Anatomy of tropical alpine plants

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Introduction

Despite recent interest in alpine ecology, we have little information on anatomy of alpine plants. This is as true of tropical alpine plants as it is of those from temperate mountain areas. The reasons for the lack of studies in anatomy of tropical alpine plants are perhaps surprising.

First, one can cite the tendency for plant anatomists to work little on comparative problems and, when they do, to work in terms of particular taxonomic groups and to express their data in systematic terms rather than in ecological ones. To be sure, interest in ecological plant anatomy has increased in the latter half of the 20th century, and one can cite more studies concerning tropical alpine plants in recent years. The curious climatic regimes of high equatorial mountains make anatomical adaptations of especial interest, as will be seen from the relatively few examples cited in this chapter. Adaptations to frost and to drought are central in tropical plants, but these adaptations are different from those in plants of extremely cold or extremely dry regions.

A second reason for lack of studies on anatomy of tropical alpine species is a by-product of the working habits characteristic of biologists. Ecologists, unless highly theoretical in orientation, tend to use the outdoors as a laboratory. For the plant anatomist, laboratory work must be done indoors, and the habit of working both in the field and in the laboratory apparently does not come easily to most plant anatomists. Indeed, few plant anatomists who do comparative work collect the material they study. Tropical alpine areas are often difficult of access, so that plant anatomists are quite unlikely to visit these areas. Perhaps more significant, plant anatomists tend not to be well trained in plant ecology and physiology, so that kinds of data needed for structure/function correlations are often not collected. Plant physiologists tend not to initiate studies in
plant anatomy very often. A collaboration among workers seems a
desirable way of proceeding with studies on anatomy of tropical alpine
plants. Such collaborations have been very few, so that the present chapter
will have the purpose of calling attention to possible findings rather than
reporting them.

A third circumstance that has delayed anatomical studies on tropical
alpine plants is the tendency for anatomical studies to favor woody species
and species of economic importance. Woody plants are often thought to
contain more anatomical diversity. In fact, herbaceous plants offer just as
many features of anatomical interest. The studies cited below indicate the
inherent interest of tropical alpine plants, and should promote further
studies by enterprising workers.

**Anatomy of rosette trees**
The chief genera of rosette trees in tropical alpine areas are *Espeletia*
(Asteraceae) in the northern Andes and *Senecio* (Asteraceae) on the high
African volcanoes. *Lobelia* (Campanulaceae, subfamily Lobelioidae; or
Lobeliaceae) is often cited, but note should be taken that the high
elevation species of *Lobelia* are not arborescent; the woodier species
of *Lobelia* tend to be at the bottom of the alpine zone or below. *Lobelia*
in the alpine zone tends to be what some authors term ‘rosulan’ (with a
very condensed stem), ‘caulorosulan’ (with a short stem, usually under
1 m). The term ‘megaherb’ is sometimes applied to plants like the tropical
alpine *Lobelia* species, although it has been used more commonly for
large-leaved herbs such as *Gunnera* or large rosette plants of subantarctic
islands (e.g. *Pleurophyllum, Stilbocarpa*). The woodiest species of *Lobelia*
in Africa can be found in the mossy forest, as in the case of *L. gibberoa*
Hems. or *L. lanuriensis* De Wild. The chief references with respect to
habit, habitat and taxonomy are: *Senecio* (Hauman 1935; Hedberg
1957, 1964; Nordenstam 1978); *Espeletia* (Smith & Koch 1935; Rock
1972); and *Lobelia* (Hauman 1933; Hedberg 1957, 1964).

Anatomy of all three genera is certainly not the same but certain main
features are similar. One can say that all three genera have a wide pith
and a thick cortex or bark (Hauman 1935; Rock 1972). The pith width
results from the action of a primary thickening meristem in *Espeletia*
(Rock 1972) and the other genera should be investigated in this respect.
There is evidence for a water storage function of the wide pith (Goldstein
& Meinzer 1983; Goldstein et al. 1984). Another possible function of the
pith is structural, providing a device for achieving a cylinder wide in
diameter (and thus structurally superior to a narrow cylinder for resistance to shear) and capable of bearing larger numbers of leaves than could a narrower stem. There seems little reason to doubt the water storage function of the stem in these genera, because in these genera the stems are succulent by any definition, whether studied in terms of anatomical preparations (Hauman 1935; Rock 1972) or by macroscopic dissections (Hedberg 1964, p. 51).

