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Cover illustration: The fruit, seed, and flower of *Quillaja saponaria* Mol. (Rosaceae), a dominant tree in the sclerophyllous vegetation of Central Chile.

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8. Underground Structures of Woody Plants in Mediterranean Ecosystems of Australia, California, and Chile

Josep Canadell and Paul H. Zedler

Interest in the possible evolutionary convergence has been the impetus for comparative studies of how organisms function in mediterranean ecosystems (Cody and Mooney 1978). For plants, stem architecture, seasonal growth patterns, nutrient relationships, and some physiological aspects have been examined to determine if convergence occurs under similar climatic constraints.

Despite the obvious importance of the below-ground component of plants, several difficulties have discouraged detailed work on this aspect of the problem. First, the soil environment in each mediterranean region is much more variable than the environment to which the above-ground part of the plant is exposed. Soil properties frequently vary significantly over very small distances. A microenvironmental mosaic is common in California and Chilean ecosystems, where rocks, steep slopes, and changes in types of bedrock are very frequent. Second, and probably most important, information is scarce because of the tedious work required to gather any type of below-ground data.

Despite these difficulties, studies are numerous enough that it is possible to assemble a preliminary picture. The objective in this chapter is to gather information on structure of root systems and on the water relations characteristic of different types of root-system morphologies. We focus exclusively on woody plants, both shrub and tree species, growing in the Pacific mediterranean ecosystems. This area includes the woodlands and heathlands in

Southeast and Southwest Australia, the chaparral and oak woodlands in California, and the matorral in Chile. We compare the root structure and rooting patterns among different regions with all available data.

Root-System Structure and Rooting Patterns

Root-System Morphologies

Because of the summer drought in regions of mediterranean climate, soil moisture in the surface horizons of the soil profile will be depleted for up to six months (Mooney et al. 1974). But in these regions precipitation is also great enough that in many situations moisture reserves can be considerable at greater depths. Two general root-system morphologies have evolved to deal with the strong spatial and temporal limitations on availability of moisture. First, some deep-rooted species can utilize moisture from lower horizons. When these species also have a well-developed shallow-root system, they are said to have a dual root system. The shallow roots in the upper soil layers enable plants to benefit from the generally higher nutrient content in the surface soils as well as to take immediate advantage of rains, especially when deep horizons are not yet recharged after the summer drought. The root systems of many sclerophyllous evergreen shrubs in the mediterranean regions have this type of morphology.

The existence of the dual root system was revealed in one of the earliest studies on root-system structure. Cannon (1914) studied three species of oaks (*Quercus douglasii*, *Q. agrifolia*, and *Q. lobata*) in California. He concluded that dual root development may be fairly common among these species. This type of root system has strong development of shallow roots within the first meter of soil, and roots penetrating to several meters, depending on the depth of the water table and the amount of rain. Cooper (1922) pointed out that the dual system was possible only when soils were friable and easily penetrated by roots. Where rock is at the surface, which it is very frequently, the roots penetrate the crevices wherever they can. The result is a rooting pattern controlled in large part by the substrate and without a clear pattern. The dual system was reported in Cooper's study for *Adenostoma fasciculatum*, *Quercus durata*, and *Arctostaphylos tomentosa* in Jasper Ridge, central California. In an area close by, Wright (1928) also found a dual type of root system in *Baccharis pilularis*. The extension of the taproot, however, varied from slight to 3.2 m.

The second basic root morphology is a shallow system. Shallow-rooted plants occur in the driest part of the water-availability gradient in the mediterranean climate regions. Such plants cope with drought by becoming dormant during dry periods. Many of the summer-deciduous species found in California and Chile are in this category (Mooney and Dunn 1970). Plants with life strategies other than summer deciduous may also display a shallow-root system, such as some species of the Southeast Australia heathland (Specht 1981a), and *Yucca whipplei* in the California chaparral (Hellmers et al. 1955).

Of the two types of root system, the deep-rooting morphology has been described as the commonest in the five mediterranean regions of the world. A deep-root system, with either one dominant taproot or many deep-penetrating roots, clearly seems to be advantageous for maximizing use of water throughout the year. Successful establishment in xeric habitats also seems highly correlated with early development of a taproot because ability to reach deep moisture layers is crucial for surviving the first summer drought after germination. Cannon (1914) observes that in various California chaparral species a deeply penetrating taproot starts to develop immediately, and elaboration of the surface network occurs later. Specht and Rayson (1957) found a seedling of *Banksia ornata* growing in the sand plains in Southeast Australia to have a taproot extending 0.5 m deep, but little development of the lateral roots. Observing one-year-old seedlings of *Quillaja saponaria*, a Chile matorral species, showed a taproot about 1 m long (Riveros et al. 1976).

The taproot as an adaptation to a climate with seasonal drought was studied experimentally by Zimmer and Grose (1958). They collected seeds of 14 *Eucalyptus* species growing across a moisture gradient in Victoria, Australia, and planted them in a greenhouse. The seedlings showed a transition from a fibrous root system for species from moist habitats to a single taproot with weak laterals for species from drier areas. Similarly, Matsuda and McBride (1986) studied how root morphology of seedlings of *Quercus douglasii*, *Q. lobata*, and *Q. agrifolia* might affect distribution of these species in the central coast ranges in California. They found that *Q. douglasii* had the longest main root. They used this along with other plant features to explain the occurrence of *Q. douglasii* on xeric sites, a pattern documented earlier by Griffin (1971). The high degree of plasticity shown by some of these *Quercus* species, however, complicates this story. For example, it has been shown that *Q. douglasii* may either tap deep water and produce few surface roots, or utilize mainly shallow soil water via a dense lateral root system. Thus *Q. douglasii* may occupy many habitats partly because of its root system's morphological plasticity (Callaway 1990).

The dual system and early development of a taproot have been also observed for plants growing in nonmediterranean climatic regions that have a seasonal drought. *Quercus turbinella*, a shrub of the Arizona chaparral, has a root system of the generalized type, with a taproot—actually many deeply penetrating roots—and a strong lateral root system (Davis 1970). Under greenhouse conditions, roots of *Q. turbinella* may grow to a length of 30 cm before leaves develop from shoots only 2 to 3 cm tall (Davis and Pase 1977).

Root-system morphologies other than the dual and the shallow types have been described in mediterranean climate ecosystems. Attempts to describe morphologies have often lacked a systematic approach because the forms are highly variable and few individuals are excavated because of the tedious work required. Some species also have highly plastic root systems that vary depending on both soil environment and stage in development. Examples are *Hibbertia montana* and *Phyllanthus calycinus*, which grow in the understory of jarrah forest in Southwest Australia. Both species initially have a taproot but it often decays, leaving a freely branching root system (Crombie et al. 1988).

Several attempts have been made to classify root-system morphologies and, more recently, their architecture as well, because it is thought to be critical to a mechanistic understanding of soil-resource acquisition (Berntson 1992, Fitter and Stickland 1992). Cannon (1949) devised a classification of root systems in which he attempted to recognize invariable characters by comparing root systems assumed to be genetically similar but grown in different habitats. He described six basic root systems differentiated by such characters as degree of development of primary and lateral roots, rooting depth, and primary root branching types. Kummerow (1981), however, considered the data set to be too narrow for a general classification of roots. He felt that this limitation particularly applied to mediterranean ecosystems, where rocky soils, steep slopes, and irregular moisture patterns provide greatly varied soil conditions that can be exploited by many species and root forms.

We have no comprehensive descriptions of the root systems in southeastern and southwestern Australia heathlands, California chaparral, and Chilean matorral, but basic information is available for the most dominant woody species in all three ecosystems. One of the most extensive studies was done by Specht and Rayson (1957), who studied the root systems of 91 woody and grass species in the heath community in Southeast Australia. Crombie et al. (1988) also looked at 22 species of trees, shrubs, and grasses in the jarrah forest in Southwest Australia, and Dodd et al. (1984) studied 551 root systems from 43 woody species in the low woodland and open forest in Southwest Australia. Unlike Kummerow's (1981) findings, Dodd et al. (1984), in their systems, found that species had a rather consistent root-system morphology, allowing them to be classified according to Cannon's schemes. Following Cannon's scheme, they described five basic root-system types to produce the broadest study on root-system morphologies in any mediterranean region. These are the five types:

Type 1. Well-developed primary (taproot) and lateral roots, neither dominant. The length of the taproot usually less than 1 m.
Type 2. Root system shallow but laterally very extensive, several times greater than its depth. Roots less than 0.5 m deep.
Type 3. Dominant, deep fibrous taproot lacking an extensive lateral root system. Rooting depth usually greater than 3 m.
Type 4. Dominant deep taproot with well-developed lateral roots near the soil surface. Lateral spread as extensive as vertical.

