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Sherwin Carlquist

Santa Barbara Botanic Garden, Santa Barbara, California

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VESTURED PITS IN *ECHIU*M (BORAGINACEAE): ISLAND WOODINESS REVISITED

SHERWIN CARLQUIST

Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, California 93105

ABSTRACT

Vestured pits are present on pits of secondary xylem vessels of all studied *Echium* species, roots as well as stems. Variations in vesturing presence do occur in the genus (across wide circular pit cavities; along margins of elliptical pit apertures; aggregated to various degrees; variously abundant), but these are difficult to define precisely and are related primarily to organography and ecology rather than to the taxonomic system. The Macaronesian species have been reported to form a single clade. Wood anatomical features other than vesturing are also closely keyed to species ecology and, in particular subclades, growth forms. Woodiness, exemplified by most species of the insular clade of *Echium*, has been claimed to have evolved as a mechanism to promote outcrossing on islands. This alleged indirect selection is questioned here. The bases for secondary woodiness on island areas are multiple and are reviewed here (lessened temperature and moisture extremes; retention of branches instead of reproducing by seed as a form of economy; lack of mammalian herbivores; superior dispersal and colonization abilities of less woody clades; ability to occupy geologically new or recently altered areas). These features may, individually and collectively, serve to increase the ability of species to become woody on islands. Vesture presence can be cited for some groups that have radiated well on Macaronesian islands (Boraginaceae, Brassicaceae) as well as on certain major land areas (*Acacia* and *Eucalyptus* on Australia all have vestured pits on vessels). Plant species can be viewed as having an umbrella of features relevant to woodiness and growth form, with thresholds in tolerance of cold, drought, etc. In an island environment, there is alleviation, moderation, and transcendence of these thresholds and restrictions so that survival of vegetative structures into the next growing season is achieved. Advantageous radiation into new growth forms is made possible by this extension of the growing season.

Key Words: adaptive radiation, Canary Islands, insular woodiness, Macaronesia, secondary woodiness

INTRODUCTION

In an earlier study of woods of *Echium* from the Canary Islands and Madeira (Carlquist 1970a), the probability that pits on *Echium* vessels are vestured was mentioned, but as workers agree, these minute structures are best studied with scanning electron microscopy (SEM). Vestured pits have since been confirmed for stems of *Echium* and certain other Boraginaceae (Miller 1977; Rabaey et al. 2010). In the present study, views of vestures not only from the outer surfaces of vessels but from inner surfaces as well have been included; the latter have not often been included in SEM studies of vestured pits. SEM exploration of *Echium* vestured pits reveals presence of vestures in roots as well as stems; vestures in roots can differ appreciably from those in stems.

The number of species included here (13) is the same as in the light microscope study (Carlquist 1970a), although the roster differs by two species. Roots and inflorescences of *E. auberianum* Webb & Berth., a high-alpine species from Tenerife with perennial roots but annual inflorescences, are included here. *Echium auberianum* is the earliest-departing lineage of the insular *Echium* clade, according to Böhle et al. (1996). One of the non-Canarian annuals, the widespread and weedy continental *E. plantagineum* L., is included. *Echium plan-*

tagineum, like many annual angiosperms, has secondary xylem. *Echium candicans*, a shrubby species, is from Madeira. The remainder of the perennial species studied here are from the Canary Islands.

The molecular tree of the entire genus *Echium* offered by Böhle et al. (1996) shows short branch length within the insular clade, indicative of a recent radiation of the insular species. It also shows that all of the *Echium* species on the Macaronesian (Atlantic) islands are descendants of a single colonization. This clade is entirely perennial and variously woody except for the annuals *E. bonnetii* Coincy and *E. pitardii* A. Chev., which are Canarian annuals. Böhle et al. (1996), although cognizant of diversity in growth form in this clade, did not consider the considerable diversity in wood anatomy (Carlquist 1970a) within the insular clade. Without reference to this diversity and to the relationships between adaptive radiation in insular echiums and their ecological preferences, Böhle et al. (1996) reached back to Wallace (1878) for an explanation. They claimed that evolution of woodiness in the island *Echium* species permits more outcrossing and production of a greater abundance of seed. Böhle et al. (1996) stated that “many differences between perennial woody habits [in the island *Echium* species] could be non-adaptive.” Thus, they cite reproductive biology as a causation of woodiness and its diversity in this clade. The occurrence of vestured pits is just one aspect of the wood anatomical diversity in *Echium*, but a review of whether selection for reproductive biology is that powerful needs re-examination in a wider context that includes ecology, physiology, and growth form. Diversity in habit, ecology, and physiology in *Echium* and other island genera seems so great that selection for a genetic system alone seems improbable.

