MORPHOGENESIS OF PROPAGULES IN VIVIPAROUS SPECIES *BRYOPHYLLUM DAIGREMONTIANUM* AND *B. CALYGINUM*

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ABSTRACT

The propagule development in two viviparous *Bryophyllum* species: *B. daigremontianum* and *B. calycinum* (Crassulaceae) has been found to proceed *via* embryoidogenesis (somatic embryo). In both species, all propagule organs arise from the dormant meristem derivatives, but there are morphogenetic differences at the latest developmental stages (in adventitious root initiation). In both species, the propagule genesis proceeds through the "globular", heartshaped and torpedoshaped stages. Comparative morphological and embryological analysis of propagules in the species in question and sexual embryos revealed a strong similarity in their developmental patterns not with standing their morphological variability. It has been suggested that two *Bryophyllum* species carry the "dormancy" gene.

The present study has confirmed that vegetative propagules of the flowering plants can be either embryoids or buds.

KEY WORDS: viviparity, vegetative propagule, embryoid, morphogenesis, *Bryophyllum*.

INTRODUCTION

Asexual reproduction plays an important role in the system of flowering plant reproduction. It comprises all types and modes of reproduction not involving meiosis and double fertilization. According to one view, two types of asexual reproduction are recognized: embryoidogenic and gemmorrhizogenic (Batygina, 1987-1994). The direction of evolution of many plants has been toward viviparity. The occurrence of seedlings on a plant has repeatedly been the subject of study and discussion (Linne, 1809; Braun, 1859; and others).

Most authors referred to viviparity the process of seed germination *in situ* (i.e. on the plant) in some species of mangroves (*Rhizophora*, *Avicenia*). Some authors, however, believed viviparity to be the process of vegetative propagule formation on various structures of the maternal plant (leaf, stem, flower) and that the process is similar to vegetative reproduction (Braun, 1859; Goebel, 1928; Victorov, 1964; and others). By viviparity a number of authors meant both the process of formation of plantlets from seeds in mangroves and of vegetative propagules in other species (Serebryakova, 1978; Genkel, 1979; and others). In 1969, van der Pijl coined the term "pseudoviviparity" to denote the process of vegetative propagule formation alone, as opposed to the true viviparity in mangroves.

The best known examples of viviparity are provided by members of the *Crassulaceae*. Belonging to this family is the genus *Bryophyllum*. A characteristic feature of this genus is the formation of vegetative propagules on the leaf. The initia-

tion and formation of these has been the focus of attention of botanists for a long time (Berge, 1877). Incomplete evidence on morphogenesis of propagules has resulted in continuing multiplicity of terminology: used "buds" (Howe, 1931; and others), "embryos" or "leaf embryos" (Naylor, 1932; Yarbrough, 1932, 1934), "foliar pseudobulbils" (Johnson, 1934; Resende, 1954), "embryoids" (Batygina, 1987), and others.

The data in the literature, a new approach to the study of reproduction systems and new experimental evidence provided further insights into the phenomenon of viviparity in flowering plants. We understand viviparity in the broad sense as the process involving the formation of generative and vegetative viviparous diaspores (propagules) (with and without alternation of generations, respectively) (Batygina, in press).

The present work is concerned with detailed studies of the genesis and patterns of development of vegetative propagules on leaves of two species belonging to the genus *Bryophyllum*: *B. daigremontianum* Hamet et Perr and *B. calycinum* Salisb.

MATERIAL AND METHODS

Two species of *Bryophyllum* – *B. daigremontianum* Hamet et Perr and *B. calycinum* Salisb. – growing in the greenhouse of the Komarov Botanical Institute (St. Petersburg) were used. Leaves of *B. daigremontianum* were also harvested in a natural habitat (Bangalore, India). For examination, leaves of the 1st-5th layer (starting from the shoot apex) were taken. In

order to initiate morphogenesis of propagules, *B. calycinum* leaves were placed in moist sand. No such treatment was given to *B. daigremontianum* leaves. Leaf regions with notches containing propagules at different stages of development were fixed in FAA and embedded in paraffin-wax. Depending on the developmental stage, the sections varied in thickness from 5 to 12. The preparations were subjected to triple staining (Kamelina, Proskurina, Zhinkina, 1992) or stained with hematoxylin and safranin. The periodic acid-Schiff reaction was used to determine insoluble polysaccharides.

