

Paedomorphosis, Secondary Woodiness, and Insular Woodiness in Plants

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TABLE OF CONTENTS

I. Abstract	
II. Introduction	
III. Historical Review	
A. Paedomorphosis, Insular Woodiness, and Secondary Woodiness	
B. Paedomorphosis	
1. Genesis of the Theory of Paedomorphosis	
2. Bailey's Refugium Theory and Major Trends in Xylem Evolution	
3. Paedomorphic Characters of the Secondary Xylem	
C. Insular Woodiness	
1. Examples of Insular Woodiness	
2. Relictual and Secondary Insular Woodiness	
3. Hypotheses to Explain the Evolution of Insular Woodiness	
D. Secondary Woodiness	
IV. Stem Structure and Wood Anatomy in <i>Xanthorhiza simplicissima</i> , <i>Coreopsis gigantea</i> , and <i>Mahonia bealei</i>	
A. Overview	
B. Organography and Anatomy	
1. <i>Xanthorhiza simplicissima</i>	
2. <i>Coreopsis gigantea</i>	
3. <i>Mahonia bealei</i>	
C. Materials and Methods	
D. Results	
1. Stem Anatomy and Xylem Characteristics of <i>Xanthorhiza simplicissima</i>	
a. Overview	
b. Vessels	
c. Rays	
d. Fibers	
e. Secondary Woodiness	

2. Stem Anatomy and Xylem Characteristics of <i>Coreopsis gigantea</i>	
a. Overview.....	
b. Parenchyma in Younger Stems.....	
c. Vessels in Younger Stems.....	
d. Parenchyma in Older Stems.....	
e. Vessels in Older Stems	
f. Rays in Older Stems.....	
g. Fibers in Older Stems	
h. Secondary Woodiness	
3. Stem Anatomy and Xylem Characteristics of <i>Mahonia bealei</i>	
a. Overview.....	
b. Vessels	
c. Rays	
d. Fibers	
e. Secondary Woodiness.....	
4. Paedomorphosis in Primitively Woody Taxa.....	
V. Discussion	
A. <i>Xanthorrhiza simplicissima</i>	
1. Vessels.....	
2. Rays	
3. Fibers	
4. Paedomorphosis	
5. Secondary Woodiness	
6. Environmental Factors and Anatomy.....	
B. <i>Coreopsis gigantea</i>	
1. Vessels	
2. Rays	
3. Fibers	
4. Paedomorphosis in the Secondary Xylem.....	
5. Secondary Woodiness	
6. Environmental Factors and Anatomy.....	
C. <i>Mahonia bealei</i>	
1. Vessels	
2. Rays	
3. Fibers	
4. Paedomorphosis	
5. Secondary Woodiness	
6. Environmental Factors and Anatomy.....	
D. Paedomorphosis in the Secondary Xylem	
1. The Baileyan Trends.....	
2. Maberly's Criticism of Paedomorphosis.....	
E. Secondary and Insular Woodiness	
F. Paedomorphosis with Primary Woodiness	
G. Paedomorphic Rays and Raylessness	
H. The Concept of Woodiness in Relationship to Plant Growth Forms	
VI. Conclusions	
VII. Acknowledgements.....	
VIII. Literature Cited	

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I. Abstract

The related concepts of paedomorphosis in the secondary xylem, insular woodiness, and secondary woodiness are reviewed and evaluated in order to clearly distinguish the phenomenon involved, and provide a firm foundation for future research in this area. The theory of paedomorphosis refers to the occurrence of certain juvenile xylem characteristics, such as scalariform perforation plates and lateral wall pitting, in the secondary xylem of shrubby, suffrutescent, pachycaulous, and lianoid growth forms. Paedomorphic characteristics are often found in insular woody species, a fact that has caused paedomorphosis to be associated with secondary woodiness. The anatomy of the secondary xylem in *Xanthorrhiza simplicissima* (Ranunculaceae), *Coreopsis gigantea* (Asteraceae), and *Mahonia bealei* (Berberidaceae) is described in order to provide specific data for discussion. These species serve as test cases for the presence of paedomorphosis, and the evolution of secondary woodiness. The secondary xylem of all three species was found to have a degree of paedomorphosis, with *Coreopsis* having the greatest number of paedomorphic characteristics, *Xanthorrhiza* having an intermediate number, and *Mahonia* possessing only a single characteristic. Plotting the occurrence of the character states woody and nonwoody on phylogenetic trees containing these taxa shows that *Coreopsis* is secondarily woody, while the ancestry of the other two species cannot be unambiguously established. These results must, however, be considered preliminary as the occurrence of secondary growth in many “herbaceous” plants often goes unreported. Although paedomorphosis is often associated with secondary woodiness, there are examples of paedomorphic wood in primitively woody taxa. One conclusion is that the degree of paedomorphosis may be a better indicator of the mechanical requirements of the shoot than of its evolutionary history.

II. Introduction

Much of the research on the secondary xylem and associated tissues such as the vascular cambium has been skewed towards typical woody dicotyledons, like trees. This focus is seen in many of the articles in the IAWA (International Association of Wood Anatomists) Journal, and in the website InsideWood (InsideWood, 2004-onwards), an online wood anatomy information and image database. This orientation is likely due to the sheer usefulness of, and commercial applications for, the secondary xylem of these plants. Much research has been geared towards understanding stem anatomy in order to advance various commercial applications of wood (Panshin & de Zeeuw, 1970). Even the efforts of Kribs (1935) to develop a broad classification of rays were affected by this focus. Kribs’ ray classification system was based on the study of a collection of mostly typical dicotyledonous woods (Carlquist, 2001).

Despite the emphasis on typical woody dicotyledons, there has been some interest in the secondary xylem of plants that are not typically woody. For example, *Arabidopsis* has recently been used as a genetic model for both primary and secondary xylem development (Chaffey et al., 2002; Melzer et al., 2008; Nieminen et al., 2004). There has also been increased interest in the secondary growth of so called herbaceous¹ plants, and in the anomalous secondary growth of plants with cambial variants (Carlquist, 2007; Rajput & Rao, 1998; Rajput & Rao, 1999; Schweingruber, 2006; Schweingruber, 2007a; Schweingruber & Landolt, 2005–2008).

This interest in non-commercial species is, of course, not a recent phenomenon. In the 19th century both Darwin and Wallace became interested in insular species of plants and animals (Darwin, 1859; Wallace, 1878). As part of this interest, they debated how woody plants could appear on islands. This phenomenon was puzzling because environmental conditions seemed to limit the successful dispersal of woody plant seeds. How could plants with limited dispersal reach islands? Such issues, as well as a general interest in the xylem anatomy of insular plants and their relatives, led scientists such as Chrysler (1937) and Carlquist (1962) to study secondary xylem with anatomical characteristics different from those of typical dicotyledons. Interest in these plants, many of them found on islands, led to the theory of paedomorphosis in the secondary xylem (Carlquist, 1962; Chrysler, 1937). The concept of secondary woodiness is also closely associated with insular woodiness, and paedomorphosis.

Insular woodiness occurs when plants from predominantly herbaceous groups have woody members that occur on islands (or in mountainous equatorial areas). Secondary woodiness refers to woodiness that is derived from herbaceous ancestors. Paedomorphosis in the secondary xylem refers to a suite of anatomical characteristics, many of which are normally associated only with the primary xylem in typical woody dicotyledons. Paedomorphic features are most often found in less woody plants that have shrubby, suffrutescent, pachycaulous, or lianoid growth forms.

Paedomorphosis in the secondary xylem, and the related concepts of insular and secondary woodiness, are explored in this paper. In addition to a review of these concepts, particular attention is directed to how the presence of secondary growth in herbaceous plants affects the theory. We also consider the secondary xylem of three species, *Xanthorhiza simplicissima* Marsh., *Coreopsis gigantea* (Kellogg) H.M. Hall, and *Mahonia bealei* (Fortune) Carr. that serve as test cases for the evolution of secondary woodiness, and the presence of paedomorphosis. The secondary xylem of these species is examined for characteristics of paedomorphosis, and their phylogenies are reviewed for evidence of secondary woodiness.

¹ The term heraceous is treated more fully in the Discussion.

III. Historical Review

A. Paedomorphosis, Insular Woodiness, and Secondary Woodiness

The theory of paedomorphosis in the secondary xylem, and the terms insular and secondary woodiness are related concepts that are complex, nuanced, and sometimes controversial. In addition (and unfortunately), these concepts are not always well defined or used consistently in the literature. Sometimes they are conflated with each other, even though they are not identical, and have important differences. For instance, a plant with certain anatomical characteristics in the secondary xylem may be described as having paedomorphic wood. Based on this, some researchers imply (or come perilously close to implying) that it must have secondary woodiness. However, without phylogenetic knowledge of its ancestors, a plant cannot be definitively said to be secondarily woody. That decision must be made in the context of its phylogenetic relationships (Carlquist, 1962). There is similar confusion about insular woodiness. Since insular woodiness can originate from either herbaceous ancestors or extinct woody ancestors, decisions about its origin are best made in a phylogenetic context (Kim et al., 1996). Due to the inherent complexities of these concepts, they must be clearly differentiated.

Even the concepts of “woody” and “woodiness,” which are used much more often in the literature, are often ambiguous. Although wood is generally understood to mean the secondary xylem of gymnosperms and dicotyledons (Evert, 2006), when applied to growth forms woodiness can mean a variety of things. For instance, a plant may have a woody stem, a woody root system, or both (Isnard et al., 2003). Woodiness in growth forms may also exist in varying degrees, from a small amount to a very substantial amount. A suffrutescent stem like that found in *Descurainia tanacetifolia* (Brassicaceae) has secondary xylem only at its base, while the remainder of the stem is herbaceous (Goodson et al., 2006). The common presence of secondary xylem in annuals and herbaceous perennials (Bowers, 1996; Bowers & Mauseth, 2008; Schweingruber & Poschlod, 2005), is sometimes referred to as wood (Chaffey et al., 2002; Melzer et al., 2008; Nieminen et al., 2004; Ye, 2002). This can result in typically herbaceous plants possessing wood, and perhaps even being termed woody (Melzer et al., 2008). At the other extreme, much of the tissue in perennial arborescent plants like *Acer rubrum* (Sapindaceae) is typical wood, produced over a number of years. Thus, whether a particular growth form is woody or not is often a matter of interpretation.

B. Paedomorphosis

1. Genesis of the Theory of Paedomorphosis

Paedomorphosis is one of the possible end results of heterochrony. Heterochrony is broadly defined as the change in both the rate of development of characters, and the timing of the appearance of these characters during development (de Beer, 1930; Gould, 1977; McNamara, 1986). Variation in growth rates, as well as

the duration and timing of the growth period, affect the relationship between size and shape of particular structures (McNamara, 1986). Organisms with different rates of development may possess adaptive advantages, which may be selected for, thus shaping evolution (McNamara, 1986; McNamara & McKinney, 2005). Heterochrony is analyzed by comparing ontogenies of related organisms. Morphological comparisons of changes in shape and size have to be used together with heterochronic time data (McKinney, 1988).

There are two different results of heterochrony: paedomorphosis and peramorphosis. Paedomorphosis results when an organism passes through fewer developmental stages than its ancestor, resulting in the adult form of the organism possessing morphological characteristics that occurred in the juveniles of its ancestor (McNamara, 1986). Peramorphosis, on the other hand, results if the organism passes through more developmental stages than its ancestor, leading to the adult form that is not represented in the ancestor (McNamara, 1986). Both paedomorphosis and peramorphosis can be achieved in more than one way. For example, paedomorphosis can occur by the reduction of the rate of morphological development through the juvenile growth stage (neoteny), by early sexual maturation (progenesis), or by the delay of the beginning of morphological development (post-displacement) (McNamara, 1986).

Paedomorphosis has been applied to the study of both animals and plants. For instance, paedomorphosis has been studied in the ammonite *Protacanthoceras tuberculatum* to investigate the evolution of its small shell (Landman, 1988). In limpets, the shell form of subclade Patellogastropoda was also achieved through paedomorphosis (Linberg, 1988). Although (Carlquist, 1962) is best known for applying the theory to plant anatomy, the concept was discussed in the literature much earlier than his seminal work. Chrysler's (1937) study of *Zamia* (Cycadaceae) provides an early glimpse of the ideas that Carlquist would later refine.

When Chrysler (1937) investigated xylem taken from a mature specimen of *Zamia floridana*, he found tracheids with scalariform lateral wall pitting throughout the xylem. This is in contrast with the other genera in the Cycadales, which have either only tracheids with bordered pits, or both tracheids with scalariform pitting (tracheids near the pith) and tracheids with bordered pits (tracheids in the later formed xylem). In the latter case, pitting changes from scalariform in the earliest formed xylem, to bordered pits in the more mature xylem (Chrysler, 1937).

Since *Zamia floridana* has a tuberous stem, or caudex, Chrysler also investigated pitting in two species which possess well defined trunks: *Z. pseudoparasitica* and *Z. tuerckheimii*. The xylem of a mature specimen of *Z. pseudoparasitica* showed a pattern of tracheids with scalariform lateral wall pitting close to the pith, tracheids with transitional lateral wall pitting further out in the stem, and tracheids with circular bordered pits closer to the phloem. The trunk of a young specimen of *Z. tuerckheimii* revealed only tracheids with scalariform lateral wall pitting (Chrysler, 1937).

These findings suggest that tracheids with scalariform lateral wall pitting are normally found only in immature cycads, or in the earliest xylem of more mature

cycads. Based on these observations, Chrysler (1937) concluded that the tuberous species *Z. floridana* is a persistent juvenile with respect to its xylem. It produces only immature xylem throughout its life. The presence of only tracheids with scalariform wall pitting indicates an arrested development in the xylem. Although he did not term it paedomorphosis, his observations are in essential agreement with the theory later formulated by Carlquist (1962).

Carlquist (1962) developed the full theory of paedomorphosis in the secondary xylem. The theory is an effort to explain why the anatomy of the secondary xylem of some less woody plants with shrubby, herbaceous, or lianoid forms does not fit the broad anatomical trends seen in the secondary xylem of typical woody dicotyledons. His hypothesis is that the anatomical changes seen in these plants are due to paedomorphosis. In this context, paedomorphosis means that certain features of the primary xylem are also found in the secondary xylem. Thus, the secondary xylem of plants with paedomorphic wood shows anatomical characteristics usually associated with the primary xylem of typical woody dicotyledons. Paedomorphic secondary xylem is either permanently juvenile, or else loses its juvenile characteristics slowly as it grows. In less woody plants, paedomorphic secondary xylem retains juvenile characteristics found in the primary xylem because the plants are either moving evolutionarily towards, or away from, true woodiness (Carlquist, 1962).

2. Bailey's Refugium Theory and Major Trends in Xylem Evolution

In formulating his theory of paedomorphosis, Carlquist (1962) drew on Bailey's (1944) refugium theory (Carlquist, 2009). This theory states that there is an evolutionary lag in the development of the tracheary elements in the primary xylem, compared to those in the secondary xylem. According to the refugium theory, vessels first originated in the secondary xylem, replacing tracheids. Over time, vessels in the secondary xylem became ever more specialized. Increasing specialization was evident in a directional series of structural changes in the elements. The changes included changes in lateral wall deposition patterns, modification of the vessel end walls, and a decrease in vessel element length. These changes did not occur as quickly in the primary xylem, so that eventually the vessels of the primary xylem were less specialized than those of the secondary xylem. As a result of this evolutionary lag, the primary xylem retains more primitive tracheary characteristics than the secondary xylem. Thus, the primary xylem serves as a refugium for these more primitive characteristics (Bailey, 1944).

In developing the refugium theory, Bailey drew on the major trends of tracheary element evolution that he helped formulate during the first half of the 20th century (Bailey, 1944; Bailey & Tupper, 1918; Frost, 1930a, b, 1931). These trends eventually became known as the Baileyan trends. They were intended to indicate the general direction of evolution in tracheary elements. Later, other researchers used the Baileyan trends to establish evolutionary direction in other xylary cell and tissue types, such as rays (Kribs, 1935) and wood parenchyma (Kribs, 1937).

Several of the major Baileyan trends concern tracheary elements, especially vessels (Bailey, 1944; Bailey & Tupper, 1918; Frost, 1930a, b, 1931). The vessels which occur in plants found earliest in the fossil record have annular or helical lateral

wall deposition patterns. Because these patterns are found earlier in the fossil record, they were considered primitive, or less advanced (see Wagner, 1969 for a critique of this idea). If these patterns were found in an extant plant, they would be considered primitive. Slightly later in the fossil record scalariform patterns appear. Finally the most advanced, or specialized, pattern appears in the record: vessels with pitted lateral walls. Within this category, vessels evolved from possessing opposite to alternate pitting.

The changes from annular to pitted lateral walls were paralleled by a series of changes in the vessel end walls. Vessels that appear earlier in the fossil record have scalariform perforation plates (bars across the opening of the end wall). More advanced vessels have fewer bars, until eventually no bars are present (simple perforation plates). The vessel elements also become shorter, and develop more transverse (less angled) end walls. Unlike the end walls of vessels with scalariform perforation plates, transverse end walls do not overlap with those of neighboring vessel elements (Bailey, 1944; Frost, 1930a, b, 1931).

Trends in the distribution of vessels were also established (Gilbert, 1940). Diffuse porous woods, where the vessel diameters remain relatively constant in a growth ring, were found to be less advanced. The ring porous condition, which consists of clearly delineated areas with larger diameter vessels (earlywood) alternating with areas of smaller vessels (latewood) was more advanced (Gilbert, 1940).

Another major trend involved the appearance and evolution of fibers. Fibers, like vessels, are absent from the earliest fossils, and so must also have evolved from tracheids. Unlike vessels, which are specialized for water conduction, fibers are adapted to a specialized support function. The less advanced form is the fiber tracheid. Fiber tracheids are intermediate in form between tracheids and true fibers. They are considered imperforate tracheary elements like tracheids, so they are capable of transporting water only through their porous pit membranes. They also have bordered lateral wall pitting, like tracheids. The more advanced form is the libriform fiber, which possesses simple pits (pits with reduced or absent borders) (Evert, 2006).

Kribs examined ray parenchyma (Kribs, 1935) and axial wood parenchyma (Kribs, 1937) to determine their evolutionary trends. In the case of axial parenchyma, he concluded that its absence is the most primitive condition. Diffuse axial parenchyma (single strands or cells scattered among the xylary fibers) is advanced. Metatracheal parenchyma (axial parenchyma in concentric rings parallel to the cambium, but independent of the vessels) is more advanced. Vascentric parenchyma (parenchyma surrounding the vessels) is the most advanced type of axial wood parenchyma (Kribs, 1937). In the case of ray parenchyma, heterogeneous rays possessing both upright and procumbent cells are most primitive. More advanced rays have increasing levels of cell homogeneity. Homogeneous rays, consisting of only ray cells with procumbent orientation, are the most advanced (Kribs, 1935).

Kribs' ray classification system was based on the study of a wood collection that contains mostly trees. As a result, it does not include categories for ray types found in less woody growth forms such as woody herbs (herbaceous plants that have evolved the ability to produce at least some limited secondary xylem) (Carlquist,

1974), or rosette trees. To correct this problem, Carlquist (2001) modified the system to include paedomorphic ray types found in less woody plants. These additions to ray types include Paedomorphic Type I, Paedomorphic Type II, and Paedomorphic Type III (Carlquist, 2001).

The Paedomorphic Type I category contains both multiseriate and uniseriate rays. Upright ray cells predominate in the multiseriate rays, with any procumbent cells restricted to the multiseriate portion of the ray. The uniseriate rays have only upright cells. Examples of plants with Paedomorphic Type I rays include *Verbesina* spp. (Asteraceae), and some species of *Euphorbia* (Euphorbiaceae) (Carlquist, 2001).

Paedomorphic Type II rays are almost exclusively multiseriate with solely or predominantly upright cells. Any procumbent cells are found in the multiseriate portion of the rays. Although uniseriate rays may occur in this type, they are uncommon. *Geranium tridens* (Geraniaceae) and *Ardisia brackenridgei* (Myrsinaceae) contain Paedomorphic Type II rays (Carlquist, 2001).

Paedomorphic Type III rays are uniseriate with exclusively upright cells. No multiseriate rays are found in this type. Plants with Paedomorphic Type III rays include *Corema conradii* and *Dracophyllum acerosum* (Ericaceae) (Carlquist, 2001).

For the most part, the Baileyan trends were initially treated as irreversible evolutionary trends. However, the xylem of a single species did not necessarily have only primitive or advanced characteristics. Depending on the level of functional organization examined, there could be a mix of the trends. Within even one cell type, vessel elements for example, one characteristic might be more advanced (simple perforation plates) while another might be less advanced (scalariform lateral wall pitting). If the secondary xylem had a preponderance of cell types with primitive or specialized characteristics, it was treated as structurally primitive or advanced (Bailey, 1944). However, in specific plants one set of characteristics could be more, or less, advanced than another (Bailey, 1944). For example, *Pentaphragma decurrens* (Pentaphragmataceae) has vessels with primitive characteristics, while the fact that it lacks rays (or has delayed ray development) is a more specialized feature (Carlquist, 1997).

All of the major trends in xylem evolution were discovered by use of a few simple methods. First, the fossil record was used to determine the specialization of a feature. For example, if tracheids appeared in the fossil record before vessels, then the tracheids were less specialized, or more primitive, than the vessels (Bailey, 1944; Frost, 1930a, b, 1931). Vessels would, in turn, be considered more advanced, or specialized, than tracheids. Second, statistical correlations were used to establish relationships between trends. A characteristic or cell type recognized as primitive due to its place in the fossil record would be compared to other characteristics whose level of advancement was not known. If a given characteristic had a high correlation with the characteristic already recognized as primitive, then it too was primitive.

For example, early researchers such as Frost (1930a, b, 1931) recognized that tracheids appeared in the fossil record before vessels. Thus, they were considered primitive. It also seemed reasonable that vessels were derived from tracheids, since vessels are found later in the fossil record, and have the same types of lateral wall pitting. In addition they both fulfill the same function, conducting water. Since tracheids are longer than vessel elements, any characteristics correlated with longer

vessel element lengths were also considered primitive, and characteristics associated with shorter vessel elements were more advanced (Bailey, 1944; Frost, 1930a, b, 1931). The use of statistical correlations was extended beyond vessels to other xylem components, such as rays and xylary parenchyma. Patterns of parenchyma distribution in the xylem as well as ray composition type were both correlated with vessel characteristics to determine primitive and advanced states (Gilbert, 1940; Kribs, 1935, 1937).

The most primitive states of the Baileyan trends tend to be found in the primary xylem of typical dicotyledonous woody plants. This region usually contains longer vessel elements with scalariform lateral wall pitting with wide lateral wall pit apertures, thin walled fibers with wide lumens (or no fibers), and tall primary rays (interfascicular regions of the primary plant body that are continuous with rays in the secondary xylem) with erect cells (Carlquist, 2001; Carlquist, 2009).

Bailey's (1944) refugium theory was an attempt to explain why the primary xylem retains these primitive features. According to this theory vessels evolved first and became more specialized in the secondary xylem. Evolution and specialization then proceeded to the late primary xylem (the metaxylem, which matures after elongation of the primary plant body is completed), and then to the early primary xylem (the protoxylem, which matures in actively elongating tissues of the primary plant body). As a result of these events, the primary xylem is left with more primitive features than the secondary xylem (Bailey, 1944; Esau, 1977).

These trends, and this explanation of their occurrence, set the stage for Carlquist's theory of paedomorphosis (Carlquist, 1962). Carlquist found that many of the more primitive xylem characteristics were expressed in the secondary xylem of herbs, woody herbs, rosette trees/shrubs, and stem succulents that were included in his study. Later studies confirmed these tendencies, and led to the description of new characters associated with paedomorphosis (Carlquist, 1974, 1983, 1989, 1997; Carlquist, 2001; Carlquist, 2003, 2009; Lens et al., 2005a). The paedomorphic characteristics described in this research include scalariform or pseudoscalariform lateral wall pitting on the vessel elements; vessel elements with simple (most common) or scalariform (less common) perforation plates; wide, thin-walled fibers and the predominance of libriform fibers, or parenchyma cells replacing fibers; either the absence of rays or delayed ray development; and rays, when present, consisting of mostly upright, or square, cells (Carlquist, 1962; Carlquist, 2001; Carlquist, 2009). Tracheids are usually absent from paedomorphic woods. Carlquist (1962) also noted that paedomorphic woods produce decreasing, or stable, vessel element lengths as the secondary xylem ages (Fig. 1).

3. Paedomorphic Characters of the Secondary Xylem

Many of the paedomorphic characteristics can be expressed independently of each other, so that not all paedomorphic woods have all of the paedomorphic characteristics. The lack of linkage between these characteristics can lead to one or two paedomorphic features occurring in xylem that otherwise has more typical

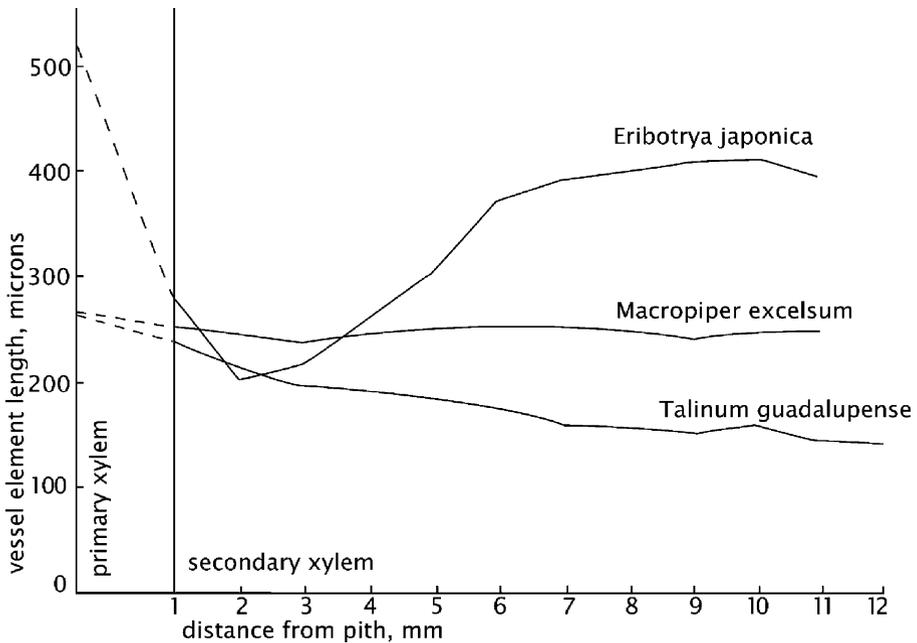


Fig. 1 Age on length curves for vessels in *Eriobotrya japonica*, *Macropiper excelsum*, and *Talinum guadalupense* (after Carlquist, 1962)

characteristics (Carlquist, 1962). Thus, there is a continuous range of paedomorphic woods from those expressing only one or two paedomorphic characteristics, to those with the full suite of characters described above.

