

Development of dorsiventrality in seedlings of *Azara serrata* R. & P. (Flacourtiaceae)

W. A. CHARLTON

Biological Sciences, Williamson Building, University of Manchester, Manchester M13 9PL, UK

SUMMARY

Azara spp. generally have dorsiventral shoots with the appearance of a large and a small 'leaf' at each node. On morphological grounds the small 'leaf' is usually considered to be derived from an upper stipule, while the lower stipule is reduced. This interpretation is reinforced by the changes during seedling development. Seedlings usually pass through a phase where the shoot is radially symmetrical and trilacunar nodes with small, glandular, non-vascular stipular structures are formed. Then nodes become more asymmetrical with the diminution of stipular development and lateral leaf trace development on one side, and accentuation on the other, and this process proceeds until the adult state is reached. Dorsiventrality depends on alternation of asymmetry at successive nodes and alternation may appear later than asymmetry. The changes in the seedling indicate that a recent interpretation of the adult structure of *Azara* based on homoeosis is not useful. The seedlings provide an interesting case in continuum morphology since they show a continuum of stipular structures from 'gland' through to 'leaf' but the continuum does not quite extend to the original leaf blade, which remains distinctive.

Key-words: *Azara serrata*, seedling, dorsiventrality, leaf, stipule, development, continuum, homoeosis.

INTRODUCTION

The genus *Azara* has dorsiventral shoots which generally present the appearance of having a large and a small leaf at each node, with the larger leaf attached towards the lower side of the shoot and the smaller towards the upper. The small 'leaf' has been interpreted as a leaf-like stipule (e.g. Warburg 1894; Troll 1937; Dormer 1944), or a leaflet (Reiche 1896). In his revision of *Azara* Sleumer (1977) called it an accessory leaf. Most authors have also identified small stipular structures. In an investigation of *A. microphylla* (Charlton 1991) it was concluded that the small 'leaf' had been derived by homoeotic replacement of the upper stipule by a 'leaf' while the lower stipule was represented by a small non-vascular structure. Two additional small stipular structures were related to the homoeotic 'leaf'. The vascular supply was consistent with reduction from an original trilacunar nodal condition. The small 'leaf' had a conspicuous terminal gland not found on the large 'leaf', which was interpreted as a residual stipular character. The replacement of 'stipule' by 'leaf' character in *Azara microphylla* is not absolutely complete, and it might therefore be taken as a case where the distinction

between 'leaf' and 'stipule' is not sharply defined, rather than one of homoeosis. The development of seedlings has now been studied in *A. serrata* to obtain more information on the relationships between 'leaf' and 'stipule'. In addition, the structure and development of the adult shoots derived from the seedlings has been investigated and will be presented separately.

MATERIALS AND METHODS

Seed was obtained from two plants of *Azara serrata* in the *Azara* collection of the National Council for the Conservation of Plants and Gardens (UK) in 1991 and 1992. Progeny from the two showed similar behaviour and are not treated separately here. Seedlings were grown in a glasshouse. They were fixed at intervals starting immediately after emergence and the distribution of leaves and stipules was noted at the time of fixation. All material was fixed in FAA fixative (Johansen 1940). Developmental morphology was studied using epi-illumination light microscopy and all material for this was stained in 0.02–0.05% alcohol-soluble nigrosin in 95% ethanol (Charlton *et al.* 1989). A set of 13 seedlings with 4–6 visible leaves (above the cotyledons) was embedded in paraffin wax by standard methods (Johansen 1940), sectioned serially at 10–15 μm and stained with aqueous toluidine blue.

OBSERVATIONS

In the subsequent account, leaves and nodes are identified by order of appearance above the cotyledons. Seedlings of *A. serrata* appear quite ordinary in their earliest stages as the first leaves above the cotyledons are without conspicuous stipules (Fig. 1a). The first two leaves, 1 and 2, are almost opposite. The next four leaves are normally spirally arranged (Fig. 1b). After the first two leaves there is a transition to a nodal condition approximating the adult state in *A. microphylla*, a larger and a smaller leaf-like structure with some smaller appendages. The transition is not abrupt, and symmetrical (or nearly so) leaves with two small lateral leafy structures often occur. Figure 1c shows forms from the early stages of growth. By the time six or seven nodes have been formed above the cotyledons the shoots are usually detectably dorsiventral and by the time the eighth node is mature larger leaves are being formed and growth has assumed the adult appearance (Fig. 1d).

