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Elaboration of stipular structures in *Azara serrata* R. & P. (Flacourtiaceae)

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SUMMARY

Several appendages are attached at each node of adult shoots of *Azara serrata*. There is always a large 'leaf', which is equivalent to the leaf blade of the early seedling leaf, and a small 'leaf' which is of stipular derivation. Other additional appendages of stipular derivation can occur. These are generally glandular, but in the early adult phase (second-season seedlings) some of them may be leaf-like. Only the large and small 'leaves' have a leaf-like vascular supply, from two traces derived from an original trilacunar nodal condition. It is suggested that *A. serrata*, and other species, may escape from conventional morphology by a cascade of stipular development and progressive elaboration, each stipular structure becoming accompanied by additional stipular structures with increasing size of the apical region as the plant develops from seedling to adult, and increasing size being accompanied by an increasing tendency to develop in a leaf-like manner. As a result there is a continuum of developmental possibilities for stipular structures, from gland to 'leaf'.

Key-words: Azara serrata, *Azara* spp., leaf, stipule, development, continuum.

INTRODUCTION

Adult shoots of *Azara* are dorsiventral, and normally give the appearance of having two leaves at each node, a large one at the lower side and a small one at the upper. The small 'leaf' has been seen as a leaf-like stipule (e.g. Warburg 1894; Troll 1937; Dormer 1944), a leaflet (Reiche 1896), and an accessory leaf (Sleumer 1977). Seedlings of *A. serrata* pass through a sequence of heteroblastic development in their first season which shows that the small 'leaf' is derived from an upper stipule, and receives its vascular supply from what was originally the upper lateral leaf trace, while the large 'leaf' shows continuity of descent from the leaf blade in the early stages of the seedling (Charlton 1994b). As Dormer (1944) suggested for *A. microphylla*, the lower lateral leaf trace has been suppressed and the development of the lower stipule has been reduced (Charlton 1994b). There appears to be a continuum of possibilities for stipular development in *A. serrata* from 'gland' to 'leaf', but the small 'leaf' of stipular origin is still distinct from the large 'leaf' which is descended from leaf blade; also, stipular structures, particularly leaf-life ones, tend to be accompanied by additional lateral stipular structures from an early stage in seedling development. In their second growing season the seedlings of *A. serrata* may carry this tendency to a further extreme and this is described here.

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 in their second and third seasons of growth were grown in a glasshouse. Shoots and shoot tips were fixed at intervals during the growing seasons. Shoots of the original parental plants were obtained in June 1993. 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). Individual nodes of some shoots were embedded in paraffin wax by standard methods (Johansen 1940), sectioned serially at 10–15 μm and stained with safranin and alcian blue. Other plants of *A. serrata* have been inspected at Batsford Park Arboretum, Gloucestershire and the Royal Botanic Garden, Edinburgh.

OBSERVATIONS

The terminology of large and small 'leaves' used in previous papers (Charlton 1991, 1994b) is maintained; extension of the possible range of stipular structures is dealt with on an *ad hoc* basis.

Shoot morphology

Seedlings of *A. serrata* can be considered to attain maturity in their second growing season, since they are then capable of forming flower primordia (which open in the next season). In their second season they produce nodes with large and small 'leaves' which are like those normally found in older established plants (Fig. 1a) but they also produce nodes with additional small leafy structures. Figure 1b shows a node with the maximum complement observed so far. In addition to the large and small 'leaves' there can be, in decreasing order of size and likelihood of appearance: a median leaf-like stipule (MLS on Fig. 1b); a lower leaf-like stipule (LLS); and an upper leaf-like stipule (ULS). No attempt has been made to quantify the distribution of these structures: however, it was evident that individual plants vary in the range they can produce, and the maximum complement of additional structures for any given plant tended to occur at the nodes produced during the most vigorous early growth. In established plants and older seedlings additional leaf-like stipules are not common; usually only a few median leaf-like stipules can be found, again in the early growth. At the time of writing (March 1994) active extension growth had begun in the 2- and 3-year old seedlings, and there were relatively fewer additional leaf-like stipules in the older plants.

