OSMOPHORES OF *AMORPHOPHALLUS RIVIERI* DURIEU (ARACEAE)

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ABSTRACT

The undertaken investigations (SEM, LM) concentrated on the distribution and the anatomy of osmophores emitting a characteristic odour of inflorescence of *Amorphophallus rivieri* Durieu. The osmophores situated at the top part of spadix (appendix), secreted a strong fragrance during the whole period of blooming, whereas those located on the stamens, in the apical and in the middle part of the spathe produced a weaker smell. The fragrance at the basis of spathe was undetectable although both the secretion and the tissue structure characteristic for osmophores located on the adaxial surface of the remaining part of the spathe were observed. The gland tissue consisted of the epidermis and of several layers of subepidermal parenchyma. The epidermis was covered by a thin, striated cuticle or sticks of wax. Moreover, there was also a small number of stomata covered with a smooth cuticle. The cells of osmophores stained intensively with neutral red. They contained numerous lipid drops, which presumably are carriers of the secreted fragrance substances. The cells of subepidermal layers were filled up with starch grains in the appendix and stamens. A considerable quantity of starch was also observed in the deeper layers of parenchyma in the spathe. The pattern of osmophores distribution corresponds with the localization of these inflorescence fragments, which emit heat, as showed in the literature.

KEY WORDS: osmophores, anatomy, *Amorphophallus rivieri*, Araceae.

INTRODUCTION

Numerous representatives of the Araceae family, are known to form inflorescence emitting a strong odour, frequently accompanied by heat production. Osmophores described in the Araceae family, i.e. glands generating smelling secretion in the flowers or inflorescences, are located in the various fragments of spadix. Most frequently the destituted of flowers terminal part of spadix, the so-called appendix, is transformed into the osmophore, which in *Amorphophallus titanum* is an example of the largest one in the world of plants and attains a length of 1,86 m (Vogel, 1990).

The fragrant substances are also produced by *Monstera* monoecious flowers (Ponchet et al. 1982), *Philodendron* staminate flowers (Vogel, 1990) and pistils of *Spathiphyllum* (Vogel, 1990). In some reports there is information that spathe also contain osmophores. Ponchet et al. (1982) discovered the presence of odoriferous compounds in spathe of *Monstera* and *Philodendron*; on the other hand, Vogel (1990) mentions the species of *Arisaema*, *Symplocarpus* and *Cryptocoryne* genera in which osmophores are also situated in this organ.

The heat production by spadix was noted in many representatives of the Araceae family (Meeuse 1975, Raskin et al. 1987, Skubatz et al. 1990, Vogel 1990, Yafuso 1993). Van der Pijl (1937), Skubatz et al. (1990) confirmed this fact in many species of *Amorphophallus*. The authors of the latter study showed as well that the heat energy was emanated not only by the staminate flowers and appendix, but also by some

particular spathe fragments during the florescence of *Amorphophallus rivieri*.

In available literature there are data indicating the independent heat and odour generation; for example, the staminate flowers of *Amorphophallus titanum* emit only heat (Van der Pijl, 1937). There is also the idea propagated, the heat emission by osmophores of the Araceae family is probably a secondary symptom of odoriferous material synthesis (Vogel, 1990).

In the present study anatomical examinations of generating heat energy of *Amorphophallus rivieri* spadix and spathe fragments were carried out to define if they are the areas of simultaneous occurrence of osmophores. The surface build and the tissue structure of these organs were compared.

Despite the fact that osmophores of many species of the Araceae family have been examined till now (Vogel, 1990), there is lack of data in literature concerning the anatomical structure of the tissues emitting fragrance in *Amorphophallus rivieri*.

MATERIAL AND METHODS

The specimens of *Amorphophallus rivieri* Durieu cultivated in pots as ornamental plants were used for examination.

The observations of fragrance emission were initiated together with the formation of inflorescence and continued during all florescence stages. The day of spathe unfolding has been

Figs 1-3. Localization of osmophores of *Amorphophallus rivieri* Durieu and structure of glandular tissue of the apical part of spadix (appendix).