Angiosperm groups other than *Echium* provide an informative context in this regard. Baker (1955) claimed that island colonists were advantaged by self-fertility. However, over time there is an overriding advantage of converting to an outcrossing pattern in the small population sizes that many island species have (Carlquist 1966). *Echium* could be said to exemplify both tendencies, but that genus is just one example. The outstanding example of adaptive radiation on islands is the tribe Madieae of Asteraceae, which has diversified extensively in the Californian Floristic Province; from that source, an amazing series of diversifications has occurred on the Hawaiian Islands (Carlquist et al. 2003). The Hawaiian species are, as one might expect, self-incompatible (Carlquist 1974; Carlquist et al. 2003). The mainland species, contrary to the situation in *Echium*, are also mostly self-incompatible (Clausen et al. 1945). Thus, there is no evidence that woodiness in the Hawaiian species has any role in their outcrossing, so should we accept the contrary hypothesis in the case of *Echium*? The various qualitative and quantitative manifestations of woodiness in the Hawaiian Madieae are closely correlated to ecology (Carlquist 1974), and that is true in the island *Echium* species as well (Carlquist 1970a).

The moist forests (laurel forest) of Macaronesia contain many of the tree species on those islands. Few species of *Echium* (*E. candicans* L.f., *E. pininana* Webb & Berth.) occur in the laurel forest. Most occur in the alpine and lower zones of scrub on these islands; these areas may have been moister in pre-human times than they are now. Böhle et al. (1996) designated no fewer than 21 island species of *Echium* as “trees,” but this differs from the descriptions of Bramwell and Bramwell (1974) and my own experience: perhaps only three species ever reach or exceed 2 m in height, and most individuals are much shorter. *Echium pininana* is the only species for which the designation “tree” could be claimed, but *E. pininana* is a monocarpic rosette plant that can flower during its second or third year in sunny places but later on if it grows beneath a tree canopy (original observations, based on garden cultivation). *Echium auberianum*, from the high-elevation cinder cones of the Teide caldera on Tenerife, is not, as Böhle et al. (1996) claimed, a “monocarpic herb,” but rather a plant with a woody caudex that is mostly root tissue (as in the horseradish, *Armoracia*), which annually sends up leaves and inflorescences after snow has melted. Thus, nearly all of the radiation in growth form in *Echium* has taken place outside of the laurel forests, and the wood of these *Echium* species is closely keyed to those marginally moist habitats (Carlquist 1970a), some of which are in the pathway of trade winds (Lems 1960). Lens et al. (2013) suggest a “possible link between secondary woodiness and increased drought resistance,” but the situation, as suggested in the Conclusions section of this paper, may be much more complicated.

The phylogeny of *Echium* offered by Böhle et al. (1996) proves very useful. These authors show a probable origin for the genus in circum-Mediterranean annuals. The first-diverging lineage of the insular clade is the caudex perennial *E. auberianum*, described above. Second to diverge is a clade of two species: the tall monocarpic rosette plant *E. pininana*, a rarity from the laurel forests of La Palma, and *E. wildpretii* Pearson ex Hook., also monocarpic, but a rosette plant with its growing point roughly at ground level (and thus not a “monocarpic rosette tree” as claimed by Böhle et al. 1996), much like the Hawaiian silversword, *Argyroxiphium sandwicense* DC. (Asteraceae),

which occupies a very similar habitat in the caldera of Haleakala, Maui. Although the often tall (to 3–4 m) stem of *E. pininana* is woody, the stem of *E. wildpretii* has only a relatively thin (ca. 2–4 mm) cylinder of secondary xylem (around a large central pith) at the time of flowering. The crown group of the insular *Echium* clade consists mostly of “candelabrum shrubs,” lower branches longer than upper branches, which most commonly reach about 1 m. According to Böhle et al. (1996), this crown group, with very short phyletic branch lengths, has radiated very recently, ultimately colonizing Madeira and the Cape Verde Islands. The data on vestured pits and related vessel features presented here follow the three clades shown in their phylogenetic construction. Wood data on one of the circum-Mediterranean annuals, *E. plantagineum*, are offered by way of comparison.

MATERIALS AND METHODS

The wood sections studied with SEM are mostly those prepared for the earlier survey of *Echium* wood anatomy (Carlquist 1970a). Slides prepared in that study were soaked in xylene to soften the Canada balsam so that the cover slips could be removed. The sections from the slides thus disassembled were retrieved and cleansed of Canada balsam with four changes of 60°C xylene. The sections were then dried between pairs of clean glass slides on which pressure was applied to maintain flatness. Two species were not included in the 1970 study. Portions of roots and inflorescence axes were removed from an herbarium specimen of *E. auberianum*, Carlquist 2695 (RSA-POM) from Cañada del Teide, boiled in water, and stored in 50% aqueous ethanol. Material of *E. plantagineum*, supplied by Annie’s Annuals and Perennials (Richmond, CA) and grown to maturity in my garden, was processed similarly. The portions of these two species stored in ethanol were hand sectioned with single-edged razor blades. Sections were subjected to three changes of distilled water at 60°C and dried as above. All sections were placed onto aluminum stubs, sputter-coated, and observed with a Hitachi S2600N scanning electron microscope (SEM). Voucher specimens and authors of binomials are specified in the captions. Identifications are based on Lems (1960) and Bramwell and Bramwell (1974). Useful geographic and climatic information is also contained in these references. The sequence of species and the groupings inferred follow the scheme of Böhle et al. (1996) although the number of gene sites used in that study was small and therefore the topology of their cladogram for the genus may lack robustness, and some of their species groupings may be subject to change.