Type 5. Nondominant shallow taproot, with pronounced branching and forking of roots. Root depth usually less than 1 m

In Dodd's study, 83% overall of the species studied had a dominant taproot that reached depths from 1 m to deeper than 4 m. Specht and Rayson (1957) found that a quarter of the heath species in Southeast Australia had deep taproots, one half had shallow taproots, and the remaining quarter (mostly herbaceous species) had fibrous roots.

Several root-excavation studies have been done in the California chaparral (Hellmers et al. 1955, Kummerow et al. 1977, Kummerow and Mangan 1981, Kummerow and Wright 1987, Miller and Ng 1977). The most extensive study was done by Hellmers et al. (1955), who studied 68 individuals in 18 species of shrubs and subshrubs in 14 locations in southern California chaparral. The different study locations had variations in soil type, texture, and depth, bedrock type, and steepness of slope. Because conditions were so variable, only two basic root-system morphologies for shrubs were recognized: shrubs with coarse major roots growing downward, where the depth of downward penetration was greater than the radial spread, and shrubs with coarse major roots growing laterally, where radial spread of roots was usually much greater than downward penetration. A third type was distinguished for subshrubs, which had a fibrous root system with great radial spread but rooting no deeper than 1.5 m.

Unlike the two other ecosystems considered, few data on root-system structure are available for Chilean matorral species (Giliberto and Estay 1978, Hoffmann and Kummerow 1978). Data are not adequate to attempt a classification, but a basic dual system seems to be fairly common for evergreen resprouters.

Dodd's classification is by far the most thorough for mediterranean species. Its five categories include most of the root types in the various classifications presented in this review, so that it could be used as a general classification for shrubs and trees in the mediterranean ecosystems. Changes on root length—depth and lateral extension—will have to be reconsidered, however, when this classification is used outside of Dodd's study area. Different soil types and species may be the cause of these possible differences.

Factors Affecting Rooting Patterns

The rooting pattern of a plant, like other aspects of morphology, is the result of environmentally influenced development of a basic genetic plan (Pearson 1974). Environmental constraints are usually so strong, however, that they are often the driving force determining root-system morphology. The primary factors controlling root development are the amount and depth of moisture and nutrients, and soil physical properties (Curl and Truelave 1986, Feldman 1984, 1988, Richards 1986). Although soil environmental factors exert strongest control on root-system morphology, morphology is also influenced, less obviously, by the environmental factors to which the aerial

Table 8.1. Above- and below-ground dimensions for woody species in Australia, California, and Chile mediterranean ecosystems

		Above-ground		Below-ground			
Species	*n*	Average height (m)	Average crown radius (m)	Maximum horizontal extension radius (m)	Maximum vertical extension (m)	Taproot	Ref.
SOUTHEAST AUSTRALIA							
Adenanthos terminalis	—	0.4	0.3	0.4	0.6	yes	1
Astroloma conostephioides	—	0.1	0.1	0.5	0.2	yes	1
Banksia marginata	—	0.7	0.2	4.1	2.4^{a}	yes	1
Banksia ornata	—	1.2	0.3	6.2	2.4^{a}	yes	1
Boronia coerulescens	—	0.3	0.2	0.3	0.3	yes	1
Calytrix alpestris	—	0.2	0.2	0.3	0.6^{a}	yes	1
Casuarina muelleriana	—	1.3	0.3	0.9	2	yes	1
Casuarina pusilla	—	0.4	0.2	2.8	2.4^{a}	yes	1
Correa rubra	—	0.3	0.3	0.5	0.6^{a}	yes	1
Cryptandra tomentosa	—	0.2	0.2	0.3	0.4	yes	1
Daviesia brevifolia	—	0.4	0.1	0.2	2	yes	1
Dillwynia hispida	—	0.2	0.1	0.3	0.3	yes	1
Euphrasia collina	—	0.3	0.1	0.2	0.3	yes	1
Gompholobium minus	—	0.2	0.2	0.3	0.3	yes	1
Hibbertia sericea	—	0.3	0.1	0.3	0.5	yes	1
Hibbertia stricta	—	0.3	0.2	0.3	0.6^{a}	yes	1
Laudonia behrii	—	0.8	0.1	0.1	2	yes	1
Leptospermum myrsinoides	—	0.9	0.2	1.2	2.3	yes	1
Leucopogon costatus	—	0.3	0.1	0.3	0.3	yes	1
Leucopogon woodsii	—	0.3	0.2	0.1	0.3	yes	1
Phyllota pleurandroides	—	0.7	0.3	2.8	2.3	yes	1
Phyllota remota	—	0.3	0.2	0.3	2.4^{a}	yes	1
Pimelea octophylla	—	0.3	0.1	0.2	0.2	yes	1
Spyridium subochreatum	—	0.4	0.2	0.6	1.9	yes	1
Xanthorrhoea australis	—	0.8	0.3	1.7	2.4	yes	1
Average		0.5 ± 0.1	0.2 ± 0.1	1.0 ± 0.3	1.2 ± 0.2		
Range		0.1–1.3	0.1–0.3	0.1–6.2	0.2–2.4		
SOUTHWEST AUSTRALIA							
Acacia barbinervis	8	0.4	0.3	0.5	1.5	yes	2
Acacia huegelii	2	0.2	0.2	1	1	yes	2
Acacia pulchella	15	0.4	0.2	0.3	0.4	yes	2
Adenanthos cygnorum	6	1.3	0.5	1.3	1.6	yes	2
Allocasuarina humilis	3	0.8	1	4	1.5	yes	2
Andersonia heterophylla	8	0.3	0.4	0.2	0.6	no	2
Aotus ericoides	2	0.5	0.5	0.2	0.4	yes	2
Astartea fascicularis	17	0.5	0.2	1.1	0.8	yes	2
Astroloma xerophyllum	4	0.6	0.6	1	0.9	no	2
Beaufortia elegans	21	0.8	0.8	1.2	1.4	yes	2
Bossiaea eriocarpa	22	0.4	0.4	1.1	0.9	yes	2
Calytrix empetroides	11	0.5	0.2	0.3	0.6	yes	2
Calytrix flavescens	13	0.3	0.4	1.6	2	yes	2
Calytrix fraseri	1	0.5	0.2	0.5	0.6	yes	2
Conospermum curvum	3	0.6	0.4	0.6	1.2	no	2
Conostephium minus	2	0.3	0.5	0.5	0.5	no	2
Conostephium pendulum	11	0.3	0.4	1.3	1.5	no	2
Daviesia juncea	3	0.5	0.6	0.5	1.8	yes	2
Eremaea pauciflora	12	0.7	0.5	6	2.4	yes	2
Eriostemon spicatus	14	0.7	0.3	0.6	0.8	yes	2
Euchilopsis linearis	12	0.6	0.9	0.4	0.4	yes	2
Gompholobium tomentosum	11	0.3	0.2	0.4	1.1*	yes	2
Hemiandra pungens	6	0.3	0.4	0.4	0.4	no	2
Hibbertia aurea	13	0.3	0.3	0.6	0.9	yes	2
Hibbertia helianthemoides	13	0.3	0.2	0.3	0.7	yes	2
Hibbertia huegelii	3	0.4	0.3	0.4	0.9	yes	2
Hibbertia hypericoides	15	0.5	0.5	1.8	2.1	yes	2
Hibbertia subvaginata	53	0.3	0.3	0.4	0.7	yes	2
Hypocalymma angustifolium	16	0.3	0.5	1.2	0.9	yes	2
Jacksonia floribunda	20	0.9	0.7	1.4	3.1	yes	2
Jacksonia furcellata	6	1.1	0.7	5	2	yes	2
Lechenaultia floribunda	3	0.1	0.2	0.2	0.3	yes	2
Leptospermum ellipticum	36	0.7	0.5	0.6	0.9	yes	2
Leucopogon conostephioides	31	0.3	0.5	0.8	0.9	no	2
Leucopogon sprengelioides	27	0.5	0.4	0.3	0.5	no	2

(continued)

Table 8.1 (*continued*)

