Ontogeny and morphology of the tuber of Dioscorea floribunda Mart. et Gal.

O P SHARMA
Department of Botany and Plant Pathology, Himachal Pradesh Krishi Vishva Vidyalaya, Palampur 176 062

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Abstract. The tuber arises from the hypocotyl due to intensive unilateral activity of the primary thickening meristem. The resulting growth thrust produces a tuber apex, which consists of a drawn-out dome of this meristem, covered by secondary cortex and having a core of conjunctive parenchyma with vascular bundles. The tuber undergoes axiate and thickening growth by activity of the primary thickening meristem in the subapical and lateral regions. The tubercle, formed by the hypocotyl plus the first internode of plumular shoot and the hypopodia of successive aerial shoots of a sympodium, undergoes secondary growth by the primary thickening meristem, initiating in the hypocotyl. Morphologically, the tuber is an integral appendage of the hypocotyl secondary body, whereas the tubercle is a sympodial rootstock, the two together forming a perennial organ through activity of the same primary thickening meristem.

Keywords. Ontogeny; morphology; tuber; Dioscorea floribunda.

1. Introduction

Dioscorea has a baffling variety of underground storage organs (Knuth 1924; Burkill 1960; Archibald 1967), broadly classified as tuber and rhizome, but without any precise morphological definition. Sparshott (1935) studied the tuber development of Testudinaria elephantipes. Koch and Bruhn (1962) examined the morphology of tuber of D. floribunda and compared it with similar tubers of three other Central American species, namely, D. chiapasensis, D. composita and D. spiculiflora. Martin and Ortiz (1963) investigated the origin and anatomy of the tubers of D. floribunda and D. spiculiflora. Sharma (1974, 1976) studied the ontogeny of annual tuber in D. glabra and of rhizome in D. deltoidea to define their morphological nature. The study is extended here to the perennial tuber of D. floribunda to determine its true morphology.

2. Materials and methods

Seeds obtained from the material introduced at the Indian Horticultural Research Institute, Bangalore, were sown in petri dishes on wet blotting paper and in sand
pots in the laboratory during May–June at Palampur (altitude 1200 m). Plants were raised in the field. Tuber formation was traced from seedling onward. Embryos dissected from germinating seeds, seedling and adult plant bases with tubers at different stages of development, and tuber pieces were fixed in formalin-acetic acid-alcohol. These were embedded in paraffin for microtome-sectioning. Sections were stained in safranin and fast green and mounted in DPX.

3. Observations

3.1. External morphology

The seed is flat and winged around (figure 1). Of the two cotyledons, one is absorbent and its sheath encloses the primordium of the second. On germination the radicle grows into primary root, while the second cotyledon emerges as a green leaf (figure 2). The plumular shoot emerges after about three weeks (figure 3). Its first leaf, a scale, subtends a perennial bud, which produces one or more aerial shoots in the first growing season (figure 4). The tuber arises from the very short hypocotyl, pushes the primary root to one side, grows downward, and bears adventitious roots (figure 3). Under Palampur conditions the tuber generally remains almost conical and terete during the first season (figure 4). Subsequent year it assumes a horizontal posture and becomes dorsiventral (figures 5, 6). Besides the main growing point, it develops several similar growing points from its sides (figures 5, 6) and becomes lobed. Adventitious roots arise profusely from its sides (figure 5). The epicotylar end of tuber produces one to few aerial shoots every year and develops into a tubercle (figures 5, 6), also called head or crown.

3.2. Ontogeny of tuber

The tuber arises from the hypocotyl below the insertion of emergent cotyledon and at the level of attachment of the sheath of absorbent cotyledon. This position is clear when a germinating seed lies with the emergent cotyledon upward, but if the seed is upside-down, the emergent cotyledon exhibits a twist at its base and the point of tuber origin is obscured.