The xylem characteristics of *Senecio*, *Espeletia* and *Lobelia* show little or no indication of xeromorphy (Carlquist 1958, 1962a, 1966, 1969; Hauman 1935; Rock 1972). Although the high-alpine species of *Lobelia* (*L. telekii* Schweinf.: Carlquist 1969) and *Espeletia* (*E. timotensis* Cuatr.: Rock 1972) have short vessel elements, the shortness of vessel elements in these species might be related indirectly to the rosette habit (rosulan) in these species rather than to xeromorphy.

Features that validate mesomorphy in wood anatomy of the three genera cited above include wide diameter of vessels, low number of vessels per group (many vessels solitary), and low number of vessels per mm² of transection (Carlquist 1958, 1962a, 1969; Rock 1972). These features are shown for *Lobelia gibberosa* in Figure 6.1. A comparison between wood of rosette trees and wood of shrubs and other kinds of trees has been offered earlier (Carlquist 1966, 1975). The latter study shows that rosette trees stand next to stem succulents in their quantitative wood characteristics. One might, in fact, call *Senecio*, *Espeletia* and *Lobelia* (montane species) stem succulents. The broad leaf surfaces would be atypical for succulents. The vessels in the rosette trees certainly do not seem to be narrow enough or dense enough to provide redundancy (or possibly other) characteristics that are common in xeromorphic woods (for a review, see Carlquist 1988).

Areas of rays, as seen in tangential sections of woods, are rather great for the rosulan species of *Espeletia* and *Lobelia*, and the lack of secondary walls on ray cells in those species (as revealed by examination with polarized light: Rock 1972) has led Rock to claim a water storage function for these rays. The rays of the more arborescent species in these genera are tall, but relatively narrow (Figure 6.2), and do not suggest a marked water storage function. Absence of growth rings (Figure 6.1) is definitely characteristic of all three genera, although A. P. Smith (personal communication) has found distinct growth rings in the stem of *S. keniodendron* at 4200 m on Mount Kenya and in *E. humbertii* Cuatr., an arborescent species, at treeline in the Venezuelan Andes. The presence of growth rings in these species probably reflects the strongly seasonal rainfall in both of
Figures 6.1–6.4. Wood sections of *Lobelia* (Campanulaceae). Figs. 6.1–6.3. *L. gibberosa* (Carlquist 2829). Fig. 6.1. Transection; note relative paucity of vessels. Fig. 6.2. Tangential section. Rays are tall, moderately wide. Fig. 6.3. Radial section; most ray cells are upright. Fig. 6.4. *Lobelia shaferi* (Yw-40053). Perforation plates from radial section, showing modified scalariform condition. Figures 6.1–6.3, magnification scale above Figure 6.1 (finest divisions = 10 μm). Figure 6.4, scale above Figure (divisions = 10 μm).
these exceptional regions. On the whole, most tropical alpine sites where rosette trees grow are not so strongly seasonal that strongly marked growth rings characteristically occur.

The slow and moderate accumulation of secondary xylem, correlated with succulence, is characteristic of the three genera cited above. In turn, this has the effect of preserving a juvenilistic secondary xylem conformation, which is being termed paedomorphosis in wood (Carlquist 1962b). Paedomorphosis has multiple expressions in wood anatomy. Horizontal subdivision of ray cells is lessened, so that erect ray cells are more abundant than would be expected in comparison to procumbent cells (Figure 6.3). Procumbent cells are found in some primary rays and little-altered primary rays, and may be related to leaf traces (Rock 1972). Lateral wall pitting of vessels in the secondary xylem often resembles that of metaxylem vessels in the three genera, in contrast to the alternate pitting that quickly succeeds metaxylem patterns in typically woody species. Simple perforation plates characterize all of the three genera, as one might expect in these families, on the basis of their numerous specialized features (Carlquist 1958, 1962a, 1969). However, occasional perforation plates that are not scalariform in the ordinary sense but much altered versions best termed multiperforate or irregularly scalariform, do occur in a very small proportion of vessel elements (Figure 6.4). The occurrence of this small proportion of multiperforate plates is very likely a manifestation of paedomorphosis, since metaxylem vessels do have scalariform perforation plates in some Campanulaceae and Asteraceae, whereas secondary xylem vessels in these families typically have simple perforation plates (Bierhorst & Zamora 1965). Mabberley (1974) confused scalariform lateral wall pitting of vessels (common in rosette trees) with scalariform perforation plates (rare in rosette trees). He also confused the theory of paedomorphosis with Bailey's (1944) idea that the primary xylem is a refugium of primitive xylem features. Mabberley's misunderstanding and consequent theorizing in terms of the Durian theory have been criticized (Carlquist 1980, 1988), and ideas of paedomorphosis in wood have continued to be accepted in the various taxonomic groups where this phenomenon is characteristic (Carlquist 1988). Predominantly herbaceous dicotyledon families that have become secondarily woody in the relatively non-seasonal climates of tropical montane areas are among the categories of dicotyledons that show paedomorphosis in wood (Cumbie 1983).

