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Combination of sequences of cell divisions in the anther wall formation in Solanaceae species

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Summary

Anther wall formation was studied in six Solanaceae species (*Bouchetia anomala, Capsicum tovari, Margaranthus solanaceus, Physalis viscosa, Withania adpressa*, and *Withania riebeckii*). Combinations of at least three different sequences of cell divisions were observed in the same species, even in the same microsporangium. These data contrast with the general idea that each species shows a single pattern or type of wall formation. The mentioned co-occurrence of cell divisions evidences the close affinity of the anther wall formation types, and the thin boundary between them. This co-occurrence also reveals different cell abilities and some kind of convergence, since two neighbour cells may go through different sequences of divisions but originate the same wall structure (= number of layers).

Key words: anther wall formation, combination of cell division, Solanaceae

Introduction

Davis (1966) established a classification of anther wall formation types to characterise particular sequences of cell divisions that produce all the wall layers. Afterwards, many authors have used that terminology to describe the antheral development in many species of different families. Within Solanaceae, the anther wall formation type has been studied in a number of species, in which the 'basic' and 'dicotyledonous' type have been reported (for a review, Carrizo García 2002b). In all the cases recorded until now, every species has a single type, while certain variability is found above the specific level (i.e. genera, tribes – Carrizo García 2002b –). The only exception to this in the family has been reported for *Solanum nigrum* L., in which the basic and dicotyledonous types appear simultaneously (Bhandari & Sharma 1987).

In a study of the anther histology carried out as a part of an integral antheral analysis of a number of Solanaceae genera (Carrizo García 2002a, b), different sequences of cell divisions have been found simultaneously in several species. As a consequence, this paper is an attempt to show these patterns and to discuss their relation to the types of wall formation defined by Davis (1966), as well as the possible meaning of the variability observed.

Materials and methods

A total of six Solanaceae species were studied, which are detailed in table 1. The observations were made under a compound light microscope in cross sections of young buds of several sizes; at least ten buds from a single individual were examined for each species. The buds were first fixed in formalin – ethyl alcohol – acetic acid, then dehydrated, included in Paraplast™, and finally sectioned. The 5–8 μm thick serial sections were coloured with Cresyl Violet (D'Ambrogio de Argüeso 1986).

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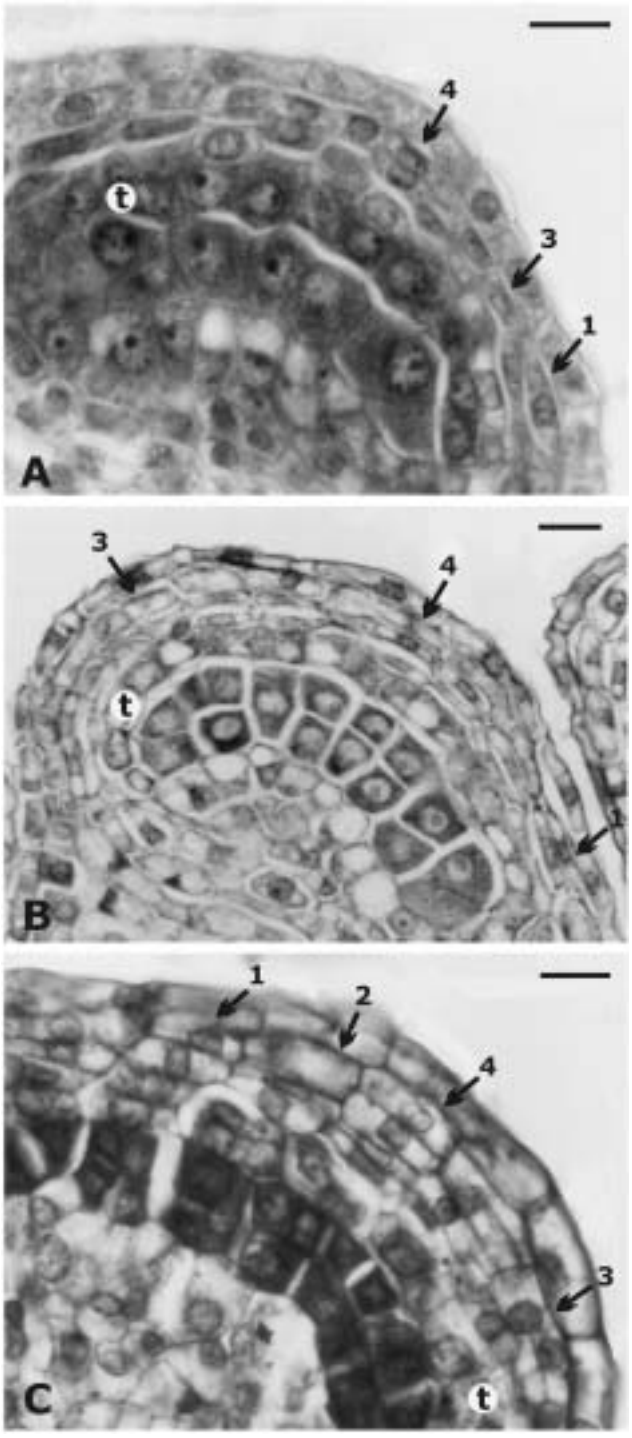

