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Ontogeny of Leaf in *Iris* (Iridaceae) and its Morphological Nature

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The initiation of leaf takes place by periclinal divisions in the second tunica layer and the cells of the outer corpus layers also contribute to the upgrowth of the leaf primordium. Further growth takes place by an adaxial meristem. As the leaf primordium grows in height, the adaxial meristem of two faces become unified and consequently an upper radial part is formed. The terete leaf of *Iris* is not simple elaborate petiole but it is equivalent to the laminar region of dicotyledonous leaves.

Key Words: *Iris*, **Leaf development, Adaxial meristem**

Introduction

The structure of the leaf in Iridaceae exhibits many features of anatomical interest due to its reported phyllodic nature. Some earlier workers (e.g. Arber 1921, Peters 1927) have studied the anatomy of *Iris* leaf in relation to its bearing on phyllode theory. However, no attempt has been made to evaluate it on the basis of ontogeny. The present study has been undertaken with a view to fill up this lacunae and to provide a broader basis for morphological interpretation of terete leaf of *Iris*.

Materials and Methods

The vegetative apices of *Iris decora* L. were collected from naturally growing populations in Mussoorie. The materials were fixed in formalin-acetic acid-alcohol (FAA) and later preserved in 70% ethanol. For histological examination the material was prepared following standard techniques (Johansen 1940). Both longitudinal and transverse sections were cut at 5–6 μm and stained with tannic acid-iron alum with safranin and orange G (Sharman 1943).

Observations

Shoot Apex Organization

The shoot apex shows a tunica-corpus organisation. The tunica is two layered and its cells are radially elongated on the flanks and tangentially elongated or

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squarish at the summit. A few cells at the summit of the tunica are enlarged and lightly stained. Divisions in the tunica are strictly anticlinal but periclinal divisions occur in inner tunica at the site of leaf initiation. The tunica surrounds the corpus where cells are irregularly arranged and divide in various planes (figure 1 A, B).

Initiation and Development of the Leaf

The leaf primordia are formed on the flank of the shoot apex. The plastochron between the initiation of two leaf primordia is fairly long; the second leaf primordium initiates when the first attains a height of 80 to 90μ. The initiation of leaf takes place by periclinal divisions in the second tunica layer, followed by similar divisions in the outer layers of the corpus (figure 2 A, E). Following initiation, the leaf primordium appears like a block-shaped protuberance which grows further by extensive anticlinal and periclinal divisions in the corpus (figure 2 B, G). Divisions in the derivatives of corpus also contribute in raising the primordium. The outer tunica divides anticlinally to keep pace with the developing primordium and gives rise to the protoderm of the young leaf. The cells of the outer tunica above the leaf primordium occasionally show periclinal divisions (figure 2 H).

When the leaf primordium is 65 to 70 microns high, an adaxial meristem develops in the subapical region of the primordium (figure 2 I). Initially, this meristem is restricted to the extreme adaxial part of the primordium, and in a longitudinal section only two or three cells show periclinal divisions. Due to localized activity of this meristem, the primordium tends to extend over the summit of the shoot apex. Gradually the adaxial meristem stimulates the adjacent cells of the subapical region and a median longitudinal section of 100 to