The primary vascular tissue of hypocotyl consists of four cotyledonary traces, one of absorbent and three of emergent cotyledon. The traces from opposite sides fuse toward the root end of hypocotyl, which is generally marked by two adventitious roots, arising directly below the cotyledons (see figure 11). The primary thickening meristem, causing the secondary growth of hypocotyl, differentiates in the perivascular parenchyma independent of the shoot apex, and does not extend into the primary root (Sharma 1975).

The tuber originates in the primary thickening meristem due to its precocious and intensive unilateral activity, which results in growth thrust at the locus, rupturing the overlying hypocotylar epidermis and primary cortex. Being not a true apical meristem, the tuber apex has a drawn-out dome of primary thickening meristem covered by a mantle of secondary cortex (figure 7). The tuber undergoes axiate growth by activity of the primary thickening meristem in the subapical region, producing conjunctive parenchyma and vascular bundles to the inside acropetally and secondary cortex to the outside (figures 7, 8). The thickening growth of tuber
Figures 1-6. Seed germination and tuberisation $\times 1$ ($\times 12.5/15.4 \text{ cm}$). 1-2. Emergence of second cotyledon. 3-4. Emergence of shoots and tuberisation. 5-6. Second year tuber, whole (5) and the same cut vertically (6).
Figures 7–10. Tuber development in vertical (7–8) and cross (9–10) sections. 7. Tuber apex, × 70 (× 12.5/15.5 cm). 8. Young tuber showing axiately growth, × 28 (× 12.5/15.5 cm). 9. Portion of tuber showing thickening growth, × 70 (× 12.5/15.5 cm). 10. Cessation of thickening growth on lower side, × 28 (× 12.5/15.5 cm).
also results from activity of the primary thickening meristem but in the lateral region (figure 9). Raphides are common in the ground parenchyma (figures 8, 9). The adventitious roots arise in the primary thickening meristem. The outer region of secondary cortex behaves as the first cork, for its cells are somewhat suberised. Inside it in the secondary cortex arises the storied cork (figure 9). Its dividing initials along with the first cork seem to have been mistaken for the temporary periderm by Martin and Ortiz (1963), who ascribed the storied cork to the outer derivatives of cortical cambium—the primary thickening meristem. Ultimately the primary thickening meristem becomes indistinguishable from the starch-rich conjunctive parenchyma and starch-free secondary cortex, both of which differentiate very close to it.

On resumption of axiate growth in subsequent year, the primary thickening meristem virtually stops its activity on the lower side, but enhances its activity dorsolaterally (figure 10). The cells of ground parenchyma show distinct radial alignment (figure 10). New growing points differentiate on the sides due to unilateral activity of the primary thickening meristem, and behave like the main growing point. Every year the tuber undergoes fresh thickening growth by activity of its primary thickening meristem. The outer region of new secondary cortex is suberised, while storied cork arises inside it. The old cork is shed.

3.3. Ontogeny of tubercle

The hypocotyl, integrating the tuber with the tubercle, is pushed aside by the precocious tuber and remains extremely short (figure 11). The activity of primary thickening meristem, originating in the hypocotyl, extends into the stunted first internode of plumular shoot. That the perennial bud is in the axil of the first leaf (scale) of plumular shoot is clear by the presence of a leaf trace near the bud (figure 12). Shoot system being sympodial, the perennial bud produces the second aerial shoot (figure 13). Its prophyll, in turn, subtends a perennial bud, in which a similar sequence is represented (figure 14). Consequently, a sympodial rootstock, the tubercle, is formed by the hypopodia (axis below the insertion of prophyll) of successive aerial shoots, but the first rootstock segment consists of the hypocotyl and first internode of plumular shoot (figure 11). In fact, the perennial-bud bearing node determines the limit of a rootstock segment and the primary thickening meristem closely follows the perennial bud (figure 14), which continues the growth of tubercle year after year. Beginning with the hypocotyl and proceeding upward segment-wise, the tubercle undergoes secondary growth by activity of the primary thickening meristem, producing conjunctive parenchyma and vascular bundles to the inside and secondary cortex to the outside. The epidermis is ruptured and sloughed off (figure 15). The primary cortex gets suberised, while storied cork arises in its inner region. Like the tuber, the tubercle undergoes secondary growth every year (figure 16). The new cork initiates in the inner region of new secondary cortex.