		Above-ground		Below-ground			
Species	*n*	Average height (m)	Average crown radius (m)	Maximum horizontal extension radius (m)	Maximum vertical extension (m)	Taproot	Ref.
Melaleuca scabra	20	0.4	0.6	1.6	2	yes	2
Melaleuca seriata	7	0.5	0.5	1.9	2.1	yes	2
Oxylobium capitatum	7	0.4	0.3	0.4	0.6	yes	2
Petrophile linearis	15	0.3	0.4	0.6	2	yes	2
Pithocarpa corymbulosa	4	0.5	0.4	0.2	0.8	yes	2
Regelia ciliata	12	0.9	0.8	1.2	0.6	yes	2
Scholtzia involucrata	11	0.3	0.5	1.9	1.9	yes	2
Stirlingia latifolia	11	0.5	0.5	1.8	2.6	yes	2
Average ± error		0.5 ± 0.1	0.4 ± 0.1	1.1 ± 0.2	1.2 ± 0.1		
Range		0.1–1.3	0.2–1.0	0.2–6.0	0.3–3.1		
SOUTH AND CENTRAL CALIFORNIA							
Adenostoma fasciculatum	13	1.5	0.9	4	2.4/7.6	yes	3
Adenostoma fasciculatum	2	1.5	1	2	2.4	yes	4
Adenostoma fasciculatum	4	0.6	0.2	1.2	1	—	5
Adenostoma fasciculatum	3	—	1	3	0.6	no	6, 7
Adenostoma sparsifolium	2	3.3	3.2	3.3	2.1	no	4
Arctostaphylos glandulosa	4	0.7	0.5	2.7	2.7/5.2	yes	3
Arctostaphylos glauca	4	2	1.1	6.4	2.6	no	3
Arctostaphylos glauca	1	1	0.5	0.6	0.3	—	5
Arctostaphylos pungens	2	—	1.5	4.5	0.6	no	6, 7
Baccharis pilularis	1	0.9	0.5	2.1	3.2	yes	8
Ceanothus crassifolius	7	2	0.8	3	1.4	yes	3
Ceanothus greggii	2	0.9	0.2	0.3	0.3	—	5
Ceanothus greggii	1	—	1.5	3.5	0.6	no	6, 7
Ceanothus greggii	2	0.8	0.5	3.4	1.4	yes	3
Ceanothus leucodermis	4	1.5	1.1	3	3.7	yes	3
Ceanothus oliganthus	3	2.1	0.8	1.7	1.8	yes	3
Cercocarpus betuloides	2	1.5	1	2.7	1.5	no	3
Diplacus longiflorus	2	0.4	0.2	0.9	0.8	no	3
Eriodictyon crassifolium	1	0.9	—	1.4	—	no	3
Eriogonum fasciculatum	4	0.4	0.4	1.5	1.2	no	3
Haplopappus pinifolius	1	—	0.4	0.6	0.3	no	6, 7
Heteromeles arbutifolia	1	1.8	0.4	0.3	0.3	—	5
Heteromeles arbutifolia	1	1.2	0.8	1.5	2.1	yes	3
Lotus scoparius	2	0.3	0.3	0.9	1.1	yes	3
Quercus chrysolepis	1	—	—	—	7.3	yes	3
Quercus dumosa	3	1.5	0.8	3.3	2.4/8.5	yes	3
Salvia apiana	1	0.6	0.6	1.8	1.5	no	3
Salvia mellifera	2	1.2	0.7	1.8	0.6	no	3
Yucca whipplei	2	0.6	0.8	3.3	0.8	no	3
Average + error		1.2 ± 0.1	0.8 ± 0.1	2.3 ± 0.3	1.7 ± 0.3		
Range		0.3–3.3	0.2–3.2	0.3–6.4	0.3–8.5		
CENTRAL CHILE							
Colliguaja odorifera	—	1	1	3.5	0.6	no	7, 9
Colliguaja odorifera	—	—	—	1.5	1	—	10
Colliguaja odorifera	2	0.4	0.1	—	0.6	—	5
Cryptocarya alba	—	3.1	1.5	3	0.6[a]	no	9
Cryptocarya alba	—	—	—	4	1	—	10
Lithrea caustica	—	1.2	1.8	4	0.6[a]	no	9
Lithrea caustica	—	—	—	7	5	yes	10
Mutisia retusa	—	1.2	—	—	—	no	9
Quillaja saponaria	—	—	—	—	8	yes	10
Retanilla ephedra	—	—	—	1	1	—	10
Satureja gilliesii	—	—	—	1	0.8	—	10
Satureja gilliesii	—	0.6	0.2	1	0.2	no	9
Satureja gilliesii	4	0.9	0.4	1	0.9	—	5
Average ± error		1.2 ± 0.1	0.8 ± 0.3	2.7 ± 0.6	1.7 ± 0.7		
Range		0.4–3.1	0.1–1.8	1.0–7.0	0.2–8.0		

(*continued*)

[a] Roots deeper than the given depth.

References: 1. Calculated from Specht and Rayson 1957. 2. Dodd et al. 1984. 3. Hellmers et al. 1955. 4. Hanes 1965. 5. Miller and Ng 1977; 6. Kummerow et al. 1977; 7. Kummerow 1980; 8. Calculated from Wright 1928. 9. Hoffmann and Kummerow 1978. 10. Giliberto and Estay 1978.

parts of the plant are subjected (Burns 1972). Competition between plants, both intraspecific and interspecific, can also contribute to the final morphology of the root system. Atkinson et al. (1976) reported that as canopy overlap among apple trees increased as a result of decreasing space between individuals, trees altered their root systems by producing many more roots growing downward, rather than horizontally. More recently, Mahall and Callaway (1992) report that the roots of desert shrubs in California can inhibit the growth of roots of their own and other species by releasing biochemical inhibitors. It is conceivable that similar interactions may be present in mediterranean regions.

Availability of soil resources, both moisture and nutrients, has been shown to strongly limit plant production in ecosystems of mediterranean South Australia, California, and central Chile (Beadle 1954, Giliberto and Estay 1978, McMaster et al. 1982, Miller and Poole 1979, Mooney and Dunn 1970, Poole and Miller 1975, Specht 1979, Specht and Rayson 1957). Thus, availability of resources in time and space is expected to heavily influence the final root form and distribution. Among the benefits of the dual root system, for example, may be that the deeper roots supply moisture that allows the surficial roots to remain active and able to exploit brief pulses of nutrients that are released when the soils are wetted after prolonged dry periods. Crick and Grime (1987) have suggested that such an ability to utilize nutrient pulses may be a characteristic feature of a stress-tolerant life history.

The three primary factors—moisture, nutrients, and physical properties—can change on a very broad spatial scale (over hundreds of kilometers) as well as on a very local scale (over just a few meters) (Beckett and Webster 1971, Kummerow and Wright 1988). At either scale, root form and distribution often follow the patterns of soil environmental variation. Kummerow (1981) and Richards (1986) suggested the idea of habitat-specific rather than species-level determination of the rooting patterns of plants. This notion led to the habitat-specific root-classification scheme mentioned in the preceding section. An example of the need for this type of root-morphology classification is the California chaparral shrub, *Adenostoma fasciculatum*. This species has been shown to have a highly plastic rooting pattern that can respond to different soil environmental conditions (Table 8.1). Cooper (1922) found roots of this species at a depth of 1 m, but nothing resembling a taproot. Later, *A. fasciculatum* was identified as a deep-rooted shrub, with a taproot extending as deep as 7.6 m (Hanes 1965, Hellmers et al. 1955). In more recent excavations, however, *A. fasciculatum* has been found growing successfully in shallow soils where the roots did not penetrate deeper than 0.6 m (Kummerow et al. 1977, Miller and Ng 1977).

Not all species, however, even in the same plant community, have the plasticity to enable them to adapt to a broad range of soil conditions. In fact, many species in the California chaparral show relatively nonplastic development of their root systems, such as *Quercus dumosa* and *Eriogonum fasciculatum*. *E. fasciculatum* is a shallow-rooting species (Kummerow et al. 1977) and remains shallow-rooted even when soils allow deeper penetration (Kummerow and Mangan 1981). Conversely, *Q. dumosa* shows a consistently deep rooting habit, and the species does not occur on shallow soils (Kummerow and Mangan 1981, Kummerow and Wright 1988). Several authors who studied the low woodland and open forest in Southwest Australia (Dodd et al. 1984) and the jarrah forest in Southeast Australia (Abbott et al. 1989) also do not agree with the idea that root-system development is determined largely by site characteristics. Dodd et al. (1984) studied 551 individual plants of 43 woody species and found that root-system morphologies were rather consistent within species. Abbott et al. (1989) showed the root-system morphology of *Eucalyptus marginata* to be under strong genetic control, because the same basic architecture was expressed regardless of soil type; Kimber (1974), however, reported varied forms for the four individuals he studied.

The explanation for the contradictory findings about genetic versus environmental control of root system morphology in different ecosystems seems to be primarily related to physical characteristics of the soil. Root morphology can be strongly influenced by the soil's physical properties, such as hardness, porosity, and bedrock depth and its degree of weathering, which can completely change the soil environment in which roots are growing. The deep sandy soils of the sand plains in South Australia allow much freer expression of root-system morphologies, than is possible in Californian and Chilean ecosystems, where rocky soils and steep slopes are common. It also seems to be the case that the genetic control of plasticity differs among species.

Depth of Root Penetration

Plant-rooting depth is influenced by many factors involving both plant and soil characteristics. Although above-ground biomass is not perfectly correlated with rooting depth, trees do tend to root more deeply than shrubs, and larger individuals send roots deeper into the soil profile than smaller individuals. The genetic component is important in determining root depth, but factors such as depth of water table and bedrock, amount of rain, hardness of substratum and degree of weathering, including presence of cracks and channels, are primary factors in controlling the rooting habit, and therefore the actual depths from which roots will be able to acquire resources.