RESULTS

Bryophyllum leaves are typical leaves of succulent plants. The *B. calycinum* leaf is oblong-ovate with rounded denticles along the margins. The *B. daigremontianum* leaf is ovate, with dentate margins. Both leaves exhibit the pinnate venation. The leaf has the midvein and two smaller veins running to the base of the lamina. The lateral veins are deflected towards the basal notches of the leaf, while the primary rib gives rise to a group of branching veins. The veins run along the leaf margins and their peripheral branches terminate in hydathodes.

Both *Bryophyllum* species produce propagules in most of the notches along the leaf margins. In basal region, propagules are laid down but normally they fail to develop. Propagules on a leaf are not initiated simultaneously. Therefore, they tend to be at different developmental stages both on a leaf and on leaves of different tiers. Propagules develop from meristems termed "dormant meristems" (Yarbrough, 1932).

At early stages of *B. calycinum* and *B. daigremontianum* leaf development, the initials of the future dormant meristem are difficult to identify, since the entire leaf primordium is composed of meristematic cells. As the leaf develops, its vascular system differentiates and marginal notches are formed (Table 1, Fig. 1.). In the leaf notch, a peg (projection) develops. Concurrent with these processes, a meristematic zone is formed which will give rise to a propagule. This zone is located in the leaf margin notch in *B. calycinum* and in the notch peg in *B. daigremontianum* (Table 1, Fig. 2; Table 3, Fig. 4a, 4b). It is worth noting that the formation of this meristematic zone proceeds concurrently with the hydathode formation. Due to leaf margin anatomical differences between the two *Bryophyllum* species, the distance between the hydathode and the meristematic zone in *B. daigremontianum* is larger than that in *B. calycinum*.

At early stages of leaf development in both species, the vascular system fails to come in contact with cells of the meristematic zone which, probably for this reason, continues to be a dormant meristem. At a later stage of leaf development, following proliferation of cells of this zone, it gives rise to 7 to 10 layers of densely cytoplasmic cells. At this developmental stage, the meristematic zone begins to come in contact with the leaf vascular system (Table 1, Fig. 2). In *B. calycinum*, the meristem comes in contact with the vascular bundle running parallel to the leaf margin. In *B. daigremontianum*, the leaf notch peg is innervated with 5 bundles branching out of the vascular bundle parallel to the leaf margin. Coming in contact with these bundles is the meristem giving rise to a propagule. The vascular bundles are surrounded by cells containing tannins. The presence of tannins in leaf cells (subepidermal layer) is a characteristic feature of some *Crassulaceae*, in particular *Bryophyllum*.

Then the process of the vegetative propagule formation commences. The earliest stages of the dormant meristem development have not been identified (the meristem is formed from a single or several cells), it is only at the later developmental stages that it would be appropriate to speak of its similarity to the sexual embryo. The sexual embryo is known to normally pass through the stages of globular, heartshaped, torpedoshaped and maturation. Similar stages can be distinguished in the propagule development in the two *Bryophyllum* species (Table 1, 2, 3). However, the "globular" stage of the *Bryophyllum* propagule differs morphologically from the globular stage of the sexual embryo.

In both species, the propagule cotyledon formation proceeds in a fashion similar to that in a normal dicotyledones' sexual embryo. At early developmental stages, one of the cotyledons is usually smaller than the other. Later they become virtually equal in size. In both species, the cotyledons differ in shape from one another. They are spherical in *B. calycinum* and wide-elliptical in *B. daigremontianum* (Table 1, Figs 4, 7-9; Table 2, Figs 1-4; Table 3).

As the cotyledons develop, the vascular system differentiates in them. Cotyledon cells contain starch. Between the cotyledons, the apical meristem is laid down. It gives rise to a plumule. The formed plumule has two leaf primordia (Table 2, Fig. 5).

