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ANATOMICAL DIVERSITY IN ROOTS OF SEVEN SPECIES
OF *ABRONIA* FROM CALIFORNIA AND
ITS ECOLOGICAL IMPLICATIONS

Janet S. Webster and Ruth C. Wilson

Introduction

Diversity in the roots of *Abronia* Juss. species (Nyctaginaceae) may provide clues to the impact of ecological conditions on the evolution of mechanical and conductive tissues in these organs. This study explores the possibility that the root-soil interface, a variable environment with differentially supportive and water-holding capacities, effectively contributes to the evolution of fibers and vessel elements in roots. Structureless, unstable soils are predicted to place added physical pressure on plants to produce "self-supportive" or soil-stabilizing structures in what is in effect a "terrestrially fluid" environment. Therefore, less stable soils should induce structural modifications in roots in response to these physical pressures coupled with the interplay between plant habit and the habitat in general.

Adaptive modifications in root anatomy as correlated with habit and habitat are hypothesized here for each of seven *Abronia* species; *A. alpina* Bdg., *A. nana* Wats ssp. *covillei* (Heimerl.) Munz, *A. turbinata* Torr., *A. villosa* S. Wats., *A. pogonantha* Heimerl., *A. maritima* Nutt. ex Wats., and *A. latifolia* Eschs. These species occur in sandy soils distributed across diverse ecological habitats; montane, desert, and coastal (Wilson 1972). Soils associated with five of these species were studied in detail (Webster 1979) and reported to be of similar texture, pH, and low organic content regardless of their geographic region.

Materials and Methods

Habit and habitat.—Sample specimens were collected and identified (according to Munz 1974) by Jan Webster and Ruth Wilson from several populations (Webster 1979) of each of five *Abronia* species during the spring and early summer of 1978. In addition, materials of *A. turbinata* (collected spring, 1968, by Wilson) and *A. alpina* (collected summer, 1969, by Wilson) were available as pickled specimens.

Voucher specimens for this study have been deposited at the California State College, San Bernardino, herbarium unless otherwise indicated for the following: montane species, *A. alpina* (1296 extremely rare from Ramshaw Meadows, Tulare Co., deposited at the Rancho Santa Ana Botanic Garden, Claremont, California), *A. nana* ssp. *covillei* (0045 from the north shore of

Big Bear Lake, San Bernardino Co.) and *A. turbinata* (1162 from Deadman's Summit Mono Lake, Mono Co.); desert species, *A. villosa* (0002 from Palm Springs, Riverside Co.) and *A. pogonantha* (0031 from east of Palmdale, Los Angeles Co.); and coastal species, *A. maritima* (0051 from San Diego, San Diego Co.) and *A. latifolia* (0059 from Oso Flaco Beach, San Luis Obispo Co.).

Photographs and illustrations of the habit and habitats of these species may be found in the works of Purer (1936), Tillett (1959, 1967), Wilson (1970, 1972, 1976), Helm (1978), and Webster (1979).

Stems of these species tend to develop into prostrate branching networks varying in length among the species, e.g., rarely exceeding 0.2 m in *A. alpina* and *A. nana* ssp. *covillei*, usually measuring less than 0.5 m in *A. turbinata* and *A. pogonantha*, generally averaging 1 m in *A. villosa*, and frequently exceeding 1.5 m in *A. maritima* and *A. latifolia*.

Abronia alpina and *A. nana* ssp. *covillei* develop compact perennial mats. Individuals of *A. turbinata* may be annual or perennial, prostrate or erect in habit, and at the desert edge or in the montane forest. Individuals studied were erect perennials from montane populations. *Abronia villosa*, a widely distributed desert annual, persists well into the summer when water is available. *Abronia pogonantha*, a short-lived desert annual, develops ascending to erect branches in contrast to the prostrate habit of *A. villosa*. *Abronia maritima* and *A. latifolia* are perennials from coastal strand and dune habitats. Vegetative resprouting from buried *A. latifolia* stems and roots was observed as a common occurrence in populations from Oso Flaco Beach, California, and from the Oregon coast.

Because loose soils in preferred *Abronia* habitats exert little resistance on root development, tortuous root morphology was not evident among the roots collected, with the exceptions of *A. alpina* and *A. nana* ssp. *covillei*. The highly compressed, accordionlike appearance of *A. alpina* roots may reflect the physical pressures of frost heaving present in alpine habitats.