Both qualitative and quantitative evidence say that some mediterranean trees have very deep root systems. For instance, jarrah trees (*Eucalyptus marginata*) in Southwest Australia generally have sinker roots, ending with a fine root system, extending to depths of 20 m (Carbon et al. 1980), and to more than 40 m into highly weathered granite (Abbott et al. 1989, Dell et al. 1983). The roots of some species of California oak trees (*Quercus wislizenii*, *Q. douglasii*, *Q. lobata*, and *Q. kelloggii*) took up water during the summer months from depths of at least 21 m (Lewis and Burghy 1964).

There are several examples of shrubs rooting to considerable depths for the Pacific mediterranean regions (Table 8.1). In the California chaparral, fine roots of *Adenostoma fasciculatum*, *A. sparsifolium*, *Quercus dumosa*, and *Q. chrysolepis* were found in tiny cracks and through fractured rocks to a depth of 7 to 9 m (Hellmers et al. 1955, Hanes 1965). Roots of *Rhus* (*Malosma*) *laurina* were found as deep as 13.2 m for one individual at the edge of a road cut (DeSouza et al. 1986). In the Arizona chaparral, *Q. turbinella* penetrated up to 6.4 m through cracks in rocky regolith (Davis 1970, 1978, Davis and Pase 1977) and to a depth of at least 9.1 m in an active mica-schist quarry (Saunier and Wagle 1967). In the Chilean matorral, roots of *Quillaja saponaria* were found 8 m deep in a well-developed fertile soil that originated from igneous porphyritic rock (Giliberto and Estay 1978). Similarly, roots 1 cm in diameter of different species were quite often found at 6 m below the surface in the kwongan of Southwest Australia near Eneabba. Only roots of *Eremaea beaufortioides*, however, were clearly identified to species (Hnatiuk and Hopkins 1980). But conversely, Dodd et al. (1984) in an extensive study of the rooting patterns of the kwongan shrubs, found only 7 of 43 woody species rooting to depths of 2 m or more.

If the soil is deep enough to allow full expression of the root system, patterns of soil moisture often are critical in shaping the final root morphology. The hardness of the substratum, however, can be a strong impediment, so that development will be freer in sandy soils because of their high permeability. Kimber (1974) found that the characteristic root depth of *Eucalyptus marginata* was greatly affected by depth of the water table. Though roots were capable of growing deeper, a water table at a depth of 15 to 20 m would limit further root penetration. Depth of *Quercus douglasii* roots seems to be controlled by the depth to which moisture can penetrate. *Q. douglasii* usually grows in dry areas where the water table is beyond its reach (Cannon 1914, Griffin 1973). Conversely, Lewis and Burghy (1964) found that several *Quercus* species, including *Q. douglasii*, reach water tables somewhat deeper than 21 m. Callaway (1990) emphasized soil-water distribution in shaping the overall root morphology of *Quercus* species in California.

If the soil is shallower than the usual depth of root penetration, and the underlying rock is not sufficiently weathered to permit passage of roots, a layer of roots usually grows at the soil–bedrock interface. If a taproot reaches the impenetrable bedrock, it will grow horizontally. But most commonly the bedrock does allow, to varying degrees, further deep root penetration through highly weathered material or through a network of cracks and channels. Examples of such penetration into the bedrock have been cited in this section. Another example is *Eucalyptus marginata*, for which roots were found to penetrate along vertical channels in lateritic bedrock in the jarrah forest ecosystem in Southwest Australia (Dell et al. 1983, Johnston et al. 1983). The channels, or preferred pathways, are permanent features of the profile, and it has been suggested that they result from dissolution of laterite by humic acid produced by the root itself (Plumb and Gosting 1973). In other cases, the bedrock structure allows passage of roots. Davis (1972) found roots of *Arctostaphylos pallida* following the planes of shale at a depth of 4 m. A contrary example is *Adenostoma fasciculatum*. It has generally been considered a deep-rooted plant, but Kummerow et al. (1977) reported that roots rarely penetrated into the cracks in granite. In fact, the benefit of penetration into granite has been questioned because of the small amount of water held in the rocks of the southern California watersheds. Rowe and Colman (1951) reported that fractured metamorphic rock below the soil profile could hold no more than 1.3 mm of water per 30 cm of rock depth.

Root penetration into unfissured bedrock has been reported for highly porous rocks. Such rocks absorb water in the wet season, releasing it to invading roots in the dry summer (Oppenheimer 1956, 1960). Some limestone rocks have surprisingly high water-storage capacity, and dwarf shrubs of the Mediterranean phrygana were observed to grow on the bare, unfissured rock in the Mediterranean Basin (Orshansky 1951). These roots behaved as if they were growing in soil. Oppenheimer (1960) also reported several cases for *Quercus* spp. and *Pistacia* spp. growing in localities where little or no soil remained. Penetration into porous rocks, however, has not been reported for the Pacific ecosystems of mediterranean type.

The distinction between maximum rooting depths and distribution of root biomass with depth must also be kept in mind. Miller and Ng (1977) observed that even deep-rooted shrubs can have the bulk of the biomass concentrated near the soil surface. Roots are often most abundant in the first 40 cm of the soil profile (Kummerow 1981, Low 1983, Miller and Ng 1977), and sometimes roots are confined mostly between 10 cm and 40 cm, avoiding the driest upper layer and also allowing better anchorage. At other times the whole root system is much shallower, most of the roots occurring in the first 20 cm, as found for six *Arctostaphylos* species in central California (Davis 1972). In species of the Southeast Australia heathland, the largest fraction of the root system is concentrated in the upper 30 cm of soil (Specht and Rayson 1957).

The highly variable data on rooting depth make it difficult to generalize. It is clear that some shrubs in all three regions are capable, at least under some circumstances, of rooting to great depth, and that mean rooting depths extend well beyond the zones of maximum nutrient concentration (2 to 20 m). Table 8.1 shows that for all the plant communities studied, mean values of root depth are between 1.2 and 1.7 m (individual values range from 0.2 to 8.5 m). Shrub species growing in the sand plains in Southwest and Southeast Australia (Table 8.1) show a somewhat shallower rooting pattern (rooting depth averages 1.2 m) than shrubs in California and Chile (where average rooting depth is 1.7 m). Relative to the above-ground development, however, shrubs in southern Australia have a more extensive root system (a smaller ratio between canopy height and root depth). The significance of the deep roots probably lies more in the access they provide to deep moisture during the times of most severe drought than in their contribution to nutrient absorption or to water absorption during times of maximum plant growth.

Horizontal Root Extension

The functions of shallow roots are to provide support for the aerial stems and to acquire water and nutrients, which are more abundant in the upper soil layers. Thus it is expected that the lateral extension of roots will be greater at or near the surface than deeper in the soil, a pattern reported for trees (Cannon 1914, Abbot et al. 1989, Incoll 1969). Roots of *Eucalyptus marginata* 1 m deep were found extending horizontally up to 20 m from the lignotuber (Abbot et al. 1989), although this has to be considered a rather exceptional distance. For trees on steep slopes the lateral root system is highly asymmetrical, with most of the roots occurring on the uphill side of the tree (Kimber 1974, Canadell and Rodà 1991). This asymmetry presumably has more to do with optimal anchoring of the plant than with improved success at obtaining water or nutrients.

In shrubs the shallow root system extends also over areas many times larger than the above-ground projected canopy area. Specht and Rayson (1957) found that species of the heathland explore between 10 and 20 times the area of their canopies. Ratios of root area to shoot area (cross-sectional projected area) for *Adenostoma fasciculatum* were 7 in a shallow soil (Kummerow et al. 1977) and 2 to 3 in deeper soils (Hellmers et al. 1955, Hanes 1965). According to the data gathered in Table 8.1, the area occupied by the roots in mediterranean species is between 2 and 6.5 times greater than that occupied by the canopy. Southeast and Southwest Australia heathland shrubs show the largest horizontal root extension among the three mediterranean regions studied.

Competition has an important part in the extension and depth to which the shallow roots grow. In the dense California chaparral and Chile matorral in shallow soils evidence is strong for species-specific rooting depths (Hoffmann and Kummerow 1978, Kummerow and Wright 1988, Wright 1987). Kummerow et al. (1977) and Hoffmann and Kummerow (1978) found a complicated network of roots, in which different species were exploiting different levels in the upper soil. Such differential rooting patterns may have arisen or at least been maintained to lessen competition.

Fine roots, commonly considered those less than 5 mm in diameter, have specific spatial distributions. Fine roots are found in variable quantities in the uppermost part of the soil profile, with the highest densities under the shrub canopy. This characteristic distribution has been related to the higher availability of nutrients under the shrub canopy (Lamont 1983). In particular cases when the top soil layer is gravel or a loose type of material, the densest layer of fine roots is at greater depth avoiding easily desiccated horizons. There is little overlap of fine roots from different individuals within the restricted area around the root crown (Kummerow et al. 1977).