Fig. 1. The general inflorescence habit of *A. rivieri*.

Osmophores occur on the adaxial spatha surface, barren part of spadix (appendix) and in staminate flowers; AP – appendix, Sp – spatha, M – staminate flowers, 0,4x.

Fig. 2. Transversal section of appendix. Osmophore (OS) consists of epidermis and several layers of tiny cells of subepidermal parenchyma. The bigger cells of brighter contents, occur in deeper located parenchyma sometimes with raphides; W – small vascular bundles visible in gland tissue adjacency, LM, 75x.

Fig. 3. Fragment of Fig. 2. The osmophore parenchyma cells consisted of dark-stained protoplasts (toluidine blue) containing numerous starch granules, LM, 300x.

accepted as the beginning of florescence. For this purpose, the examined fragments of spadix and spathe were cut off and put into separate air-tight containers. After several hours the presence or absence of odour was recorded.

The tests of osmophore tissue presence were conducted by means of hand made slides of fresh pistillate and staminate flowers, apical part of spadix (appendix) and the upper, middle and lower parts of spathe by staining them with 1% neutral red. The starch contents was examined by means of Lugol fluid, and the lipid compounds in cells means and cutinized walls were stained with Sudan III.

The number of stomata counted per 1 mm² area was fixed as the average of ten measurements by means of the light microscope.

The spathe and spadix surface was also observed by means of the scanning electron microscope. To this end, the inflorescence fragments were fixed in buffered 3% glutar aldehyde for four hours at room temperature. After several washings and postfixation in 0,1 M osmium tetroxide at temperature of 4°C, they were dehydrated in ethanol sequence (concentration rising from 10% to 99,8%), and carried into acetone. The inflorescence fragments, dried with CO₂ at critical point were coated with gold and observed by means of the BS-340 TES-LA microscope.

Some part of the fixed material was embedded in epoxy resin Spurr and cut into semi-thin slices (0,75-1 µm) and next stained with 0,05% toluidine blue.

RESULTS

The intense fragrance emitted by the appendix and the weaker smell emanated by stamens were scented in the first and second florescence days. The next day the odour of little intensity was issued from the upper and middle part of adaxial spathe surface.

Appendix

Appendix of *Amorphophallus rivieri* is of pink-violet colour conditioned by the presence of anthocyan in some epidermis cells and in 1-2 layers of the located beneath parenchyma. Its surface is marked by the oblong, unevenly spaced furrows (Fig. 1).

The transversal section of the appendix showed a slight undulation of the surface and an arrangement of the outer tissues, characteristic for osmophores of homogenous structure, distinguishable by the lack of differences in dimensions of cells they were formed of (Figs 2, 3). The gland's emitting layer was constituted by a thin-walled epidermis. The subepidermal parenchyma comprising 2-7 layers of rather closely arranged cells containing numerous amyloplasts, the cytoplasm intensely stained with toluidine blue and the moderately sized vacuoles corresponded with the structure features of the tissue producing secretion, as was confirmed by histochemical tests. Small vascular bundles were found in the immediate vicinity of the gland tissue.

The deeper located layers of basic ground tissue consisting of larger cells, with more extensive vacuoles and simultaneously smaller starch contents, presumably made the additional osmophore storage tissue. The parenchyma pith in the central part of the spadix contained a very well-developed ventilating system, which consisted of large intercellular spaces.

The conducted by means of SEM observations of the epidermis surface of osmophore, located in the spadix, showed

the presence of anisotropically set wax sticks, hindering the determination of cell outlines (Figs 4, 5).

The stomata appeared both in places of osmophore protuberances and within burrow limits, relatively in inconsiderable frequency, for eight per 1 mm² were noted. They were surrounded by massive cuticle rings, forming the superficial integument (Figs 5, 6, 7).

Some places of the epidermis surface were free from wax coating. In these places and around the stomata the spherical protuberances of 2 µm in diameter were observed by means of SEM, (Figs 6, 8), the presence of which might be probably connected with fragrance emitting compounds. It seems very probable that they made the secretion droplets getting through the cell wall.