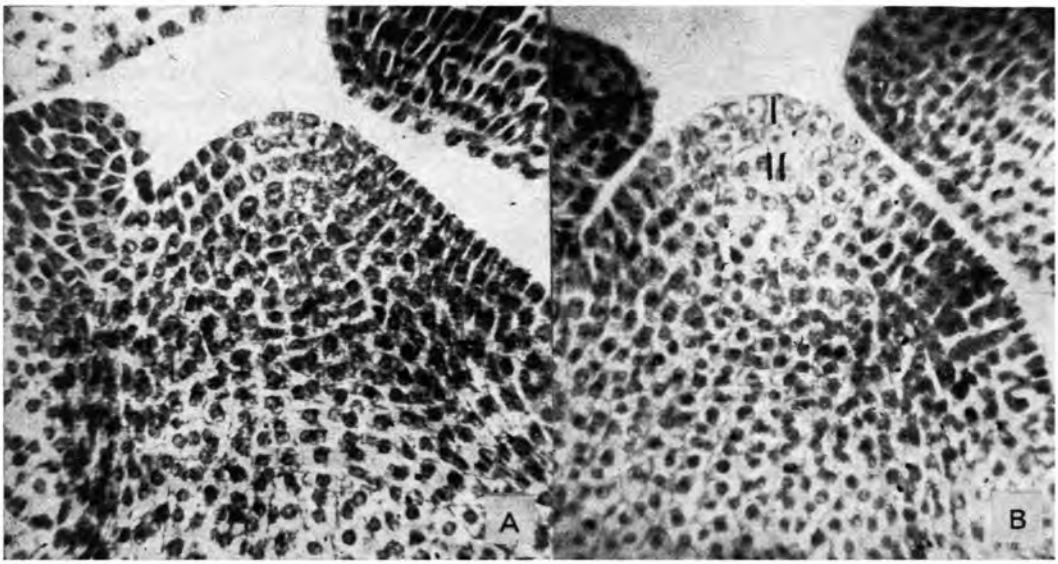

Figure 1 **A, B** Shoot apex organization in *Iris decora*. A B Median longitudinal sections of the shoot apex of *Iris decora* at two successive stages of the formation of leaf primordium (× 400) I Tunica, II Corpus

