root infection of *Epipactis pontica* was the lowest in comparison to the root infection of *E. palustris* and *E. helleborine*.

Keywords: *Orchidaceae*, *Epipactis pontica*, roots, anatomy, mycorrhiza.

Introduction

The genus *Epipactis* has approximately 50 species, thus it belongs among the richest genuses in Europe. In the area of the Czech republic 15 species and

in the Slovak republic 18 species are known at present (MEREĎA 1996). The species *Epipactis pontica* was identified in 1975. Recently it has been found in the Slovak republic (VLČKO 1994, 1995). Its occurence was also proved in the area of the Czech republic near Bylnice in the Bílé Karpaty Mountains (BATOUŠEK 1996). FUCHS & ZIEGENSPECK (1925) contributed to obtaining the knowledge of the root anatomy and histology of many Europian orchid species. Their scientific knowledge and conclusions were taken and cited by the other authors (e. g. GOEBEL 1932, SOLEREDER & MEYER 1933, SCHMEIL & SEYBOLD 1940, GUTTENBERG 1956, 1968 et al.). During the past years JURČÁK (2003) has been engaged in the anatomical and mycorrhizal conditions of terrestrial Central European orchids – including some exponents of the genus *Epipactis*.

As it is known, *Epipactis pontica* roots have never been microscopically studied. The aim of this work was the characterisation of anatomical-histological structures and mycorrhizal conditions of this recently found species. JATIOVÁ & ŠMITÁK (1996) mentioned that *Epipactis pontica* belongs among the critically endangered species (C1). Accordingly only the roots of one specimen were used for this. This specimen was taken from the locality near Bylnice in connection with the acquisition of the herbarium evidence.

Material and methods

The plant material was obtained at the end of the growing season (5th October). The roots were rinsed in water, fixed for 48 hours in FAA and then stored in glycerol-ethanol (1:1). Transverse sections were made with a manually operated microtom, their thickness was about 15 μm. The temporary microscopical preparations were coloured in an aqueous safranin and fluoroglucinol solution. Starch was detected with Lugol's solution. A different intensity of the fungal infection was found in different root zones, so the transverse sections were not causal but they were made throught three root zones – the apical (it is distanced 8 ± 3 mm behind the root apex), middle (in the middle of the root lenght) and basal root zone (5 ± 3 mm from the stool). In sum 10 roots were processed, only the undisturbed ones were chosen to determine these zones.

The total number of all cells and infected cells of rhisodermis (including root hairs) and primary cortex was counted in each transverse section. Three cell types were distinguished among the infected cells: passage cells, trophocytes and phagocytes. For the quantitative expression of the fungal infection AIMen (Anatomical index of endotrophic mycorrhiza) was used which was proposed and used by JURČÁK (2003). The AIMen expresses the number of the infected cells to all cells of the examined structure, after multiplying by one hundred it is expressed in per cent. In reviewing the mycotrophy intensity the AIMen provides a more exact expression of the fungal infection in comparison with the verbal evaluation of the mycotrophy used by e.g. PROCHÁZKA (1980), PROCHÁZKA & VELÍSEK (1983).

Photomicroscope Olympus BX-40 was used to research microscopically and to make the photodocumentation. The counts of the found uninfected and infected cells are shown in Tables and Figures.

Results

Anatomical conditions

From the apical zone three tissue layers of adventitious roots can be well discerned (Fig. 1 A - C): an outermost layer (rhisodermis), ground tissue (primary cortex), and stele tissue (central cylinder).

The rhisodermis comprises of small, thin walled, prosenchymatous cells of isodiametric shape in section (Fig. 2). Their outer cell walls showed a moderate positive reaction to lignin and were locally covered by detritus elements through which fungal hyphae passed. This layer is called hyphae cover. Some rhisodermal cells placed bellow this hyphae cover were deformed and their walls were squeezed inside the cells.

Most roots carried root hairs through their full lenght. The lenght of the root hairs varies from 200 to 600 μm. A part of the root hairs was infected by fungal hyphae (Fig. 5, 6, 8), a part of them did not contain any hyphae (Fig. 4, 9, 10 A, B). These fungal hyphae generally deformed the apical zones of the infected root hairs (Fig. 6). The deformations occured even in the root hairs without the hyphae in the transverse sections of the basal zones of the roots (Fig. 9, 10 A, B). It is supposed that these root hairs were infected in former times, too. Spores of some fungus were discovered in the apical zone of one root hair (Fig. 7 A, B).

