ANATOMICAL STUDIES ON SUCCULENT CLADOSES IN CASUARINA EQUISETIFOLIA LINN.

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ABSTRACT

Casuarina equisetifolia Linn. is a well-known xerophytic plant of the tropics and sub-tropics with thin, wiry, cladodes. Contrastingly in coastal plants of Malaya and Singapore succulent branches are formed. The anatomical characters of the fleshy cladodes and the shoot apices are described in this paper, in comparison with the normal, non-succulent structures. Causal factors for the succulent habit in this plant are indicated and the significance of such a variation is comparatively discussed with reference to corresponding literature.

INTRODUCTION

Succulent habit and the storing of water in the parenchymatous tissue are characteristics of xerophytes and halophytes. In the leaves of certain halophytes mesophyll may become modified into succulent tissue or in stems there may be excess of parenchyma storing water. Many well-known examples are mentioned in standard reference works on plant anatomy or ecology (Haberlandt, 1969; Mullan, 1931, 1933; Cronquist, 1961; Burstrom and Odhnoff, 1964; Kochar, 1968). In certain plants succulence is a genetical character and in others it may develop due to the influence of edaphic and environmental factors and therefore their structures can be altered experimentally. Experiments in which succulent plants were used either to determine the water holding capacity of the tissues or their salt tolerance are summarized in earlier papers (Delf, 1915; Keller, 1923). In Casuarina equisetifolia Linn., a well-known xerophytic plant, fleshy cladodes were noticed in some of the trees growing near the sea-coast in contrast to the non-succulent, thin, wiry cladodes of inland plants. In this paper the anatomical and morphogenetic variations of two types of such cladodes are compared.
**Succulent Cladodes in Casuarina equisetifolia Linn.**

**Materials and Methods**

Normal and fleshy twigs were collected and fixed in F.A.A. Customary methods were followed for dehydration and embedding. Pretreatment of the material, before embedding, with hydrofluoric acid, was helpful. The stem sections were stained with safranin green and the shoot apices with safranin tannic acid and ferric chloride combination (Sass, 1958).

**Observations**

*C. equisetifolia* is a common pioneer tree, growing on sandy soil in east coast of Malaya. The seed germination, establishment and growth of seedlings, succession of other seedlings under the shade of *Casuarina* plants, leading towards the establishment of coastal forests, are discussed earlier (Corner, 1952). In certain areas the gradual development of *Casuarina* forest, from seedlings to mature trees of 33–50 m. tall, also may be seen. During the field trips in the last 5 years to Jason Bay area, South Johore, and in southern islands of Singapore many abnormal, drooping, branches were noticed in certain trees. The terminal portions of these branches were bigger in size, fleshy, and light green in colour, unlike the normal ones which were small, thin and dark green (Figs. 1, 2). In many trees only the terminal branches were fleshy whereas the other laterals towards the main axis of the tree were normal. Such fleshy drooping branches were more common on the trees standing next to the sea, directly exposed to the sea breeze. Although such fleshy branches were observed all round the year their number on different trees was much greater during November to January months, the monsoon period in this region.

The fleshy and robust growth was observed at the terminal portions of the branches as well as in some of the laterals close to them (Fig. 1 a). The tips of the fleshy branches conspicuously extended beyond the laterals, while in the non-succulent branches the laterals extended beyond the main tip (Figs. 1, a–c, 2, a, b). The internodal length, diameter of both the main axis and the lateral branches of fleshy and normal cladodes are given in Table I.

The internodal length of the fleshy cladodes at the distal ends of the main axes was about 2–3 times greater but their lengths decreased on lateral branches. The diameter of the thin and lateral axes of fleshy branches was about 2–3 times more when compared with the normal branches.
TABLE I

<table>
<thead>
<tr>
<th>Main axis</th>
<th>Lateral branch</th>
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<tr>
<td>Internodal length</td>
<td>Diameter</td>
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<tr>
<td>Normal branch</td>
<td>..</td>
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<tr>
<td>Fleshy branch</td>
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* Each figure represents an average of 20 readings.

The young stem of *C. equisetifolia* showed variable number of ridges and grooves, from 7-12, in the materials collected from Seychelle Islands, Madagascar, India, Australia and New Caledonia (Metcalfe and Chalk, 1950; Lowson and Sahni, 1963). In Singapore and Malaysian plants the cladodes of normal branches in transection showed seven or eight ridges and corresponding number of grooves (Figs. 3, 8). The structure of the stem is well recorded and it also shows considerable variations in materials collected at different geographical locations of the world with regard to the density and kind of tissue present (Metcalfe and Chalk, 1950). For this reason the main points of stem anatomy, as they refer to local plants, are given here.

