Ecophysiological Considerations for Restoration

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Theory and Application

- Ecophysiological traits can be used to determine tolerances to environmental conditions and to estimate rates of nutrient cycling.
- Measurements of traits related to light, water, and soil nutrient acquisition may help practitioners select plant palettes for restoration projects.
- Trait differences between native and nonnative species may be used to assemble invasion-resistant communities.
- Comparing ecophysiological traits between plants in restored and intact communities provides an additional metric for defining the success of restoration projects.

Plant restoration activities can be positively or negatively affected by changes in the abiotic or biotic environment from that of the pre-disturbance condition, such as invasion by nonnative species and changes in aboveground microclimate, soil structure, or soil nutrients. A thorough understanding of the ecophysiological mechanisms of adaptation that describe the potential for a plant to persist in a habitat allows a more accurate assessment of 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 vary in their capacity 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 more slowly, if at all. Individual plants also vary in the rate at which they take up carbon, nitrogen, and water, and these differences will influence rates of nutrient cycling and other ecosystem functions. Ecophysiological traits that influence ecosystem functioning are referred to as *effect* traits (Suding et al. 2008).

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This chapter describes how measurements of ecophysiological traits can explain a plant's tolerance to variations in abiotic and biotic conditions and its capacity to cycle nutrients in ecological systems. We describe the basic light, water, and soil nutrient requirements of plants, as well as plant responses to variation in the availability of these requirements. We also describe how commonly measured ecophysiological traits can be used to predict restoration outcomes, to assess the success of restoration projects, and to aid in the design of restoration projects.

Ecophysiological Measurements

Measurements of ecophysiological traits can provide valuable information to restoration practitioners and researchers (Taiz and Zeiger 1998; Cornelissen et al. 2003; Lambers et al. 2008). Trait measurements may be used to assess the health of individuals, the quality of the environment, the environmental tolerance of species (their ecological niche), and the role of a species within the community (McGill et al. 2006; Violle et al. 2007; Fortunel et al. 2009). When average species trait values are weighted by their abundance to calculate community-weighted mean trait values, they can also provide information on ecosystem-level processes such as nutrient cycling (Diaz et al. 2007; Lavorel 2013). Trait data can help with decisions regarding necessary site preparation, selections of species to add to the landscape, and methods for removing invasive species (Kimball et al., 2015). Measurements may also be used to assess ecosystem processes, something that is increasingly suggested as a measure of the progress or success of restoration projects (Benayas et al. 2009; Wortley et al. 2013).

Several ecophysiological traits are routinely measured to determine tolerance and rates of nutrient cycling (table 6-1). Commonly measured leaf-level traits include instantaneous photosynthetic and transpiration rates, typically measured with portable gas exchange systems containing infrared gas analyzers, or IRGAs. With an IRGA system, it is possible to measure the rate at which carbon is fixed (photosynthesis) and water is lost (transpiration) under ambient or manipulated conditions. The ratio of carbon gain to water loss is a measure of drought tolerance or water-use efficiency (WUE). Many IRGAs allow users to alter the CO_2 concentration available to plants, leaf temperature (within a small range), and available light, making it possible to collect response curve data from which critical maximum and minimum values, as well as optima and thresholds, can be determined (Farquhar et al. 1980; Harley et al. 1992). Leaves can also be collected and processed to determine carbon content, nitrogen content, and stable carbon isotope ratios. The ratio of heavy to light stable isotopes of carbon in a leaf is correlated with long-term intrinsic WUE (Farquhar et al. 1989).

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TABLE 6-1.

Some frequently measured physiological traits, common abbreviations, units of measurement, and how they are measured, followed by what high values of such traits can indicate in terms of environmental conditions (compared among sites), environmental tolerances (compared among species), the ecological niche (for a given species), and effects on ecosystem processes (using community-weighted metrics across species).

