PRIMARY VASCULAR ORGANIZATION OF *TESSARIA ABSINTHIOIDES* (COMPOSITAE)

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Abstract

The primary vascular system of the shoot of *Tessaria absinthioides* was studied by the use of serial cross sections. It is a system of the open type, with eight sympodia, 2/5 helical phyllotaxy and trilacunar three-trace nodes. All the bundles are interpreted as leaf traces diverging towards the left along a sinistrorse genetic spiral. Leaf insertion is of the separated type and there are two sets (2 + 3) of contact parastichies in the apex. The phylogenetic implications of these characters are discussed.

Introduction

The primary vascular system in seed plants varies greatly in pattern and complexity from one taxon to another (Beck *et al.*, 1982). Its organization, which is directly related to the phyllotaxy reflects the intrinsic continuity of stem and leaves (Wardlaw, 1968; Namboodiri & Beck, 1968; Devadas & Beck, 1972).

Although the stelar concept (Fahn, 1974; Esau, 1977) has given an idea of the unity of plant structure, it has also contributed to consider the vascular system as something rigid and artificial (Esau, 1954). The study of the morphology and ontogeny of vascular bundles through serial sections of both the shoot apex and young stem has served to elucidate the architectural pattern of the primary vascular system, thus providing an understanding of the relationships between bundles (Devadas & Beck, 1971).

Stem stelar structure has been used to interpret the phylogenetic and taxonomic relations of various taxa (Ezelarab & Dormer, 1963; Philipson & Balfour, 1963; Benzig, 1967; Jensen, 1968; Namboodiri & Beck, 1968; Rodin & Paliwal, 1970). Although Compositae is recognized as a clearly defined family, and as such has drawn attention of several research groups interested in documenting its phylogenetic relations, few papers could be found on its primary vascular organization (Esau, 1945; Carlquist, 1959; St. Omer & Moseley, 1981).

The aim of the present paper is to determine the architecture of the primary vascular system of *Tessaria absinthioides* and to contribute to understand the phylogenetic position of the tribe Inuleae.

Materials and Methods

Plants of *Tessaria absinthioides* (Hook. et Arn.) D.C. were collected from two sites, Bahia Blanca and Pradere, in the south west of Buenos Aires Province.