It is also important to remember that not all of the characters initially mentioned in association with paedomorphosis are the juvenile states found in the primary xylem. While the term “paedomorphosis” leads one to expect that only juvenile states will be found in paedomorphic wood, the original concept of paedomorphosis was more subtle. While certain paedomorphic characteristics, like vessels with scalariform lateral wall pitting, are associated with the primary xylem (at least in typically woody species), other paedomorphic characteristics, such as the presence of libriform fibers and simple perforation plates, are not. These features were initially included in lists of paedomorphic characters because their occurrence was thought to be correlated with other paedomorphic characteristics, which are truly juvenile (Carlquist, 1962; Carlquist, 2001). However, the widespread occurrence of libriform fibers in groups such as the Asteraceae (Carlquist, 1966), and the common occurrence of simple perforation plates in the secondary xylem of many species suggests that these correlations are only apparent, and may be due to limited sampling (Table 1) (Schweingruber, 2006; Schweingruber, 2007a). That fact that libriform fibers and simple perforation plates sometimes co-occur with paedomorphic characters does not mean that they are correlated with them across a wide range of taxa. This has been recognized in recent treatments of paedomorphosis, which claim no relationship between fiber type and paedomorphosis (Carlquist, 2009). For

Table 1 Secondary Growth in Species of Brassicaceae, Violaceae and Ranunculaceae^a

Family	Species	Secondary Growth Rings	Rays	Perforation Plates	Growth Form ^b
Brassicaceae	<i>Alyssum alyssoides</i> (L.) L.	one	rayless	simple	T
Brassicaceae	<i>Anastatica hierochuntina</i> L.	one	3–7 seriate	simple	T
Brassicaceae	<i>Arabidopsis thaliana</i> (L.) Heyhn.	one	rayless	simple	T
Brassicaceae	<i>Arabis procurrens</i> Waldst. & Kit.	–	rayless	–	T
Brassicaceae	<i>Brassica rapa</i> L.	one	3–10 seriate	simple	T
Brassicaceae	<i>Camelina pilosa</i> (DC.) Vasilcz.	–	1–3 seriate	–	T
Brassicaceae	<i>Capsella bursa-pastoris</i> (L.) Medik.	one	2–3 seriate or rayless	simple	T
Brassicaceae	<i>Capsella rubella</i> Reuter	one	rayless	simple	T
Brassicaceae	<i>Cardamine amara</i> L.	–	rayless	–	T
Brassicaceae	<i>Cardamine flexuosa</i> Width.	one	rayless	simple	T
Brassicaceae	<i>Clypeola jonthlaspi</i> L.	one	rayless	simple	T
Brassicaceae	<i>Coronopus squamatus</i> (Forsk.) Asch.	one	rayless	simple	T
Brassicaceae	<i>Descurainia Sophia</i> (L.) Prantl.	one	1–3 seriate	simple	T
Brassicaceae	<i>Diplotaxis muralis</i> (L.) DC	one	3–7 seriate	simple	T
Brassicaceae	<i>Draba nemorosa</i> L.	one	rayless	simple	T
Brassicaceae	<i>Erophila verna</i> (L.) DC	one	rayless	–	T
Brassicaceae	<i>Hornungia petraea</i> (L.) Rchb.	one	rayless	–	T
Brassicaceae	<i>Lepidium densiflorum</i> Schrad.	one	rayless	simple	T
Brassicaceae	<i>Matthiola parviflora</i> R. Br.	one	rayless	–	T
Brassicaceae	<i>Notoceras bicornae</i> Willk.	one	rayless	simple	T
Brassicaceae	<i>Pseuderucaria clavata</i> (Boiss. & Reut.) O.E.Schulz	–	4–10 seriate	–	T
Brassicaceae	<i>Rhaphinastrium rugosum</i> (L.) All.	one	2–4 seriate	simple	T
Brassicaceae	<i>Sinapis arvensis</i> L.	one	1–3 seriate	simple	T
Brassicaceae	<i>Sinapis flexuosa</i> Poir.	one	1–3 seriate	–	T
Brassicaceae	<i>Sisymbrium altissimum</i> L.	one	1–3 seriate	simple	T
Brassicaceae	<i>Sisymbrium andinum</i> Phil.	one	1–4 seriate	simple	T
Brassicaceae	<i>Sisymbrium irio</i> L.	one	1–4 seriate	simple	T
Brassicaceae	<i>Sisymbrium Sophia</i> L.	–	1–3 seriate	–	T
Brassicaceae	<i>Thlaspi arvense</i> L.	–	rayless	–	T
Brassicaceae	<i>Thlaspi bonariense</i> Poir.	–	rayless	–	T
Brassicaceae	<i>Thlaspi perfoliatum</i> L.	one	rayless	simple	T
Violaceae	<i>Hybanthus communis</i> Taub	± distinct	Paedomorphic Type III	simple	C
Violaceae	<i>Viola arborescens</i> L.	distinct	rayless	simple	C
Violaceae	<i>Viola biflora</i> L.	indistinct	rayless	simple	H
Violaceae	<i>Viola calcarata</i> L.	distinct	rayless	simple	H
Violaceae	<i>Viola canadensis</i> L.	distinct	rayless	simple	H
Violaceae	<i>Viola canina</i> L.	distinct	rayless	simple	H
Violaceae	<i>Viola elatior</i> Fries	distinct	rayless	simple	H
Violaceae	<i>Viola hirta</i> L.	distinct	rayless	simple	H
Violaceae	<i>Viola labradorica</i> Schrank	distinct	rayless	simple	H
Violaceae	<i>Viola mirabilis</i> L.	distinct	rayless	simple	H
Violaceae	<i>Viola odorata</i> L.	distinct to indistinct	rayless	simple	H
Violaceae	<i>Viola palustris</i> L.	indistinct	rayless	simple	H
Violaceae	<i>Viola reichenbachiana</i> Jordan ex Boreau	distinct	rayless	simple	H

Table 1 (continued)

Family	Species	Secondary Growth Rings	Rays	Perforation Plates	Growth Form ^b
Violaceae	<i>Viola rupestris</i> F.W. Schmidt	distinct	rayless	simple	H
Violaceae	<i>Viola suavis</i> Bieb.	distinct	rayless	simple	H
Violaceae	<i>Viola tricolor</i> L.	distinct	rayless	simple	H
Ranunculaceae	<i>Aconitum lyctonum</i> ssp. <i>vulparia</i> Nyman	none	rayless	simple	H
Ranunculaceae	<i>Aconitum napellus</i> ssp. <i>lusitanicum</i> Rouy	none	none	simple	H
Ranunculaceae	<i>Aconitum variegatum</i> ssp. <i>paniculatum</i> (Arcang.) Negodi	none	none	simple	H
Ranunculaceae	<i>Actaea spicata</i> L.	distinct	primary only	simple	H
Ranunculaceae	<i>Adonis flammea</i> Jacq.	one	2–3 seriate	simple	T
Ranunculaceae	<i>Anemonastrum narcissiflorum</i> Holub	indistinct	primary only	simple	H
Ranunculaceae	<i>Anemone narcissiflora</i> L.	indistinct	primary only	simple	H
Ranunculaceae	<i>Anemone nemorosa</i> L.	none	none	simple	H
Ranunculaceae	<i>Anemone ranunculoides</i> L.	none	none	simple	H
Ranunculaceae	<i>Aquilegia coerulea</i> James	distinct	primary only	simple	H
Ranunculaceae	<i>Aquilegia vulgaris</i> L.	distinct	primary only	simple	H
Ranunculaceae	<i>Clematis alpina</i> ssp. <i>alpina</i> (L.) Miller	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Clematis alpina</i> ssp. <i>Sibirica</i> (L.) O. Kunze	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Clematis campaniflora</i> Brot.	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Clematis cirrhosa</i> L.	distinct	primary rays dominant		liana
Ranunculaceae	<i>Clematis columbianae</i> Nutall.	distinct	primary only	simple	liana
Ranunculaceae	<i>Clematis flammula</i> L.	distinct	primary rays dominant	simple	C
Ranunculaceae	<i>Clematis hirsutissima</i> Pursh	distinct	primary rays dominant	simple	C
Ranunculaceae	<i>Clematis montevidensis</i> Spreng	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Clematis recta</i> L.	distinct	primary rays dominant	simple	C
Ranunculaceae	<i>Clematis vitalba</i> L.	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Clematis viticella</i> L.	distinct	primary rays dominant	simple	liana
Ranunculaceae	<i>Consolida regalis</i> Gray.	one	1–3 seriate	simple	T
Ranunculaceae	<i>Eranthis hiemalis</i> (L.) Salisb.	none	none	simple	H
Ranunculaceae	<i>Helleborus foetidus</i> L.	distinct	primary rays dominant	simple	H
Ranunculaceae	<i>Helleborus viridis</i> L.	distinct	primary rays dominant	simple	H
Ranunculaceae	<i>Hepatica nobilis</i> Schreb.	indistinct	primary rays only	simple	H
Ranunculaceae	<i>Nigella arvensis</i> L.	one	rayless	simple	T
Ranunculaceae	<i>Nigella damascene</i> L.	one	rayless	simple	T
Ranunculaceae	<i>Pulsatilla alpina</i> ssp. <i>alpina</i> (L.) Delabre	distinct to indistinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla alpina</i> ssp. <i>apiifolia</i> (Scop.) Nyman	distinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla alpina</i> ssp. <i>millefoliata</i> (Bertol.) D.M. Moser	distinct	primary rays only	simple	H

Table 1 (continued)

Family	Species	Secondary Growth Rings	Rays	Perforation Plates	Growth Form ^b
Ranunculaceae	<i>Pulsatilla montana</i> (Hoppe) Rchb.	distinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla multifida</i> (E.Pritz.) Juz.	distinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla patens</i> (L.) Mill.	distinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla vernalis</i> (L.) Mill.	distinct	primary rays only	simple	H
Ranunculaceae	<i>Pulsatilla vulgaris</i> ssp. <i>vulgaris</i> Mill.	distinct	primary rays only	simple	H
Ranunculaceae	<i>Ranunculus aconitifolius</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus acris</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus alismifolius</i> Geyer	none	none	simple	H
Ranunculaceae	<i>Ranunculus alpestris</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus bulbosus</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus circinatus</i> Sibth.	none	none	simple	Hydro
Ranunculaceae	<i>Ranunculus cortusifolius</i> Willd.	none	none	simple	H
Ranunculaceae	<i>Ranunculus ficaria</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus flammula</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus glacialis</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus kuepferi</i> Greuter et Burdet	none	none	simple	H
Ranunculaceae	<i>Ranunculus lanuginosus</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus montanus</i> Willd.	none	none	simple	H
Ranunculaceae	<i>Ranunculus repens</i> L.	none	none	simple	H
Ranunculaceae	<i>Ranunculus serpens</i> Schrank	none	none	simple	H
Ranunculaceae	<i>Ranunculus trichophyllus</i> Chaix	none	none	simple	Hydro
Ranunculaceae	<i>Thalictrum alpinum</i> L. cf.	distinct	large primary & secondary	simple	H
Ranunculaceae	<i>Thalictrum foetidum</i> L.	indistinct	primary rays dominant	simple	H
Ranunculaceae	<i>Trollius albiflorus</i> (A. Gray) Rydberg	none	none	simple	H
Ranunculaceae	<i>Trollius europaeus</i> L.	none	none	simple	—

^a Data from Schweingruber and Landolt (2005–2008) and Schweingruber (personal communication)

^b Growth Forms: C—Chamaephytes=Dwarf shrubs. H—Hemicryptophytes=Perennial plants with periodic shoot reduction. Hydro—Hydrophytes. T—Therophytes=Annuals

instance, Lens et al. (2007) used only the presence of extremely short vessel elements, the occurrence of wide scalariform intervessel pits, and absence of rays (or the presence of exclusively upright cells in multiseriate rays), as indicators of paedomorphosis.

Perhaps the most characteristic feature of paedomorphic woods is the age-on-length curve that describes changes in vessel element length across the secondary xylem (Fig. 1) (Carlquist, 1962; Carlquist, 2001; Carlquist, 2009). Typical paedomorphic wood has either vessel elements that decrease in length as the secondary xylem grows (typified by *Talinum guadalupense*, Portulacaceae; Fig. 1), or has vessel elements whose lengths initially decrease, but then remain roughly constant through the remainder of the secondary xylem (typified by *Macropiper excelsum*, Piperaceae; Fig. 1) (Carlquist, 1962; Carlquist, 2001; Carlquist, 2009). When vessel element lengths in the secondary xylem are graphed in age-on-length

curves, the former case shows a negatively sloped curve, while the latter shows a nearly flat curve (Fig. 1) (Carlquist, 1962).

These two patterns of vessel element length contrast with the typical pattern seen in normal woody dicotyledons, such as *Eriobotrya japonica* (Rosaceae) (Fig. 1). In *E. japonica* the earliest formed vessel elements of the secondary xylem continue the decrease in length seen in the primary xylem. However, at some point fairly early in the process of secondary growth, the vessel elements begin to increase in length. As secondary growth continues, vessel element lengths level off, and eventually may even decline somewhat. The paedomorphic age-on-length curves described above are similar to the descending portion (found mainly in the primary xylem) of age-on-length curves for typical woody dicotyledons (Carlquist, 1962, 2009).

Nearly flat age-on-length curves have been reported for vessel elements in several woody annuals of the Asteraceae, such as *Dicoria canescens*, *Gnaphalium californicum*, and *Helianthus annuus* (Carlquist, 1962). They are also found in stem succulents like *Cereus gigantea* (Cactaceae) and *Senecio praecox* (Asteraceae), rosette trees like *Carica candamarcensis* (Caricaceae), and woody herbs like *Sonchus leptcephalus* (Asteraceae) (Carlquist, 1962).

Negatively sloped age-on-length curves are also reported in some woody annuals of the Asteraceae, including *Ambrosia hispida*, *Blepharizonia plumosa*, *Cirsium californicum*, and *Madia sativa*. They also occur in the stem succulents *Begonia coccinea* (Begoniaceae) and *Brighamia insignis* (Campanulaceae), in the rosette tree *Scaevola kauaiensis* (Goodeniaceae) (Carlquist, 1962), in *Impatiens arguta*, *I. niarniamensis* (Balsaminaceae) (Lens et al., 2005a), and in all species in *Corema* and *Empetrum* (both Ericaceae) (Carlquist, 1989).

The developmental mechanics that lead to negative age-on-length curves are straight forward. In a typical woody dicotyledon, transverse divisions in fusiform cambial initials increase as the primary xylem is formed so that vessel element length gradually decreases. During the transition from the primary to secondary xylem, the number of transverse divisions is reduced and intrusive growth of the fusiform cambial initials causes cell elongation so that the vessel elements become longer. Eventually, the number of transverse divisions increases and intrusive growth declines, so that vessel element length plateaus, then drops slightly. In paedomorphic wood the transverse divisions in the fusiform cambial initials continue, and there is little cell elongation. If these patterns are maintained indefinitely, a plot of vessel element lengths will give a negatively sloped age-on-length curve. If they continue for a shorter time, then the age-on-length curve will flatten out after the initial brief negative slope (Carlquist, 2001).

Whether the negatively sloped or flat age-on-length curves found in paedomorphic woods offer any functional advantage is unknown. It may simply be that since many paedomorphic woods are found in short, rosette shrubs that have thick parenchyma-filled stems, the increased mechanical strength offered by longer vessel elements is less important, and is not selected for. Longer vessels are stronger because the areas where the vessel elements abut are mechanically weaker than the lateral walls of the vessel elements. Thus, for a given vessel length, longer vessel elements provide fewer potential weak points than shorter vessel elements. In short, rosette shrubs, the parenchyma may provide sufficient mechanical strength for the growth form (Carlquist, 2001).

Scalariform (or scalariform-transitional) and pseudoscalariform lateral wall pitting between vessels, and between vessels and parenchyma cells, is another anatomical feature still considered indicative of paedomorphic secondary xylem. Scalariform lateral wall pitting occurs in vessels with flattened sides (facets) where two vessels meet, or more commonly, where vessels contact rays. The width of the pits corresponds to the width of the flattened side of the vessels. In pseudoscalariform lateral wall pitting the pits are either shorter, or longer, than the flattened vessel sides. When they are longer, they extend part of the way around the circumference of the vessel (Carlquist, 2001). When they are shorter, the pits do not reach to the sides of the flattened walls. Pseudoscalariform lateral wall pitting is usually found only in plants with paedomorphosis (Carlquist, 1962; Carlquist, 2001). *Begonia coccinea*, *Cereus gigantea*, *Carica candamarcensis*, *Chimantaea mirabilis*, *Espeletia hartwegiana*, *Phoenicoseris regia*, and *Senecio praecox* (all Asteraceae), as well as *Pentaphragma decurrens* (Pentaphragmataceae), and *Impatiens niarniamensis* (Carlquist, 1962, 1997; Lens et al., 2005a) are examples of plants with scalariform wall pitting, and paedomorphic woods. Except for *Chimantaea mirabilis*, all of these plants also have tall pit apertures. Tall pit apertures are another characteristic of paedomorphic woods (Carlquist, 1962, 1997; Lens et al., 2005a). Vessels with scalariform or pseudoscalariform lateral wall pitting have less cell wall strength due to the larger size of the pit apertures, and are common in highly parenchymatized woods. Since the parenchyma in these plants provides mechanical strength through cell turgor, it may be that there is no negative selection against these paedomorphic characteristics (Carlquist, 2001).

Most plants with paedomorphic wood have vessels with simple perforation plates, though the presence of simple perforation plates is not in itself an indication of paedomorphosis (Carlquist, 2001; Carlquist, 2009). Simple perforation plates occur in paedomorphic wood that has been identified as such by other characters (scalariform lateral wall pitting, etc.), but by themselves they do not contribute to this determination. Although Carlquist (1962) initially listed them as a characteristic of paedomorphic wood, more recent treatments have recognized the presence of simple perforation plates as an advanced character (Carlquist, 2009).

The occurrence of scalariform perforation plates in the secondary xylem is a more reliable indication of paedomorphosis. In the families Campanulaceae, Pentaphragmataceae, Valerianaceae, and Asteraceae scalariform perforation plates are occasionally found in the secondary xylem. In the genera where they occur, they are an indication of paedomorphosis since they are more common in the primary xylem and early secondary xylem (Carlquist, 1983, 1997). For example, scalariform perforation plates are found in the vessel elements of three species of *Pentaphragma* (*P. decurrens*, *P. horsfieldii*, and *P. sp.*), all of which have paedomorphic wood (Carlquist, 1997). In the Campanulaceae and Pentaphragmataceae the plants that have scalariform perforation plates are mesophytes living in moist forest understories. In these environments transpiration rates are likely to be lower, so increased rates of hydraulic flow promoted by simple perforation plates are not critical. As a result, scalariform perforation plates may persist because they are not selected against (Carlquist, 1983, 1997).

In many plants with paedomorphic secondary xylem, axial parenchyma is usually extremely abundant, and may be the only axial component of the secondary

xylem apart from vessels. This is often a continuation of the primary xylem structure in these plants, which is heavily parenchymatized and has few, if any fibers (Carlquist, 1962; Carlquist, 2001). In contrast, typical woody dicotyledons have secondary xylem with fibers and/or tracheids in addition to vessels and axial parenchyma, as well as heavily parenchymatized primary xylem (Carlquist, 1962). Abundant axial parenchyma is found in the paedomorphic wood of plants such as *Impatiens niamniamensis* (Balsaminaceae) (Lens et al., 2005a), *Carica candamarcensis* (Caricaceae), *Wunderlichia mirabilis* (Asteraceae), *Scaevola kauaiensis* (Goodeniaceae), *Brighamia insignis* (Campanulaceae), and *Talinum guadalupense* (Portulacaceae) (Carlquist, 1962). Recently, however, the use of abundant axial parenchyma as an indication of paedomorphic secondary xylem has been called into question (Carlquist, 2009). While its physiological activities (the storage of starch and the conduction of sugars) are linked to those of the rays (the radial conduction of sugars), its evolution has not been directly linked to ray evolution. Unlike rays, the distribution of axial parenchyma does not show heterochronic changes (Carlquist, 2009).

Some paedomorphic woods have relatively wide, thin-walled libriform fibers, or fiber tracheids (Carlquist, 1962; Carlquist, 2001). Tracheids are uncommon in paedomorphic wood (Carlquist, 2001). *Impatiens arguta* (Lens et al., 2005a), *Begonia coccinea* (Begoniaceae), *Cereus gigantea* (Cactaceae), *Senecio praecox* and *Sonchus leptcephalus* (both Asteraceae) all have thin-walled, wide libriform fibers (Carlquist, 1962), but these types of fibers are also common in many less woody plants, especially those of the Asteraceae (Carlquist, 1966), and are not currently considered indications of paedomorphosis (Carlquist, 2009). Fiber tracheids are found in the branching canes of *Chloranthus erectus* (Chloranthaceae), a species reported to have other paedomorphic characteristics such as upright ray cells and scalariform perforation plates (Carlquist, 1992). They also occur in the rayless, paedomorphic wood of *Pentaphragma decurrens* and *P. horsfieldii* (Carlquist, 1992), but again are not currently considered primary indications of paedomorphosis.

Paedomorphic secondary xylem is also distinguished by the presence of rays with exclusively, or at least predominantly, upright (or square) ray parenchyma cells, with few or no procumbent cells (Carlquist, 1962, 1970, 1983, 1989; Carlquist, 2001; Carlquist, 2009). However, in some species with paedomorphic wood a few rows of procumbent cells may occur in the middle of larger rays consisting of largely upright ray cells (Carlquist, 1962). The predominance of upright ray cells in paedomorphic wood is in contrast to most typical woody dicotyledons, where procumbent ray cells are usually more common (Mauseth, 1988). In paedomorphic wood, the interfascicular regions of the primary xylem (primary or pith rays) often contain mainly upright parenchyma cells, and this phenomenon continues into the rays of the secondary xylem (Carlquist, 1962, 2009).

The orientation of ray cells (in radial sections) is related to the direction of travel of solutes in the xylem: procumbent ray cells conduct solutes radially, while upright ray cells conduct solutes vertically, as well as some radial transport (Carlquist, 2009).

The increased number of upright ray cells in paedomorphic wood results from a decrease in the transverse divisions of the ray initials (Carlquist, 2001). This phenomenon is seen in *Impatiens niamniamensis* (Balsaminaceae) (Lens et al.,

2005a), *Vernonia salviniae* and *Wunderlichia mirabilis* (Asteraceae), *Brighamia insignis*, *Trematolobelia macrostachys* and *Delissea undulata* (Campanulaceae), *Lobelia gibberoa* (Lobeliaceae), and in some members of Polygonaceae such as *Antigonon leptopus* (Carlquist, 1962, 2003).

When they are present, paedomorphic rays are frequently high and wide (Carlquist, 1962, 2009; Lens et al., 2005a; Lens et al., 2007). These types of rays are considered paedomorphic because, in typical woody dicotyledons, the primary rays are often higher and wider than the rays of the secondary xylem. As a result, high and wide rays that continue from the primary into the secondary xylem are a juvenile feature, and have been used as an indication of paedomorphic wood (Carlquist, 1962, 2009).

Raylessness is also a characteristic of paedomorphic wood (Carlquist, 1970; Carlquist, 2001; Carlquist, 2009). The rayless condition can persist for the life of the plant, as seen in *Impatiens arguta* (Lens et al., 2005a), and in *Plantago princeps* (Plantaginaceae) (Carlquist, 2001), *Viola trachelifolia* (Violaceae) (Carlquist, 2001), *Stylidium* (Stylidiaceae), *Besleria* (Gesneriaceae), and *Aeonium* (Crassulaceae) (Carlquist, 2001). In other cases, transverse divisions in what will become ray initials are delayed, but divisions eventually begin and the plant develops rays as the amount of secondary xylem increases. This happens in *Cyrtandra* c.f. *propinqua*, and *Ixanthus viscosus* (both Gesneriaceae; Carlquist, 1974), and in at least one species of *Pentaphragma* (Carlquist, 1997; Carlquist, 2001).

In some species that lack rays (e.g., *Plantago princeps*), some fiber tracheids appear to be derived from areas of the cambium that would normally produce rays (Carlquist, 1970). The substitution of fiber tracheids for ray cells in rayless species may be a means of providing additional structural support for these stems. In some woody species with short lived stems, fiber tracheids may provide adequate support given the limited structural needs. As a result, raylessness may be positively selected for in these species (Carlquist, 2001).

The number of paedomorphic characteristics expressed in the secondary xylem is a measure of the degree of paedomorphosis present in a taxon. For example, the only paedomorphic characters found in the three *Pentaphragma* ssp. investigated by Carlquist (1997) are raylessness (or perhaps delayed ray development), vessel elements with scalariform lateral wall pitting, and the occurrence of occasional scalariform perforation plates. In other taxa, several paedomorphic characteristics occur in the secondary xylem. For instance, *Foeniculum vulgare* (Apiaceae) has a negatively sloped age-on-length curve, vessel elements with scalariform lateral wall pitting and wide pit apertures, and mostly erect ray cells (Carlquist, 1962). Though both of these species have paedomorphic secondary xylem, *F. vulgare* shows a greater degree of paedomorphosis.

Although paedomorphic anatomical characteristics are indications of juvenile wood, by themselves they should not be used to make decisions about whether the ancestry of a plant is herbaceous or woody. Although they may provide circumstantial evidence, they are first and foremost structural characters that must be interpreted in some theoretical framework. They cannot be conclusive by themselves because paedomorphosis can exist in plants with either woody or herbaceous ancestors (Carlquist, 1962). Questions of ancestry should be resolved in a phylogenetic context, as discussed more fully below.

C. Insular Woodiness

1. Examples of Insular Woodiness

Many plants with paedomorphic wood are found on islands. Insular woodiness refers to the woodiness of island plants that occur in predominantly herbaceous groups. In this context, insular means oceanic islands, continental islands, or mountainous areas near the equator. Equatorial highlands share certain characteristics with islands, such as relatively uniform yearly climates. In a sense they are “islands” of isolated flora and fauna that are distinctly different from that of the surrounding lowlands. Examples of equatorial highlands include the New Guinea highlands, the highlands of Colombia and Venezuela, and Mt. Kenya in eastern Africa (Carlquist, 1974).

Woodiness refers to the amount of secondary xylem in comparison to relatives on the mainland, or at lower elevations (Carlquist, 1970, 1974). *Sonchus leptcephalus* (Asteraceae; Canary Islands), *Brighamia insignis*, *Delissea undulata* and *Lobelia gibberoa* (Campanulaceae; Hawaiian Islands), *Scaevola kauaiensis* (Goodeniaceae; Southern Polynesian Islands), *Talinum guadalupense* (Portulacaceae; California islands), *Chimantea mirabilis* (Asteraceae; Guiana Highlands), and *Carica candamarcensis* (Caricaceae; Andes) are examples of species that have paedomorphic secondary xylem, and also insular woodiness (Carlquist, 1962, 1974).

Oceanic islands differ from continental islands in geologic origin, age, and their source of biota. Oceanic islands such as the Hawaiian and Canary Islands are of volcanic origin, and are geologically much younger than continental islands. Often they are more isolated than continental islands (but there are exceptions such as the Canaries, which are only 322 km from continental Africa) (Givnish, 1982). The entire flora and fauna of oceanic islands are necessarily derived from colonization from the mainland (Hubbell, 1968). Continental islands like New Zealand, Madagascar, and the California Islands (except perhaps Guadalupe) were once attached to continents, but were separated by rising sea levels (Hubbell, 1968; Thorne, 1969). As a result of their geologic origins, they are typically much older, and are frequently less isolated than oceanic islands (Thorne, 1969). During the time they were joined to the continents they shared the same flora and fauna. As a result, at least part of their biota is derived from direct continental contact (Hubbell, 1968).

Plants with insular woodiness have a wide variety of growth forms. Some are rosette herbs that have extended vegetative periods. This extended growth period produces elongated stems that eventually flower. Examples of plants with this growth form can be found on Hawaii (*Wilkesia gymnoxiphium*, Asteraceae), the Canary Islands (*Echium pininana*, Boraginaceae), and the Kenyan plateau (*Dendrosenecio keniodendron*, Asteraceae). Sometimes plants with rosette growth forms develop lateral branches at the base, which converts the monocarpic rosette into a shrub. The shrub-like growth form of *Stephanomeria blairii* (Asteraceae; San Clemente Island, CA) is an example of this growth form (Carlquist, 1974).

Other insular woody plants produce lateral branches from nodes beneath the inflorescences to produce a candelabrum-like growth form, as seen in some species of *Echium* (Boraginaceae; Macaronesia). Another example of a plant with this

growth form is *Euphorbia candelabrum* (Euphorbiaceae; Kenyan plateau). Axillary inflorescences that continue to grow indefinitely may occur in some woody growth forms, like *Plantago robusta* (Plantaginaceae; St. Helena), and *P. arborescens* (Canary Islands) (Carlquist, 1974). Some shrubby genera have increased in height on islands. One example of this phenomenon is the genus *Sarcopygme* (Rubiaceae, Borneo) (Carlquist, 1974).

Woody arborescent plants with erect, bloated trunks and thick main branches (the “bottle tree” or pachycaulous habit) also occur on islands. *Dendrosicyos socotrana* (Cucurbitaceae) from Socotra Island off the coast of Yemen is an example of this type of plant (Olson, 2003). Other species are woody, tree-like, and grow in very dry conditions. *Sida eggersii* (Malvaceae; West Indies) is an example of one of these species (Carlquist, 1974). Other examples are *Senecio vaccinioides* (Asteraceae) and *Hesperomeles ferruginea* (Rosaceae) from the páramos of the Andes (Carlquist, 1974).

2. Relictual and Secondary Insular Woodiness

There are two broad hypotheses for the origin of insular woodiness. One hypothesis is that plants with insular woodiness are relicts, descendants of woody continental species that are now extinct (Carlquist, 1974; Mort et al., 2004). In some cases, where the woody island plants are nearly herbaceous, they may have evolved from woody ancestors, reducing the amount of secondary growth in the process (Carlquist, 1974). This type of relictual woodiness has been described in taxa from Macaronesia (Barber et al., 2002; Goodson et al., 2006). In Macaronesia, at least some woody taxa are descended from woody continental ancestors that were once abundant, but were apparently driven to extinction either in Europe during the Pleistocene glaciation, or in Africa by desertification. In this scenario, insular woodiness is an ancestral character state, or plesiomorphy.

The second hypothesis is that plants with insular woodiness evolved from herbaceous continental ancestors (Barber et al., 2002; Carlquist, 1974; Goodson et al., 2006; Mort et al., 2002). In this scenario, insular woodiness is a derived character state, or apomorphy. Insular woodiness of this type is also a form of secondary woodiness. Although relictual insular woodiness has been found in all seven species of *Descurainia* (Brassicaceae, Canary Islands) (Goodson et al., 2006), and for all fourteen species of *Pericallis* (Asteraceae, Macaronesia) (Swenson & Manns, 2003), the evolution of secondary woodiness on islands is more common (Mort et al., 2002).

Distinguishing between a relictual and secondary origin of insular woodiness can be difficult. Many island plants have diverged so greatly from mainland ancestors that it is difficult to place them in phylogenetic analyses (Givnish, 1998; Kim et al., 1996). Typical problems involve determining the source of the original island colonizers, determining when the colonization took place, estimating the number of introductions, and determining the ancestors of the island genera (Givnish, 1998). Although morphological data has often been used to address these problems, it is sometimes difficult to tell whether a shared character state is due to common ancestry, or convergent evolution (Givnish, 1998). To address this problem, molecular sequences have increasingly been used, sometimes

in conjunction with morphological data, to determine the origin of insular woodiness.