The primary cortex consists of three parts: exo-, mezo- and endodermis (Fig. 11). Parenchymal cells make up both exodermis and mesodermis.

The exodermis was mostly formed by 1 or 2 layers of small thin walled cells without intercellular spaces. In comparison with the exodermis, the mesodermis comprised of much (distinctively) bigger cells with intercellular spaces. Distribution of the cells infected by the fungal hyphae was not concentric or else regular. However, more infected cells were situated in the outermost layers of the primary cortex aside from the apical, the middle or the basal zone. Bellow the exodermis the passage cells were predominant. The other infected cells (trophocytes and phagocytes) were mostly situated deeper (Fig. 12). The mesodermal cells located more closely to the central cylinder often contained small amyloplasts (Fig. 11, 13 A, B, 14 A, B).

The endodermis was always formed by a single-layer of cells. In the endodermis, 3 or 4 thick walled impermeable cells (oriented towards phloem elements) changed with 3 to 5 thin walled permeable cells (oriented towards xylem elements) from the apical zones (Fig. 14 A, B). The radial cell walls of thin walled cells were regularly lignified. The lignification of the radial cell walls of the thick walled cells occured sporadically. Either the external cell walls (adjoining the mesodermis) or the inner ones (adjoining the pericycle) of some cells showed the lignification.

The pericycle surrounding the central cylinder (actinostele) was formed by a single layer of thin walled cells. The cell walls of the pericycle cells adjoining the protoxylem elements were lignified. The vascular bundles in the central cylinder of the examined roots were radial, hexarch (Fig. 13 A), pentarch (Fig. 13 B) or tetrarch (Fig. 14 A, B). Sectors of the primary phloem made isles strongly different from the xylem. The primary xylem was distinguished to outwardly situated protoxylem (oriented towards the pericycle) and central distributed metaxylem. The xylem elements, including the metaxylem ones, had relavitely small diameters. From the qualitatively-anatomical point of view the inner structures are similar to the knowledge of the adventitious root anatomy of the genus *Epipactis*.

Mycorrhizal conditions

On the surface of the rhisodermis, there were sectors covered by either a thin, sporadically interrupted, or a thick layer of detritus elements. The fungal hyphae penetrate through this layer called hyphae cover. This hyphae cover is the outer source of the fungal hyphae which could enter the rhisosphere only at a limited distance (e.g. Fig. 3 A, B, 5).

The hyphae from the hyphae cover mostly entered the inner root structures either by penetration of the rhisodermal cells or in an apoplastic fashion. The rhisodermal cells under the hyphae cover were mostly deformed. Their external cell walls were scraped inward the protoplast. Strongly infected cells of the rhisodermis decayed and their fragments merged and made the hyphae cover.

Some root hairs were infected by the fungal hyphae, especially in the transverse sections of the apical, but also the middle root zone (Fig. 5, 6, 8). The hyphae from the hyphae cover infect the root hairs by passing directly through their bases, or through nearby cells of the rhisodermis. The communication of the fungal hyphae (their entry or exit) between the root hairs and the external environment (the rhisosphere) was not found. The fungal hyphae deformed apex of the root hairs (Fig. 6, 8) mostly to spiral shapes. These deformations were held even after the death of the hyphae (Fig. 4, 10 A, B). Spores of some fungus were discovered in one root hair (Fig. 7 A, B).

The mycorrhizal cells, i.e. the passage cells, the trophocytes and the phagocytes, occured in the primary cortex of all the examined roots (Fig. 11, 12). The pasage cells dominated in the outermost layers of the mesodermis. The trophocytes and the phagocytes were typical for the middle part of the mesodermis. The remaining layers of the mesodermis were devoid of the hyphae. These parts of the primary cortex were characterized with the amyloplasts. The fungal hyphae in the infected layers of the primary cortex widened either from a cell to another through attenuations in the cell walls (Fig. 12) or at first they passed among the cell walls and then entered the cells through the attenuations. The mycorrhizal cell types were not placed in the regular, i.e. concentric layers. The mycorrhizal cells of some roots formed small isles which were situated under the rhisodermis covered by a thicker hyphae cover.

For data about counts of the root hairs and the cells of the primary cortex of all the examined roots in each root zones see Table 1.