Apical shoot segments 1-3 cm long were fixed in FAA and stored in 70% ethanol. Specimens were dehydrated and paraffin embedded according to conventional methods (Johansen, 1940). Serial cross sections 10-20 μm thick were cut and stained with
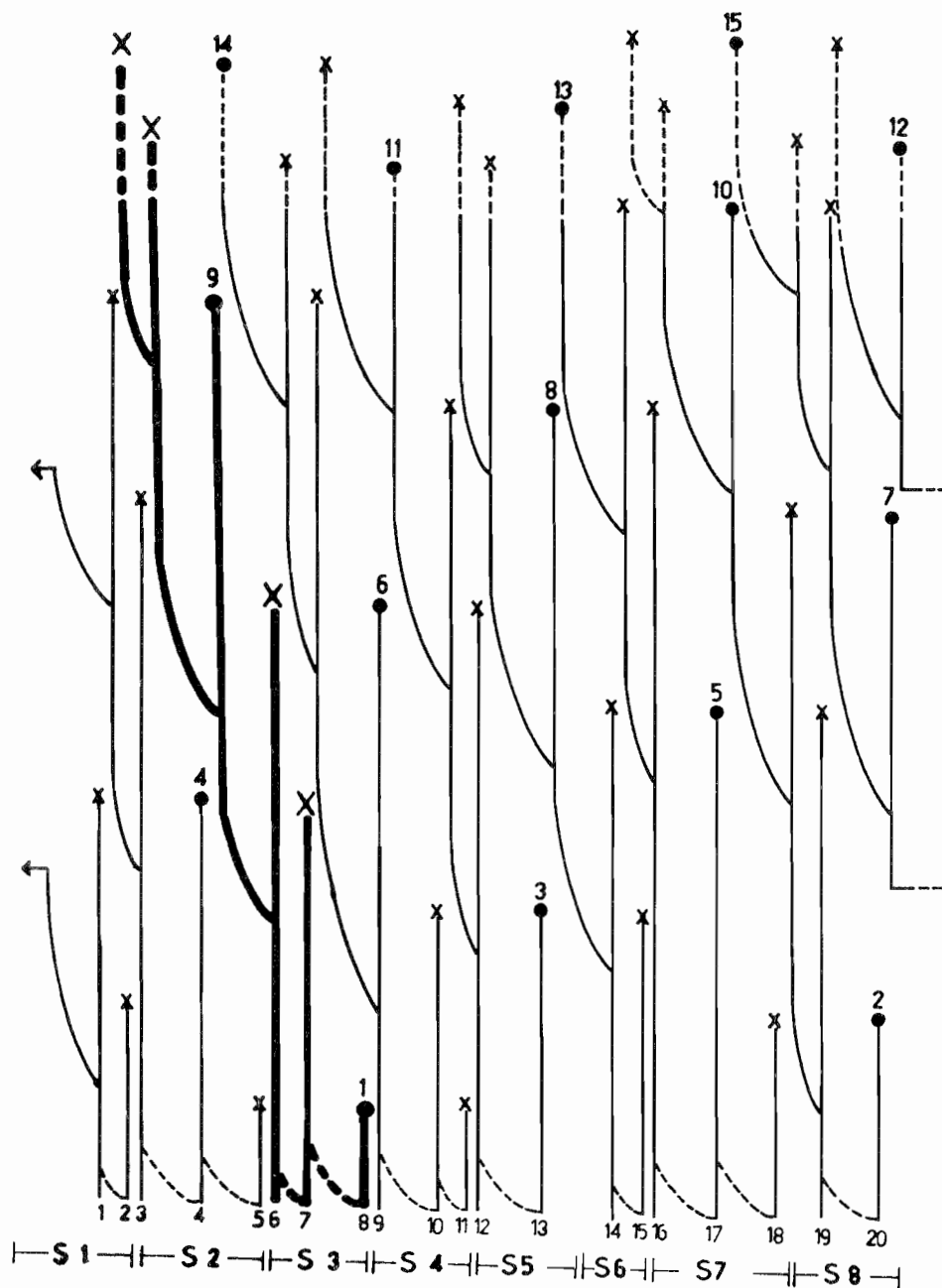
Fig.1. Two dimensional diagram of the primary vascular system as if split open lengthwise and viewed from the inside. Leaves numbered in increasing order from the bottom. Upper broken lines indicate traces of young shortened inter nodes. The bundles are numbered from 1 to 20 as in Fig.2: broken lines show their connections below the segment depicted. Sympodium 3 drawn with thick lines. S = sympodium, o = medium trace, x = lateral trace.

safranin-fast green. Line drawings of bundles and leaf traces were made from the serial sections using a Wild M20 microscope fitted with a drawing tube.

Reconstructions of the primary vascular system were depicted as if the stem were split open lengthwise and viewed from the inside. Photographs were obtained using a Zeiss II photomicroscope.

Results

Tessaria absinthioides is a sub-shrub, with rhizomes and gemmiferous roots as means of perennation and vegetative propagation. Aerial shoots 1-1.5 m high with basal and upper leaves are produced each spring. Basal leaves are sessile, 22-60 mm long x 3-6 mm wide, with entire margins and scattered hairs; upper ones are alternate, oblanceolate, sub-sessile, whitish pubescent, 50-80 mm long x 5-15 mm wide and toothed at their margins.