Characteristic features of the *B. daigremontianum* and *B. calycinum* propagules are the absence of the main root apical meristem and the formation of the adventitious root system.

In *B. daigremontianum*, initiation of adventitious roots occurs in the region of "hypocotyl" at the late torpedo stage. At this stage, the propagule exhibits well-developed cotyledons with a formed vascular system and starch in their cells, and a plumule with two primordia. The vascular bundles of the cotyledons enter the "hypocotyl" stele (Table 2, Fig. 5).

In *B. calycinum*, adventitious root initiation occurs at the stage when the cotyledons are well developed, the formation of vascular system begins, but starch is still lacking in the cotyledon cells. The plumule is not yet differentiated at this stage of propagule development. The adventitious roots are linked to the leaf vascular supply. Subsequently, the roots pierce the leaf tissues and emerge into the notch (Table 1, Fig. 5).

In propagules of both species, the roots are formed asynchronously. The detachment of the plantlets from the leaf occurs due to the formation of an abscission layer of cells a proportion of which contains tannins. This process occurs within 20 to 25 days of the propagule initiation in *B. calycinum* and within 30 to 35 days in *B. daigremontianum* (Table 2, Fig. 8). The timing of propagule detachment from the maternal plant varies according to environmental conditions. The propagule becomes independent (autonomous) as soon as it loses its link with the leaf vascular system and develops adventitious roots. In *B. daigremontianum*, this occurs at the late torpedo stage (Table 2, Fig. 5). The *B. calycinum* propagule becomes independent when its adventitious roots emerge into the leaf notch. Propagules may remain on the maternal leaf up to the stage where six pairs of leaves are formed in them. The *B. daigremontianum* propagules with three pairs of leaves are capable of producing new propagules on the third pair of leaves under conditions of high humidity and long day.

The examined *Bryophyllum* species have basically similar modes of propagule development (Table 3). The propagule has cotyledons with a well-developed vascular system and reserve substances in the form of starch, a plumule and a "hypocotyl". In both species, following the formation of cotyledons, the connection with the maternal plant vascular system

is established for a period of time. Propagules have been found to exhibit variations in their genesis. These concern the structure of a basal part, the timing and site of adventitious root initiation.

Comparative morphological and histological studies of vegetative propagules in the two *Bryophyllum* species suggest that these structures should be viewed as somatic embryos, and not as buds. Their features, such as origin from the residual meristem (dormant meristem), passage through major developmental stages typical for the sexual embryo (globular, heartshaped, torpedoshaped), presence of cotyledons and of a well-developed plumule, the bipolarity of their development, suggest that the *Bryophyllum* propagule can be regarded as a kind of somatic embryo. The specific character of this somatic embryo is the formation of adventitious roots from the dormant meristem derivatives. This pattern of development is similar to that of root development in *Nelumbo* and *Triticum*. A transient connection between the propagule and the leaf vascular supply is no evidence for the former being a bud, since the bipolar structure arising from the leaf epidermal cell in *Crassula multicava* L. is also linked to the maternal organism.

DISCUSSION

The nature of propagules occurring on the leaves of various *Bryophyllum* species has been discussed in the literature for more than 100 years (Strasburger, 1835; Hofmeister, 1868; Loeb, 1915; Goebel, 1928; Sinnott, 1960). Despite thorough studies by Berge (1877) of the *Bryophyllum calycinum* leaf structure and of vegetative propagule formation, the propagule morphogenesis and factors responsible for it are still an open question. This is probably the reason for there being no consensus in interpreting these structures and for multiplicity of terminology in describing them: "buds" (Howe, 1931), "adventive buds" (Strasburger, 1835; Haccius, 1969), "foliar buds" (Freeland, 1933), "foliar pseudobulbils" (Johanson, 1934; Resende, 1954), "embryos" or "foliar embryos" (Naylor, 1932; Yarbrough, 1932), "leaf-embryos" (Warden, 1968), "leaf-plantlet meristems" (= "leaf-embryos") (Warden, 1971/1972), "embryoids" (Batygina, 1989) and others.