Trait	Units	Measured	Environment	Tolerances	Niche	Ecosystem Processes
Maximum photo-synthetic rate (A_{max})	μmol CO_2 m^{-2} s^{-1}	Gas exchange system with infrared gas analyzer	Favorable	Suitable for environment	Competitor	High C cycling
Water-use efficiency (WUE)	μmol CO_2 mol^{-1} H_2O	Gas exchange system with infrared gas analyzer	More xeric	Ability to tolerate dry conditions	Stress tolerator	Low water cycling
Midday water potential (Ψ_{md})	MPa	Pressure chamber	Mesic	Lower ability to tolerate dry conditions	Less stress tolerant	High plant water flux
Relative growth rate (RGR)	$g\ g^{-1}\ day^{-1}$	Size through time	Favorable	Suitable for environment	Competitor	High NPP; High C cycling
Leaf longevity (LL)	days	Mark leaves and revisit	Less favorable	Greater stress tolerance	Stress tolerator	Low nutrient cycling
Specific leaf area (SLA)	$g\ m^{-2}$	Determine leaf area, divide by dry weight	Favorable	Suitable for environment	Competitor	High nutrient cycling
Root mass ratio (RMR)	g root g^{-1} plant	Harvest plants, separate roots, dry and weigh	More stressful	Ability to tolerate dry conditions	Stress tolerator	More even water cycling throughout year
Leaf N content (leaf N)	$mg\ g^{-1}$	Grind up leaves and analyze content	More N available for uptake	Higher growth potential or greater cold tolerance	Colonizer	High N cycling
Intrinsic water-use efficiency ($\delta^{13}C$)	‰	Grind up leaves; analyze stable isotope ratios (send to stable isotope facility)	Xeric	Ability to tolerate dry conditions	Stress tolerator	Low water cycling

leaf longevity, require marking individual plant modules and returning to take measurements through time, or by performing sequential harvests of individuals in the same population through time (Hunt et al. 2002). Harvesting an individual plant and measuring leaf, stem, root, and reproductive material enables determination of biomass allocation patterns, such as root:shoot, specific leaf area (SLA, the ratio of leaf area to leaf mass), and root mass ratio (RMR, the ratio of root mass to total biomass). Predawn and midday water potential measurements on stems can be collected with a pressure chamber, providing information on soil water availability and plant water stress, respectively (Slatyer 1967).

Many traits are typically correlated, leading ecologists to search for the ideal mix of non-redundant traits that provides information about where species fall along different trade-off axes (Westoby et al. 2002; Reich 2014). For example, a global analysis of six leaf traits from 2,548 plant species identified trait correlations that differentiated species with short leaf lifetimes, fast gas exchange rates, and high nutrient concentrations from those species with long leaf lifetimes, slow gas exchange rates, and low nutrient concentrations (Wright et al. 2004). Some studies suggest that parallel trade-offs occur belowground. For example, specific root length (SRL) indicates greater absorptive root length per unit biomass, so it may be the belowground analog of SLA. Species with a high resource acquisition strategy might have high SRL, high root respiration rate (Tjoelker et al. 2005), and low root lifespan (Eissenstat et al. 2000; McCormack et al. 2012). Many studies measure belowground biomass allocation (table 6-1), such as RMR and root-to-shoot biomass ratio (R:S), to assess species' responses to water and soil nutrient availability (Drenovsky et al. 2008; Funk and Zachary 2010). However, root-to-shoot and other allocation ratios may not be good predictors of resource acquisition (Aerts and Chapin 2000). For example, species may achieve high water uptake with a low root allocation but high SRL, suggesting that morphological and physiological traits should be examined in concert. Similarly, while the global pattern of leaf trait correlations suggests that only a few key traits need to be measured, some community types (such as those dominated by herbaceous species) show different patterns of leaf trait correlations (Funk and Cornwell 2013). Thus, measurements of multiple traits are likely necessary to provide the most useful information for restoration.

Ecophysiological Requirements and Stressors

Understanding the environmental conditions required for plants to persist may be critical to the success of restoration projects. Below, we describe the importance of light, water, and soil nutrients, providing examples for how these abiotic requirements and stressors influence plants in restoration settings.