Smaller stipular structures also occur between and beside the major structures at a node. At the simpler nodes with only a large and small 'leaf' there are glandular structures and sometimes radially symmetrical structures with glandular tips (Fig. 1c). There is a single axillary bud situated in the angle between axis and large and small 'leaves'. At more complex nodes additional glandular structures occur between adjacent leaf-like structures and beside the outer ones (Fig. 1d). Also in more complex nodes

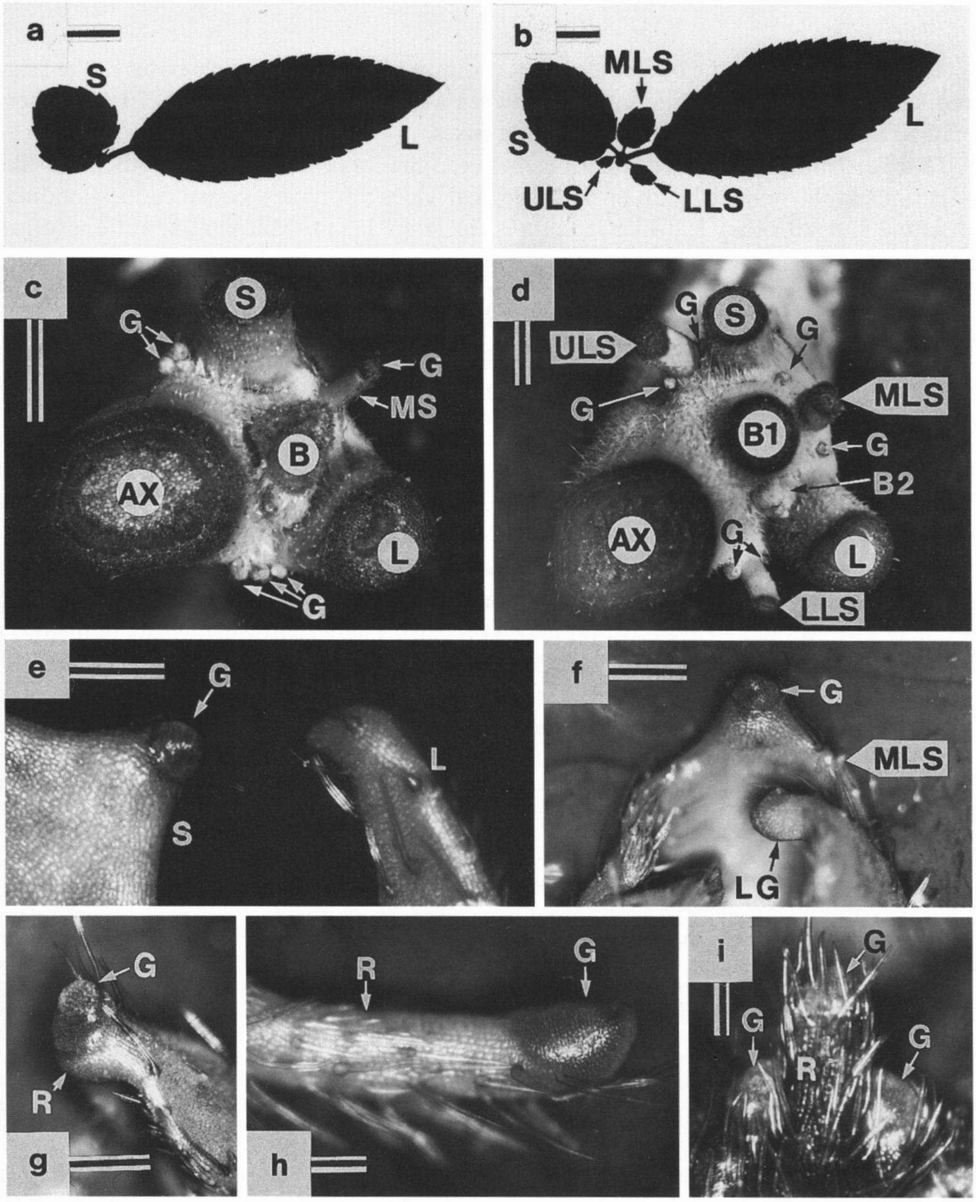


Fig. 1. (a) Silhouette of a node showing only large and small 'leaves' L and S. Bar = 1 cm. (b) Silhouette of node showing large and small 'leaves' L and S, also additional stipular structures: upper leaf-like stipule ULS; median leaf-like stipule MLS; lower leaf-like stipule LLS. Bar = 1 cm. (c) Node corresponding to that shown in (a), with stem AX, large 'leaf' L, small 'leaf' S, and axillary bud B trimmed to near the base. G denotes glandular stipular structure or glandular head of stipular structure; MS is a radially symmetrical stipular structure inserted between L and S. Bar = 1 mm. (d) Node corresponding to that shown in (b). Large and small 'leaves' L and S, the upper, median, and lower leaf-like stipules (ULS, MLS and LLS, respectively), and the main axillary bud B1 are all trimmed down. Glandular stipular structures are labelled G; B2 is an additional bud in the