

## *Ecophysiological Constraints on Plant Responses in a Restoration Setting*

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Plant restoration activities can be positively or negatively impacted by changes in the abiotic environment, such as changes in aboveground microclimate, soil structure, or soil nutrients, from that of the predisturbance condition. Through an understanding of the ecophysiological and biochemical mechanisms of adaptation that describe the potential for a plant to persist in a habitat or location, one can better assess the impact of an altered environment on future plant performance and restoration outcomes. This feature of plants is often referred to as *tolerance*. Plant species differ in their capacities to tolerate different biotic and abiotic stressors and this tolerance can be the basis for why some species are capable of reestablishing themselves quickly in a restoration setting, whereas the reestablishment of other species proceeds at a much slower rate, if at all. This chapter focuses on two basic ecophysiological themes that relate to the capacity to become reestablished and tolerate variations in abiotic conditions: (1) light and energy relations in aboveground processes, and (2) water and nutrient relations in belowground processes. We describe the basic requirements of plants, as well as the types of stressors and plant responses associated with these themes. We also describe specific examples that relate to needs required for mitigation in a restoration context, where mitigation could refer to improving factors that impact the reestablishment of particular species or of an ecosystem process.

It is important to recognize that in some cases the physical environment (aerial microclimate or soil conditions) may have been so extensively modified by a previous disturbance or land-use activity that plant reestablishment may not be possible in the short term, because anthropogenic activity has irreversibly altered the environment (Suding et al. 2004). In such cases, reestablishment of historically present species may not be possible or practical. An example of such an extreme would include reestablishment of particular native species in portions of the north central United States (e.g., Iowa and Indiana) where extensive belowground tile systems were installed a century ago to convert swamp regions into fertile agricultural lands (Prince 1997). A second example is the portions of Australia where historical conversion of forest to agricultural lands has resulted in salt migration to the soil surface that makes plant establishment difficult (Cocks 2003; Eberbach 2003). Lastly, tailings that have accumulated from mining activities in the western United States, as well as other places in the world, have resulted in soils that either are so contaminated with toxic elements that no species can persist or simply lack the basic soil structure that allows plants to get established

(Shaw 1990). Nonetheless, efforts to restore vegetation to these significantly altered ecosystems can and should benefit from understanding the ecophysiological principles that allow tolerance of stressors associated with these altered systems.

### Light and Energy Balance: Aboveground Processes

Photosynthesis is the basic process whereby the simultaneous capture of carbon dioxide from the atmosphere and photons from the sun results in the formation of the organic compounds used as the building blocks of growth in plants. In general, neither of these two essential substrates for photosynthesis differs in concentration between pristine habitats and those disturbed sites undergoing restoration. What may differ, though, is the light profile within the vegetation, which becomes relevant if plant species vary in their tolerances of light levels. In this regard, it is prudent to recognize that different species have quite different tolerances in the degree to which their leaves will persist when exposed to full sunlight conditions. In addition, plants with different photosynthetic pathways may have a differential capacity to utilize light resources for photosynthetic carbon gain, especially when considering a restoration setting involving herbaceous species. Three major photosynthetic pathways exist:  $C_3$ ,  $C_4$ , and Crassulacean Acid Metabolism (CAM) (Farquhar et al. 1989; Sage and Monson 1999; Taiz and Zieger 1999). However, owing to slow growth rates and relatively low abundances of CAM species worldwide, only  $C_3$  and  $C_4$  photosynthesis are particularly relevant to restoration activities in most cases. These two pathways share similar biochemical and structural features to capture the sun's photons, and as a result produce ATP and NADPH to drive the photosynthetic reduction of  $CO_2$  to form sugars. Where the two pathways differ is in how carbon dioxide is fixed, which results in  $C_4$  taxa typically having a greater capacity to fix carbon than  $C_3$  taxa in the same environment, particularly in warm and high-light conditions.

#### $C_3$ Versus $C_4$ Photosynthesis

$C_3$  photosynthesis is the ancestral pathway common to all taxonomic lines (Ehleringer and Monson 1993; Sage and Monson 1999). During photosynthesis, carbon dioxide diffuses into leaves through stomata and then diffuses to chloroplasts where it combines with ribulose biphosphate (a 5-C molecule) via ribulose biphosphate carboxylase (Rubisco) to form two molecules of phosphoglycerate (a 3-C molecule), which can then be transformed into usable sugar molecules. However, Rubisco can also combine ribulose biphosphate with atmospheric oxygen to form one molecule of phosphoglycerate and one molecule of glycolate. The glycolate produced cannot be directly transformed into a usable sugar and must thereby be processed through a biochemical "salvage" pathway referred to as *photorespiration* that results ultimately in the generation of carbon dioxide. Although Rubisco has a much greater affinity for  $CO_2$  than  $O_2$ , photorespiration reduces overall photosynthetic carbon gain in  $C_3$  plants in proportion to the ratio of ambient  $CO_2$  vs.  $O_2$  (the two competing substrates for Rubisco). Under current atmospheric conditions of 0.037%  $CO_2$  and 21%  $O_2$ , the reduction of net carbon gain is about 35% and this inefficiency increases even more as temperatures increase.