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Light

Photosynthesis is the basic process whereby the simultaneous capture of carbon dioxide from the atmosphere and of photons from the sun results in the formation of the organic compounds used as the building blocks of growth in plants (Lambers et al. 2008). In general, neither of these two essential substrates for photosynthesis differs in concentration between pristine habitats and disturbed sites undergoing restoration. What may differ, though, is the light profile within the vegetation, which may be altered due to physical disturbance or invasion by nonnative species with different phenology, growth rate, or maximum height than natives. Since plant species differ in their light tolerances and preferences, it is important to consider whether light availability at a site matches the needs of plants to be restored (Baltzer and Thomas 2007).

Photosynthetic light saturation can occur at light levels that are as low as 5%–20% of midday sunlight for leaves of understory plants or shade leaves of large trees (Givnish 1988; Funk and Lerdau 2004). Two factors that determine the light level at which photosynthesis does not increase further are stomatal conductance and leaf protein content (typically estimated by leaf nitrogen content). Each of these factors respond to the plant's growth environment (e.g., soil nutrient availability, vapor pressure deficit), with the upper limits often well correlated with leaf life expectancy (Reich et al. 1999). Stomatal conductance is a measure of how open the stomatal pores are that allow the inward diffusion of CO_2 for photosynthesis. Since stomatal pores also control the outward flux of water, water stress (described below) tends to result in reduced stomatal conductance (to prevent water loss) and consequently lower photosynthetic rates. The same applies for protein content. Since the majority of leaf protein is associated with photosynthetic activity (Evans 1989), reduction in leaf protein content will reduce photosynthetic rates, particularly under water stress. The successful establishment of plants in a restoration setting will thus depend on a sufficient supply of nutrient resources to build plant tissues and support photosynthetic activities, and adequate water supplied to leaves to maintain stomatal conductance and the inward diffusion of CO_2.

Exposure to light levels far greater than those experienced during development, such as for greenhouse plants transplanted to the field, or shade plants exposed to higher light levels than they might experience under more natural conditions, can create a significant challenge for plants in a restoration context. *Photoinhibition* (a reduction of photosynthetic rates at high light levels) can occur when leaves are exposed to sunlight above the light saturation point, as shown in figure 6-1 (Adir et al. 2003; Demmig-Adams 2003). The effects of photoinhibition can include a reduction in photosynthetic capacity and loss of chlorophyll (bleaching), potentially causing leaf mortality and leading to reduced plant estab-

lishment. The excess light energy absorbed beyond light saturation can oxidize and damage cellular components unless a mechanism is available to dissipate this energy. Some species have evolved protective mechanisms, such as xanthophyll, that can minimize the damage to leaves caused by excess light availability (Adir et al. 2003; Demmig-Adams 2003; Adams et al. 2004). Sometimes light levels are too high for these protections to be effective, as for plants that naturally grow in shade but are exposed to high light during transplanting, or plants exposed to water stress and high temperature conditions.

In sites needing restoration, shade-loving plants may need to be shaded during establishment, and this can occur by planting next to existing "nurse plants" that facilitate establishment (Butterfield and Briggs 2011). High light levels in disturbed sites can also be problematic due to increased competition from fast-growing, shade-intolerant invasive species (Cabin et al. 2000; Loh and Daehler 2008; Chen et al. 2013). Working in a disturbed Hawaiian rainforest, Funk and McDaniel (2010) found that shading with mesh screens reduced the growth of invasive grass species and increased survival and growth of native woody seedlings.
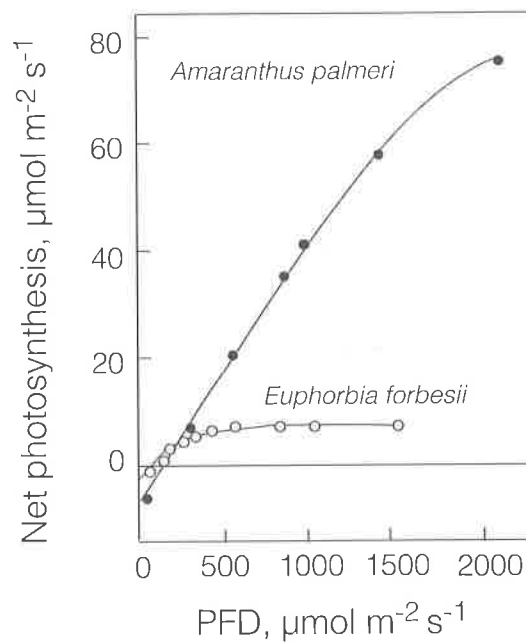
Figure 6-1. The response of photosynthesis (μmol/m²/s, as measured with an infrared gas analyzer) to changes in light availability (Photon Flux Density in μmol/m²/s) for two C_4 species adapted to different light conditions. *Amaranthus palmeri* is a desert annual, adapted to high light environments. *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).