The zone of the root hairs is not delimitated on the roots. Totally 194 root hairs in all the zones of the examined roots were found. The highest share of the root hairs number was in the apical zones (sections A - 90 root hairs) and decreased towards the basal zones (63 root hairs in the middle zone - sections B, and 41 root hairs in the bazal zones - sections C). Only 30 from 194 root hairs were infected by the fungal hyphae (i.e. the AIMen = 15.46%). The ratio of the infected root hairs was not equal with regard to the root zones. In the basal zones, i.e. in the oldest parts of the roots, and in the apical zones there were the highest number of infected root hairs (the AIMen = 17.07% in sections C, and 14.4% in sections A). The middle zones of the roots were the least infected (the AIMen = 6.3%).

The average number of the cells of the primary cortex was 433 cells/section. Overall 12.996 cells were evaluated, from which only 1.691 cells contained the fungal hyphae. The total infection of the cells of the primary cortex was lower by 2.45% with respect to the root hairs. It can be said that the fungal hyphae from the hyphae cover marched shorter distance and that is why the infection of the root hairs is higher than in the case of the cells of the primary cortex. In comparison to the root hairs the distribution of the primary cortex cells infected by the fungal hyphae is more balanced (Tab. 1) but the difference is in the cell infection, which was highest in the middle zones (the AIMen = 14.53% in sections B). The apical and the basal zones had almost the same ratio of the mycorrhizal cells (the AIMen = 12.08% in sections A, and 12.36% in sections C). It is possible to conclude that the infection starts in the youngest, apical zones, ends in the oldest, basal zones and develops in the middle zones, and that is why the ratio of the mycorrhizal cells is highest there.

For the relationship between the intensity of the fungal infection of the root hairs and the cells of the primary cortex and the lenght of the roots see Figure 15, from which the dependence between the root lenght and the intensity of the infection of the primary cortex cells results. The dependence is obvious especially in the case of the shorter roots (the lenghts 20 – 48 mm) – the longer the root, the higher the ratio of the mycorrhizal cells (the AIMen is higher). In the case of the longer roots (the lenghts 80 – 170 mm) there are fluctuations in the mentioned dependence. It is possible to conclude that if the shorter roots are still in their growth, the higher share of the mycorrhizal cells will support the growth.

It was found by observing the distribution of mycorrhizal cell types (i.e. passage cells, tropho- and phagocytes) that they are not spread regularly but quite equally (Fig. 16). The share of the passage cells was the lowest in the basal zones (the AIMem = 3.16% in C zones) and the highest in the middle zones (the AIMen = 4.27% in B zones). The share of the trophocytes as well as the phagocytes was the highest in the middle zones (the AIMen = 4.88% for trophocytes and 5.38% for phagocytes in B zones).

With respect to the relationship between the root lenght and the types of the mycorrhizal cells (Fig. 17) it is possible to say that the longer roots have a higher

intensity of the infection as well as the shares of the particular types of the mycorrhizal cells. The longest root showed the highest share of the tropho- and phagocytes.

Overall 13.01% of the primary cortex cells of all the roots were infected by the fungal hyphae. The highest share displayed the trophocytes (the AIMen = 4.85%) and the phagocytes (the AIMen = 4.40%), the lowest one displayed the passage cells (the AIMen = 3.75%).

Discussion

Opinions that the fungal hyphae of the terrestial orchids stand for the absorb function of the root hairs still appear. Radiation of the fungal hyphae from the root hairs into their surroundings was mentioned and microphotographically documented by e.g. CUDLÍN (1974) in *Platanthera bifolia*. It might be a secondary penetration of the fungal hyphae from a not fixed, i.e. living plant material. The communication of the fungal hyphae between the root hairs and their surroundings was discovered during the root study of Czech orchids in the bloom phase (JURČÁK 2003) as an exceptional, rather than general phenomenon. If the mentioned type of the communication appeared, the fungal hyphae would enter the root surroundings only at a short distance. In common the fungal hyphae communicate between the rhisodermal cells and the rhisodermal surface with the developed hyphae cover. If they get out of their hyphae cover, it was also at short distances. This was repeatedly found in the roots of *Epipactis pontica*, too (Fig. 3 A, B, 5). No microscopic evidence of the fungal hyphae forming a long distance communication system typical for the ectotrophic mycorrhiza (MEJSTŘÍK 1988) was found for the orchid mycorrhiza. In the roots of *Epipactis pontica* it was microscopically found that the fungal hyphae colonized the roots (some parts of the root hairs, the cells of the rhisodermis and the primary cortex) and only the nearest surroudings of the roots (i.e. the hyphae cover from which they leave into the rhisosphere only at a small distance). It is possible to say that the fungal hyphae getting out in longer distances were broken off during the collection and their processing, but no fragments of these fungal hyphae were found even microscopically.