Plant–Soil Water Relations

The patterns of change in soil moisture content with depth and time, and the corresponding drying and rewetting cycles, are decisive in determining species composition in an environment. Plants with different rooting habits show different seasonal courses of water potential, and the length of water stress and the distribution of soil moisture with depth will determine whether or not a species can succeed in a particular environment.

Species show differential rooting patterns along moisture gradients in the mediterranean-climate regions. Deep- and shallow-rooted plants are adapted to different degrees of aridity, along with other morphological and physiological characteristics. Generally, deep-rooted evergreen species are more abundant in wetter parts of the mediterranean regions, whereas shallow-rooted drought-deciduous species dominate in the driest areas.

Water Relations in Evergreen Species

Evergreen species growing within an area have been shown to differ in rooting habit, implying differences in exploitation of resources with depth. Evidence of such stratification has been shown directly by excavations and indirectly by measurements of drying and rewetting patterns for soil and plant tissue during drought cycles (Poole and Miller 1975, 1978, Riveros et al. 1976, Dodd et al. 1984).

Dodd et al. (1984) studied xylem pressure potential curves of 30 species during the summer drought in the sand plains in Southwest Australia. The close relationships between water stress and root morphologies were found. Davis and Mooney (1986) studied four co-occurring chaparral shrubs, and found strong evidence that different species share the soil-moisture resource by using different portions of it. At the height of the drought, the water potentials of the deep-rooted *Quercus durata* corresponded to soil-moisture potentials at a depth of 2 m. *Adenostoma fasciculatum* and *Heteromeles arbutifolia* had roots intermediate in depth, and water potentials corresponding to soil moisture at 0.75 m, and water-potential values for the shallow-rooted *Rhamnus californica* were equivalent to soil potentials at 0.5 m depth. For the Chilean matorral, seven of the most abundant shrub species showed a seasonal course of water stress closely related to their rooting habit (Giliberto and Estay 1978). *Lithrea caustica* and *Quillaja saponaria*, with deeper and more extensive roots, had higher and less variable xylem potentials throughout the year, but *Satureja gilliesii*, *Colliguaja odorifera*, *Retanilla ephedra*, and *Cryptocarya alba*, with shallower root systems, underwent greater and more variable water stress.

Competition for the scarce soil resources also causes partitioning among different species in the semiarid woodlands in East Australia (Hodgkinson 1992). Trees and shrubs compete for soil moisture, and partial stratification of roots is found between life forms. The trees, with their deeper roots, take up water from shallow and deep soil layers, the latter enabling them to tap additional soil water not available to the shrubs. The shrubs thus had the lowest xylem pressure potentials during the dry periods. A similar situation was reported for trees and understory species in the jarrah forest in Southwest Australia (Crombie et al. 1988). Water relations in both examples were closely related to root morphology.

Using data compiled from several studies, the drought response of the different evergreen species from the mediterranean-climate regions can be grouped in two main categories: species with shallow-rooting characteristics (less than 1 m), and those with deep-rooting characteristics (about 2 m and more). An intermediate category combining characteristics of these two groups might also be considered.

Shallow-rooted species become highly stressed, reaching water potentials between – 40 and – 60 bars by the end of the summer drought (Dodd et al. 1984, Giliberto and Estay 1978, Griffin 1973, Poole and Miller 1975). Summer rains bring relief, and plants resume growth immediately after rains come in early winter. Generally, shallow-rooted species have higher leaf conductances, greater transpiration and photosynthetic rates, and lower osmotic potentials when water is available, and annual fluctuations in plant water potentials and growth are greater than in deep-rooted species (Poole and Miller 1975, 1978). Medium-rooted species behave essentially like shallow-rooted species, though with reduced water stress.

Deep-rooted species show smaller seasonal variation in water potentials. They either undergo no water stress at all, or are stressed for a much shorter time at the end of the summer drought. They often are able to maintain high rates of transpiration during the summer by drawing groundwater from deep soil horizons or directly from the water table. For instance, *Heteromeles arbutifolia* was found to maintain a positive carbon balance all year (Mooney and Chu 1974). Pairs of closely related species have been studied for the influence of some morphological traits, especially the rooting patterns, on the length of the water stress period. *Arbutus menziesii* occurs under conditions of a shorter water-stress period than *H. arbutifolia* is able to endure (Morrow and Mooney 1974). Similarly, *Adenostoma fasciculatum* has fairly restricted activity during the summer, but *A. sparsifolium* remains physiologically active during the summer drought (Hanes 1965). For both, differences in the rooting pattern were partially responsible for such results.

Species dependent upon the water table for moisture supply often show a quite sudden start and end to water stress that does not correspond directly to variations in climate or soil moisture content. Rather, the descent of the water table beyond a critical point seems to cause the abrupt changes (Dodd et al. 1984).

For deep-rooted species, sporadic rains do not always relieve water stress during the summer drought, because the soil profile is not recharged at depth. But even species that also have well-developed shallow roots are not always able to take full advantage of the surface moisture. Hart and Radosevich (1987) showed that surface roots of commonly deep-rooted species, such as *Adenostoma fasciculatum*, seem to lose their ability to respond to increased soil moisture after rainfall. But roots of *Arctostaphylos stanfordiana*, a shallow-rooted shrub, maintain their capacity for quick absorption (Hart and Radosevich 1987).

Water Relations in Drought-Deciduous Species

In the most xeric conditions of the mediterranean-climate regions in California and Chile, summer-deciduous species replace evergreen ones in the chaparral and matorral communities. Sometimes, however, patches of summer-deciduous species are found in the middle of chaparral and matorral, in response to dry microclimatic conditions, highly disturbed areas, barren rocky slopes, road cuts, or peculiar soil types such as heavy clays (Harrison et al. 1971). Overall, the drought-deciduous species occupy areas where the low available moisture during the dry season would not allow evergreen species to succeed.

The defining trait of the drought-deciduous species is reduced leaf area during summer. These species also, compared with evergreens, have higher photosynthetic and transpiration rates, and they are highly responsive to the long summer–fall drought. As a result of their habitat and root system characteristics, drought-deciduous shrubs undergo stronger and earlier water stress than evergreen species (Miller and Poole 1979). In fact, one of the main structural differences between life forms is their root system (Mooney and Dunn 1970). Generally, summer-deciduous shrubs have a shallow root system but evergreen species are deeper rooted. The primary evidence for this difference comes from the study by Hellmers et al. (1955). Overall, summer-deciduous shrubs, considered to be drought evaders, are considered better adapted to withstand prolonged summer drought than evergreen species.

Contrary to the generalities above, Gill and Mahall (1986) found almost identical seasonal courses of water potential in the co-occurring chaparral evergreen *Ceanothus megacarpus* and the coastal sage summer-deciduous *Salvia mellifera*. The latter did not initiate or terminate growth significantly earlier in the season than the evergreen species. These findings suggest that the soil volumes occupied by roots of evergreen and deciduous shrubs may not necessarily be different, as previously thought. But the validity of the generalization about evergreen–deciduous differences can be defended: (1) *C. megacarpus* is a nonresprouting obligate seeder and among the most shallowly rooted evergreen species (Barnes 1979); and (2) *C. megacarpus* belongs to a section of its genus known to have a number of highly evolved drought-resisting traits (Nobs 1963). It is to be expected that the most droughtresistant evergreens are also the most shallowly rooted, and that these species co-occur with summer-deciduous species at specific points along the moisture-availability gradient. More research is needed, particularly in determining root growth and activity patterns of both groups of plants (Mooney 1989).

Drought-deciduous species have not been described in the Southeast and Southwest Australia heathland, although they have a counterpart in evergreen shallow-rooted species. Under water stress, these evergreen species apparently enter a state of anabiosis, but unlike the drought-deciduous species, they retain much of their leaf canopy (Specht 1981b). It is possible that retention of the evergreen habit across the moisture gradient may be explained at least in part by the soils' nutrient deficiency and the resulting high cost of deciduousness (Specht 1963, Stock et al. 1992).

Lignotubers

Occurrence and Terminology

We define the lignotuber as a woody swollen structure at the stem base, from which roots or rhizomes or both grow. Its size can vary among species from a few cm to almost 2 m in diameter (Jacobs 1955). This structure is genetically determined (Mullette and Bamber 1978) and it appears early in seedling development. Seedlings of most *Eucalyptus* species develop a lignotuber within the first one or two growing seasons after germination (Noble 1984), and between 3 and 5 months were needed for the lignotuber to become apparent in 11 shrub species studied in the Chile matorral (Montenegro et al. 1983).

