VII. DOMATIA IN SEEDLINGS

In recent years considerable interest has been taken in the characteristics of seeds and seedlings, especially those of rainforest species. The rapid destruction of the world's rainforests is the cause of great concern to many. Efforts at rehabilitation and reafforestation can be assisted considerably if seedlings can be readily recognised and their ecological requirements ascertained. Many botanists such as Duke (1965, 1969) and Burger (1972) are endeavouring to add information on this aspect of rainforest ecology. Systematic botanists also find characters of seedling morphology and anatomy useful as evidence of relationships at various levels of taxonomy, and also in some cases, Bailey (1956), as evidence in phylogenetic studies.

One character which occurs in many rainforest species is the presence of domatia — small structures occurring on the lower surface of the leaf blade in or very close to the vein axils. They may be in the form of a pit in the leaf tissue, a pocket formed by a connection of tissue across a vein axil, a tuft of hairs or a dome of tissue elevated above the leaf surface with an opening in or near the centre. These four — pit, pocket, hair-tuft and dome — are, following Jacobs (1966a), the basic elemental types. In some cases, a domatium may have a structure in which elements are combined. Domatia occur only in woody dicotyledons, trees, shrubs or vines, and in the majority of cases, those species are of humid forest origin. Often they are quite distinctive and their presence has been used as a supporting character in systematic studies of tropical and subtropical floras. To date they have not been recorded in seedlings.

If seedling characters of any kind are to be useful it is necessary to define what one is to regard as a seedling. In his extensive study of seedlings of European species and those few tropical and subtropical ones being grown in hothouses in Europe, Lubbock (1892) noted that the first leaves are generally simple or at any rate, simpler than those which follow, and the numerous illustrations in his book are of plants with, at the most, four to six leaves. Goebel (1900) called the first stages after germination 'juvenile', but found, as have all morphologists, that it is often impossible to draw a sharp line between these 'juvenile stages' and the adult form. The differences between the two sections of the developmental history may be slight with a gradual transition between them. However, in some cases there may be quite obvious distinctions between the juvenile and adult leaf morphology. Goebel introduced the terms 'homoblastic' and 'heteroblastic' to describe these two types of development. Allsopp (1967) also noted these differences and referred to the seedling (or sporeling) leaves as primary leaves, and reserved the term 'juvenile' for leaves of plants having sharply separated juvenile and adult stages. However, the separation may in some cases be one of duration rather than of actual morphology.

Duke (1965, 1969) provides considerable data especially on the 'eophylls', a term introduced by Tomlinson (1960) for the first few leaves with green expanded lamina developed by the seedlings of palms, as opposed to the rudimentary scale leaves of fixed number which precede

them. Duke's illustrations show maximum number of eophylls as six to eight with the majority of specimens bearing two eophylls.

Jacobs (1966a) has noted that in Alnus glutinosa "the seedling stage lasts about one year after germination which means that the first leaves produced by one year old seedlings are still juvenile", but records that domatia were present in the first year plants of Alnus glutinosa and also of Corylus avellana, but absent in first year seedlings of Acer campestre. In this latter species and also in Tilia cordata domatia had developed in the third year seedlings.

Burger (1972) defines two stages of growth — the "first stage is chosen: a. for a seedling which possesses epigeous cotyledons which develops a first leaf, b. for a seedling with hypogeous cotyledons which develops a first fully grown leaf", while the second stage is chosen "for a plant which has already developed some almost normal leaves (young form)." In the descriptions, the sequence and the numbers of the leaves are mentioned. It seems that this precision is needed in the definition of the 'seedling stage', at least in the circumstance of any particular character.

The first reference to the time of development of domatia in the young plant was made (as have many other first observations on domatia) by Hamilton (1897) who noted that "often juvenile plants do not have domatia." When Poole (1950) published studies on New Zealand Nothofagus species, he had checked the distinction made by Du Rietz (1931) that domatia occur in Nothofagus fusca but not in N. truncata, by examining "all the herbarium specimens available and in a number of forests" where he found that domatia occur in N. fusca "on trees and saplings above 6ft—10ft high" (2-3 m). "On seedlings or saplings below this height they are usually not present."

In the introduction to his paper 'On domatia', Jacobs (1966a) in the definition stated that they are produced on "maturing adult stage leaves" and later, as noted above, that the seedling stage lasts about one year in Alnus. "Absence of domatia is to be added to the points by which juvenile leaves in Alnus (and probably in other genera) differ from adult leaves." However, it is reported in a footnote (p. 297) that F.B. Sampson (pers. comm. M. Jacobs) states that domatia are absent in juvenile leaves of Pennantia corymbosa (Icacinaceae) but do occur in those of Carpodetus serrata (Escalloniaceae) which has juvenile leaves "somewhat smaller, less regularly lobed, and far less coriaceous than those on adult plants" which also bear domatia. In his short paper 'The Study of Seedlings' Jacobs (1966b) records some of the characters of seedling leaves — "and they never have domatia".