Some examples will illustrate how these studies have been conducted. Goodson et al. (2006) used sequences from seven non-coding chloroplast regions (cpDNA; *rps16* intron, *trnDGUCtrnEUUC*, *trnEUUC-trnTGGU*, *psbZ-trnJMAU*, *rpoB-trnCGCA*, *ndhFrp132*, *ndhC-trnVUAC*) along with internal transcribed spacers (ITS) of the ribosomal DNA to investigate the phylogeny of *Descurainia* (Brassicaceae), a genus of perennial woody shrubs found in the Canary Islands. Low divergence among the cpDNA and ITS sequences of the seven species supports a recent introduction of the genus to the islands in a single colonization event. Phylogenetic reconstruction demonstrates that *D. tanacetifolia* is the closest mainland relative to the insular species of *Descurainia*. This species is perennial, with subspecies *D. tanacetifolia* ssp. *suffruticosa* being suffrutescent (woody at the base of the stem). The authors conclude that woodiness was likely present in the continental ancestors of the Canarian *Descurainia*, making insular woodiness relictual in *Descurainia* (Goodson et al., 2006). They also note that the closest continental relatives to other Canarian woody, perennial endemics in genera such as *Bencomia* (Rosaceae), *Convolvulus* (Convolvulaceae), and *Isoplexis* (Plantaginaceae) are suffrutescent perennials or shrubs.

Other studies have also found relictual woodiness on islands. A phylogenetic analysis of the fourteen species of *Pericallis* (Asteraceae) found in Macaronesia was based on morphological, molecular and combined data sets (Swenson & Manns, 2003). *Pericallis* contains both woody subshrubs and herbaceous perennials. Although not conclusive, the analysis provided evidence that the ancestral state for *Pericallis* is woody, not herbaceous (Swenson & Manns, 2003).

Firm support for relictual insular woodiness has been found for *Lactoris fernandeziana* (Lactoridaceae, Juan Fernandez Islands), based on anatomical, developmental, and molecular data (Fuertes-Aguilar et al., 2002; Mort et al., 2002). A molecular study using two chloroplast genes also supports relictual insular woodiness for the Canary Islands species *Plocama pendula* (Rubiaceae) (Andersson & Rova, 1999; Bremer, 1996; Fuertes-Aguilar et al., 2002; Goodson et al., 2006). *Tolpis* (Asteraceae), a mostly woody genus from Macaronesia, has also been found to possess relictual insular woodiness (Mort et al., 2002). In a similar manner, the molecular phylogeny for all species of *Dendrosenecio* (Asteraceae) suggests that its east African highlands ancestors were at least semi-woody (Knox & Palmer, 1995).

The hypothesis that insular woodiness is derived from mainland, herbaceous ancestors is supported in a number of taxa. *Sideritis* (Lamiaceae) is a genus of rosette plants, suffrutescent perennials, and arborescent shrubs in Macaronesia, and of suffrutescent annuals and perennials on the mainland (Barber et al., 2002). Phylogenetic analysis based on chloroplast and ITS sequences indicates an increase in woodiness among the insular members, although the ancestral habit was not firmly identified (Barber et al., 2002). The range of habit on the islands was interpreted as evidence that the taxa with insular woodiness are derived from herbaceous ancestors (Barber et al., 2002).

Molecular analyses also support derivation of insular woodiness from herbaceous ancestors in all species of *Sonchus* (Asteraceae; Macaronesia), *Lavatera phoenicea* (Malvaceae; Canary Islands), most species of *Echium* (Boraginaceae; Macaronesia),

in *Aichryson bethencourtianum*, *A. tortuosum* and all species of *Aeonium* (all Crassulaceae; Macaronesia), and all species of the Hawaiian silversword genera *Argyroxiphium*, *Wilkesia* and *Dubautia* (Asteraceae) (Baldwin & Sanderson, 1998; Bohle et al., 1996; Fairfield et al., 2004; Fuertes-Aguilar et al., 2002; Kim et al., 1996; Mort et al., 2002).

3. Hypotheses to Explain the Evolution of Insular Woodiness

There are several hypotheses that attempt to explain why plants with secondary insular woodiness have evolved from herbaceous ancestors. Two of the older hypotheses are Darwin's (1859) competition hypothesis, and Wallace's (1878) longevity hypothesis.

When Darwin (1839) visited the Galapagos Islands during his famous voyage on the *Beagle*, he noticed that the tree sunflowers (*Scalesia*, Asteraceae) growing there were woody. He hypothesized, based on their observed distributions, that while trees were unlikely to reach the islands (he was unsure why this was), herbaceous plants would be successful. The herbaceous plants that were successful could gain a competitive advantage by growing taller. This would lead to selective pressure for increased woodiness, which would eventually lead to arborescence (Darwin, 1859; Givnish, 1998). Since seeds or spores of land plants have to be capable of dispersing over long distances to reach and colonize islands (Givnish, 1998), the large size and lower viability of seeds from continental trees may preclude them from colonizing islands (Carlquist, 1974). The fact that the open, or partially open, habitats found on islands early in their colonization lend themselves to colonization by sun adapted herbs also supports Darwin's hypothesis. Open habitats are likely to be visited by birds that release seeds via endozoochory (dispersal of seeds from the digestive tract) or ectozoochory (dispersal of seeds stuck to feathers or skin) from similar environments on the mainland. As the colonists become established, there will be a gradual increase in plant coverage, which will select for the evolution of increased stature that will likely be accompanied by increased woodiness. Thus, some of the colonists gain an advantage over other plants in the competition for light by growing taller (Givnish, 1998). The increase in woodiness that accompanies the change from open to forest habitats is sometimes referred to as an ecological shift (Carlquist, 1974). In many cases the woodier herbs are found in the understory in less open habitats, or occupy forested areas. They may also grow in scrub habitats (Carlquist, 1974).

Darwin's competition hypothesis has been supported by simulation models and quantitative measurements in several studies (Givnish, 1982; Givnish, 1998; Tilman, 1988). In the ALLOCATE simulation 100 species that differed in their allocation to roots, leaves, and stems competed for a limiting resource and light over ten simulated years (Tilman, 1988). In nutrient poor soil, species with a high allocation to leaves (and high relative growth rates) initially dominated. These species were eventually out competed by species that had lower allocations to leaves, but greater allocations to roots. None of the plants which dominated at any point in nutrient poor soil had high allocations to stems. They were rosette plants. In three other scenarios, each having progressively richer soils, species with a high

allocation to leaves and low allocation to stems initially dominated. However, over time these species were replaced by plants with higher allocations to stems and roots. The dominant species at the end of the ten year simulation period had a greater allocation to stems than leaves in all three of the nutrient rich plots (Tilman, 1988). This suggests that woody plants will be favored under these conditions.

Field studies and observations also support the competition model. A study of 72 herbaceous species found along a gradient from a dry oak to a floodplain forest used data on leaf coverage (the average density of foliage within a m^2 plot) and maximum leaf height (plant size) to investigate the adaptive significance of height in herbaceous plants in forests (Givnish, 1982). Each species was placed into a maximum leaf height category, and leaf coverage for each was estimated at 13 intervals for each plot. Maximum leaf height was correlated with the average density of leaf coverage in the habitat. With each 7% increase in herbaceous leaf cover, maximum leaf height roughly doubled (Givnish, 1982). The correlation between plant height and percent cover confirms a prediction of Darwin's hypothesis.

A similar relationship between leaf height and density of leaf coverage was found in a field study of orchids in the northeastern United States. Taller species like *Cypripedium reginae*, *Platanthera (Habenaria) ciliaris*, and *P. (Habenaria) dilatata* were found in habitats such as meadows, bogs, and swamps where there are dense layers of herbaceous competitors. Species of intermediate height like *Cypripedium candidum*, and members of the genera *Calopogon* and *Arethusa*, occurred in less dense communities. The shortest orchids were found in habitats with low densities of competitors, heavy shade, or both. For example, the basal leaved *Habenaria straminea* grew in open sites with little competing vegetation, while the caulescent *Cypripedium arietinum* was found in shady woods with low densities of competitors (Givnish, 1982).

In contrast to Darwin's competition hypothesis, Wallace (1878) hypothesized that woodiness would evolve in herbaceous island colonists as a way to extend their life span. With greater longevity would come more flowers, which would allow a greater chance for cross-pollination by insect pollinators, which were then thought to be less common on islands (Carlquist, 1974; Givnish, 1998; Jorgensen & Olesen, 2001; Wallace, 1878). Unfortunately, this hypothesis has not been well supported. First, many plants can self-pollinate, obviating the need for insect pollination. Also, it turns out that insect pollinators are not uniformly rare on islands. They tend to be either very abundant (if they have no competitors), or else they are entirely absent if they have not dispersed to the island (Carlquist, 1974; Givnish, 1998).

Some support for Wallace's (1878) longevity hypothesis has come from a study of *Echium*, a genus of mostly woody perennials from Macaronesia. All but two of the island species (*E. bonnetii* and *E. pitardii*) are woody, while the continental species of *Echium* are predominately herbaceous (Bohle et al., 1996). The study used noncoding DNA from the chloroplast (*trnT*_{UGU}-*trnL*_{UAA} spacer, *trnL*_{UAA} intron, *trnL*_{UAA}-*trnF*_{GAA} spacer) and nuclear genomes (18S-5.8S ITS-1 region). The DNA was isolated, amplified and sequenced, and the sequences were aligned visually. Phylogenetic trees were constructed using maximum parsimony and neighbor

joining methods. The resulting phylogeny supports the idea that the island species are derived from continental ancestors. In addition, two length polymorphisms (indels) in common between the island and the continental species provided support for a single, mainland-to-island invasion, with rapid speciation by the colonizers (Bohle et al., 1996).

The woody habit of insular *Echium* has been hypothesized to be an adaptation that helped prevent inbreeding depression in the geographically isolated founding populations (Bohle et al., 1996). *Echium* is insect pollinated. Since the islands of Macaronesia are insect poor, it is unlikely that its initial environment on the islands would have contained many insects. Under these conditions, increased woodiness would extend the life of the plant and would be expected to provide an opportunity for increased pollination. Since the mainland, herbaceous members of *Echium* show inbreeding depression, it is likely that the colonizing species would also have had this characteristic. This would have led to selection for outbreeding among the founding members of the species. Selection for outbreeding could be expected to lead to the large inflorescences found in the current island species. These large inflorescences could help attract pollinators, while the woody habit would provide the structural support necessary to produce the inflorescences.

A third hypothesis for the evolution of woodiness in insular plants was stimulated by the observation that islands have moderate climates (Carlquist, 1974; Jorgensen & Olesen, 2001). Island climates are either uniform throughout the year, or else have their climatic extremes moderated by oceanic influences. Climatic moderation includes moderate annual temperatures, adequate and uniform rainfall, and high humidity. Moderate annual temperatures means temperature ranges of 10–25°C (Hawaii, Fiji, New Caledonia), or 5–20°C (Juan Fernandez, St. Helena). Annual rainfall of at least 1,000 mm is found on islands such as Juan Fernandez and St. Helena, at least at sea level. In association with rainfall, high humidity resulting from the nearby ocean can provide insulation against temperature fluctuations. High humidity also helps reduce transpiration, as well as evaporation from the soil. Humidity in some locations in Hawaii averages 81%, while in the Canary Islands 75% humidity is not uncommon (Carlquist, 1974). Moderation in these components provides a release from seasonality for the island plants, so that continuous growth is possible. Continuous growth allows a root system that can support more leaf growth and greater arborescence (woodiness), which permits additional photosynthesis (Carlquist, 1974).

Some small evidence against this hypothesis comes from the *Echium* study (Bohle et al., 1996). In moderate climates comparable to that of Macaronesia, such as the Iberian Peninsula, this hypothesis predicts that *Echium* should be woody, as it is in Macaronesia. However, all species of *Echium* on the Iberian Peninsula are herbaceous.

The final hypothesis for the evolution of insular woodiness is related to the absence of herbivores on islands. The presence of large herbivores tends to select for rapid completion of plant life cycles in order to avoid predation. Release from this selective pressure allows plants to complete their life cycles, and to exploit climatic moderation. Thus, rather than being consumed, the plants enjoy year-round growth, which eventually favors the evolution of increased woodiness and perennial growth forms (Carlquist, 1974; Jorgensen & Olesen, 2001). Supporting this idea is the fact

that on islands where herbivores have been introduced predatory pressure has prevented the reproduction of some woody plants. On these islands, only annuals and woody plants on inaccessible cliffs tend to survive. On other islands such as Hawaii, the effect of long-term herbivory is drastic enough to threaten the survival of some woody, and woody herbaceous species (Carlquist, 1974).

D. Secondary Woodiness

Like paedomorphosis and insular woodiness, the term secondary woodiness is not always used consistently in the literature. Secondary woodiness is best described as the evolution of secondary xylem in plants with herbaceous ancestors (Carlquist, 1974, 1992; Lens et al., 2005a). The term itself suggests that woodiness was lost, and then reappeared during later evolution (Isnard et al., 2003). It also implies that primary woodiness, a term rarely used in the literature, exists. Primary woodiness may be inferred to mean woodiness derived from a woody ancestor (i.e., plesiomorphic woodiness) (Carlquist, 1995b; Carlquist, 2003).

As has been made clear above, neither the existence of paedomorphosis nor insular woodiness means that secondary woodiness must necessarily be present. It is true that many plants with paedomorphic wood are secondarily woody, and that insular woodiness is frequently associated with secondary woodiness, but the correlations between these characteristics are not absolute. The mere existence of paedomorphic characteristics is insufficient to determine if a plant has secondary woodiness. Likewise, the existence of insular woodiness is not incontrovertible evidence of secondary woodiness (Kim et al., 1996). In some cases, insular woodiness has been found to be plesiomorphic (relictual). Nor can insular woodiness be equated with paedomorphosis. Plants with insular woodiness may or may not have paedomorphic wood. Phylogenetic analysis must be used to resolve these questions. We return to these points in the [Discussion](#).

IV. Stem Structure and Wood Anatomy in *Xanthorhiza simplicissima*, *Coreopsis gigantea*, and *Mahonia bealei*

A. Overview

In order to investigate the relationship between paedomorphosis and secondary woodiness in a specific context, three potentially secondary woody species were chosen for study. Carlquist (1995b) reports the presence of paedomorphic rays in *Xanthorhiza simplicissima*, and suggests that this species may be secondarily woody. However, he recommends study of larger, older stems to confirm the ray type (Carlquist, 1995b). Both Carlquist (1974, 1985) and Thorne (1969) consider *Coreopsis gigantea* to be an example of insular woodiness, but neither addresses the issue of secondary woodiness. Carlquist (1995b) suggested that *Mahonia bealei* might be secondarily woody based on interpretations of the position of the genus in published cladograms (Loconte & Estes, 1989; Qiu et al., 1993). Loconte and Estes (1989) hypothesize a woody ancestor for Berberidaceae, with a shift to herbaceousness, and then a shift back to woodiness for the branch bearing the

genera *Berberis* and *Mahonia*. Investigation of these three species provides the opportunity to discuss the concepts of paedomorphosis, insular and secondary woodiness in a specific context.

B. Organography and Anatomy

1. *Xanthorhiza simplicissima*

Xanthorhiza simplicissima (yellowroot) is a monotypic, perennial, small deciduous shrub. Its stems rarely reach more than a meter in height, and 3–10 mm in diameter. Younger stems are relatively erect, while older stems may become partly procumbent (Fig. 2a). Very young stems have a ring of lignified primary fiber bundles similar to those found in species of *Clematis* (Isnard et al., 2003). Older stems have dense wood with small groups of relatively narrow diameter vessels, and conspicuous large unlignified rays. The dense wood found in *X. simplicissima* is rare in the Ranunculaceae (Isnard et al., 2003; Rowe et al., 2004).

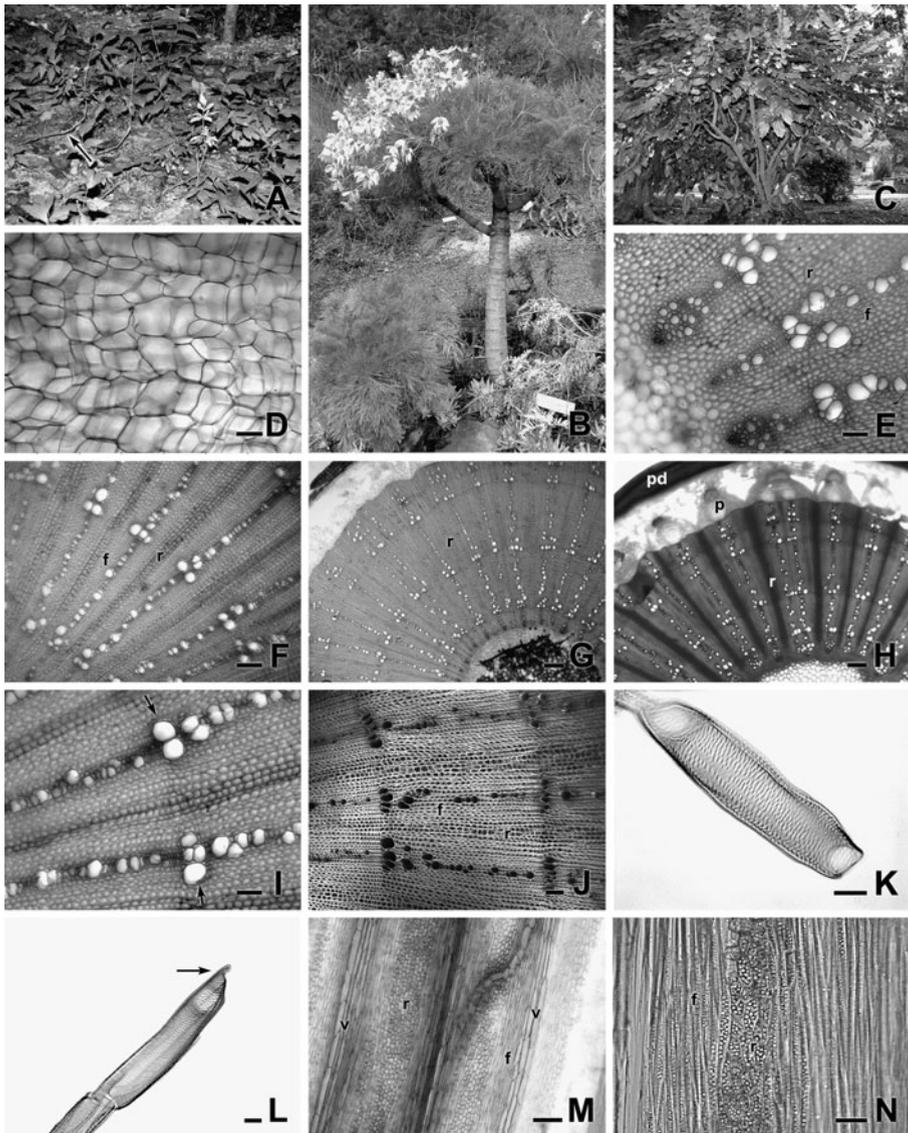
The leaves of *X. simplicissima* are alternate, pinnately or bipinnately compound, are usually divided into three to five leaflets that are serrate to deeply toothed, and have long slender petioles (Fig. 2a). The bark is gray-brown and smooth, with the inner bark yellow-colored due to the presence of berberine. The flowers are yellow to purple-brown, have five petals, and appear in early spring. Individuals are usually found in shady, damp woods near water, from New England to northern Florida. Yellowroot was widely used for medicinal purposes by Amerindians. It has also been used in folk medicine in the American South (Reed, 2004; Seiler et al., 2008).

Many Ranunculaceae are reported to be annuals with short-lived stems and only primary growth, though recent studies have begun to question these descriptions (Table 1) (Schweingruber & Landolt, 2005–2008). *Clematis* and *Xanthorhiza*, at least, are exceptions to these rules for they have distinctly woody stems. However, in neither case are the stems strongly self-supporting. Growth forms in these genera include lianas, creepers, and small shrubs which are either partially self-supporting or procumbent (Isnard et al., 2003; Rowe et al., 2004).

Fig. 2 a. *Xanthorhiza simplicissima* growing along a stream bank in southern Guilford County, NC. Note the weak stems that become horizontal with growth (arrow). b. *Coreopsis gigantea* at the Berkeley Botanical Garden. c. *Mahonia bealei* growing on the UNCG campus. D–N. *Xanthorhiza simplicissima*. All images LM except J, confocal. d. Pith cells in tangential section. bar=50 µm. e. Transverse section. Primary, and earliest formed secondary xylem. The vessels are embedded in fibers (f). r ray. bar=50 µm. f. Transverse section of two growth rings with vessels embedded in fibers (f), separated by rays (r). bar=100 µm. g. Transverse section of pith and five rings of secondary xylem. r=rays. bar=200 µm. h. Xylem with five growth rings in transverse section. The rays (r) are all continuous with the interfascicular regions of the primary plant body. p=phloem, pd=periderm, bar=200 µm. i. Transverse section of larger vessels of the earlywood at the transition (arrows) between growth rings. bar=50 µm. j. Two transitions between growth rings are clearly visible in transverse section, as are differences in cell wall thickness between the rays (r) and fibers (f). bar=40 µm. k. Maceration. Vessel element with an alternating pattern of pits, and simple perforation plates. bar=20 µm. l. Maceration. Vessel element with caudate tip (arrow). bar=20 µm. m. Tangential section with portions of a high ray (r), non-storied vessels (v), and non-storied fibers (f). bar=200 µm. n. Tangential section showing non-storied, starch-filled ray cells (r), surrounded by non-storied fibers (f). The fibers closest to the rays contain starch. bar=50 µm

2. *Coreopsis gigantea*

Although most Asteraceae are herbaceous, some family members have structural forms that include herbs, shrubs, and trees (Cronquist, 1955; Heywood et al., 1977; Metcalfe & Chalk, 1950). Of these forms, the herbs and shrubs tend to be found in regions where there is the greatest phyletic diversity of other taxa. This is frequently the xeric montane areas of subtropical and tropical North and South America. In contrast, trees or tree-like forms tend to be found in areas of low phyletic diversity, such as middle and low tropical or subtropical rain forests. They also occur as insular endemics (Heywood et al., 1977).



Coreopsis gigantea, giant Coreopsis, is a perennial shrub ranging from 0.45 m to 1.2 m tall (Fig. 2b). It occurs on rocky ocean cliffs and dunes of the coast sage shrub and coastal strand plant communities of California. It is drought tolerant, grows best under full sun, and lives in well-drained soil. The leaves are fern-like and pinnately divided into linear segments clustered at the ends of the branches. It blooms March to May with flowers that resemble the common daisy. The heads occur in cymes on long scapiform peduncles. Although Carlquist (1985) classified *C. gigantea* as an herb due to its degree of succulence, it does not fit well into this, or any, common category of growth forms. The trunk of *C. gigantea* is sturdy, though somewhat more pliable than a small tree. It usually has a cluster of small branches at the top (Fig. 2b) (Keil, 1993; USDA & NRCS, 2009).

3. *Mahonia bealei*

The Berberidaceae consists of both herbs and shrubs from mostly Northern temperate regions, with some species from the Andes. Species occur in habitats ranging from forest understories, to arid regions and deserts. The family often contains alkaloids such as berberine, an isoquinoline that colors the wood yellow (Judd et al., 2002; Metcalfe & Chalk, 1950). Phylogenetic study places the family as the sister group to the Ranunculaceae (Hoot et al., 1999). The 70 species of *Mahonia* are evergreen shrubs native to eastern Asia, North and Central America. Several species are grown ornamentally.

Mahonia bealei is a typical example of the cultivated members of the genus. It is a 0.5–4(–8) meters tall evergreen, perennial shrub native to eastern Asia (Fig. 2c). In China it occurs in forests, forest margins, weedy slopes, streamsides, roadsides, and thickets at 500–2000 m (Ying et al., 2010). Its leaves are alternate and pinnately compound, and composed of nine to fifteen opposite, ovate leaflets that have spiny dentate margins. The yellow flowers emerge in spring and, in late summer, produce blue-black berries covered in a waxy white bloom. It grows in a rounded, open, irregular habit with upright branching (Kling et al., 2008).

C. Materials and Methods

Specimens of *Xanthorhiza simplicissima* Marsh. (Fig. 2a) were collected from three sites in North Carolina: Guilford County (the Randleman Lake area), Randolph County (Little River at Pisgah Covered Bridge; voucher: NCU 589175, 589174), and Transylvania County (the Avery Creek area of Pisgah National Forest). *Coreopsis gigantea* (Kellogg) H. M. Hall (Fig. 2b) was collected from the University of California at Berkeley Botanical Garden (accession number: 60.0129). *Mahonia bealei* (Fortune) Carr. (Fig. 2c) was collected in Guilford County, North Carolina on the campus of the University of North Carolina at Greensboro (voucher: NCU 589177, 578176), and at 309 Waverly Way, Greensboro, NC.

All plant material was stripped of leaves, and the stems cut into short sections of approximately 2.5 cm length. The sections were then fixed in either FAA (formalin-acetic acid-alcohol), or Karnovsky's fixative (Berlyn & Miksche, 1976; Ruzin, 1999).

Following fixation, slides for microscopic study were made from either stem sections, or macerated tissue. Stems with diameters of 3.5, 4.0, 4.5, 5.0, and

6.0 mm were used for measurements and observations of *Xanthorhiza simplicissima*, with the larger diameters (4.5, 5.0, 6.0 mm) utilized predominately. A small stem with a diameter of 19.0–23.0 mm, and a larger stem with a diameter of 52.0–58.0 mm were used from *Coreopsis gigantea*. Mostly larger stems (8.0, 8.5, 9.5 mm diameters) were sectioned for *M. bealei*, but some 6.0 mm diameter stems were also used. Stem sections (transverse, radial, and tangential) were made either by hand using a razor blade, or with an American Optical Model 860 sliding microtome.

After sectioning, all sections were transferred to 50% ethyl alcohol. The sections were then stained with 1% safranin in 95% ethyl alcohol, which was sometimes followed with fast green (Ruzin, 1999). Following staining, the sections were either mounted directly, or washed with 95% and 100% ethyl alcohols, and finally Clear Rite II (Richard-Allan Scientific, Kalamazoo, MI), in place of Xylene. The sections were placed on glass slides and covered with either Richard-Allan Slide Preparation Mounting Medium (Richard-Allan Scientific, Kalamazoo, MI) or, for sections mounted from aqueous media, Karo Light Corn Syrup (ACH Food Companies, Inc., Memphis, TN), followed by cover slips.

For observation with the confocal microscope specimens fixed in FAA were sectioned by hand using a razor blade to prepare transverse, tangential, or radial sections. The sections were stained with 1% safranin in 50% ethyl alcohol for twenty to thirty minutes, and then dehydrated through a graded acetone series at 15–30 minute intervals, at concentrations of 30%, 50%, 75%, 90%, and 100% acetone. The sections were then rehydrated through a graded acetone series (90%, 75%, 50%, 30%, 10% acetone) to distilled water using the same time intervals (Kitin et al., 2002; Kitin et al., 2000). Finally, the sections were cleared in a graded glycerol series (25%, 50%, 75%, 100% glycerol). Specimens were kept in each glycerol solution for at least one hour. The cleared sections were mounted on glass slides using 100% glycerol, cover slipped, and photographed with an Olympus FluoView™ FV500 confocal laser scanning microscope (Kitin et al., 2000).

Macerations were prepared following Gifford's method after first removing the periderm from the stems (Ruzin, 1999). Once maceration was complete, the tissue samples were washed with distilled water and transferred to 50% ethyl alcohol. Samples were placed on glass slides, teased apart, and stained for ten minutes with 1% safranin in 95% ethyl alcohol. The stained tissue was washed in several changes of 95% followed by 100% ethyl alcohol. A final wash with Clear Rite was completed before the macerations were placed on slides and covered with Richard-Allan Mounting Medium (Ruzin, 1999).

Olympus CH-2 and Leitz Ortholux II light microscopes were used to take measurements of cells and tissues, as well as for general tissue observation. Photographs were taken on a Nikon Eclipse E600 light microscope equipped with a Diagnostic Instruments, Inc. Model 2.2.1 Revision 2 digital camera, and SPOT Advanced Software 4.0.8, and on a Leitz Ortholux II light microscope equipped with a Leica DFC420 digital camera and Image-Pro Express 6.0 software. Field photographs were taken with a Nikon CoolPix 5700 model digital camera. The tonal qualities of the images were adjusted, labels were added, and plates assembled with Adobe Photoshop CS, CS3 and CS4. Figure 1 was redrawn from Carlquist (1962) in Adobe Illustrator CS.

Cell dimensions were measured at the longest and widest points of the cells. For vessel elements, measurements included the cell walls and caudate tips. Measurements for vessel elements and fibers came from macerations. Trends of vessel element lengths across the secondary xylem were determined from measurements taken from radial sections. Vessel element lengths were measured across the width of the xylem, from xylem formed at the edge of the pith to that adjacent to the vascular cambium.

Widths of rays were measured in tangential sections, while ray cell dimensions (height and width) were measured in radial sections. Tangential sections were used to determine if vessel elements exhibited storying (adjacent elements with end walls aligned with each other). Radial sections also provided insight into the extent of vessel, ray, and fiber storying. The mean number of vessels per group, vessel restriction patterns, and vessel distribution were determined from transverse sections.