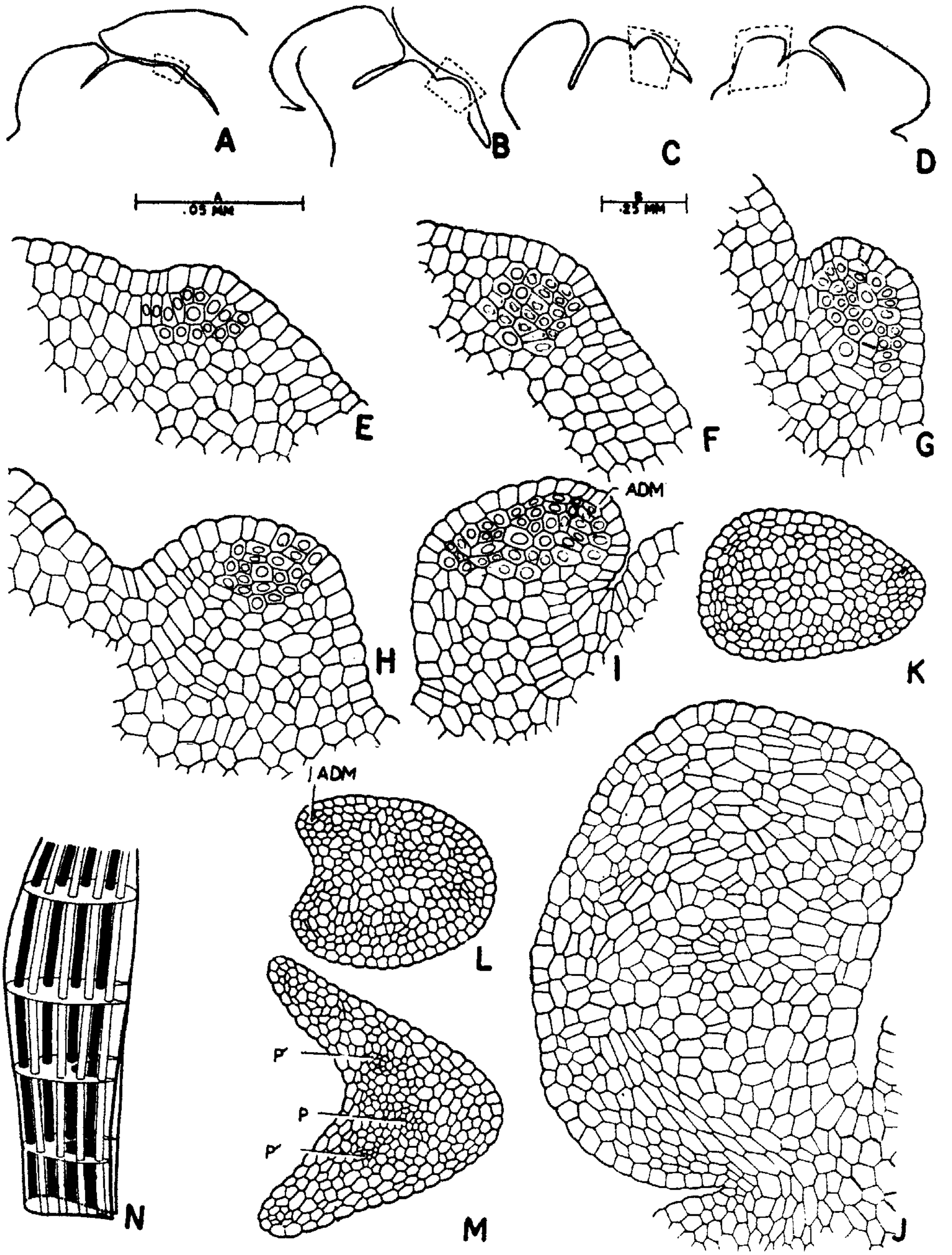

Figure 2 A–N Initiation and development of leaf in *Iris decora*. *A–D* Outline of median longitudinal sections (MLS) of the shoot apices at successive stages of leaf development; *E*, A portion of the shoot apex marked in figure A magnified showing initiating divisions of leaf; *F*; A part of the MLS of the shoot apex showing divisions in the corpus; *G*, A part of the MLS of the shoot apex as marked in figure B magnified; *H*, A part of the median longitudinal section of the shoot apex at a stage when the leaf primordium is 70μ high; *I*, A part of the median longitudinal section of leaf primordium as marked in figure C magnified; *J*, Median longitudinal section of a 240μ high primordium marked in figure *D; K, L, M*, *TS* of *ca.* 100μ, 160μ and 230μ high leaf primordia respectively, *N*, A three dimensional diagrammatic representation of the course of vascular bundle in *Iris* leaf
ADM, Adaxial meristem; P Median procambial strand; P', Lateral procambial strands derived from P Scale A for figures E–M; Scale B for figures A–D

110μ high primordium shows the meristem along the entire adaxial surface (figure 2C, I). Transactions of primordia at this stage also confirm the presence of adaxial meristem along the entire adaxial surface (figure 2 K). The meristem along the median line of the adaxial surface becomes sluggish while the one along the two margins is still active in a primordium 160 to 170 microns high (figure 2 L). This marginal meristematic activity initiates the lateral growth and accounts for the surface expansion of bifacial sheathing base of the leaf.

The marginal meristem, however, ceases to function gradually when the primordium attains a height of 225 to 250μ. Concomitantly the marginal adaxial meristems undergo fusion and form the submarginal meristem. The intensity of activity of this submarginal meristem (unified adaxial meristem) gradually increases and it is responsible for the radial growth of the distal part of the leaf. In the subsequent stages of development, the submarginal meristem is more active than the basal meristem as in mature leaves the basal bifacial part is shorter than the distal unifacial part. After the radial extension of primordium sets in, the intercalary growth starts which results in further elongation of the leaf (figure 2 D, J).

Procambial Differentiation

When the leaf primordium is between 230 and 240μ high, some cells between the adaxial and abaxial surfaces of the primordium show vertical divisions. This makes the locus of initiation of the procambial strand. A transection of the leaf primordium at this stage shows this strand occupying the central position. Initially a single median procambial strand differentiates in acropetal direction in the leaf primordium which later gives several lateral branches in paired succession, one on either side at a time (figure 2M). As in the distal part, the margins of the sheathing leaf base become confluent, the procambial strands show a radial arrangement (figure 2N).

Discussion

The leaves of *Iris* initiate by periclinal divisions in the cells of the second tunica layer accompanied by anticlinal and periclinal divisions in the subjacent layers of the corpus. The latter divisions augment to the initial height of the primordium, a developmental relationship also encountered by Rudiger (1939) and Kaufman (1959).