axil of large 'leaf' L. Bar = 1 mm. (e) Tips of a young large and small 'leaf' L and S from the same node, showing presence of conspicuous gland G at the tip of S and absence of a similar structure at the tip of L. Bar = 200 µm. (f) A young median leaf-like stipule MLS with gland G at the tip, and gland LG at the tip of a marginal serration. Bar = 250 µm. (g) Tip of a leaf-like stipule with a radially-symmetrical region R below gland G. Bar = 200 µm. (h) A radially symmetrical stipular structure R with terminal gland G. Bar = 100 µm. (i) Glandular stipular structure with short radially symmetrical region R and glandular head G, with two additional glandular structures G. Bar = 100 µm.

there is, in addition to the bud in the usual position between the petiole bases of the large and small 'leaves', an additional bud between axis and large 'leaf' (Fig. 1d) and there may be another even smaller bud in some cases.

There are morphological distinctions between the large 'leaf' and any other leaf-like structures at the node. The tip of the large 'leaf' does not have a conspicuous glandular structure but all other leaf-like structures do (Fig. 1e, f). Marginal serrations of all leaf-like structures have glandular tips (e.g. Fig. 1f). The larger leaf-like structures are flattened right up to the terminal gland (Fig. 1e, f) but in smaller ones the gland may be inserted on a terminal portion with radial symmetry (Fig. 1g).