Statistical analyses were carried out with Minitab 15 statistical software (Minitab Inc., 2006), and SPSS (SPSS, 2006). Scatterplots with least squares regression lines of vessel element lengths from across the width of the xylem were constructed in SPSS and refined in Adobe Illustrator CS3. LOWESS (Locally Weighted Scatterplot Smoother) curves were also plotted in SPSS. LOWESS is a robust method of smoothing scatterplots by using locally weighted regression, which minimizes the influence of outliers on the smoothed lines (Cleveland, 1979, 1981).

A word of caution about the statistical analysis is appropriate. Since only a few plant samples were taken from a limited number of sites, it is not statistically valid to make inferences about the species populations based on these results. To ensure statistically robust inferences about the population, an appropriate random sampling design would be necessary (Ramsey & Schafer, 2002). While most plant anatomical studies fall short in this area, means are still calculated and used in traditional plant studies. In light of this fact, the means and other measurements provided here may still provide useful insights.

To determine if the study species are secondarily woody, the character states “woody” and “nonwoody” were plotted on recent phylogenies containing the study taxa. The tree of Kim et al. (2004a) was used to determine the origin of woodiness in *Xanthorhiza*. For *Coreopsis* we used Mort et al.’s (2004) phylogeny of the western clade of *Coreopsis* (Archibald et al., 2005; Mort et al., 2004). Kim et al.’s (2004a) phylogeny of the Berberidaceae was the basis for determining if secondary woodiness is present in *Mahonia*.

In order to determine if the other taxa on these phylogenetic trees are woody, a character matrix was created based on the published descriptions of each taxon. Information such as habit, longevity, and morphological descriptions of the taxa were used to judge the likelihood of woodiness in the taxa (Tables 2, 3, and 4). Except for in *Coreopsis*, determinations of woodiness were based on our subjective probability of the presence of a significant amount of fibrous wood in each species. Use of this rather strict definition of wood is necessary because recent work has shown that many taxa previously considered to lack secondary growth actually possess it (Dietz & Ullmann, 1997; Dietz & Schweingruber, 2002; Krumbiegel & Kästner, 1993; Schweingruber, 2006; Schweingruber, 2007a; Schweingruber & Poschlod, 2005; Schweingruber & Landolt, 2005–2008). We return to this issue in the Discussion. Once each of the taxa was assigned a character state (woody or

Table 2 Probability Assessment for the Presence of Fibrous Wood in Taxa Related to *Xanthorrhiza*

Taxon	Habit	Habit References	Duration	Duration References	Description	Description References	Probability of Wood	Character Coding
<i>Copitis</i>	Herbaceous	Kim et al., 2004a	Perennial	USDA & NRCS, 2009	Stem height 7.6–15.2 cm	Novak & Lemmon, 2005	Very low	Absent
	Herbaceous (<i>C. trifolia</i> , <i>C. laciniata</i> , <i>C. groenlandia</i>)	Bratton, 1976; Halpern, 1989; USDA & NRCS, 2009	(<i>C. trifolia</i>)	USDA & NRCS, 2009	Small stature herb	Halpern, 1989		
<i>Xanthorrhiza</i>	Woody	Kim et al., 2004a	Perennial	Isnard et al., 2003	The wood is like that of a small shrub.	Carlquist, 1995a	Very high	Present
	Woody shrub or subshrub	Isnard et al., 2003			It produces weakly upright woody stems. It grows no more than 60 cm tall.	Isnard et al., 2003		
<i>Ranunculus</i>	Herbaceous	Hoot, 1991; Iudd et al., 2002; Kim et al., 2004a; Stebbins, 1938	Perennial	Hoot, 1991	<i>R. repens</i> is a creeping low growing perennial herb with prostrate to nearly erect stems (20–30 cm tall).	Miller, 2003	Low to moderate; absence confirmed from Schweingruber & Landolt, 2005–2008	Absent
	Herbaceous (<i>R. repens</i> ; <i>R. longirostris</i> , <i>R. hispidus</i>)	Miller, 2003; USDA & NRCS, 2009	Perennial (<i>R. repens</i> ; <i>R. longirostris</i> , <i>R. hispidus</i>)	USDA & NRCS, 2009				
<i>Hydrastis</i>	Herbaceous	Kim et al., 2004a	Perennial	Stebbins, 1938	<i>R. longirostris</i> is a semi-erect perennial herb (30.5 cm tall), <i>R. hispidus</i> is a perennial herb with a single erect stem (76.2 cm tall).	USDA & NRCS, 2009		
	Herbaceous (<i>H. canadensis</i>)	Sinclair & Catling, 2001						
<i>Glaucidium</i>	Herbaceous	Kim et al., 2004a	Perennial	Sinclair & Catling, 2001	<i>H. canadensis</i> is a herbaceous perennial with a stem 30 cm tall that grows in mesic woods.	Sinclair & Catling, 2001	Presence of wood confirmed from Carlquist, 1995a	Present
	Herbaceous (<i>G. palmatum</i>)	Sinclair & Catling, 2001						
<i>Caulophyllum</i>	Herbaceous	Kim et al., 2004a	Perennial	Kumazawa, 1930	<i>G. palmatum</i> is an herbaceous perennial (45–60 cm tall).	Kumazawa, 1930	Presence of wood confirmed from Carlquist, 1995a	Present
	Herbaceous	Kumazawa, 1930						
<i>Nandina</i>	Herbaceous (<i>C. thalictroides</i>)	Kim et al., 2004a; Mescham, 1980	Perennial (<i>C. thalictroides</i>)	USDA & NRCS, 2009	<i>C. thalictroides</i> is an erect herbaceous perennial with a multiple stem growth form (76.2 cm tall).	USDA & NRCS, 2009	Moderate	Absent
	Woody	Kim & Jansen, 1998; USDA & NRCS, 2009						
<i>Nandina</i>	Herbaceous (<i>C. thalictroides</i>)	Kim & Jansen, 1998; USDA & NRCS, 2009	Perennial (<i>C. thalictroides</i>)	USDA & NRCS, 2009	<i>N. domestica</i> is an evergreen shrub that grows 180 cm tall. It is found in multistemmed	Florida Exotic Pest Council, 2008	Very high	Present
	Woody	Florida's Plant Encyclopedia, 2008; Kim & Jansen, 1998;	Evergreen perennial	Florida Exotic Pest Plant Council, 2008; Floridatlas				

Table 2 (continued)

Taxon	Habit	Habit References	Duration	Duration References	Description	Description References	Probability of Wood	Character Coding
	Shrub	Kim et al., 2004a Florida Exotic Pest Plant Council, 2008; Florida's Plant Encyclopedia, 2008; Loconte & Estes, 1989		Plant Encyclopedia, 2008	clumps. <i>N. domesica</i> is a woody evergreen shrub with multiple nonbranching stems (180–240 cm tall).	Florida's Plant Encyclopedia, 2008		
<i>Menispermum</i>	Woody	Kim et al., 2004a; Myers, 1924; Stebbins, 1938 USDA & NRCS, 2009	Perennial	USDA & NRCS, 2009	The stem of <i>M. canadense</i> contains 8 vascular bundles.	Dormer, 1954	Very high	Present
	Vine (<i>M. canadense</i>)							
	Vine or liana (<i>M. canadense</i>)	Myers, 1924			<i>M. canadense</i> is a vine or liana twining to 5 m. It usually twines around a small tree or shrub. It has vascular bundles and medullary rays.	Myers, 1924		
<i>Tinospora</i>	Woody	Kim et al., 2004a	Perennial	Foreman, 1988	<i>T. caffra</i> is a liana which twines around its host.	Senbeta et al., 2005	Very high	Present
	Woody (<i>T. caffra</i> , <i>T. siamensis</i>)	Foreman, 1988; Senbeta et al., 2005			<i>T. siamensis</i> is a slender woody climber up to 10 m tall. Its glabrous stems are up to 2 cm in diameter.	Foreman, 1988		
<i>Akacia</i>	Woody	Kim et al., 2004a	Perennial (<i>A. quinata</i>)	Swearingen et al., 2006	<i>A. quinata</i> is a woody perennial plant that grows as either a climbing vine, or as ground cover.	Swearingen et al., 2006	Very high	Present
	Woody (<i>A. quinata</i>)	Swearingen et al., 2006						
<i>Singnifanchétia</i>	Woody	Gianoli, 2004; Kim et al., 2004a Loconte & Estes, 1989	Perennial	Fern, 1997–2003	<i>S. chinensis</i> is a deciduous climber that twines around other plants. It grows 15 m tall.	Fern, 1997–2003	Very high	Present
<i>Decaisnea</i>	Vine							
	Woody	Kim et al., 2004a; Stebbins, 1938	Perennial	Fern, 1997–2003	<i>D. fargesii</i> is a deciduous shrub which grows 4 m tall.	Fern, 1997–2003	Very high	Present
	Woody (<i>D. fargesii</i>)	Baneroff, 1930						
	Shrub	Loconte & Estes, 1989						

<i>Circaea</i>	Herbaceous	Kim et al., 2004a; Locoite & Estes, 1989; Takhtajan, 1997 eFloras, 2008	Annual or perennial	Takhtajan, 1997	C. <i>agrestis</i> is an herb 3–10 cm tall.	eFloras, 2008	Very low	Absent
<i>Kingdonia</i>	Herbaceous (C. <i>agrestis</i>)	Balfour & Smith, 1914; Kim et al., 2004a; Laconte & Estes, 1989	Perennial	Balfour & Smith, 1914	<i>K. uniflora</i> is a glabrous plant with a flowering stem 7–12 cm tall. The stem has one basal leaf.	Balfour & Smith, 1914	Low	Absent
<i>Dicentra</i>	Herbaceous	Kim et al., 2004a	Perennial (D. <i>cullaria</i> , D. <i>spectabilis</i>)	eFloras, 2008	<i>D. cullaria</i> is a perennial with a scapose stalk.	eFloras, 2008	Low, but 2 ^o growth confirmed from Schweingruber & Landolt, 2005–2008	Absent
<i>Pteridophyllum</i>	Herbaceous	Walton & Hufford, 1994	Geophyte			Kemper Center for Home Gardening, 2001–2009		
<i>Hypocoon</i>	Herbaceous (P. <i>racemosum</i>)	Kadereit et al., 1995; Kim et al., 2004a	Perennial	Tani et al., 2001	<i>D. spectabilis</i> is an herbaceous perennial 30.5–91.4 cm tall.	Tani et al., 2001	Low	Absent
<i>Clematis</i>	Shrub, half-shrub	Tani et al., 2001	Perennial or biennial	Kadereit et al., 1995	<i>P. racemosum</i> is an evergreen perennial herb found in the understory.			
<i>Euptelea</i>	Woody	eFloras, 2008; Kim et al., 2004a	Annual	eFloras, 2008	<i>H. leptocarpum</i> is a procumbent to erect annual, profusely branched at the base. The stem is 15–30 cm tall, with basal leaves.	eFloras, 2008	Low to moderate	Absent
	Deciduous tree (E. <i>polyandra</i> , E. <i>pleiosperma</i>)	USDA & NRCS, 2009	Annual (H. <i>imberbe</i> , H. <i>pendulum</i>)	USDA & NRCS, 2009				
	Tree or shrub (E. <i>polyandra</i>)	Tamura, 1993	Perennial with woody base	Tamura, 1993	Wood has been described by Carlquist.	Carlquist, 1995a	Very high	Present
		Kim et al., 2004a	Perennial	Fern, 1997–2003	<i>E. polyandra</i> is a deciduous tree (8 m tall). <i>E. pleiosperma</i> is a deciduous tree (9 m tall).	Fern, 1997–2003	Very high	Present

Table 3 Probability Assessment for the Presence of Woody Tissue in Taxa Related to *Coreopsis*

Species	Habit	Habit References	Duration	Duration References	Description	Description References	Probability of Wood	Character Coding
<i>Coreopsis douglasii</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Small (6–20 cm tall) annual with leaves entirely basal	Smith, 1984	Very low	Absent
<i>C. californica</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Annual (10–30 cm tall) with leaves entirely basal	Smith, 1984	Low	Absent
<i>C. stillmanii</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Small (8–20 cm tall) annual with leaves mostly or entirely basal	Smith, 1984	Very low	Absent
<i>C. bigelovii</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Annual (10–35 cm tall) with leaves mostly basal	Smith, 1984	Low to moderate	Absent
<i>C. hamiltonii</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Herbaceous annual, somewhat fleshy stemmed	Smith, 1975	Low to moderate	Absent
<i>C. callitropsidea</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Annual	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Annual (8–40 cm tall)	Smith, 1984	Low to moderate	Absent
<i>C. gigantea</i>	Herbaceous	Jansen et al., 1987; Smith, 1975	Perennial	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Herbaceous annual, somewhat fleshy stemmed Perennial with stout thick stems and large dissected leaves	Smith, 1975 Crawford & Whitkus, 1988	Very high	Present
<i>C. maritima</i> ^a	Herbaceous	Jansen et al., 1987; Smith, 1975	Perennial	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004; Smith, 1975	Large (1–2 m tall) fleshy stemmed (stems 4–10 cm in diameter) perennial Herbaceous perennial, fleshy stemmed Perennial with stout thick stem	Smith, 1984 Smith, 1975 Crawford & Whitkus, 1988	High	Present
<i>C. petrophila</i>	Woody Frustrucose	Jansen et al., 1987 Smith, 1975	Perennial	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004	Smaller (0.3–0.8 m) perennial, with hollow stems (1–2 cm in diameter) Herbaceous perennial, fleshy stemmed	Smith, 1984 Smith, 1975	Very high	Present
Section Pseudo-	Suffrutucose to fruticose Suffrutucose	Crawford, 1976 Crawford, 1976	Perennial	Archibald et al., 2005;	Stems 30–150 cm tall, profusely branched, glabrate Fruticose small shrub Suffrutucose to fruticose	Crawford, 1976 Smith, 1975	Very high	Present

Agaristia (for <i>C. senaria</i>)			Mort et al., 2004						
<i>C. nutica</i>	Woody Suffruticose to fruticose	Jansen et al., 1987 Sherff, 1936 Crawford, 1976	Perennial	Archibald et al., 2005; Jansen et al., 1987; Mort et al., 2004	Large shrub over 3 m tall, with most individuals 1–3 m tall Small shrub.	Crawford, 1982 Smith, 1975	Very high	Present	
<i>C. cyclocarpa</i>	Woody	Jansen et al., 1987; Crawford, 1982	Perennial	Archibald et al., 2005; Crawford, 1982; Jansen et al., 1987; Mort et al., 2004; Sherff, 1936; Smith, 1975	Herbaceous with several stems from the base Woody perennial Herbaceous perennial	Smith, 1975 Crawford, 1982 Sherff, 1936	High	Present	
<i>Dalhlia coccinea</i>	Herbaceous Suffruticose	Sherff, 1936; Smith, 1975 Crawford, 1976, 1982	Perennial	Archibald et al., 2005; Mort et al., 2004	Tuberous perennial	Harris, 2008	Low to moderate	Absent	

^a *C. maritima* is in the same section as *C. gigantea* (sect. Tuckermannia). Synthetic hybrids between these species are highly fertile, and they may be semispecies (Crawford & Whitkus, 1988).

Table 4 Probability Assessment for the Presence of Fibrous Wood in Taxa Related to *Mahonia*^a

Genus	Habit	Habit References	Duration	Duration References	Description	Description References	Probability of Wood	Character Coding
<i>Vanconveria</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	USDA & NRCS, 2009	<i>V. hexandra</i> is perennial with long basal stems (20.3–40.6 cm).	Turner & Gustafson, 2006	Low, but 2° growth confirmed from Schweingruber & Landolt, 2005–2008	Absent
<i>Epimedium</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Kang, 1990	<i>E. koreanum</i> is a low rhizomatous perennial herb that grows to 30 cm.	Kang, 1990	Low, but 2° growth confirmed from Schweingruber & Landolt, 2005–2008	Absent
<i>Sinopodophyllum</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989	Perennial	Xiao et al., 2006	<i>Sinopodophyllum hexandrum</i> is a perennial herb.	Xiao et al., 2006	Low	Absent
<i>Achlys</i>	Herbaceous	Fukada, 1967; Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Fukada, 1967	<i>A. triphylla</i> and <i>A. japonica</i> are perennial herbs with branched, creeping rhizomes.	Fukada, 1967	Low	Absent
<i>Diphylleia</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Radford et al., 1968	<i>A. californica</i> is a slender erect perennial herb, to 39 cm.	Fukada & Baker, 1970	Very low	Absent
<i>Dryosma</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Woodson, 1928	<i>Diphylleia</i> has stems with scattered vascular bundles.	Judd et al., 2002	Low to moderate	Absent
<i>Podophyllum</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Jones & Watson, 2001	<i>D. cymosa</i> is a rhizomatous perennial herb 40–100 cm tall.	Radford et al., 1968	Very low	Absent
<i>Platiorhegma</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Fern, 1997–2003	<i>D. pleiantha</i> is an herbaceous caulescent perennial.	Woodson, 1928	Low	Absent
<i>Jeffersonia</i>	Herbaceous	Baskin & Baskin, 1989; Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Baskin & Baskin, 1989; Radford et al., 1968	<i>Podophyllum</i> has stems with scattered vascular bundles.	Judd et al., 2002	Very low	Absent
<i>Ranzania</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Schmid, 2002	<i>P. dubia</i> (<i>Jeffersonia dubia</i>) is a perennial that grows to 20 cm.	Fern, 1997–2003	Low	Absent
					<i>J. diphylla</i> is a rhizomatous, acaulescent, perennial herb.	Radford et al., 1968	Low	Absent
					<i>J. diphylla</i> is an herbaceous perennial found in mesic deciduous forest habitats.	Baskin & Baskin, 1989	Low	Absent
					<i>R. japonica</i> (<i>Podophyllum japonicum</i>) is a small rhizomatous perennial that	Schmid, 2002	Low	Absent

<i>Mahonia</i>	Woody Shrub	Kim & Jansen, 1998 Loconte & Estes, 1989; Meacham, 1980	Perennial	Rehder, 2001	grows 30.5 cm tall. Evergreen unarmed shrubs, rarely small trees.	Rehder, 2001	Very high	Present
<i>Berberis</i>	Woody Shrub	Kim & Jansen, 1998 Loconte & Estes, 1989; Meacham, 1980	Perennial	Rehder, 2001	Evergreen or deciduous spiny shrubs, rarely Small trees.	Rehder, 2001	Very high	Present
<i>Gymnospermium</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	Ying et al., 2010.	Small perennial tuberous herb with yellow flowers, height 5 cm.	Ying et al., 2010.	Low	Absent
<i>Leontice</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989; Meacham, 1980	Perennial	eFloras, 2008	<i>Leontice evermannii</i> is a perennial herb, 30-50 cm tall.	eFloras, 2008	Low	Absent
<i>Caulophyllum</i>	Herbaceous	Kim & Jansen, 1998; Loconte & Estes, 1989	Perennial	eFloras, 2008; USDA & NRCS, 2009	The genus consists of understory deciduous herbs that grow 20-90 cm tall. A perennial with multiple stems.	eFloras, 2008; USDA & NRCS, 2009	Low	Absent

^a *Nandina*, *Clematis*, *Hydrastis* and *Gitaucidium* are in Table 2.

nonwoody), Mesquite 2.0 was used to plot woodiness on the published phylogenetic trees of the taxa (Maddison & Maddison, 2009).

To investigate the occurrence of paedomorphic wood in primitively woody taxa we plotted data on the co-occurrence of scalariform perforation plates and uniseriate homocellular rays with upright cells (Paedomorphic Ray Type III) on a phylogeny of the Ericaceae (Kron et al., 2002). The data for these plots was extracted from the Xylem Database (Schweingruber & Landolt, 2005–2008). We choose the Ericaceae for analysis because Meylan and Butterfield (1978) report several species with these paedomorphic characteristics.

D. Results

1. Stem Anatomy and Xylem Characteristics of *Xanthorrhiza simplicissima*

a. Overview. Transverse sections of *Xanthorrhiza simplicissima* reveal a pith composed of large thin-walled, isodiametric parenchyma cells. In radial and tangential views, these cells appear somewhat oval with horizontal sides that are often parallel, and flattened (Fig. 2d). At the pith/xylem interface, the parenchyma cells of the pith tend to have an upright (vertical) orientation.

Close to the xylem, the cells are smaller in transverse section and, at the base of the earliest formed vessel groups, they transition to much smaller, radially elongated, oval shaped cells (Fig. 2e). These cells gradually assume somewhat rectangular shapes between the strands of vessels, which radiate outward from the earliest formed clusters of vessels. Proceeding radially outwards, the parenchyma cell strands (primary rays) become the rays of the secondary xylem. No rays form within the primary vascular bundles, or their radial extensions. All of the vessels lie between the rays, and are embedded in fiber cells. The fiber cells are smaller than the ray cells, and are oval or rounded in outline, as seen in cross-section (Fig. 2e, f).

The xylem occupies a major proportion of the stem, especially in older stems, and forms a cylinder around the pith (Fig. 2g). The secondary xylem is composed only of vessels, rays, and fibers, with few or no tracheids. No axial parenchyma or fiber tracheids were found. Curved arches of tissue composed of parenchyma cells interspersed with half moons of partially crushed phloem occur just outside the secondary xylem and vascular cambium. The phloem is frequently capped with small arches of fibers. Beyond the fibers lies the periderm (Fig. 2h).

b. Vessels. Vessels form a prominent feature of the secondary xylem. In transverse section they appear rounded or oval, and may have flattened sides, especially where they come into contact with other vessels. The vessels occur in single, or occasionally double, radial strands that radiate outwards from the beginning of a growth ring (Figs. 2f–h). They are distributed in a semi-ring porous pattern. A typical growth ring is marked by a short tangential band of wider diameter vessels at the beginning of the ring, followed by a discontinuous strand of smaller vessels that ends at the margin of the next growth ring (Fig. 2i). In many transverse sections, a darker stained line of cells can be seen at the end of a growth ring. This is due to the slightly smaller cell size of the fibers and ray cells produced at this position (Fig. 2j). Almost all of the vessels are restricted to the central part of the

area between the rays, with no contact with the parenchyma cells of the rays (Fig. 2i).

There are a substantial number of single vessels that are separated from one another by intervening fiber cells. There are also a substantial number of pore multiples, vessel groups containing two, three, or more vessels (Fig. 2e). Extremely high numbers of vessels making contact in a group are not common, but there are examples of groups with ten, sixteen, or even more vessels. The mean number of vessels in a group is 2.5 ($n=26$; $SE=0.1$).

The mean length of the vessel elements is 249.4 μm ($n=50$; $SE=9.4$), and the mean width is 32.9 μm ($n=50$; $SE=1.6$). Narrow, oval shaped pits in alternating rows are found on the secondary walls of the vessel elements. The pits are numerous, lack borders, and cover much of the lateral surface of the vessels. No examples of vessel elements with annular rings, helices, scalariform or reticulate secondary wall deposition patterns were found. Therefore, the only part of the surface of the primary wall that is not covered by the secondary wall is the part exposed due to the pit apertures (openings) (Fig. 2k).

The vessel elements have simple perforation plates set in end walls that are slightly to fairly oblique (Fig. 2k), with noticeable caudate tips, which can be relatively long (Fig. 2l).

There is no overall vessel element storying, though it is occasionally possible to find elements in adjacent vessels that are aligned with each other (Fig. 2m).

A graph of vessel element lengths across the xylem with a Locally Weighted Scatterplot Smoother line fitted shows vessel element length decreasing with distance from the pith (Fig. 3b). More recently formed vessel elements have shorter lengths than the older vessel elements. The resulting curve has an overall negative slope (Fig. 3b). When a linear regression line is fitted to the same data points, a negatively sloped line also results ($p=0.00$, $r^2=0.104$; Fig. 3a).

c. Rays. Rays in *Xanthorhiza simplicissima* are multiseriate, and are composed of upright (or square) ray cells (Paedomorphic Type II). In transverse sections, they originate as two to four cell wide primary rays in the earliest formed (primary) xylem, and gradually widen as they extend across the secondary xylem towards the vascular cambium. The rays do not branch, and no rays originate within the vascular bundles (Fig. 2e–h). The ray cells tend to be somewhat rectangular in outline in transverse views (Fig. 2e, j). In tangential view they may be rounded, but most are oval or elongated oval in shape (Fig. 2m). Some of the elongated ray cells have flattened or angled ends (Fig. 2n). Many are densely packed with inclusions that may be starch grains (Fig. 2n). The lateral cell walls of the cells have scattered, oval-shaped pits, which may occur in an alternate pattern, when they occur frequently.

The rays tend to be tall, and always extended past the end of the tangential sections. Due to this, maximum ray height could not be measured. They are at least 6 mm high, the size of the largest sections. The rays have a mean width of 150.3 μm ($n=26$; $SE=12.4$), or 9.6 cells ($n=26$; $SE=0.8$). In tangential section most of the rays have uniseriate ends, some terminating in a single cell. However, it is also common to find rays where the uniseriate ends extend for four or five cells. None of the rays are storied (Fig. 2n). All ray cells are upright when seen in radial section. Mean ray cell height is 55.1 μm ($n=54$; $SE=2.2$), and mean width is 22.4 μm ($n=54$; $SE=0.9$).

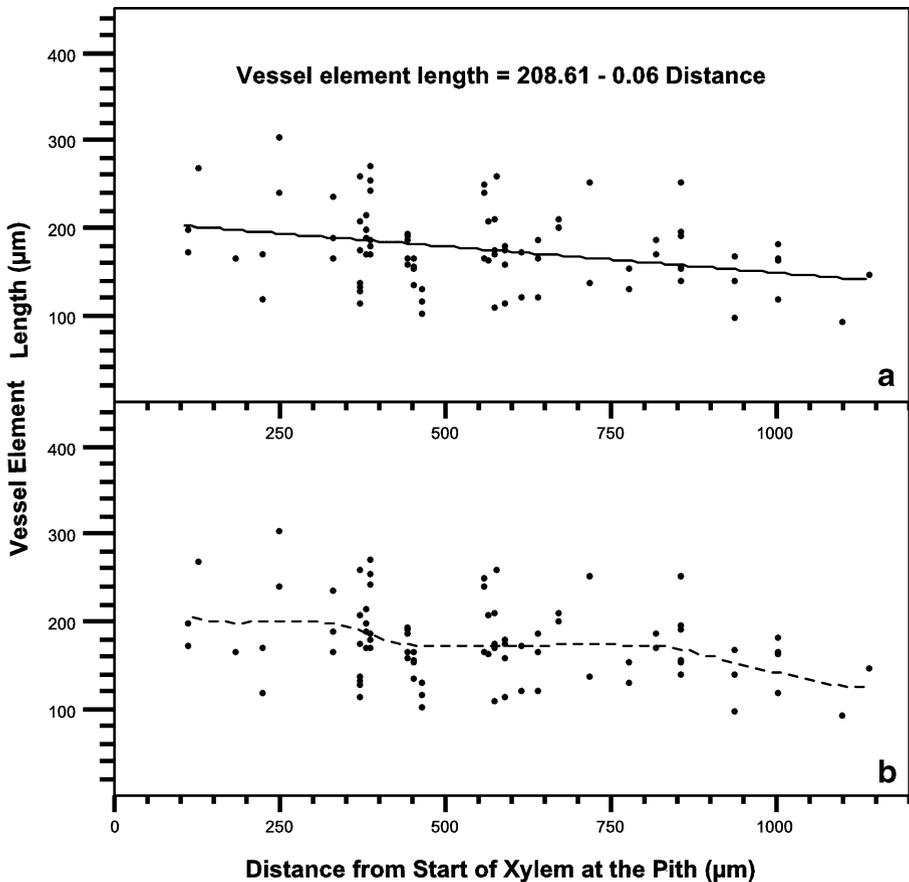


Fig. 3 Age-on-length curves for *Xanthorhiza simplicissima*. **a.** Negatively sloped regression line. **b.** LOWESS (Locally Weighted Scatterplot Smoother) curve showing the same negative trend

d. Fibers. Only libriform fibers are found in the secondary xylem. This fiber type characteristically has tapered ends, although forked ends can be found occasionally. In transverse section the fibers are rounded or somewhat oval, with small lumens (Fig. 2e, i, j). The fibers have pit apertures that have no apparent borders, and resemble slits (simple pits). Their mean length is 351.1 μm ($n=50$; $\text{SE}=8.8$), and mean width (including the cell wall) is 15.9 μm ($n=50$; $\text{SE}=0.5$).

Libriform fibers are very abundant throughout the secondary xylem, forming a matrix in which the vessels and rays are embedded (Fig. 2h). Some of the fibers close to ray cells appear to contain starch grains (Fig. 2n). Fiber cells farther away from the rays do not. No storying occurs in the libriform fibers (Fig. 2m, n).

e. Secondary Woodiness. Based on our character state determination (Table 2), and the phylogenetic tree of Kim et al. (2004a), the ancestral state of *X. simplicissima* is equivocal (Fig. 4). The outgroup, *Euptelea*, is a deciduous tree (Kim et al., 2004a).