Consider several views on the origin of meristem in *Bryophyllum* leaf notches and on the development of propagules. Thus, Beals (1923) believed the propagule to be formed as a result of division of phloem cells, i.e. endogenously. The author does not touch upon the problem of development of meristem in leaf notches. However, already Berge (1877), and subsequently (Hofmeister, 1868; Howe, 1931; Naylor, 1932; Yarbrough, 1932; Freeland, 1933; and others), studied *Bryophyllum* leaf meristems giving rise to propagules. They noted that in the leaf, which is 1-2 mm in size, the meristem is located in leaf notches. According to Yarbrough (1932), this meristem is not in contact with the leaf vascular supply. He termed it "dormant meristem", believing that it retains the meristematic property for a long time due to its isolated position. Such meristems were also localized in *B. daigremontianum* leaves (2.5-3 mm) (Johanson, 1934). Among the *Crassulaceae*, there are other representatives which develop propagules on leaves, as in *Crassula multicava* (McVeigh, 1938). In this species, propagules are only formed from derivatives of the leaf epidermis or leaf stalk cells. In *Crassulaceae* the vegetative propagule can be initiated exogenously. In *C. multicava*, all parts of the propagule are formed by proliferation of epidermal cells. More recently, a similar situation was reported

in *Ranunculus sceleratus* L. (Konar, Nataraja, 1965; Konar, Thomas, Street, 1973). In *R. sceleratus*, the vegetative propagule is represented by an embryoid which, like the *C. multicava* propagule, develops from epidermal cell derivatives. It should be noted that at no stage of its development is the embryoid in contact with the vascular system of the maternal organism (*in situ*, *in vivo*). This is in contrast to what is observed in *C. multicava* where the propagule establishes, at a late stage of its development, a link with the leaf vascular system.

Our data suggest that in the *Bryophyllum* species the viviparous propagule, with all its organs, is completely formed by proliferation of dormant meristem cells. In spite of the fact that the two *Bryophyllum* species develop adventitious roots by different mechanisms (in the hypocotyl in *B. daigremontianum* and from leaf marginal meristem in *B. calycinum*), the basal part of the bipolar propagule is differentiated from derivatives of dormant meristem cells in both species. The transient connection of the *Bryophyllum* bipolar propagule with the leaf vascular system is not established immediately following the formation of the propagule, and it disappears at a late stage of the propagule development. The period during which the propagule acquires autonomy (i.e. becomes independent of the maternal organism) spans different stages of its development, ranging in *B. daigremontianum* from the stage where the propagule shows well-developed cotyledons, the plumule is not yet differentiated and the roots just begin to form to the propagule which has 2 to 6 pairs of leaves and well-developed adventitious roots. In *B. calycinum*, this period is shorter. A similar pattern of propagule autonomization has been observed in sexual embryos (Batygina, Vasilyeva, 1987).

Comparative embryological study of development of sexual embryos, viviparous propagules, and embryoids formed in the *in vitro* culture suggests that the term "embryoid" is more appropriate in describing vegetative propagules in various *Bryophyllum* species and in *Crassula multicava* than the terms proposed by other authors. Comparative morphological analysis of sexual embryos, viviparous propagules and embryoids at different stages of development that have been obtained in the *in vitro* culture revealed their high morphological variation.

Therefore, we follow the point of view of Naylor (1932), Yarbrough (1932) and McVeigh (1938) who proposed that viviparous propagules of *Bryophyllum* and *Crassula* be referred to as "foliar embryos" or "embryos". It is probably for the reason of the term "embryoid" having been accepted in the literature more recently that the authors make use of it. The term "dormant meristem" appears to be an appealing one. Its legitimacy is supported by new evidence on viviparous maize mutants (Meinke et al., 1994). It is not inconceivable that the *viviparous* gene will be discovered in various *Bryophyllum* species as well.