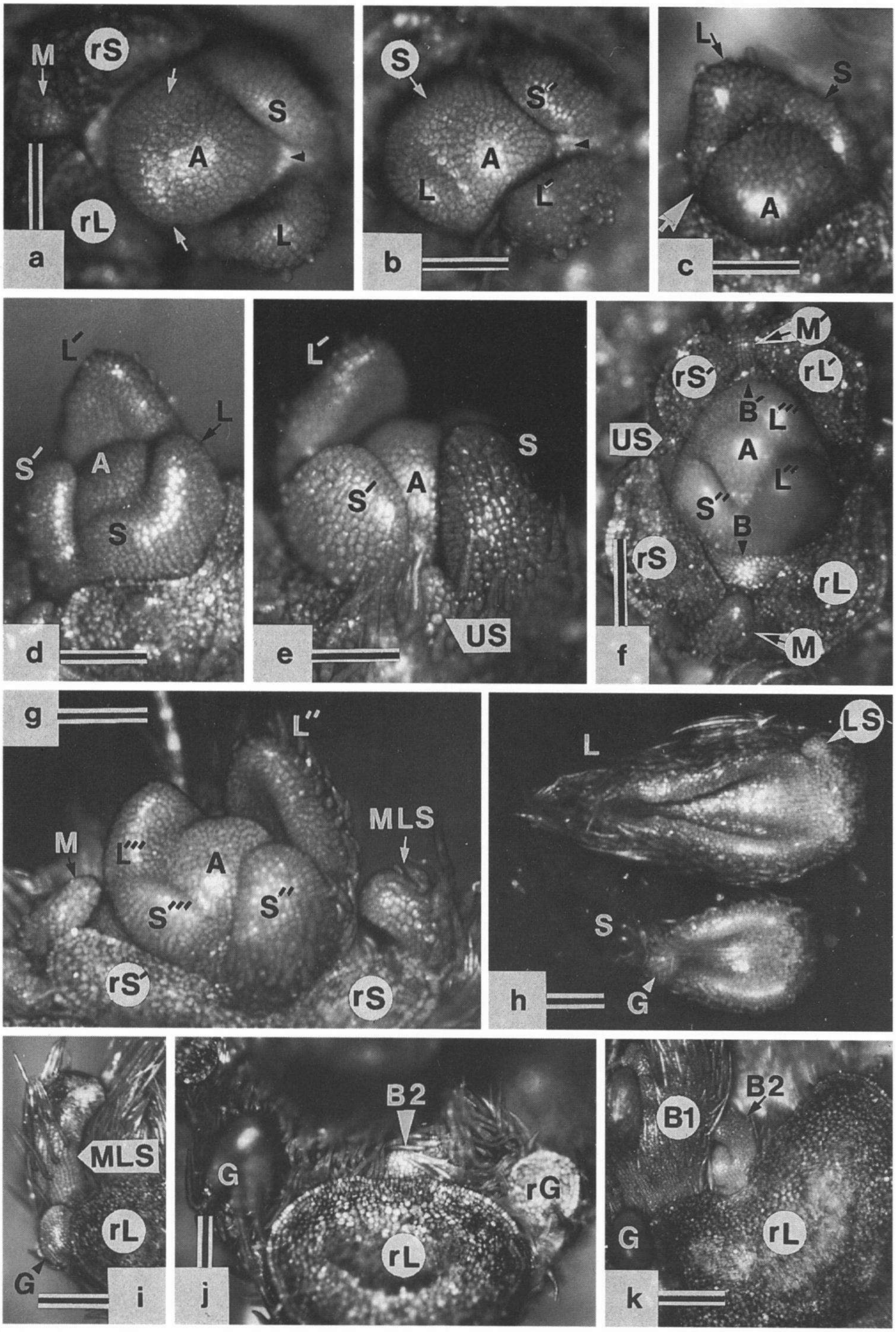
In the adult shoots, radially symmetrical stipular structures range from quite substantial (Figs 1c, h) to small (Fig 1i) and small glandular structures are sometimes inserted beside them (Fig. 1c, i).

Developmental morphology

Development of leaf primordia in shoots in their second season is at first very similar to the process in the later stages of the first season. A leaf primordium arises as an asymmetrical crescent (Fig. 2a) which becomes divided into two regions corresponding to the large and small 'leaves' at that node (Fig. 2b). There is little evidence of any lower stipule primordium at this stage (Fig. 2c). The primordia of large and small leaves arise as outgrowths of a common leaf buttress (Fig. 2d); the shoot apex is somewhat tilted towards the upper side of the shoot and the buttress is obliquely inserted (Fig. 2d, also Fig. 2g).

Primordia of additional stipular structures are somewhat variable in their position and timing of appearance. The development of covering trichomes makes it difficult to