For consistency with the presentation of Charlton (1991), the form attained by the seedlings which corresponds to the adult condition in *A. microphylla* will be described

Fig. 1. (a) Seedlings showing leaves 1–4 above the cotyledons. Bar=1 cm. (b) Spiral arrangement of leaves 3–5. Bar=1 cm. (c) Representatives of leaves 3–5 showing various forms of symmetry. Bar=1 cm. (d) Later stage, showing dorsiventral arrangement. Linked labels S and L show small and large 'leaf' at the same node. Bar=2 cm. (e) Small glandular stipular structures (arrows) at the base of (removed) leaf 3 (rL3). Bar=0.5 mm. (f) Leaf 3, glandular stipular structure G with additional smaller structure G'. Bar=100 μm . (g) Base of leaf 4 (rL4) with two expanded stipular structures LS and additional glands G. Bar=0.5 mm. (h) Leaf primordia 1 and 2 with initiation of stipular structure (arrow). Bar=100 μm . (i) Older leaves 1 and 2 with small stipular structures (arrows). Bar=200 μm . (j) Early stage of development of leaf 5; A is shoot apex, arrows indicate edges of primordium. rL4 is the base of the preceding leaf. Bar=100 μm . (k) and (l) Two views of the same primordium of leaf 3. L3 is leaf blade, A shoot apex, arrows indicate stipular primordia. Bar=100 μm . (m) Older leaf 3 (L3), stipular structure remaining small (arrow). L4 is next leaf. Bar=200 μm . (n) Leaf 4 (L4) with stipular primordium (arrow) and shoot apex A. Bar=100 μm .

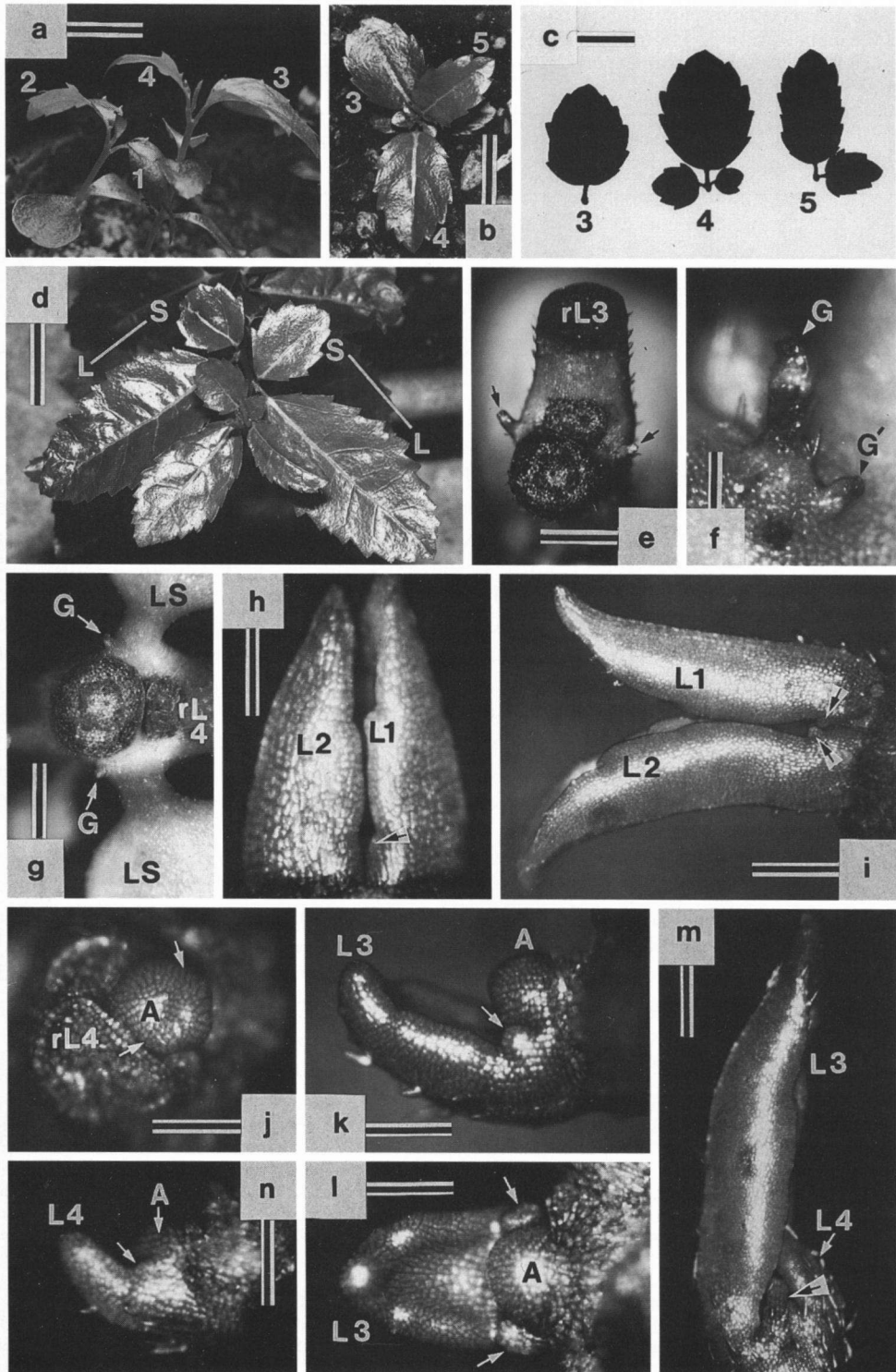


Table 1. Frequencies of flattened, expanded stipular structures and glandular stipular structures as the main stipular components at nodes 3–7 in seedlings of *A. serrata*, with results of χ^2 tests (at 1 d.f.) for deviation from an expectation of equal frequencies of each type of stipular structure as found in the adult state

Node number	Flattened, expanded stipular structure	Glandular stipular structure	χ^2 value for deviation from equal frequencies
3	21	161	107.7**
4	96	70	4.1*
5	53	65	1.2NS
6	43	33	1.3NS
7	24	18	0.9NS

* $P < 0.05$; ** $P < 0.01$.