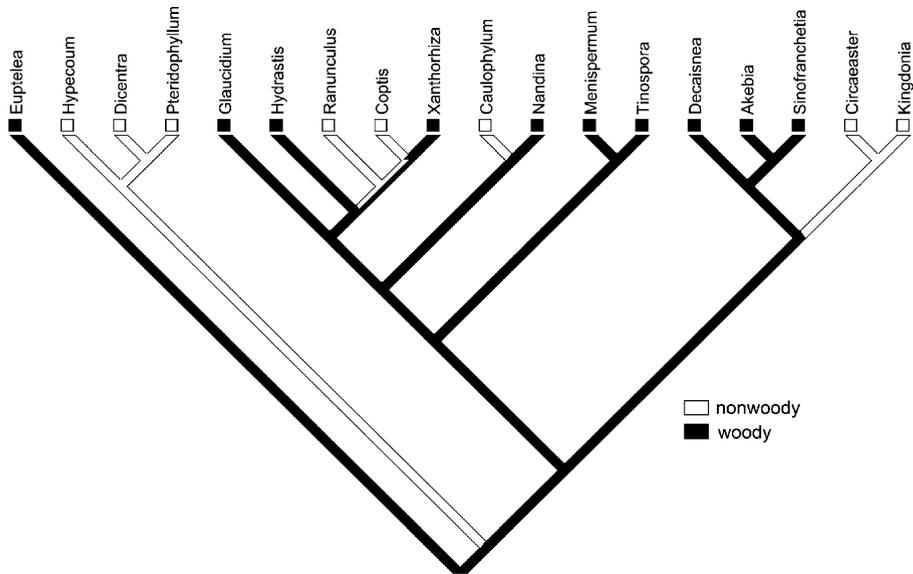


Fig. 4 Character mapping of woody and nonwoody taxa on Kim et al.'s (2004a) phylogeny of the early-diverging dicots. The data for character state determinations is in Table 2. For purposes of this exercise determinations of woodiness were based on the assessed probability of the presence of a significant amount of fibrous wood. According to these criteria, it is not possible to say with certainty whether *Xanthorhiza simplicissima* is secondarily woody or not

2. Stem Anatomy and Xylem Characteristics of *Coreopsis gigantea*

a. Overview. Transverse sections show a stem and xylem anatomy quite different from *Xanthorhiza simplicissima*. In general, ground tissue made up of parenchyma cells and containing vascular bundles of xylem and phloem arranged in a ring dominates *Coreopsis gigantea* stems (Fig. 5a). While some observations were based on young stems, measurements for assessing paedomorphosis were based on larger stems because they have more substantial amounts of secondary xylem. There are also developmental differences between the stem and xylem anatomy of young (smaller) and older (larger) stems.

b. Parenchyma in Younger Stems. Parenchyma cells throughout younger stems are thin walled. In the center of the stem, in transverse section, they are rounded, or slightly oval in outline, and frequently have flattened sides where they make contact with adjacent parenchyma cells. In general, the cells are smaller toward the vascular bundle region, and then become larger again moving towards the outside of the stem, and in the cortex. However, parenchyma cells found in the outer part of the stem tend to be smaller than those located in the center of the pith. Within the pith, the cells are much smaller near the earliest formed vessels of the vascular bundles than in the center. In some cases, they retain their rounded shape; in others they are more oval, or even elongated, near the vessels. A ring of secretory canals occurs in the pith, close to the earliest formed vessels (Fig. 5b).

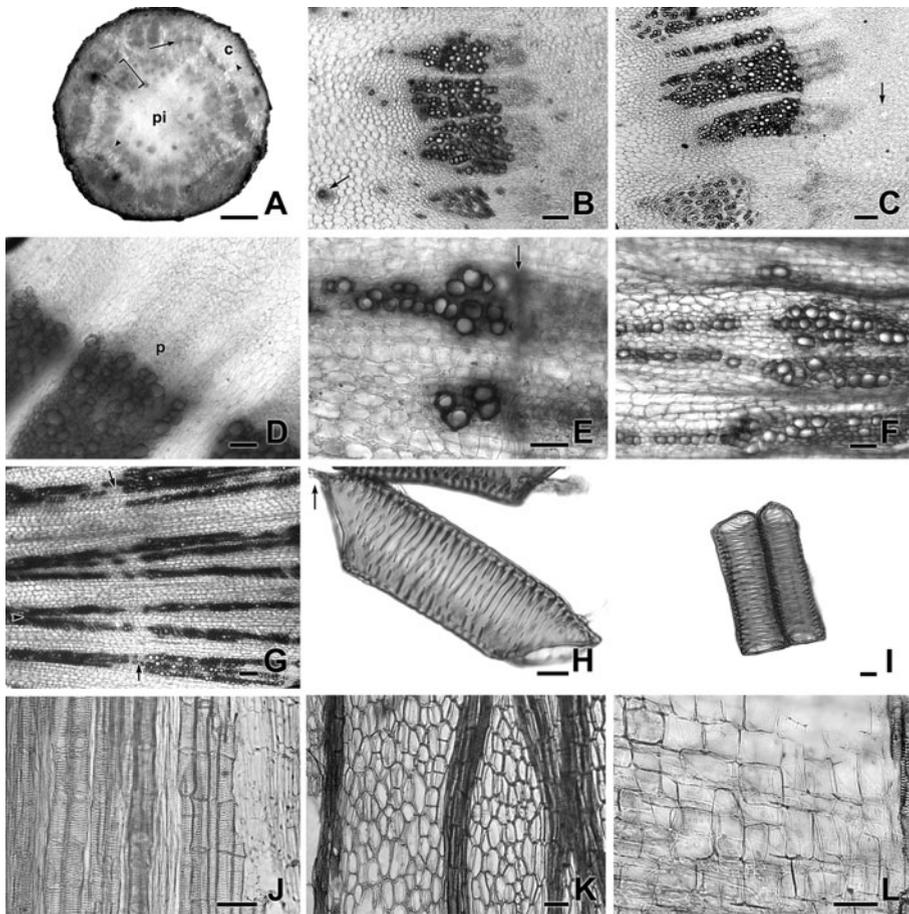


Fig. 5 *Coreopsis gigantea*. All images LM. **a.** Full stem transverse section showing large pith (*pi*), vascular system with secondary growth (bracket), cambium (*arrow*), phloem, cortex (*c*) and secretory cavities (*arrow heads*). bar=1.0 cm. **b.** Transverse section of the vascular zone from a young stem with limited secondary growth. The rays are continuous with the interfascicular regions (primary rays) of the primary plant body. bar=200 μ m. **c.** Transverse section of the vascular zone from a slightly older stem. Rays of various sizes separate the bundles. bar=200 μ m. **d.** Transverse section with primary and secondary phloem (*p*) exterior to the secondary xylem in a young stem. bar=100 μ m. **e.** Transverse section with clusters of larger diameter vessels (earlywood) just interior to the cambium (*arrow*) marking the beginning of a growth ring. bar=100 μ m. **f.** Older stem with secondary growth, in transverse section. Interrupted vessel strands mark the transition between growth rings. bar=100 μ m. **g.** Junction of two growth rings (between *arrows*) in a transverse section of an older stem. Formation of new rays (*arrowhead*) occurs as the stem grows in diameter. bar=200 μ m. **h.** Maceration. Vessel with a pseudoscalariform lateral wall deposition pattern, and caudate tip (*arrow*). bar=20 μ m. **i.** Maceration. Two adjacent vessels with less oblique end walls, simple perforation plates, and less pronounced caudate tips. bar=20 μ m. **j.** Tangential section. Vessel storying. bar=100 μ m. **k.** Ray parenchyma cell shape in tangential section. bar=100 μ m. **l.** Radial section. Ray constituted of predominately square and upright parenchyma cells, with a few procumbent cells. bar=100 μ m

The rays are all multiseriate, with no uniseriate rays (Paedomorphic Type II). The majority of the ray parenchyma is produced by the action of the vascular cambium during secondary growth (Fig. 5c), and occurs between the smaller fascicular regions. Some of the smaller ray cells are shaped like elongated ovals, while others are only slightly oval shaped. Elongated, oval shaped parenchyma cells are most common where the rays are narrow. In very narrow rays, elongated parenchyma cells with somewhat flattened ends, tending towards a rectangular shape, are also seen. These rectangular parenchyma cells are also present between phloem strands, as a continuation of the xylary rays. If the rays are wide, the constituent parenchyma cells are more rounded.

Just outside the most recently formed vessels lie strands of phloem embedded in parenchyma (Fig. 5d). A second ring of secretory canals lies outside the outer boundary of the phloem (Fig. 5c). The parenchyma cells located in this region have more rounded outlines, becoming oval-shaped outside the secondary phloem, near the third ring of secretory canals in the outer cortex, just inside the periderm (Fig. 5b, c). These outermost parenchyma cells have an upright orientation when seen in radial or tangential section.

c. Vessels in Younger Stems. Vessels typically occur in short wedge-shaped or roughly rectangular groups, as seen in transverse section. Some vascular bundles lie close to each other, with narrow interfascicular regions. Others are separated by much wider interfascicular regions (Fig. 5c). This difference probably reflects the position of the section in relation to anastomoses between vascular strands. The vessels themselves are usually arranged in multiple, discontinuous, radially oriented strands (Fig. 5b). Vessels found on the borders of the bundles often make contact with the parenchyma of the interfascicular regions. Beyond this, however, it is difficult to determine a distinct pattern of distribution of the vessels in the vascular bundles. For example, there may or may not be gaps in the vessel strands, and obvious trends in the diameter of the vessels are hard to discern. At least in some cases, there may be gaps in the vessel strands at the same positions in adjacent bundles. These gaps likely signal the transition from one growth increment to the next.

d. Parenchyma in Older Stems. Many of the observations made on the transverse sections of younger stems hold true for the older stems, but there are some differences. There is a tendency for the parenchyma cells in the middle of wide rays to be noticeably larger than those lying close to the vessels. The cells tend to be round at the stem center, elongated-oval shaped between the vascular strands, and are somewhat rectangular adjacent to the most recently formed vessels. In the vicinity of the youngest vessels many of the ray parenchyma cells are rectangular, or elongated ovals with flattened ends. The rays tend to be more consistent in width when compared to younger stems, although there are exceptions.

e. Vessels in Older Stems. Vessels in larger stems are distributed in a semi-ring porous pattern. Strands of vessels typically extend radially from a cluster of vessels at the beginning of a growth increment. Vessels located on the borders of vessel groups often make contact with the parenchyma cells in the adjacent rays.

The vessel clusters, which consist of larger diameter vessels (sometimes only marginally larger), have a tangential or sometimes a diagonal orientation in transverse

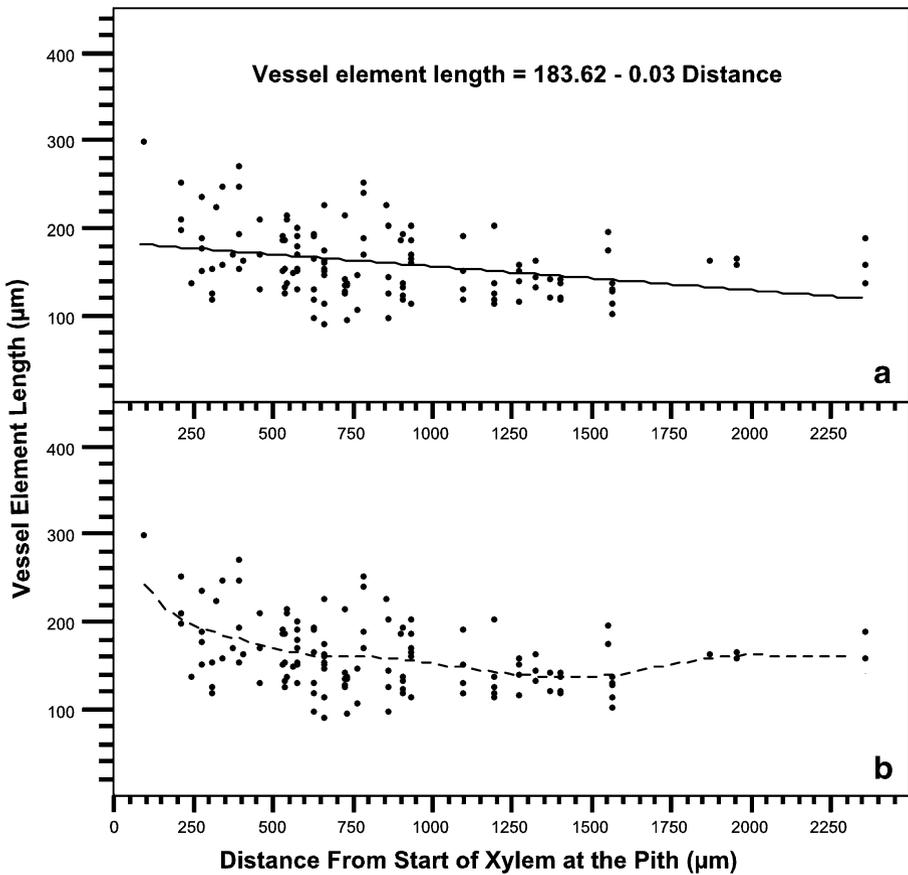


Fig. 6 Age-on-length curve for a 22 mm stem of *Coreopsis gigantea*. **a.** Negatively sloped regression line. **b.** LOWESS (Locally Weighted Scatterplot Smoother) curve showing an initial steep decline in vessel lengths, followed by a flattening of the curve

sections, and are not always well defined. They may consist of only one or two large diameter vessels (Fig. 5e). These conglomerations of vessels represent the earlywood (i.e. springwood). The vessel strands that extend from these clusters form the latewood (i.e. summerwood, Fig. 5f). The vessel strands are discontinuous in that they often contain single vessels that do not make contact with each other, as well as groups of two or three vessels in contact with each other. Mean group size is 1.7 vessels ($n=26$; $SE=0.1$), although the range extends to 11 vessels per group.

There is often a noticeable space at the end of the latewood where the vessel strands end in parenchyma, or in a few fibers (Fig. 5f, g). Another tangential cluster of vessels occurs radially outside this area (Fig. 5f), beginning a new growth increment. Thus, in older stems the vessels exhibit a repeating pattern of a tangential vessel cluster, a radiating strand of vessels, and a band of parenchyma. The cambial zone can be seen as a darker staining ring where the vessel strands terminate (Fig. 5e).

The vessel elements have a mean length of 180.2 μm ($n=50$; $SE=5.9$), and a mean width of 51.6 μm ($n=50$; $SE=1.8$), as determined from macerations. They frequently

widen in circumference at their ends, and occasionally have slight caudate tips (Fig. 5h). Most often they have fairly transverse or perhaps slightly oblique end walls. A few of the vessel elements have helical lateral wall deposition patterns, but the majority have helical transitional to scalariform, or pseudo-scalariform deposition patterns (Fig. 5i). Scalariform lateral wall patterns are the most common. No lateral wall pits are visible on the vessel elements (Fig. 5h, i). The end walls have simple perforation plates. The vessels tend to show storying in tangential views (Fig. 5j).

Graphs of vessel element lengths measured across the width of the xylem from a 22 mm stem show a decrease in vessel element length, with more recently formed vessel elements having shorter lengths than the earlier formed elements (Fig. 6). The resulting LOWESS curve initially declines, then levels out (Fig. 6b). The overall slope is negative. When a linear regression line is fitted to the data, a negatively sloped line results ($p=0.00$, $r^2=0.101$; Fig. 6a).

A second set of vessel lengths from a stem with a 58.0 mm diameter also produced a consistently negatively sloped curve, as did a linear regression line fitted to this data ($p=0.00$, $r^2=0.175$; Fig. 7). A third set of data points taken from the

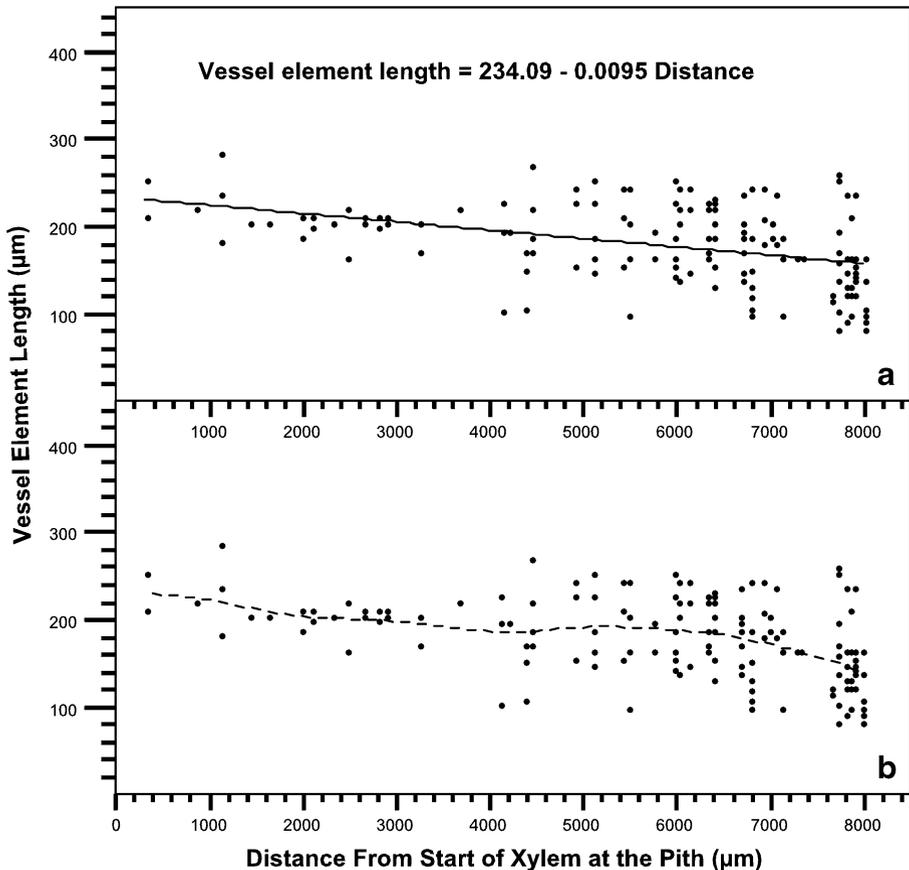


Fig. 7 Age-on-length curve for a 58 mm stem of *Coreopsis gigantea*. **a.** Negatively sloped regression line. **b.** LOWESS curve showing the same negative trend

same 58.0 mm stem produced a nearly flat curve, and a linear regression line with essentially no slope ($p=0.67$, $r^2=0.001$; Fig. 8).

f. Rays in Older Stems. Like their younger counterparts, older stems have multiseriate, non-storied rays (Paedomorphic Type II). In radial sections the shapes of the parenchyma cells follow the same general trends as seen in transverse sections. The stem center has larger, rounded parenchyma cells, while the cells around the earliest formed vessels are oval or sometimes a little elongated, and tend to have an upright orientation. Moving radially outward rounded parenchyma cells still occur between the vessel strands, but vertically oriented cells increase in number and become more common, especially immediately adjacent to vessels. New rays may form amid the vessels, splitting the radial files of cells (Fig. 5g, arrowhead).

Tangential sections of older stems show the same general tendencies in parenchyma cell shape as in younger stems, but rounded parenchyma cells are much less common. Elongated, oval parenchyma cells with vertical orientations

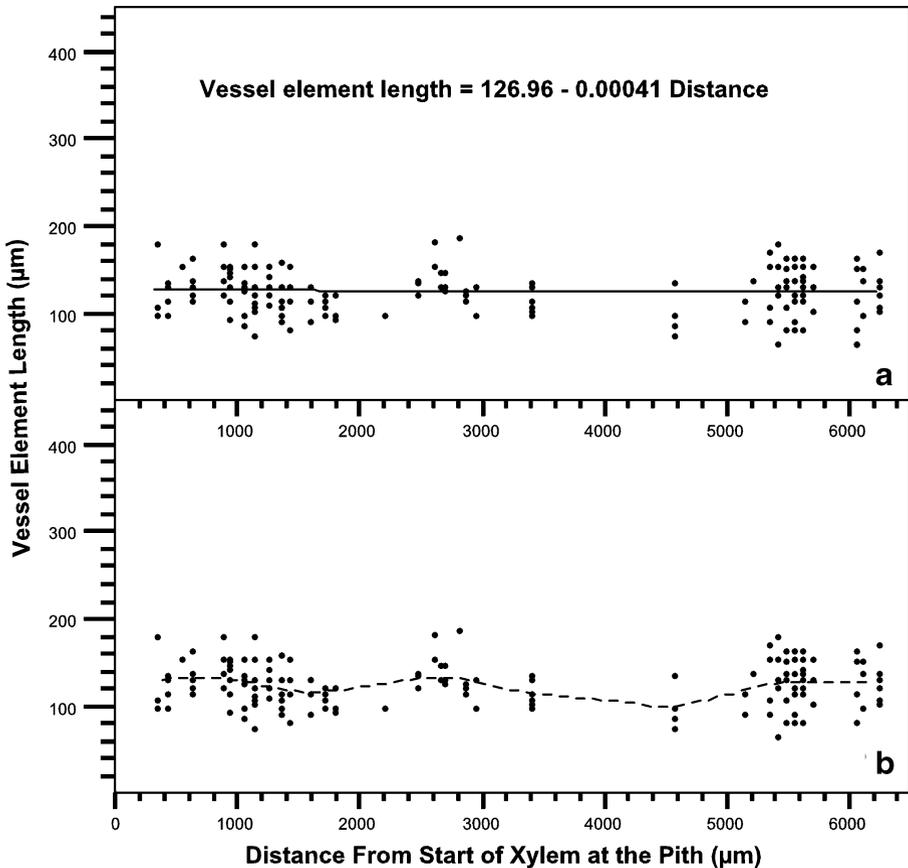


Fig. 8 Age-on-length curve for another portion of the same 58 mm stem represented in Fig. 7 (*Coreopsis gigantea*). **a.** Flat regression line. **b.** LOWESS curve showing the same lack of trend

predominate (Fig. 5k). The parenchyma cells directly adjacent to vessels, and in very narrow rays between strands of vessels, are typically narrower than in other locations. The cells in these areas are also more elongated and have angled, slightly pointed or flattened ends. Some of the cells are coffin shaped (Fig. 5k).

The height of the rays in tangential section could not be determined because they exceeded the height of the sections (5.67 mm). Mean width of the most recently formed rays is 134.5 μm ($n=20$; $\text{SE}=17.5$), or 5.6 cells ($n=20$; $\text{SE}=0.50$) (Fig. 5k).

Radial sections reveal ray parenchyma cells that are rectangular in outline. Of these, most are upright, with a few squarish cells intermixed. Only a few procumbent cells are found. Measured in radial section, the mean height of the cells is 113.2 μm ($n=50$; $\text{SE}=3.7$), and the mean ray cell width is 69.5 μm ($n=50$; $\text{SE}=2.4$) (Fig. 5l).

g. Fibers in Older Stems. Libriform fibers are not common, but do occur in the xylem of *Coreopsis gigantea*. In transverse section the fibers appear rounded or oval in outline. Macerations show that most are tapered, although examples of fibers with forked ends can occasionally be found. The fibers have a mean length of 336.7 μm ($n=53$; $\text{SE}=10.7$), and a mean width of 27.1 μm ($n=53$; $\text{SE}=1.1$).

When they occur, libriform fibers are closely associated with vessels, and normally are found next to single vessels or groups of vessels. If they are not immediately adjacent to a vessel, they are separated by only a few parenchyma cells. The fibers never occur as isolated cells in areas of parenchyma far from the vessels. Wherever they are located, they usually occur in either strands of single fibers, or strands that are 2–4 fibers wide. A few fiber strands are considerably wider, 7–8 fibers in width. Many of the multiseriate fiber strands are storied, at least to some degree.

Other than vessels, libriform fibers, and parenchyma cells, no other cell types occur in the xylem. There is no evidence for tracheids or fiber-tracheids.

h. Secondary Woodiness. Plotting woodiness on a phylogenetic tree of the *Coreopsis* species from western United States, Mexico, and Central America, supports the secondary derivation of woodiness in *C. gigantea* (Fig. 9).

3. Stem Anatomy and Xylem Characteristics of *Mahonia bealei*

a. Overview. The stem anatomy of *Mahonia bealei* resembles that of *Xanthorrhiza simplicissima*. Like *Xanthorrhiza*, transverse sections of *M. bealei* show a prominent pith composed of parenchyma cells, surrounded by a cylinder of xylem (Fig. 10a). Just beyond the vascular cambium are arches of compressed phloem mixed with parenchyma, which form convex protrusions capped by phloem fibers. The parenchyma cells located to the outside of the phloem are larger than those in the rays. Irregular shaped fiber bundles are scattered among the parenchyma cells of the cortex (Fig. 10a).

In the main part of the pith, parenchyma cells tend to be fairly large and round (Fig. 10b). In radial and tangential sections the parenchyma cells are in vertical files, are upright, and are rectangular or squarish (Fig. 10c). Their end walls are often angled, and their side walls may be curved, or at least not parallel, so that the files of cells appear

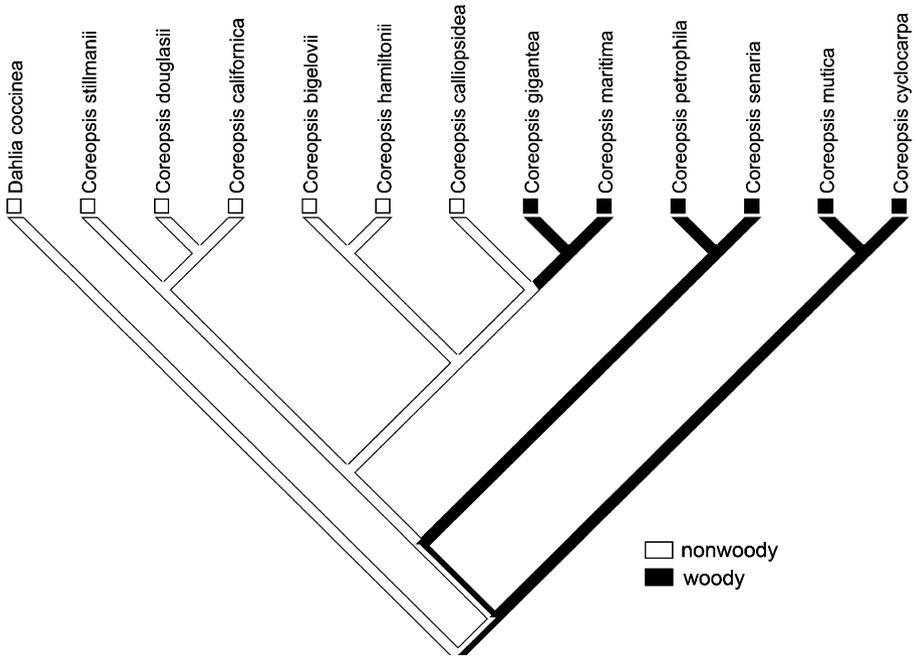


Fig. 9 Character mapping of woody and nonwoody taxa on Mort et al.'s (2004) phylogeny of the western clade of *Coreopsis*. For purposes of this exercise, woody is defined as the possession of significant amounts of secondary xylem. The data for character state determinations is in Table 3. According to these criteria *Coreopsis gigantea* is secondarily woody

irregular. The pith cells often contain rhomboidal crystals, and appear to have thicker cell walls than the parenchyma cells of *Xanthorhiza* or *Coreopsis* (Fig. 10c).

In transverse section, the parenchyma cells of the pith are generally smaller and more oval shaped closer to the xylem than in the pith center. The primary xylem consists of a V-shaped cluster of vessels embedded within a fiber matrix. The pith parenchyma extends past these wedges to form “arms” on each side of the primary bundles. Proceeding radially outward on each side of the bundles, the parenchyma cells make a transition from oval, slightly elongated cells to more rectangular cells. They have usually assumed the rectangular outline of typical xylary ray cells by the position where the initial wedge shaped cluster of vessels merges into the secondary xylem (Fig. 10d). The parenchyma cells found surrounding the arches of secondary phloem are the smallest of all parenchyma cells in transverse section.

b. Vessels. Vessels are a prominent feature of the secondary xylem of *Mahonia bealei*. They are rounded or oval in cross-section, commonly with flattened sides where they abut other vessels. The vessels of the secondary xylem are embedded in a matrix of fibers, in discontinuous radial strands. These strands contain both single vessels, as well as groups of vessels in contact with each other. Clusters containing large numbers of multiple vessels are not uncommon. Vessel groups of 24, 33, and 63 can be observed. However, single vessels and groups of two or three vessels also occur. The mean number of vessels per group is 6.7 vessels ($n=25$; $SE=0.3$) (Fig. 10e).