$C_4$  photosynthesis appears to have evolved multiple times and most likely as a result of low carbon dioxide conditions (Ehleringer et al. 1997; Sage and Monson 1999). It is a modifica-

tion of the  $C_3$  pathway that spatially restricts the  $C_3$  photosynthetic cycle to the interior portions of a leaf, such as bundle sheath cells as shown in Figure 3.1. In the outer cells of  $C_4$  pathway leaves, PEP carboxylase takes up carbon dioxide (actually bicarbonate) at a high rate to produce oxaloacetate (a 4-C molecule). The 4-C molecules diffuse into the interior bundle sheath cells where a decarboxylation reaction occurs and the resulting carbon dioxide is fixed into organic matter using the  $C_3$  photosynthetic cycle. Because of the greater enzymatic activity of PEP carboxylase relative to Rubisco, the PEP carboxylation activity results in a pump-like mechanism that creates high carbon dioxide concentrations at the leaf interior where the Rubisco portion of the photosynthetic cycle takes place. Thus, photorespiratory carbon dioxide loss does not occur in  $C_4$  plants.

$C_4$  plants tend to have a higher photosynthetic rate relative to  $C_3$  plants because they lack photorespiratory activity. They usually also have higher growth rates, particularly in warm climates. Not surprisingly, many of the most common invasive species on disturbed sites in temperate to tropical regions possess  $C_4$  photosynthesis. Indeed, some of the world's worst weeds are  $C_4$  taxa (Sage and Monson 1999). Thus, in any restoration activity, it is important to recognize the often-superior competitive ability of  $C_4$  taxa, especially if the objective is to reestablish  $C_3$ , nonwoody vegetation. This competitive advantage comes from the ability of  $C_4$  plants to take advantage of today's relatively low carbon dioxide atmosphere. Additionally, on open, disturbed sites, warm microclimatic conditions, especially during the summer, also favor  $C_4$  taxa over  $C_3$  taxa, because the high temperatures at the soil surface tend to increase photorespiration and reduce net photosynthetic carbon gain in  $C_3$  taxa. Ironically, with human burning of fossils fuels resulting in increased atmospheric carbon dioxide levels, it is pos-

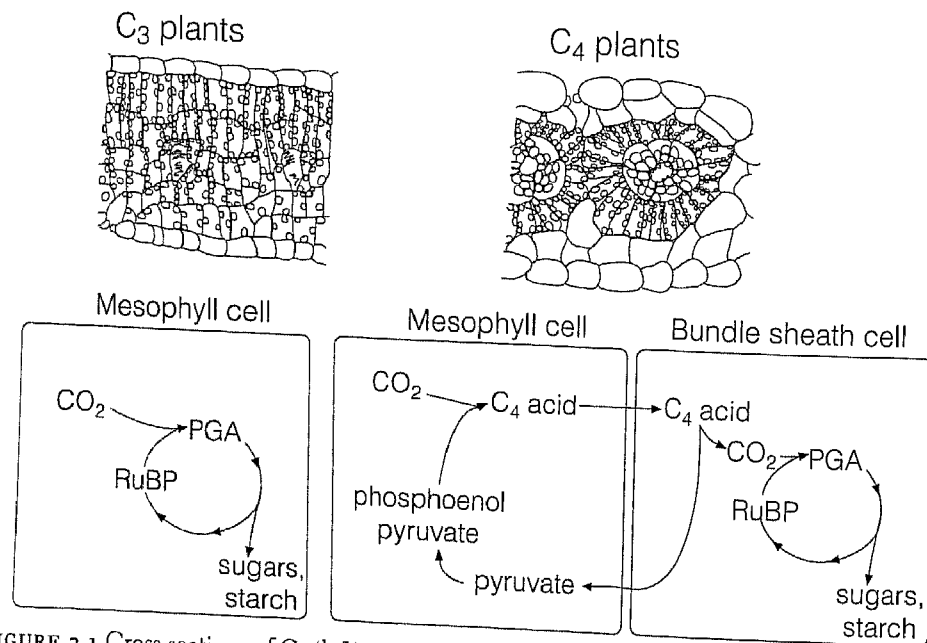


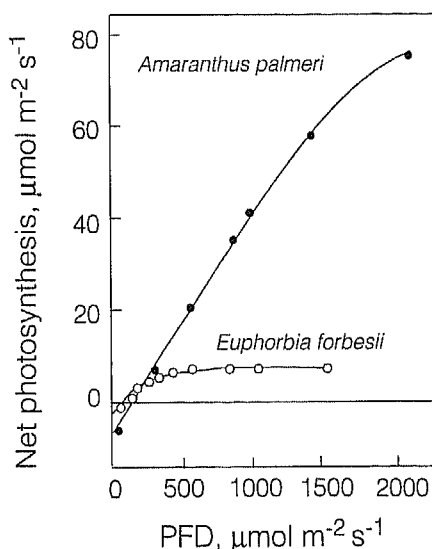
FIGURE 3.1 Cross-sections of  $C_3$  (left) and  $C_4$  (right) plant leaves and schematic representations for each photosynthetic pathway showing the basic differences in carbon dioxide fixation. Note that  $C_4$  plants have the  $C_3$  photosynthetic pathway, but it is restricted to interior cells.

sible that the competitive advantage of  $C_4$  over  $C_3$  taxa today will diminish in the next century (Ehleringer et al. 2004).