RESULTS

1. *Echium auberianum* clade (Fig. 1)

The wood of the perennial root of *E. auberianum* is distinctive in that the background cells (Fig. 1A) are not thick-walled fibers as in the other species (Carlquist 1970a), but rather thin-walled fibers that very likely could be living fibers. These could account for the meristematic nature of the root of *E. auberianum*, which produces leaves and annual inflorescences at ground level. The vessels of the roots (Fig. 1A–E) are circular in outline and typically have elliptical pits as seen on the inner vessel surfaces (Fig. 1A, B). Vessel-to-vessel interfaces bear alternate oval pits, as seen from outer vessel surfaces (Fig. 1C). Pits between vessels

Fig. 1. SEM images of root (A–E) and inflorescence axis (F) of *Echium auberianum* Webb & Berth., *Carlquist 2495* (RSA-POM).—A. Oblique transverse section, showing portions of two vessels and the thin-walled nature of libriform fibers.—B–E. Longitudinal sections of root secondary xylem.—B. Luminal surface of vessel, showing vestures in the pit apertures and some helical relief on the wall surface.—C–F. Pits seen from outer surfaces of vessels.—C. Alternate pits, with moderate lateral elongation of pits; vestures are along pit aperture margins.—D. Portions of two vessels; pits are various in size and shape.—E. Scalariform and transitional pitting; density and size of vestures is varied.—F. Portion of inflorescence axis longitudinal section, protoxylem at left, metaxylem at right; vestures are lacking.

and thin-walled fibers can be pseudoscalariform or transitional (Fig. 1D, E). All of these pits are prominently vested. The vestures are at margins of pit apertures. As seen from the insides of vessels, they extend across the pit cavity (Fig. 1B) and are variously grouped.

Only primary xylem was observed in the inflorescence axes of *E. auberianum* (Fig. 1F). There is an abrupt transition from helical primary xylem vessels (Fig. 1F, at left) to scalariform primary xylem vessels (Fig. 1F, right $\frac{3}{4}$ of image). These primary xylem vessels lack vestures.

Fig. 2. SEM images of longitudinal sections of stem secondary xylem of *Echium plantagineum* L., cultivated in Santa Barbara (A) and *E. wildpretii* Pearson ex Hook. f., *Carlquist* 2498 (RSA-POM) (B–F).—A. Luminal surface of vessel; pits are small, circular.—B. Outer surface of a fiber-tracheid; pits are bordered but do not have vestures.—C. Outer surface of vessel; pit cavities are circular, densely vested towards the pit canal.—D. Luminal surface of a vessel, showing vestures densely placed along the pit aperture.—E. Luminal surface of a vessel; prominent helical thickenings are present; no vestures visible in this portion.—F. Pit cavities and apertures are elliptical rather than circular, and bear vestures along the pit apertures.

2. *Echium plantagineum*: a continental species

The continental species of *Echium*, a sister clade to the insular species (Böhle et al. 1996), are annuals or biennials with

normal cambial activity, but with, as in the case of most eudicot annuals, limited amounts of secondary xylem. There are vestured pits in the vessels of *E. plantagineum* secondary xylem (Fig. 2A).

3. *A monocarpic clade: E. wildpretii and E. pininana*

In Böhle et al. (1996) the most basal branch of the insular clade consists of *E. auberianum*, but the next branch of that clade consists of a pair of species, *E. wildpretii* and *E. pininana*. The former is an acaulescent rosette plant, the latter a markedly caulescent and rather woody but unbranched rosette plant.

The imperforate tracheary elements of *E. wildpretii* (Fig. 2B) and most other species have bordered pits that are moderately sparse and not vested, and thus are best designated as fiber-tracheids. These characteristics are associated with imperforate tracheary elements that are not active in the conductive process. The moderate figure for vessels per group in *Echium* (1.5 to 2.5) indicates this also, according to the criteria developed earlier (Carlquist 1984). In Penaeaceae, a myrtalean family with vested pits, imperforate tracheary elements have vestures and are best designated as tracheids because vestures are definitely associated with cells that are conductive (Carlquist 2017).

The vessel-to-vessel pits of *E. wildpretii*, as seen from the inner surfaces of vessels, have elongate pit apertures that may lack vestures (Fig. 3E), although vestures are present on some vessel inner surfaces (Fig. 2D). Vestures are definitely present in outer surfaces of *E. wildpretii* vessels, whether the pit cavities are circular (Fig. 2C) or elliptical (Fig. 2F).