Short (less than 0.25 m), virtually unbranched roots of *A. alpina*, *A. turbinata*, and *A. pogonantha* were readily extracted from their loose soils, whereas the somewhat longer branched roots of *A. nana* ssp. *covillei* were difficult to collect because of rocky inclusions in their soil. Roots of *A. villosa*, *A. maritima*, and *A. latifolia* were difficult to collect in their entirety simply because of their length. Extensive root systems, measuring up to 2.5 m, were recorded for *A. maritima* and *A. latifolia*. Roots measuring up to 10 cm in diameter were collected from *A. latifolia* populations located in moist protected habitats within the middune range of this species.

Root tissue preparation.—Root specimens were fixed at the time of collection in FAA. For histological analyses, root segments were cut from roots about 1 cm below the apparent stem-root transitional zone (Webster 1979). These tissues were dehydrated in a standard TBA series, embedded in paraffin, sectioned, and stained with safranin O and fast green (Johansen

Fig. 1. Representation of 0.25- and 0.20-mm grids from the improved Neubauer counting chamber overlayed on a root transection showing quadrat locations for inner and outer root regions.

1940). The segment directly below the first segment was macerated in Jeffery's fluid and stained with safranin O.

Quantitative evaluation of fibers and vessel elements.—Length and width measurements were taken at the longest and widest dimensions of fibers and vessel elements from a minimum of 20 cells for each sample specimen as macerated materials allowed.

For the quantitative evaluation of root diversity associated with anomalous vascular growth, two growth regions were recognized, an inner central region and an outer peripheral region. Five quadrats, one inner and four outer (Fig. 1) were evaluated for each root specimen. Fiber, vessel element, and crystal counts were taken from root transections overlayed with an improved Neubauer hemacytometer counting chamber (Fig. 1). Quadrat size was adjusted in proportion to the diameter of each root specimen evaluated (Webster 1979).

Total numbers for fibers, vessel elements, and crystals were recorded for each quadrat, converted to number per mm^2 , and reported as the mean number per mm^2 for each species. These means became the basis for T-tests and calculated ratios and indices.

Indices of vulnerability and mesomorphy were calculated and evaluated after Calquist (1977a, 1977b):

$$\text{vulnerability} = \frac{\text{vessel-element width in } \mu\text{m}}{\text{vessel number per mm squared}}$$

$$\text{and mesomorphy} = \frac{\text{vessel-element length} \times \text{vessel width } \mu\text{m}}{\text{vessel number per mm squared}}.$$

Figs. 2-9. *Abronia* root tissues and cell types for six species from California. Central portions of the root (Fig. 2-7) are positioned toward the middle of the page. Transections enlarged to 1,000 μ m scale. Macerated tissues (Fig. 8-9) enlarged to 500 μ m scale.—2. *Abronia nana* ssp. *covillei*.—3. *Abronia turbinata*.—4. *Abronia villosa*.—5. *Abronia pogonantha*.—6. *Abronia maritima*.—7. *Abronia latifolia*.—8. *Abronia maritima*.—9. *Abronia latifolia*.

Values for these indices were converted to relative percents vulnerability and xeromorphy (100 percent minus relative percent mesomorphy) by setting the highest value in each case at 100 percent and arranging all other values as percentages of the highest value.

Species abbreviations used in Tables and Figures in this paper are as follows: *A. alpina* (alp), *A. nana* ssp. *covillei* (nan), *A. turbinata* (tur), *A. villosa* (vil), *A. pogonantha* (pog), *A. maritima* (mar) and *A. latifolia* (lat).

Anatomical Descriptions

Tissue patterns.—Although secondary anomalous growth from multiple cambia compounds the problem of tissue and cell analysis, distinctive patterns are evident for each species of *Abronia* studied (Fig. 2–7).

Libriform fibers and vessel elements typical of the species of *Abronia* are represented by *A. maritima* and *A. latifolia* macerated tissues (Fig. 8–9). Simple perforated transverse end walls characterized the vessel elements of the species studied. Some oblique, tailed vessels were observed in *A. villosa* macerated tissues. Within each successive band of differentiation, vessel elements range from narrow cells with spiral or helical secondary wall thickenings, to wider elements with scalariform to nearly circular, alternate lateral wall pitting (Fig. 10–23).

In younger, relatively undifferentiated portions of *Abronia* roots new bundle sites are seen as clusters of four or five vessels scattered in the ground parenchyma around the central vascular region. With each successive concentric band fewer and fewer vessels are seen. In older regions of the same root the expansion of these sites is evidenced by the presence of additional vascular bundles and differentiated cell types. Each newly differentiating region produces bundles of vessel elements and phloem components, parenchyma cells, and in some species bands of fibers (Fig. 2–7, 10–23). Elongated, often lignified axial parenchyma cells appear to replace fibers in the roots of the montane species.