4. Discussion

In Dioscorea deltoidea (Sharma 1976), normal activity of primary thickening meristem in the hypocotyl transforms it into a distinct but transitory tuber-like structure,
which at its epicotylar end passes into a sympodial rhizome. It is formed by the hypopodia of successive aerial shoots (mostly dormant), but the first rhizome segment consists of the hypocotyl and the stunted first internode of plumular shoot. The rhizome undergoes secondary growth every year by the activity of a primary thickening meristem. In *D. glabra* (Sharma 1974), precociously unilateral activity of primary thickening meristem in the hypocotyl produces a seedling tuber—an integral appendage of hypocotyl secondary body (Sharma 1978). The hypocotyl itself is inconspicuous, passing above into a sympodial rootstock, but (i) annually only one rootstock segment is produced, (ii) every year the old tuber and the associated rootstock segment die, and (iii) the hypopodium of new aerial shoot, like the hypocotyl, produces a new tuber (Sharma 1974). When examined with this background, the tuber of *D. floribunda* has two components, the main tuber and its tubercle. Developmentally, the tuber proper is similar to an annual tuber and the tubercle to a rhizome. Morphologically, therefore, the tuber proper is an integral appendage of the hypocotyl secondary body, whereas the tubercle is a sympodial rootstock, the two together forming a perennial organ through activity of the same primary thickening meristem. On the contrary, Koch and Bruhn (1962) interpreted the tuber as a hypocotyl—the whole hypocotyl after it has undergone differential secondary growth. The present study does not support this view, for the tuber first originates from the hypocotyl unilaterally as an appendage of its secondary body and only then undergoes differential growth.

The tuberous hypocotyl of *D. deltoidea* (Sharma 1976), the hypocotyl with the main tuber of *D. floribunda*, and the hypocotyl with seedling tuber, or the hypopodium with adult tuber of *D. glabra* (Sharma 1974) are homologous structures. Phylogenetically, they seem to represent three of the many different phases in the evolution of tuber in *Dioscorea*. The situation in *D. deltoidea* conforms almost to the prototype, while *D. floribunda* and *D. glabra* represent the derived conditions due to the modified activity of their primary thickening meristem in the hypocotyl or hypopodium.

According to Martin and Ortiz (1963), in *D. floribunda* (i) primary growth of the tuber is by multiplication and thickening of the primary thickening meristem and by differentiation of the cells so produced, (ii) growth of the tuber in diameter is a type of secondary growth caused by the activity of a cambium-like layer in the cortex, and (iii) this layer is a direct continuation of the primary thickening meristem near the apex of the tuber. In fact, the primary thickening meristem is originally responsible for the secondary growth of hypocotyl, but due to its precocious and intensive unilateral activity this meristem brings about tuber genesis. Thus, the primary body of hypocotyl is the primary body of tuber also, but the primary hypocotylar tissues dermal—fundamental and vascular—do not extend to the tuber proper, which develops purely due to secondary growth in two phases, axiate and thickening.

The observations of Sparshott (1935) on the perennial tuber of *D. elephantipes* (*Testudinaria elephantipes*), though interpreted in terms of a single cotyledon, point clearly to the composite nature of the tuber as in *D. floribunda*. 

Abbreviations

ae, absorbent cotyledon; ar, adventitious root; as, aerial shoot; c, storied cork; co, secondary cortex; cp, conjunctive parenchyma; d, vascular bundle; e, epidermis; ec, emergent cotyledon; i, raphides; l, scale leaf; m, primary thickening meristem; p, prophyll; pb, perennial bud; ps, plumular shoot; r, primary root; s, seed; t, tuber; tu, tubercle.
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