Fig. 2. Standard labels are: L=large 'leaf' or its primordium; S=small 'leaf' or its primordium; A=shoot apex; B=site of main axillary bud; r denotes a removed structure; where the same structures from different nodes are visible, primes (′) are used to distinguish them. (a) Initiation of leaf primordium (between white arrows). A black arrowhead between L and S indicates the prospective site of an axillary bud. The primordium of an additional stipular structure M appears between rL and rS. Bar=100 µm. (b) Older stage of primordial development; regions of large 'leaf' L and small 'leaf' S are now distinct. The arrow between L′ and S′ indicates a prospective axillary bud site. Bar=100 µm. (c) View of a primordium from the adaxial side, showing regions of large 'leaf' L and small 'leaf' S. Arrow indicates the position where a lower stipule primordium might be expected to arise. Bar=100 µm. (d) Side view of shoot apex with two primordia each showing large and small 'leaf' components. The shoot apex is tilted towards the upper side of the shoot (i.e. towards the side at which the small 'leaves' are inserted) and the insertion of the complex L and S is somewhat oblique. Bar=100 µm. (e) Partly dissected shoot tip showing relative sizes of large and small 'leaf' primordia at the time a primordium of an additional upper stipular structure US is detectable beside S. Bar=100 µm. (f) Overhead view of partly dissected shoot tip, showing structures at four nodes. Two additional median stipular structures M and M′ are visible between rL and rS, and between rL′ and rS′; the primordium of an additional upper stipular structure is visible at the base of rS′; the sites of the axillary buds B and B′ are visible at the older nodes. Bar=100 µm. (g) Side view of a partly dissected shoot tip showing structures at four nodes. At the oldest node MLS is an additional median leaf-like stipule situated between base of small 'leaf' rS and the corresponding large 'leaf' (not visible). At the next younger node M is a median stipular structure in the same position relative to rS′ and the corresponding large 'leaf'; it is somewhat curved towards the shoot apex and will probably become leafy. Bar=100 µm. (h) Young large and small 'leaves' from the same node (fourth down from the apex) showing similar form, except for the presence of the gland G at the tip of the small 'leaf' which is curved towards the adaxial side. At the base of the large 'leaf' LS is the primordium of a lower stipular structure. Bar=100 µm. (i) Young median leafy stipular structure MLS (at ninth node down from the apex), with additional gland G, seen from the side. Bar=200 µm. (j) Site of an additional bud B2 in the axil of a large 'leaf' rL (eighth node down from apex). Bar=100 µm. (k) Well-developed additional bud B2 in the axil of large 'leaf' rL beside main bud B1. Bar=200 µm.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determine precise details for the later ones. They can appear at the edge of the leaf buttress (e.g. Fig. 2e). Those arising in the median position, between large and small 'leaves', plainly arise from a residual area of the original leaf buttress (Fig. 2a, f, g). Late-developing ones may appear to arise from the edges of pre-existing leafy structures (e.g. Fig. 2f, h). It is not possible to determine at first how any of the additional structures might develop. However, those which develop as leafy structures show a pronounced curvature towards the shoot apex (Fig. 2g) while radially symmetrical structures tend to remain straight (e.g. Fig. 1c, h). The primordium of the small 'leaf' also tends to show something of this curvature, which is less apparent in the large 'leaf' (Fig. 2h). The smallest stipular structures arise beside the bases of larger ones (Fig. 2i).