Fig. 1. Combinations of sequences of cell divisions in the anther wall formation in Solanaceae. **A:** sequences 1, 3, and 4 in *Bouchetia anomala*. **B:** sequences 1, 3, and 4 in *Margaranthus solanaceus.* **C:** sequences 1, 2, 3, and 4 in *Withania adpressa*. References. T: tapetum, 1: sequence 1, 2: sequence 2, 3: sequence 3, 4: sequence 4. Scale bars: 15 μm.

Results

Each microsporangium shows in all the species investigated a primary parietal layer between the epidermis and the sporogenous tissue. The cells of the primary parietal layer divide periclinally once, forming two secondary parietal layers, the outer and the inner. From the cells of these two layers, four main sequences of cell divisions could be observed, which can be summarised as follows:

Sequence 1. The cells of both secondary parietal layers divide periclinally, originating four new layers. From the epidermis inwards, the layers formed are endothecium, two middle layers and tapetum (Figs. 1 A–C).

Sequence 2. The cells of both secondary parietal layers divide periclinally, originating the endothecium, two middle layers, and the tapetum; the middle layers continue dividing after the tapetum has differentiated itself (Fig. C). Thus, the final number of layers (always higher than four) depends on the number of subsequent divisions that have taken place.

Sequence 3. Only the cells of the outer secondary parietal layer divide periclinally, while the inner secondary parietal layer directly differentiates as tapetum. The layers thus formed are endothecium, a single middle layer, and tapetum (Figs. 1 A–C).

Sequence 4. Only the cells of the outer secondary parietal layer divide periclinally, but subsequent cell divisions can occur in the cells of the resulting middle layer (Figs. 1 A–C), and sometimes also in the endothecial cells (Fig. 1C). The tapetum differentiates itself directly from the inner secondary parietal layer. The layers thus defined are endothecium, two or three middle layers (which depends on the number of subsequent cell divisions), and tapetum.

Different combinations of these four sequences appear in each species, even in the same microsporangium. Thus, in *Bouchetia anomala*, *Physalis viscosa*, *Margaranthus solanaceus*, *Capsicum tovari*, and *Withania riebeckii*, sequences 1, 3 and 4 are observed (Figs. 1A, B). In any of these five species, one subsequent division in cells of the middle layer is the commonest in sequence 4, while new divisions rarely occur in the future endothecium (Figs. 1A, B). Thus, the epidermis, the endothecium, one to three middle layers, and the tapetum form the mature anther wall.

A combination of sequences 2 and 4 is found in *Withania adpressa* (Fig. 1C). Usually, there are later divisions in cells of the middle layers in these two sequences, as well as in the endothecium in sequence 4 (Fig. 1C), but they do not follow any observable pattern. Besides, sequences 1 and 3 may appear rarely (Fig. 1C). Therefore, the epidermis, the endothecium, one to three middle layers, and the tapetum form the mature anther wall.

Table 1. Species studied and collection data (voucher specimens deposited at CORD).

Species	Collection data
Bouchetia anomala (Miers) Britton et Rusby	Argentina, Di Fulvio 491
Capsicum tovari Eshbaugh, Smith et Nickrent	Argentina, cult., Botanical Museum of Córdoba, Carrizo García
Margaranthus solanaceus Schltdl.	Netherlands, cult., Nijmegen Botanical Garden, Carrizo García
Physalis viscosa L.	Argentina, Carrizo García
Withania adpressa Battand.	Netherlands, cult., Nijmegen Botanical Garden, Carrizo García
Withania riebeckii Balf.	Netherlands, cult., Nijmegen Botanical Garden, Carrizo García

Discussion

The types of anther wall formation defined by DAVIS (1966) have received contrasting importance, since they have been used without objections by many authors, completely ignored by others, and also criticised by some others (VARGHESE & CHOWDHURY 1972; BHATNAGAR & KAPIL 1979; JOHRI et al. 1992). The four sequences identified in this work may be related to the types of wall formation defined by DAVIS (1966). Thus, sequences 1 and 2 would be equivalent to the basic type, but sequence 2 develops subsequent divisions in the middle layers. Sequences 3 and 4 may be considered, respectively, the dicotyledonous type and a derived case of this one due to the subsequent divisions in the middle layers and/or endothecium. Even though sequences 2 and 4 initially follow a particular type, the subsequent divisions make a difference.