Echium pininana (Fig. 3A–F) has vessel-to-vessel pits that are relatively large and richly vested. This vesturing is visible as seen on the inner surfaces of vessels (Fig. 3A–D) as well as on the outer surfaces (Fig. 3E–F). The pits of roots (Fig. 3A) are relatively sparsely vested. In the sample studied, pits at the base of the stem (Fig. 3B) have vestures that are branched like coralloid outgrowths of the pit aperture and adjacent cavity. Farther up the stem, one sees a phenomenon not mentioned to any appreciable extent in literature on vested pits: small vestures coat the surfaces of branches from the pit apertures of vessel-to-vessel pits (Fig. 3C–D). In secondary xylem at the base of the single inflorescence of *E. pininana*, vesturing is somewhat sparse in vessel-to-vessel pits (Fig. 3E, F). Grouping of vestures on flange-like branches of secondary wall material are abundant on some of these (Fig. 3E), but less evident on others (Fig. 3F).

4. *The crown group of insular Echium species (Fig. 4–6)*

All of the insular species of *Echium* other than *E. auberianum*, *E. wildpretii*, and *E. pininana* form a close crown group according to the phylogenetic construction of Böhle et al. (1996). All of the species of this crown group included here are shrubs that differ from each other in size and ecology and therefore also, not surprisingly, in quantitative and qualitative wood features (Carlquist 1970a). Differences in pitting and vesturing details are therefore to be expected. Of the species presented here, most are from dry regions below the laurel forests; the crown group species with the most mesic habitats are probably *E. giganteum*, from the north-facing slopes of Tenerife, and *E. candicans*, from openings in the laurel forests of Madeira. These two species have notably low values for numbers of vessels per group in the genus (1.3, 1.5), likely indicative of more mesomorphic wood (Carlquist 1984). The highest figure in the genus is 4.4 vessels per group in *E. wildpretii* (Carlquist 1970a), from alpine regions of El Teide.

The pitting of vessels of *E. onosmifolium* Webb & Berth. is distinctively elliptical as seen from inner surfaces (Fig. 4A, B). These narrow pit apertures are associated with irregularly

thickened vessels walls (Fig. 4A, B). Outer surfaces of vessels in *E. onosmifolium* reveal circular pit cavities (Fig. 4C). Grouping of vestures and attachment of vestures to platelets or flanges is evident in Fig. 4B–C.

Echium strictum L.f. vessels have notably thick walls (Fig. D). The vestures occur as attachments to pit cavity or pit canal margins (Fig. 4D–E) rather than as outgrowths of flanges. The inner surfaces of vessels in *E. strictum* do not bear helical thickenings (Fig. 4E).

Echium hierrense Webb ex Bolle vessels show irregular thickenings (Fig. 4F). The inner pit apertures are elliptical, and the vestures tend to be variously aggregated.

Echium decaisnei Webb & Berth. has some imperforate tracheary elements that may be considered tracheids or vasicentric tracheids because of wide pit borders (Fig. 5A) and presence of a few vestures (Fig. 5B). The outer surfaces of vessels of *E. decaisnei* (Fig. 5C) exhibit vestures scattered across the pit cavity—pit canal juncture.

Echium webbii Coincy (Fig. 5D–E) has elliptical pit apertures as seen from the inner surfaces of the vessels (Fig. 5D). From the outer surfaces the pit cavity—pit canal junctures bear scattered vestures.

In *E. virescens* DC., the pit apertures as seen from the inner vessel surface are very narrow, but with rounded ends (Fig. 5E). When seen from the outer vessels surface, this narrow shape is also evident (Fig. 5F). The vestures all seem attached to margins of the pit cavity, rather than grouped or adherent to flanges or branches of secondary wall material.

As seen from inside the vessels, pits of *E. leucophaeum* (H. Christ) Webb ex Sprague & Hutch. (Fig. 6A, D) are rounded in shape and crowded with vestures. Some vessels have narrower pits (Fig. 6B) in which the vestures are aggregated into coralloid branches. As seen from the outer surfaces of vessels, pits of *E. leucophaeum* have circular apertures with vestures confined to the pit canal more than to the pit cavity (Fig. 6C).

Echium giganteum L.f. (Fig. 6E) has circular pits with numerous vestures. In *E. candicans* (Fig. 6F) the pits are notably large and bear abundant vestures, which are variously interconnected and supported.

CONCLUSIONS

Vesture Patterns in Echium

1. *Imperforate tracheary elements.*—Imperforate tracheary elements in *Echium* have borders on pits, but the pits are too sparse and the borders are too small to qualify them as tracheids. Not surprisingly, these fiber-tracheids also lack vestures on pits. The sole exception observed was in *E. decaisnei*. Thus, in most *Echium* species, imperforate tracheary elements do not contribute to conductive safety, as they undoubtedly do, for example, in Penaeaceae (Carlquist 2017). Conductive safety in *Echium* is thus shifted to such xeromorphic features as narrow vessel diameter, latewood of growth rings, higher vessel density, and such foliar characters as drought-deciduousness of leaves. The presence of vestures in vessels becomes potentially important in *Echium* when comparing the genus to other Macaronesian elements.