NS, not significant.

in the terms previously used, so that each node is considered to bear a large 'leaf', a small 'leaf', radially symmetrical 'stipules' which are partly glandular, and sessile 'glands'. However, as the seedlings develop through their early stages they produce a continuum of stipular structures which makes it difficult to maintain a consistent terminology. Leaves 1, 2 and 3 generally each have two small glandular structures, one at each side of the petiole base (Fig. 1e) and similar and successively larger structures appear at higher nodes. At node 3 and above each is often accompanied by a similar but smaller structure at the side furthest from the petiole of the associated leaf (Fig. 1f). At node 3, and with increased frequency at upper nodes (Table 1), instead of a radially symmetrical glandular structure as the main stipular component there is often an expanded, flattened structure. However, overall there is a continuous gradation between small glandular structures and leaf-like appendages. The latter are distinctly petiolate (except the smallest) and have marginal serrations like the main part of the leaf (Fig. 1c). The tips of all serrations and the tip of the stipular structure are glandular but the tip of the leaf itself is not conspicuously so. Like the radially symmetrical glandular structures, the flattened appendages are often accompanied by additional glandular structures (Fig. 1g, and see also Figs 2b, 3i) in a similar lateral position. For operational convenience, we can describe the node as bearing a leaf and we can call the associated appendages stipular structures: leaf-like, glandular, or additional.

Fig. 2. (a) Leaf 4 (L4) with two stipular structures (arrows) arching over shoot apex A. Bar=100 μ m. (b) Later stage of leaf 4 (L4) showing expanded stipule (arrow) and small accessory structure (X). L5 is next older leaf. Bar=200 μ m. (c) and (d) Two views of a primordium of leaf 7 (L7), with lateral extension S which will form a small 'leaf'. A is shoot apex. Bar=100 μ m. (e) and (f) Two views of an older leaf 7 (L7) in which S has grown up and arches over shoot apex A. The arrow in (f) indicates where the stipular structure will arise at the side opposite to S. Bar=100 μ m. (g) and (h) Two views of a yet older leaf 7 (L7). S is the small 'leaf' of L7 and the arrow in (h) indicates a small stipular structure at the opposite side of L7. L8 is the next leaf. Bar=100 μ m. (i)–(m) Details of leaves 12–15. Bars=100 μ m. (i) Initiation of primordium (between arrows) on shoot apex A. L and S are large and small 'leaves' at the next older node; * marks the site where the associated axillary bud will arise. (j) Primordium showing distinction between regions of large 'leaf' L and small 'leaf' S, also shoot apex A, and next older primordium with small leaf S' and (removed) large 'leaf' rL'. (k), (l) and (m). Older primordia. (k) and (l) are views of the same dissection. L and S are large and small 'leaves' of the older primordium, L' and S' of the younger, A is shoot apex. Arrows indicate primordia of additional stipular structures: in (k) at the outer edge of S; in (l) at the side of L opposite to S; in (m) between L and S.