In the second day of anthesis droplets of lipid compounds in the epidermis and occasionally in parenchyma cells were observed (histochemical test). On the surface of the epidermis also the presence of bigger droplets of orange secretion, and in some places the appearance of a layer of a substance, similar in colour and adhering closely to the external walls of epidermis cells, was noted. The following days of anthesis the presence of few lipid droplets, concentrated mainly in epidermis cells adjacent to the stomata, have been recorded. The lipid drops observed by means of the light microscope and the globular protuberances on the external walls of epidermis cells, visible by means of the scanning microscope, indicate the probable connection between secretion and fragrance emission.

Stamens

In the structure of stamens there appears a distinct adaptation to pollen liberation by the apical part of the head. The particular anatomical stamen features, i.e. the arrangement of parenchyma layers in subepidermal position, with the endothecium beneath them (Fig. 9) suggest that the superficial areas of the outer walls may also perform another function. The presence of lipid drops inside the thick-walled epidermis cells and on their surface, the intensely stained ingredients of epidermis protoplasts and of the adjacent parenchyma, as well as the very numerous starch grains in parenchyma cells correspond with the characteristics of secretory glands generating fragrance substances. The stamens' smell emission stated in the beginning of the observations was confirmed by the anatomical structure of these organs.

The relatively short filament, ca 1/4 of stamen's length, characterizes the formation of a great number of stomata and the occurrence of large intercellular spaces. The presence of lipid secretion in the filament cells or on its surface has not been observed.

Spathe

The spathe differed considerably in the thickness and inner structure in its basal and apical parts. The lower part distinguished itself by the biggest fleshing (2,76 mm) (Figs 10, 12), the middle part attained the medial thickness (1,64 mm) and the apical part was the thinnest one (0,33 mm) (Fig. 11).

The basal part of spathe attracted attention by its intensely stained (red-brown) adaxial surface covered with papilliform convexities (Fig. 10). Considering their interior structure, some similarity with the double layer osmophore construction of the highly undulated surface was stated (Fig. 12). The epidermis of the observed papillae had relatively thin, conically protruded external walls and showed the character of emission epithelium because of the dense, intensely staining cytoplasmatic contents and big cell nuclei (Fig. 13). During

Figs 4-8. Osmophore surface covering appendix, SEM

Fig. 4. Wax sticks on the surface of epidermis cells, 2400x.

Fig. 5. Stoma located in hollow, surrounded by cuticle ring forming the striated layer beside, 2400x.

Fig. 6. Numerous globular protuberances of cuticle surface in stoma adjacency, 2400x.

Fig. 7. Enlarged stoma from Fig. 6 consisting of massive cuticle ring in peripheral part, 3600x.

Fig. 8. Fragment of epidermis without wax coating, consisting of numerous spherical cuticle protrusions formed presumably by secretion accumulation, 2420x.

Fig. 9. Transversal section of stamen head with subepidermal located parenchyma (m) and multilayer endothecium (e), LM, 320x.

fragrance emission by the spadix observed were also relatively large lipid drops on the papillae surface of the spatha, frequently in close adjacency of stomata. Lipid drops of considerably smaller size were also observed in the epidermis cells and subepidermal papillae parenchyma. However, the smell was not stated in this part of spatha. The number of stomata amounted to 1.8 per 1 mm^2 .

On the transversal section of the papilliform convexities, under the epidermis mesophyll was observed, consisting of bigger cells than the epidermal ones. (Fig. 13). The large air-spaces appeared beneath the stomata. A great amount of amyloplasts containing starch granules was present in the deeper located basic ground tissue cells, particularly around vascular bundles.

The vascular bundles, in the shape of massive bands, penetrated the central part of the spatha and, in the form of branches, reached its upper and lower surface. The parenchyma, located in the central region, was characterized by the presence of very large air-spaces (Fig. 12), forming a ventilating system similar to the one which appeared in the deeper layers of the spadix tissues. A rather considerable number of stomata in the abaxial epidermis was stated: 62 per 1 mm^2 (Fig. 18).