### High Light as a Stressor

Photosynthetic uptake of carbon dioxide in leaves of both  $C_3$  and  $C_4$  taxa increases with increasing sunlight. This is expected since two of the essential substrates for photosynthetic carbon gain are the ATP and NADPH generated by the light reactions of photosynthesis. Eventually a plateau is reached where there is no further increase in photosynthetic carbon dioxide uptake with increasing light levels (Figure 3.2). While several factors determine the light level at which photosynthesis does not increase further, the two most common features not associated with the light reactions of photosynthesis are stomatal conductance and leaf protein content (typically estimated by leaf nitrogen content). Each of these factors responds to the plant's growth environment, with the upper limits often well correlated with leaf life expectancy (Reich et al. 1999). Stomatal conductance is a measure of how wide open the stomatal pores are that allow the inward diffusion of carbon dioxide for photosynthesis. Water stress (described below) tends to result in reduced stomatal conductance, reduced photosynthetic rates, and for the light saturation point of photosynthesis to occur at lower light levels.

The same response applies for protein content. Since the majority of leaf protein is associated with photosynthetic activity, reduction in leaf protein content will reduce photosynthetic rates, particularly under water stress. The successful establishment of plants in a



**FIGURE 3.2** The response of photosynthesis (as measured by carbon dioxide fixation rate) to changes in the sunlight (photon fluxdensity, PFD) for two  $C_4$  species adapted to different light conditions. *Amaranthus palmeri* is a desert annual, adapted to high-light environments. *Euphorbia forbesii* is a shade-adapted species from the forests of Hawaii. Note the correlation between maximum photosynthetic rate and sunlight level at which photosynthesis saturates. Modified from Pearcy and Ehleringer (1984).

restoration setting will depend on both a sufficient supply of nutrient resources to build plant tissues and support photosynthetic activities and on sufficient amounts of water supplied to leaves to maintain stomatal conductance for the inward diffusion of carbon dioxide.

Exposure to light levels far in excess of those experienced during development, such as for greenhouse plants transplanted to the field or for shade plants exposed to higher light levels than they might be exposed to under more natural conditions, can create a significant challenge for plants in a restoration context. That is, once photosynthetic light saturation is achieved, as shown in Figure 3.2, high light levels can become a stressor (Demmig-Adams 1998), inhibiting plant establishment and potentially causing leaf mortality. Photosynthetic light saturation can occur at light levels that are as little as 5%–20% of midday sunlight for leaves of understory plants or shade leaves of large trees. High light can also become a stressor if the photosynthetic apparatus generates too much ATP and NADPH (the products of the light reactions) and thus exceeds the ability of these substrates to be utilized in the dark reactions. In this case, carbon dioxide availability for the dark reactions generally limits overall photosynthesis (often due to stomatal diffusion limitation).

Another type of light stress is photoinhibition, a process that can occur when leaves are exposed to sunlight levels that are above the light saturation point, as shown in Figure 3.2 (Adir et al. 2003; Demmig-Adams 2003). The excess energy from the light reactions of photosynthesis oxidizes cellular components unless a mechanism is available to dissipate this energy. The effects of photoinhibition can include a reduction in photosynthetic capacity and loss of chlorophyll (bleaching). There are protective mechanisms within a leaf to minimize the potential damage caused by excess light availability (Demmig-Adams 1998; Adir et al. 2003; Adams et al. 2004), including the xanthophyll cycle, where excessive energy is dissipated without causing chlorophyll pigment loss (Demmig-Adams 2003). However, sometimes the light level exposure is too high for protection to be effective, as for plants that naturally grow in shade but are exposed to high light during transplanting, or plants exposed to water stresses and high temperature conditions. Here, exposure to high light does constitute a stress that results in photoinhibition and degradation of protein components of the photosynthetic apparatus (Demmig-Adams 1998; Jiao et al. 2004). When leaves of low-light adapted or acclimated plants are exposed to high light levels, the photoinhibitory effects often result in a photosynthetic light response curve (e.g., Figure 3.2) in which photosynthetic rates actually decline at higher light levels, such as in the case of some tropical tree species (Langenheim et al. 1984).