The absence of identifiable libriform fibers and the tendency for vessel differentiation predominantly along radial planes rather than along tangential planes in the roots of montane species (Fig. 2, 3, 10–15) set these species apart from *Abronia* species studied from other habitats (Fig. 4–7, 16–23). This radial expansion leads to the intrusion of products from one cambial layer into another. These “intrusive bundles” are most evident in *A. alpina* and *A. nana* ssp. *covillei* (Fig. 2) and less evident in *A. turbinata* (Fig. 3).

Concentric patterns of vascular tissue without the intrusion of the successive layers are evident in roots of desert and coastal species (Fig. 4–7). Bundles in these species differentiate vessels and fibers predominantly along tangential planes and to a lesser degree along radial planes. Fiber bands associated with each cambial layer are especially evident in *A. villosa* (Fig.

Figs. 10–23. *Abronia* root transections, even numbers, and near median tangential sections, odd numbers, from seven California species detailing vascular bundles, fibers, and vessel elements. Outer edges of the roots are positioned to the left. All figures are enlarged to the 500 μm scale.—10–11. *Abronia alpina*.—12–13. *Abronia nana* ssp. *covillei*.—14–15. *Abronia turbinata*.—16–17. *Abronia villosa*.—18–19. *Abronia pogonantha*.—20–21. *Abronia maritima*.—22–23. *Abronia latifolia*.

4) and *A. maritima* (Fig. 6) roots. Of special note are the wide bands of fibers developed at the outer edge of *A. pogonantha* (Fig. 5) roots. By contrast, roots of *A. latifolia* develop only a few fibers in their central, primary regions and little or no fibrous tissue in their outer regions. Vascular bundles of *A. latifolia* are separated widely by storage parenchyma both radially and tangentially (Fig. 7).

Figs. 10-23. Continued.

Table 1. Arithmetic means and ratios for anatomical characters of roots from seven species of *Abronia* from California.

Anatomical characters	Species ^a and habitat group						
	Montane			Desert		Coastal	
	alp	nan	tur	vil	pog	mar	lat
MEAN VALUES							
Vessel elements							
width (μm)	21.0	23.0	38.0	86.0	56.0	90.0	77.0
length (μm)	107.0	144.0	108.0	148.0	147.0	153.0	166.0
Vessel no./mm sq.							
inner region							
small	226.8	121.8	89.7	167.0	178.9	43.2	54.2
large	58.9	67.8	12.9	106.2	120.1	30.4	21.0
small + large	285.8	189.6	102.7	273.5	298.9	37.6	75.3
outer region							
small	59.8	53.9	36.0	64.2	88.6	23.8	2.4
large	24.9	29.4	10.0	52.8	45.4	15.1	1.5
small + large	84.7	85.4	46.0	117.1	134.0	38.9	3.9
Fiber size							
width (μm)	— ^b	—	—	20.0	20.0	18.0	19.0
length (μm)	—	—	—	397.0	339.0	400.0	348.0
Fiber no./mm sq.							
inner region	—	—	—	102.6	—	219.6	14.8
outer region	—	—	—	156.4	396.6	438.6	—
Crystals no./mm sq.							
inner region	26.4	24.5	6.1	16.9	13.6	11.8	6.1
outer region	40.1	49.6	9.9	22.6	11.1	16.8	4.9
RATIOS							
Fiber/vessel element (length)	—	—	—	2.7	2.3	2.6	2.1
Vulnerability	0.20	0.24	0.73	0.64	0.37	2.14	6.42
Mesomorphy	21.0	34.0	79.0	95.0	54.0	328.0	1065.0

^a Key to species abbreviations see Materials and Methods.^b — = Fibers absent.

Lateral roots appear to develop only from the primary pericycle. These lateral roots grow intrusively and interrupt tissue patterns in these areas.

Raphides develop in parenchyma cells, in inner and outer regions of the roots. At this time, no consistent patterns can be associated with their deposition or correlated with species habitat.

Quantitative evaluation of fibers and vessel elements.—Arithmetic means for values from fiber, vessel element, and crystal measurements and counts are presented in Table 1. Interspecific T-test comparisons of these means

Figs. 24–25. Quantitative evaluation of fiber and vessel-element parameters from seven species of *Abronia* correlated with habitat.—24. Mean number per mm² for the total functional root unit based on data collected from both outer and inner root transection regions shown in Table 1.—25. Relative percent xeromorphy and vulnerability contrasted for each of seven *Abronia* species from California.

show fewer significant differences at the 99% level among species from the same habitat than among species from different habitats. Species from different habitat groups differed by at least 75% of the vessel element characters. This suggests functional divergence and convergence in response to ecological conditions.