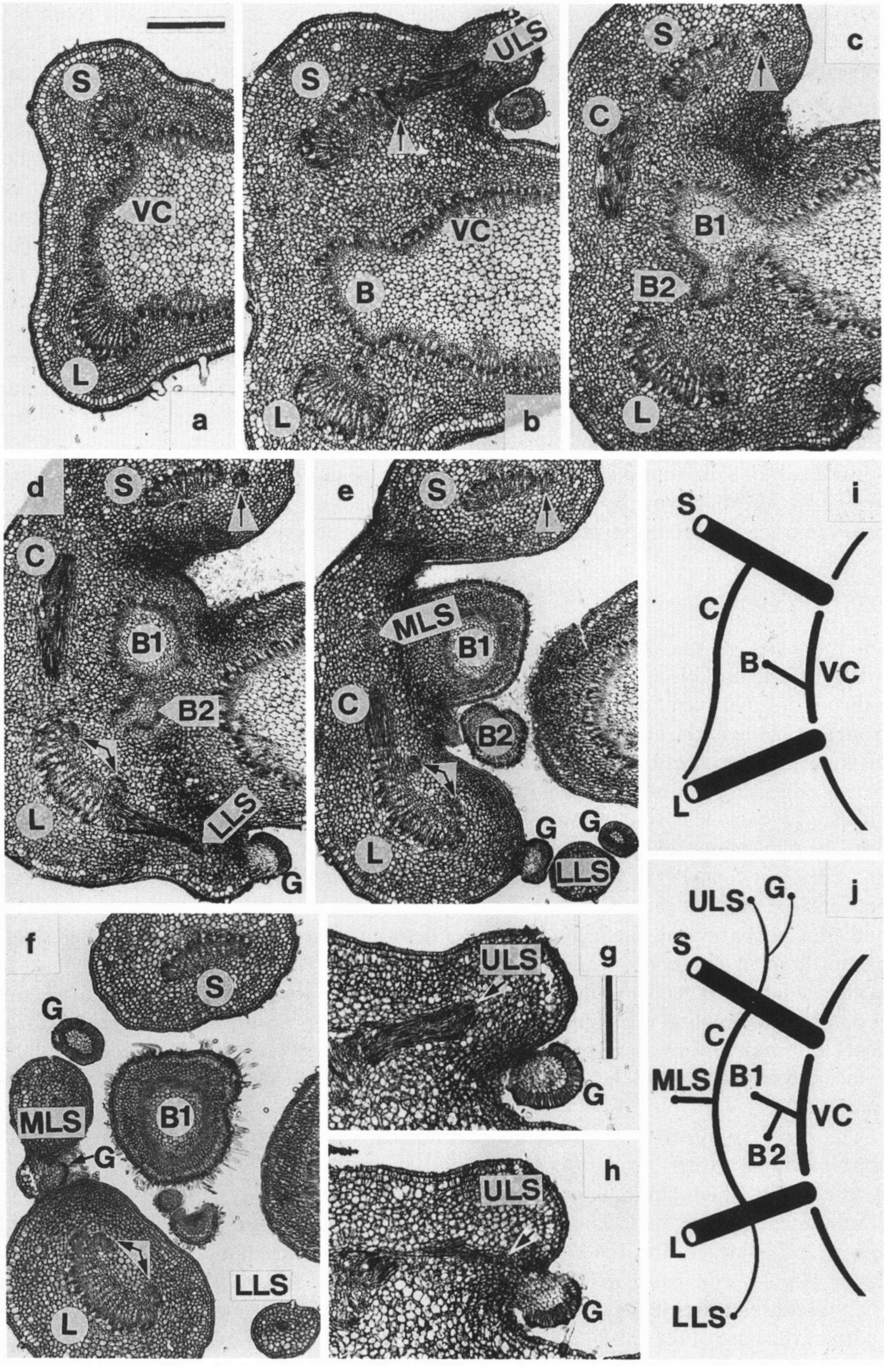
There is a small triangular area between the shoot apex and the primordia of large and small 'leaves' (Fig. 2a, b, f) which gives rise to the axillary bud, or the main axillary bud if there is more than one. The first additional bud arises separately in the axil of the large 'leaf' at the midline of insertion of its petiole, beside the main bud (Fig. 2j, k). Details of origin of further buds have not been seen.

Vascular structure

Where there is only large and small 'leaf' plus small stipular structures the nodal vasculature corresponds to that of the later nodes of seedlings of *A. serrata* in their first season (Charlton 1994b) and is similar to that previously described for adult *A. microphylla* (Charlton 1991). Two traces depart from the stem vasculature and one runs into the large 'leaf', one into the small 'leaf'. The trace of the small 'leaf' gives off a branch which forms a connecting trace running towards the trace of the large 'leaf' and turning to run beside it before eventually fusing with it. The bud trace departs from the stem vasculature above the closure of the gap left by the trace to the large 'leaf'. This form of vasculature is shown in diagrammatic form in Fig. 3i for comparison with the more elaborate forms of vasculature.