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While shading structures might not be feasible on large scales, reestablishing the canopy through seeding or planting of fast-growing native species can lower light levels and promote the growth of slower-growing, shade-tolerant native species. Restoration practitioners may also be challenged by systems that receive too little light. The recruitment of native tree seedlings in a seasonally dry forest in Hawaii was suppressed due to shading by alien fountain grass (*Pennisetum setaceum*), demonstrating that restoration, especially by natural recruitment, must be preceded by removal of fountain grass (Cabin et al. 2000). Similarly, native shrub establishment in a California coastal sage scrub community was inhibited when fast growing annuals shaded the shrub seedlings. The authors concluded that some type of weed maintenance (e.g., mowing, manual pulling) and planting of native perennials without native annuals is required for native perennial establishment in that system (Kimball, Lulow et al. 2014).

Solar radiation also affects microclimate variation that contributes to the small-scale topographic heterogeneity influencing natural and restoration success of both plant and animal systems (chap. 10). For example, plants may experience a microclimate in which air and leaf temperatures near the soil surface can be significantly hotter during the day and significantly cooler at night than those experienced at greater heights (fig. 6-2). During the day, the sun's energy is absorbed by the soil surface, potentially raising surface temperatures to dangerously 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 ground (fig. 6-2). Metabolic activities, such as rates of photosynthesis and respiration, are a function of leaf temperature, so we would expect the highest rates to occur in leaves nearest the soil surface. However, near-surface temperatures can also exceed critical maximum temperatures, thereby posing a thermal stress, especially for establishing seedlings, since their rooting depths, water transport capacities, and carbon reserves are likely to be lower than for mature, established plants. Environmental variation also influences plants at a larger scale, such as through slope aspect and steepness. Slopes that receive more solar radiation will be warmer and drier, and this will influence plant performance (Kulpa et al. 2012). For example, when identical methods were used to restore native plant cover to a highly degraded site in California, cover on the north-facing slope was significantly higher than on the south-facing slope three years after seeding and planting (Kimball et al., 2015). Although native grass and forb establishment was impacted by slope aspect, native shrubs were able to establish fairly well on both slopes, indicating practitioners in this system may have greater success restoring shrubs than other functional groups on south-facing slopes (fig. 6-3).

Leaf temperatures often can be elevated 1°C–10°C above air temperatures (Funk and Lerdau 2004; Lambers et al. 2008). Leaf temperatures will rise until
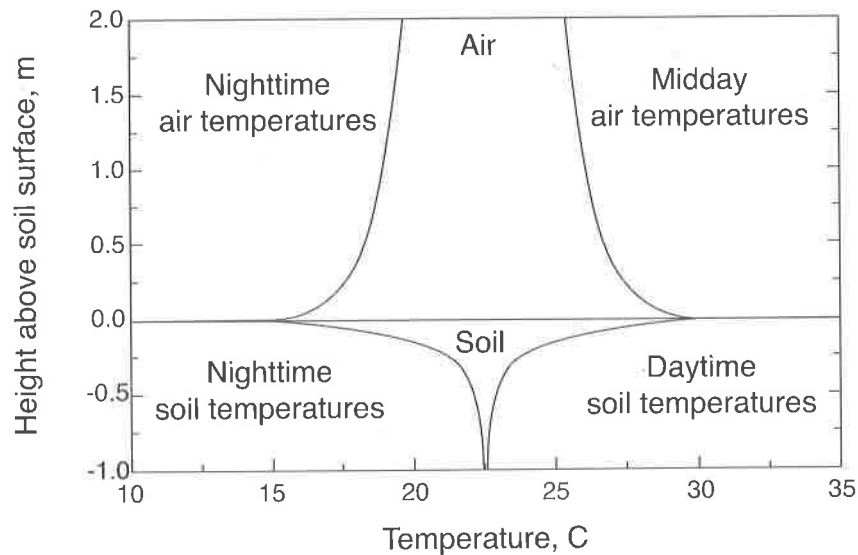
Figure 6-2. Microclimate profile of air temperature as a function of height above the soil surface during midday and nighttime conditions.