The leaf anatomy of the three genera of rosette trees cited above suggests forms of xeromorphy in species of higher elevations: leaves of the lower elevation species are thinner, broader, and lacking in the various
features that connote xeromorphy. This has been noted by Rock (1972) for *Espeletia*, and can be readily observed in the leaves of *Senecio* and *Lobelia*; both of these genera have leaves less complex than those of *Espeletia*. *Espeletia* has pockets on the abaxial surfaces of leaves ('areolar cavities' of Rock). Water storage undoubtedly does occur in the thicker leaves of the high elevation species of all three genera, although identifying exactly which cells in the leaf store water and to what degree they do so is not easy (Rock 1972). Hypodermis occurs in leaves both in *Espeletia* (Rock 1972) and *Senecio* (Hauman 1935), and may serve a water storage function.

Distinctive functions performed by the leaves in the high elevation species of all three genera can be described in anatomical terms. Old leaves clothe the stems in *Senecio keniodendron* (Hedberg 1964) and *Espeletia* (Cuatrecasas 1934), and have the effect of preventing freezing of the stems (Goldstein & Meinzer 1983). The immediate anatomical cause of this behavior is failure of formation of an abscission layer in these genera; that has not been established by observations, but can be supposed with reasonable assurance.

All three genera of rosette trees cited above have nyctinastic leaf movements (Hedberg 1964; Smith 1974). The anatomical structure underlying this behavior has not been established. One would expect that parenchyma cells near the petiole base and on its abaxial side would fill with water during the night. Nyctinastic movements in rosulan and caulorosulan plants can be seen in some other plants as well as the tropical alpine rosette trees; beet and chard (*Beta vulgaris* L.) show such daily cycles, for example.

Hairs on leaves of some species of *Senecio*, *Espeletia* and *Lobelia* are sufficiently dense so as to be significant in the insulating qualities of the leaves (Hedberg 1964). These hairs are, in all three genera, elongate uniseriate hairs, sometimes densely borne (Hauman 1935; Rock 1972). Some species of *Senecio* have hairs only on petioles of leaves (Hauman 1935), but this is a maturation effect. On primordia of these *Senecio* leaves, hairs occur over the entire surface, but differential loss occurs as leaves in particular species mature (original observation).

### Sclerophyllous shrubs

Hedberg & Hedberg (1979) find that tropical alpine plants fall into the categories of rosette plants, tussock grasses, acaulescent rosette plants, cushion plants, and sclerophyllous shrubs. Acaulescent rosette plants of
tropical alpine regions have been little studied anatomically, but superficial examination suggests no profound differences in leaf texture or stem nature from related rosette plants of other geographical regions. Likewise, tussock grasses, although a distinctive element in tropical alpine zones, seem unlikely to differ modally as a group from tussock grasses in other regions. As individual species, however, species comparisons would doubtless prove interesting.

Haleakala and other Hawaiian volcanoes

Leaf anatomy has been studied synoptically for very few tropical alpine sclerophyllous shrubs, but the Hawaiian species of Geranium, all of which are high elevation plants, have distinctive modes of leaf anatomy (Carlquist & Bissing 1976). In addition to features of gross morphology (leaf area, number of leaf teeth) that distinguish the species, such anatomical characters as outer epidermal wall thickness and leaf thickness can be combined to form an index to the relative mesomorphy or xeromorphy of particular species. Hypodermis prominence increases with xeromorphy of species locality, lending credence to the idea that hypodermis is often a water storage tissue. Geranium tridens Hillebrand has isolateral leaves, whereas the other species have bifacial leaves. The felty covering of hairs on at least some surfaces of the leaves of the high elevation species G. cuneatum Hillebrand and G. tridens is highly reflective, and although trichomes on leaves ordinarily do not lower ultraviolet light absorption by leaves very much, in extreme situations this might be one possible function. This and other potential functions of trichomes in these species are worthy of investigation.