The primary vascular system of the stem is of the open type, with eight sympodia, 2/5 helical phyllotaxy and trilacunar three-trace nodes (Figs. 1,2). During early developmental stages, in the absence of secondary growth, the vascular bundle, 17-20 in each cross section (Fig.2), are interpreted as groups of leaf traces, no bundle remaining axial during the entire course of its development. Following the traces acropetally (Fig.1) they always diverge towards the left side, constituting the sympodia, and each one traverses several (3-4) internodes, as an identifiable unit, before separating from the rest and entering the corresponding leaf. Unions between adjacent sympodia are seen only occasionally
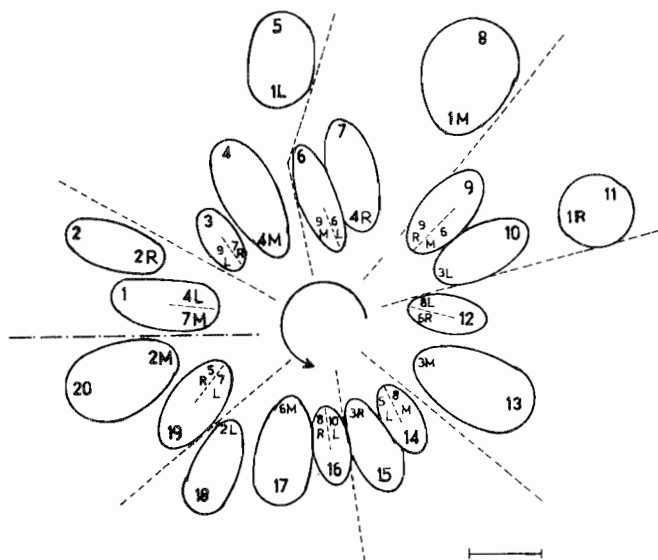

Fig.2. Diagram of cross section of stem corresponding to the bottom of Fig.1. Bundles numbered as in Fig.1. Curved arrow indicate sinistrorse genetic spiral. Broken lines delimit sympodial sectors. Dotted-dashed line indicate imaginary cut to depict diagram in Fig.1. M = median trace, R = right lateal trace, L = left lateral trace Scale = 200 μm.

Each sympodium (Fig.3) contributes one median (M), one right lateral (R), and one left lateral (L) trace to non- successive leaves; thus each sympodium is seen to connect leaves in the following sequence; **nM, n + 3R, n + 3 + 2L, n + 3 + 2 + 3M** and so on successively. Each leaf is connected by three adjacent sympodia (Fig.4) with two other leaves, two and three nodes farther down, so that **R** of a leaf **n** comes from **M** of the leaf **n-3, M** of the leaf **n** comes from **L** of the same leaf **n-3** and **L** of the leaf **n** from **R** of the leaf **n-2**.

This sequence determines the open system, made up of eight sympodia, with two of these intervening between those from which the median traces of the successive leaves diverge (Fig.1). Although along each sympodium there are eight leaves between two leaf traces of the same category (Fig.1), whether median or lateral, the phyllotaxy is nevertheless2/5 and not 3/8, because the·system rotates during its development.

The vascularization of two successive leaves does not overlap (Fig.1), thus determining leaf insertion of the separated type (Dormer, 1972), with one or two bundles remaining between them, depending on the level of internode being observed.
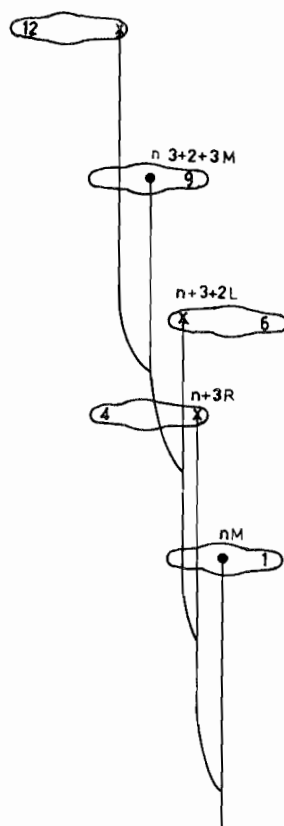