The traces to additional leaf-like structures at the more complex nodes of *A. serrata* almost all arise as branches from traces corresponding to those which occur in the simpler forms of nodes. Figure 3a–f shows sections from a series taken through a node

Fig. 3. Vascular anatomy of node. Standard labels are as follows: VC=vascular cylinder of stem; G=gland or occasionally trace to gland. Vascular traces (and sometimes the organs they supply) are labelled: S=trace to small 'leaf'; L=trace to large 'leaf'; ULS=trace to upper leaf-like stipule; MLS=trace to median leaf-like stipule; LLS=trace to lower leaf-like stipule; C=connecting trace; B=trace to bud(s); B1=trace to main bud; B2=trace to additional bud. Figures (a)–(f) are from one series of sections proceeding upwards through a node with all possible appendages. All at same scale. Bar=300 μm on (a). (a) Departure of main traces to the two 'leaves' from vascular cylinder. (b) Departure of trace to upper leafy stipule, with appearance of extra small trace (arrow); also departure of bud trace. (c) Part of the connecting trace C joining the two main traces is visible. Extra small trace (arrow) seen in (b) runs parallel with main trace S. Bud trace begins to resolve into separate traces to main and additional buds. (d) As (c) but also showing separation of the bud traces, the departure of the trace to the lower leaf-like stipule, and two further extra small traces (double arrow) parallel to main trace L. (e) As (d) but higher in the node, showing trace to median leaf-like stipule. Two glands are associated with the lower leaf-like stipule. (f) The small extra trace running parallel to S in lower sections is no longer visible, having fused with S, but the small traces (double arrow) accompanying L are still visible. The connecting trace between S and L is not visible, having joined completely with L. There is a gland at either side of the median leaf-like stipule. (g) and (h) Adjacent sections from another node. Bar=200 μm on (g). (g) Upper leaf-like stipule receives a substantial trace (arrow). (h) A small branch (arrow) runs towards the gland beside the leaf-like stipule. (i) Diagram of the nodal vasculature as formed in the later stages of the first season of growth (for comparison with following figure). (j) Diagram showing the most elaborate nodal vasculature found in plants in the second season of growth.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with the maximum complement of appendages. The upper leaf-like stipule receives a trace which branches off from the trace to the small 'leaf' (Fig. 3b). A connecting trace runs almost straight across from the trace of the small 'leaf' to the trace of the large 'leaf' (Fig. 3c–e), and the trace to the median leaf-like stipule branches off from the connecting trace (Fig. 3e). The trace to the lower leaf-like stipule arises as a branch from the trace to the large 'leaf' (Fig. 3d). Glandular structures inserted beside additional leafy stipules are not usually vascularized (Fig. 3b, d–f) but occasionally the glandular structure at the outer upper edge of the node, adjacent to the upper leaf-like stipule, receives a small trace which branches off from the trace to the upper leaf-like stipule (Fig. 3g, h). A bud trace branches off from the stem vasculature above the closure of the gap left by the large 'leaf' trace (Fig. 3b). The trace to an additional bud arises as a branch from the main bud trace (Fig. 3c, d).

Small additional traces branch off from the main leaf traces, and run parallel to them, at the departure of traces connecting to upper and lower leaf-like stipules (Fig. 3b, c and 3d, e, f respectively), or without direct relationship to other events (Fig. 3d–f). When followed upwards the small traces rejoin the main ones (e.g. Fig. 3e, f).

Figure 3i is a diagrammatic representation of a node from the late stages of the first season of seedling growth, to provide comparison with Fig. 3j, which shows all the possible traces to lateral structures which have been observed so far.

DISCUSSION

On the basis of the changes during the first season of growth of the seedlings it was concluded that there was a continuum between 'gland' and 'leaf', but there was still a distinction between 'leaf' of stipular origin from 'leaf' showing continuity of descent from leaf blade in the early stages of seedling development. In the more elaborate forms of node in *A. serrata* the 'leaf' of stipular origin has become more leaf-like since the cross-connecting strand between the traces of the large and small 'leaves' connects directly to each leaf trace in the same way. It could also be argued that the large 'leaf' becomes more like an independent leaf, since it can have a bud placed directly in its axil. Charlton (1991) suggested for *A. microphylla* that, instead of the single bud between the bases of the two 'leaves', one might expect each 'leaf' to subtend an axillary bud; but probably the single bud site was determined in relation to the initial single primordium at the node. Based on the suggestion of Snow & Snow (1942) that an axillary bud is induced by the axillant leaf, it appears that in the elaborate nodes of *A. serrata* the first bud is formed in relation to the initial primordium, and then the large 'leaf' induces the formation of its own individual axillary bud. If a bud were similarly associated with the small 'leaf' this would be a further step along the continuum to leaf character.