The middle part of the spatha distinguished itself with a smooth adaxial surface, without papilliform appendages. In the third day of anthesis a weakly perceptible fragrance emitted by the adaxial surface of this part was noticed. Lipid drops of different size were observed on the adaxial epidermis cell surface, in their protoplasts and in the first layer of subepidermal parenchyma. The intense vacuole stain as effect of neutral red treatment was stated in the cells of both tissues. A small quantity of stomata was noted both in adaxial and abaxial epidermis, 4.5 and 3.5 per 1 mm^2 respectively. The presence of large intercellular air-spaces was observed in the central part of the parenchyma. The vascular bundles were concentrated at the subepidermal mesophyll of the spatha proximal region.

The upper part of spatha was lamellate and reached only 12% of the basal part thickness (Fig. 11). The neutral red colouring of the cellular vacuomes of tissues located peripheral-

ly occurred only in the third day of anthesis, just like in the lower located region. Numerous lipid drops appeared on the adaxial epidermis surface at that time, the presence of odour was also noted. The epidermis of both the surfaces was marked by an insignificant number of stomata; on the adaxial surface it amounted to 1.5 per 1 mm^2 and on the abaxial one – 2 stomata per 1 mm^2 .

The external walls of multangular adaxial epidermis cells, observed by means of SEM, were covered with a striated cuticle coat (Figs 14, 15). The cyclocytic stoma in the apical part of each convexity was found (Figs 13, 14, 15). The stomata cells were protected with a massive layer of smooth cuticle, considerably convexed at the anticlinal walls. The external cuticular lists covering the vestibule of stoma were distinctly marked around it (Fig. 16). The presence of globular formations of maximum dimensions equal to the distance between cuticle stripes ($1.5\text{--}2 \text{ }\mu\text{m}$) was stated on the walls of spatha epidermis cells, just like the ones on the epidermis surface covering the appendix (Fig. 17). The presence of these protuberances may also indicate the secretory character of the inflorescence part described.

DISCUSSION

In the present study it was stated that the appendix of *A. rivieri* emitted an intense fragrance during the whole period of anthesis, while the stamens, the apical and the middle parts of spatha emitted a considerably weaker smell in the third day since its unfolding. Simultaneously, the presence of lipid compounds droplets was proved on the surface and inside the stamens' epidermis cells, spatha and the apical part of spadix which, according to Vogel (1990), are carriers of the secreted fragrance substances in many representatives of the *Araceae* family. According to the pre-cited author, the components of aromatic secretion of the *Araceae* family, among others terpenoids, are of lipophilic character. The author thinks that they may probably migrate in the form of liquid together with their carriers through the wall layers of epidermis cells, including

Figs 10-13. The structure of spatha osmophores.

Fig. 10. Exposed fragment of adaxial, basal part of spatha (SP) and spadix consisting of pistillate (F) and staminate flowers (M), 0.8x.

Fig. 11. Transversal section of apical, lamellar part of spatha. Vascular bundles visible in mesophyll, beneath proximal epidermis, and deeper – large intercellular spaces, LM, 35x.

Fig. 12. Transversal section of basal part of spatha, consisting of numerous papillae on the adaxial surface and smooth abaxial surface. Mesophyll located in the middle with many air-spaces, LM, 35x.

Fig. 13. Fragment of transversal section of papilla with intensely stained epidermis cells possessing big nuclei (arrow) and conical external walls covered with striated cuticle. Stoma visible in apical part, LM, 220x.

Figs 14-18. The surface of spatha osmophores, SEM.

Fig. 14. Stoma on a small protrusion, next epidermis cells covered with striated cuticle, 890x.

Fig. 15. Stoma with massive cover made of cuticle, 890x.

Fig. 16. Stoma with thick cuticular lists around the vestibule filled probably with secretion, 2200x.

Fig. 17. Numerous, spherical cuticle protuberances on epidermis cells surface of adaxial, middle part of spatha, 2200x.

Fig. 18. Stoma from the basal part of abaxial spatha surface, LM, 970x.