The phenotypic expression of such a structure may be determined by environmental factors, however, because some species have been found both with and without a lignotuber depending on the environmental conditions. Species may have a lignotuber even though closely related species living in the same region do not. Nonlignotuberous and lignotuberous species of the *Lehmannianae* (a group of *Eucalyptus* species) occur side by side in habitats that are prone to fire in Southwest Australia (Carr et al. 1983). In the California chaparral the lignotuber-forming *Arctostaphylos glandulosa* grows in the same habitats as *A. glauca*, which does not form a lignotuber. On the other hand, specific environmental factors that are not yet clear may be important selective forces for such a feature. Orshan et al. (1984) studied a transect through different mediterranean ecosystems in Chile, from the coast to the high mountains. They found that the proportion of species with lignotubers changed from 29% at the immediate coast to 73% in the coastal range, and from there the percentage gradually decreased with increasing altitude until only 5% of the species had lignotubers at 2000 m.

All mediterranean-climate regions of the world have trees and shrubs that develop lignotubers, although it is not a character exclusive to these regions (James 1984). A survey of 429 kwongan species in the open woodland and heathlands in Southwest Australia reported that 44 species were lignotuberous (Dodd et al. 1984). This number accounted for more than a quarter of the 163 kwongan woody shrub and tree species shown to have resprouting capacity after fire. In the heathland of Dark Island in Southeast Australia, however, no species were found with either epicormic buds or lignotubers, even though a large percentage of the plants were able to survive a fire (Specht and Rayson 1957). In the California chaparral, lignotubers are described for many of the commonest species: *Adenostoma fasciculatum*, *A. sparsifolium*, *Arctostaphylos glandulosa*, *A. vestita*, *A. patula*, *Ceanothus* sect. *Ceanothus*, *Quercus dumosa*, and *Rhus* (*Malosma*) *laurina* (DeSouza et al. 1986, Hanes 1965, Hellmers et al. 1955, Jepson 1916, Kummerow 1981, Kummerow and Mangan 1981). For the Chile matorral, lignotubers are reported to form in dominant species that include evergreen, summer semideciduous, and summer-deciduous shrubs: *Colliguaja odorifera*, *Quillaja saponaria*, *Lithrea caustica*, *Cryptocarya alba*, and many others (Hoffmann and Kummerow 1978, Montenegro et al. 1983).

Lignotubers are also called burls, root crowns, or rootstocks by different authors, even when referring to the same species (see *Adenostoma fasciculatum* in Hellmers et al. 1955 and Kummerow 1981). The name burl has often been used to describe the woody swellings when applied to the Ericaceae (Jepson 1916, Garland and Marion 1960). Root crowns and rootstocks have been used as nonspecific, general labels for any type of massive woody structure at the junction of stem base and roots, regardless of whether or not it is genetically determined. At present, anatomy and possible functions of the so-called lignotubers and burls are not known well enough for them to be considered different structures. In fact, Kummerow and Ellis (1989) say that the terms lignotuber and burl, at least in California, are commonly used interchangeably. We believe that the distinction between a structure that is genetically determined and one that is induced by environmental conditions is important. Therefore we suggest using lignotuber in the narrow sense for genetically determined swollen woody structures at the stem base. We propose that burl, or basal burl if more precision is desired, be used as the broader name for woody swellings at the stem base applicable to all such structures whether or not they are genetically determined. We justify our suggestion by origin and usage. Burl is a traditional label applied to any pronounced woody swelling on a tree or shrub. Lignotuber is a scientific term and thus may be applied in a restrictive sense without contradicting popular usage.

Anatomy, Morphology, and Development

Initiation, development, and anatomy of lignotubers have been studied for some species of *Eucalyptus* in great detail (Kerr 1925, Carr et al. 1983, 1984a, 1984b). Recently, thorough work has also been done on the lignotuber ontogeny of *Quercus suber* in the Mediterranean Region (Molinas and Verdaguer 1993a,b). But our knowledge is limited for the rest of the lignotuberous species.

Typically the lignotuber arises in the axils of the cotyledons as a pair of lateral outgrowths, which gradually increase in size until they meet, forming a swelling that encircles the stem (Kerr 1925). In lignotuberous species of the *Lehmannianae*, lignotuber formation is preceded by the appearance of a crescent-shaped array of accessory buds, adaxial to the axillary bud. Lignotubers may be formed at successive nodes, but those with only one upper accessory bud (which may be present even in nonlignotuberous species) do not form lignotubers (Carr et al. 1983). Carr et al. (1984a) found four modes of lignotuber initiation after studying the morphological development of the lignotubers of 13 species that represented five taxonomic groups in *Lehmannianae*.

For the California chaparral species, lignotubers have been defined as clumps of secondary wood that develop from the transition zone between the hypocotyl and the main root of seedlings (Kummerow and Mangan 1981). Usually, to this genetically determined woody swollen structure, bases of stems and roots become incorporated into the lignotuber tissue, presenting a complex and contorted structure.

The lignotubers are quite distinct in their structure, and should not be confused with enlarged portions of stems whose tissues retain their characteristic organization. Lignotuber tissues differ from stem tissues in quantitative aspects, but the types of tissues are the same: cambium, phloem, rhytidome, sapwood, heartwood, and kino veins (Bamber and Mullette 1978). For example, the lignotuber of *Eucalyptus gummifera* has shorter wood fibers, a greater proportion of axial parenchyma of the wood, and less expansion of the axial parenchyma of the outer phloem than in the stem tissues. Carr et al. (1984a) found that in eucalypt seedlings the lignotuber cambium differs from the stem cambium in a number of ways, including size and frequency of ray initials, lengths of the fusiform initials, and composition of the xylem produced.

Lignotuber formation is an inherited characteristic, but like other genetically determined characteristics, it may not be expressed under some circumstances (Kerr 1925, Beadle 1968, Mullette and Bamber 1978). Full penetrance of the genes involved in lignotuber formation for *Eucalyptus* spp. is reported to be affected by both climatic and edaphic factors. Beadle (1954, 1968) proposed that the lignotuber was an adaptation to poor soils, because high levels of P and N restricted its development in seedlings of *Eucalyptus oleosa*, *E. saligna*, and *E. gummifera*. Mullette and Bamber (1978), however, found that, on the contrary, an increase in soil P levels stimulated lignotuber development in *E. gummifera*. Jahnke et al. (1983) studied two geographic provenances of *E. camaldulensis*, one normally lignotuberous and the other nonlignotuberous; plants of both provenances were raised under combinations of soil N and P levels. Lignotubers were not formed in plants of the southern provenance regardless of the nutritional treatment. For the northern provenance the percentage of seedlings that developed a lignotuber was highest at high levels of P associated with low to intermediate levels of N. Therefore, although we know that different soil N and P availability affects lignotuber expression and development, a consistent trend in nutritional effects is not apparent, perhaps because of interaction by factors not considered.

Differential lignotuber development is found within species, resulting in varied sizes and morphologies. For many of the *Eucalyptus* species, lignotubers ranging between 15 mm and 150 mm in diameter have been described, but other species like the mallee forms of eucalypts have lignotubers 1 to 2 m in diameter (Jacobs 1955). A multistemmed *E. gummifera* mallee had one massive lignotuber 75 m^2 in area (Mullette 1978). The Chilean matorral shrub and small tree *Lithrea caustica* was reported to have a lignotuber as heavy as 67 kg (dry mass) (Hoffmann and Kummerow 1978). A *Quercus dumosa* lignotuber of 15 kg was found in the California chaparral, and a lignotuber as heavy as 52 kg was reported for *Q. turbinella* in the Arizona chaparral (Davis and Pase 1977). In the Mediterranean Basin, Canadell and Rodà (1991) reported a lignotuber mass of 317 kg for a *Q. ilex* (tree).

The lignotubers of some eucalypts may be evident only in the juvenile stages of plant development, because as plants grow the lignotubers may merge with the main stem (Pryor 1976). If lignotuberous plants are subjected to above-ground removal (e.g., by fire) and subsequent resprouting, though, the lignotuber rapidly enlarges, both because the tissues grow and because the stem bases merge within the lignotuber structure. Repeated stem harvesting for charcoal manufacturing was the cause of the massive lignotubers of *Lithrea caustica* and *Cryptocarya alba* found in the Chilean matorral (Hoffmann and Kummerow 1978).

Frazier's (1993) study of hybridization between a sprouting, lignotuberous species of *Ceanothus* and nonsprouting species provides the only data on inheritance and genetic control of the lignotuber. In a study of naturally occurring hybrids he found that most morphological traits had character states very close to the midpoint of the two parental types. In contrast, he found that degree of lignotuber development, though intermediate, was much closer to that of the nonsprouting species. The presumption is that the hybrids would therefore have little or no capacity to resprout after fire. This finding is surprising since lignotuber structure would be expected to be a quantitative character affected by many genes. Therefore, either the burl is determined by few genes and one or more recessive alleles or some developmental constraint or ecological factor selects against the "half-burl" condition.

