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Nodal Spine Pairs Present in the Mimosoid *Prosopis juliflora* Are Not Stipules but Define a Distinct Class of Lateral Organs

Vishakha Sharma, Sushil Kumar*

National Institute of Plant Genome Research (NIPGR), New Delhi, India.
Email: *sushil2000_01@yahoo.co.in

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ABSTRACT

The descriptions of *Prosopis juliflora* of subfamily mimosoideae in the family leguminosae, given in the floras of arid and semi-arid regions of the world, including the flora of Delhi, state that the spine pairs seen in association with compound leaf on nodes are stipules. The suggestions that spines are stipules were tested by morphological and histological examination of nodes of *P. juliflora* plants growing in the Arawalli range at New Delhi. The nascent nodes on growing branches of *P. juliflora* were observed to produce a pair of knife-like free bifacial stipules together with a leaf and a pair of spines. The stipules were missing from the mature nodes of the same branches whose young nodes carried stipule pairs, suggesting that the stipules were deciduous whereas leaves and spines were persistent. Anatomically, spines were observed to be appendages to stem and located adjacent to leaf petiole away from stipules. Vasculature of stipules was independent. The observations allowed the conclusion that *P. juliflora* nodes form regular stipules and spines produced on them are stem-like distinct lateral organs. It is suggested that nodal spine pairs borne on plant nodes in general are lateral organs different from stipules, leaves and secondary inflorescences.

Keywords: Lateral Organs; Leaf; Mimosoideae; *Pisum sativum*; Spines; Stipules

1. Introduction

Shoot architecture of angiospermic plants is largely dependent on the size, structure and relative arrangement of its vascularised lateral organs, formed on nodes of the main stem and branches [1]. Leaves and stipules in the vegetative phase and these and flower/fruit bearing secondary inflorescences in the reproductive phase are the principal lateral organs of most angiosperms [2]. Stipules are known to occur only in about a third of angiosperm species [3]. Usually formed in pairs, one on either side of the site of attachment of leaf to stem, stipules demonstrate enormous inter-species variation in size and structure [4]. Stipules are vestigial/inconspicuous in some species [4]. In other stipulate species, scaly, tendriller, spiny or foliaceous stipules of varying sizes and patterns have been treated as species specific taxonomic characters [3,4]. The genetic programmes of stipule differentiation have begun to be investigated [5-8]. In *Pisum sativum*, a model species for the study of stipule, leaf and flower/inflorescence development processes, the *cochleata* (*coch*), *stipule reduced* (*st*) and *coch st* mutants in the background of leaf mutants and 1-N-napthylpthalmic acid (NPA, an auxin transport inhibitor) treated *COCH ST* shoots have been observed to produce nearly all of the reported patterns/morphologies of stipules, including tendriller stipules, except the scaly and spiny stipules [7-10]. These observations indicated parallel homoplasy [10,11] in the network of genes involved in the determination of the large majority of angiosperm stipule types and sharing of genes between leaf and stipule differentiation [9,10].

Spine (or thorn) pairs produced at nodes are reported as stipules in some species of very different families [2-4]. Nodal spine pairs are a characteristic of several species of the genera such as *Acacia*, *Mimosa* and *Prosopis* of the subfamily mimosoideae of the leguminoseae family [12-18]. Following two considerations led us to hypothesize that spines are lateral organs that are distinct from secondary inflorescences, leaves and stipules. 1) spines are radial structures, contrastingly different from most other types of stipules which are bifacial like leaves and leaflets [3,4]; 2) Spine-like stipules have not been observed among the genetic and induced stipule variants in *P. sativum*, a member of subfamily papilionoideae closely related to subfamily mimosoideae in the same family leguminosae [7-9]. The hypothesis was tested on

*Corresponding author.

Prosopis juliflora (Swartz) D.C. whose nodes are reported to carry spines as stipules. The nascently formed vegetative nodes and aged nodes were examined for their lateral organs morphologically and histologically. The study revealed that *P. juliflora* nodes bear small, free and bifacial deciduous stipules, and the spines are distinct lateral organs having origins of vasculature in stem, independent of that for stipules.

2. Materials and Methods

Areas of Aravalli range in and around the institute's campus were surveyed for adult plants of *P. juliflora* (Mimosoideae) and *Eagle marmelos* (Linnaeus) C. S. (Rutaceae) some of which were tagged for investigation. *E. marmelos* served as a control species in these experiments. Branches clipped from the identified trees were separated into nascent and mature nodes which were scanned using a Hewlett Packard PSC scanner and photographed using NIKON SMZ 1500 Stereozoom Microscope (Tokyo, Japan) and photographed with Nikon DXM 1200 cc digital camera. The nodes were fixed in formalin acetic alcohol and sectioned transversally with hand held rajor. Sections were stained with dilute safranine and observed microscopically with Nikon E100 microscope at 40× magnification. Microphotographs were taken by attaching microscope to Nikon 8400 digital camera.