TABLE 1. Comparison of fragrance and heat emission and histochemical localization of glandular tissue in inflorescences of *Amorphophallus rivieri* Durieu. (Literature data and results of present study).

Parts of inflorescence	Fragrance emission according Arcangeli (1983) and Vogel (1990)	Heat emission according Skubatz et al. (1990)	Results of authors' investigations		
			Fragrance emission	Reaction after neutral red treatment	Presence of lipid substances in epidermis and on its surface
Appendix	+	+	+++*	+	+
Staminate flowers	—	++	++	+	+
Spatha:					
– apical part	—	++	+	+	+
– middle part	—	+	+	+	+
– basal part	—	+	—	+	+

* The intensity of smell or thermal effect is marked by adequate number of +.

the cuticle, which shows a high penetrability for those substances and usually is rather thin in osmophores.

In result of investigations carried out by means of SEM, microglobules partly sunk in the layers of the epidermis cell wall covering the appendix, were observed, as well as on the epidermis surface of the spatha basal part (adaxial surface). We may suppose they are the secretion drops inhered in the external part of the cell wall.

The preparatory test presence for of secernent tissue confirmed its appearance on the surface of the apical part of spadix, stamens and the adaxial surface of spatha. These results are only partially consistent with literature data (Table 1), according to which the appendix is the place of osmophore appearance in *A. rivieri* (Arcangeli 1883, Stern et al. 1987, Vogel 1990).

Despite the fact that microscope observations indicated the presence of secernent tissue, the emission of smell, perceptible for man, in the lower part of the spatha was not stated. The secretion of intense fragrance by the appendix and the production of secretion of a weaker, or undetectable for man, smell by other parts of *A. rivieri* inflorescence may be directly connected with the adaptation to pollination by various groups of insects. From the point of view of pollination ecology, the inflorescences of the genus *Amorphophallus* are simultaneously classified to the categories of flowers visited by beetles (cantarophily) and dung-flies (sapromyophily) (Kugler 1970, Faegri and Van der Pijl, 1971). Whereas there is no doubt that the flowers pollinated by beetles (saprophagans and coprophagans) attract pollinators, above all, by the specific odour (aminoid), it is not quite certain whether the similar smell is the substantial attractant for flies (Faegri and Van der Pijl, 1971). According to the pre-cited authors the flowers pollinated by flies may distinguish themselves by a smell imperceptible for man.

The odour production of varied quality by the precised parts of the same flower or inflorescence, or smell generation of different intensity in the flower is a well-known phenomenon described for many species (Kugler, 1970, Vogel, 1990).

The glandular tissue situated on the spadix and spatha indicated some differences in the structure. The appendix was covered with epidermis, which contained a wax coat forming characteristic sticks, while the external epidermis walls of the adaxial spatha surface were conically protruded, equipped with a thin layer of striated cuticle. In both cases the epider-

mis was featured by an inconsiderable amount of stomata: appendix – 8 per 1 mm², spatha – 1.5-4.5 per 1 mm².

The stomata occurring on both the organs were marked by a massive cover: as a cuticular shield in the shape of ring around the stomata cells (spadix) and as a smooth cuticular coat with a slot above the stoma (spatha) protecting the whole stomata. Both their structure and their small number seem to correspond with the xeromorphy symptoms.

In many species the secernent epithelium of osmophores was devoid of stomata (Stern et al. 1987, Vogel 1990). However, their presence was noted on the osmophore surface of spadix of some of the *Araceae* and in *Ceropegia* (Vogel 1990). The above mentioned author thinks that stomata do not play on essential role in smell emission, but they may take some part in it, because in water originating from transpiration of some representatives of the Aroideae family odour substances were found.

The glandular-tissue cells in spadix formed a stratum under the epidermis consisting of 2-7 coats of rather dense system. They distinguished themselves by a high content of starch. The bigger and deeper situated ground-tissue cells were equipped with starch as well.

Apart from the epidermis, in some places of the spatha 1-2 layers of subepidermal parenchyma showed glandular-tissue properties (dense cytoplasm, big nuclei, intense effect of "life staining"). The deeper located parenchyma was characterized by a loose structure. Storing of starch occurred in the deeper situated ground-tissue layers, around the vascular bundles. According to Vogel's suggestion (1990) there is the possibility of secretion transport by the vascular bundles from deeper located places of its origination.

