

Chapter 2

Morpho-Anatomical Traits for Plant Adaptation to Drought

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Abstract Plant resistance to drought relies on adaptive strategies based on the timing of phenophases and on the presence of structural traits mainly related to: (1) increase of water uptake and storage; (2) reduction of water loss during dry periods; and (3) mechanical reinforcement of tissues to prevent wilting that may lead to irreversible collapse and damage of cells. In this chapter, after a few evolutionary considerations, we focus on the adaptive value of the main phenological, morphological and anatomical properties. We report the common existence of such traits in both desert and semiarid environments, especially in Mediterranean-type ecosystems. All morpho-anatomical characteristics are interpreted considering that plant resistance to drought also depends on the ability to respond to multiple stressors. We conclude that various combinations of anatomical features can contribute in different degrees to the adaptive capacity of plants to drought.

2.1 Introduction

Shortage of water is a constraint to life that recurs more and more in many regions of the world due to global climate change (IPCC 2007). Increasing drought has an impact on the survival of plants in natural ecosystems, while it also results in reduced yields in crops.

Climate change in semiarid regions is expected to trigger desertification processes; these can have serious consequences considering that semiarid woody

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ecosystems sustain a considerable part of the world's terrestrial biomass, net primary productivity and biodiversity (Atjay et al. 1979). Mediterranean ecosystems are particularly fragile and characterised by two stress periods during the year, namely summer drought and winter cold (Mitrakos 1980). In these ecosystems, the impacts of human-induced climate change are estimated to be highest (Hulme et al. 1999) and future changes are likely to aggravate significantly the existing environmental, structural and socio-economical problems. Here, global climate change will cause significant alteration in temperature regimes and precipitation patterns as well as an increase in both the frequency and intensity of extreme events (e.g. heat waves, floods, droughts) (IPCC 2007). Understanding the response of plants to increasing drought would be desirable in the light of global and regional changes not only to forecast population dynamics in natural ecosystems, but also to adjust management practices in agriculture. All biogeochemical processes are climate driven, and thus, increasing drought could not only impact the C-gains and C-losses of ecosystems, but may influence plant growth by affecting phenology and determining modifications at biochemical, physiological and anatomical levels (Schwartz 1999; Morison and Morecroft 2006).

Every plant organ is ideally designed to fulfil metabolic and physiological processes in specific environmental conditions. In environments characterised by arid conditions, plant survival depends upon the ability to harmonise structure and function to withstand desiccation without permanent damage (Maximov 1931). These plants show structural alterations that are mainly related to water saving (e.g. water storage and reduction of water losses) and mechanical reinforcement of tissues (e.g. thickening and straightening of cell walls) (Shields 1950; Fahn 1964; De Micco and Aronne 2007). Mechanical reinforcement may prevent phenomena such as collapse and damage of cells, associated with irreversible wilting, and hence the loss of functionality during water deficit.

In this chapter, we discuss the adaptive value of some morphological and anatomical traits in the various organs of plants growing under dry conditions. A specific focus is on woody plants of semiarid Mediterranean-type ecosystems. More specifically, we start from general considerations about phenological features, also in relation to growth forms; subsequently, we discuss plant structural attributes linked with water storage, reduced water loss and efficiency and safety of water transport in the xylem. The role of some attributes is considered at the ultrastructural level. Moreover, structures that reinforce tissues and defend them against predators and excess of light are pondered considering that plant resistance to drought is also associated with the ability to respond to the action of multiple stressors.

All morpho-anatomical attributes are interpreted under the perspective that not single traits but suites of anatomical features are responsible for the adaptive capacity of plants in a specific environment.

2.2 Evolution of Plant Life Forms

The evolution of terrestrial vascular plants, from the primordial aquatic organisms to higher terrestrial plants, has been accompanied by increasing complexity in the structure and functions of their vegetative and reproductive organs. Many environmental factors drove the evolution of morpho-functional traits during the key 'moment' when organisms moved from the aquatic environment to colonise the lands. Indeed, some factors, including atmosphere composition and radiation, were changing during land plant evolution. On the other hand, gravity also played an important role during land colonisation, because plants, loosing hydrostatic pressure, perceived it with different intensity (Graham 1993; Rozema et al. 1997; Bateman et al. 1998). However, the major factor was water availability: the first land plants faced the problem of solving the conflict between water retention and the metabolic requirement to exchange gases with the atmosphere for photosynthesis (Niklas 1986).

The evolutionary history of plants is rich with examples of how specific traits arose to fulfil specific needs (e.g. for water translocation, for reproduction, to withstand mechanical stress, etc.) due to changing environmental conditions (Raven 1977) (Fig. 2.1). Although such traits involve any life organisation levels (from the development of multifaceted metabolic pathways up to organogenesis), there is common agreement that the development of specific forms and functions is controlled by mechanical and physiological constraints (Niklas 1986). A need for simplifying the variability of plant shape and size has lead to the application of plant functional types (Smith et al. 1997). Each of them might be considered the result of the interconnections between traits evolved at different levels (e.g. cytological, anatomical, phenological, physiological, biochemical and molecular) and designed to accomplish specific functions. Whilst single traits can be related to many functions, on the other hand, multiple traits can act in cooperation to achieve a specific aim through the development of definite adaptive strategies.

Focusing on the strategies to withstand water shortage, the adaptation mechanisms become more and more developed and complex moving from wet areas towards arid areas, where the regularity of drought events leads to the development of multifarious strategies (Monneveux and Belhassen 1996). Pursuing the need to avoid drying out of tissues, there is common agreement on the presence of an adaptive link between the leaf gas exchange capacity and hydraulic efficiency in above- and below-ground organs, as well as at the whole plant level (Brodribb 2010). The existence of a strong relation between leaf photosynthetic capacity and hydraulic supply of water to leaves has been shown in a group of conifers and angiosperm species, both vessel bearing and vessel less (Brodribb and Field 2000).