### *Microclimatic Stressors*

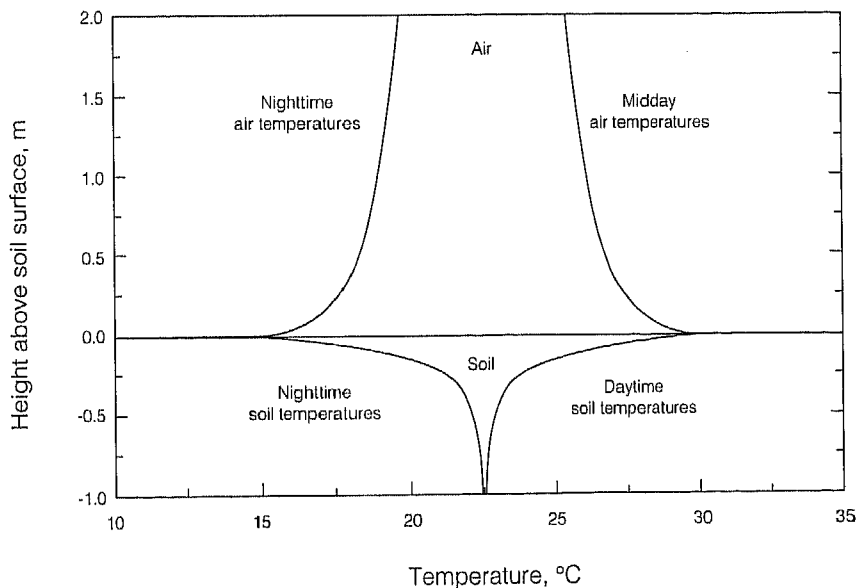
Microclimate variation contributes greatly to the small-scale topographic heterogeneity that plays an important role in the ecology of both plant and animal systems (Larkin et al., this volume). For example, plants may experience a microclimate in which the air and leaf temperatures in the 0.5 m above the soil surface can be significantly hotter during the day and significantly cooler at night than those experienced at greater heights. Microclimatic conditions such as these can be considered stressors because they can result in tissue desiccation, protein degradation, high respiration, and other biochemical dysfunctions. The vicinity of the soil surface is the harshest of environments because plant tissues are potentially exposed to both contrasting stressors, especially during the sensitive period of plant establishment.

During the day, the sun's energy is absorbed by the soil surface, potentially raising the temperature of the soil surface to particularly high levels on sunny days. A portion of the surface heat is transferred to the air by convection, raising the air temperature nearest the surface, and creating an air temperature profile that is hottest near the soil surface (Figure 3.3). Now consider two plants of differing heights with leaves in the same microclimate profile. Metabolic rates, such as rates of photosynthesis, respiration, and transpiration, are a function of leaf temperature. So, we would expect the highest transpiration rates and respiration rates to occur in leaves nearest the soil surface. This poses a thermal stress, especially during seedling establishment, since the rooting depths, water transport capacities, and carbon reserves are likely to be lower in young, establishing plants than in mature, established plants. The impact of a soil-surface microclimate stress can be even greater under certain conditions and ultimately result in mortality. This is because leaf temperatures often can be elevated 1°–10°C above air temperatures.

The difference between leaf and air temperatures will depend on the net leaf energy balance, qualitatively described as:

$$\text{absorbed solar} + \text{infrared radiation} = \text{infrared reradiation} + \text{convection} + \text{transpiration},$$

where the solar and infrared radiation absorbed by a leaf represent the energy gained by a leaf that must, in turn, be dissipated through reradiation, convection, and transpiration. Leaf temperatures will rise until the energy absorbed by a leaf equals the amount of energy dissipated by these three processes. Thus, leaf temperatures will normally exceed air temperatures by an amount reflecting the net energy gain. If leaves are able to transpire at a high rate or if leaves are small so that convection rates are potentially high, then leaf temperatures may be similar to air temperatures. However, seedlings with large leaves near the surface, or leaves not able



**FIGURE 3.3** Microclimate profile of air temperatures, a function of height above the soil surface during midday and nighttime conditions.

to dissipate heat through transpirational cooling, will have higher temperatures than that of the adjacent air. Over time, these elevated leaf temperatures can result in dehydration and leaf mortality of young seedlings getting established. Not surprisingly there is strong selective pressure for leaf tissues to grow beyond the soil surface in order to reduce transpiration rates and reduce respiratory carbon losses. Having leaves even 2–3 cm above the soil surface is enough to greatly reduce transpiration rates. This is one reason why screens and other shading structures are so important in promoting establishment of seedlings in a restoration setting: they reduce the net energy load incident on the seedling.

At the critical stage of seedling establishment, spring nighttime conditions at the soil surface in some habitats can also represent a thermal stress. This is because at night the coldest part of the microclimatic profile on a bare surface is at the soil surface (Figure 3.3). Here energy is lost by reradiation; the radiative loss from the soil is greater than the absorption of infrared radiation from a nighttime sky, resulting in falling soil and leaf temperatures at the soil surface. During early spring conditions in temperate regions, frost develops at the soil surface as a result of this thermal imbalance. Again, emerging seedling tissues at the soil surface are most vulnerable to this freezing stress, which can often be avoided by leaf and bud tissues that are elevated 5–10 cm above the soil surface. Increasing wind speed (and therefore convective heat transfer to the surface) will reduce the magnitude of the cooling effect in the microclimatic profile, but often the air is most stable at night and so wind speeds are typically low.

### Water and Nutrients: Belowground Processes

Many terrestrial restoration settings are associated with significantly altered soil conditions. These include disturbances that have completely replaced surface soils (such as in mining operations); changes in the composition of soil components (such as the addition of clay particles or the loss of organic matter); altered bulk soil densities (such as those associated with compaction); losses of microbes (such as mycorrhizae and nitrogen-fixing bacteria); and the addition of contaminants (such as heavy metals from a smelting operation). Such activities may affect both the availability and distribution of belowground resources and alter the ability of plants to acquire the critical resources essential for growth. The extent to which the belowground environment has changed can strongly dictate the potential for recovery owing to highly sensitive nutrient and water dependencies of vegetation. In many cases belowground alterations, even subtle structural changes in soil compaction or increases in some elements, will preclude native ecosystem restoration. In contrast to these terrestrial cases, the restoration challenge of wetland ecosystems is often increased surface salinities that alter plant/water relations, thereby reducing the likelihood of plant establishment (Handa and Jeffrie, 2000; Zedler et al. 2003).