In normal cladodes a thick cuticle (7.5 μ) was present on the epidermis enclosing certain refractive bodies (Fig. 4). At the grooves a number of uniseriate hairs and stomata were present and the former were more conspicuous in the free hand sections than in microtome sections (Figs. 4, 6). Hypodermis, restricted at the ridges, was 1-2 layered with sclerenchyma at the margins and parenchyma in the centre (Fig. 4). From the central parenchyma a group of sclerenchyma cells, ‘T’-shaped in appearance, extended towards the leaf trace bundles dividing the palisade tissue into two well-defined sectors (Figs. 3, 4); such a condition was also recorded in the material collected from the Mediterranean region (Metcalfe and Chalk, 1950).

The extension of sclerenchyma group, especially the length of the vertical arm of the ‘T’ was variable. In some it joined with the leaf trace bundle whereas in others it stopped in the upper or middle portion of the cortex (Figs. 3, 5). In longitudinal sections of the cladode the orientation and arch-like condition was clearer where the sclerenchyma touched the
vascular tissues only at regular and equidistant points. The palisade parenchyma was usually two-layered. Between the leaf trace (opposite to
ridges) and cauline bundles (opposite to the grooves) and likewise between palisade tissue and cauline bundles there were 2–3 and 7–8 layers of parenchyma respectively (Figs. 4, 6). The number of leaf traces as well as cauline bundles was equal to the number of grooves or ridges present in the stem. Tannin bodies and druses were common in the parenchyma of both cortical and stelar regions. The idioblasts with druses were of the same size as the surrounding parenchyma cells (Fig. 4).

In fleshy stems, collected either from a single plant or different plants, the number of grooves and ridges was variable from 10–12. The cuticle was thinner (4.5 μ) in fleshy stems and refractive bodies on cuticle were few or absent. Hypodermis was similar to those in non-succulent cladodes. There was a quantitative increase of palisade and ground parenchyma tissue in proportion to the increased size of the ridge and the cross-sectional area of the central cylinder (Figs. 4, 6). Counting across the ridge there were 17–20 palisade cells from the groove to the central sclerenchyma strand in contrast to 8–10 cells of the normal stem. The palisade layers were 3–4 in number (Fig. 6). The parenchyma was present abundantly below the palisade tissue, surrounding the leaf trace and cauline bundles in contrast with 7–8 layers of normal stems (Figs. 4, 6). Further, most of these cells were 2–3 times bigger in size and tannin deposits were lacking in them when compared with their counterparts in normal stem. Idioblasts with druses were very much smaller in size unlike the surrounding cells, indicating the limited cell enlargement of the idioblasts. Structurally the vascular bundles were similar to those in the normal stem, but there was an increase in the number of xylem and phloem cells in both the bundles. The individual cell size, as determined by the transectional cell area, was less in tracheids, vessels and sieve tubes. Even the sclerenchyma cells that organized caps above these bundles were smaller in their cross-sectional area. Pith cells were larger with few or no idioblasts in them. Thus it became obvious that the bigger size and succulent nature of the stem was largely due to the corresponding increase of palisade and ground parenchyma in cortical and stelar regions of the stem.

The shoot apices of normal and fleshy stems were studied. In the shoot apex of normal plants the leaf primordia were compactly arranged, showing alternate arrangement, and the tips of these extended over the pro-meristem (Fig. 7). The cells in the main apex as well as in the lateral structures were filled with tannin or other cell contents and thus were darkly stained (Figs. 7–9). The apex was dome-shaped and at the maximum phase it measured 42.6 μ high (a–b) and 82.6 μ wide (c–d) and consisted of 12–14
rows of cells across the axis c–d. Histological zonation was clear and there were three distinct tunica layers, with a tendency towards the formation of a fourth layer in some of them (Fig. 9). The corpus tissue consisted of three layers of cells and it gradually merged with the rib meristem which consisted of enlarged vacuolated cells (Fig. 9). The rib meristem was distinct, the demarcating zone starting from 7 or 8 layers deep from the summit of the apex and the cells of the peripheral meristem were darkly-stained than those of other histogens.

The increased size of fleshy shoots was very evident in the longisections of both the main axis and the lateral branches. The leaf primordia varied in their arrangement from the alternate to the opposite condition (Figs. 10, 11). The cells in them were thin-walled, vacuolate, with very few cell contents in contrast to the tissue arrangement of the normal branches (Figs. 7, 10). The promeristem was bigger in size (a–b 56·4 μ; c–d 113·4 μ). The two tunica layers were well defined and the corpus zone was narrower with 1–2 cell layers. The peripheral meristem was 3–4 layered including the protoderm (Figs. 11, 12). The rib meristem was most prominent with enlarged thin-walled cells and it was identified from the fifth layer starting from the summit of the apex (Fig. 12). Some of the cells had 2–3 nuclei in them, and tannin id oblasts were completely wanting. Only the maximal phases of shoot apices in normal and fleshy stems are compared here.