2. *Organographic distribution of vestures.*—All vegetative organs in *Echium* have vestures on bordered pits of secondary xylem, although no vestures were observed in leaves or

Fig. 3. SEM images of luminal (A–D) and outer (E–F) faces of longitudinal sections of secondary xylem vessels of *Echium pininana* Webb & Berth., *Carlquist 2730* (RSA-POM).—A. Root. Vestures are grouped irregularly.—B. Lower stem. Vestures are grouped into fascicles.—C–D. Mid-level of stem.—C. Vestures are densely aggregated into secondary wall portions that traverse the oval pit aperture.—D. Vestures are attached to irregular portions of secondary wall material attached to pit aperture margins.—E–F. Pits from stem just below an inflorescence axis.—E. Vestures attached irregularly along the margins of a circular pit cavity.—F. Vestures mostly not attached to each other, along the cavity of a circular pit.

inflorescence axes. Although vestures are more abundant in pits of vessels in stems, wood of all roots observed also has some vestures, although they are less abundant than those of stems.

3. Diversity in vesture positioning.—Recent work on vestured pits has, logically, explored whether vestures are present or ab-

sent in particular families and genera (Jansen et al. 1998, 2001). A few workers (Bailey 1933; van Vliet 1978) have noticed varied configurations in the way that vestures are aggregated or attached to pits, or noted the presence of vestures not merely within pits, but on luminal vessel walls (Meylan and Butterfield 1978; Carlquist 1982, 1989, 2016, 2017), where vestures

Fig. 4. SEM images of luminal surfaces (A–B, E–F), outer vessel surface (C), and vessel wall in sectional view (D) from longitudinal sections of stem secondary xylem of *Echium* species.—A–C. *Echium onosmifolium* Webb & Berth., *Carlquist 2584* (RSA-POM).—A. Portion of surface to show widely elliptical nature of pits and surface sculpture of lumen surface.—B. Vestures are aggregated on supporting structures.—C. Circular pit aperture; vestures are mostly aggregated on plate-like structures.—D–E. *Echium strictum* L.f., *Carlquist 2511* (RSA-POM).—D. Vestures (arrow) adhere to the transition between the pit canal and the pit cavity.—E. Vestures are both single and aggregated into small groups.—F. *Echium hierrense* Webb, *Carlquist 4343* (RSA-POM). Vessel wall lightly textured or striate, vestures are crowded in the pit apertures.

extend beyond pit apertures in various configurations. Much more work is needed in angiosperms as a whole, but some kinds of diversity within *Echium* are evident from the present study. The diversity is largely correlated with pit shape and vessel wall thickness.

Narrow elliptical pit apertures are associated with vestures along the edges of the pit aperture facing the vessel lumen (as in *E. auberianum*, Fig. 1A–E, and the metaxylem of *E. wildpretii*, Fig. 2B–F). Adherence of vestures to the pit aperture edges suffices to position the vesture tips on either side

Fig. 5. SEM images of outer surfaces (A, C, E, G) and luminal surfaces (B, D, F) from longitudinal sections of stem secondary xylem of *Echium* species.—A–C. *Echium decaisnei* Webb, *Carlquist* 2548 (RSA-POM).—A, B. Bordered pit from an imperforate tracheary element.—A. Vestures absent or nearly so.—B. Vestures present in the narrow pit aperture.—C. Vessel wall. Circular pit membrane, showing vestures across the transition between pit cavity and pit canal, some attached in fascicles.—D–E. *Echium webbii* Coincy, *Carlquist* 4342 (RSA-POM).—D. Elliptical pit aperture, within which vesture bases may be seen.—E. Pit cavity–pit canal transition bears groupings of vestures.—F–G. *Echium virescens* DC., *Carlquist* 4346 (RSA-POM).—F. Narrowly elliptical pit aperture; vestures almost occlude pit aperture.—G. Vestures densely placed in pit cavity–pit canal transition.

of the pit aperture sufficiently far across the pit aperture for the vestures to be in the path of the conductive stream through the pit. Thus we can connect the positioning of vestures in narrow pits with the idea that these globose structures func-

tion, as discussed below, in creating safety in the conductive process.

If the vessel wall is thick, vestures may form on the pit aperture margins—not facing the vessel but rather facing the pit cavity

Fig. 6. SEM images of luminal surfaces (A, B, D) and outer surfaces (C, E, F) from longitudinal sections of stem secondary xylem of *Echium* species.—A–D. *Echium leucophaeum*, Carlquist 2517 (RSA-POM).—A portion of wall to show vestures at the same level as the lumen surface.—B. Two pits in which vestures branch in coraloid fashion.—C. Vestures aggregated in pit cavity–pit canal transition.—D. Vestures much aggregated.—E. *Echium giganteum* L.f., Carlquist 2539 (RSA-POM). Small pit; most vestures grouped.—F. *Echium candicans* L.f., Carlquist 2647 (RSA-POM). Most vestures attached to structures that extend from the pit aperture margin.