the energy absorbed by a leaf equals the energy dissipated by re-radiation, convection, and transpiration. 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 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. In restoration settings, seedlings are frequently planted with tree guards to reduce herbivory, but an experimental study in Australia found that plastic tree guards increased leaf temperature and mortality, while guards constructed out of shade cloth created a more favorable microclimate for seedling establishment (Close et al. 2009). Adding shading structures, utilizing existing nurse plants, or reestablishing canopy trees can also promote favorable microclimates: they reduce the net energy load incident on the seedling (Loh and Daehler 2008; Funk and McDaniel 2010).

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 (fig. 6-2). Here energy is lost by re-radiation; the radiative loss from the soil is greater than the absorption of infrared radiation from a nighttime sky, resulting in low soil and leaf temperatures. During early spring conditions in temperate regions, frost may develop at the soil surface as a result of this thermal imbalance.
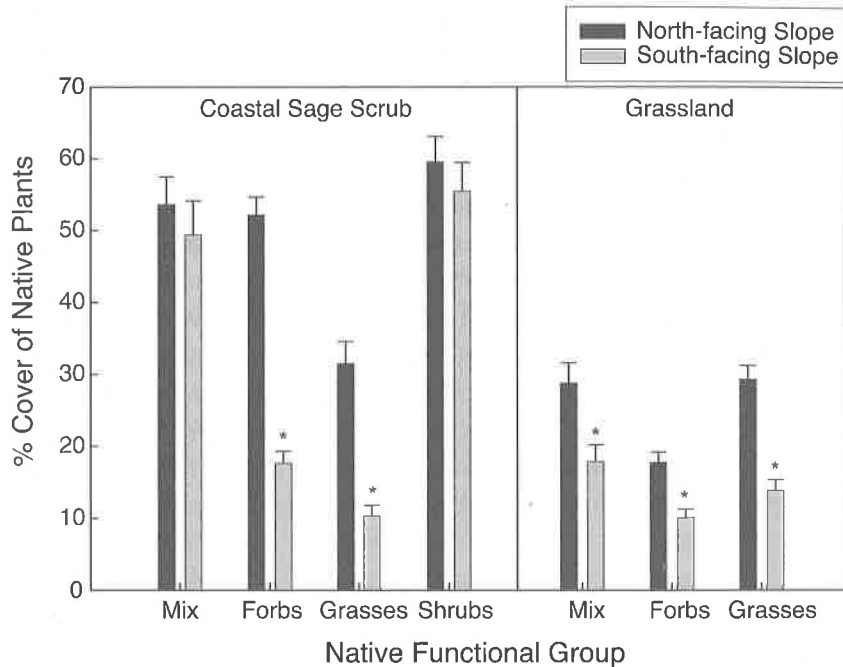
Figure 6-3. Post-restoration % cover of native plants on North- and South-facing slopes. Identical methods were used to restore native coastal sage scrub and grassland species on each slope, but aspect had a significant effect on the establishment of grasses and forbs. * indicates cover on S-facing slopes was significantly lower than N-facing slopes for that functional group of plants. Data are from the West Loma Ecological Restoration Experiment (described in case study box 6-1).

Cold tolerance can be a major limitation to seedling establishment in restoration of shrub (Hou and Romo 1998) and tree seedlings (Gurney et al. 2011), making it important to select cold hardy species. Tissues of emerging seedlings at the soil surface are most vulnerable to freezing stress, which can often be avoided by leaf and bud tissues that are raised 5–10 cm above the soil surface. Frost damage to seedlings may be minimized by adding protective structures or by planting seedlings under the canopy of existing nurse plants to prevent radiative heat loss from the soil (Scowcroft and Jeffrey 1999; Curran et al. 2010).