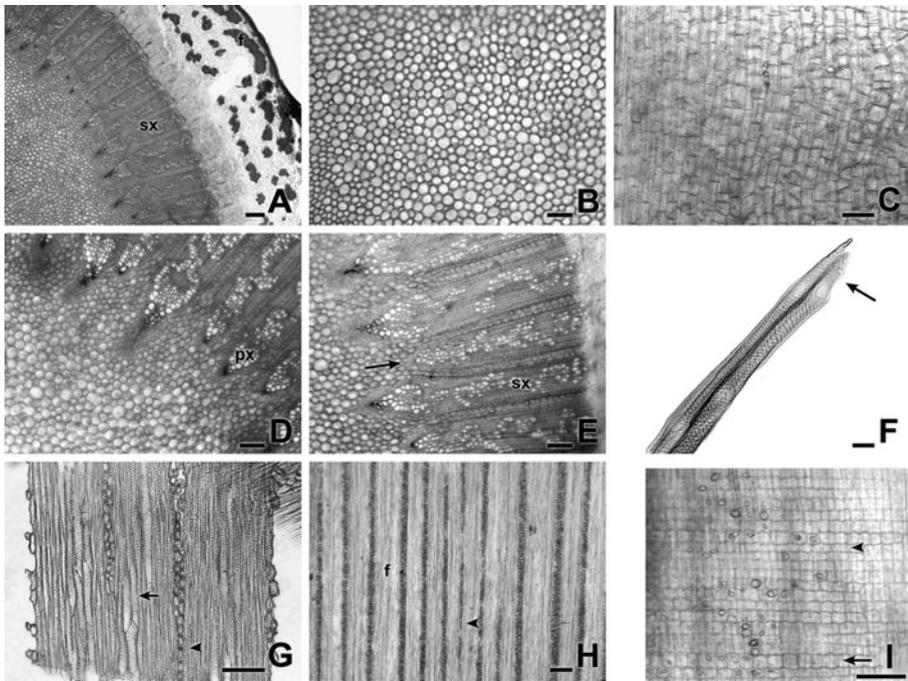


Fig. 10 All sections LM. **a.** Transverse section showing a central pith of parenchyma surrounded by a vascular cylinder of primary and secondary xylem (*sx*). Fiber bundles (*f*) lie in the cortex. bar=200 μ m. **b.** Transverse section of parenchyma cells in the pith. bar=100 μ m. **c.** Radial section showing upright, rectangular parenchyma cells in the pith. bar=100 μ m. **d.** Transverse section of the outer portion of the pith, primary (*px*) and some secondary xylem showing the transition from primary ray to the rays of the secondary plant body. bar=100 μ m. **e.** Transverse section of primary and secondary xylem (*sx*) with no clear growth rings. Bundles of secondary xylem may form in continuity with the primary xylem, or opposite a primary ray (*arrow*). bar=100 μ m. **f.** Maceration. Vessel element with an extended caudate tip (*arrow*), oblique end wall, a helical lateral wall deposition pattern, and simple perforation plate. bar=20 μ m. **g.** Tangential section showing occasional vessel storing (*arrow*) in the secondary xylem. The uniseriate end of a ray is also visible (*arrow head*). bar=100 μ m. **h.** Tangential section of fibers (*f*) and rays (one uniseriate), some with uniseriate ends (*arrow head*). bar=200 μ m. **i.** Radial section showing procumbent (*arrow head*), square, and upright (*arrow*) files of ray cells, some with rhomboidal inclusions. bar=100 μ m

The radial strands of vessels are broken into segments by areas of the fiber matrix (Fig. 10e). These fiber areas may be fairly large, producing a large break in the strand, or only a few fibers wide. In general, the vessels formed just exterior to a break are normally slightly larger than those farther out in the strand. In many strands, however, this is not a consistent trend, and changes in vessel diameter may not be readily apparent. Since there are differences in vessel diameter, the vessel distribution can be called semi-ring porous, though no obvious growth rings are evident (Fig. 10d, e).

The discontinuous vessel strands form a zigzag pattern between two xylary rays, although some sections of a strand may be radially or tangentially oriented (Fig. 10e). Vessels in a strand fairly commonly contact one of the rays. Only one or two vessels may be in contact with a ray, or many vessels may be in contact (Fig. 10e).

The vessel elements have helical secondary wall deposition patterns and simple perforation plates, with at least moderately oblique end walls. Often one or both of

the end walls have a caudate tip, which are occasionally extended (Fig. 10f). Simple lateral wall pitting can be seen on most vessel elements. The pitting is in the form of narrow oval pits (frequently slit-like) in an alternating pattern that tends to follow the groove formed between the helices on the lateral wall. The mean length of vessel elements is $257.5 \mu\text{m}$ ($n=50$; $SE=9.2$), and the mean width is $24.7 \mu\text{m}$ ($n=50$; $SE=1.1$). Storying is only occasionally present (Fig. 7g).

Vasicentric tracheids are present, and are most commonly associated with smaller vessel elements. They have the same type of lateral wall deposition pattern and lateral wall pitting as vessel elements, but are long and narrow in diameter. No measurements were made of their length or width.

An age-on-length curve fitted with a Locally Weighted Scatterplot Smoother line shows that vessel element length remains roughly constant across the xylem. The more recently formed elements have similar lengths to those of older elements (Fig. 11b). When a linear regression line is fitted to the same data, a nearly flat line results ($p=0.832$, $r^2=0.00$; Fig. 11a).

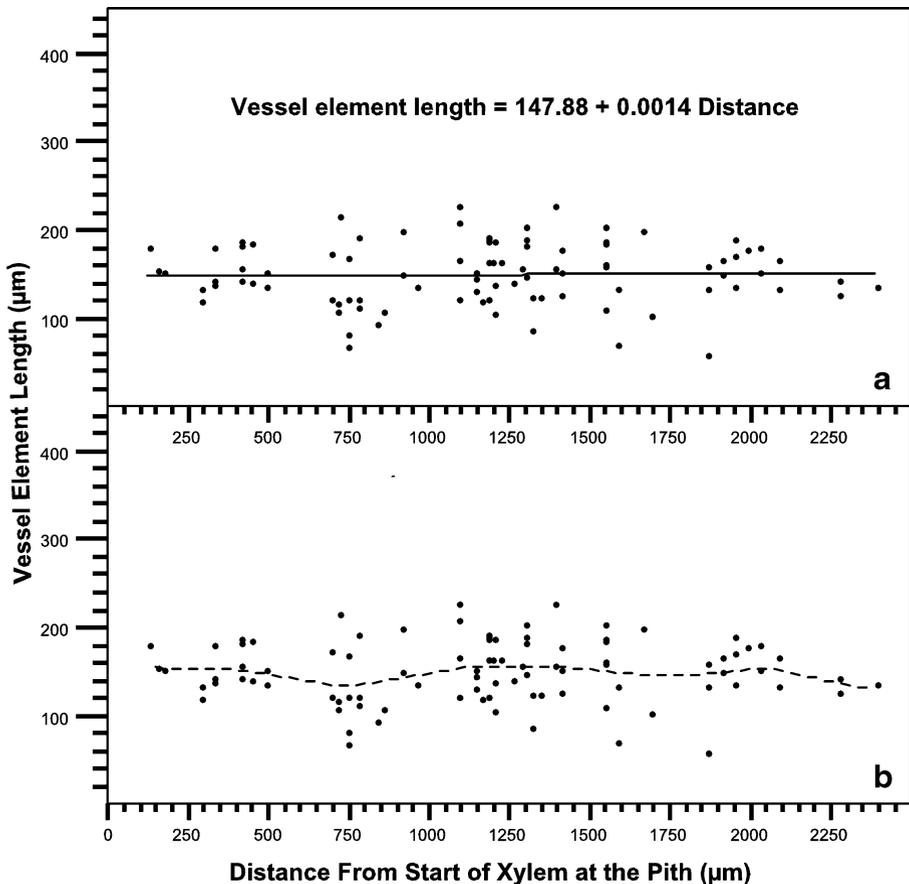


Fig. 11 Age-on-length curve for *Mahonia bealei*. **a.** Flat regression line. **b.** LOWESS curve showing the same lack of trend

c. Rays. Kribs Heterogeneous Type I rays are a prominent feature of the secondary xylem of *M. bealei*. They begin as interfascicular regions of the primary plant body (primary rays), and extend in an unbranched file of cells through the secondary plant body, widening radially, before ending outside the phloem (Fig. 10e, h). As seen in transverse sections, the rays are usually only one or two cells wide at the pith, but may be three to four cells wide in some cases. Most are multiseriate, but occasional uniseriate rays also occur. Ray height could not be determined because they extended beyond the limits of the tangential sections (5.67 mm) (Fig. 10h). A few small, uniseriate rays occur where the radial strands of vessels and fibers anastomose (Fig. 10h, arrowhead), but uniseriate rays are not typical and were not measured. Ray width is relatively constant when seen in tangential section. Mean ray width is 63.8 μm ($n=27$; SE=2.9), or 3.7 ray cells ($n=27$; SE =0.126) (Fig. 10h). Few of the rays exhibit the convex shape commonly seen in tangential sections of other species (Fig. 5k).

Although most of the rays are multiseriate (typically 2–4 seriate), many have uniseriate portions. The alternation between multiseriate and uniseriate sections occurs in no particular pattern. Often very short rays are uniseriate for their entire height. The ends of the rays are also uniseriate, either in the form of a single ray cell, or as an extended uniseriate tip, five cells or longer (Fig. 10h).

In tangential section, the ray cells may be rounded, oval, or ovoid in shape. A mix of these shapes occurs in both multiseriate and uniseriate rays. Often the oval and ovoid shaped cells are found on the margins of the ray with their longer axes oriented vertically, or in the uniseriate portions of a ray. None of the rays are storied (Fig. 10h).

In radial section the rays are a mix of both procumbent and upright cells, with no clear domination by either type. A radial file of cells usually contains cells of a single shape, but there are exceptions. In some instances several files of procumbent cells will alternate with several rows of upright cells, with no discernable pattern of alternation (Fig. 10i). Procumbent cells have a mean height of 25.5 μm ($n=30$; SE=1.0), and a mean width of 46.1 μm ($n=30$; SE=2.1). Upright cells have a mean height of 34.0 μm ($n=20$; SE=1.4), and a mean width of 31.4 μm ($n=20$; SE=0.8). The mean height for all ray cells is 28.9 μm ($n=50$; SE=1.0), and the mean width is 40.3 μm ($n=50$; SE=1.7).

d. Fibers. The secondary xylem of *Mahonia bealei* contains many libriform fibers surrounding the vessels and rays, and forming a matrix in which the other cell types are embedded. The fibers have simple pits and appear round or oval in transverse section (Fig. 10e). They are commonly elongated with pointed ends. Mean fiber length is 387.1 μm ($n=50$; SE=14.5), and mean width is 15.5 μm ($n=50$; SE=0.5). Some storying occurs, but is restricted to limited areas of two to four adjacent fibers.

e. Secondary Woodiness. Plotting woodiness on Kim et al.'s (2004b) phylogenetic tree of the Berberidaceae yields an equivocal reconstruction of the ancestral state for *Mahonia bealei* (Fig. 12). *Mahonia* and *Berberis* (both woody) are sister to the nonwoody *Ranzania*, but the presence of a woody outgroup, and their proximity to *Nandina* (woody) leads to an ambiguous ancestral state reconstruction. Based on the

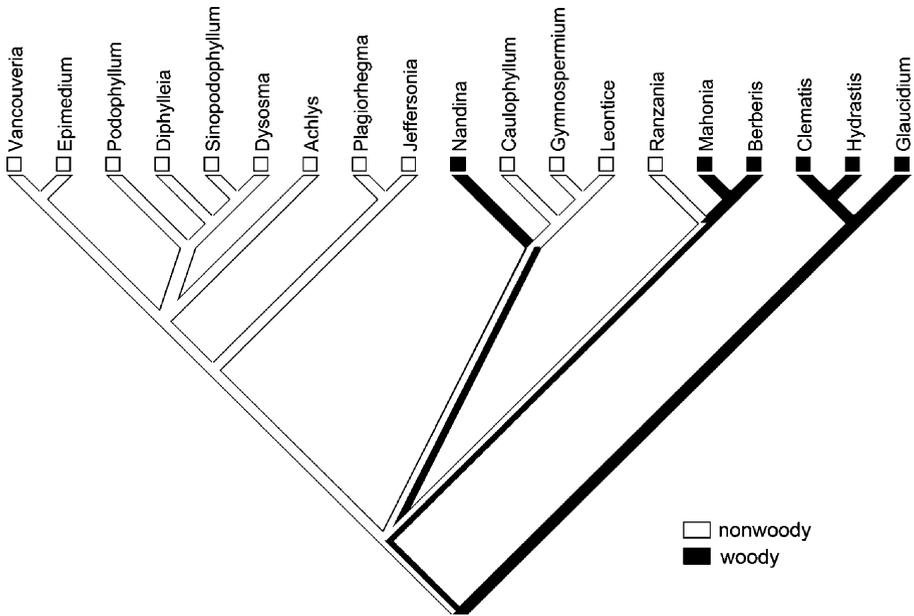


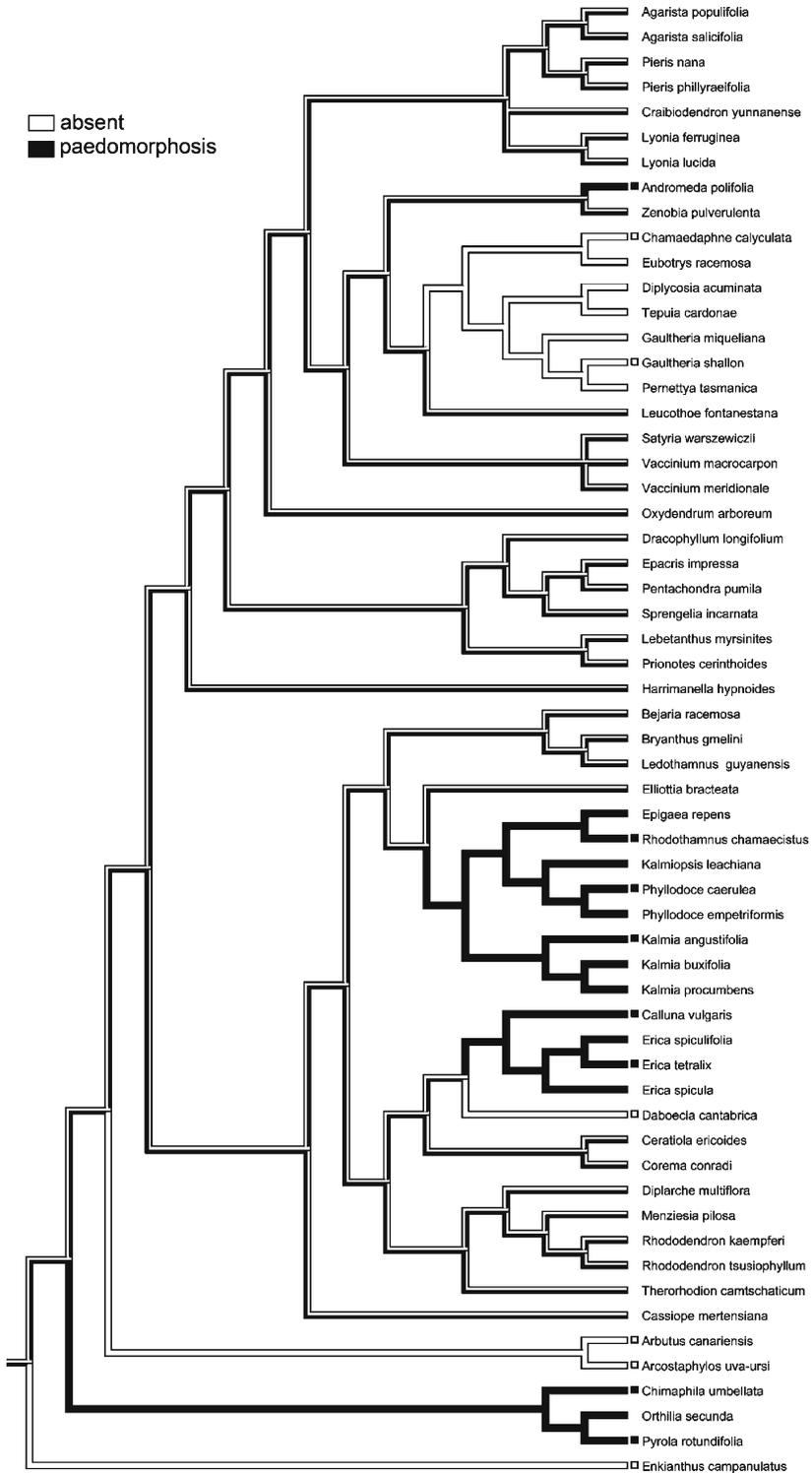
Fig. 12 Character mapping of woody and nonwoody taxa on Kim et al.'s (2004b) phylogeny of the Berberidaceae. The data for character state determinations is in Table 4. For purposes of this exercise determinations of woodiness were based on the assessed probability of the presence of a significant amount of fibrous wood. According to these criteria, it is not possible to say whether *Mahonia bealei* is secondarily woody or not

character state changes on this tree we cannot determine if their woodiness was derived from a woody or nonwoody ancestor.

4. Paedomorphosis in Primitively Woody Taxa

A plot of the co-occurrence of scalariform perforation plates and Paedomorphic Type III rays on a phylogeny of the Ericaceae (Kron et al., 2002) suggests that paedomorphic wood has evolved several times independently in the family (Fig. 13). However, the large amount of missing data weakens this conclusion, as it is possible that the family possessed paedomorphic wood as a primitive characteristic, with the evolution of non-paedomorphic wood occurring several times. In either case, paedomorphic wood occurs within a primitively woody family and so cannot be used as *prima facie* evidence of secondary woodiness.

Fig. 13 Character mapping of the co-occurrence of the characters scalariform perforation plates and Paedomorphic Type III rays (i.e., of paedomorphic wood) on Kron et al.'s (2002, Fig. 7) phylogeny of the woody family Ericaceae. Character states were determined from the Xylem Database (Schweingruber and Landolt, 2005–2008). The characteristics of terminal taxa without associated symbols (□, ■) are unknown. The character mapping shows that either paedomorphic wood arose independently several times in the family, or the whole family possesses paedomorphic wood, and there have been several reversions to normal wood. In either case, paedomorphic wood occurs within a primitively woody family and so cannot be used as *prima facie* evidence of secondary woodiness



This plot, and the data in the Xylem Database (Schweingruber & Landolt, 2005–2008), also make it clear that the taxa *Chimaphila umbellata* and *Pyrola rotundifolia*, which are normally considered nonwoody, produce enough secondary xylem to be considered at least marginally woody. Both species produce secondary xylem with abundant fibers, and can easily be called woody under most definitions of this term.

V. Discussion

A. *Xanthorrhiza simplicissima*

I. Vessels

Our results agree with Carlquist (1995a) that the vessels are distributed in a semi-ring porous pattern, are restricted to the central part of the fascicular areas, and have no contact with the rays. However, the mean length of the vessel elements found here (249.4 μm) is longer than the mean length reported by Carlquist (1995b: 167.0 μm), and much shorter than the mean length in dicotyledonous woods overall (649.0 μm ; Metcalfe & Chalk, 1950). Unfortunately, measures of sample variability are not available in the literature, so we are unable to determine if these differences are statistically significant. We also found a difference in mean vessel element width: 32.9 μm , compared to 20.0 μm reported by Carlquist (1995a). Finally, the mean number of vessels per group reported in this study (2.5) is less than that reported in the literature (4.5; Carlquist, 1995a).

These differences may be a consequence of the samples used or, in some cases, of the measurement methods. Neither we nor Carlquist used a true random sampling procedure in selecting stems for study. Carlquist (1995a) used samples from only one site, while we only sampled three relatively similar sites. Although working with a limited number of samples is common in anatomical and systematic studies, it should not be surprising that occasional differences in measurements are found. While there is evidence that at least some characteristics of xylem anatomy (vessel diameter and density, for instance) are affected by environmental conditions, it is not clear how plastic these characteristics are, or whether these effects could account for the observed discrepancies between our and Carlquist's measurements (Arnold & Mauseth, 1999). If they can account for the discrepancies, the differences could be due to sampling error. For instance, although vessel elements in our sample seem substantially longer and wider than those reported by Carlquist (1995a), they may be within the normal range of intraspecific variation (Pieter Bass, personal communication). Also, differences in vessel element lengths might be explained if Carlquist (1995a) used more mature stems than we did. In pedomorphic woods, mean vessel element length can decrease over time. It is possible that if larger, older stems were sampled mean vessel element length might be shorter. More extensive sampling would be needed to confirm this hypothesis.

Although we used a different method of measurement than Carlquist (1995a), this difference cannot account for the observed differences in vessel diameter. We used wall thickness plus lumen diameter as our measure of vessel element width, while Carlquist

(1995a) used only lumen diameter. Since he gives wall thickness as 1 μm , even doubling this to account for the two walls only brings his measurements to 22.0 μm , significantly less than the 32.9 μm (SE=1.6) that we found. Clearly, differences in method can account for only a small part of the overall difference in means.

It has been argued that a larger number of vessels per group, and narrower vessel elements, are advantageous in drier environments (Mauseth, 1988). Cavitation (introduction of air bubbles into a vessel) is an increased danger in drier (or colder) areas. A larger number of vessels per group offers greater protection against this danger through transport path redundancy. If a vessel in a cluster suffers cavitation, conductivity can continue in the other vessels. There is, however, no experimental evidence that greater vessel grouping correlates with greater cavitation resistance. In contrast, there is a strong correlation between the area of inter-vessel pitting and vulnerability to cavitation (Hacke et al., 2006; Wheeler et al., 2005). This observation complicates the speculative link between vessel grouping and cavitation resistance. It implies a trade-off between the advantages of extensive interconnection for redundancy versus the disadvantages for increasing the probability for air-seeding between vessels. There is evidence that narrower vessels (which tend to have less pit area per vessel) may be less prone to cavitation than wider vessels (Sperry et al., 2006). Thus, vessel groupings composed of narrower vessels would, hypothetically, be more resistant to cavitation than the same grouping of larger ones. Although the discrepancy between our measurements and those of Carlquist (1995a) might be explained if his sample came from a drier location (implying more vessels per group), the possible validity of this hypothesis is lessened by the above considerations.

If short vessel element lengths are an adaptation to more xeric environments as Carlquist has suggested (Carlquist, 1985), adaptation to a dryer environment might also explain why our measurements of mean vessel element length are longer than those from his study.

2. Rays

Both we and Carlquist (1995b) found multiseriate rays composed of mostly upright cells. The rays are Paedomorphic Type II (Carlquist, 2001), and are extensions of the primary rays (Carlquist, 1995b).

3. Fibers

Our descriptions of libriform fibers agree well with those in the literature. The mean length of xylary fibers reported here is 351.1 μm , compared to a mean of 342.0 μm in Carlquist (1995b). Though no measures of variability are available for Carlquist's data, these values would seem to be within the normal range of sampling error. In both cases, mean fiber lengths are much shorter than the mean length reported for dicotyledonous woods as a whole (1,317.5 μm ; Metcalfe & Chalk, 1950). When compared with the difference in vessel element lengths between the studies, the similarity in fiber lengths can be taken as support for the hypothesis that the differences in vessel element lengths and widths are adaptive.

The libriform fibers are typically non-storied, and are found adjacent to the rays and vessels (Carlquist, 1995b). The ratio of imperforate tracheary element length to vessel

element length is 2.05 (Carlquist, 1995b), and 1.4 (this study). These ratios are typical for species with libriform fibers. If tracheids or fiber-tracheids were present in the wood, a lower ratio (closer to 1.0) would be expected (Carlquist, 1995b).

4. Paedomorphosis

Trends in vessel element length as found in the negatively sloped age-on-length curve, and the presence of upright ray cells, support Carlquist's (1995b) report of paedomorphic wood in this species. Although the age-on-length graph shows a negatively sloped curve, there is only a weak linear association between vessel element length and distance from the start of the xylem ($r^2=0.104$, $p=0.00$).

5. Secondary Woodiness

Plotting woodiness on a phylogeny of early diverging dicots (Kim et al., 2004a), yields three character state changes leading to a nonwoody habit (Fig. 4). Although one of these took place in a group that contains *Xanthorrhiza simplicissima*, the presence of woody tissue in *Glaucidium* and *Hydrastis* (Carlquist, 1995b), as well as in the more basal members of the clade (*Nandina*, *Menispermum*, *Tinospora*) result in an equivocal ancestral state for *Xanthorrhiza*.

In making this assessment we equated woodiness with the possession of significant amounts of fibrous secondary xylem. A number of authors have shown that the possession of secondary growth is much more common than the possession of fibrous secondary xylem, and is more widespread than has been traditionally assumed (Dietz & Ullmann, 1997; Dietz & Schweingruber, 2002; Krumbiegel & Kästner, 1993; Schweingruber, 2006; Schweingruber, 2007a; Schweingruber & Poschlod, 2005; Schweingruber & Landolt, 2005–2008). Even herbaceous plants like *Dicentra* can have more than one secondary growth increment (Schweingruber & Landolt, 2005–2008). Equating the possession of wood with the occurrence of secondary growth and replotting what data is available on the occurrence of secondary growth in the “herbaceous” taxa (Table 2) does not alter our conclusion, though it does change which taxa are labeled nonwoody.

6. Environmental Factors and Anatomy

Several of the xylem characteristics of *Xanthorrhiza simplicissima* are likely adaptations to its environment. In the southeastern United States, *X. simplicissima* is most frequently found in the understory of mature forests, in the moist areas around streams (eFloras, 2008; Rowe et al., 2004). Although it is found in both the coastal plain and piedmont, it is most common in the Appalachian Mountains in a belt running from the deep southern United States (northern Florida and Texas) into New England (USDA & NRCS, 2009). In this area, the climate produces clear cut growing seasons where spring and early summer bring higher temperatures and increased rainfall. Later in the year lower temperatures halt growth.

Like the ring-porous condition, the semi-ring porous distribution of vessels is a response to seasonal fluctuations in rainfall and temperature. The relatively low number of vessels per group indicates that any added safety of redundant vessels is

not needed in the moist, shaded conditions where *X. simplicissima* grows. Given conditions of heavy shade and moist soil, it is likely that high vessel conductivity is not required to maintain transpiration rates. Another indication that transpiration may not be excessive is that the leaf surface area of *X. simplicissima* is fairly small. This condition may be correlated with the fact that mean vessel width is much lower than that of dicotyledons as a whole (Metcalf & Chalk, 1950).

The paedomorphic features of *X. simplicissima*—a negatively sloped age-on-length curve, and the presence of rays with upright cells—may indicate an adaptation to providing an intermediate amount of mechanical strength. Although the presence of libriform fibers and the pitted lateral wall deposition pattern of the vessels create a dense wood, the rays and short vessel elements tend to offset this increased strength (Carlquist, 2001). Perhaps the greatest factor affecting mechanical strength is the limited amount of secondary growth. With limited secondary growth, stem diameter is not significantly increased (Rowe et al., 2004). The fact that many of the plants seen in the field are somewhat procumbent supports this view. The hypothesis that paedomorphosis represents a relaxation of selection for mechanical strength is discussed more fully below (Carlquist, 2001).

B. Coreopsis gigantea

There is less anatomical data available on *Coreopsis gigantea* than *Xanthorrhiza simplicissima*. What is available is largely in agreement with our results.

1. Vessels

Vessels in *C. gigantea* are distributed in a semi-ring porous pattern, and tend to be storied. Carlquist (1985), reports semi-ring porous wood,² but does not discuss storied. The mean length and width of the vessel elements in this study is 180.2 μm , and 51.6 μm respectively. The mean number of vessels per group is 1.7. Measurements from the literature are 210.0 μm and 36.7 μm for length and width, respectively, and of 2.2 vessels per group (Carlquist, 1985). Whether these differences are statistically significant cannot be determined due to the lack of variability measures reported in the literature. As in *Xanthorrhiza simplicissima*, neither we nor Carlquist (1985) used true random samples. As a result, sampling error could play a role in accounting for the different measurements.

A second possibility to account for the differences involves the age-on-length curves. Two of the three vessel element length data sets show a drop in vessel element length as the distance from the pith increases. If our samples came from larger, older stems as compared to those of Carlquist (1985), then we would expect our measurements to yield a shorter mean length. However, no details on the age or size of the plants sampled by Carlquist (1985) are available.

As discussed above, differences in methodology in measuring the vessel element widths can account for only some of the difference in mean vessel element width

² For the purposes of this discussion we have amended our definition of wood as fibrous secondary xylem to include the highly parenchymatized secondary xylem of *Coreopsis gigantea*. We return to this issue in the last section of the Discussion.

between the two studies. Carlquist (1985) measured vessel diameter on the basis of the lumen, while we measured the lumen plus wall thickness. This discrepancy explains part, but not all, of the difference in mean vessel element width found in the two studies. Vessel wall thickness would have to be substantial to account for the total difference in means.

A final possibility to account for the difference in means is the source of the samples. Carlquist's (1985) plants were field collected, while ours came from the Berkeley Botanical Garden. Cultivated plants usually have more mesomorphic characteristics than wild material of the same species (Bissing, 1982). However, known differences of this type are not sufficient to account for the difference in means observed here (Bissing, 1982). The inconsistent trends among the measurements of vessel size and distribution also do not support the hypothesis that the samples we used were from a more mesic habitat. Our mean vessel element width is greater and mean vessels per group is lower than the same parameters measured by Carlquist (1985), which is consistent with a more mesic habitat for our samples. However, our mean vessel element length should be longer than Carlquist's (1985), and it is not.

All vessel elements seen in this study have simple perforation plates. There is, however, some variability in lateral wall deposition patterns, related to the age of the vessels and whether they are located in the primary or secondary xylem. Vessels with helical wall deposition patterns are found in the primary xylem, while helical transitional to scalariform secondary wall deposition patterns are found in later formed vessels of the secondary xylem. There is no lateral wall pitting in the conventional sense of scalariform, transitional, opposite, or alternate pits. The term pseudoscalariform pitting may better describe the type of pitting found in this species. In pseudoscalariform pitting, smaller pits are interspersed with other wider pits, many of which extend around the circumference to more than one wall facet (Carlquist, 2001).

