Evolutionary patterns in seed formation of the Bulgarian taxa of Thalictrum (Ranunculaceae)

Abstract

A detailed cytoembryological study of seed development in the eight Bulgarian Thalictrum taxa showed that embryogeny conforms to the primitive Onagrad type and the endosperm is nuclear. Some advanced features were found in mature seeds, in which respect T. simplex subsp. rhodopaeum, by the formation of a primordial plumule and procambial vessels, appears to represent the highest evolutionary level known for the whole family. These and other data demonstrate that the evolution of cytoembryological features within the genus Thalictrum shows both parallelism and heterobathmy.

Introduction

The family Ranunculaceae is well known for showing a remarkable combination of primitive and advanced characteristics. Thalictrum species are of particular interest because of scantiness of relevant information. A comparative embryological study of the Bulgarian Thalictrum taxa (Daskalova 1984) has shown that they have retained some primitive features while at the same time developing new, progressive ones. Against this background, the results of a comparative cytoembryological study of their seed development are presented here.

Material and methods

Seed from the eight Bulgarian species and subspecies of Thalictrum (Panov 1970, but with T. minus not subdivided) was collected between 1976 and 1980 in the wild, from native populations (Table 1). The plants from which seeds were taken have been deposited in SOM as voucher specimens, and are indicated in the text and table by their respective collecting numbers (prefixed with T-).
Table 1. A list of cytoembryologically studied populations and voucher specimens.

<table>
<thead>
<tr>
<th>Thalictrum</th>
<th>Locality (voucher No.)</th>
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<tr>
<td>aquilegiifolium L. subsp.</td>
<td>Mt Vitosa, grassy places by the river Drenovicka in the Botanic Garden (T-11237)</td>
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<tr>
<td>aquilegiifolium</td>
<td>Mt Slavjanka, in Pinus sylvestris wood mixed with Fagus sylvatica and Picea abies above the village Panil (T-12504)</td>
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<tr>
<td>storgosiacum Panov</td>
<td>Mt Pirin, grassy places in Pinus heldreichii wood by the hut &quot;Javorov&quot;, 1800 m (T-12519)</td>
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<tr>
<td>foetidum L.</td>
<td>Danube plain, grassy and rocky places at &quot;Kajlaka&quot; near Pleven (T-14500)</td>
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<tr>
<td>minus L.</td>
<td>Krajste, grassy and stony places by the river Erma near Tran (T-1406)</td>
</tr>
<tr>
<td>simplex L. subsp. simplex</td>
<td>Stara planina, Kotlenska part, grassy and rocky places at &quot;Barmukbair&quot; (T-11203)</td>
</tr>
<tr>
<td>simplex subsp. rhodopae-um (Rech. f.) Panov</td>
<td>Western boundary mts, Vlahina planina, grassy places by the frontier (T-1199)</td>
</tr>
<tr>
<td>lucidum L.</td>
<td>Krajste, Cepan subregion, grassy places by Belidjiehan (T-13504)</td>
</tr>
<tr>
<td>flavum L.</td>
<td>Sofija region, wet meadows by the village Gorubljane (T-12505)</td>
</tr>
<tr>
<td></td>
<td>Danube plain, distr. Lom, wet places and meadows by the village Orsoja (T-13507)</td>
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</table>

The material was fixed in Navashin’s mixture, embedded in paraffin using the classical methods, and sectioned with a rotary microtome. The microtome sections were stained in Heidenhain’s haematoxylin.

Results and discussion

The first division of the primary endosperm nucleus is not followed by wall formation, and the endosperm is nuclear as in all other Thalictrum species studied so far (Overton 1904, Vijayaraghavan & Bhandari 1970) and, generally, in all Ranunculaceae (Tamura 1965).

The first division of the zygote is transversal, as in all other members of the family (Davis 1966), and terminal and basal cells are formed (Fig. 1). The further embryogeny conforms to the Onagrad type, considered to be primitive (Fig. 2).

In the mature seed, the endosperm occupies the whole cavity (Fig. 2-4), surrounding a small, typically dicotyledonous embryo (Fig. 1-3) which consists of a short massive

Fig. 1-7. Seed formation in Bulgarian Thalictrum species. – 1, First division of the zygote in T. foetidum (× 2000); 2, seed of T. aquilegiifolium (× 200); 3, seed of T. flavum (× 200); 4, seed of T. simplex (× 200); 5, mature embryo in T. flavum (× 1500); 6, mature embryo in T. minus (× 1500); 7, mature embryo in T. simplex (× 1500).
suspensor, a radicle, a hypocotyl, a shoot apex, and cotyledons. According to these characteristics the mature seeds are similar to the “rudimentary type” in Martin’s (1946) seed classification, which is considered to be the most primitive type in angiosperms. As a rule, the embryo is not differentiated when it is detached.

In the mature seed, however, some progressive features were found that are unevenly distributed over the studied taxa, among which the degrees of correlation between embryo and whole seed and of cotyledonal development vary. The weakest correlation and lowermost degree of cotyledonal development were found in *Thalictrum aquilegiifolium* subsp. *aquilegiifolium* (T-11237, Fig. 2), followed in this order by *T. lucidum* (T-12505), *T. flavum* (T-13507, Fig. 3, 5), *T. foetidum* (T-1406), and *T. minus* (T-11203, Fig. 6). The strongest correlation between embryo and whole seed, and the highest degree of cotyledonal development – features that are considered as advanced – were found in *T. simplex* subsp. *rhodopaenium* (T-1199, Fig. 4).

According to our results, and due to the observed formation of a primordial plumula and procambial vessels (Fig. 7), the mature seeds of *Thalictrum simplex* subsp. *rhodopaenium* would represent the highest evolutionary level known so far, not only in the genus *Thalictrum* (Overton 1904, Vijayaraghavan & Bhandari 1970, Ivanova 1971), but in the *Ranunculaceae* as a whole (Sokolovskaja 1981).

The foregoing results, when combined with further embryological data established by us (Daskalova 1984), demonstrate that the evolution of cytoembryological features within the genus *Thalictrum* shows both parallelism and heterobathy.

References


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