Sclerophyllous shrubs of Haleakala and the other Hawaiian volcanoes experience climatic regimes sufficiently extreme that adaptations by wood are of significance and, in fact, characterize all of the species in the alpine zones of these mountains. To be sure, alpine conditions are equalled only by desert areas in transpiration potential (Smith & Geller 1979), but freezing also occurs. Many Hawaiian alpine genera are also represented in dry lowland areas (Carlquist 1970).

Wood of dryland evergreen shrubs of Mediterranean-type climates is characterized, to a surprisingly large extent, by the occurrence of vasicentric tracheids and, to a lesser degree, true tracheids (Carlquist 1985). Vasicentric tracheids and true tracheids offer subsidiary conductive systems that could maintain water columns to leaves even if all vessels embolize. In addition, they offer redundancy in the conductive system by virtue of being
Figures 6.5–6.9. Wood preparations of Hawaiian alpine plants. Figs. 6.5, 6.6. *Geranium tridens* (Carlquist 546). Fig. 6.5. Transection of wood; a fascicular area is in the center; the rays, at either side, are filled with dark-staining compounds. Fig. 6.6. Tangential section of wood, with fascicular area at left (vessels and vasicentric tracheids in centre of that area, ray at right). Figs. 6.7–6.9. *Dubautia menziesii* (Carlquist H17). Fig. 6.7. Transection of wood, ray in center and at right; vessels are narrow and grade into vasicentric tracheids. Fig. 6.8. Tangential section, ray at right; most cells are narrow vessels or vasicentric tracheids. Fig. 6.9. Cells from a wood maceration; a vasicentric tracheid is visible, above (diagonally
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Conductive cells additional to vessels, and merely redundancy alone could explain the effectiveness of this cell type in resisting the effects of drought or freezing.

Vasicentric tracheids, despite their rarity in the world flora, prove to be common in the Haleakala alpine flora. *G. tridens* (Figures 6.5, 6.6) and the other Hawaiian species of *Geranium* have vasicentric tracheids (original data). In *Geranium*, the central portions of each fascicular area (zones in wood between rays) consists of vessels and vasicentric tracheids, whereas the margins of the fascicular areas adjacent to rays consist of libriform fibers. Vasicentric tracheids are abundant in wood of the high-alpine species *G. tridens*, but are less abundant in wood of the more mesomorphic species from lower on Haleakala, *G. arboreum* A. Gray.

Vasicentric tracheids are relatively uncommon in the large family Asteraceae (Carlquist 1985), but are abundant in the Haleakala species of this family. Wood of *Dubautia menziesii* (A. Gray) Keck, which may be found at the summit of Haleakala, features patches of what appear to be variously narrow vessels (Figures 6.7–6.9). In macerations, many of these prove to be vasicentric tracheids. *Tetramolopium humile* Hillebrand also occurs at the summit of Haleakala, and is a dramatic example of vasicentric tracheid presence. In the wood of this species (Figures 6.10, 6.11), vasicentric tracheids outnumber narrow vessels; only a few libriform fibers are present (Carlquist 1960). Vasicentric tracheids appear to increase in abundance in various phylads in proportion to the dryness experienced by any given species (Carlquist 1985). This may explain why vasicentric tracheids are more abundant in *T. humile*, which has roots shallower than those of *D. menziesii*. In addition, *D. menziesii* has thick and markedly succulent leaves (Carlquist 1959a), in contrast to those of *T. humile*, which appear to have little water storage capacity although their upright orientation may reduce transpiration somewhat. Physiological measures show that leaves of Hawaiian species of *Dubautia* in dry localities have mechanisms for dealing with limited water availability compared to species from more mesic localities (Robichaux & Canfield 1985).

Other species with vasicentric tracheids that occur near the summit of Haleakala include *Santalum haleakalae* Hillebrand (Santalaceae) and *Argyroxyphium sandwicense* DC. (Asteraceae). The latter is considered in detail later.