A lignotuber should always be at least as old as the aerial part of the plant, and because it has the potential to persist even when the above-ground parts of the plant are lost, it could be much older. Although attempts have been made to determine the age of lignotubers, only a few studies have provided reliable data. Traditional techniques for dating wood are not applicable to lignotubers because their highly contorted wood makes it impossible to read the annual growth rings. In fact, only carbon dating can be considered reliable enough for lignotuber aging. The first radiocarbon dating for a lignotuber was published by Grant Taylor and Rafter (1963). They determined an age of 200 years for a sample taken from the central part of a lignotuber 1.2 m in diameter of the mallee *Eucalyptus oleosa*. Later, Wellington et al. (1979) confirmed the age of large lignotubers of *E. oleosa*. They analyzed samples from different parts of a lignotuber almost 2 m in diameter found in one of the oldest eucalypt populations in Southwest New South Wales. The oldest radiocarbon age was 330 ± 70 years. For the California chaparral shrub *Adenostoma sparsifolium*, an age of 200 ± 65 years was established for a lignotuber 0.3 m in diameter (Hanes 1965).

Other complexities in lignotuber growth and survival may make it difficult or impossible to determine the age of a genet from the lignotuber. In the California chaparral, we have observed that *Arctostaphylos glandulosa* and *Adenostoma fasciculatum* shrubs frequently consist of small, roughly circular clusters of stems that suggest a gradual outward expansion from a central point in a "fairy-ring" pattern. Examining excavated burls often reveals a more axial portion consisting of decayed wood, and an outer portion of new healthy burl. We believe this condition indicates that after fire, central portions of the burl atrophy, and regenerated tissues tend to form on the outer margins of the burl. Repetitions of this cycle could lead to fragmentation of the genets into a more-or-less circular arrangement of ramets. This tendency is particularly strong in *Arctostaphylos glandulosa*, which has extensive populations consisting of thousands of stems in which it is nearly impossible to recognize subclusters corresponding to individual genets. S. Davis (pers. comm.) has discovered almost perfectly symmetrical annular clones of *Malosma laurina* 10-15 meters in diameter in the Malibu area of southern California. If our suspicions are correct, aging living lignotubers in such species may give only a minimal estimate of the age of the genet.

Functions and Adaptive Meaning

Little is known about the actual function of the lignotuber in mediterranean ecosystems. In fact, little or no direct experimental evidence is available on the functions of the lignotuber for any ecosystem in which lignotuberous plants occur. Functions have often been inferred from studies on structure, anatomy, and nutrient contents of the lignotuber tissues, but direct quantitative observations are few.

The lignotuber has been considered an adaptation to uncertainty in the habitat, especially to stresses such as defoliation and prolonged drought or fire, which cause total or partial loss of the plant's above-ground parts (Carr et al. 1983). Frost can cause widespread above-ground mortality and even death in mediterranean-climate regions (O'Brien 1989). It is not, however, the only possible type of adaptation to these sorts of stresses, because lignotuberous and nonlignotuberous species often grow with equal success side by side.

The lignotuber has a decisive role in plant survival after disturbances and stresses. Successful regeneration after logging in the jarrah forest in SE Australia depends upon the presence of well-developed lignotuberous growth at the time the disturbance occurs (van Noort 1960). The presence of large subterranean lignotubers in the *Eucalyptus gummifera* mallee, ensuring regeneration after damage, is a clear advantage in the harsh environments in which it grows (Mullette 1978, Gill 1981). Having a well-developed lignotuber is also advantageous in surviving wildfires in the California chaparral, where some lignotuberous species show no mortality at all after fire (Rundel et al. 1987). Even at the seedling stage, a lignotuber can strongly influence survival. Noble (1984) stated that the lignotuber of eucalypts enhances the seedlings' ability to survive perturbations such as drought, grazing, and fire.

The occurrence of lignotubers in the Chilean matorral, a vegetation in which fire, is thought to have been less important than other mediterranean shrub types demonstrates the diversity of environmental pressures that can drive selection for the lignotuber (Montenegro et al. 1983). In Chile, drought and grazing are suggested as primarily selective forces favoring lignotuber development.

We postulate a dual function for the lignotuber. First, it stores concealed buds (a source of meristematic tissue), and second, it stores resources such as carbohydrates and nutrients. Both functions may allow rapid regrowth after above-ground parts are removed (Chattaway 1958, Specht 1981a), and therefore make the lignotuber a structure especially adapted to environments subjected to recurrent disturbance.

It is well known that the rapid resprouting capacity of some plants is related to the large numbers of concealed buds held in the lignotuber. Zammit (1988) studied the capacity of *Banksia oblongifolia* lignotubers to resprout within intervals in which it was assumed that new buds were not produced. About 30% of the buds remained dormant after the first clipping, and about 10% after the second and third clippings. No lignotubers survived four clippings over the 15-month experimental period. Kummerow and Ellis (1989) reported a figure of 120 sprouts per lignotuber on ten 54-year-old *Adenostoma fasciculatum* individuals two years after a fire. And in the Mediterranean Basin a lignotuber 1304 cm^2 in area of a tree heath, *Erica arborea*, was found to have 1268 sprouts nine months after clipping (J. Canadell unpub.).

Without disturbance, the buds held in the lignotuber are inhibited by apical dominance, and only when the stem is injured or cut off is the inhibition removed so that the buds can sprout (Blake and Carrodus 1970). Some authors, however, have found that a few species have the capacity to continuously sprout from the lignotuber, without fire or any other identifiable disturbance (Mesléard and Lepart 1989, Malanson and Westman 1985, Lacey 1983). Clipping studies indicate that it is not the plant's nutritional status that prevents development of the dormant buds (Blake 1972).

A close relationship binds lignotuber characteristics such as its size and the depth at which it is located, to its relative resistance to fire. Plants with a large lignotuber have a better chance to survive a fire than do plants with smaller ones (Rundel et al. 1987). Similarly, plants with a lignotuber deeper in the soil profile have a higher chance of surviving, for the soil's insulating properties prevent the dormant buds from being killed (Auld 1990, Flinn and Wein 1977). Bradstock and Myerscough (1988) showed that in *Banksia serrata* and *Isopogon anemonifolius*, young juveniles are the stage in the life cycle most sensitive to frequent fires. Insufficient lignotuber development was concluded to be the cause of their mortality. Experiments with *Angophora hispida*, a species common in the heathlands, woodlands, and dry sclerophyll forests in Southeast Australia, revealed that size and depth of the developing lignotuber interacted to influence the degree of plant survival. Only plants with lignotuber volumes greater than 5000 mm^3 showed no mortality after clipping and burning treatments (Auld 1990); a similar pattern was found by Noble (1984) for three *Eucalyptus* species. And the size of lignotubers in five-year-old *Banksia serrata* juveniles governed survival under simulated low-intensity fires (Bradstock and Myerscough 1988).

The lignotuber's function as a storage organ for carbohydrates and mineral nutrients is studied much less often. Some of the strongest evidence that the lignotuber acts as a carbon-storage structure comes from studies of anatomical and chemical content. Montenegro et al. (1983) studied the anatomy of one-year-old shrub seedlings in the Chilean matorral. Starch was found not only in the rays and cortex cells, but also in the axial parenchyma of the secondary xylem, the layers of periderm and parenchymatous cells being more numerous in the lignotuber than in the main stem. Important quantities of starch were contained in the parenchymatous cells. In the lignotuber the axial parenchyma is made up of paratracheal bands one to three cells wide, but the normal stem is made up of one cell layer. From these findings it is concluded that the lignotuber can be considered a storage organ for starch. Carrodus and Blake (1970), however, found inconsistent anatomical support for the carbohydrate-storage function of the lignotuber of *Eucalyptus obliqua*. Starch was restricted to the parenchymatous cells of the rays and cortex. No starch was observed in the tracheid or fiber-tracheids, as had been reported by Chattaway (1958), and their starch content was similar to that found in the adjacent taproots and stems. Lopez (1983) reported starch grains in axial and ray parenchyma of *Quercus dumosa* lignotubers in the California chaparral. But tissues concentrations of both nitrogen and non-structural carbohydrates showed no differences between lignotubers and stems.

Some studies used the tissue chemical composition of the lignotuber as support for the lignotuber function as a store of nutrients. Dell et al. (1985) found that phosphorus concentrations were three times higher in the lignotubers than in the stem wood of *Eucalyptus marginata*. This excess resulted from the more abundant storage parenchyma in the lignotuber. It was suggested that the *E. marginata* lignotuber may be a phosphorus storage organ that enables these trees to survive on nutrient-deficient soils, especially soils low in phosphorus. On the other hand, Mullette and Bamber (1978) did not find statistical differences in mineral nutrient concentrations between lignotuber and stem tissues for *E. gummifera*. But considering the great biomass of the mallee lignotubers, they concluded that the lignotuber is an important storage organ for inorganic nutrients. In the chaparral, Lopez (1983) also states that although concentrations in lignotubers may be low, the vast amount of biomass means that large quantities of both carbohydrates and nutrients could be present. He suggests that the lignotuber serves as a source of food reserves, which is especially important for resprouting after fire.