There are two types of vegetative propagules arising by embryoidogenesis and gemmorrhizogenesis (homophase reproduction) (Batygina, in press). The present work deals with morphogenesis of the *Bryophyllum* vegetative propagule arising by embryoidogenesis. A similar pattern of the vegetative propagule morphogenesis has been reported in another species, *Crassula multicava*, belonging to the *Crassulaceae* family.

Viviparity *sensu lato* is the process of plantlet (propagule) formation on a plant *via* embryogenesis (heterophase reproduction), embryoidogenesis and gemmorrhizogenesis. It is an intermediate form between the typical seed reproduction and the typical vegetative propagation.

Figs 1-11. Morphogenesis of vegetative propagule of *Bryophyllum* (schematically).

1a-4a, 11a – The different stages of leaf development. in *B. calycinum*. 1b-4b, 11b and in *B. daigremontianum*. 1-6 – early stages of development of vegetative propagule in both species. 7-10 – successive stages of development of vegetative propagule of *B. daigremontianum*. 7.1-10.1 – *B. calycinum* 11 – plantlet of *Bryophyllum*.

Figs 1-9. Successive stages of the development of meristematic zone which will give rise to a propagule in the notch of the leaf of *B. calycinum*.

Fig. 1. Notch (n) from the youngest leaf.

Fig. 2. Notch, showing a group of meristematic cells at edge of the leaf and its vascular bundle (v b).

Fig. 3. Early "globular stage" of propagule formation.

Fig. 4. Heartshaped stage of propagule formation (c – cotyledon).

Fig. 5. The propagule at the late stage of development. Cross section of the leaf (c – cotyledon, r – adventitious root, v b – vascular bundle of leaf).

Figs 6-9. The successive stages of development of cotyledons (c) of propagule in the notch of the leaf. SEM. 6, 7 – x300, 8 – x200, 9 – x600.

Figs 1-7. Some stages of propagule development in leaf notch of the *B. daigremontianum*.

Fig. 1. Heartshaped stage of propagule formation (c – cotyledon).

Fig. 2, 3 Heartshaped stage of propagule formation in the peg of leaf notch. SEM, x100.

Fig. 3. Top view SEM, x320.

Fig. 4. Torpedoshaped stage of propagule formation. SEM, x200.

Fig. 5. Late torpedoshaped stage. Cross section of the peg (c – cotyledon, ad r – adventitious root, pl – plumule, w h – basal widening of hypocotyl). LM.

Fig. 6. The basal part of plantlet, showing one cotyledon (c), basal widening of hypocotyl (w h) and adventitious roots (ad r), the second cotyledon is not visible (e l – edge of leaf). The beginning formation of abscission layer of propagule is visible.

Fig. 7. The peg of notch, showing the zone (z) which is left after abscission of the plantlet. SEM, x.78.

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MORFOGENEZA ROZMNOŻEK ŻYWORODNYCH GATUNKÓW
BRYOPHYLLUM DAIGREMONTIANUM I *B. CALYGINUM*

STRESZCZENIE

Rozmnożki dwu żyworo-dnych gatunków *Bryophyllum* (*B. daigremontianum* i *B. calycinum* (*Crassulaceae*) rozwijały się drogą embriogenezy (zarodek somatyczny). Organy wszystkich rozmnożek obu gatunków powstają z pochodnych uśpionego merystemu ale przejawiają w późniejszych stadiach rozwoju – przy inicjacji korzeni przybyszowych. Rozmnożki obu gatunków przechodzą stadium "globularne", sercowate i torpedowate. Z porównania embriologii i morfologii rozmnożek i zarodków płciowych obu gatunków wynika, że ich rozwój jest bardzo podobny, chociaż ich morfologia jest różna.

Potwierdziliśmy, że wegetatywne rozmnożki roślin kwiatowych mogą być embrioidami lub pąkami. Przy-puszczamy, że oba gatunki *Bryophyllum* mają spoczynkowy gen.

SŁOWA KLUCZOWE: żyworo-dność, rozmnożki wegetatywne, embroid, morfogeneza, *Bryophyllum*.