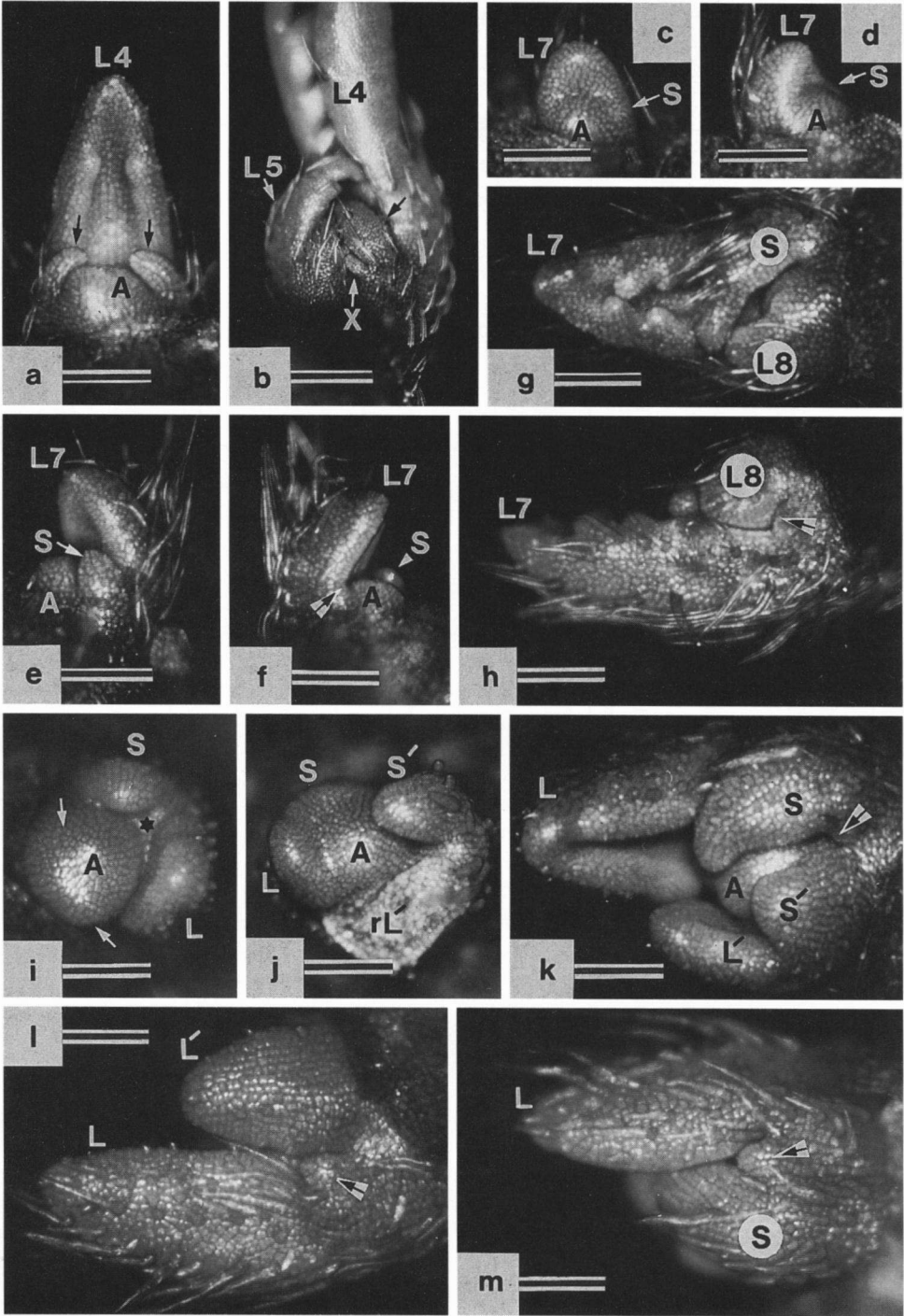


Table 2. Frequencies of occurrence of features of vascular supply to nodes 1-8 in 13 serially sectioned seedlings. There are 13 replicates for each node except 7 and 8, which are combined to give a sample of 8. *A. microphylla*-type nodes are those showing an approximation to the adult condition in *A. microphylla*, with one trace running into a large 'leaf' and one into an expanded stipular structure or small 'leaf', with a cross-connecting trace between the two

Node	Median trace only	Median plus one lateral trace	Medial plus two lateral traces	Lateral trace running only into leaf blade	Lateral trace branching, running into leaf blade and into flattened, expanded stipular structure	Proportion of <i>A. microphylla</i> -type nodes (%)
1	13	0	0	0	0	0
2	10	3	0	3	0	0
3	0	0	13	25	1	0
4	0	0	13	9	17	0
5	0	4	9	6	16	31
6	0	7	6	6	13	54
7 and 8	0	7	1	0	9	88

Leaf development in the early stages of seedling growth

Early stages of leaf and appendage development are shown in leaves 1–4, and 7 as representative stages. The earliest stages of development of leaves 1 and 2 occur before emergence of the seedling. Their stipular structures appear initially as small lateral outgrowths from the basal margins of primordia at quite a late stage, up to 300 µm tall or more (Fig. 1h) and they remain small (Fig. 1i). Primordia of leaves up to position 5 or 6 appear initially as symmetrical crescents (Fig. 1j). Stipular structures of leaf 3 appear earlier at the basal margins of the primordium, when it approaches 250 µm tall, and are relatively larger (Fig. 1k, l) than those of leaves 1 and 2, though they usually develop only into small glandular structures (Table 1, Fig. 1m). Stipules of leaf 4 also appear at the basal margin of the leaf primordium (Fig. 1n) when it is about 150 µm tall, i.e. earlier again than in the preceding leaf, and the stipules become relatively larger in proportion to the leaf blade, particularly if they are expanded (Fig. 2a, b) as is common (Table 1). While the insertion of leaves 3 and 4 is quite symmetrical at first, by leaf 7 the insertion is usually asymmetrical at an early stage (Fig. 2c, d). Leaf 7 normally has one flattened leaf-like stipular appendage and one glandular stipular structure, and the leaf primordium becomes asymmetrical because the region which gives rise to the leaf-like appendage develops as a lateral extension of the primordium (Fig. 2c, d). Consequently, this appears as a separate upwardly growing primordium at the leaf base (Fig. 2e) in contrast to the other stipular structure, which arises from the basal region of the leaf margin (Fig. 2f). While the leaf-like structure usually becomes substantial (Fig. 2g), the glandular structure may remain small for some time (Fig. 2h).

Leaf development in later stages of seedling growth

The structures at nodes 12–15 were used as examples of the later stages of seedling growth; they are not distinguished in the subsequent description. They correspond quite closely to the adult condition in *A. microphylla* and can be described in the same terms, i.e. a small upper 'leaf' and a large lower 'leaf'. They arise as rather asymmetrical crescentic primordia (Fig. 2i) which rapidly resolve into the upgrowths of the large and small 'leaves' (Fig. 2i, j). As in *A. microphylla* a single axillary bud arises from the triangular area between the large and small 'leaves' and the shoot apex (Fig. 2i). As development of the leaf proceeds, additional stipular structures arise in the same locations as in *A. microphylla* (Charlton 1991): at the upper edge of the small 'leaf' (Fig. 2k), at the lower edge of the large 'leaf' (Fig. 2l), and between the large and small 'leaves' (Fig. 2m). These develop into glandular structures.