Burger (1972) described seedlings of one hundred and eighty eight species of trees of South East Asia — of these only four are species recorded as having domatia. Either they do not occur on the seedlings of those species or they could occur on leaves produced after the recording of details of the specimens when they could still be regarded as primary or seedling leaves. There is also the possibility that they were not noticed. It must be admitted that in some cases domatia are so small that a lens may be necessary to see them clearly, and on the usually smaller leaves of seedlings they are indeed very small structures.

The first work in which an actual recording of the presence of domatia in seedlings was made was in an experimental growth by De Barros (1960) of seed of two varieties of Coffea arabica L. This was carried out as a study of the origin and development of domatia in that species, the seeds and seedlings being grown under acarid and insect-free conditions. She records that the cotyledons and the first leaves developed domatia normally and besides showing that acarids play no part in their production, the experiment illustrated the fact that seedlings of Coffea arabica do possess domatia, even on the cotyledons and the first plumular leaf. The occurrence of domatia in cotyledons seems most unusual and I have checked this on seedlings of Coffea arabica which had developed the first plumular leaf. So far there has been no sign of domatia. Further observations will continue to be made to check this report.

During the course of a current investigation into various aspects of domatia in the Queensland flora seeds of a number of domatia-bearing species have been allowed to germinate and the seedlings checked regularly in order to note the stage of development of domatia. This work has yielded some interesting comparisons with those results observed by others who have made studies of leaf domatia. As developmental anatomy of domatia from bud to mature leaf forms part of the main research being undertaken, it is now possible to extend this aspect to cover development of domatia in the seedling stage of growth.

The following data have been derived from specimens grown from seed collected in rainforests in various parts of Queensland and northern New South Wales. In order to overcome any possibility of misunderstanding, in the present work the position of occurrence of leaf domatia in seedlings has been measured by the leaf number counting from the cotyledons. In the case of specimens whose first few leaves were lost before observation, the number of nodes up to the domatia bearing leaf has been used as an indicator of leaf position. In these cases it is possible that the domatia had already been present on the lost leaves. The numbers after certain specimens indicate J.G. Tracey Seedling numbers — and refer to herbarium specimens of seedlings grown by Mr. J.G. Tracey, CSIRO Rain Forest Ecology Division, Brisbane, Qld. They were germinated and grown in rainforest soil — usually that of the site of collection without any soil sterilisation or added fertiliser. The other specimens were raised under usual horticultural conditions without fertiliser. Specimens designated a, b, c, etc. were not from the same seed source but were grown by different persons under varying conditions. In some, examination with a lens is necessary in order to see the domatia clearly but this can also be the case in the adult plant. However, in the seedlings of other species they are quite obvious, even the protuberance on the adaxial surface being clearly visible to the naked eye, e.g. in seedlings of Endiandra discolor, Alangium villosum, Pennantia cunninghamii. Domatia usually are of the same type as in the adult leaves, but as would be expected on a leaf of much smaller size are comparably smaller than the adult form. In some species the occurrence on the seedling leaf differs from the typical adult pattern being usually fewer in number, and the position may not be constant.

In all, sixty specimens of seedlings comprising 35 species of 14 families have been observed to possess domatia, in most cases in leaves occurring below node 12, the majority in leaves at node 3, node 4 or node 7. Further anatomical studies will determine whether these domatia are in a reduced form or are one stage of a developmental sequence.

In studying heteroblastic development in vascular plants Allsopp (1967) has pointed out that "the normal ontogenetic changes may be confused with those directly induced by the environment". In the light of this, the question then arises as to whether or not the induction of domatia in seedlings is environmentally induced. Those cases which have been found to occur in different specimens of the same species were in seedlings grown under varied conditions and not in a simulated, controlled rainforest type environment. Even in the few cases where very young seedlings have been transplanted from the forest to bush house conditions, the domatia still developed.

Seed of other species is continually being sought from collectors in different regions so as to obtain material which may provide additional evidence of the occurrence of domatia in seedlings.

Family Species	Domatia recorded	Comments
ANACARDIACEAE		
Euroschinus falcata	leaf 13	
Pleiogynium timorense	leaf 12	Small pockets in primary axils on lowest pair of leaflets ½ cm long.
Rhodosphaera rhodanthema	leaf 7	Plant 14½ cm high. Very shallow pits in primary axils.
ALANGIACEAE		
Alangium villosum (101)	leaf 1	On leaf 1 in primary axils only, leaf 6 in primary and secondary axils. Typical adult pattern of occurrence in almost every vein axil of the lamina by leaf 10.
BORAGINACEAE		
Ehretia acuminata	leaf 20	
COMBRETACEAE		
Terminalia melanocarpa (278)	leaf 5	Very small pocket; pit in secondary axil.