The early asymmetry of *Azara* leaf primordia, once shoot dorsiventrality is well-established, is rather similar to that found in some cases with the rotated-lamina syndrome, in which laminae face towards one side of the shoot from an early stage of development (Charlton 1993a–c, 1994a), i.e. the upper stipule arises earlier than the lower, and is larger, and the axillary bud appears in the triangular area between axis, upper stipule, and base of leaf blade. In the cases of rotated-lamina syndrome the triangular area arises by asymmetrical development of the leaf buttress, extends the full width of the base of the leaf blade, and is associated with the rotation of the lamina base, but in *Azara* the area is smaller and does not lead to any rotation effect.

First-season seedlings show progressive elaboration of stipular structures at one side of the leaf (the upper in dorsiventral shoots) and diminution at the other side. In the second-season seedlings it is apparent that there is yet further elaboration of stipular development at the upper side, with the possible production of additional leaf-like structures in the median and upper positions; there is also some increase at the lower side, with possible production of a lower leaf-like stipule. The asymmetry of the nodal assembly is maintained but it is further elaborated. The additional elaboration is associated with increase in size of the shoot apex and leaf primordia, cf. Fig. 2i, j in Charlton (1994b) and Fig. 2a, b in the present paper. As established plants and the older seedlings seem to show less elaboration than the second-season seedlings there is an impression that some homeostatic mechanism finally is invoked that stabilizes the degree of complexity of node that is produced.

The progressive elaboration can be seen as the result of a cascade mechanism operating from the earliest stages of seedling development. Even at the third node above the cotyledons glandular stipular structures can be accompanied by additional smaller lateral glands. As the shoot apex, and the primordia initiated on it, become larger during the development of the seedling, primordia of stipular structures are larger and more likely to have additional lateral primordia. These themselves become more likely to have additional lateral primordia as the size increase continues. Accompanying this cascade, the liability of a stipular structure to develop in a leaf-like manner increases with the size of the system. Together these features generate the continuum from 'gland' to 'leaf', and the same kind of suggestion could be made for the case of *Acacia longipedunculata* described by Rutishauser & Sattler (1986).

In fact, when the departures from 'conventional' leaf and stipule morphologies are seen in this light, *Azara serrata* and *A. microphylla* have only escaped from convention in two small details: the cascade of successive orders of additional stipular structures, and the very leaf-like character which stipular structures can assume. These details are superimposed on the dorsiventrality of the shoot, which involves accentuation of stipular and vascular development on one side of the leaf and reduction on the other and, as in many other cases, depends on asymmetry of shoot apex and leaf primordium. Details in Glück (1919) and Sleumer (1977) suggest that there is a range of degree of dorsiventrality among *Azara* spp. and it would be interesting to see how independent this is of the proposed cascade.

Azara therefore provides an interesting and individual case in plant morphology. It produces quite unconventional shoots by means of quite small departures from 'conventional' morphology. In terms of process morphology (Sattler 1990, 1992) the stipules can show process combinations similar to those characteristic of simple leaves, i.e. the development of dorsiventral symmetry and a laminar structure, or they can maintain radial symmetry. These processes are not entirely mutually exclusive since stipular structures with dorsiventral leaf-like features may have a radially symmetrical tip of a kind not found in the leaf blade itself. Structures of stipular origin show a continuum from 'gland' to 'leaf'. Nevertheless, there is structures evidence, and evidence from the changes during the development of the seedling, that a 'leaf' of stipular origin is still distinct from a leaf with continuity of descent from leaf blade of the early seedling leaves. On the interpretation of a cascade of stipular development and progressive elaboration, the perceived 'continuum' may not even represent a blurring of the distinction between 'leaf' and 'stipule'. However, the various interpretations are not clearly mutually exclusive; they are complementary in the sense of Rutishauser & Sattler (1985).

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