During evolution, two strategies of water use arose in plants leading to the two plant types known as desiccation tolerant (poikilohydric) and non-desiccation tolerant (homoiohydric) (Schulze et al. 2005). Poikilohydric organisms act as purely physical systems whose water content tends to reach the equilibrium with the humidity of the environment (e.g. lichens, some mosses). Such organisms do

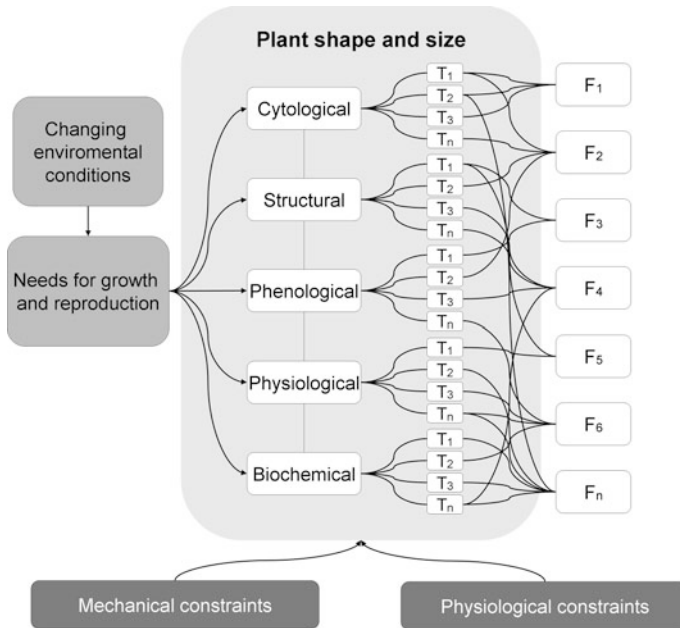


Fig. 2.1 Schematic view of how plant shape and size, depending on the combination of different traits (T_i) expressed at various organisation levels, are primed by the need to respond to environmental inputs and constrained by mechanical and physiological limitations. Single traits or combinations of them are responsible for specific adaptive strategies to fulfil precise functions (F_i)

not possess mechanisms to prevent desiccation: they consequently dry out and remain dormant when water availability decreases, but can rehydrate when water becomes available again. On the other hand, homoiohydric organisms (e.g. some ferns, flowering plants) are able to maintain high water content in their tissues independently on the conditions of the surrounding environment. Higher plants are homoiohydric. Among them, three types of resistance to drought are typically classified, namely escape, avoidance and tolerance strategies. The boundaries between these types are not clear-cut since they are not mutually exclusive (Levitt 1980). Escaping is a strategy based on the ability to complete the life cycle before the period of water shortage. In this case, plants do not experience water deficit because they are able to modulate their vegetative and reproductive phenology according to the most favourable seasons (Aronne and Wilcock 1997). Dehydration-avoidance strategies are based on the ability to maintain tissue water potential as high as possible through a variety of adaptive traits involving the minimisation of water loss and optimisation of water uptake. The reduction of transpiration occurs in water-saving plants, while water spenders rely on other means, such as osmotic adjustment, to prevent desiccation (Levitt 1980). Tolerance strategies occur in plants able to endure low tissue water potential through adaptive traits involving osmotic adjustment and the formation of more compact and stiff tissues.

Extreme desiccation tolerant plants, known as resurrection plants, can be found in angiosperms monocotyledonous and dicotyledonous plants (mainly in the Scrophulariaceae and Myrothamnaceae families). They are able to severely dehydrate, still fully recovering after rehydration as poikilohydric organisms.

Since escaping, avoidance and tolerance mechanisms can occur contemporarily in the same organism (Ludlow 1989), a definite classification of morpho-functional adaptive traits into the different strategies is not significant: the same traits can be beneficial for each of them. Such traits are generally constitutive rather than stress induced (Chaves et al. 2003).

2.3 Modulation of Growth: Phenology and Growth Forms

Apart from resurrection plants, some authors agree that the term drought resistant does not apply to many higher plants because they evolved different avoidance reactions based on the restriction of growth events into time windows when water supply is satisfactory (Greene et al. 2011). Such reactions include the shedding of aerial organs to reduce water loss due to transpiration or the regulation of plant phenology.

Most annual plants are a typical example of avoidance: the shortness of life cycle is accompanied by the completion of their reproductive cycle before the dry season. There is evidence that the transition between phenophases can be affected by increasing aridity depending on species-specific phenotypic plasticity, which is also influenced by the environment. According to Aronson et al. (1992), while desert plants respond to imposed drought by shortening their growth cycles with early seed maturation and senescence, Mediterranean annuals do not change phenophases promptly. More recently, Franks et al. (2007) demonstrated that flowering timing evolves rapidly (i.e. in a few generations) to escape drought.

For other biological types, including perennials and woody plants, adaptation to drought depends either on the evolutionary modification of specific organs, such as deep taproots or storage organs, or the onset of specific *habit* (e.g. shrub). In plants growing in deserts, morpho-anatomical traits to withstand long and severe periods of drought rely on: (1) the extreme reduction of leaves into thorns and (2) the development of succulent stems which perform photosynthesis and accumulate water in parenchyma tissues. In semiarid ecosystems, dominant forms of plant life include the evergreen sclerophyllous, drought deciduous and seasonally dimorphic shrubs which represent the main adaptive strategies of woody perennial species to water stress. The dominant role of shrubs in semiarid environments resides in the fact that they can grow in areas of high environmental stress where trees cannot survive (Rundel 1991; Wilson 1995). The different leaf shedding models derive from the diverse ability of plants to employ favourable periods to photosynthesise and allocate resources for growth, reproduction, or storage.

It is interesting that, although it is recognised that water shortage is the main limiting factor in Mediterranean-type ecosystems, here most woody perennials

undertake highly resource demanding processes just during summer. As an example, Aronne and Wilcock (1997) found that less than one-fifth of the woody perennial species occurring in a Mediterranean shrubland avoided summer aridity by reproducing in spring; the remaining species either undertook most of the whole cycle in the summer or spent the arid period developing their fruits. In Mediterranean ecosystems, such timing of growth is possible because of the occurrence of specific morphological, anatomical, physiological and reproductive attributes. They concern all the organs, from leaves to the finest roots, and include sclerophylly, specialised xylem traits and root architecture, that enhance plant survival (Aronne and Wilcock 1994; Aronne and De Micco 2001; Lamont 1983; di Castri et al. 1981; Kummerow 1989; Rhizopoulou and Mitrakos 1990; Matosevic et al. 1997; De Micco and Aronne 2008; De Micco et al. 2008).

The timing of leaf shedding is also linked with periods of xylem growth in woody species. Indeed, the duration of cambial activity, as well as structural and chemical properties of the formed wood, is dependent on environmental factors, especially water availability. Summer deciduous plants, with drought-avoiding behaviour, are characterised by single summer dormancy in cambial activity (Cherubini et al. 2003), which results in the formation of annual rings as recorded in *Cistus ladanifer* L. (Patón et al. 1998). However, the occurrence of two periods of dormancy in cambial activity in seasonally dimorphic species leads to the formation of false rings as recorded in *Cistus incanus* L. (De Micco and Aronne 2009). False rings, often referred to as Intra-Annual Density Fluctuations (IADFs) or double rings, are frequent in woods of Mediterranean environments and are triggered by specific patterns of cambial activity. Here, IADFs are caused by the interruption of the normal course of growth due to a sudden drought event, thus determining a zone of wood characterised by an abrupt change in wood anatomical properties (Schulman 1938; De Micco et al. 2007, 2012; Battipaglia et al. 2010). Such specific anatomical properties arise in response to drought to enhance safer (i.e. less subject to cavitation or embolism), though slower, water transport (we will specify this in the paragraph 2.6). The analysis of the variation of anatomical properties and isotope composition along IADFs, being correlated to stomatal regulation, has proved to be useful to reconstruct phenological events from wood structure, thus unravelling how woody species vary their role of carbon sink in different environmental conditions triggered by climate change or regional modifications of land use (Battipaglia et al. 2010).