### *Tolerances Associated with Minerals in Soils*

Most plants take up nutrients through their roots, specifically through single-celled roots that probe the aqueous soil environment surrounding a root. A common practice in restoration settings is to surface supply some of the critical macronutrients for plant growth—particularly calcium, iron, magnesium, nitrogen, phosphorus, and sulfur—as fertilizer (Bloomfield et al. 1982; Cione et al. 2002; Bradshaw 2004). Mineral nutrients, such as nitrate and ammonium,

are highly soluble in soil water and have a relatively high diffusion rate in a water solution, facilitating their uptake. The uptake of nutrients by roots is an active, energy-dependent process, in contrast to the uptake of water, which is a largely passive process. The uptake of minerals is facilitated by their solubilities, but this also makes these same minerals highly leachable from soils, especially in high-precipitation environments. Of the mineral elements extracted from the soil, nitrogen is the element needed in highest concentration within leaves as an essential component of proteins, pigments, and nucleic acids, which explains why high additions of nitrogen are particularly important (Bradshaw 1983, 1984). Some pioneer species that readily establish in restoration settings have the ability to produce their own nutrient nitrogen, avoiding the requirement that nitrogen be supplied in the soil. These plants are known as nitrogen-fixers, and they accumulate organic nitrogen through nitrogen fixation in association with a bacterial symbiont.

Often the surface area and lateral extension of a root hair are inadequate to provide sufficient exposure for roots to all essential nutrients available in the soil. This is particularly true for phosphorus, an essential element that has a low solubility and low diffusivity in the soil water solution. Thus, fungal associations are essential to establishment and nutrient uptake by most higher plants (Lambers et al. 1998; Chapin et al. 2002; Fitter and Hay 2002). Fungal hyphae are able to extend up to several orders of magnitude farther away from the root than can root hairs, creating such an effective mineral-uptake situation that many plants do not grow or have significantly reduced growth rates in the absence of their symbiotic mycorrhizal partners. Reclamation studies have provided some of the strongest evidence of the critical roles of mycorrhizal associations for the establishment of plants in a restoration setting (Allen 1991; Caravaca et al. 2003; Querejeta et al. 2003). Disturbance processes (e.g., strip mining activities) that precede the restoration phase often kill or remove mycorrhizal spores, requiring that seeds or transplanted seedlings on restoration sites be provided a fungal inoculum.

Terrestrial restoration settings often differ from more natural habitats by an abundance of toxic elements in the soil (Bradshaw 1983, 1984, 2004; Shaw 1990). The three most common mineral-related challenges to restoration are highly saline soils (discussed later), soils with altered pH levels, and high-metal-toxicity soils. The physiological impacts of these three stressors on plants are as different as the solutions applied in a restoration setting. Interestingly, there are often populations or taxa adapted to these unusual soil regimes, with the tolerance mechanism being either as accumulators or excluders. Studies of genetic variation for tolerance to heavy metals have also been extremely insightful. For example, the ability of different grass species to invade and colonize mine spoils is related to genetic variation in non-related features (Shaw 1990; MacNair 1993).

Altered soil pH levels have multiple effects on plant roots and tolerances are fairly general. Directly, pH can have a negative impact through the effect of excess  $H^+$  or  $OH^-$  on membrane integrity and ion uptake systems. Indirectly, pH can influence the solubility of metals that are toxic to plants. In contrast, heavy-metal tolerance in plants is often fairly specific and limited to a single metal, rather than species being tolerant of a wide range of heavy metals (Shaw 1990). For instance, aluminum toxicity ( $Al^{3+}$ ) occurs in acidic soils and is a major constraint on plant growth in all but calcifuge ("chalk-escaping," "acid-loving") species, which hyper-accumulate aluminum (Jansen et al. 2002). The presence of  $Al^{3+}$  generally reduces root elongation and uptake rates of essential cations such as calcium and magnesium