Caption for Figs. 6.5–6.9 (cont.).

placed), its lower tip touches a pair of vasicentric tracheids and a parenchyma cell. Figures 6.5–6.9, magnification scale above Figure 6.5 (divisions = 10 µm).
Figures 6.10–6.13. Wood sections of Hawaiian alpine and Andean superpáramo plants. Figs. 6.10, 6.11. *Tetramolopium humile* (Carlquist H18). Fig. 6.10. Transection. Vague growth rings evident; cells that appear to be libriform fibers are mostly vasicentric tracheids. Fig. 6.11. Tangential section, showing rays and narrow vessels (very few libriform fibers are present in this particular section). Figs. 6.12, 6.13. *Loricaria thuyoides* (Yw-20733). Fig. 6.12. Transection. No growth rings are evident; narrow vessels are scattered among vasicentric tracheids and a few parenchyma cells. Fig. 6.13. Tangential section; rays at left and right; axial parenchyma portion is mostly vasicentric tracheids. Figures 6.10–6.13, magnification scale above Figure 6.5.
A wood in which the entire background is composed of tracheids (thereby termed ‘true tracheids’ for purposes of clarity in my 1985 paper) offers a maximum of potential safety in terms of water-column failure. Woods with true tracheids comprise a minority of angiosperms, and many of these species appear to be restricted to wet habitats, in accordance with the ideas, seemingly supported by work in wood evolution, that claim angiosperms to have originated under moist conditions (Carlquist 1975, 1988). However, these phylads, by virtue of greater conductive safety of woods, would be ideal for dry areas if vessels can have simplified perforation plates and other vegetative structures can be modified for dryland water economy. Such species do appear to occur in dryland areas quite commonly (Carlquist 1985). On Haleakala and other Hawaiian alpine areas, this type of wood anatomy is represented in *Styphelia tameiameiae* (Cham.) F. Muell. (Epacridaceae) and *Vaccinium* spp.

**Páramos**

Although the anatomy of particular species listed from the Colombian páramos by Cuatrecasas (1934) is mostly unknown, one can cite types of wood anatomy reported for the genera to which they belong. There is usually little qualitative difference among congers with respect to wood anatomy, so this indirect form of reportage can be used as a first approximation. Cuatrecasas lists as main shrubby associates of *Espeletia* the following: *Alchemilla* spp. (Rosaceae); *Berberis quiundiensis* Kunth (Berberidaceae); *Diplostephiun* spp. (Asteraceae); *Gaultheria* spp. (Ericaceae); *Hypericum* spp.—especially *H. laricifolium* Juss. (Clusiaceae); *Miconia salicifolia* Naud. (Melastomataceae); *Myrteola vassinioides* (HBK.) Berg (Myrtaceae); *Senecio rigidfolius* Badillo (Asteraceae); and *Vaccinium* spp. (Ericaceae). Of these, *Hypericum* and *Berberis* were cited as having vasicentric tracheids in my 1985 survey. *Alchemilla, Gaultheria, Myrteola* and *Vaccinium* all have true tracheids (Metcalfe & Chalk 1950; Carlquist 1985). Rock (1972) reports that *Diplostephiun venezuelense* Cuatr. and *Senecio rigidifolius* have vascular tracheids – tracheids formed in latewood (although often confused with vasicentric tracheids by various authors). Thus, only *Miconia salicifolia* belongs to a genus for which one of these unusual wood adaptations is not reported; very likely, it has other distinctive forms of wood xeromorphy.

The superpáramo areas, higher than the zone where *Espeletia* occurs, are drier and colder than the páramos. The genus *Loricaria* occurs in the superpáramo. *Loricaria thuyoides* (Lam.) Sch. Bip. (Asteraceae) belongs
to a family in which libriform fibers are to be expected in wood. However, *Loricaria* has tracheids so abundant that libriform fibers have vanished altogether (Figures 6.12, 6.13). Termed vascular tracheids for this species earlier (Carlquist 1961), these tracheids now must be termed vasicentric tracheids (Carlquist 1985). The wood of *Loricaria* offers optimal safety, rather like a conifer wood in high redundancy of conducting cells, most of which are tracheids. Like a conifer, *Loricaria* is microphyllous.