3. Results

In accordance with the description given in floras, the adult nodes of *P. juliflora* and *E. marmelos* carried attached to stem a compound leaf and on each side of it a spine (**Figures 1(a)** and **(d)**). The young nodes of *E. marmelos* had the same composition of lateral organs as the mature nodes of *E. marmelos*. However, all the young nodes of *P. juliflora* carried, besides leaf and a pair of spines, a pair of free bifacial stipules of small size (**Figure 1(b)**). From side to side the arrangement of lateral organs on the young nodes of *P. juliflora* was visualized as stipule-spine-leaf-spine-stipule (**Figure 1(a)**). The sections at the nodes of the two species (**Figures 1(c)** and **(f)**) showed that the vasculatures of spines were located side by side as stem appendages. The vasculatures of the stipules in *P. juliflora* were on the periphery of those for leaf petiole (**Figure 1(c)**). In both *P. juliflora* and *E. marmelos* the the spine bases were seen behind the leaf petiole in the nascent nodes, however, in the mature nodes the spines occupied positions lateral to leaf petiole, apparently due to increase in the stem girth.

The stem sections at the nodes of *P. juliflora* and *E. marmelos* (**Figures 1(c)** and **(f)**) showed that spines were a part of stem. The outer tissues of stem continued uninterruptedly around the spines, although spines appeared

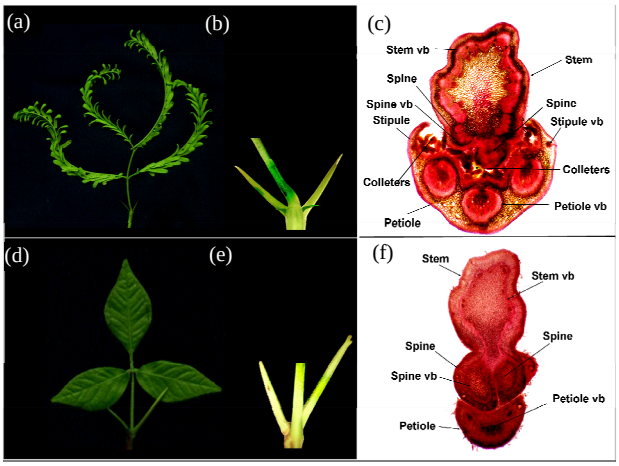

Figure 1. Composition of lateral organs at the vegetative nodes of *Prosopis juliflora* ((a), (b) and (c)) and *Eagle marmelos* ((d), (e) and (f)). (a) and (d), Lateral organs at a node: (a) = Bipinnate petiolated leaf, a pair of spines and a pair of stipules in *P. juliflora*; (d) = Trifoliate petiolated leaf and a pair of spines in *Eagle marmelos*. (b) and (e), Magnified view of node: (b) = Stem node bearing a leaf petiole in the center, a pair of large spines and a pair of smaller stipules in *P. juliflora*; (e) = Stem node bearing a leaf petiole in the center and a spine is seen on each side on the back of petiole in *E. marmelos*. (c) and (f), Transverse sections of stem nodes: (c) = Colleters (epidermal glands) lie in between the stem and leaf petiole. Spines appear as stem appendages. Stipules have vascular bundles (vb) independent from the tripartite vasculature for leaf petiole. (f) = Stem and leaf petiole are separate. Spines appear as stem appendages. The petiole has tripartite structure.

to have vascular bundle(s) well separated from the vasculature of the stem. The vasculature of petioles in both *P. juliflora* and *E. marmelos* (**Figures 1(c)** and **(f)**) was tripartite. The morphological absence of stipules in *E. marmelos* was in conformity with the absence of any extra vasculature in the petiole, unlike the petiole of *P. juliflora* in which distinct vascular bundles for the stipules could be visualized.

4. Discussion

In this study the lateral organs borne on the vegetative nodes of *P. juliflora*, a taxon of the subfamily mimosoideae of leguminosae family, and *E. marmelos* of the distant family Rutaceae were examined comparatively for some important morphological and histological features. *E. marmelos* nodes were observed to bear a leaf and a pair of spines. Whereas in this system, the vascular bundles of leaf had distinct origin from stem, those for spines appeared as stem appendages. The tissues of spines were anatomically (cell morphology-wise) similar in appearance to those in the stem. This indicated that spines of *E. marmelos* were stem-like radial lateral or-

gans. In *P. juliflora*, the position of spines with respect to leaf petiole and stem on the nodes was similar to that in *E. marmelos*. The internal structure of spines of the two species was also similar. Therefore, it was concluded that spines are stem like lateral organs. The nodes of *P. juliflora* demonstrated the presence of vasculatures for stipules at the edges of petiole. Absence of extra vasculature at nodes in *E. marmelos* was in agreement with the absence of stipules.

The morphological and histological observations allowed the inference that stipules and spines were distict lateral organs in *P. juliflora*. Since stipules were absent from the mature nodes of *P. juliflora* due to their deciduous nature, while leaf and spines were persistent, it was concluded that stipules and leaf were also distinct lateral organs. Anatomical homology between the spines of very different/distant species *P. juliflora* and *E. marmelos* led to the suggestion that the radial nodal spine pairs, present in taxonomically different species, are independent stem-like lateral organs that are distinct from stipules which are usually bifacial.

It is thought that spines exemplify determinate stem growth. The gene network responsible for differentiation and growth of stem is expected to be shared by spines with modifications of some genetic regulatory events. Spines perhaps provide a novel model of organ development processes.

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