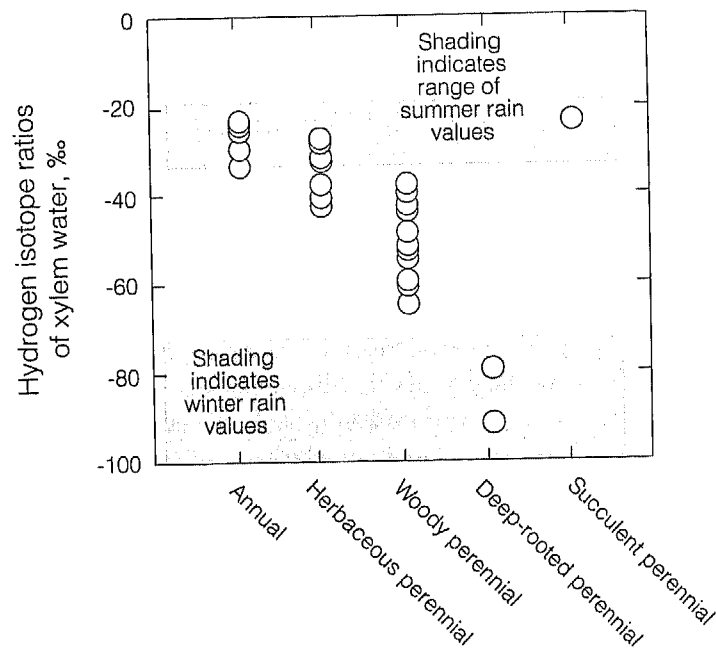


(Fuente-Martinez and Herrera-Estrella 1999). Zinc, cadmium, copper, iron, and other metals can have negative effects on plant metabolism when present in the soil in high concentrations (Shaw 1990; Rout and Das 2003). While much is known about whether tolerant species accumulate or avoid these metals, much less is known about the specific mechanisms of adaptation. In many cases, genotype-specific tolerance has been identified (MacNair 1993). However, there is limited molecular-level information on the mechanisms of tolerance and sensitivity to the metal among species (Pollard et al. 2002; Assuncao et al. 2003). This is a promising area of restoration ecology research (Fuente-Martinez and Herrera-Estrella 1999; Prasad and Freitas 2003). With the advances in genetics and the rise of new molecular tools such as micro-array analyses, it may soon be possible to pinpoint the specific molecular mechanism(s) that underlie the differing capabilities of species to persist in restoration settings with high soil metal concentrations.

### *Water Availability and Acquisition*

As with nutrients, the acquisition of water via belowground plant structures may be significantly altered in a restored habitat, owing to effects on both water availability and plant function (i.e., uptake and transport). The former is primarily a hydrological issue, influenced by soil properties, soil salinity, and climate (Sperry 2000). However, ecological effects, such as competition for water by neighboring plants (Ehleringer et al. 1991) and hydraulic redistribution of water from deep to shallow depths (Burgess et al. 1998), can also play an important role in altering the abundance of water resources. At the plant functional level, basic water uptake via roots is generally similar among most species, but the degrees of sensitivity to water limitation or water excess result in strongly varied responses. In natural systems, these differences can determine species distributions, and in restored systems may dictate a plant's ability to survive (Lambers et al. 1998). Basic rooting zones for water uptake differ between juvenile and adult plants for many perennial species (Donovan and Ehleringer 1992, 1994). Water acquisition can also be increased by mycorrhizal associations (found in many species) and by specific plant adaptations, such as hydraulic redistribution (generally defined as the movement of soil water through root systems from areas of high water availability to areas with lower water availability). Direct interception of moisture, such as fog, may also be critical to the establishment and maintenance of both tree and understory species in restoration of maritime terrestrial ecosystems (Burgess and Dawson 2004). Facilitating the maintenance or recovery of these biotic contributions to resource enhancement may be particularly crucial to restoration. For example, mycorrhizae abundance and their association with plants have been shown to be sensitive to nutrient supplementation (e.g., Egerton-Warburton and Allen 2000; Corkidi et al. 2002), a common practice in many restoration projects.

In a natural setting, plant species within the community often exhibit pronounced differences in effective rooting depth, with root density and effective rooting depth for water uptake varying within the soil profile (Dawson and Ehleringer 1998). This is illustrated in a study from the southwestern United States (Figure 3.4), which showed that the hydrogen isotope ratio of xylem water quantitatively reflects the depth in the soil from which water was derived. Summertime precipitation events resulted in upper-surface soil layers having a hydrogen isotope ratio of ca.  $-20\%$ , whereas wintertime precipitation events had ratios closer to ca.  $-90\%$ . Following a summer rain event, a large fraction of the vegetation did not use that



**FIGURE 3.4** Hydrogen isotope ratios of xylem water showing flux-weighted sources of water used by different annual and perennial species following strong summer rains in an arid land community of the Colorado Plateau in the southwestern United States. Modified from Ehleringer et al. (1991).

resource at all, or used only a portion of that new moisture as a transpiration source. Some species appeared to utilize soil water from surface and deeper soil layers equally, while others utilized moisture from recent summer rains or moisture from stored winter rains. Uptake of nitrogen from the soil and uptake of water need not come from the same rooting depths, as roots often exhibit resource acquisition specialization (Gebauer and Ehleringer 2000; Gebauer et al. 2002). Therefore, to increase the probability of restoration, it becomes critical to know both the actual rooting distributions as well as the depths from which plants extract nutrient and water resources.

#### *Water Limitation Stressors and Biotic Feedbacks*

Many studies underscore the importance of water availability and water acquisition in sustaining community properties and ecosystem processes (Chapin et al. 2002). Stresses owing to the lack of water constitute the majority of these examples, in part because water limitation, rather than water excess, is more prevalent as a stress and has a greater overall negative impact on productivity. This is due in great part to reduced carbon gain owing to stomatal closure, but water stress also decreases cellular and biochemical functions, and may negatively affect production by altering structural integrity. Thus, it comes as no surprise that reductions in water availability are easily capable of altering entire communities and ecosystems (such as found in stream diversions) (Naeem, this volume).