Vascular supply

Table 2 gives a summary of the variations of vascular supply at nodes 1–8 in the serially sectioned seedlings. Each cotyledon receives a single vascular trace from the stem vascular cylinder, and so does leaf 1 (Fig. 3a, b). Sometimes leaf 2 receives a small lateral trace in addition (Fig. 3a, b). The glandular stipular structures are normally not vascularized, though one exception was found among all nodes of the sectioned seedlings. At node 3 in all the sectioned seedlings a median vascular trace and two smaller lateral vascular traces departed from the stem vasculature (Fig. 3c) and there were no leaf-like stipular structures at this node. The lateral traces ran into the petiole of the leaf without branching (Fig. 3d, e). At node 4 there were also two lateral traces in all cases. Where there were two leaf-like stipular structures the lateral traces ran into

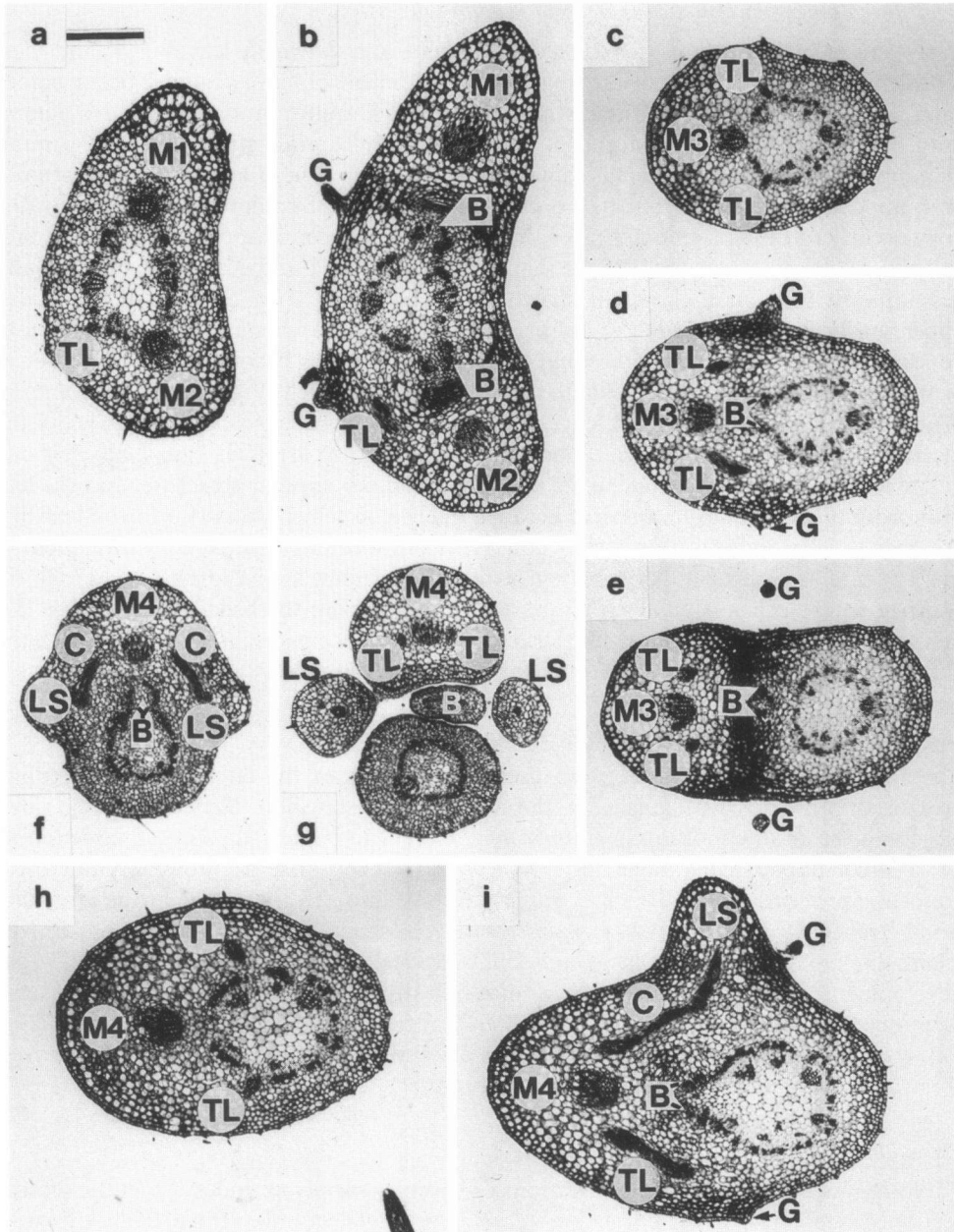


Fig. 3. Vasculature at nodes of leaves 1-4. Median leaf traces are labelled M plus the leaf number; TL denotes lateral leaf trace; LS is an expanded stipular structure or the trace running into it; C is a connecting trace running from a trace LS towards the median trace; B denotes axillary bud or its trace(s); G denotes non-vascular glandular structure. All photographs are at same scale; on (a) bar = 300 μ m. (a) and (b) Sections from a series through nodes 1 and 2. Leaf 2 receives one lateral trace. (c), (d) and (e) A series through a symmetrical node 3 with two lateral leaf traces and two non-vascular glandular structures. (f) and (g) A node with two expanded stipular structures supplied from the lateral leaf traces. (h) and (i) An asymmetrical node 4 with two lateral traces, one supplying an expanded stipular structure (see also Fig. 4a).