The capacity to use light is also influenced by biochemical differences among the three major photosynthetic pathways: C_3, C_4, and CAM (Taiz and Zeiger 1998; Sage and Monson 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. C_3 photosynthesis is the ancestral pathway common to all taxonomic lines (Ehleringer and Monson 1993; Sage and Monson 1999). C_4 photosynthesis is a modification of the C_3 pathway

that spatially restricts the C_3 photosynthetic cycle to the interior portions of a leaf thereby preventing *photorespiration,* a process that occurs when rubisco (ribulose bisphosphate), the key enzyme in the first step of carbon fixation, combines with atmospheric oxygen rather than CO_2. C_4 plants tend to have higher photosynthetic rates relative to C_3 plants because they lack photorespiratory activity. They can 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. C_4 grasses, including species in the genera *Andropogon* and *Pennisetum,* have been particularly well studied and can have significant impacts on rates of nutrient cycling and fire frequency (D'Antonio and Vitousek 1992; Reed et al. 2005; Litton et al. 2008). Restoration in communities invaded by C_4 grasses can be stymied by high fire tolerance and nitrogen use efficiency of C_4 grasses, rendering common management practices, such as fire and reduction of soil nutrient availability, less effective (Stevens and Falk 2009).

Water

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 differences in rooting depths and structures (Schenk and Jackson 2002), 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 availability of water resources. The absence of canopy trees has also been shown to increase leaf-to-air vapor pressure difference, which leads to increased transpiration of remaining plants, and hastens drought and water stress in the system (Lambers et al. 2008). This negative feedback can lead to slow but pronounced changes in species function and composition, resulting ultimately in type conversion to a relatively more xerophytic flora, an alternative state that may be resilient to restoration (Suding, Gross, and Houseman 2004). For example, in the Hawaiian dry forest, conversion to nonnative grasses has led to competition with natives for water, making it difficult to establish native trees in restoration projects (Cabin et al. 2002). Alternatively, removing canopy species can benefit native recruitment in systems experiencing drought. The removal of invasive canopy species in tropical systems, which reduce soil water availability through high rates of transpiration and rainfall interception, can lead to higher soil water availability for establishing native species despite higher midday vapor pressure deficit (Michaud et al. 2015). Similarly, in the southwestern United States, canopy thinning results in higher access to

water by native Ponderosa pines because the practice allows more snow to reach the soil surface, increasing soil moisture recharge (Kerhoulas et al. 2013).

Water acquisition can be increased by mycorrhizal associations (found in many species) and by specific plant adaptations, including hydraulic lift (generally defined as the movement of soil water through root systems from areas of high water availability to areas with lower water availability) and direct interception of moisture, such as fog (Lambers et al. 2008). Facilitating the maintenance or recovery of these biotic contributions to resource enhancement may be particularly crucial to restoration. For example, 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). 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. Water that condenses onto redwood foliage can directly enter the leaf, which is where the water is most needed (Burgess and Dawson 2004).

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, 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; McDowell et al. 2010).

Leaf stomata have the greatest effect on regulating water fluxes from plants (Jones 1998). Stomata are sensitive to both plant water status and relative humidity, and generally close during periods of water stress (Kozlowski and Pallardy 2002; Sperry et al. 2002). There is no single stomatal response exhibited by all plants to humidity and water-deficit stresses; rather, stomatal pores of different species exhibit a wide range of sensitivities. Cultivated and noncultivated populations of the same species can also exhibit differences in rates of stomatal conductance and carbon fixation, potentially influencing the competitive environment in restoration settings (Lambert et al. 2011).