2.4 From the Resistant Dry Seed to the Fragile Seedling

Adaptive strategies against drought have been studied in adult plants of many arid and semiarid ecosystems. Much less information is available about the occurrence of defence strategies during the first phases of plant life after seed germination, although it is recognised that interspecific differences in seedling survival and juvenile growth performance along resource gradients are key factors controlling

plant community structure and dynamics (Fenner and Kitajima 1999). Plant communities are first shaped by seed dispersal, which impose the habitat where the plants grow in, and then by the effect of environmental factors on seed survival, germination, seedling establishment and growth (Schupp 1995). Seedling establishment seems to be one of the most critical phases in the regeneration process by sexual reproduction. Once new gene combinations have been produced with the formation of seeds capable to germinate, survival and growth at early stages of plant development are major bottlenecks to successfully complete the reproductive cycle and to achieve canopy occupancy as demonstrated in tropical and cool-temperate forests (Fenner and Kitajima 1999; Sánchez-Gómez et al. 2006). Indeed, even if a species has a very specialised reproductive system that allows successful seed production and dispersal, other ecological factors may constrain seed germination and subsequent seedling establishment, growth and survival (Traveset et al. 2001). Seedling survival depends on the ability to cope with numerous environmental factors such as water availability, temperature, radiation, pathogens, herbivory and competitive interactions (Moles and Westoby 2004). However, the main reason for seedling mortality is drought which constraints the recruitment processes in time and/or in space (García-Fayos and Verdú 1998; Moles and Westoby 2004). Therefore, in arid regions recruitment occurs in restricted rainfall periods or in limited wet areas (Pugnaire et al. 2006; Padilla and Pugnaire 2007). Wherever dry periods, interspersed between rain events, are frequent, two aspects are fundamental in order to ensure rapid seedling establishment: prompt anchoring of juvenile seedlings to the substrate and immediate water absorption (Young and Martens 1991; Aronne and De Micco 2004). Given that the high desiccation tolerance of the embryo in the dry seed is rapidly lost during germination, survival highly depends on the rapidity in overtaking the early life stages.

Higher seedling survival is often linked to larger biomass allocation to roots. This allows a better water and nutrient uptake due to the possibility to explore larger volumes and deeper layers of soil (Davis 1989; Padilla et al. 2007). Survival of deep-rooted seedlings after drought is higher if compared to shallow-rooted ones, although this relation can be influenced by other species-specific factors (Padilla and Pugnaire 2007). Also the size of seeds seems to affect seedling survival during periods of water shortage because larger seeds are characterised by larger storage reserves which allow the development of larger seedlings with more expanded roots than smaller seeds (Fenner and Kitajima 1999). Nevertheless, by means of an experiment involving some Mediterranean woody species, Padilla et al. (2007) demonstrated the importance of water availability during the first stages of development of seedlings regardless of seed size. There is also evidence that root elongation is increased in drought-tolerant species and in species growing in dry sites, suggesting that root plasticity is under genetic control (Sharp et al. 2004). However, to what extent root plasticity is controlled by genetic principles or environmental constraints has not been clarified yet (Padilla et al. 2007). Actually, it is likely that many characters, such as seed size and vital strategy, act together in determining the capability of seedling establishment. As an example, rooting depth

in seedlings of wild species has been shown to increase in response to drought especially in species that regenerate mainly from seeds after disturbance (seeders) (Reader et al. 1993). Moreover, growth reactions to water shortage can be influenced by the interaction with other factors, mainly with irradiance. More specifically, contrasting hypotheses attempt to explain the effects of drought on seedling performance along gradients of irradiance. According to the trade-off hypothesis, the effects of light limitation are more negative under drought conditions: the reduced carbohydrates produced by photosynthesis enhance the conflicts between the simultaneous demands for allocation of resources to develop both above-ground and below-ground biomass (Kubiske et al. 1996). On the other hand, many experiments support the facilitation hypothesis by which drought is less harmful under shadier conditions (Sánchez-Gómez et al. 2006). According to this hypothesis, so-called “nurse plants” facilitate growth and development of other plant species (target species) beneath their canopy. Indeed, they create microhabitats that are more favourable for seed germination and/or seedling establishment. The nursing effect has been used to restore vegetation in arid and subarid zones in recent years (Ren et al. 2008).

Apart from biomass root/shoot ratio and root length, many other morphological parameters affect seedling establishment in Mediterranean environments. The development of specialised tissues, such as hypocotyl hairs, during seedling emergence has been shown to have composite positive effects involving facilitation of water uptake and prompt physical support (Aronne and De Micco 2004). Other anatomical traits favouring adaptation to drought, such as small diameter roots and specialised tissues to avoid water loss, are common also in adult plants and will be analysed in the following paragraphs.

2.5 Transpiration and Leaf Xeromorphy

Water absorbed by plant roots is lost in the atmosphere mostly through leaf transpiration. Transpiration rates vary widely among plant groups: from 10 to 0.1 g of water $\text{dm}^{-2}\text{h}^{-1}$ in hygrophytes and xerophytes respectively (Monneveux and Belhassen 1996). Plants in arid and semiarid environments show leaves with xeromorphic traits designed to reduce transpiration to a minimum under drought conditions. The reduction of transpiration can be reached through various means including leaf shedding (i.e. in drought deciduous species) as well as decrease of leaf number, leaf size and branching. In extreme conditions shedding of twigs, branches or larger portions of plants also occurs. In plants that appear leafless under drought conditions, photosynthesis is achieved thanks to green branches, stems or retained petioles (Fahn 1964). Sclerophylly of plants is also considered an adaption to drought: hard leaves do not suffer from permanent damage due to wilting and can completely recovery when favourable conditions are restored.