Abronia alpina differed in as few as 12.5 percent of the characters when compared with *A. nana* ssp. *covillei*, and in as many as 87.5 percent when compared to either *A. maritima* or *A. latifolia*. *Abronia turbinata* was least like the other montane species because of its tendency to produce succulent roots. *Abronia pogonantha* and *A. latifolia* represent extremes in both habit and habitat. They differed in 100 percent of the vessel element characters measured.

Figure 24 shows trends correlated with habitat groups for the increase or decrease in number per mm² of mechanical and conductive tissues. If fibers and vessel elements are considered together as contributing to support, then total support tissue is seen to increase from *A. latifolia* to *A. turbinata* to *A. nana* ssp. *covillei* to *A. alpina* to *A. villosa* to *A. maritima* and to *A. pogonantha*, respectively. Fibers are distributed to the outer regions in bands in *A. pogonantha* roots (Table 1).

The number of vessels per mm² is consistently higher in primary vascular tissue, inner region, than in secondary tissues produced by successive cambia. This reflects the presence of parenchyma from primary ground tissue and the addition of axial parenchyma associated with differentiating bundles. Numbers of vessels are seen to be higher in the species from the more xeric habitats, montane and desert, and lower in the species from the more mesic habitats, coastal (Table 1 and Fig. 24).

Vessel elements are shorter and narrower (about 1/3) in montane species than in coastal species (Table 1).

Fiber to vessel-element length ratios (Table 1) appear to fall close to values reported (2.6: Carlquist 1975, p. 141) for woods from specialized dicotyledons with simple perforation plates and libriform fibers.

Ratios of vulnerability and mesomorphy (Table 1) and percent xeromorphy and vulnerability (Fig. 25) indicate that montane species, alpine perennials in particular, show the highest degree of xeromorphy and the lowest vulnerability. Habit must be considered in the evaluation of any anatomical digressions from what might be predicted for desert annuals. Because these annuals grow in the least xeric months of the desert cycle, they show higher vulnerability and higher mesomorphy (Table 1) than the alpine species, yet still more xeromorphy than the coastal species (Fig. 25). Clearly, vulnerability and mesomorphy (Table 1) increase in species from dry, high-elevation alpine habitats to yellow-pine forest and desert habitats to coastal habitats, respectively.

Ecological Implications

That wood anatomy can be important in the analysis of how a group adapts to various ecological situations, and which factors, e.g., habit, rainfall, temperature, or soil are most influential in inducing changes in wood has been clearly exemplified by the studies of Carlquist (1966, 1975, 1977a, 1977b to cite only a few). Therefore, the hypothesis that anatomical modifications can be correlated with habitat, is of special interest when applied to roots (traditionally considered conservative in their evolution) of species from a single genus distributed across diverse ecological habitats.

Trends shown by values derived from the study of root anatomy in *Abronia* species are not unlike those discovered by Carlquist (cited above) for the

woody stems of numerous plants with different habits from different habitats.

Because of the cortical origin of anomalous cambia and differentiation of axial parenchyma from these cambia, groups of vessel elements in *Abronia* roots are separated by bands of parenchyma. Nevertheless numbers of vessels compare well with those from woods with normal cambia (Compositae: Carlquist 1966) and with averages from world flora comparisons (Carlquist 1977b, Table 6). Carlquist (1977b) reports that annuals representative of the world flora have wider ($61\ \mu\text{m}$) and shorter ($186\ \mu\text{m}$) vessel elements with a vulnerability (V) of 0.38 while desert shrubs ($29\ \mu\text{m}$ wide $\times$ $218\ \mu\text{m}$ long with $V = 0.08$) and arctic shrubs ($27\ \mu\text{m}$ wide $\times$ $245\ \mu\text{m}$ long with $V = 0.1$) tend to be narrower and longer. Stem succulents were reported to have vessel elements that were $72\ \mu\text{m}$ wide $\times$ $259\ \mu\text{m}$ long and $V = 1.33$. The parallels in *Abronia* species are evident, e.g., alpine species ($21\ \mu\text{m}$ wide $\times$ $107\ \mu\text{m}$ long with $V = 0.21$) and desert species which are annuals (56 – $86\ \mu\text{m}$ wide $\times$ 147 – $148\ \mu\text{m}$ long with $V = 0.54$ – 0.95 for *A. pogonantha* and *A. villosa* respectively). Succulence is seen in *A. turbinata* among the montane species and is striking in *A. latifolia* ($77\ \mu\text{m}$ wide $\times$ $166\ \mu\text{m}$ long with $V = 6.42$). Although *A. maritima* is located on the coast, its position on fore-dunes undoubtedly accounts for its increased fiber production and thus reduced number of vessels per mm^2 .