In the characteristics of mycorrhiza and mycotrophy of the Czech orchid species BURGEFF (1932 cit. ex. PROCHÁDZKA 1980) mentioned that the mycorrhizal cells form three zones in the primary cortex (the outer zone of the mycelium development, the middle zone of digested cells and the inner zone of reserved cells). In the direction from the root surface CUDLÍN (1974) distinguished these cell types: trophocytes, phagocytes with undigested residues of the fungal hyphae and phagocytes with living cells. In *Cephalanthera damasonium* he demonstrated the more or less regular distribution of these cell types with the fact that the phagocytes with the living cells were distributed in the middle layers of the primary cortex.

Three types of mycorrhizal cells were distinguished in the examined roots of *Epipactis pontica* with respect to the immediate situation of the fungal hyphae development:

1) Passage cells - i.e. cells infected by the fungal hyphae which branch out and expand in relativelly smaller amount in the cells. During the next development the cells evolve slowly throught the stage of the fungal hyphae expansion and extinction. Their mycorrhizal cycle is therefore long. The passage cells occur mostly in the exodermis or outermost layers of the mesodermis since in their cells there is relatively the least starch reserve in amyloplasts.

2) Trophocytes - represent cells with the expressive development of the fungal hyphae which fully use the starch in the amyloplasts. The trophocytes are in the evolutional stage of the mycorrhizal cells, when the parasitism of the mycobiont predominates over the phycobiont.

3) Phagocytes - in these cells the phycobiont consume all the starch reserves and the situation is opposite to the trophocytes, i.e. the phycobiont parasites on the phycobiont.

In *Epipactis pontica* roots the distribution of the tropho- and the phagocytes was not equal. In the cycle of the mycorrhizal cells other temporary stages can be distinguished: the initiative, the elaborative and the terminative stadium. A part of the cells, which had passed throught all mycorrhizal stages, showed the character of a repeated, i.e. secondary infection in the phagocyte stage. The mycorrhizal process is highly dynamic so that the trophocytes and phagocytes lay-out cannot be stable or regular.

PROCHÁDZKA (1980) classified Czech orchids into four groups according to the intensity of mycotrophy and its relationship to autotrophy. The representatives of *Epipactis* genus were placed into the third group (i.e. species which are mycotrophical during the germination and in the stadium of mycorrhisoms). In the adult age they are slightly mycotrophical (*Epipactis palustris*), medium-mycotrophical (*Epipactis helleborine*) or highly mycotrophical (*Epipactis microphylla* and *E. purpurata*). This classification is not correct due to the absence of exact standards for the evaluation of the mycotrophy intensity in the adult age. The AIMen was therefore used as the mycotrophy intensity criterion. JURČÁK (2003) proposed and determinated the AIMen for 13 Czech stool and tuberose orchid species (including two species of *Epipactis* genus). Quantitatively the AIMen is an exact numeral expression of the mycotrophy intensity of examined structures (roothairs, cells of the rhisodermis and the primary cortex), which are infected by the fungal hyphae.

It is obvious that this criterion need not be in harmony with the physiological productivity of the mycobiont. For comparison the ascertained AIMen of *Epipactis palustris* and *E. helleborine* (JURČÁK 2003) and the AIMen of the examined *Epipactis pontica* are shown in Table 2.

From Table 2 it is obvious that *Epipactis pontica* has a much higher (2x) intensity of the fungal infection of the root hairs than *E. helleborine*. On 5 roots of *Epipactis helleborine* only 24 root hairs were found (8 with infection), while on 10 examined roots of *Epipactis pontica* 194 root hairs were discovered (therefrom

30 infected). Lower share of the infected root hairs of *E. pontica* might have been due to later collection of the plant material at the end of growing season (in October), while *Epipactis helleborine* was collected during the flowerage. Even various ecological factors of the habitats may cause the differences in the intensity.