**DISCUSSION**

Different causal factors are identified that would induce the formation of succulent tissues in certain plants. Goebel (1900) considered optimum level of sodium chloride tolerance in succulent plants which also restricted relatively poor number of species in the sea-shore vegetation. Certain shore plants like *Lotus corniculatus, Plantago major, Atriplex rosea, Blitum polymorphum, Scrophularia* sp. produced fleshy leaves in contrast to their inland counterparts. Plants of *Lepidium sativum* were cultivated both on shore and inland and the former group developed succulent nature. It was suggested that the succulence of the leaf depended on the proportion of salts in the soil (Goebel, 1900). Leaves of *Bacharis halimifolia* exposed to the ocean spray were succulent, when compared with others on the same plant that were not sprayed (Boyce, 1954). Nitrogen deficiency in the soil was considered as another reason for succulent habit in certain plants (Esau, 1965). The influence of Cl-ions and excess of salt in the soil leading to the succulent habit of plants were reported by different authors (Mullan, 1933; Burstrom and Odhnoff, 1964).
In the present case the succulent nature of the stems was largely due to the edaphic conditions including the salt content of the soil. Because only those plants that were on the coastal margin developed fleshy stems and others towards inland 33-66 m. from the coastal margin did not have any. Further the roots of the former plants were much closer to the seawater, and possibly subjected to greater salt concentration of the soil. The effect of direct ocean spray also seemed to play an important part. Root nodules with nitrogen fixing bacteria were found in the local *Casuarina* plants indicating additional supply of atmospheric nitrogen (Corner, 1952).

There appears to be no previous description of the shoot apex structure of *Casuarina* and the importance of such studies in various angiosperms was emphasized earlier (Gifford, 1954; Gifford and Corson, 1971). The apex of the fleshy shoot was much larger in size, and there was a distinct variation with regard to the reduced number of tunica and corpus layers accompanied by a quantitative increase of rib meristem tissue. The variation noticed in leaf arrangement is a significant change between the non-succulent and succulent forms. Earlier workers have noticed that the phyllotaxis is affected by the vigour and nutritional status of the plant (Champion, 1961; Cutter, 1965; Loiseau, 1957). Though no quantitative studies were made to arrive at definite figures it was generally observed that the fleshy shoots were more vigorous in their growth, when compared with the normal ones.

The nature and development of the water storage cells, the water retaining capacity of succulents and their physiology are described in various works mentioned earlier. In case of desert plants, it was recorded that the succulent plant organs swell rapidly when moisture was abundant and during the period of drought they shrivelled and became depleted of water (Daubenmire, 1965). The leaves of certain halophytes increased twice in their thickness during the rainy season owing to the expansion of the aqueous tissue (Mullan, 1931). Increased number of succulent shoots were seen in *Casuarina* plants during monsoon period, when abundant soil moisture and comparatively high humidity existed, than during the other months of the year and this is similar to the observations made on desert plants (see Daubenmire). Except for fleshy leaves of mangrove plants or halophytes, where succulence is brought about by either epidermis or palisade tissue, in others the tissue concerned is the ground parenchyma (Mullan, 1931). The same feature is seen in the species presently investigated, namely, *Casuarina equisetifolia*. 
Fig. 1. *a, b.* Terminal portions of main and lateral branches respectively showing succulent condition. *(c)* End portion of a normal branch. Fig. 2. *(a)* Distal portion of the branch in 1 *a* enlarged to show the succulent cladodes. *(b)* Part of the normal branch showing main axis and lateral cladodes (cm. scale).
Figs. 7–12. Fig. 7. L.S. shoot apex of a normal branch, note the compact arrangement of cladodes, × 52. Fig. 8. Part of Fig. 12 enlarged to show the tissue arrangement in the main axis and at the base of the cladodes, note compact arrangement of parenchyma with many idioblasts, × 190. Fig. 9. Apex at maximal phase, enlarged to show 3 tunica layers, 4th is incompletely demarcated, × 520. Fig. 10. L.S. shoot apex of a fleshy branch, note the prominent parenchyma in main axis as well as at the base of fleshy cladodes, × 52. Fig. 11. Part of apical region enlarged to show the tissue arrangement, × 234. Fig. 12. Apex of the fleshy branch enlarged to show the broad dome, 2 tunica layers, thinner peripheral and broader rib meristem, × 425. In Figs. 9 and 12, a–b, and c–d show the length and breadth of the dome respectively, at maximal phase of the apices.
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REFERENCES