Following uptake, the transport of water through a plant is achieved by the presence of a water potential gradient from the site of water uptake (the soil) to the site of water loss (air). Commonly referred to as the soil-plant-air continuum (SPAC), this water transport mechanism is largely passive and driven by leaf-level transpiration, but because transport depends on the maintenance of this gradient, it is critical that management of each end-member (soil and air) accompany restoration of the transport medium (plant). Although the SPAC gradient is passively derived, the actual water fluxes are regulated by biotic factors, such as stomatal function and hydraulic architecture, and environmental factors, such as the leaf-to-air vapor pressure difference (Sperry 2000; Sperry et al. 2002).

Over the past decade or so, it has become clear that plant hydraulic architecture plays a fundamental role in governing the flow of water through plants. Given that water in the xylem is held under tension, low soil moisture availability and high evaporation demand can cause xylem within plant stems and roots to lose its conductive ability (i.e., cavitate), resulting in a disruption of water flow from the soil to the transpiring leaf surfaces. Different plant species have contrasting "vulnerability" curves, which describe the relationship between the plant water potential (a measure of water stress) and xylem cavitation (a measure of the plant's ability to move water between roots and leaves) (Figure 3.5). The xylem tissues transporting water between roots and shoots of plant species from more mesic habitats tend to cavitate at higher plant water potentials. The steep changes in cavitation that can occur over a narrow plant water potential range underscore the importance of maintaining adequate soil moisture, especially during the development and establishment of plants in a restored community.

Leaf stomata have the greatest effect on regulating water fluxes from plants (Boyer 1985). Stomata are sensitive to both plant water status and relative humidity, and generally close during periods of water stress (Kozlowski and Pallardy 2002; Sperry 2002). There is not a single stomatal response exhibited by all plants to humidity and water-deficit stresses, but rather stomatal pores of different species exhibit a wide range of sensitivities (Schulze and Caldwell 1994; Flexas et al. 2004). To the extent that plants in a restoration setting are influenced by

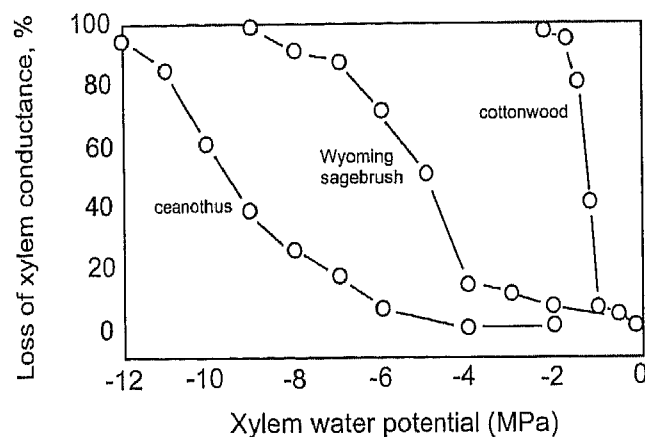


FIGURE 3.5 Vulnerability curves for three contrasting perennial species, showing loss of xylem conductance (xylem embolism) within the plant hydraulic system as a function of plant water potential. Modified from Sperry (2000).

pronounced diurnal or seasonal changes in humidity, both transpiration and photosynthesis rates will exhibit similar dynamics.

The differential rooting depths and sensitivities of stomata to humidity describe a fundamental water-relations challenge in restoring species within arid ecosystems. However, facilitation by shading to alter the microclimate can be a viable mechanism permitting species with differing rooting depths to become established. Maestre et al. (2001) described establishment of three desired shrub species (*Medicago arborea*, *Quercus coccifera*, and *Pistacia lentiscus*) in a Mediterranean restoration setting using the tussock of *Stipa tenacissima* (alpha grass) to facilitate establishment. It is likely that the differential use of soil moisture in surface and deeper soil layers by the grass and shrubs species, respectively, afforded an opportunity to both reduce the energy load on developing perennials and avoid competition for water at depth. With better knowledge of the differential rooting depths for water uptake of juvenile and adult perennials, it is possible to devise irrigation routines that increase the probability that perennials will become established in a restoration setting.

Variation of water availability, uptake, and transport, and the factors that affect them in restoration settings should follow patterns similar to those found under natural conditions. However, in light of the altered soil conditions typical of most projects, future restoration efforts would benefit from designs that explicitly incorporate the ecological importance of water relations, especially if the restoration objectives include efforts to recover some semblance of a normal or sustainable hydrological cycle. Indeed, because water availability is found repeatedly to be the resource most limiting to plant and ecosystem production (Chapin et al. 2002), recognizing the factors that govern water acquisition and transport is critical to restoration programs. What we don't know is which water-use traits are most difficult to recover in restoration programs and the degree to which water limitation influences the success of such efforts.

In recent years, the integration of ecophysiology and ecosystem ecology has promoted greater recognition of biotic feedbacks and their importance in sustaining water resources of ecosystems. The feedback framework has proved useful in elucidating the functional importance of species within a community, and identifying which species should be considered keystone from a functional perspective (Naeem, this volume). For example, fog-water interception and subsequent fog drip caused by redwood trees in the coastal forests of northwestern California have been shown to contribute substantial portions of the monthly water consumption by understory species (Dawson 1998). In the absence of these tall trees, summer soil moisture input for understory and shrub species would be nil since rainfall is absent during the summer in this ecosystem. Similarly, belowground water redistribution (hydraulic lift) by key tree species within eastern deciduous forests can enhance water availability in the upper soil layers, not only to the tree species itself, but also to many forb and herbaceous species in the tree's immediate proximity (Dawson 1993, 1996).