However, for the evaluation of the mycotrophy level the intensity of the primary cortex cells infection is important. The highest value showed the roots of *Epipactis helleborine* (the AIMen = 29.88%), followed by *E. palustris* (the AIMen = 17.35%), while *E. pontica* had the lowest intensity (the AIMen = 13.01%). From this point of view *Epipactis pontica* seems to be only slightly mycotrophic species. This evaluation is temporary. The marked differences in the intensity of the primary cortex infection of the compared *Epipactis* species might be qualified as an objective display of phycobiont-mycobiont interaction, but they may also be misrepresented by: a) different period of plant collection, b) different conditions of their places, c) amount of treated plant material limited by the protection of plant species.

It will be necessary to use uniform standards (e.g. the period of the collection in the same phenological phase of plant growth) and above all gradually obtain statements from more plant specimens for the objective evaluation and the comparison of the intensity of the fungal infection (thereby the level of the mycotrophy). These statements can serve for a more objective assessment and evalution of phycobiont–mycobiont interactionts, which can contribute to the protection of the plant species.

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Fig. 1. – Fig. 14.

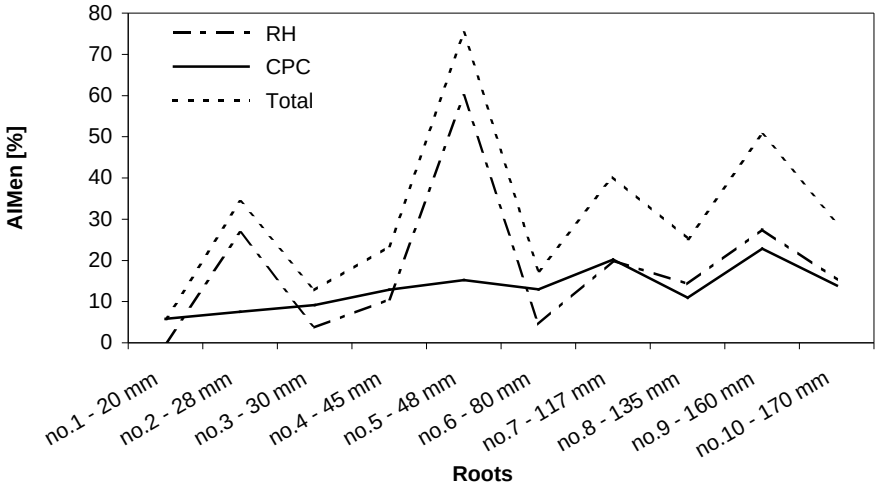

Fig. 15. Relationship between the root length and the intensity (the AIMen) of root hairs and primary cortex cells infection (RH = root hairs, CPC = cells of the primary cortex).

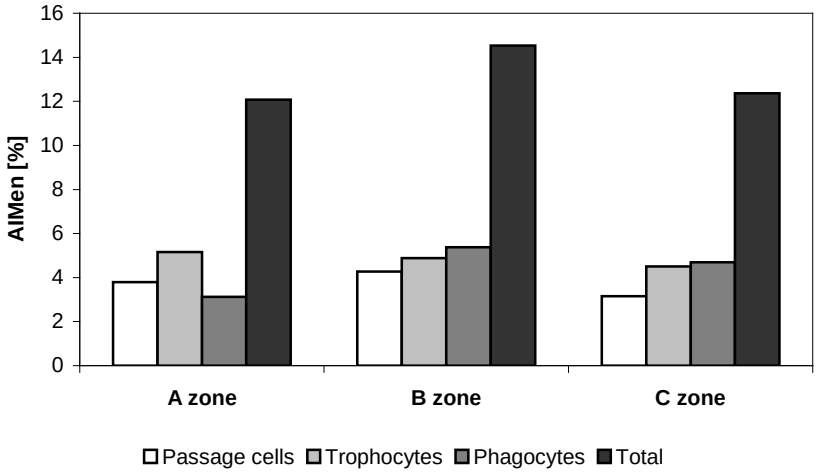

Fig. 16. Distribution of infected cells of the primary cortex in sections (A, B, C) with regard to their AIMen.