Rates of stomatal conductance also reflect environmental conditions, including moisture levels in the air and the soil. The California native shrub, *Salvia api-*

ana, exhibited lower stomatal conductance during the first year of growth when seeded with native forbs than when seeded in a mix of native shrubs without forbs (case study box 6-1; Bell et al., forthcoming). These results suggest greater water usage by the herbaceous forbs compared to perennial shrubs, and demonstrate how the selection of plant palette can influence water use (fig. 6-4). Determining the abiotic goals of a restoration project in advance (for example, increased versus decreased amounts of surface water flow) will allow practitioners to select plants with ecophysiological traits that help achieve those goals.

Differential rooting depths, such as that found between shrubs and herbaceous species, and variable sensitivities of stomata to humidity describe a fundamental water-relations challenge in restoring species within arid ecosystems. 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) established 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. In this case, 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 radiation load on developing perennials and avoid competition for water at depth. With better knowledge of the differential rooting depths for water uptake of juvenile
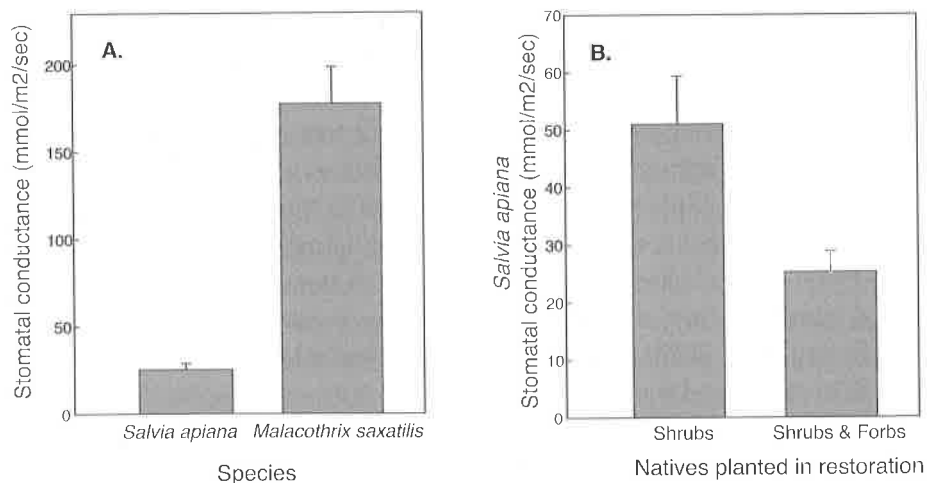
Figure 6-4. A. Stomatal conductance values for the shrub, *Salvia apiana*, and the herbaceous forb, *Malacothrix saxatilis*, measured in the same restoration plot in coastal sage scrub (Santa Ana Mountains, CA). B. Conductance values for the shrub, *Salvia apiana*, when planted with other native shrubs and when planted with a mix of shrubs and forbs.

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Case Study Box 6-1
The West Loma Ecological Restoration Experiment

By Sarah Kimball, Travis E. Huxman, and Megan Lulow
Collaboration between UC Irvine's Center for Environmental Biology,
the Irvine Ranch Conservancy, and OC Parks

Santa Ana Mountains, CA: Different combinations of native Coastal Sage Scrub and Grassland species were added to the landscape, which was initially dominated by Eurasian grass and forb species. Restoration was conducted in strips with functional groups (shrubs, forbs, and grasses) seeded alone or in combination to determine the mixture of natives with community-weighted traits that best limit subsequent invasion by nonnative species.

Case Study 6-1. Student interns with the Center for Environmental Biology collect plant density data on the top of the South-facing slope at the West Loma Ecological Restoration Experiment. In the background, blocks restored to coastal sage scrub and native grassland on the North-facing slope are visible.

Test of theory: Incorporation of ecophysiological traits that may be used to assemble invasion-resistant communities (hypothesis of limiting similarity).
The limiting similarity hypothesis predicts that communities are more resistant to invasion when they contain natives with traits similar to the most common invasive species.

UC Irvine's Center for Environmental Biology collaborated with the Irvine Ranch Conservancy and OC Parks to test this hypothesis by restoring natives with a diversity of trait combinations. Trait measurements were conducted on native and nonnative species, and community-weighted trait values were related to the abundance of nonnative species in the different plots.

Expected outcome: Plots with the highest functional diversity values and with community-weighted mean values most similar to abundant nonnatives would be more resistant to invasion by nonnative species.