Sclerophylls are widely distributed in arid and semiarid environments together with seasonally dimorphic species. Sclerophylly has been interpreted as a

phenomenon linked also to other functions as protection against pathogens or as response to scarce nutrient availability (Salleo and Nardini 2000). However, there is evidence that stiff, leathery leaves are widespread in species adapted to drought occurring in various environments throughout the world. Sclerophyllous leaves are characterised by reinforcing tissues (e.g. thick-walled epidermal cells, sclereids, etc.) which prevent the collapse of the whole structure when water availability is scarce (drought hypothesis), thus reducing the risk for mechanical damage. Under drought conditions, a sclerophyllous leaf slightly reduces its volume thanks to thick cuticle and thick-walled epidermal cells, but thin-walled mesophyll cells severely shrink resulting in an increase of intercellular spaces. This allows photosynthesis to remain active also in conditions of severe water stress when other leaf types wilt (Shields 1950).

Seasonally dimorphic species are characterised by a seasonal reduction in their transpiring surface: larger winter mesomorphic leaves growing on dolichoblasts (long twigs) are shed at the beginning of the arid season and are replaced by smaller summer xeromorphic leaves on new brachyblasts (short twigs) (Orshan 1964; Aronne and De Micco 2001).

In both sclerophyllous and summer leaves of seasonally dimorphic plants there are many similar traits allowing to withstand drought conditions. Such characteristics regard not only the morphological appearance of leaves on axes but also their anatomical properties both inside (e.g. features of palisade and spongy parenchyma tissues) and at surface levels (e.g. deposition of protective layers and features of stomata).

It is well accepted that phenomena such as paraheliotropism, steep leaf inclination and changes in the colour, due to alteration of pigment content, are frequent in dry habitats. They help reducing solar irradiation and consequently decrease leaf heating and transpiration rates as well as avoid damage to photosystems and phenomena of photo inhibition (Aronne and De Micco 2001; Arena et al. 2008). The lamina folding and the leaf rolling are valuable mechanisms to reduce transpiration (Fig. 2.2a). Leaf rolling, is frequent in grasses adapted to drought and is induced by turgor loss of bulliform cells occurring in the epidermis (Fig. 2.2b) or of other specialised mesophyll cells (Shields 1950).

Adaptation to drought conditions is achieved also through the low ratio of the external leaf surface to its volume. This is generally also accompanied by the occurrence of a compact structure (Fig. 2.2a, c) made of small mesophyll cells with thick cell walls, reduced intercellular spaces and a more compact network of veins. The increased leaf stiffness, although limiting gas exchange, might reduce water losses enhancing high leaf tissue density and dry mass per area (Fahn 1964; Mooney and Dunn 1970; Niinemets 2001). More recently, the decrease of total diffusion conductance throughout intercellular spaces from substomatal cavities to chloroplasts has been linked not only to reduced aquaporin conductance, but also to precise anatomical traits such as the reduction of chloroplast surface area exposed to intercellular space per unit leaf area (Miyazawa et al. 2008; Tosens et al. 2012). The presence of additional layers of palisade parenchyma at the expense of spongy tissue (Fig. 2.2 a, c, d) is also considered a way to increase the

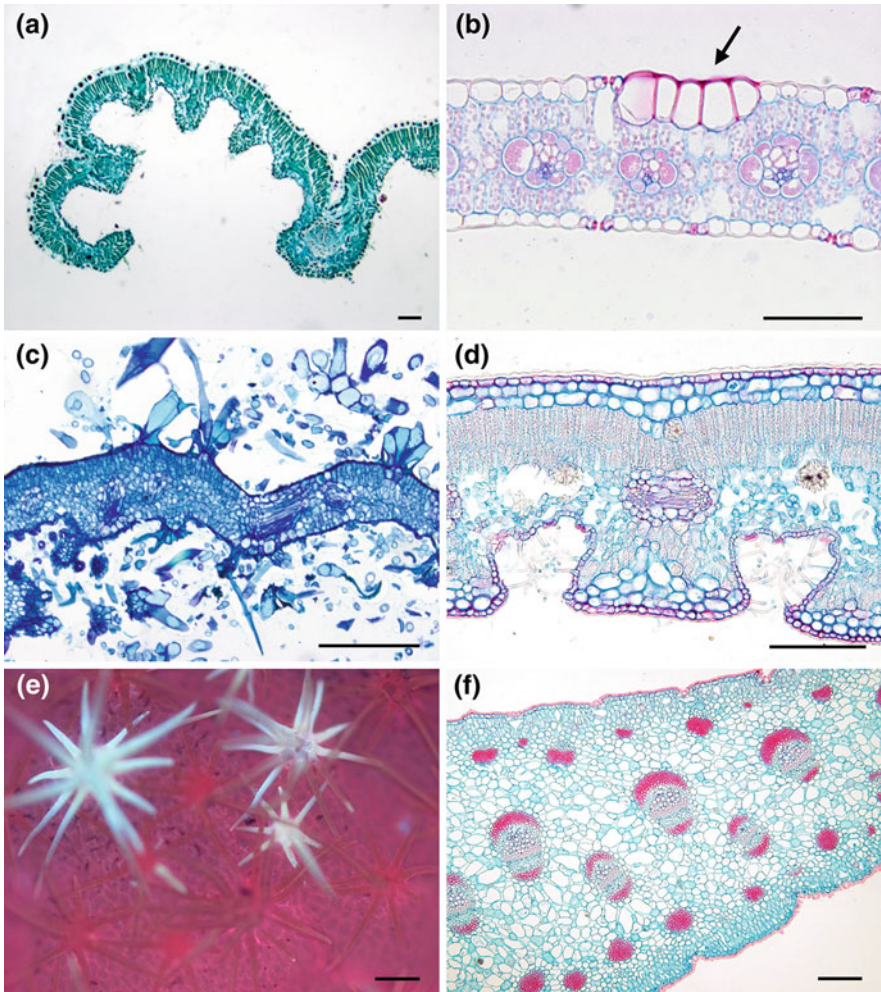


Fig. 2.2 Light (a–d, f) and epi-fluorescence (e) microscopy views of leaf cross-sections (a–d, f) and lamina surface (e) showing anatomical traits for resistance to drought: **a.** Folded lamina and compact structure in *Cistus monspeliensis* L.; **b.** Bulliform cells (arrow) in *Zea mais* L.; **c.** High leaf density and high frequency of trichomes in *Cistus incanus* L.; **d.** Additional layers of epidermis and palisade parenchyma, and stomata concentrated in crypts in *Nerium oleander* L.; **e.** High frequency of suberised trichomes in *C. incanus* L.; **f.** Thick cuticle, sunken stomata and water-storage parenchyma in *Yucca* sp. Bars correspond to 100 µm

path of water through intercellular spaces to reach stomata; this would be a strategy to increase water use efficiency (ratio of carbon dioxide fixed to water lost) (Lewis 1972). In xeric leaves, additional layers of palisade parenchyma can develop also adjacent to the lower epidermis leading to isobilateral anatomical structure which, together with steep leaf inclination, allows the optimisation of

light interception in the early morning hours and in late afternoon. The increase of mesophyll thickness enhances the photosynthetic capacity if it is accompanied by an increase in the number of chloroplasts exposed near the surface area facing the intercellular spaces (Oguchi et al. 2005). However, other factors, including leaf developmental stage and light availability, are known to interact with drought in determining modifications of mesophyll and chloroplast differentiation, and ultimately of mesophyll diffusion conductance and photosynthetic capacity (Tosens et al. 2012).