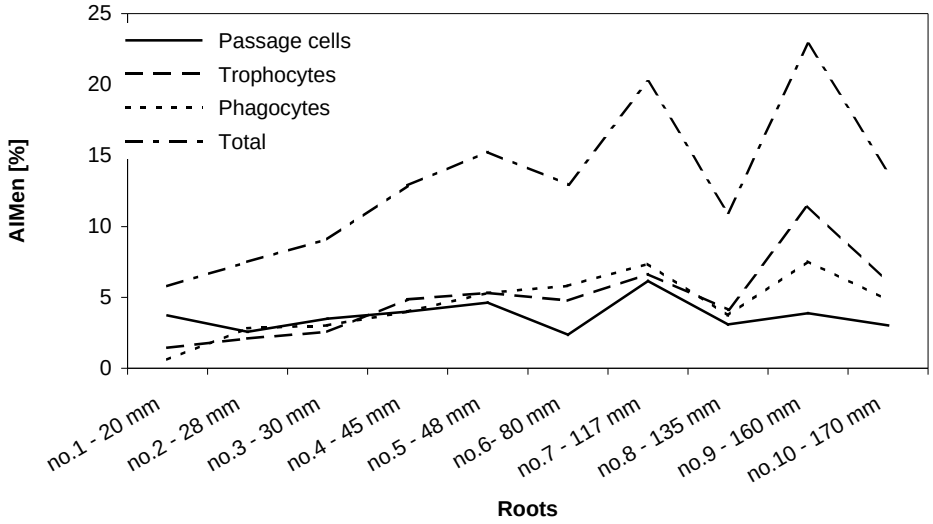

Fig. 17. Relationship between the distribution of infected cells and the root length, with regard to their AlMen.

Tab. 1. Summary of quantitative statements of root hairs and primary cortex cells infection by fungal hyphae.

Root no. length	Root zone	Root hairs number			Primary cortex cells number		
		total	with hyphae	the AIMen [%]	total	with hyphae	the AIMen [%]
1. 20 mm	A	9	0	0	479	35	7.31
	B	10	0	0	490	40	8.16
	C	3	0	0	479	9	1.88
2. 28 mm	A	3	0	0	432	15	3.47
	B	12	4	33.3	422	36	8.53
	C	0	0	0	420	45	10.71
3. 30 mm	A	14	0	0	427	30	7.02
	B	7	1	14.3	434	46	10.6
	C	6	0	0	420	42	10
4. 45 mm	A	9	1	11.1	468	111	23.29
	B	6	1	16.67	452	54	11.95
	C	4	0	0	499	20	4.01
5. 48 mm	A	6	4	66.67	436	36	8.26
	B	1	1	100	432	78	18.05
	C	3	1	33.3	488	94	19.26
6. 80 mm	A	6	0	0	396	42	10.61
	B	9	0	0	378	48	12.70
	C	7	1	14.29	356	58	16.29
7. 117 mm	A	5	1	20	436	71	16.28
	B	0	0	0	416	94	22.60
	C	5	1	20	366	81	22.13
8. 135 mm	A	5	2	40	468	53	11.32
	B	7	0	0	522	56	8.81
	C	2	0	0	458	49	10.70
9. 160 mm	A	18	4	22.22	327	85	25.99
	B	4	3	75	458	102	22.27
	C	7	1	14.29	448	95	21.20
10. 170 mm	A	15	1	6.67	334	30	8.98
	B	7	0	0	421	89	21.14
	C	4	3	75	434	47	10.83
Total in zones	A	90	13	14.4	4.203	508	12.08
	B	63	10	6.3	4.425	643	14.53
	C	41	7	17.07	4.368	540	12.36
Total (Σ=A+B+C)		194	30	15.46	12.996	1.691	13.01

Tab. 2. Intensity of the fungal infection of *Epipactis pontica* in comparison with *Epipactis palustris* and *Epipactis helleborine* according to the AIMen.

Taxon (number of examined roots)	Root zone	AIMen (in %)		
		Root hairs	Cells of the rhisodermis	Cells of the primary cortex
Epipactis palustris (6 roots)	A	0,00 [1]	7,21	5,36
	B	0,00 [1]	1,95	4,21
	C	0,00 [1]	20,47	42,50
Total	A+B+C	0,00	8,69	17,35
Epipactis helleborine (5 roots)	A	40,00	11.33	5,37
	B	0,00	13,70	51,52
	C	35,29	10,56	34,33
Total	A+B+C	33,33	12,00	29,88
Epipactis pontica (10 roots)	A	14,40	unvalued	12,08
	B	6,3	unvalued	14,53
	C	17,07	unvalued	12,36
Total	A+B+C	15,46	---	13,01

[1] found only 4 root hairs without any fungal hyphae