Fig.3. Diagram illustrating sequence of connections of the traces from one sympodium to non-successive leaves. M = median trace. R = right lateral trace. L = left lateral trace.
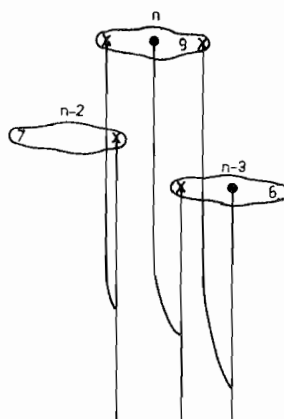
Fig.4. Diagram illustrating the connections of the traces of one leaf with three adjacent sympodia
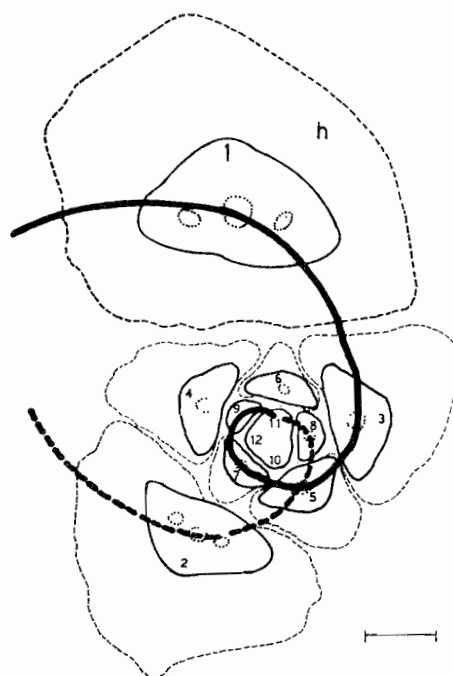

Fig.5. Diagram of cross section through shoot tip with young leaves numbered from below to the apex. One pair of 2 + 3 contact parastichies are indicated by entire and broken lines respectively. h = hairs. dotted circules = procambium and traces. Scale = 200 μm
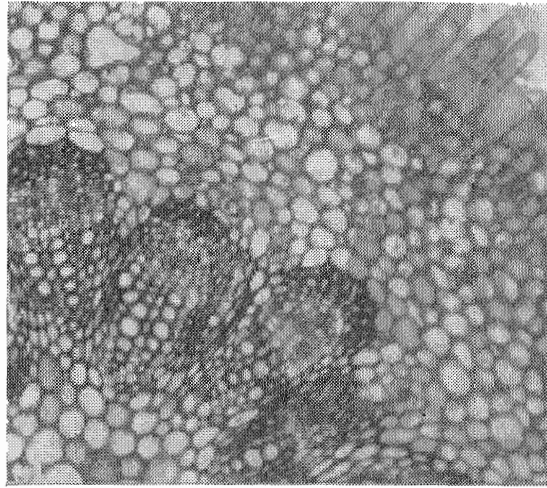
Fig.6. Cross section through an internode. h = hairs. Scale = 10 μm

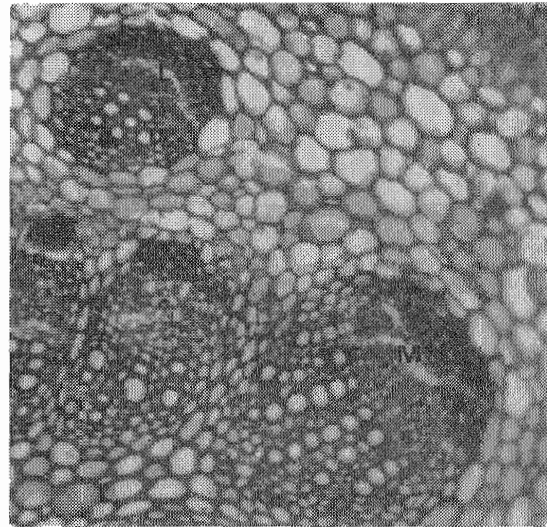

Fig.7. Cross section near a node. M = median trace. L = left lateral trace. Scale = 100 μm.