Water losses are also severely affected by the characteristics of stomata. Adaptation to drought involves the decrease of stomata size, while stomata density shows a more plastic response to environmental changes. In a recent experiment, Xu and Zhou (2008) demonstrated that stomatal density increases under moderate water deficit, while it declines under severe drought. There is much information on how reduction of transpiration can be rapidly achieved through a physiological control of stomatal opening. However, stomatal closure is strongly controlled by hydraulic architecture of leaves and stems that determines the critical thresholds for vulnerability to cavitation (Sperry 2000). Plants of arid and semiarid environments show sunken stomata, often covered by resinous masses and wax layers or confined in deep crypts of the lamina (Fig. 2.2d) (Fahn 1964; Monneveux and Belhassen 1996). These crypts are often occluded by wax tubules or trichomes which might further reduce transpiration. However, the occurrence of stomata plugged with cuticular structures has been also shown as an adaptation to excess water in plants growing in rainforests and cloud forests: these plugs help maintaining photosynthetic activity by preventing the formation of a continuous water film that would impede diffusion of CO₂ into the leaf (Field et al. 1998). The presence of plugged and/or sunken stomata and hairy leaves is not exclusive of plants of arid environments and is also related to other functions such as protection against herbivory (Bongers 1973; Koster and Baas 1981). Although xeromorphic leaves are generally more hairy than mesomorphic ones (Fig. 2.2c, e), there is common agreement on the fact that dead trichomes participate in the reduction of transpiration when stomata are closed, while living trichomes might themselves increase water losses (Shields 1950).

Xeromorphic leaves are also characterised by the presence of a thick cuticle. The hydraulic permeability of the cuticle depends on its thickness, chemical composition and crystal forms of cuticular waxes embedded in the cuticle or deposited over it. Water permeability of cuticle is lower in xeromorphic than in mesomorphic leaves and it has been demonstrated that the properties of this barrier at leaf interface with atmosphere are genetically controlled (Riederer and Schreiber 2001). Cuticular water permeability also depends on relative humidity, decreasing as environment dries out thanks to chemical properties of cutin and wax domains (Bargel et al. 2004). Moreover, different cuticle composition can determine changes in reflectance thus indirectly affecting lamina heating (Monneveux and Belhassen 1996). Indeed, the occurrence of cuticular waxes, by increasing leaf reflectance at the visible and infrared light wavelengths, can reduce photoinhibition of photosynthesis and transpiration rates, having a positive effect on water use

efficiency. Besides, UV radiation is also attenuated by the presence of flavonoids in the cuticle matrix or at the surface of epicuticular waxes (Bargel et al. 2004). Phenolic compounds can also filter excess radiation either in form of vacuolar accumulations in glandular leaf hairs, in epidermal and parenchyma cells, or linked to membranes throughout mesophyll cells as also shown in cortical cells of green photosynthesising twigs (Tattini et al. 2000; De Micco and Aronne 2007). Such phenolics also have an indirect role in adaptation to drought since, being feeding deterrents, they protect plants from permanent damage due to grazing and pathogen attacks. This is critical since development of spare organs would require an extra-additional energetic cost which is often unaffordable under drought conditions.

The above-reported traits are linked to the reduction of transpiration; however, xeromorphic leaves can be also characterised by the presence of multilayered epidermis or parenchyma tissues devoted to water storage (Fig. 2.2f). Such water-storage tissues show lower osmotic pressure than photosynthesising cells which, under conditions of low water availability, can obtain water from the water-storage cells. The latter are generally thin-walled cells which can shrink easily, though rapidly recover when water becomes available again (Fahn 1964). In xeromorphic leaves, the recovery of cell turgidity after shrinking without suffering mechanical damage is favoured by the occurrence of the so-called concertina cells whose involuted cell walls help rapid enlargement when water becomes available again (Aronne and De Micco 2001).

2.6 The Role of the Stem and Evolutionary Trends in Wood Anatomy

Symptoms of adaptation to drought in stems have to be searched in the presence of peripheral structures reducing water loss, in the formation of water-storage tissues and in the characteristics of the water transport system. Regarding water saving, it relies on the properties of thick cuticle and thick-walled epidermal cells as well as on the occurrence of suberized subepidermal layers in young organs or interxylary cork rings in older stems. Such structures constitute barriers arranged “in series” as hydraulic resistors regulating water exchanges at the plant–atmosphere interface (De Micco and Aronne 2011). Water storage is achieved through the presence of succulent stems, below-ground structures such as bulbs and rhizomes, and living wood fibres or living xylem parenchyma containing reserve materials (Fahn 1964).

Apart from the analysis of structures which reduce water loss or serve in water storage, most studies have focused on adaptive traits regulating the transport of water from roots to leaves. Considering the metabolic cost for the synthesis of xylem tissue, plants tailoring xylem formation to fit the expected evapo-transpirational demand of leaves should have an adaptive advantage during evolution (Sperry 2003). In the last few decades, there has been increasing interest in the

study of the relationships between wood anatomy and environmental factors. In general, most wood anatomical traits can be interpreted based on their functional significance in the survival strategies of the species. They determine the hydraulic conductivity (efficiency) and vulnerability to cavitation (safety) of a given wood as well as the biomechanics of stems and branches (Zimmermann 1983; Carlquist 1975; Baas et al. 1983, 2004; Baas and Schweingruber 1987; Tyree and Sperry 1989; Niklas 1992; Tyree et al. 1994; Hacke and Sperry 2001). Adaptation to drought can be achieved through a sort of compromise between the need to maintain high conductivity when water is available, and to prevent embolism under conditions of aridity. The main ecological trends in wood anatomy highlight that, moving from mesic to xeric areas, woods tend to be less efficient in water flow, but more resistant to embolism and more robust (Fig. 2.3). In Mediterranean environments, this general tendency is often accompanied by a change of the plant habit from trees to evergreen/drought deciduous shrubs (De Micco et al. 2008). For many wood anatomical features, the existence of direct or indirect proportionality with the properties of efficiency/safety of water transport can be traced (Fig. 2.3). Such relations are sometimes ambiguous, considering that different combinations of various characteristics can tip the balance towards one extreme or the other. This balance between efficiency and safety is well achieved by many shrub species from Mediterranean semiarid ecosystems which have wood specialised for high conductivity when water is available (simple perforation plates, wide earlywood vessels, etc.), but also for safety during drought periods (narrow latewood vessels, vascentric tracheids, etc.) (Carlquist 1988, 1989).