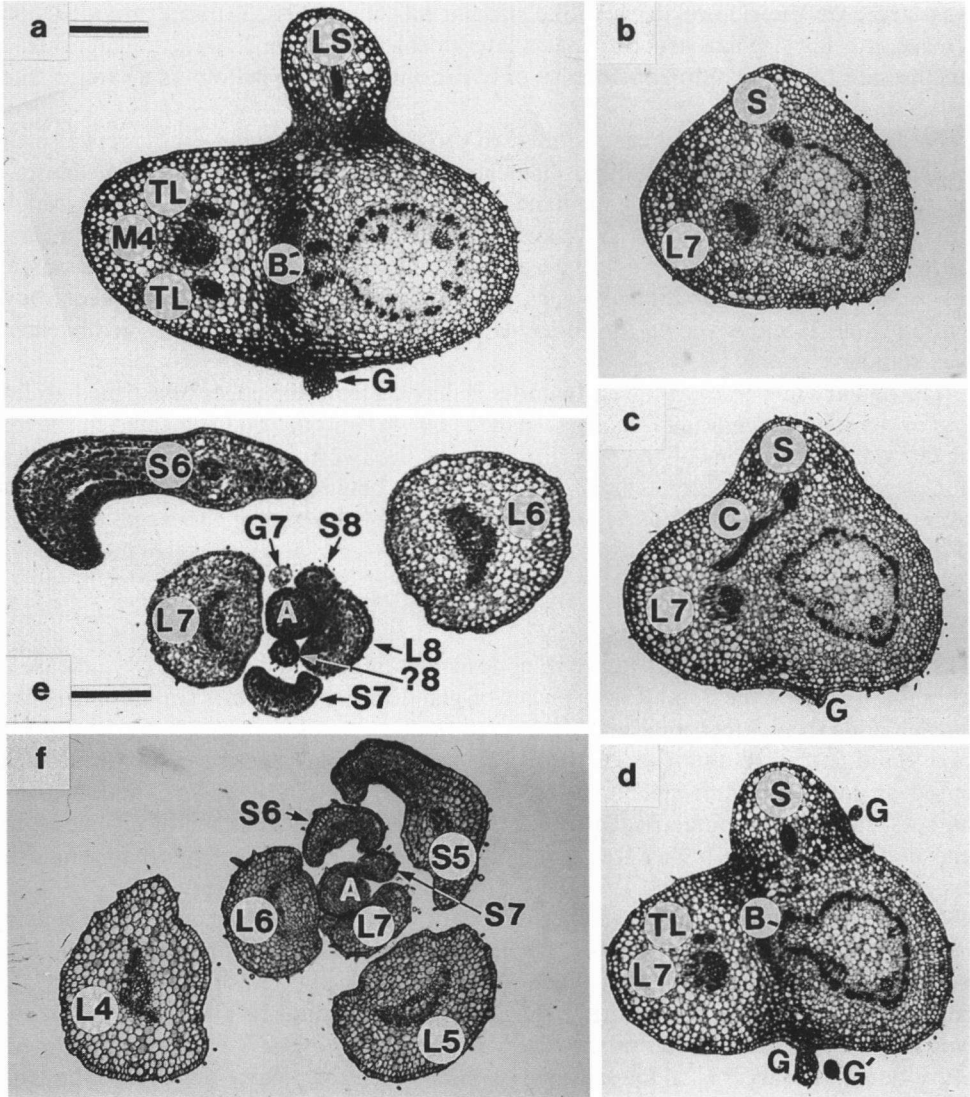


Fig. 4. (a)–(d) Nodal vasculature. All are at the same scale; on (a) bar=300 μ m. (a) Vasculature at node 4 (continued from Fig. 3i). Median leaf trace is labelled M4; TL denotes lateral leaf trace; LS is an expanded stipular structure with a trace running into it; B denotes axillary bud or its trace(s); G denotes non-vascular glandular structure. (b)–(d) Sections from a series through a node 7 showing two-trace vasculature approximating the condition in *A. microphylla*. L7 is trace to large ‘leaf’; S is the trace to the small ‘leaf’; C is a connecting trace running from a trace S towards the median trace; TL is lateral leaf traces; B is bud trace; G are non-vascular glandular structures. (e), (f) Transverse sections through buds, at same scale. On (e) bar=200 μ m. L is large ‘leaf’; S is small ‘leaf’; G is non-vascular glandular structure; components are numbered according to the nodal position above the cotyledons; A is shoot apex. (e) A bud with spiral phyllotaxis and a succession of leaves with the same symmetry; the symmetry is probably beginning to change at node 8 where there are two large lateral primordia, S8 and ?8. (f) A bud with alternating symmetry and consequent dorsiventrality.

the petiole as lateral leaf traces but also branched to supply the stipular structures (Fig. 3f, g). Where there was one leaf-like and one glandular stipular structure the lateral trace

was larger on the side of the leaf-like stipular structure (Fig. 3h) and provided both a trace into the stipular structure and a lateral leaf trace (Figs 3i, 4a); the lateral trace on the side of the glandular structure only ran into the leaf petiole as a lateral trace (Figs 3i, 4a).