If values of vulnerability of 0.30 and below are considered extremely xeromorphic and represent plants with exceptionally numerous, narrow vessels and therefore redundancy (Carlquist 1977a), then *A. alpina* and *A. nana* ssp. *covillei* fall into this category. If values of vulnerability of less than 1.0 are considered xeromorphic (Carlquist 1977b) then the montane and desert species fall into this category. If values of vulnerability greater than 1.0 are considered mesomorphic then the coastal species fall into this category. Using Carlquist's (1977b) values for mesomorphy, one finds that montane and desert species fall easily into the xerophyte category ($M = 75$ or below) and the coastal species fall into the mesophyte category ($M = 200$ or more). Similar trends are seen among Compositae (Carlquist 1966) for values arranged according to rainfall. Mesic groups developed wider-longer ($66\ \mu\text{m} \times 282\ \mu\text{m}$) vessels. Desert groups produced narrower-shorter ($34\ \mu\text{m} \times 155\ \mu\text{m}$) vessels. Annuals tended to be more mesic than perennials, $46\ \mu\text{m}$ wide $\times$ $186\ \mu\text{m}$ long and $39\ \mu\text{m}$ wide $\times$ $152\ \mu\text{m}$ long, respectively.

One interesting note regarding the range of cell dimensions among the seven species of *Abronia* can be made by a comparison with the 14 tribes of Compositae (Carlquist 1966). *Abronia* species ranged from 21 – $90\ \mu\text{m}$ in vessel width, 107 – $166\ \mu\text{m}$ in vessel-element length and 339 – $400\ \mu\text{m}$ in fiber length compared to Compositae which ranged from 33 – $96\ \mu\text{m}$ in vessel width, 155 – $300\ \mu\text{m}$ in vessel-element length and 301 – $448\ \mu\text{m}$ in fiber length. The maximum Compositae vessel-element length is twice that of the *Abron-*

ia species. This difference in length may reflect the fact that *Abronia* species produce secondary vascular bundles by anomalous cambia. These cambia arise in the cortical parenchyma and may produce shorter elements than normal cambia (Carlquist 1975). Nevertheless, trends in vessel-element length are still present among the species and differ significantly at the 99% level.

To answer the question of what mitigating influences foliar structures might have as sources for departure from a particular xylem formulation, results from foliar studies of four *Abronia* species (Helm 1978) are noted here. Helm (1978) examined trends in leaf xeromorphy for four species of *Abronia*. He identified trends associated with trichome numbers, morphology and size, and stomatal number and size in an attempt to classify the species as either xeromorphic or mesomorphic. Interestingly, these findings correlate with the classification of the roots studied here. Leaf types were ranked (Helm 1978) from most xeromorphic to least xeromorphic as follows: *A. alpina* to *A. nana* ssp. *covillei* to *A. villosa* to *A. maritima*, respectively.

The loss of fibers in the perennial montane species is of special interest relative to implications associated with habit and habitat. Loss of fibers in roots and stems associated with habit are described by Gibson (1978). He reports that roots of *Pterocactus tuberosus* (Pfeiff.) Britt. & Rose., a poorly known Argentine geophyte, never form fibers in secondary xylem, "not even in the most rapidly growing lateral roots." In addition, Gibson (1977) noted that species of Opuntioideae with low, lax growth habits and limited secondary growth either postpone production of wood fibers for many years or eliminate them entirely.

Not only decreases in fibers but increases in fibers are of special interest. Both *A. maritima* and *A. pogonantha* roots produce relatively more fibers per mm² (438.6 and 396.6 respectively) than the other species studied. In the case of *A. maritima* one might speculate that its foredune habitat subject to wind and wave action would select for roots with greater resilience and stabilizing structures, thus increased fibers. Likewise, *A. pogonantha* from exposed wind-swept desert habitats may increase fibers in its roots in response to habitat as well as to the effects of the wind on its erect stems. Fibers in *A. pogonantha* are deposited to the outer edges and constitute a tubular structure. Fibers in this outer region may also be correlated with its shallow root system and annual habit which is more subject to drought effects at the end of its growing season.

With these data and studies in mind it seems safe to conclude that anatomical differences seen within the roots of *Abronia* species are an integral part of the adaptive processes *Abronia* species have undergone within their ecologically distinct habitats.

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