ELAEOCARPACEAE		
Elaeocarpus grandis	(a) leaf 4	Plant 12½ cm. Fine pit opening nearer to lateral vein than to the midrib.
"	(b) leaf 7	
"	(c) leaf 1	
"	(d) leaf 3	
"	(e) leaf 3	
"	(f) leaf 7	
"	(g) leaf 6	
E.largiflorens (27)	leaf 5	
E.obovatus	(a) leaf 7	Pocket type; delicate tissue forming.
"	(b) leaf 8	A distinct pocket.
E.reticulatus	leaf 7	Pocket type.
"	leaf 8	Plant 19 cm. Pocket type with delicate covering.
ICACINACEAE		
Pennantia cunninghamii	(a) leaf 2	One pit domatium in primary axil with two in secondary axils.
"	(b) leaf 3	One domatium in primary and one in secondary axils.
"	(c) leaf 5	Pit type in primary axils.
"	(d) leaf 5	Domatia in two secondary axils only; by leaf 9 they occurred in both primary and secondary axils.
		In all cases a slight protuberance visible on the adaxial leaf surface.
LAURACEAE		
Cryptocarya triplinervis (830)	leaf 3	Very small pocket.
Endiandra discolor (190)	leaf 4	Domatia of large adult type with visible protuberance on adaxial surface of lamina
MELIACEAE		
Dysoxylum fraseranum (42)	(a) leaf 2	First two leaves are trifoliolate. Domatia occur in opposite axils at base of upper leaflet of leaf 2.
"	(b) leaf 3	

second specimens		
" (418)	(a) leaf 3	
"	(b) leaf 4	Plant 8 cm high; short pocket with hairs inside.
D.muelleri (43)	(a) leaf 5	Small seedling.
"	(b) leaf 8	Plant 15 cm.
D.rufum (664)	(a) leaf 1	First seven leaves simple; pocket domatia on leaf 1.
"	(b) leaf 11	Plant 20-25 cm high; first ten leaves missing.
Toona australis (119)	leaf 3	One domatium in terminal leaflet.
"	leaf 4	(3 leaflets).
Turraea brownii	leaf 4	Hair tuft domatium.
OLEACEAE		
Olea paniculata	leaf 6	
RUBIACEAE		
Coelospermum paniculatum (148)	node 3	On third pair of leaves after the cotyledons "domatia along midrib starting to show up".
Morinda jasminoides	node 12	Two opposite leaves each with one domatium in upper part of the lamina - round pit type.
SAPINDACEAE		
Arytera distylis	leaf 8	
A.divaricata	(a) leaf 4	
"	(b) leaf 5	
"	(c) leaf 6	
Cupaniopsis foveolata	leaf 4	Present also on leaf 7 and leaf 10 of same specimen.
C.serrata	leaf 3	Very small pocket domatium with hairs on the rim.
C.serrata var. tomentella (310)	leaf 8	Specimen transplated from forest; leaflets (4 x 1½ cm); pocket type.

Mischocarpus exangulatus (322)	leaf 4	First 4-6 leaves simple; domatia small pocket in leaf 4, then domed pocket in leaf 7 (compound leaf of 2 leaflets). Developing miniature leaflets of leaf 8 at apex show obvious development of domatia.
" (135)	leaf 7	Very small pocket type domatia in primary axils.
Sarcopteryx stipitata	leaf 8	
Toechima dasyrrachne	leaf 6	Specimens collected as small seedlings; leaves to node 5 missing at time of observation. Domatia in almost all primary axils in the leaflets of leaf 6.
" (53)	leaf 6	Specimen raised from seed. Domatia very small pockets with hairs, similar to the adult form.
T.erythrocarpum (259)	leaf 7	Small pocket type on uppermost leaflets.
T.tenax	(a) leaf 7	Plant 12½ cm high; leaves to node 6 missing at time of observation; five pocket type with hairs.
"	(b) leaf 4	
"	(c) leaf 4	
STERCULIACEAE		
Argyrodendron actinophyllum (385)	leaf 4	First 13 leaves simple, 14th leaf trifoliolate; pocket domatia on leaf 4.
"	(a) leaf 2	Simple leaf.
"	(b) leaf 1	Two leaves present on this specimen both simple and both with domatia.
VERBENACEAE		
Premna lignumvitae (294)	node 5	Opposite leaves, both with elongated pocket type domatia with hairs at the rim.
VITACEAE		
Cissus antarctica (1031)	leaf 1	Small pocket type covered on the outside with hairs.
"	(a) leaf 7	First adult sized leaf - shallow pocket domatia.
"	(b) leaf 2	

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