Node 5 had a majority of cases similar to those at nodes 3 and 4, but it was also the earliest to show any cases with vascular structure corresponding to that of adult *A. microphylla*. These nodes have a median trace and only one lateral trace that ran straight into the single leaf-like stipule and gave off a branch, which ran across to the median trace and then ran beside it as a lateral trace. At the other side of the node was an unvascularized glandular stipular structure. This arrangement was more frequent above leaf 5 (Table 2) and is shown for node 7 (Fig. 4b–d). By nodes 12–15 this arrangement was standard.

The axillary bud trace at the early nodes is derived from the edges of the median leaf gap in the stem vasculature (e.g. Figs 3b, d, e, f, i, 4a) and the bud is located in the axil of the main component of the leaf (Fig. 3g). As the two-trace condition is reached at nodes with large and small 'leaf' the bud arises between the two 'leaves' and the stem, and the bud trace departs above the closure of the gap of the large 'leaf' trace (Fig. 4c, d).

Symmetry and dorsiventrality

The structures produced at successive nodes show in general a progressive increase in asymmetry. Using the overall frequencies of glandular and leaf-like stipular structures at each node from 3 to 7 to generate expected frequencies of nodes with two leaf-like or two glandular structures (symmetrical), or two dissimilar structures (asymmetrical) based on random occurrence, it can be shown statistically that nodes 3 and 4 have a higher frequency of symmetrical arrangements than would be expected by chance alone, and nodes 5–7 have a higher frequency of asymmetrical arrangements than would be expected by chance (Table 3).

In about half of the seedlings (24 of the 59 with visible leaf 5) the change to asymmetry occurred while the phyllotaxis was still spiral, and the sense of asymmetry remained the same in successive leaves for a few nodes (Fig. 4e) before alternation of a symmetry and consequent dorsiventrality occurred. The change from spiral to alternating symmetry was not entirely abrupt: e.g. in the bud shown in Fig. 4e leaf 8 has two large lateral appendages; the larger is on the same side as in the preceding leaves 6 and 7, so the sense of symmetry is continued, but the leaf is less asymmetrical than its predecessors. In other cases, leaf asymmetry alternated in successive leaves as soon as it appeared so that dorsiventrality appeared simultaneously (Fig. 4f).

DISCUSSION

Seedling development and interpretations of adult morphology of Azara

The description of the small 'leaf' as a 'leaf-like stipule' (or equivalent terms) by earlier authors (Warburg 1894; Troll 1937; Dormer 1944) certainly reflects its derivation by progressive elaboration of the stipular structures found in the early stages of the seedling. The derivation invalidates Reiche's (1896) suggestion that the small 'leaf' is a leaflet.

Table 3. Frequencies of symmetrical and asymmetrical arrangements of nodes 3–6, i.e. of nodes with two similar or two dissimilar stipular structures, expected frequencies based on the overall frequency of each kind of stipule, and χ^2 values for the deviation from expectation at that nodal position. The χ^2 value for node 3 is in parentheses because the expected frequency at that node for two flattened, expanded stipular structures is lower than that normally accepted in χ^2 tests but may actually be acceptable (see Cochran 1954)

Node		Symmetrical		Asymmetrical	χ^2 value (1 d.f.)
		Two glandular stipular structures	Two flattened, expanded stipular structures	One of each kind of stipular structure	
3	Observed	74	4	13	} (8.2**)
	Expected	71.2	1.2	18.6	
4	Observed	20	33	30	} 5.6*
	Expected	14.8	27.8	40.5	
5	Observed	11	5	43	} 13.2**
	Expected	17.9	11.9	29.2	
6	Observed	3	8	27	} 7.6**
	Expected	7.2	12.2	18.7	
7	Observed	0	3	18	} 11.8**
	Expected	3.9	6.9	10.3	

* $P < 0.05$; ** $P < 0.01$.

Charlton (1991) suggested for *A. microphylla* that the small 'leaf' represented a homoeotic replacement of 'stipule' by 'leaf'. It is now debatable whether an approach based on homoeosis is useful here. The stipular modifications in *A. serrata* can hardly be considered in the same light as a homoeotic mutation since there is a gradual elaboration of stipular structure as the seedling develops and the stipular structures on the two sides of the leaf are differently affected. The same argument presumably applies to *A. microphylla*. The continuum of developmental possibilities for stipular structures in *A. serrata* also make it difficult to apply even the looser definitions of homoeosis, e.g. homoeotic replacement in the broad sense, as defined by Sattler (1988), where part of an organ is replaced by a structure resembling the whole original organ.