Afroalpine

The shrubby flora of alpine East Africa contains the following genera of shrubs according to the flora of Hedberg (1957): *Alchemilla* spp. (Rosaceae); *Anthospermum usambarense* K. Schum. and *Galium* spp. (Rubiaceae); *Blaeria* spp., *Erica arborea* L. and *Philippia* spp. (Ericaceae); *Crassocephalum* spp. and *Helichrysum* spp. (Asteraceae); *Hypericum* spp. (Clusiaceae); *Pelargonium whytei* Bask. (Geraniaceae); *Protea kilimandscharica* Engl. (Proteaceae); and *Thesium kilimandscharicum* Engl. (Santalaceae). Of these, the genera *Hypericum* and *Protea*, and the families Geraniaceae and Santalaceae have been shown to possess vasicentric tracheids. True tracheids are known in *Anthospermum* (Koek-Noorman & Puff 1983) and *Galium* (Carlquist 1985) of the Rubiaceae. *Erica* has true tracheids (Carlquist 1985), and very likely the other ericaceous genera cited, *Blaeria* and *Philippia*, do also. *Alchemilla* belongs to a tribe of Rosaceae characterized by true tracheids, according to my unpublished observations. Thus, the majority of shrubs in the African alpine flora have either vasicentric tracheids or true tracheids, and very likely have other wood features adapted for these extreme sites. The species of *Helichrysum* should be studied for possible wood xeromorphy, as should *Adenocarpus mannii* (Hook f.) Hook f., a legume shrub of the region. *Crassocephalum* tends to occur in moist areas at the bottom of the alpine zone.

*Argyroxyphium*, a unique tropical Alpine genus

*Argyroxyphium* (Asteraceae, tribe Heliantheae, subtribe Madinnae), endemic to the Hawaiian Islands, is quite distinctive in its adaptations to tropical (or subtropical) alpine zones, despite the fact that it hybridizes (very infrequently in nature) with *Dubautia*. As a rosette plant, *A. sandwicense* DC. (Figure 6.14) shows no cessation in growth, and that is demonstrated in wood anatomy of all species as well, since growth rings are absent (Figure 6.17). The rosette of *A. sandwicense* undoubtedly
Anatomy protects the apical meristem from frost by virtue of its hairs and the dense crowding of leaves. In *A. kauense* (Rock & Neal) Deg. & Deg., short trunks are formed below the rosettes, suggesting, in comparison to *A. sandwicense*, that *A. sandwicense* is constrained by frost and that *A. kauense* has been released from it by virtue of its lower elevation habitat.

The brilliant appearance of leaves in *A. sandwicense* is produced by non-glandular trichomes that are flattened in their distal portions (Figure 6.16) and highly reflective, giving the plant the name silversword. This suggests that protection from UV may be a selective factor, although trichome covers of leaves often function in reducing transpiration by serving as a windbreak or offer a moderate degree of insulation against frost. Separation of these factors presents an interesting challenge for future investigators.