The transverse projection of the apex (Fig.5) shows the primordia numbered in increasing order following the sinistrorse direction of the genetic spiral. One pair of contact parastichies can be observed, constituting a spiral system of the type 2 + 3.

During the course of development the traces change in size, shape and composition. In the internodes the bundles are tangentially flattened (Fig.6) and form a ring with narrow interfascicular regions. In the nodal region, as they enter the leaves, they take on a circular form (Fig.7). The traces are composed of primary xylem and phloem in the internodes farthest away from the apex, and of phloem and procambium or procambium alone as they approach the apex. The sequence of tissue differentiation is the typical of most Dicotyledons; the phloem differentiates and matures acropetally prior to xylem, which does so bidirectionally.

Discussion

The results of the present paper indicate that the vascular system in *Tessaria absinthioides* is composed of leaf traces or groups of them, since none of the bundles are axial in the sense that they do not run through the stem indefinitely. Esau (1954) and O'Neil (1961)describe for *Helianthus* and *Lupinus albus*, respectively, primary vascular systems without axial bundles. This interpretation is not in agreement with that of Devadas & Beck (1972), who consider that each sympodium is formed by axial bundles from which the leaf traces diverge.

The most remarkable feature in the primary vascular system of *T. absinthioides* is the presence of eight sympodia with 2/5 phyllotaxy. This is explained by the fact that the whole vascular system rotates during the course of development, so that the sympodia do not remain parallel to the orthostichies (Beck *et al.*, 1982). Vascular patterns with more than five sympodia are uncommon among Angiosperms (Beck *et al.*, 1982). These authors found only three species of Angiosperms with eight sympodia and helical phyllotaxy: *Cotyledon paniculata, Petalostemon* sp., and *Sutherlandia frutescens*, none of them with 2/5 phyllotaxy, and only the last two with trilacunar nodes.

The number of bundles in each cross section is related to the number of sympodia, the quantity of leaf traces per leaf, and the number of internodes traversed by these traces (Devadas & Beck, 1972). In *T. absinthioides*, much overlapping does not occur, keeping a more or less constant number of 17-20 bundles in each cross section.

On the basis of the intimate relationship between phyllotaxy and vascular system (Cutter, 1959; Esau, 1965; Namboodiri & Beck, 1968) it is possible to determine the arrangement of bundles by looking at the direction of the genetic spiral, the direction of trace divergence, and the number of sympodia. In *T. absinthioides* the genetic spiral is sinistrorse, the traces diverge towards the left (as seen from the inside), and there are eight sympodia, in agreement with Namboodiri & Beck (1968) who demonstrated that in systems with 8 and 21 sympodia the direction of the genetic spiral is opposed to the direction of trace divergence (when viewed from the outside), even though Beck *et al.*, (1982) say that there is no correlation between these two characters.

From the phylogenetic point of view, *T. absinthioides* has some of the characters considered primitive as open vascular system and helical phyllotaxy, but lacks others as parallelism of sympodia and orthostichies, presence of five sympodia, and short traces (Namboodiri & Beck, 1968; Devadas & Beck, 1972,; Beck *et al.*, 1982). Taking into

account the fact that it remains unclear whether trilacunar nodes with three traces are primitive or evolved in nature (Dickison, 1975), then *T. absinthioides* is a species which can be defined neither as totally primitive nor totally evolved.

This ambiguity in the phylogenetic position of this species can be partly due to the fact that although it belongs to the Compositae, one of the most evolved families, it is classified in the tribe Inuleae, closely related to the Heliantheae, one of the most primitive tribes in the family (Cronquist, 1955).

Acknowledgement

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