Xeric conditions apparently favoured selection for short elements with simple perforations while scalariform ones remained generally restricted to plant taxa with a mesic or boreal/alpine ecology (Baas 1986; Carlquist 1975). Simple perforation plates are a more evolved character than scalariform ones (Bailey and Tupper 1918; Wheeler and Baas 1991) and they offer the capability for conducting larger volumes of water per unit of time when water is available (Carlquist 1975; Christman and Sperry 2010). However, according to Sperry (2003), scalariform perforation plates would be advantageous under drought conditions because they favour refilling of embolised vessels in a passive way. More specifically, a scalariform perforation would divide large gas bubbles into smaller ones which may dissolve more rapidly than fewer, larger bubbles in refilling vessels with simple perforation plates.

Xeromorphic woods are generally characterised by an increased number of narrow vessels. Under dry conditions, the redundancy of conducting cells permit water transport despite deactivation of a part of the tissue (Carlquist 1975; Baas et al. 1983). Conductivity being proportional to the fourth power of the vessel radius (Van der Oever et al. 1981; Zimmermann 1983), narrow vessels only allow slow water flow rate. However, narrow vessels are valuable for safety since they guarantee water transport also when larger vessels are embolised (Carlquist 1975).

In arid and semiarid environments, vessel size may be limited also by the need to reduce intervessel pitting and embolism by air seeding which is a phenomenon described as gas being drawn through pit membrane pores (Wheeler et al. 2005;

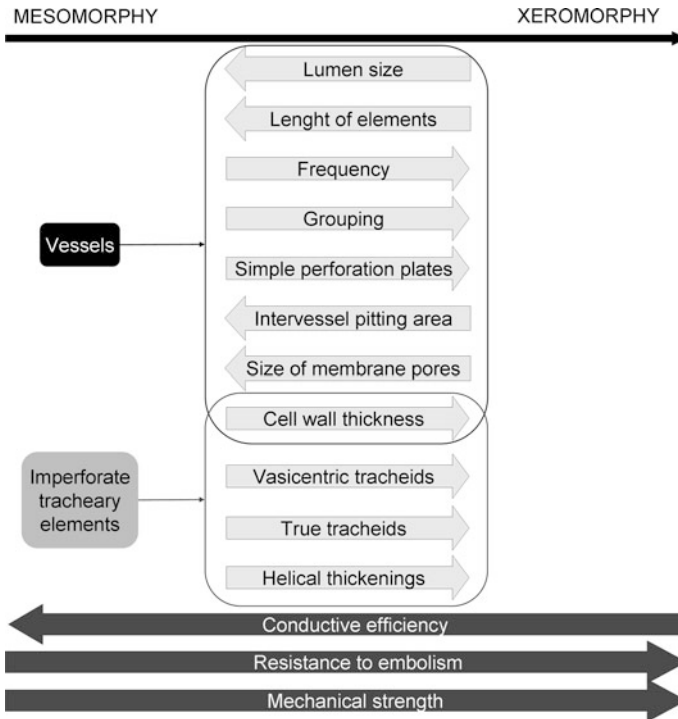


Fig. 2.3 Schematic view of the direct and inverse proportionality between the main attributes of xylem elements and functional traits of efficiency/safety against embolism and implosion. Different combinations of these traits might play a role in species geographical distribution in mesic and xeric areas

Sperry et al. 2006). The porosity of pit membranes between adjacent vessels might be designed to solve the conflict between the functional requirements to minimise vascular resistance, which favours thin, porous membranes, and to limit embolism spreading, which requires robust membranes and smaller pores. Indeed, a decrease in total pit area per vessel causes a decrease in the average size of membrane pore, and hence an increase in safety from cavitation (Wheeler et al. 2005). In the light of these considerations, traits such as pit membrane permeability, pit membrane area between vessels and pore size can be considered important adaptive traits potentially driving ecological differences between species (Jansen et al. 2009).

Vessel grouping is another phenomenon, favouring safety, common in the arid desert and Mediterranean flora (Carlquist 1989). Recently, the first empirical evidence of the positive relation between vessel grouping and cavitation resistance has been reported for seven *Acer* species (Lens et al. 2011). If a particular vessel in a group embolises, the surrounding active vessels maintain the three-dimensional conductive pathway. Almost the same role can be played by vasicentric tracheids which are distributed in sheaths around the vessels, especially in woods of

semiarid ecosystems. According to Carlquist (1989), such tracheids have been “re-invented” in clades that have evolved more specialised woods where primitive tracheids have been supplanted by non-conducting fibre elements. The other mode of tracheid reinvention is represented by “vascular tracheids” that are formed only at the end of growth ring (Carlquist 1989). However, as in the case of very narrow vessels, the conductive rate through tracheids is extremely low but this is presumably not a problem since low transpiration and low conductive rates may be expected during periods of drought.

Another common property of woods from xeric floras is the occurrence of helical thickening in vessels.

Thickness and density of vessel sculpturing in *Acer* species has been shown to be correlated with resistance to cavitation (Lens et al. 2011). Apart from the increase of mechanical strength, helical sculpturing has a role in preventing the incidence and spreading of cavitation, because it increases wall surface and thereby water bonding to the surface (Carlquist 1989; Kohonen and Helland 2009). In woods of xeric environments, helical thickenings increase mechanical strength which can be also guaranteed by the presence of vessels and imperforate tracheary elements with very thick walls and narrow lumen (Sperry 2003).

Besides, other features, such as length of conduit elements, play an important role in defining efficiency of water transport and resistance to negative pressures, but, being correlated to vessel lumen diameter, are less studied.

In general, adaptation to drought can be achieved by means of various combinations of wood anatomical traits. The lack or the low expression of a specific trait can be compensated by the occurrence of other features addressed to the same goal; for example, greater wall thickness in any species may compensate for a lesser amount of imperforate tracheary elements when vessel frequency is very high as shown in *Cistus monspeliensis* L. by De Micco et al. (2008). Moreover, wood adaptive attributes can be considered additive (Carlquist 1989); such a property would explain species distribution along gradients of water availability in semiarid ecosystems such as Mediterranean types. In these ecosystems, moving from more mesic to arid areas there is a change in habit from deciduous to evergreen and seasonally dimorphic/drought deciduous that is also accompanied by an increasing occurrence of attributes in wood anatomy allowing adaptation to drought conditions (De Micco et al. 2008; De Micco and Aronne 2009).