(Fig. 4D, arrow). In this case, the channel (sometimes termed “pit channel” in wood anatomical literature) is free from vestures, but all vestures face the pit cavity (yet do not touch the pit membrane).

Sometimes in elliptical pits, the vestures are conjoined as coraloid fascicles (Fig. 3B). This configuration is not unique

to *Echium*, but has been described in Myrtales (van Vliet 1978) and Brassicaceae (Carlquist 2016). One can think of it as protracted growth of secondary wall material at a few sites so that the vesture tips are numerous and can potentially be involved in contacting the water within a pit in a living plant.

A third modality of vesture occurrence can be seen in pit cavities that are circular rather than elliptical. In these, a number of flanges of secondary wall of various dimensions traverse the pit cavity and bear vestures on their surfaces (Fig. 3C, 4C). Sometimes, the flanges appear formed of aggregated vestures, suggesting a kind of ontogenetic sequence in formation of an ever-increasing number of globular vesture tips before the vessel is mature and is added to the conductive xylem (Fig. 3D). In this view, the sparser pits in secondary xylem just below the inflorescence in *E. pininana* (Fig. 4E, F) would represent a foreshortened ontogeny. There is as yet no evidence for this speculation, but these various appearances need to be studied ontogenetically (by means of transmission electron microscopy) to determine how vestures grow before vessel maturation. Pits with the greatest number and density of vestures are found in *E. candicans*, *E. onosmifolium*, and *E. pininana*. Annual species of *Echium*, judging from the small sample, have vestured pits that are small and have fewer vestures.

Vestures as an Evolutionary Advantage

The occurrence of vestured pits in angiosperms is clearly not random (Jansen et al. 2001). Jansen et al. (2004) claimed that vestures are more common in warm, subtropical climates. If we look at key genera and key localities, the picture changes. We see that some systematic groupings that have vestured pits, like *Echium* (which is not in warm subtropical climates) have been able to radiate spectacularly. One remarkable example, omitted by Jansen et al. (2004) is Brassicaceae (3710 species), all studied species of which have vestured pits (Carlquist 2016). Brassicaceae are chiefly boreal to cold temperate; in fact, the family is known in cultivation for frost resistance (Bouwkamp 1969). Frozen ground, for species with shallow roots (such as many Brassicaceae), is physiologically arid. This may help us to understand how alpine regions on the Canary Islands and Madeira, as well as dry lowlands, support numerous Brassicaceae. All of the Fabaceae in the Canary Islands (e.g., *Spartocytisus*) have vestured pits.

If we look at key angiosperm families and genera, we see that presence of vestures goes hand in hand with radiation into dry and geologically new habitats, followed by speciation in which some non-xeric habitats are occupied. The most spectacular of these is perhaps *Eucalyptus* in Australia. The other major tree genus in Australia, *Acacia* s. l. (Fabaceae), also has vestured pits (Evans et al. 2006). Other Myrtaceae (*Leptospermum*, *Callistemon*, *Verticordia*) in Australia also have vestured pits (Jansen et al. 2008) and are prominent in the Australian flora.

In the Hawaiian Islands, the two major tree genera are *Acacia* (Fabaceae) and *Metrosideros* (Myrtaceae). Both of these colonize dry situations (including new lava) well, but also penetrate into some moister situations. Three genera that are among the most pervasive woody weeds in Hawaii also have vestured pits: *Leucaena* (Fabaceae), *Miconia* (Melastomataceae), and *Psidium* (Myrtaceae).

The physiological significance of vesturing and other forms of sculpturing on vessel walls has been hypothesized to be prevention of embolism formation—and perhaps reversal of embolisms (Carlquist 1983). This hypothesis is supported by the data on wettability of textured inner vessel surfaces (Kohonen 2006; Kohonen and Helland 2009) and by experimental evidence showing the patchiness of wettability on vessel surfaces (McCully et al.

2014). A review of possible functions of vestured pits is offered by Jansen et al. (2003).