Kaplan (1975), who made an extensive study of unifacial monocotyledonous leaves, commented that the monocotyledonous leaves consist of a distal unifacial sector and a proximal bifacial sheath. He is of the opinion that variations in the leaf morphology in a range of monocotyledonous taxa are, therefore, due to reciprocal elaboration and suppression of these two sectors or both.

The duration and intensity of the activity of different meristems are responsible for the marginal, radial and apical growth of the leaf primordium in *Iris*. Initially a subapical meristem appears which is localized to the extreme adaxial part of the primordium. This meristem later extends over the entire adaxial face, but soon it looses its activity along the median line separating two marginal groups of meristems which are responsible for the formation of the basal bifacial part of the leaf. The adaxial marginal meristem soon becomes unified and forms submarginal meristem which is responsible for the radial growth of the leaf. Thus the activity of marginal meristem forms the basal bifacial part and the submarginal meristem the radial part of the leaf (cf. Kaplan 1970).

Morphological Nature of Iris Leaf

There has been a great deal of controversy regarding the morphological nature of unifacial leaves and the leaf of *Iris* calls for some comments. DeCandolle (1827), on the basis of similarity in the appearance of ensiform leaves and petiolar phyllodes of *Acacia*, interpreted them as debladed expanded petioles or phyllodes. This view received support from the anatomical studies of Arber (1918, 1921, 1925). She finds parallelism in form and striate venation between unifacial monocotyledonous appendages and petiolar in phyllodes *Acacia*.

Arber's view was criticized by Gaisberg (1922), Peters (1927) and Troll (1939, 1955). According to these investigators while the phyllodes of *Acacia* and *Oxalis* show rudimentary lamina at the distal end of the flattened petiole, no such structure could be observed in the unifacial monocotyledonous leaves in any stage of development. According to Troll (1939), the radial organisation of vascular strands which is a diagnostic feature of petiole is also known to occur in "rib-like" regions of the blades of some taxa and, therefore, the unifacial part of the leaf represents an undifferentiated lamina and petiole. Surprisingly enough, Arber (1950) also expressed similar view in her later writings, "......in the light of the more recent knowledge, it seems better to modify this interpretation, and to regard such a leaf a fixation of whole phyllode at its prelaminar stage".

An another interpretation was put forward by the German School on the basis of ontogenetic studies. Thielke (1948) and Roth (1949, 1957) consider the unifacial leaf of monocotyledons as an entirely new structure which is derived as a result of a special type of meristematic growth on the abaxial side of leaf primordium and exhibits a course of development which is quite different from that of the dorsiventral leaves. They called it as sympodial development. Roth (1949) interpreted the sheathing base of unifacial leaf as equivalent to entire dorsiventral leaf and the unifacial axis as the new part developed from abaxial secondary apex without any counterpart in conventional dorsiventral leaf. This interpretation led her to conclude such leaves are phylogenetically derived forms.

According to Hagemann (1970), there is no basic difference in the leaf primordium of an unifacial and a bifacial leaf. Both types of leaf primordia are equivalently dorsiventral at inception and have active marginal meristem. Cessation of activity of this meristem results in the unifacial sector. Thus Hagemann (1970, 1973) concludes that leaf is fundamentally a bifacial organ and radial sector of leaf should be referred to as 'subunifacial' or 'unifacialoid'. Hagemann's view got an equivocal support from Kaplan (1970 a, b) and Stevensen (1973).

The present ontogenetic study on the leaf of *Iris* reveals that the proximal part of the leaf is bifacial as the adaxial marginal meristem forms the blade but the growth of the blade is rather checked due to a different growth pattern towards the distal end of the leaf. This is in agreement with Hagemann's (1970) concept that the primordia of unifacial leaves are also dorsiventral at inception. Thus the terete leaf of *Iris* is not simple elaborate petiole but equivalent to the laminar region of dicotyledonous leaves (cf. Kaplan 1973).

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