The absence of certain canopy trees has also been shown to increase leaf-to-air vapor pressure difference (recall Figure 3.4), which leads to increased transpiration of remaining plants and hastens drought and water stress in the system. This negative feedback can lead to slow but pronounced changes in species function and composition, ultimately resulting in type conversion to a relatively more xerophytic flora. The danger of such wholesale conversions is the possibility of a system reverting to an alternative state that may be resilient to restoration (Suding et al. 2004; Suding and Gross, this volume).

### Salinizing and Groundwater Shifts at Landscape Scales

Human activities affect the hydrology of entire river basins, and modern high-nutrient agricultural systems leach nutrients into groundwater systems. Perhaps nowhere is the hydrologically driven restoration challenge made clearer than in riparian zones. Existing ecological and agroecological systems can alter the salinity and water relations of a region such that restoration activities become challenged by an altered groundwater system (David et al. 1997; Kozlowski 2002; Cocks 2003; Eberback 2003). Conversely the tiling of waterlogged soils to drain marshes and other wetlands can alter the surface-groundwater dynamics irreversibly, to the extent that reestablishment of native communities becomes challenging, at best, or even impossible in the foreseeable future (Prince 1997).

One extreme example is the hydrologically driven restoration effort being made in western Australia, where both the challenges and the needs for restoration come face to face. Here the emergence of an extensive and highly productive wheat agriculture economy over the past century has replaced trees as the dominant plant type across the landscape (Bell 1999; Eberbach 2003). The forest-to-crop conversion during this time period has resulted in lower overall transpiration water fluxes across the landscape and, consequently, the rise of a saline groundwater table that now has the potential to jeopardize the stability of the wheat-driven economy. The rising saline water table also is likely to impact nearby salt-intolerant ecosystems (Cramer and Hobbs 2002).

In this instance, restoration for a mix of stable agricultural and natural vegetation requires lowering of the groundwater by the reintroduction of tree and perennial shrub species capable of drawing down the water table with their higher-than-wheat transpiration rates (Bell 1999). This would seem initially possible given the higher and more continuous transpiration rates by a dense forest stand. Cocks (2003) suggests that native biodiversity could be maintained by planting native trees with higher water-flux rates, which might be harvested periodically for bioenergy, wood products, and fuel. Yet salinity is also likely to reduce transpiration rates by perennial species in the short term, through its impact on water potential and stomatal conductance. Lefroy and Stirzaker (1999) predict that an extensive agroforestry effort would be required to manage the rising saline water tables. However, Hatton et al. (2003) recently concluded that even with extensive revegetation of the landscape, this effort might be inadequate to achieve a stable hydrogeochemical state given the magnitude of the historical crop-related activities. Clearly the situation in western Australia presents an exciting opportunity for restoration ecology, ecophysiological, and agricultural interests to work together to identify feasible alternatives and implement measures that will offer a sustainable future for the region.

### Summary

In the most ideal research, plant ecophysiological performance in a restored setting should be compared to that of reference plants in a natural ecosystem. Such studies provide the best opportunity for identifying performance expectations and ultimately attaining restoration goals. Thus, field-based comparative experiments are likely to offer the greatest insights for restoration, but in the past, this research tended to be time-intensive and technologically expensive—burdens that often precluded adequate sample sizes. However, improved techno-

logical capabilities over the past two decades, such as lightweight, portable, gas-exchange systems and compact data loggers, have made field ecophysiological assessments much more rapid and tractable. In addition, the use of proxies, such as stable isotopes that correlate well with long-term, integrated, ecophysiological function, provide a relatively easy means by which to monitor plant performance and predict restoration outcomes. Careful selection of which ecophysiological variables to monitor, and on which species, also helps to refine such studies—the variables should be based on the stresses that are expected to have the greatest impact on plant survival (e.g., water potential in an arid system or light response in a high-light environment) and for those species that best represent the reference ecosystem. Simple proxies, such as leaf area and stem elongation, can provide a decent integrated evaluation of stress response, but if certain ecosystem functions, such as water or carbon fluxes, are an objective of restoration, more sophisticated measurements may be necessary. In all cases, however, ecophysiological trait values that match the expected ranges seen in reference plants should be included in the performance standards of a restoration project.

It is clear that not all plant species exhibit the same sets of physiological response curves or stress tolerances. Thus, changes in the state of aboveground microclimate conditions and belowground resource states are likely to produce different species responses that might be predictable once the basic ecophysiological characteristics of the key species are understood. Restoration involves not only an understanding of the role of the physical environment as a driver of plant performance, but also an appreciation of the biotic feedbacks that influence plant performance directly. An appreciation of these basic ecophysiological mechanisms of adaptation and physiological environmental responses can shed fundamental insights that inform the practice of ecological restoration, as well as help guide restoration ecology research and restoration experiments. Furthermore, because restoration settings often pose unique environmental challenges to plants, ecophysiological studies in these settings may also provide significant new insights about plant ecophysiological function.

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