The leaves of *A. sandwicense* as seen in transection (Figure 6.15) contain some of the most remarkable foliar adaptations known. *Argyroxyphium* leaves are thick, related to the innovation of three sets of bundles as opposed to the single set of bundles (as is typical in angiosperm leaves) in the related genera *Dubautia* and *Wilkesia* (Carlquist 1957, 1959a). In terms of form alone, the reduction of surface to volume ratio represents a xeromorphic adaptation. What is much more surprising, however, is the development of massive water-retaining gels in the intercellular spaces of the leaf (Carlquist 1957). This may be observed on living plants: the gels can be squeezed from a broken leaf. These gels are not without parallel in Asteraceae, for they occur in other genera of subtribe Madiinæ: *Blepharizonia*, *Hemizonia* and *Madia* (Carlquist 1959b). The leaves of the ‘greenswords’ — *A. grayanum* (Hillebr.) Degener and *A. virescens* Hillebr. — have gel storage also, as does the bog species *A. caliginis* Forbes (formerly spelt *A. caligini*), which is evidently a recent entrant into the bog habitat from a dryland ancestry. The leaves of *A. caliginis* do show some adaptation to the bog habitat in their development of more massive hydathodes near the leaf margins than occurs in *A. sandwicense*. The gels in *Argyroxyphium* represent a form of water storage, and the distribution within Madiinæ and within the plants in the annual species dramatizes this function (Carlquist 1959b). The occurrence of the gels in annual species shows that these accumulations are probably not related to frost resistance. The effectiveness of the gels in the water economy of *Argyroxyphium* leaves has been quantified by the study of Robichaux & Morse (1990) and physiological data on the functioning of leaves are compared for *A. sandwicense* and *Dubautia menziesii* by Robichaux et al. (1990).
Figures 6.14–6.18. *Argyroxyphium* habit and anatomical details. Fig. 6.14. Flowering individual of *Argyroxyphium sandwicense*, Haleakala Crater, 7 July 1966. Fig. 6.15. Leaf from *A. sandwicense*, transection, showing that most of the central portion of the leaf is filled with a gel. Fig. 6.16. Transection of hairs from leaf surface of *A. sandwicense*; distal portion of trichomes is flat in transection. Figs. 6.17, 6.18. *A. kauense* (Carlquist 2110). Fig. 6.17. Wood transection, showing that vessels are narrow and tend to grade into vasicentric tracheids. Fig. 6.18. Tangential section; bordered pits can be seen in many fibriiform cells; most of these are vasicentric tracheids, but some narrow vessels are present (ray at right).
The wood of *Argyroxyphium* (Figures 6.17, 6.18) features the presence of a few vasicentric tracheids. Because these occur in other alpine Asteraceae of the Hawaiian Islands cited above, *Dubautia menziesii* and *Tetramolopium humile*, this may not seem very remarkable until one notes that vasicentric tracheids are rare in woods of Asteraceae (Carlquist 1988). The multiseriate rays of *Argyroxyphium* wood represent relatively little-altered primary rays (pith rays), as is expected in a rosulan (*A. sandwicense*) or caulorosulan (*A. grayanum, A. kauense*) plant. Vessel diameter is less in *A. sandwicense* than in the bog species *A. caliginis* and *A. grayanum* (Carlquist 1958), indicating that even though the stem of *A. sandwicense* is thick and could be regarded as potentially capable of water storage, the wood is xeromorphic. The vessels of *A. kauense* (Fig. 6.17) are intermediate in diameter between these two extremes.

The glandular trichomes on the inflorescences of *Argyroxyphium* secrete a resin-like substance. This is probably not a mechanism for reduction of transpiration, but rather a means for deterring insect predation; it is very viscid and bitter, and often coats the epidermis of most inflorescence structures. Abundance of these secretions in the annual tarweeds shows that their presence is not related to frost resistance.

The sum of anatomical features of *Argyroxyphium* shows close and intricate adaptation to the dryland habitats of alpine Hawaii. The two bog species are held to be recent derivatives in which time has been insufficient for much change in that adaptation—either loss of xeromorphic features or introduction of mesomorphic ones. However, even in the bog species, some degree of xeromorphic adaptation may still be of positive value. In fact, on clear days in the Puu Kukui bog where these species grow, leaf heating and transpiration are very likely pronounced.

**Cushion plants**

One would like to be able to describe the nature of leaf anatomy and other anatomical characters of the cushion plants so characteristic of high elevations in the equatorial Andes (notably *Azorella* of the Apiaceae). Cushion plants are less characteristic of other tropical alpine areas, but one may see mat-like growth forms not dissimilar to cushion plants in such tropical areas as alpine New Guinea, and the adaptations of mat-like
plants in tropical alpine areas may not be far removed from those of cushion plants.

Napp-Zinn (1984, pp. 171–88) reviews the literature on leaf anatomy of Andean plants, and that literature proves to be rather considerable. However, Napp-Zinn’s tables group plants of particular Andean habitats, despite the fact that within each habitat a wide range of habits is represented. That may account for the fact that, while some generalizations concerning leaf anatomy of the Andean alpine plants are entertained by Napp-Zinn (1984), he seems to feel these generalizations do not hold. What one wants is a comparison of leaves of cushion plants of different genera similar in habit and leaf size. Alternatively, one could develop valuable understanding of ecological leaf anatomy by comparing for a particular genus, such as Azorella, species from a range of habits (including cushion plants) and habitats. When the ranges in leaf anatomy for several such genera represented in tropical alpine areas are compared, we may have an idea of anatomical modalities related to the cushion plant habitat and their significance. Ideally, one would like to see development of physiological data concomitant with study of anatomy of these plants.

References


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