Bases for Insular Woodiness

In earlier decades, woodiness of genera such as *Echium*, *Senecio*, or *Lobelia* on island areas (or equatorial peaks, the “sky islands”) was interpreted as a relictual feature, and that the less woody species on continental areas were derived from them (Bramwell 1972). Genera such as *Plantago* (Carlquist 1970b) and others woodier on islands than elsewhere (Carlquist 1974) were shown rather decisively to be secondarily woody; the Hawaiian flora, not well known to Europeans, proved important in this regard. The wood of secondarily woody species on islands is different in its protracted juvenilism (Carlquist 1962). The construction of phylogenies based on molecular data, such as that of Böhle et al. on *Echium*, has confirmed the existence of secondary woodiness in island representatives of predominantly herbaceous genera. Acceptance of insular woodiness, however, did not lead to a uniform explanation. Böhle et al. (1996) considered that woodiness in the insular species of *Echium* is “non-adaptive” in itself, and is a mere byproduct of selection for greater outcrossing and greater seed production, reviving an idea of Wallace (1878). The concept of Böhle et al. (1996) that woodiness in *Echium* is merely a byproduct of selection for increased seed production (by virtue of longevity) and greater outcrossing (continental species are self-fertile whereas insular *Echiums* are self-sterile), is improbable on the basis of the great variety in growth form, length of flowering season, and other diversity within the genus. Members of the silversword complex on the Hawaiian Islands (*Argyroxiphium*, *Dubautia*, and *Wilkesia* of Asteraceae, tribe Madieae) are all self-sterile and mostly appreciably woody, but the continental Madieae from which this complex is derived are also self-sterile (Clausen et al. 1945), counter to the *Echium* pattern. Lens et al. (2013) entertained a “possible link between secondary woodiness and increased drought resistance, based on the Canarian flora.” Certainly some areas of the Canary Islands do appear dry, although the pressure of several centuries of grazing by introduced herbivores undoubtedly makes the Canarian landscape look more desolate today than it was in pre-human times, when uplands as well as north-facing Canarian lowlands in the path of moist trade winds (Lems 1960) were very likely more heavily vegetated. “Insular woodiness” in the Hawaiian flora is mainly restricted to the wet forest (lobelioids, Goodeniaceae), and is least evident in dry lowlands or alpine areas.

Perhaps the most obvious reason for insular woodiness of genera such as *Echium* or *Plantago* is a kind of biological economy. Survival as seeds or even as a ground-level caudex every year means that branches leading to the production of leaves, necessary antecedents for flowering and seed production, must die every year, wasting an investment of photosynthates. If branches can be perennial, continued growth can increase the height and mass of an individual plant, thereby resulting in habitat occupancies and growth forms unavailable to an annual. Greater seed production per individual plant can also be achieved, although this may or may not be greater than a seed output produced by a smaller group of individuals that are larger and longer-lived.

Other reasons offered for insular woodiness have been cited earlier (Carlquist 1974). Release from frost by mild temperature regimens related to oceanic influences permits a year-long potential growing season (except at upper elevations). Island ar-

eas reasonably close to the shoreline often experience increased humidity, resulting in larger shrub size and larger leaves, as on the Californian Channel Islands. Freedom from browsing, trampling, and uprooting by mammalian herbivores can be cited on oceanic islands devoid of mammals in pre-human times. "High Islands" like the Hawaiian or Juan Fernandez Islands offer ecology suitable for forest trees (as evidenced by their many tree weeds), but continental forest trees often have larger or less dispersible fruits and seeds, whereas less woody groups (Asteraceae) excel at long-distance dispersal and colonization of volcanic islands. Geological newness and instability may also provide some colonization opportunities, and may help explain woodiness of some genera in areas with minimal frost such as cismontane California (*Dendromecon*, *Eriogonum*, *Senecio*, *Haplopappus*) and the Andes (*Bocconia*, *Coriaria*, *Fuchsia*) as well as on insular areas.

One feature that is difficult to quantify, and therefore difficult to demonstrate, is the ability of many angiosperms to adapt to dry seasons, whereas adaptation to winter freezing is more difficult. One series of examples can be found in equatorial alpine floras, such as those of the East African volcanoes or the upper elevations of New Guinea, where one can see temperate genera of Asteraceae (*Senecio*), Campanulaceae (subfamily Lobelioideae), Gentianaceae (*Gentiana*), Plantaginaceae (*Plantago*), and Ranunculaceae (*Ranunculus*). On such "sky islands" on the other hand, there are no derivatives of the tropical genera one sees at lower elevations on these mountains. In other words, long-distance dispersal of plants suited to moderate amounts of frost at night (mostly North Temperate genera) is accomplished much more easily than adaptation to cold by any of the downslope tropical genera.

Release from Continental Restrictions as an Umbrella Explanation for Insular Woodiness

One can hypothesize, after reviewing the numerous cases of secondary woodiness in genera and secondary woodiness on islands in particular, that more than one causal scenario exists. Different genera and species can have different stories. However, as an umbrella explanation, one can consider that plants with enough resistance to drought, cold, and other factors limiting speciation on continental islands can colonize and, thanks to a longer (often year-long) and milder potential growing season, develop greater vegetative mass and radiate into growth forms and habitats they do not occupy on continental areas. We need to compare island and continental representatives of particular clades, and just as important as understanding why woodiness occurs on islands is understanding what circumstances favor annuals (or perennials in which branches die back to the ground at the end of a growth season) on continental areas. Surviving primarily in the form of seeds, with attendant sacrifice of vegetative apparatus, is held to be non-economical and not a pathway toward radiation in size or growth form, as mentioned above. In extreme cases, as in the Mojave Desert of California, annuals may go for many years without germinating, periods of time that perennials and woody shrubs often cannot tolerate without losing parts of a plant or dying. Annuals have the potential advantage of germinating only in years when seeds can be produced, and growing more and more abundantly in exceptionally good years, thus expanding the seed bank maximally. However, the range of adaptations within annuals is limited. How can they

escape these limitations and shift into producing vegetative mass that is not sacrificed annually?