The literature is mixed in its support of the vessel element characteristics we found in *C. gigantea*. Carlquist (1974) found scalariform, or near scalariform, lateral wall pitting in the vessel elements. He later reported the predominate occurrence of simple perforation plates, but found no helical sculpturing (defined as secondary wall thickening connecting the pit apertures) as a secondary wall deposition pattern (Carlquist, 1985).

This difference can probably be ascribed to the confusing terminology used to describe vessel element secondary wall deposition patterns, and vessel element secondary wall pitting. If we exclude transitional forms (which are common), secondary wall deposition patterns can be categorized as annular, helical, scalariform, reticulate, and pitted (Evert, 2006; Mauseth, 1988). In these forms, the area of the primary wall not covered by the patterned secondary wall is available for diffusion. Lateral wall pitting can be in a scalariform, opposite, or alternate pattern, and the pits can be bordered or nonbordered. With the exception of the pitted secondary wall deposition pattern, pitting is usually described independently of the wall deposition patterns (Evert, 2006; Mauseth, 1988).

While the terms lateral wall pitting and lateral wall deposition pattern describe two different things, they may occur together. For example, it is conceivable that a vessel element can have a helical secondary wall deposition pattern, as well as alternate pits. In this case the primary wall is exposed at the pit apertures, which lie in an alternating pattern. Additional secondary wall material overlays this in the form

of a raised helical band. This pattern of lateral wall deposition and pitting can be seen in *Mahonia bealei* (Fig. 10f).

The common usage of the term scalariform in the literature tends to conflate the terms scalariform secondary wall deposition pattern and scalariform pitting. Strictly speaking, these are two different concepts. A scalariform secondary wall deposition pattern refers to the raised deposits of secondary wall material. In contrast, scalariform secondary wall pitting refers to the pattern of the pits themselves. Often, however, these terms are used interchangeably. In the case of *C. gigantea*, the literature probably describes the same phenomenon in vessel element characteristics as our research, but in different terms (Carlquist, 1985).

2. Rays

In smaller diameter stems, only a limited amount of xylem is produced from the fascicular cambium. As a result, the primary rays (interfascicular regions) are wide. The parenchyma cells of these rays divide to keep up with the production of xylem by the fascicular cambium. Over time, interfascicular cambium forms in the parenchyma of the primary rays, and eventually merges with the fascicular cambium to form the vascular cambium (Mauseth, 1988). The vascular cambium then produces the secondary xylem and phloem in a continuous cylinder, which is clearly visible in larger stem sections.

In *C. gigantea* the xylary rays appear more as interfascicular regions in the secondary xylem than as typical rays. In more typical woody dicots, rays appear in transverse section as radial bands of parenchyma cells with clearly delineated borders, set in a matrix of other cells such as libriform fibers. In *C. gigantea* libriform fibers are not extremely common, and ray parenchyma often occurs immediately adjacent to the vessel elements of the secondary xylem. As a result, the borders of the rays are less defined than those in fibrous woods. Rays with very diffuse borders have also been reported in the annual *Calepina irregularis* (Brassicaceae) (Schweingruber, 2006).

In transverse section the secondary rays are fairly wide. This is due in part to the narrow strands of vessels, and the limited amount of associated fibers produced in the secondary xylem. The width of the secondary rays is also due to the fact that they are the continuation of wide primary rays (Mauseth, 1988).

3. Fibers

There is no comparable information on libriform fibers available from the literature.

4. Paedomorphosis in the Secondary Xylem

The data and observations reported here support the hypothesis that the secondary xylem of *C. gigantea* is paedomorphic. The age-on-length curves, pseudoscalariform pattern of secondary lateral wall pitting, and upright ray parenchyma cells, all provide evidence of paedomorphosis (Carlquist, 1962, 2009).

Both negatively sloped and flat age-on-length curves were found in *C. gigantea*. The fact that we found both negatively sloped and flat lines may be a result of the fact that

little of the variation is explained by the regression lines. The r^2 values (0.101, 0.175, 0.001) make it obvious that there is no strong linear association between vessel element length and the distance from the start of the xylem. It may be that we were unable to detect a negative slope in the second sample from the 58.0 mm stem because of this, or because our second set of measurement only covered 6.2 mm of xylem instead of the 8.0 mm covered by the first sample. Alternatively, it is possible that reports of the existence of two types of paedomorphic curves are in error (Carlquist, 1962; Carlquist, 1989; Carlquist, 2001; Carlquist, 2009; Lens et al., 2009). The high amount of variability in vessel element lengths may make it impossible to differentiate negatively sloped from flat curves. Sampling stems of different size classes in a single species, along with publication of measures of goodness of fit, are needed to provide evidence to distinguish between these hypotheses. In any case, the vessel element length data in all three graphs indicate paedomorphosis.

5. Secondary Woodiness

There is little discussion in the literature on whether *Coreopsis gigantea* is woody, or possesses secondary woodiness. Carlquist considers it as an example of a woody herb, and lists it in his catalogue of woody herbs on islands (Carlquist, 1974). He also includes it as a member of the woody genera in the Munz flora of southern California (Carlquist, 1985; Munz, 1974). Thorne also lists it as an example of insular woodiness (Thorne, 1969).

Our character mapping on Mort et al.'s (2004) phylogeny of the western clade of *Coreopsis* shows that *C. gigantea* is secondarily woody, but the ancestral state for the genus remains in doubt (Fig. 9). Higher level phylogenies of the whole genus, and of tribe Heliantheae, help resolve this question. Kim et al. (1999) constructed a phylogeny of *Coreopsis* based on ITS sequences. In it, they used two outgroups basal to *Coreopsis*: *Fitchia speciosa*, and *Dahlia coccinea*/*Dahlia macdougalii*. *Fitchia speciosa* is a tree (USDA & NRCS, 2009), and is basal to *Dahlia*. *Dahlia* is nonwoody (Harris, 2008; Saylor, 2008; Vivar-Evans et al., 2006). This study suggests that the ancestor of *Coreopsis* lacked wood. A more recent study used nuclear 18S-26S rDNA internal transcribed spacer (ITS) sequences to construct a phylogeny of the Heliantheae, the tribe that contains *Coreopsis* (Baldwin et al., 2002). This study also supports an ancestral perennial, herbaceous state for *Coreopsis* (Baldwin et al., 2002).

The use of the term woody to describe the mature stems of *Coreopsis* is somewhat problematic, especially in light of our use of this term to refer to secondary xylem with a high percentage of fibers. The secondary xylem of *C. gigantea* shares more similarities with the wood of so-called herbaceous perennials than to the secondary xylem of highly fibrous woody species (Dietz & Ullmann, 1997; Dietz & Schweingruber, 2002; Krumbiegel & Kästner, 1993; Schweingruber, 2006; Schweingruber, 2007a; Schweingruber & Poschlod, 2005; Schweingruber & Landolt, 2005–2008). We return to this problem in the general discussion.

6. Environmental Factors and Anatomy

Coreopsis gigantea is found on the Channel Islands of southern California, and along a narrow strip of the mainland bordering seven counties in central and

southern California (Monterey, San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Riverside, San Diego; Consortium of California Herbaria, 2008). It usually grows on cliffs and sand dunes, exposed to the effects of the nearby ocean. In general, this area has a Mediterranean climate. Temperatures are mild and relatively stable, but there are seasonal differences in rainfall. Winters are wet, while summers tend to be dry (Keil, 1993; Ritter, 2006; USDA & NRCS, 2009).

Some of the xylem characteristics of *Coreopsis gigantea* seem to be an adaptation to this climate and habitat. While its vessels have a semi-ring porous distribution, it can be difficult to distinguish larger diameter vessels from smaller vessels in transverse sections. True growth rings bordered by a complete lack of vessels or the presence of a terminal fiber band are lacking. Instead, there are breaks in the radial vascular strands indicating seasonal disruptions of growth.

The low number of vessels per group may also be an adaptation to mesic conditions. It is possible that the large amount of parenchymatous tissue helps to store water, lessening any adaptive value of large vessel groups, which may be advantageous in xeric environments (Carlquist, 1985; Mauseth, 1988). Its shallow root system, fern-like leaves, and moderate vessel widths also indicate a lesser need for the high vessel conductivity that accompanies high transpiration rates. All of these factors are consistent with an adaptation to a mild climate without strong seasonality.

Of the three species studied here, *C. gigantea* has the highest number of paedomorphic features. Several of its xylem characteristics support the hypothesis that paedomorphosis represents a release from selection for mechanical strength (Carlquist, 2001). Although branches do occur, *C. gigantea* is not a tall plant, and its shoots do not appear to offer much wind resistance. As a result, its need for mechanical strength would seem to be minimal. The abundant parenchyma in its stem offers sufficient turgor to support the stem, without the need for extensive support from sclerenchyma. In conventional woods, rays offer less strength than the fibers they displace, and may weaken the wood. However, in *C. gigantea*, fibers are uncommon and rays may provide all the strength that is needed.

C. Mahonia bealei

Our results for *Mahonia bealei* are in general agreement with published findings on this species (Carlquist, 1995a).

1. Vessels

The mean length (257.5 μm) and width (24.7 μm) of the vessel elements reported here are comparable to the published means for this species (272.0 and 13.0 μm , respectively; Carlquist (1995b)). We found a mean of 6.7 vessels per group, compared with a mean of 11.8 vessels per group reported in the literature (Carlquist, 1995a).

The difference in vessel lengths can almost certainly be attributed to sampling error, though measures of variability are not available from the literature to verify this. The lower mean width of the vessel elements can be partially explained by the fact that Carlquist (1995b) only measured the lumen. If we estimate the combined thickness of the two cell walls as 2.0 μm , and subtract this amount from our measurements, it

brings our measurements to 22.7 μm , at least a bit closer to Carlquist's (1995b) figure of 13.0 μm . The remaining difference in vessel width could easily be due to intraspecific variation or, if the differences are statically significant, could, along with the higher number of vessels per group indicate greater xeric adaptation; although we might also expect to see shorter vessel element lengths in xeric adapted plants. This hypothesis may be supported if Carlquist's collection was from the field (ours was cultivated), though the greater availability of water to cultivated plants may not necessarily lead to greatly increased mesomorphic characteristics (Bissing, 1982).

2. Rays

There are no reports of ray cell dimensions in the literature. Carlquist (1995b) estimates ray height as 2.4 mm based on tangential sections. This seems low as our maximum section height, which the rays exceed, was 5.67 mm. Mean ray width is 63.8 μm , or 3.7 cells. This compares to a ray width of 4.4 cells reported in the literature (Carlquist, 1995a).

3. Fibers

Mean fiber length is 387.1 μm , and mean fiber width is 15.5 μm . This is shorter than the mean length of 541.0 μm measured by Carlquist (1995b). Although we found limited fiber storying, our results can easily be reconciled with Carlquist's (1995b) report of no fiber storying. The difference is likely due to a difference in interpretation. Fiber storying is certainly rare.

4. Paedomorphosis

Mahonia bealei has the fewest paedomorphic features of the three species studied here. As a result, it has only a minimal degree of paedomorphosis. The only indication of paedomorphosis is the flat age-on-length curve of vessel element lengths. Since $r^2=0.00$ ($p=0.832$) none of the observed variation is explained by this line, which is not significantly different from zero.

The weak paedomorphosis found in *Mahonia bealei* can perhaps best be understood in light of the hypothesis that paedomorphosis represents a relaxation of selection for mechanical strength. *Mahonia bealei* has limited branching, can grow up to 4 (–8) meters tall (Ying et al., 2010), and can be top heavy (Fig. 2c). This habit requires more mechanical strength than do the habits of the other species investigated here. Attempts to section its stems demonstrate the density of its wood. All of these facts support the hypothesis that there is an inverse relationship between degree of paedomorphosis and mechanical strength (Carlquist, 2001).

5. Secondary Woodiness

Loconte and Estes (1989) produced a morphological phylogeny of Berberidaceae that shows a woody ancestry for Berberidaceae, then a shift to herbaceousness, with a reversion to woodiness in the *Berberis/Mahonia* branch. They support their conclusion that *Berberis* and *Mahonia* are secondarily woody by citing the

apomorphic characteristics of the wood anatomy: ring porosity, little or no wood parenchyma, and homogenous, uniseriate rays (Loconte & Estes, 1989; Shen, 1954).

The *rbcL* maximum-parsimony tree generated in Qiu et al.'s (1993) study of the Magnoliidae places Papaverales basal to Ranunculales. The Papaverales are usually reported to consist of herbaceous plants (*Dicentra* and *Papaver* were used as representatives of the order in the study). Since the Ranunculales contains many woody genera (*Mahonia*, *Xanthorhiza*, *Cissampelos*, *Cocculus*, *Akebia*, and *Euptelea* are included in the tree, along with *Caltha*, which is herbaceous), the implication is that *Mahonia* has herbaceous ancestry (Qiu et al., 1993). However, recent work has shown that both *Dicentra* and *Papaver* have secondary growth (Schweingruber & Landolt, 2005–2008). *Dicentra formosa* produces distinct rings of secondary xylem, as do *Papaver alpinum*, *P. auranthiacum*, and *P. variegatum*. *Papaver dubium*, *P. rhoeas*, and *P. somniferum* are annuals that produce a single ring of secondary xylem (Schweingruber & Landolt, 2005–2008). These findings weaken the case for the herbaceous ancestry of *Mahonia*.

Judd et al. (2002) lists several apomorphies for the genus *Berberis*, including secondary woodiness (Judd et al., 2002). Though they do not discuss *Mahonia*, the proximity of *Mahonia* to *Berberis* on Loconte and Estes' (1989) tree suggests that Judd et al. (2002) would also consider it secondarily woody.

Kim and Jansen (1998) used chloroplast DNA restriction sites to construct the phylogeny of 16 genera of the Berberidaceae. They recognized four basic groups in the family, corresponding to the four groups based on base chromosome number of 6, 7, 8 and 10. These same groups were also recovered in an earlier study (Kim & Jansen, 1996). Kim et al. (2004b) used the chloroplast gene *ndhF* to further investigate the phylogeny of the family in the hope of resolving the relationships between the chromosomal groups discovered earlier (Kim & Jansen, 1998). Though they failed in this goal, they were able to provide strong support for retaining *Nandina* in the Berberidaceae. The retention of *Nandina* is relevant because it has woody stems, and because its position on the tree influences our character state reconstruction.

Our character state mapping on Kim et al.'s (2004b) phylogeny was unable to resolve the phylogenetic history of woodiness in *Mahonia* and *Berberis* (Fig. 12). Plotting the same data on Kim and Jansen's (1998) phylogeny suggests that these taxa are primarily woody. The difference in these conclusions is due largely to the position of *Nandina* in the two studies. Kim and Jansen (1998) place it as sister to the rest of the family, whereas in Kim et al.'s (2004b) study it is strongly supported as the sister group to the clade that contains *Caulophyllum*, *Leontice* and *Gymnospermium* (Fig. 12). Phylogenetic reconstructions of character state history are strongly dependent on the shape of the underlying phylogeny, and on the character states assigned to the terminal taxa (Olson, 2007).

6. Environmental Factors and Anatomy

The genus *Mahonia* is native to the Pacific Northwest of the United States, as well as Central America and Asia. Although *M. bealei* is used widely as a landscaping shrub throughout the United States, it originated in China. Its semi-ring porous pattern of vessel distribution suggests that it is adapted to a climate with a clearly

delineated growing season. We assume, of course, that these characters are not so plastic that they have been influenced by the local, North Carolina climate. Although trends in the vessel strands are not always consistent, the first part of the growth ring consists of noticeably larger diameter vessels, which means growth is initiated with higher temperature and plentiful water. Later in the ring the vessel diameters are smaller, which may indicate an adaptation to less rainfall.

Mahonia bealei has a higher number of vessels per group than in either *Xanthorhiza simplicissima* or *Coreopsis gigantea*. This, together with the presence of vasicentric tracheids and fairly narrow vessels, may provide a margin of safety in case of fluctuations in water supply. Narrow vessels and tracheids have been shown to resist cavitation better than wide ones (Hacke & Sperry, 2001; Sperry et al., 2006). Its vessels also have helical lateral wall deposition patterns, which may allow for some deformation of the vessel walls. This feature could help prevent implosion of the vessels due to extreme negative pressure resulting from dry conditions.

D. Paedomorphosis in the Secondary Xylem

Carlquist (2009) recently placed paedomorphosis in the secondary xylem in the context of heterochrony in the xylem of angiosperms. According to his synthesis, there is a continuum of heterochronic events in the xylem. On one end of the continuum, plants like the monocots Gunneraceae, Nelumbonaceae, and Nymphaeaceae have lost cambial activity, resulting in a permanently juvenile xylem. Juvenile features of these plants include sympodial, less woody growth forms, decreasing vessel element lengths across the primary xylem, and raylessness (or exclusively upright ray cells). On the opposite end of the continuum are typical woody plants like trees and shrubs. These plants have an active vascular cambium that produces secondary xylem with mature (adult) characteristics very early in life. They have woody monopodial growth forms. Their vessel elements decrease in length in the primary xylem, but then increase in length in early secondary xylem before leveling off in later secondary xylem. Ray cells tend to be mostly or exclusively procumbent. Plants with paedomorphic secondary xylem fall between these extremes, but lie towards the monocot end of the spectrum. They possess at least some of the paedomorphic characters discussed in the Introduction (Carlquist, 2009).

1. The Baileyan Trends

Carlquist based part of his theory of paedomorphosis on Bailey's (1944) refugium theory (Carlquist, 2009). Bailey (1944) proposed that advanced wood features, by which he means features adapted for maximum conductance, first evolved in the secondary xylem, and then later appeared in the primary xylem. This evolutionary scenario explains why the primary xylem tends to retain more primitive (less optimal) tracheary elements (Bailey, 1944; Carlquist, 1962; Mauseth, 1988). According to Carlquist's (1962) paedomorphic theory, anatomical features that occur in the primary xylem of typical woody plants also occur in the secondary xylem. Therefore, in paedomorphic wood, some of the features of the secondary xylem will be primitive, in the Baileyan sense (Carlquist, 1962).

Since the Baileyan trends serve as an underpinning to Carlquist's (1962) theory, it is good to at least briefly examine possible weaknesses in the assumptions behind these trends. Although Carlquist (1962) uses the trends as a point of reference, his theory actually serves as a partial refutation of them.

All the major Baileyan trends were discovered either by the use of the fossil record to determine the timing of a character's appearance, or through correlations with the primitive features so discovered (Bailey, 1944; Bailey & Tupper, 1918; Frost, 1930a, b, 1931; Kribs, 1935, 1937; Tippe, 1938). Bailey's general trends were confirmed by Wheeler and Baas (1991) through a study of the frequency of woody character state occurrences in a database of 1200 fossil woods. Unlike a previous survey (Chalk, 1937), Wheeler and Baas (1991) were able to relate their observed frequencies to geological periods. Although not all of Bailey's trends were supported (septate fibers are more common in the fossil record than Bailey would have predicted), most were.

A problem with using correlation methods in these ways is that they may not be tracking changes in the characters themselves, but changes in the relative abundance of taxonomic groups in the fossil record (or sampling errors in the database). For instance, the low percentage of species with short ($< 350 \mu\text{m}$) vessel elements in the Cretaceous may be an indication of the composition of the flora, not of the primitive nature of short elements (Wheeler & Baas, 1991). Warren (Herb) Wagner long ago recognized this problem, and warned against it (Wagner, 1969). Neither Chalk (1937) nor Wheeler and Baas (1991) summarized the taxonomic distribution of the fossils, which would at least partially address this criticism. In some cases the taxonomic identity of the fossils was not even known (Wheeler & Baas, 1991). These types of methods would have greater validity if they were conducted within a phylogenetic context, which would address the problem of species abundance.

Although the Baileyan trends are still accepted as reasonable descriptions of the general course of xylem evolution (Evert, 2006), some of their underlying assumptions limit their usefulness. The fact that the trends were developed outside of a taxonomic framework, and were therefore treated as irreversible, was originally seen as one of their strengths (Tippe, 1938). Homoplasies in the trends are now known, with the instance of parallelisms outnumbering reversals by a factor of two (Baas & Wheeler, 1996). The existence of homoplasies makes it necessary to test the assumed primitive conditions implied by the trends in the context of each new study. They can no longer be considered irreversible.

The assumption that water conduction was the major driving force behind the evolution of vessels has also been questioned (Mauseth, 1988; Sperry, 2003). It is now more common to view the different types of tracheary elements as having evolved in response to the environmental and physical demands put on the particular vascular tissue (Mauseth, 1988). Plants with only primary xylem grow under different conditions, and have different physiological needs than older plants of the same species that have developed secondary xylem. Since different demands are put upon their vascular systems, the tracheary elements must assume different structural forms, and must have evolved to meet these demands. For example, younger plants may be shorter, so that root pressure may be sufficient to move water and minerals up through the xylem. In this case, tracheids and narrower vessels may suffice.

Older, taller plants are dependent on cohesion-tension to move water, and may need wider vessels to meet their water transportation needs, and longer vessel elements to provide additional structural strength (Mauseth, 1988).

There are, of course, tall plants like the conifers that do not rely on wide vessels to meet their water requirements. Instead, they use tracheids as water conduits. However, since conifers are often found in habitats with limited resources (such as areas of low soil fertility), the lower resource requirements of their xylem may offer an advantage that outweighs conductivity. Thus tracheids, which are found in less dense woods that require less energy and less structural compounds to construct, are able to meet both the conductive and resource needs of conifers (Hacke & Sperry, 2001; Sperry, 2003).

Ecological wood anatomy has also shown that certain environmental factors like seasonality, nutrient availability, and temperature have strong correlations with wood structure (Endress et al., 2000). In experiments with the cacti *Cereus peruvianus* and *C. tetragonus*, reduction of vessel density and vessel diameter was triggered by reducing the availability of nitrogen and phosphorous in the soil (Arnold & Mauseth, 1999). While these may be only short-term responses, it seems reasonable that long-term selection pressure could reverse at least some of the major evolutionary trends.

Functional studies have provided additional insights into xylem evolution. For example, there are inherent trade-offs between conductivity and safety. Wider vessels may offer greater conductivity, but increase the risk of cavitation through the formation of bubbles in the water column from freeze-thaw cycles, or from drought (Hacke & Sperry, 2001). Larger lateral wall pits also enhance conductivity, but weaken the vessel wall. The extent of lateral wall pitting may even be more important than lumen diameter in safety issues (Sperry, 2003; Sperry et al., 2006). The increased porosity of the pit membranes also offers increased conductivity, but this increases the risk of air seeding, which causes cavitation (Sperry, 2003). Thicker vessel walls offer greater safety against collapse caused by negative pressure; however, there is a greater cost to the plant since there is a greater investment in wall material (Sperry, 2003).

Transpiration rate is another driving force behind the evolution of tracheary elements. Most of the water taken in by plants is lost due to transpiration that occurs during the gas exchange associated with photosynthesis. Transpiration rate can be affected by several factors including size of the leaves, the number of stomata, water availability, and CO₂ concentration in the atmosphere (Sperry, 2003). There is evidence that early plants did not need highly conductive tracheary elements because of the much higher CO₂ levels at that time. The highly favorable exchange rate for CO₂ versus water greatly reduced the cost of transpiration. These factors might at least partially explain the tracheary element morphology seen in early fossil plants (Feild et al., 2004). Feild et al. (2004) also argue that these ancestral characters were adapted to the high water availability and the low evaporative demand in the tropical, rainy environments of the early plants.

Although these considerations weaken the validity of the Baileyan trends, the trends still offer some insight into xylem evolution. Bailey's refugium theory, however, is much weaker and does not adequately explain how primary xylem and secondary xylem differ. The primary xylem can only be described as an evolutionary

time capsule if the trends are irreversible, or if each of Bailey's primitive states could be shown to be primitive for the angiosperms as a whole. In the latter case, the trends would be similar to morphological transition series: multistate characters with restricted transitions between the states (Swofford and Begle, 1993). Characters like this are hypotheses of evolutionary transformations that must be tested through correlations with other characters in a parsimony framework. These types of analyses would likely show that in some taxa the primary xylem retains many primitive states, while in others it does not. The structure of the primary xylem is shaped both by the selective pressures placed on the young plant (Mauseth, 1988), and by historical, lineage specific events. During the period when the primary xylem serves as the main conductive tissue, young plants frequently have lower transpiration demands. They may be shaded in the understory, or have smaller masses of leaves with correspondingly fewer stomata. They are also smaller, so that the fibers and heavier vessel element lateral wall deposition patterns seen in the secondary xylem are not needed for structural support (Mauseth, 1988). These requirements may differ in different taxa, leading to different structures of the primary xylem.

Research on the genetic and cellular mechanisms behind secondary growth also provides insight into the linkage between the primary xylem and the secondary xylem. Plants like *Arabidopsis thaliana* that normally have only primary growth can be induced to produce secondary xylem (Nieminen et al., 2004). It has also been shown that the genes responsible for the production of secondary xylem in loblolly pine have homologs in *Arabidopsis*. Thus, the primary xylem has structural differences from secondary xylem partly because of the different expression of the same gene families (Groover, 2005; Nieminen et al., 2004).

2. Mabberley's Criticism of Paedomorphosis

Mabberley (1974) disagreed with Carlquist's (1962) use of age-on-length curves for vessel elements as a basis for his theory of paedomorphosis. Mabberley noted that plants like *Talinum guadalupense*, with a negatively sloped age-on-length curve, and *Macropiper excelsum*, with a flat age-on-length curve, are pachycauls. Pachycaulous plants have thick, often parenchymatous, stems with piths that become progressively wider higher in the stem. Mabberley argued that even if the vessel element measurements that produced the curves were taken at the same height, they were not taken from geometrically equivalent parts of the plants. This necessarily produces different types of curves due to the differences in pith radii in the pachycaulous and leptocaulous (a typical tree or shrub) plants (Mabberley, 1974).

Basic geometry illustrates why different curves will be produced from plants with different pith radii. The increase in the amount of xylem is dependent on two factors: the number of cambial initials available for division, and the rate of cell division. The number of cambial initials available for division is given by the formula $(2\pi r)/x$, where x =the tangential width of cambial initials, r =the radius of the pith and secondary xylem, and $2\pi r$ =the circumference of the vascular cambium. As is apparent from this formula, the smaller the radius, the smaller the circumference, and the fewer the cambial initial cells available for division (Mabberley, 1974). Under these conditions the rate of anticlinal cell division becomes important in increasing the circumference of the cambium. If the rate of anticlinal division cannot keep up

with the periclinal divisions that add cells to the secondary xylem, then the increased circumference must be made up by apical intrusive growth of the initials (Evert, 2006). Intrusive growth increases the number of initials available in the circumference by causing initials from a lower level to intrude between the initials of a higher level. Later transverse divisions in the elongated initials results in two shorter cells, where there was originally only a single long cell (Mabberley, 1974). As the radius of the stem increases and these processes continue, there are more cambial initials available for radial anticlinal division, and the need for intrusive growth is reduced. As a result, when vessel element length is plotted against distance from the center of the stem there is a steep rise in vessel element length in the earlier formed secondary xylem, then a reduction, and eventually a plateau (Mabberley, 1974).

Pachycaulous plants like *Macropiper excelsum* and *Talinum guadalupense* have wide piths, that become wider upwards. The greater radius means that there are more cambial initials available for anticlinal division, so it is easier for these divisions to keep up with the increase in secondary xylem (Mabberley, 1974). Therefore, there is less need for intrusive growth to increase the number of initials, and vessel element lengths do not increase. Since these plants start with a wide pith, a plot of their vessel element lengths resembles the latter part of the age-on-length curves for a typical woody plant. However, if vessel elements were measured at the base of a pachycaulous plant, the age-on-length curve would resemble the full curve (Mabberley, 1974).

Since the age-on-length curves produced by the pachycaulous plants in Carlquist's (1962) study can be explained by the wider pith at the location where the measurements were taken rather than by paedomorphosis, Mabberley (1974) argues that the theory of paedomorphosis is not supported by the curves. Measurements of vessel element lengths at geometrically equivalent locations are necessary to support the theory (Mabberley, 1974).

Research done since Carlquist's (1962) initial study demonstrates the incorrectness of Mabberley's (1974) conclusion. Negatively sloped age-on-length curves have been found in a number of non-pachycaulous plants, including those in this study. In the Rubiaceae, *Arcytophyllum setosum* (shrub), *Emmeorrhiza umbellata* (perennial climbing herb), *Hedyotis fruticosa* (shrub or small tree), *Spermacoce verticillata* (woody herb or subshrub), and *Phylloentas schimperiana* (woody herb or shrub) all have negatively sloped curves (Lens et al., 2009). Other examples of non-pachycaulous plants with negatively sloped curves are *Impatiens arguta*, *I. niarnniensis* (both herbaceous, Balsaminaceae) (Lens et al., 2005a), *Coris monspeliensis*, *Lysimachia kalalauensis*, *L. vulgaris* (small to medium trees and shrubs, Myrsinaceae) (Lens et al., 2005b), and all species in *Corema* and *Empetrum* (shrubs, Ericaceae) (Carlquist, 1989). Flat age-on-length curves have been found in *Arcytophyllum lavarum* (subshrub), *Diodella sarmentosa* (perennial climbing herb), *Hedyotis lessertiana* (shrub or small tree), *Spermacoce macrocephala* (subshrub), and *Kadua cordata* (subshrub or shrub) (all Rubiaceae; Lens et al., 2009).