Following the continuum approach of Rutishauser (1984) and Rutishauser & Sattler (1986), Charlton (1991) suggested that a case could be made in *A. microphylla* for the existence of a continuum between 'gland' and 'stipule'. The heteroblastic changes in the seedling of *A. serrata* support this view and require its extension on account of the developmental possibilities for stipular structures. There is a continuum from non-vascularized glandular structures to leaf-like stipules, i.e. to 'leaf' at the same lateral position of insertion at the leaf base. But a small 'leaf' formed in such a position which indicates that it is of stipular origin still differs in some details from a large 'leaf' formed in a position with continuity of descent from 'leaf blade' in the seedling. It has a conspicuous terminal gland, lacking in the large 'leaf', and the vascular traces to the

axillary bud are positionally related to the gap left in the stem vasculature by the departure of the trace to the large 'leaf'. It can still be argued that the large 'leaf' is distinct from the continuum of structures of stipular origin.

Charlton (1991) suggested for *A. microphylla* that homoeotic replacement of 'stipule' by 'leaf' included the production of additional stipular structures accompanying the homoeotic 'leaf'. Even if an approach based on homoeosis is rejected in favour of a continuum approach, leaf-like development of a stipular structure could be accompanied by correlated induction/production of additional 'stipules' in relation to the 'leaf'. A similar process may occur in *Pisum* (see Marx 1977). During the development of the seedling of *A. serrata*, however, additional smaller lateral structures begin to accompany the primary stipular structures even before these have shown any tendencies towards leaf-like development. Consequently, production of additional lateral stipular structures seems to be an innate feature of *A. serrata* unrelated to the actual nature of the primary stipular structures.

Dormer (1944) suggested that the dorsiventral shoots of *Lotononis corymbosa* and *Azara microphylla* demonstrated a correlation between lateral leaf trace and stipule development, so that the nodal condition with only two traces had arisen as a result of the suppression of one stipule (the lower) and the corresponding lateral leaf trace. The situation in the seedlings of *A. serrata* partly bears out this suggestion: all progress from unilacunar to trilacunar nodes before nodes with the full degree of leaf asymmetry and the two-trace nodal condition are formed, and in the majority of seedlings at least one trilacunar node is formed in which the two lateral traces supply two expanded stipular structures. However, the seedlings produce stipular structures before they produce lateral leaf traces so the correlation between the two is not absolute.

Azara and the leaf-stipule concept

Rutishauser & Sattler (1986) have reviewed the problems, morphological and philosophical, encountered in defining the boundary between 'leaf' and 'stipule'. The situation in *Azara* is difficult to cope with under any single concept. The 'leaf' evidently remains distinct from the 'stipular' structures in three ways: even the most leaf-like stipular structures always have a conspicuous glandular tip which is lacking in the 'leaf'; they develop as lateral components of the whole leaf primordium; and the changes in the vasculature as the seedlings develop indicate that the vasculature supplying any 'stipular' structures is derived from a lateral vascular trace supplying the 'leaf' itself. Yet there is a continuum of 'stipular' structures extending from small glands to expanded leafy structures, and primary 'stipular' structures themselves behave like leaves in having lateral accessory 'stipular' structures. Thus at each node, once a condition corresponding to the adult state in *A. microphylla* has been reached, there is a leaf blade accompanied by representatives of a continuum of stipular structures extending from glands to very leaf-like structures. The situation is one in which there is still evidence of the 'classical' distinction between leaf and stipule (cf. Rutishauser & Sattler 1985), but only small changes in detail in the three areas above would suffice to extend the continuum through to 'leaf'. In that case, if the heteroblastic series of the seedling indicated that one of the apparently equivalent 'leaves' at a node was derived from a stipular structure and the other was not, one might still be faced with the philosophical problem "can a 'leaf' ever be considered to be a leaf?"

Leaf and shoot symmetry

Seedling development in plants showing extreme shoot dorsiventrality and leaf asymmetry has been examined in detail in few cases. Charlton (1993a) examined the development of the seedling of *Ulmus glabra*. The seedling axis normally becomes distichous and dorsiventral at an early stage, and leaf asymmetry appears at the same time or later. Charlton (1993b) suggested that control of development in the adult dorsiventral shoots of *Ulmus* and similar cases resided in alternating states of asymmetry in the shoot apex. However, Charlton (1994) also showed in *Magnolia* that asymmetry could alternate node by node, producing a dorsiventral shoot, or could remain in the same sense and produce a spirally arranged shoot, and some species could produce both forms of symmetry (even within the same shoot). A shoot apex in a state of asymmetry can therefore produce a dorsiventral shoot if the sense of asymmetry alternates, or a spirally organized shoot if the state of asymmetry is maintained; both forms are distinct from a form without any asymmetry. In *Azara*, it appears, dorsiventrality resides in an alternation of asymmetry, as in these other cases; in the seedling the development of asymmetry is sometimes accompanied by alternation of asymmetry, sometimes not. As in *Magnolia* (Charlton 1994) asymmetry is not always firmly linked to dorsiventrality.

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