Among the numerous wood anatomical attributes, two groups can be distinguished: those quite conserved and stable are mainly qualitative traits (e.g. porosity and morphology of xylem elements); the others regard quantitative attributes which are characterised by high plasticity under changing environmental conditions. Actually, even within the same plant, specific wood anatomical traits, such as vessel size and cell walls thickness, can quantitatively vary according to the season in a sort of seasonal dimorphism leading to the development of summer tree rings safer than winter tree rings as recently shown in the shrub *Cistus incanus* (De Micco and Aronne 2009). Hence, this high plasticity of specific wood anatomical traits is responsible for their intra-annual variability that can be linked with environmental fluctuations and used as proxy of growth cycles.

2.7 Some Adaptive Traits at the Root Level

A well-established response of plants to drought is the modification of the root/shoot dry matter ratio which tips in favour of the former. This determines an increase of root density over leaf area, a phenomenon bringing the advantages already discussed for seedlings. Adaptive strategies to drought are based also on many other traits which regard both root architecture and anatomy.

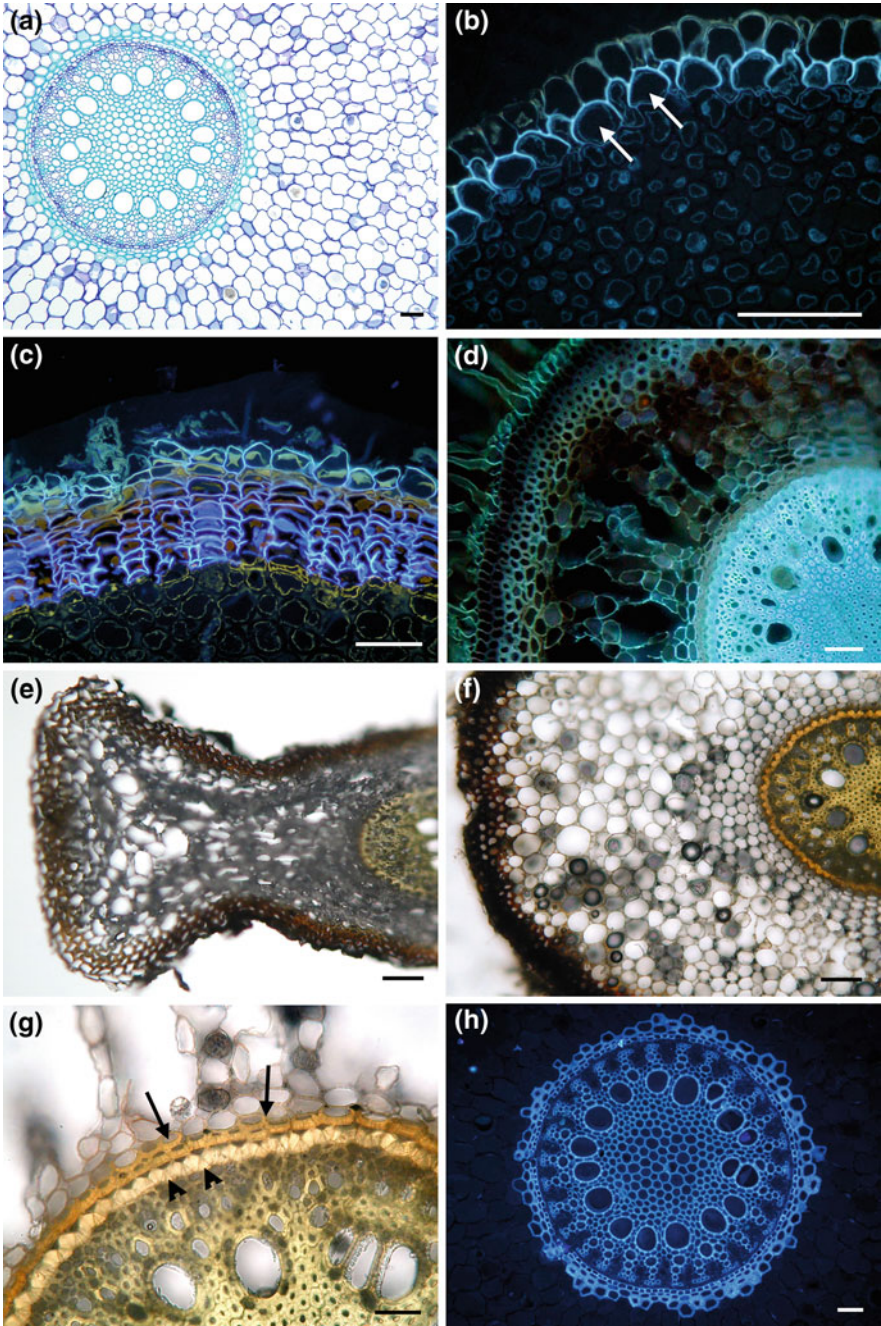
At the beginning of the twentieth century, there was a common idea that roots of arid environments had to grow very deep in the soil to withstand long periods of severe drought. Later it has been demonstrated that there is a variety of adaptive strategies. Among these, three types of root architecture are described for perennial species. The first type, typical of succulent species, is made of shallow roots, not growing deeper than about 20 cm. The second type comprises both long roots growing parallel to each other, a few metres deep, and shallow adventitious roots designed for quick uptake of water after brief precipitations. The third system is characterised by many lateral roots about 1 m long, accompanied by very long taproots which can develop tens of metres long (Phillips 1963; Kummerow 1981). Such taproots reach very deep layers of soil where phreatic water is permanently present, thus avoiding seasonal fluctuations of water availability. In some species such as *Agave deserti* Engelm, the root system is made of established and rain-induced roots which are produced on established ones within a few hours of rains and are shed when the soil dries (Hunt et al. 1987). Although representing an additional production cost for the plant, rain-induced roots confer an adaptive advantage in desert environments since they are characterised by higher hydraulic conductivity than established ones. In semiarid environments, both root systems characterised by shallow and deep roots coexist (Kummerow 1981). Moreover, in the Chilean matorral and Californian chaparral, some species have been reported to be strictly interconnected to each other (Kummerow 1981). Although main types of root architecture have been described, it is also commonly accepted that the distribution of roots throughout a soil is largely affected by moisture content of the superficial layers more than of deeper layers (Blum 1996).

As regards inner structure, the adaptive function of specific root attributes is commonly accepted even if consistent evolutionary trends among plant groups and along mesic–xeric gradients are less investigated than in stems. Xeromorphism at root level relies on the presence of traits linked to the regulation of water uptake, the avoidance of water loss and the formation of water-storage tissues (Fig. 2.4a).