The papillate outgrowths of ca 0.5 mm height, covering at the base the adaxial part of spatha in *Amorphophallus rivieri*, except of the secretory function, might act as "food bodies" for insects, just like the homologous outgrowths in *A. variabilis*, described by Van der Pijl (1937). However, the significance of such bodies is not clear in many species, because insects do not feed on them (Faegri and Van der Pijl 1971). It was shown in *Sauromatum guttatum* (Meeuse et al. 1984) that the osmophore tissue is located in clubshaped "food bodies" on the spadix, which, in the opinion of the mentioned authors, does also not exclude the performance of nutritious functions by them.

The liberation of heat accompanying fragrance emission by the secretory glands of the *Araceae* family is the result of an intense respiration process of a special course (Vogel 1990). The considerable role in heat generation in representatives of this family is played by salicylic acid inducing the complex process, the effect of which is heat radiation (Raskin et al. 1987, Skubatz et al. 1990). Many authors accept that the heat created by inflorescences of the *Araceae* family accelerates the transpiration of fragrance substances (Dahlgren et al. 1985, Vogel 1990, Yafuso 1993).

From Skubatz's et al. report (1990) it results that the different inflorescence parts of *A. rivieri* emit heat during anthesis of diverse thermal effect (Table 1). The highest temperature was recorded for staminate flowers and the apical part of the spathe (24°), whereas the appendix and the lower spathe fragments showed a weaker heat generation (22°C). It was shown in the present study that the heat liberating inflorescence parts are simultaneously the place of osmophore appearance. However, at the basal part of the spathe no perceptible odour was recorded (Table 1). The adaptation of the internal structure of the mentioned organs to the intense respiration which conditions heat emission, was noted. This adaptation is based on a very well developed intercellular space system. In the foregoing situation, the fact of appearance in the described organs of *A. rivieri* of a small quantity of stomata, except the abaxial surface of the basal part of spathe, may be striking.

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OSMOFORY *AMORPHOPHALLUS RIVIERI* DURIEU (*ARACEAE*)

STRESZCZENIE

Przeprowadzone badania (SEM, LM) dotyczyły rozmieszczenia i budowy anatomicznej osmoforów emitujących charakterystyczny zapach kwiatostanu dziwidła Riviera (*Amorphophallus rivieri* Durieu). Osmofory, które znajdowały się na szczytowym odcinku kolby (appendix), wydzielaly silną woń przez cały okres kwitnienia, natomiast położone na główce przęcikowej oraz w apikalnej i środkowej części podsadki (spatha) produkowały słabszy zapach w trzecim dniu kwitnienia. Przy podstawie podsadki nie stwierdzono wyczuwalnego zapachu, chociaż obserwowano obecność wydzielin i budowę tkanek charakterystyczną dla osmoforów występujących na doosiowej powierzchni pozostałej części tego organu. Tkanę gruczołową stanowiła epiderma oraz kilka warstw leżącego pod nią miękiszu. Epidermę pokrywała cienka, prążkowana kutykula lub pałeczki wosku. Cechowała ją również niewielka liczba aparatów szparkowych osłoniętych gładką kutykulą. Komórki osmoforów wybarwily się intensywnie czerwienią obojętną. Zawierały liczne krople lipidowe, które przypuszczalnie są nośnikami wydzielanych substancji zapachowych. Subepidermalne warstwy gruczołowe składały się z komórek obficie wypełnionych ziarnami skrobi (appendix, przęciiki) lub też znaczną ilość skrobi obserwowano w głębiej położonych pokładach miękiszu (spatha). Miejsca występowania osmoforów odpowiadają lokalizacji fragmentów kwiatostanu, z których jak wykazano w literaturze, emitowane jest ciepło.

SŁOWA KLUCZOWE: osmofony, anatomia, dziwidło Riviera, *Amorphophallus rivieri*, *Araceae*.