The preceding section detailing possible explanations for insular woodiness mentions extremes of temperature, moisture, geological/ecological opportunity, herbivore pressure, growing season length, and saturation by species richness (harmony/disharmony). The lessening of one or more of these extremes is considered essential for secondary woodiness to occur. The nature of the island habitat permits alleviation of the extremes, and for a given species, that alleviation makes the difference between retaining the original habit versus expanding into woodier growth forms. Vested pits in *Echium*, for example, might permit extension of the growing season and survival of branches into the following year if just enough moderation in moisture and temperature extremes were to occur. In another group of plants, say Crassulaceae, another tool for surviving dry periods (Crassulacean acid metabolism) might become effective on the Canaries to a degree it could not on continental areas, and enough geologically open areas in various ecological niches on the Canaries might permit speciation of a genus (*Aeonium*) to an extent not possible on a continental area. Unraveling each story is sufficiently complex that we may wish for simpler thoroughgoing explanations instead of umbrella explanations, but just as there are many species on a given island, each has particular factors limiting its expansion and we should not expect all species to have the same story. For some clades, a combination of extremes may be alleviated: frost, absence of herbivores, and drought, for example. Plants can be said to have tolerance levels for how many leaves must be lost, how many branches can be sacrificed, without jeopardizing survival and adding to the plant body. We can imagine that on continental areas, *Echium* species are, for example, resistant to drought, perhaps by virtue of having vested pits. Continental conditions, however, have extremes of drought that would not permit these species to persist through the driest months. On an island area, a moderate increase in moisture would permit them to survive the dry season, forming perennial growth forms, the descendants of which could radiate into diverse species.

Possible Examples of the "Alleviation of Continental Restrictions" Umbrella Hypothesis in the Canarian Flora

The mechanisms for tolerating extremes—extremes that are alleviated in island situations—may be difficult to catalogue, but below is an incomplete and introductory attempt to do so.

1. Drought deciduousness: this includes not merely loss of leaves during a dry season, but formation of smaller leaves during drier months: Asteraceae (*Argyranthemum*), Boraginaceae (*Echium*), Brassicaceae (*Descurainia*), Caryophyllaceae, Lamiaceae, Malvaceae
2. Vested pits: asclepioid Apocynaceae, Boraginaceae (*Echium*), Brassicaceae (possibly all), Cistaceae, Fabaceae (Jansen et al. 1998, 2001)
3. Succulence: asclepioid Apocynaceae (*Ceropegia*), Asteraceae (*Sonchus*), Crassulaceae, Euphorbiaceae.
4. Broom habit (renewal buds at ground level, flowering branches annual or short-lived perennial, but caudex and roots perennial): Boraginaceae (*Echium auberianum*), Brassicaceae, Caryophyllaceae, Lamiaceae.

5. Dense covering of leaves by hairs that may provide a boundary layer reducing transpiration: Asteraceae, Brassicaceae, Caryophyllaceae, Lamiaceae, Solanaceae.
6. Ability to form narrow vessels, more numerous per square mm of wood transection: Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Lamiaceae.

If we view each example that likely represents increased secondary woodiness on an island area individually, we may better be able to see which features of, and to what extent, alleviation of continental restrictions on growth forms has probably happened. Genera are not uniform in this respect. *Echium* has shown different adaptations in different species. By allowing *Echium pininana* to naturalize in my garden since 1968, I have been able to see that plants in full sun flower within three years, but in even moderate amounts of shade, they remain vegetative for much longer periods of time. Perhaps unexpectedly, during a series of drought years (2001–2016) very few plants flowered, although few died. Natural recruitment of at least some individuals has occurred following rains every year. Observing plants of this species over a period of almost 50 years has permitted observations of responses to varied climatic conditions from one year to another. This suggests that longitudinal observations may be as important as uniform garden conditions in studying the capabilities of a species. The plants naturalized after their initial planting of seeds. Growth of a range of *Echium* species under uniform garden conditions in Claremont, California, where several degrees of winter frost occur, showed that some lowland species were killed, whereas upland species survived (Carlquist 1974). Such observations and experiments can lead to controlled-environment studies, such as those done on sugar beets (Snyder and Wittwer 1959) and other commercial species, in which flowering is delayed or prevented and degrees of stem elongation are produced. Such tests will doubtless help us take the next steps in understanding how insular woodiness occurs. Much is known about change in growth form and woodiness in commercially important plants: we need to extend these findings to island plants.

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