The most outstanding fact presented here is that different sequences of cell divisions occur simultaneously in the same species. Up to the present, it has been usual to mention a single sequence of cell divisions for each species in Solanaceae, a sequence that was identified as a particular type of wall formation (CARRIZO GARCÍA 2002b). The only exception found in the family was *Solanum nigrum*, in which the basic and dicotyledonous types were recorded in different microsporangia of the same anther (BHANDARI & SHARMA 1987). Another peculiar feature found in all the species described here is that different sequences occur simultaneously even in the same microsporangium. Nevertheless, in spite of the co-occurrence of sequences, all of them agree in some way with the basic and dicotyledonous types, which are the only two types recorded in Solanaceae until now (for a review, CARRIZO GARCÍA 2002b).

BRUNKENER (1975), BHATNAGAR & KAPIL (1979), and HERMANN & PALSER (2000) reported several cases of variability in the anther wall formation. BRUNKENER (1975) studied a number of angiosperm species, and in some of them this author observed two or three different types of wall formation in the same microsporangium. The possible combinations were basic and monocotyledonous types (e.g. *Delphinium californicum* TORR. ET GRAY – Ranunculaceae –, *Populus tremula* L. – Salicaceae –), basic and dicotyledonous (e.g. *Ranunculus repens* L. – Ranunculaceae – , *Lupinus* sp. – Fabaceae –), dicotyledonous and monocotyledonous (e.g. *Ulmus glabra* HUDS. – Ulmaceae –, *Salix caprea* L. – Salicaceae –), and basic, dicotyledonous and monocotyledonous (e.g. *Ricinus communis* L. – Euphorbiaceae –, *Acacia* sp. – Mimosaceae –). BHATNAGAR & KAPIL (1979) studied only one species, *Bischofia javanica* BL. (Euphorbiaceae), in which they observed the basic type in some microsporangia, while the dicotyledonous and monocotyledonous types were present in others in the same anther. Moreover, they also registered subsequent divisions in the middle layers in the two last cases. Like in *Solanum nigrum* (BHANDARI & SHARMA 1987), different types of wall formation appear in different microsporangia, but not in the same one as in the six species described here and in those species studied by BRUNKENER (1975). On their part, HERMANN & PALSER (2000) observed the most atypical cases in four species of different Ericaceae genera. These species follow the same pattern until the secondary parietal layers are formed, but 'the subsequent development … is rather erratic so it does not follow a fixed pattern that might be expected of the types in Davis' classification'. This is a different and extreme case, since no type could be observed. The variation found was also present within the same microsporangium.

All the examples mentioned above show the variability that can be found in the anther wall formation, ranging from a family (e.g. Solanaceae, Salicaceae, Euphorbiaceae) up to a single species, and even in the same anther and microsporangium. BHATNAGAR & KAPIL (1979) have affirmed that the variability found in *Bischofia javanica* shows that Davis' terminology is inadequate, a proposition that was repeated afterwards by JOHRI et al. (1992). This position seems rather categori-

cal, since some species develop exactly as some of the types defined by Davis (e.g. dicotyledonous type in *Salpichroa* – Carrizo García (2000) – or basic type in *Nicotiana glauca* Graham – Carrizo García (2002b) –). The co-occurrence of different sequences, even in the same microsporangium, perhaps denotes the close affinity of the types of wall formation, for they are distinguished by the occurrence or not of a single cell division. Maybe it would be more appropriate to consider that it is possible to find species that may not follow a single type, or show variations, and recognize that the boundaries between the types can be trespassed.

As regards the subsequent cell divisions reported in sequences 2 and 4, Davis (1966) mentioned their possible occurrence, but did not give them too much importance. It has been already pointed out that the mentioned subsequent cell divisions cannot be ignored, since they reveal different cell abilities, and they define the anther wall structure (Carrizo García 2002b). Concerning the species studied here, it can be said that a particular number of wall layers may be formed in different ways in the same microsporangium (e.g. sequences 1 and 4), a fact that reveals some kind of convergence. More precisely, two neighbour cells may behave differently, i.e. go through different sequences of cell divisions, but originate the same number of layers, that is the anther wall structure. Finally, the combination of different sequences of cell divisions in the same microsporangium raise questions about the causes of the different cell behaviour of neighbour cells since usually the same one has been observed in all the secondary parietal cells in a particular species.

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