E. Secondary and Insular Woodiness

The use of wood characteristics, either with or without paedomorphosis, to determine the ancestry of taxa (Lens et al., 2009; Lens et al., 2005a) can be

problematical. Evolutionary relationships among genera can be difficult to uncover, and simple morphological assessments used outside of a phylogenetic context have limitations in reconstructing the ancestral origins of woodiness. This is especially true in insular woody genera, where problems in determining whether a species was introduced by single or multiple colonization events, the time of radiation, and the continental relatives and geographic sources of the original colonizers are especially difficult (Kim et al., 1996).

The evolution of woodiness in *Tolpis* (Asteraceae) provides a cautionary tale on determining the direction of evolution of woodiness in general, and insular woodiness in particular. *Tolpis* is a genus of ca. 16 species in Macaronesia and the nearby continents of Europe and Africa. All but two of these have woody stems. The two nonwoody species are annual herbaceous plants: *Tolpis coronopifolia* (Macaronesia, Canary Islands) and *Tolpis barbata* (Mediterranean area of Europe and Africa). Both of these species can grow as biennials under certain environmental conditions, in which case they occasionally develop woody stem bases (Moore et al., 2002).

Moore et al. (2002) constructed a phylogeny of *Tolpis* based on chloroplast DNA restriction site variation. Restriction site mutants were coded as absent or present, and parsimony analyses were done to generate phylogenetic trees. The geographic distribution of the extant species was then mapped on each clade, resulting in nine equally parsimonious reconstructions of dispersal history (Moore et al., 2002).

The topology of the strict consensus tree shows that woodiness is plesiomorphic in *Tolpis*. *Tolpis* has primary woodiness, while the annual herbaceous habit evolved twice, independently. The two herbaceous species are derived from woody ancestors (Moore et al., 2002).

The nine equally parsimonious reconstructions of dispersal history fall into two groups. The first group, consisting of eight reconstructions, implies that *Tolpis* colonized the Madeira Islands from the continent, followed by extinction of the genus on the continent, and then subsequent continental recolonization from Macaronesia. There is little agreement among the reconstructions on which island group in Macaronesia is the source of the existing continental species. The second group, consisting of the ninth reconstruction, requires four separate introductions of *Tolpis* from the continent.

To refine the analysis, minimum geographic distances required for travel between the regions were assigned to each dispersal event in each of the nine scenarios. Ranking the nine reconstructions by minimum distance required favors the first group of reconstructions, those involving continental extinction and recolonization (Moore et al., 2002).

While the authors make it clear that the data does not exclude the possibility of the evolution of woodiness in Macaronesia (it only supports the plesiomorphy of woodiness in the extant taxa), a natural interpretation of their results is that the initial colonists to Macaronesia were woody. If any of the eight, group one, dispersal reconstructions are correct, then the extant herbaceous continental species *T. barbata* evolved from woody Macaronesian ancestors (Moore et al., 2002).

It is intriguing that a woody continental species of *Tolpis* may have colonized Macaronesia, with resulting speciation throughout the archipelagos, extinction of the woody continental species, followed by a recolonization of the continent by an herbaceous species derived from a woody Macaronesian ancestor. Contrast this scenario with what would be more natural to assume based only on the distribution

of woody and nonwoody taxa. Given the current distribution, it would be natural to assume that an herbaceous species from the continent colonized Macaronesia, and that woodiness evolved as the species spread throughout the islands. After all, the extant continental species of *Tolpis* is herbaceous (*T. barbata*), while all but one of the *Tolpis* spp. in Macaronesia are woody. The results of this study make it evident that the evolution of woodiness can be complex, and that its study requires more than knowledge of the distribution of woody and nonwoody taxa.

A second example illustrates the complexities involved in the evolution of woodiness, and the evolution of insular woodiness in particular. Eleven species of *Convolvulus* (Convolvulaceae) are endemic to Macaronesia (the status of a twelfth species, the weedy annual *C. siculus*, is uncertain). All are woody. The eleven endemic species fall into two distinct groups, climbers and non-climbers (Carine et al., 2004).

Carine et al. (2004) used data from the nuclear ribosomal internal transcribed spacer (ITS), and the 17S and 26S gene regions to construct a phylogeny of the *Convolvulus* spp. in Macaronesia, and their closest relatives. Forty-three species of *Convolvulus* were sampled, including nine of the eleven species endemic to Macaronesia. The non-Macaronesian species consisted of *Convolvulus* species from the Mediterranean and western Asia, as well as some closely related species included as outgroups. The aligned sequence data was used in a parsimony analysis (Carine et al., 2004).

The topology of the consensus tree shows two major clades, one consisting of perennial non-climbing species (mostly shrubs and subshrubs), and the other composed of annual or perennial herbs and suffrutescent plants. The *Convolvulus* species endemic to Macaronesia are resolved as two distinct clades nested within these two groups (Carine et al., 2004). These phylogenetic relationships imply that there were two independent colonizations of Macaronesia from distantly related lineages of *Convolvulus* (Carine et al., 2004). The erect shrubs (*C. caput-medusae*, *C. scoparius*, *C. floridus*) resulted from one colonization, while the climbers (*C. canariensis*, *C. fruticulosus*, *C. lopezocasi*, *C. massonii*, *C. glandulosus*, *C. volubilis*) originated from another. The analysis also shows that woodiness is plesiomorphic in the erect shrubs, while it is derived in the climbers (Carine et al., 2004).

Just as in *Tolpis*, the example of *Convolvulus* shows that plants with insular woodiness are not necessarily secondarily woody. Although none of the species of *Convolvulus* were examined for paedomorphic characteristics, the implications are clear. Intuitive assessments of morphology used to determine relationships and the evolutionary origins of woodiness, while useful, should be supplemented with additional information and analyses. Phylogenetics, particularly molecular phylogenies, provides a useful supplemental tool to anatomical and morphological analyses.

F. Paedomorphosis with Primary Woodiness

Although a significant amount of work suggests a link between paedomorphic wood and secondary woodiness, there is no required connection between these two phenomena. In some studies, plants with paedomorphic secondary xylem have been shown to be secondarily woody through phylogenetic analysis. In others, the presence of paedomorphic wood has been used to suggest, *ipso facto*, secondary woodiness (Lens et al., 2009; Lens et al., 2005a). However, plotting the co-

occurrence of scalariform perforation plates and Paedomorphic Type I rays on the phylogeny of the Ericaceae shows that at least these two characteristics of paedomorphic wood can also occur in the context of primary woodiness (Fig. 13). The plots showing the evolution of woodiness in the taxa related to *Xanthorrhiza* and *Mahonia* (Figs. 4, 12) also demonstrate that the relationship between paedomorphosis and secondary woodiness is not straightforward.

Both of these lines of evidence suggest that paedomorphic wood cannot be used as the sole basis for ascertaining the existence of secondary woodiness. Since plants with paedomorphic woodiness can be either primarily or secondarily woody, the evolutionary source of their woodiness is best determined through phylogenetic analysis. Whether primary or secondary woodiness exists should not be based on anatomical or morphological analyses alone.

The wood anatomy of the Cactaceae also provides evidence that paedomorphic characteristics are sometimes found in primarily woody species. The Cactaceae is a very diverse family, all of which produce some secondary xylem. The family includes trees, vines, dwarf plants such as the globose cacti, giants such as the huge columnar cacti, epiphytes, and geophytes. The wood anatomy of the family reflects this structural diversity (Mauseth, 2006a).

All genera of the Cactaceae are woody in the sense that they have a vascular cambium that produces secondary xylem and phloem. In some cases, like the dwarf globose cacti that are only 2–3 cm in diameter, they may not produce much secondary xylem, but some occurs in all genera (Mauseth, 2006a). To meet the diverse structural needs of the species a variety of types of secondary xylem are produced, including fibrous wood, wide band tracheid wood, dimorphic wood, trimorphic wood, and parenchymatous wood (Mauseth, 2004, 2006b; Mauseth & Plemons, 1995; Mauseth & Plemons-Rodriguez, 1998; Mauseth & Stone-Palmquist, 2001). Both the shoot and the root may produce the same type of wood, or wood type may vary by organ. Wood type may also change over time in the same organ (Mauseth & Stone-Palmquist, 2001).

Fibrous wood, which contains vessels embedded in a matrix of fibers, is predominant in genera with tall branching or columnar forms, and in long scrambling plants. For example, fibrous wood is found in *Monvillea diffusa*, *Cereus hankeanus*, and *Pilosocereus lanuginosus* (Mauseth & Plemons-Rodriguez, 1998). This wood may be monomorphic in both seedlings and adults, or it may be dimorphic. Monomorphic fibrous wood is commonly found in tall woody species like *Pereskia sacharosa* (Mauseth & Plemons-Rodriguez, 1998). In other genera fibrous wood is only one stage in a dimorphic or trimorphic wood.

Wood with wide band tracheids is found in almost all genera of Cactaceae (Mauseth, 2004, 2006b). This type of wood consists mainly of vessels embedded in a matrix of tracheids. The tracheids are short and barrel shaped, and have annular or helical secondary wall deposition material projecting deeply into the lumen. The term “wide band” refers to the appearance of the annular or helical projections, which resemble bands (Mauseth, 2004).

Wide band tracheids offer a major adaptive advantage: the annular or helical bands allow the tracheids to expand and contract with changing moisture conditions. In this way the volume of each tracheid can be matched to the amount of water it contains. Coupled with the fact that these woods lack fibers, the presence of wide band tracheids allows the stem to contract under dry conditions, and expand under

wet. As a result, the risk of cavitation is reduced. Tracheids with more rigid cell walls have fixed volumes, and lack this advantage (Mauseth, 2004).

Wide band tracheid wood is monomorphic in some species, and is the first form of wood produced in some dimorphic and trimorphic species (Mauseth & Plemons, 1995). It is present as the monomorphic wood in *Astrophytum ornatum*, *Echinocactus knuthianus*, and *Blossfeldia liliputana*. These are small, globose or broad, columnar cacti (Mauseth, 2004; Mauseth & Plemons-Rodriguez, 1998).

In some dimorphic species, such as *Buiningia aurea*, *Oreocereus selsianus*, and *Vatricania guentheri*, wide band tracheid wood is produced, followed by more typical fibrous wood. In many of the dimorphic species, secondary rays are not common, and are often narrow (only 1–3 cells wide) when they occur. In other dimorphic species wide band tracheid wood is followed by parenchymatous wood, with vessels embedded in parenchyma. Species with this type of wood include *Echinopsis tubiflora*, *Gymnocalycium marsoneri*, and *Parodia maassii*. Secondary rays in these species are also narrow and sparse. In *E. tubiflora*, there is delayed development of the secondary rays so that no rays develop in the secondary xylem until the vessels are abundant. The final type of dimorphic wood contains fibrous wood as the first stage, followed by a second stage of parenchymatous wood. This is found in such species as *Hylocereus venezuelensis* and *Stephanocereus leucostele* (Mauseth & Plemons, 1995).

In trimorphic species wide band tracheid wood is followed by fibrous wood, and then parenchymatous wood as a final phase. Trimorphic wood occurs in *Melocactus intortus*, *Melocactus bellavistensis*, and *Arrojadoa braunii* (Mauseth & Plemons, 1995).

Parenchymatous wood is not extremely common, but has been found in 16 species to date. It usually occurs as a stage in dimorphic or trimorphic wood, in mostly short globose plants (Mauseth & Plemons-Rodriguez, 1998; Mauseth & Stone-Palmquist, 2001). However, the roots of species such as *Acanthocereus sicariiguensis*, *Corryocactus megarhizus*, and *Copiapoa coquimbana* have monomorphic parenchymatous wood (Mauseth & Plemons-Rodriguez, 1998).

As the previous discussion indicates, there is a correlation between wood anatomy and plant structure in Cactaceae. Adult species with short globose structure tend to have wide band tracheid wood or parenchymatous wood, or a dimorphic form containing both types. In these plants cell turgor is sufficient to provide structural support. Species with tall columnar adults or branching forms tend to have fibrous wood, either throughout their entire life cycle or as the major portion of a dimorphic wood. In many of these species, turgor pressure provides adequate support while the plant is small. As the plant enlarges, fibrous wood begins to be produced and provides greater support (Mauseth, 2006b; Mauseth & Plemons, 1995; Mauseth & Plemons-Rodriguez, 1998).

In general, monomorphic wood is found in species where the structure of the adult is very similar to the young plant. Dimorphic wood is usually found in species where there is a change in structural form from seedling to adult. For example, species like *Astrophytum ornatum* and *Gymnocalycium oenanthemum* have short and broad young shoots whose turgor is sufficient to support the plant. Their juvenile wood contains wide band tracheids. As they grow in height turgor provides insufficient support, and they switch to producing fibrous wood (Mauseth & Stone-Palmquist, 2001).

Both adult wood with wide band tracheids and adult parenchymatous wood can be considered pedomorphic. In many of the plants with adult parenchymatous wood

the structure of the wood resembles that of the primary xylem (Mauseth & Plemons, 1995). Both tissues consist of vessels embedded in a parenchymatous matrix. In at least some genera the primary xylem also possesses wide band tracheids (Mauseth & Plemons, 1995). In addition, in at least one species (*Echinopsis tubiflora*) there is delayed ray development, another characteristic of paedomorphic wood. In monomorphic wood these characteristics exist for the life of the plant, while in dimorphic and trimorphic woods they exist for a prolonged period before a different type of wood is produced. These features, while somewhat different from those described by Carlquist (1962), are paedomorphic because they occur in the primary and persist into the secondary xylem.

As mentioned above, all Cactaceae have a vascular cambium that produces secondary xylem and phloem. The ancestors of the family are also thought to be woody, probably woody non-succulent trees or large shrubs with fibrous wood. The sister group to the rest of the family, *Pereskia*, possess monomorphic, fibrous wood (Edwards et al., 2005; Mauseth, 2006b; Mauseth & Stone-Palmquist, 2001). It has also been argued that the genera that possess either monotypic wide band tracheid wood, parenchymatous wood, or these wood types as a prolonged stage in dimorphic wood, are moving evolutionarily away from typical fibrous wood towards less woodiness (Mauseth & Plemons, 1995; Mauseth & Stone-Palmquist, 2001). It seems that these types of paedomorphic woods are derived from woody ancestors in the Cactaceae.

Although research on wood anatomy in Cactaceae has not focused on paedomorphosis, the presence of paedomorphic characters in these woods provides another example of paedomorphic wood in species with primary woodiness. Unless additional research provides support for an exclusive link between paedomorphic wood and secondary woodiness, it is better to use phylogenetic analysis in conjunction with wood anatomy to gauge whether primary or secondary woodiness exists.

The fact that paedomorphic wood is produced by the plant when turgor is sufficient for its structural needs supports Carlquist's hypothesis that paedomorphic wood represents a relaxation of selection for mechanical strength (Carlquist, 2001). It may be that that paedomorphic wood arose through a heterochronic shift in flowering time when previously immature plants became capable of flowering. With no need for additional structural support, the plants continued to produce juvenile wood. Thus, juvenile features of the secondary xylem are the only ones expressed by the genes of these plants, while the genetic program for producing fibrous wood has been repressed (Mauseth, 2004; Mauseth & Stone-Palmquist, 2001).

G. Paedomorphic Rays and Raylessness

Carlquist (1962) first suggested that raylessness was associated with paedomorphosis in his classic paper on paedomorphosis, and developed his ideas more fully in relation to insular species of *Plantago* (Carlquist, 1970). In this paper he noted the correlation between rayless and other paedomorphic characters, after which he and others began to use raylessness as an indication of paedomorphosis (Lens et al., 2007).

A brief justification for considering raylessness a paedomorphic character was presented in Carlquist (2009). Here he says [Raylessness occurs] "in a small number

of eudicot species, and in some of these rays eventually form. The fact that ray formation is delayed is thus the expression of juvenilism.” To understand this argument we must first understand how multiseriate and uniseriate rays form at the beginning of secondary growth (Barghoorn, 1940, 1941a, b).

At least in the species Barghoorn (1940, 1941a, b) investigated, multiseriate rays form from the interfascicular regions of the primary plant body (the primary rays), as radial continuations of these regions. Uniseriate rays form only in the fascicular regions, after secondary growth has begun. Additional multiseriate rays may also form in the fascicular regions. As secondary growth continues, multiseriate rays may become divided to form smaller rays, and uniseriate rays may disappear. These processes occur through the replacement of ray initials with fusiform initials, and may take place gradually (Barghoorn, 1941b). As the ray initials lengthen, the resulting ray cells become more upright. It should be possible to follow the disappearance of rays in an individual in serial tangential sections, which should show a gradual lengthening of the ray cells before they are replaced by tracheary elements, or fibers. The presence of rays with diffuse lateral borders in *Calepina irregularis* (Brassicaceae) may be a stage in this process (Schweingruber, 2006).

In rayless species the transformation of ray to fusiform initials takes place as soon as secondary growth begins in the interfascicular regions (Barghoorn, 1941b). The cells of the primary rays are immediately converted to fibers or tracheary elements. In the fascicular regions uniseriate rays simply never form. If we consider only the fascicular regions of rayless species, the juvenile process of ray formation is delayed, or never occurs. Raylessness is thus an expression of paedomorphosis, as is the possession of only uniseriate rays. If we consider the interfascicular region, the conversion of ray to fusiform initials, which usually occurs later in growth, now occurs at the beginning of secondary growth. This process results in a form of peramorphosis (acceleration), the expression of mature characteristics in a juvenile. So, somewhat paradoxically, rayless wood can be seen as both paedomorphic and peramorphosis depending on whether one focuses on the fascicular or interfascicular regions.

In summarizing these mechanisms it is important to note that Barghoorn’s (1940; 1941a; b) results are based on a limited sample of more or less typical woody species. As far as we are aware, his results have not been corroborated on species with a wider range of secondary growth types (Krumbiegel & Kästner, 1993; Schweingruber & Landolt, 2005–2008).

If the absence of rays is a functional adaptation to a reduced need for lateral transport, the presence of solely uniseriate rays with upright cells (Paedomorphic Type III rays) might be a transitional stage between multiseriate rays (Paedomorphic Types I and II) and raylessness. Woods such as those of *Archeria traversii* and *A. fasciculata* (Ericaceae) (Meylan & Butterfield, 1978) have mainly uniseriate rays consisting of upright cells, and are shrubby (up to 5 m tall). Their woods at least superficially resemble those found in truly rayless species like those of *Veronica* section *Hebe* (Scrophulariaceae) (Meylan & Butterfield, 1978; Philip Garnock-Jones, personal communication). If Barghoorn (1941b) is correct that raylessness results from the substitution of fusiform shaped fibers for ray cells, then it seems reasonable that the formation of upright parenchyma cells in uniseriate rays is a transitional stage between multiseriate rays and the rayless condition.

H. The Concept of Woodiness in Relationship to Plant Growth Forms

The concept of a woody plant is central to the theory of paedomorphosis, and to this paper (Carlquist, 1962). At the outset we tried to restrict our use of the term woody to refer to the possession of fibrous wood, but our work on *Coreopsis* has shown the futility of this restriction. If we learn only one thing from Carlquist's voluminous work on xylem evolution, it should be that the concept of a woody plant is badly in need of refinement.

The fact that woody plants can readily evolve from nonwoody ancestors in a variety of environments shows that the xylem evolution is very labile. Not only does secondary xylem occur in numerous lineages, but the organ in which it evolves may vary. It may be absent from the stem, but found in the root system (Liu & Zhang, 2007; von Arx & Dietz, 2006). For example, in many dwarf *Opuntias* (Cactaceae) only fascicular cambium is formed in the stem. This cambium produces only a few vessels and some xylary parenchyma. Yet the roots of these species form large amounts of wood (James Mauseth, personal communication). The degree of woodiness may also vary within the same organ over time. *Cereus aethiops* (Cactaceae) serves as an extreme example of this phenomenon. Its shoot and root systems initially produce typical fibrous wood. However, some of its roots become greatly enlarged and switch to producing parenchymatous wood, while its slender roots continue to produce fibrous wood (Mauseth & Stone-Palmquist, 2001).

Carlquist (1962) cites a number of examples of annuals with flat age-on-length curves to bolster his case that these curves can be considered equivalent to the descending portions of normal age-on-length curves (Fig. 1). The implication is that even annuals can possess significant amounts of secondary xylem.

In the Ericaceae, the taxa *Chimaphila umbellata* and *Pyrola rotundifolia* have traditionally been considered nonwoody (Kron et al., 2002). However, both have reasonable amounts of typical fibrous wood at the root/shoot junction (Schweingruber & Landolt, 2005–2008), and could be considered woody according to conventional definitions. Even the annual *Linum usitatissimum* (flax; Linaceae) produces significant amounts of secondary growth (Bowers, 1996). These examples show that woodiness is not an all-or-nothing phenomenon, but rather occurs along a continuum (Table 1) (Schweingruber & Landolt, 2005–2008).

This point is reinforced by the work of Krumbiegel and Kästner (1993), who describe seven forms of secondary growth in the shoots (and two in the roots) of annuals: (1) Secondary growth restricted to the vascular bundles (two subtypes). (2) Fascicular and interfascicular cambia formed, but secondary lignified cells only produced opposite the primary bundles. (3) Fascicular and interfascicular cambia formed, with secondary lignified cells produced in both regions (two subtypes). (4) As in type 3, but with growth occurring in the fascicular regions prior to the formation of a complete cambial ring (two subtypes). (5) A complete, active cambial ring is present at the beginning of shoot differentiation so that it is difficult to determine the boundary between primary and secondary growth (two subtypes). (6) Secondary growth produced by successive cambia. (7) Fascicular cambia present, and interfascicular secondary growth produced by cell divisions in the inner layer of the cortex.

These seven types of secondary growth produce plants that, though they all have secondary xylem, are not all woody, at least not in the conventional sense (Krumbiegel & Kästner, 1993). Bower's (1996) use of the term arborescent instead of woody is an implicit recognition of this problem. Although he does not discuss these terms in detail, Bower (1996) distinguishes herbaceous from arborescent, not from woody. This pairing of terms puts the emphasis on the growth form, not the presence or absence of secondary xylem.

These observations also call into question the concept of herbaceousness. Currently, the term herbaceous is used in two senses. In addition to referring to stems without secondary growth, it is used to refer to plants that die back at the end of the growing season. If an herb like *Trifolium alpinum* can have up to 50 annual growth increments (Schweingruber & Poschlod, 2005), then the equation of herbaceous with a lack of secondary growth must be spurious. Even annuals such as *Capsella bursa-pastoris* and *Cardamine flexuosa* (among many others, Table 1) are capable of significant amounts of secondary growth. When annuals germinate in the winter and flower in the spring, two growth rings are often present (Schweingruber, 2007a; Schweingruber & Landolt, 2005–2008), producing even more terminological confusion.

That so called herbaceous plants can produce secondary growth is also evident from recent work on tobacco and *Arabidopsis* (Oh et al., 2003). Neither of these plants normally produces secondary xylem. However, under special conditions they can both be induced to do so. For example, when *Arabidopsis* has its inflorescences removed and is grown under short days it produces rayless secondary xylem (Oh et al., 2003). In addition, mutations in the genes *SOC1* and *FUL* cause considerable amounts of secondary xylem to be produced under both long and short photoperiods (Melzer et al., 2008). Clearly, even herbaceous annuals like *Arabidopsis* must have the genes for secondary growth. All that is needed to trigger the development of secondary xylem is a change in environmental conditions. This, in turn, alters gene expression and produces a woody tissue (Groover, 2005).

An interesting question is whether *any* aspect of the genetics required for the production of normal wood has been lost in groups with both herbaceous and woody members. The species of *Ranunculus* that have been studied in Europe lack all secondary growth (Table 1) (Schweingruber & Landolt, 2005–2008), yet occur nested within woody taxa (Fig. 4). It would be interesting to know if any of its species has retained the genes necessary for the production of woody tissue. This question could be approached by comparing the part of the genome responsible for xylogenesis from a plant like *Populus*, whose genome has been completely sequenced, to its genetic counterpart in *Ranunculus*.

These observations strongly suggest that the meaning of the term herbaceous must either be radically changed so that it includes plants with secondary growth, or restricted to the relatively few plants that truly have no secondary growth. The vast majority of herbs are not, in fact, herbaceous (Bowers, 1996; Krumbiegel & Kästner, 1993).

The use of the terms herbaceous for plants whose above ground parts do not perennate, and woody for those that do, is also problematical because these usages ignore the form with which the die back occurs. Many plants perennate by

retaining buds at, or just above, the soil surface. These plants are neither traditionally herbaceous, nor woody. Many of the plants in which Carlquist describes paedomorphic wood fit into this class. Although some of them can be described as suffrutescent, this term, like herbaceous, conflates growth form with the presence of wood. Suffrutescent plants are shrubs with stems that are woody only at the base. When the full range of growth forms is taken into account, we have to agree with Fritz Schweingruber (2007b) when he says “Anatomical characteristics would appear to have little influence on a plant’s growth form.” It would be better to use terms that do not conflate these seemingly unrelated aspects of plant form.

Raunkiær proposed just such terms in his classification system of plant life forms (Raunkiær, 1904, 1934). Phanerophytes have buds that survive unfavorable seasons on aerial, negatively geotropic shoots. Trees are typical phanerophytes. In chamaephytes the surviving buds are born on shoots very close to the ground. Hemicryptophytes bear their perennating buds at the soil surface, while in cryptophytes the buds are buried in the soil. The final category is therophytes (annuals): plants that pass unfavorable seasons as seeds (Raunkiær, 1904, 1934). Later work by other authors has extended the classification system to non-vascular and tropical plants (Ellenberg & Mueller-Dombois, 1967). None of these classifications are routinely used in discussions of plant anatomy, though they are clearly applicable (Schweingruber, 2006; Schweingruber, 2007a; Schweingruber & Landolt, 2005–2008).

Adopting Raunkiær’s terminology would allow the disambiguation of the terms woody and herbaceous. These terms could then be used for the presence and absence of secondary growth, respectively. Growth forms would be described by an independent set of terms that would more accurately reflect how plants perennate. Disambiguating these terms would do away with hybrid categories such as “woody herbs.” This category makes as much sense as the seldom used “herbaceous trees.”

VI. Conclusions

The theory of paedomorphosis in the secondary xylem is an explanation for certain character and character state trends found in the secondary xylem of plants that often have shrubby, suffrutescent, pachycaulous, or lianoid growth forms. These characteristics include a decreasing, or stable, length of vessel elements as the xylem ages; the presence of scalariform perforation plates; scalariform or pseudoscalariform lateral wall pitting; and the absence of rays, delayed ray development, or rays consisting solely of upright cells. Earlier reports that paedomorphic wood can be identified by the presence of libriform fibers and simple perforation plates are no longer considered valid.

Many species described as having paedomorphic wood are found on islands, so the concept of insular woodiness is closely associated with paedomorphosis and with the occurrence of secondary woodiness. Although paedomorphosis is often associated with secondary woodiness, there is no necessary association between the phenomena, and secondary woodiness cannot be identified based solely on the

possession of paedomorphic wood. The possession of secondary woodiness is best determined following phylogenetic analysis.

All three species investigated here were found to have a degree of paedomorphosis, with *Coreopsis gigantea* having the largest number of paedomorphic characteristics. *Mahonia bealei* has only a single paedomorphic character (a flat age-on-length curve), while *Xanthorhiza simplicissima* has an intermediate number. Repeated measures of vessel element lengths across the secondary xylem of a single mature stem of *C. gigantea* produced both negatively sloped and flat age-on-length curves, suggesting that there may be no statistical difference between descending and flat curves. Plotting the character states woody and nonwoody on phylogenetic trees containing these taxa shows that *Coreopsis gigantea* is secondarily woody, while the ancestral state of the other two species is equivocal. However, the validity of these reconstructions is at least somewhat questionable due to the often unreported occurrence of secondary growth in "herbaceous" plants.

The presence of paedomorphic secondary xylem has been suggested as a response to relaxed selection for mechanical strength (Carlquist, 2001). The xylem structure of the three species investigated here is consistent with this hypothesis. Their apparent mechanical strength is inversely correlated with their degree of paedomorphosis. Given this inverse relationship, it is possible that the presence of paedomorphic wood may be more of a consequence of a plant's growth habit than its possession of secondary woodiness. The occurrence of paedomorphic wood in primitively woody species would seem to obviate any causative relationship between paedomorphosis and secondary woodiness. Additional research is needed to explore the link between paedomorphosis and mechanical strength by examining the correlation between the occurrence of paedomorphic xylem, stem strength, and growth habit in a phylogenetic context.

The frequent occurrence of secondary growth in plants such as annuals and suffrutescent shrubs calls into doubt the use of terms such as woody and herbaceous to distinguish plants with, and without secondary xylem. These terms conflate two independent aspects of plant form, growth habit and the presence of secondary xylem. If these terms are to remain useful, their use must be restricted to one of their two meanings. Since better alternatives exist for the description of growth forms, it would be better to restrict them to the description of the presence or absence of secondary growth. The term herbaceous should only be used for plants that truly lack secondary growth, such as species of *Ranunculus* sampled here.

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