The presence of small diameter roots under reduced water availability is considered as a strategy aimed to maximise absorptive surfaces, thus increasing rates of water and nutrient uptake (Eissenstat 1992). The control of water loss is also exerted by the presence of specialised tissues such as a rhizodermis with thickened outer cell walls, a well-developed suberised exodermis, often accompanied by many layers of thin- or thick-walled suberised cells (Fig. 2.4b–d). The presence of suberised layers of cells, at the periphery of the root, represents an important

mechanism not only in the selection of nutrient uptake but especially because it regulates the inverse flux of water that, in extreme drought conditions, could pass from the root to the soil (Hose et al. 2001). It has been experimentally shown that the limitation imposed to root radial hydraulic conductivity by suberized layers increases during root development and during soil drying (North and Nobel 1995). After crossing epidermis and exodermis, water has to pass through the cortical parenchyma. The reduced number of cortical layers is considered of adaptive advantage under drought conditions because it shortens the way between the soil and the stele favouring quick radial water transport (Fahn 1964). However, considering the inverse flux of water under drought conditions, the rupture of cortical cells is considered a strategy to create cortical lacunae which interrupt the radial pathway for water movement from the stele to the soil (Fig. 2.4d) (Robards et al. 1979). In *Agave deserti* Engelm, the development of intercellular cortical lacunae has been shown to reduce radial conductivity across root cortex in response to soil drying (North and Nobel 1995). The opening of large fractures, especially in the outermost cortical layers, could also open a path for easy water release as found in *Opuntia ficus-indica* (L.) Miller under drying soil conditions (North and Nobel 1996). Recently, it has been also speculated that the presence of cortical lacunae is beneficial under drought conditions because it reduces root metabolic costs by transforming living cortical cells in air volume (Zhu et al. 2010). However, the formation of cortical lacunae can weaken root mechanical strength, making it more vulnerable in soils prone to swelling-shrinkage cycles consequent to frequent fluctuations in water availability (Striker et al. 2007). This weakening of root strength can be counterbalanced by the general finding of increased development of lignified tissues with cells characterised by thicker walls in various structures (e.g. additional sclerenchyma, increased vascular system, lignified pith) (Fig. 2.4d, h) (Mostajeran and Rahimi-Eichi 2008). The shrinkage of cortical parenchyma cells in roots growing under drought conditions is a common finding (Peña-Valdivia et al. 2010); however this phenomenon can be considered reversible especially when cell walls are reinforced by the deposition of suberin as shown in *Lygeum* spp. (Fig. 2.4e, f).

The development of endodermis with thicker cell walls and the formation of additional layers of cells with suberised walls around the stele (Fig. 2.4g, h) are considered means to prevent the desiccation of meristematic tissues such as the pericycle and other tissues inside the stele (North and Nobel 1992). Water deficit induces the formation of an higher number of endodermal cells with Casparian bands closer to root tip in *Opuntia ficus-indica* (North and Nobel 1996). This phenomenon is accompanied by other anatomical changes, including the formation of a higher number of suberised peridermal layers (phellem) which reduce water permeability of cortex as measured also in other species (Schönherr and Ziegler 1980). The relevance of the apoplastic barriers in controlling water flow depends on root developmental stage: in young unstressed roots, most of the radial hydraulic resistance is more evenly distributed across cortical layers, while in water-stressed old plants it is mainly due to exodermis and endodermis (Steudle 2000).



- ◀ **Fig. 2.4** Light (a, e–g) and epi-fluorescence (b–d, h) microscopy views of root cross-sections showing anatomical traits for resistance to drought: **a.** Water-storage parenchyma in *Asparagus acutifolius* L.; **b.** Suberised exodermis (arrows) in *Primula palinuri* Petagna; **c.** Suberised subepidermal cells in *Primula palinuri* Petagna; **d.** Suberised rhizodermis, thickened subepidermal cells and cortical lacunae in *Lygeum* spp.; **e, f.** Cortical parenchyma cells respectively shrunk and recovered after rewetting in *Lygeum* spp.; **g.** Endodermis (arrowheads) with thickened cell walls and additional layers of thick-walled cells (arrows) around the stele in *Lygeum* spp.; **h.** Additional layers of cells with thickened walls around the stele and lignified pith in *Asparagus acutifolius* L. Bars correspond to 100 μ m

Once the water has entered the stele, it needs to be transported efficiently throughout the plant to maintain a continuous water supply to the leaves. In xeric conditions, plants have evolved morpho-functional traits that change root hydraulic conductance as a mechanism for regulating transpiration complementary to those played by aerial organs (Trubat et al. 2006). It is recognised that the efficiency of water transport and the hydraulic safety of vascular system are fundamental for the survival of plants in arid environments. Indeed, in the context of climate changes, considering an increase in the frequency of drought and of overall higher temperatures, vegetation of arid and semiarid environments have to cope with increased xylem vessel cavitation. Within this scenario, in these environments, the adaptive capacity of species is strictly linked to the characteristics of their xylem in the root as in the stem. Indeed, within the same plant, conductivity shows strong variability between different root types growing with different directions and at different depths, a phenomenon which should optimise water flow according to changing water availability (Fahn 1964; De Micco and Aronne 2010).

As final consideration, we may emphasise that plants showing different root architecture and various combinations of anatomical traits allowing adaptation to drought coexist in the same arid and semiarid environments. Moreover, it has been shown that water stress triggers a wide variety of root morphological and anatomical responses: various traits are adjusted with different intensities and trends in different species and even in different cultivars within species (Shao et al. 2008; Peña-Valdivia et al. 2010). A comprehensive understanding of the different mechanisms of root adaptation to water deficit remains a valuable goal because roots can be considered sensors that detect changes of water availability in soil and influence the resistance to drought at the whole plant level.

2.8 Conclusion

The importance of the strict relationship between structure and function in plants has been recently recalled, considering that major metabolic and physiological processes are ultimately regulated by the physics of the plant's structure (Brodrribb 2009). The coordination between structure and function in plants is apparent when considering ecological trends in the evolution of morpho-anatomical traits. Such a

coordination is especially strong under stressful conditions, when structural investment is regulated for reaching optimal carbon allocation to guarantee growth, survival and reproduction. A wide variation of morphological and anatomical traits accompanies plants of different ecosystems in a sort of harmonisation between plant response and environmental constraints to improve adaptation.

Adaptation to drought is based on many morpho-anatomical traits expressed in different organs at different levels. Since they are not mutually exclusive, different combinations of traits lead to different adaptive strategies. Moreover, various degrees of adaptation can coexist, allowing quite different biological forms to share the same environment. Survival against drought also relies on the capacity of plants to simultaneously cope with other stress factors, such as predation and excess radiation.

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