In conclusion, although it is tempting to accept the dual function of the lignotuber—protection for concealed buds and storage of resources—the only direct evidence available is about the lignotuber's function as a bud store. The concealed buds held in the lignotuber are essential in regeneration after above-ground destruction. The lignotuber as an organ for carbohydrate and nutrient reserves has been inferred from indirect evidence, which does not necessarily point out that the lignotuber has storage functions distinct from that of stems and roots. Furthermore, physiology of plant processes cannot be inferred from anatomical and chemical tissue studies. Carbohydrates stored in the lignotuber nevertheless do have a critical role during the period before plants start to resprout. Regrowth has been observed to be delayed for up to half a year in some species. The carbon stored in the lignotuber may then be critical in maintaining respiration, although carbon stored in the roots may be equally important.

A Hypothesis to Explain the Evolutionary Origin of Lignotubers

Lignotubers are widely distributed geographically, and are not unique to vegetation that experiences severe summer drought (Axelrod 1975). They also occur in many families, suggesting that one or a very few fundamental selective pressures mostly independent of the morphology and physiology of the individual species account for their origin. We suggest that a universal selective pressure arises from the constraints of plant architecture. Specifically, we believe that a multiple-stemmed woody plant (shrub) has a limited range of possible responses to damage to its canopy.

Our model postulates the original condition to be a long-lived, usually multiple-stemmed woody shrub. A plant of this type must forage for water or nutrients over a wide area and therefore has a root system that is deep, or extensive, or both. Maximum size and therefore maximum fitness is achieved only after a relatively long period of growth and a large investment in roots. The strategy for such species is based on producing multiple stems from a central root crown and returning water and nutrient resources to the cluster of stems at the center. This conservative, spatially fixed soil foraging contrasts to a more active strategy such as lateral expansion by producing stems from root sprouts or rhizomes. Such mobile foraging strategies are not compatible with reliance on deep, extensive, and energetically costly root systems.

Assuming that longevity is an element in the strategy, the canopy needs to recover after fire, drought, and herbivory. Several factors would favor having the replacement stems arise from buds lower on the stems. First, buds placed lower would have a higher probability of survival, especially when burned. Second, regeneration from more highly placed buds would tend to produce weaker and more disease-prone stems because deadwood remaining from the old stem would often be incorporated into the new stem (Fig 8.1).

At least two factors would also favor an increase in the number of buds. The simple numerical advantage is probably of primary importance. The more buds, the more likely it is that at least one will survive to produce a new stem. Returning to the importance of the root system, the proliferation of stems may be useful to maximize the area of photosynthetic canopy and thus maximize the survival of root biomass. Multiple buds and sprouts are also a hedge against herbivory, to which resprouting shrubs are particularly susceptible.

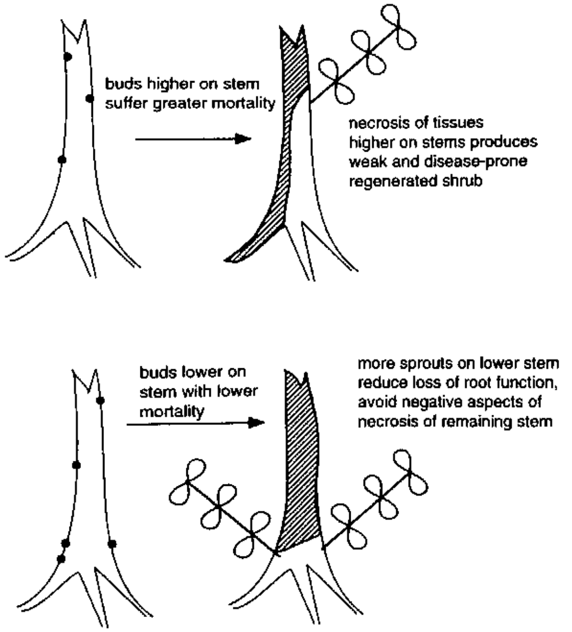

Figure 8.1. Diagrammatic representation of the hypothesized primary causes for the origin of the lignotuber. Buds placed lower have a higher probability of surviving disturbance and regenerating sounder structure. The final stage in the evolution would increase number and storage capacity by enlarging basal diameter.

Because bud number is limited by the circumference of the stem, selective pressure to increase the number requires an increase in stem diameter at the base of the plant. Concomitant with the increase in number is the need to ensure that resprouting will be rapid and vigorous. This requirement favors storage of energy reserves in the lignotuber, as suggested earlier.

All these factors acting together will move species toward a lignotuber. Species that lack a burl until after they have suffered severe canopy removal do not contradict our argument. Rather they seem to illustrate an intermediate condition in which buds are concentrated low on the plant, but in which strong selection to increase the number has been lacking.

The absence of a lignotuber in the so-called obligate-seeder species—that is, species that fail to resprout after fire and must reestablish by seed—is consistent with our hypothesis. The regenerative function of the lignotuber matters primarily because of its utility in plant response to relatively rare massive disturbance. Species benefit from a lignotuber only if the interval between massively disturbing events is significantly shorter than the life span.

Our model stresses regeneration of multiple-stemmed woody plants, but tree forms also have a lignotuber. If the probability is reasonably high that the above-ground portion of the tree will be killed by fire, the lignotuber could serve the same function in maximizing bud survival as it does for a multiple-stemmed shrub, in a manner consistent with our hypothesis. This appears to be the sequence in Australian eucalypts, where trees often exist for an extended period in the understory as multiple-stemmed shrub-form individuals with lignotubers (Florence 1981). Such individuals may be repeatedly burned and grazed before an opportunity to recruit into the canopy is presented. Florence (1981) hypothesizes that forming an extensive root system may be a critical aspect of this juvenile stage. If, however, the death of the main stem were very rare, our model would not be valid, and the presence of the lignotuber would have to be explained by some other benefit conferred on the plant.

Conclusions

Data on root structure and morphology are still somewhat scarce for woody species in mediterranean ecosystems, yet basic conclusions can be arrived at from this review.

Root morphology has been shown to have high intra- and interspecific variability. When soils allow free development of the root system, root structure is primarily determined by the species's genetic makeup. Soil features such as rockiness, steep slopes, and changes in bedrock at small spatial scales, however, cause habitat-dependent variability, which may completely alter the root system's structure. This alteration is common in the California chaparral and Chile matorral, where species-level classification has often been unsuccessful. On the other hand, the sand plains in Southeast and Southwest Australia present less constriction to root-system development, enabling the structure of the root system to develop more freely. In that case, classifications characterizing root-system structures at the species level have been more successful.

Of the different root-system morphologies, the dual type is quite common among evergreen species in the Pacific mediterranean ecosystems. It is distinguished by a taproot, which may be either a single dominant root, or multiple nondominant roots that may easily reach between 1.5 m and 2.5 m deep. Examples of roots reaching soil horizons deeper than 4 m have been reported. About 70% of the species in Table 8.1 have shown taproots. The dual type of root system also shows a well-developed lateral root system that may extend over areas several times the size of the canopy.

The dual system seems particularly well suited to mediterranean climate conditions because it enables plants to utilize moisture from deep horizons during part of the summer drought. For that reason, plants are able to photosynthesize all year during wet years. In fact, this type of root system seems to be an adaptation to a seasonal drought regardless of when the drought occurs. Thus, climates other than mediterranean with a pronounced seasonal drought also show a dual type of root system.

Unlike the relatively deep root system of the evergreen species, drought-deciduous species, which occur in the driest extreme of the mediterranean climate, commonly show a shallower root system. They are therefore much more sensitive to drought and usually have a shorter growing season.

Possession of a lignotuber is common among resprouting shrubs in the mediterranean ecosystems studied. *Eucalyptus* species, which dominate the overstory in the mediterranean forest and woodlands in Southeast and Southwest Australia, show one of the most extensive developments of the lignotuber. Although lignotubers are characteristic of mediterranean ecosystems, they are also found in regions with other climatic regimes and therefore probably are a very ancient and very general solution to problems faced by woody plants. Environmental disturbances and stresses such as drought, defoliation, and fire are suggested as possible evolutionary forces.

A dual function is postulated for the lignotuber. With little doubt, a major function is to store concealed buds that resprout after a disturbance. A second function is to store carbohydrates and nutrients, as inferred from anatomical and nutrient tissue-analysis studies. Both functions may allow rapid recovery of the plant after the above-ground parts are removed. It has yet to be experimentally proven, though, if plants use these resources during resprouting, and if so, the extent to which they are used. Also still unclear is the possible role of the lignotuber during periods between disturbances.

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