Case Study Box 6-1 continued

> **Progress:** In the first year, invasibility did not differ among seed mixes, but each native functional group had greater establishment in plots with lower native diversity. After three years of growth, shrub-only plots were less invaded, which appeared to be related to these plots containing natives with greater cumulative water extraction capacities that suppressed invader performance.
>
> **References:** Fargione et al. 2003; Emery 2007; Kimball et al. 2014b; Kimball et al. 2015; Bell et al. forthcoming.

and adult perennials, it is possible to devise irrigation routines that increase the probability that perennials will become established in a restoration setting.

Over the past few decades, it has become clear that plant hydraulic architecture plays a fundamental role in governing the flow of water through plants (Maherali et al. 2004; McDowell et al. 2011). 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) (fig. 6-5). The xylem tissues transporting water between roots and shoots of species from more mesic habitats tend to cavitate at higher plant water potentials (Maherali et al. 2004). The steep changes in cavitation that can occur over a narrow water potential range underscores the importance of maintaining adequate soil moisture or selecting less vulnerable species during the development and establishment of plants in a restored community.

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. Specifically, 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 (Knapp and Smith 2001; Huxman, Smith et al. 2004), recognizing the factors that govern water acquisition and transport is critical to restoration programs. The choice of native plants in restoration projects can influence local hydrologic processes such as runoff. For example, restoring a heavily grazed site from nonnative, invasive
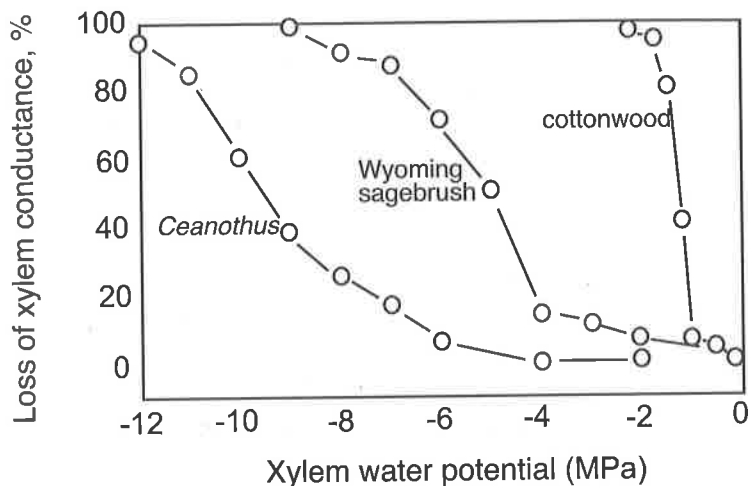
Figure 6-5. Vulnerability curves for three contrasting perennial species, showing loss of xylem conductance (xylem embolism) within the plant hydraulic system as a function of plant water potential. Modified from Sperry (2000).

grasses to grassland would likely result in greater surface flow of water than restoring the same area to shrubland. In mixed communities, plant species often exhibit pronounced differences in rooting properties, with root density and effective rooting depth for water uptake varying within the soil profile (Dawson and Ehleringer 1998). Additionally, rooting zones differ between juvenile and adult plants for many perennial species (Donovan and Ehleringer 1992, 1994). As many restoration projects involve planting perennials as seedlings, there may be increased competition for water during the initial year of plant establishment, when the young perennials have similar root depths to annuals and perennial grasses (Eliason and Allen 1997; Schenk and Jackson 2002; Bell et al., forthcoming).

The timing of rain events, in addition to the total amount of precipitation, has important implications for plant fitness (Huxman, Snyder et al. 2004; Kimball et al. 2012). Since patterns of precipitation are expected to change in response to increasing atmospheric CO_2 levels, this becomes important to consider when selecting plant palettes for restoration. Rare plants are increasingly being transplanted beyond their current ranges to match predicted future climate predictions (Kreyling et al. 2011). Measurements of ecophysiological traits can be a key tool in identifying environmental preferences, and such knowledge could be applied to restore sustainable plant communities for future climatic conditions. While this idea has been identified in academic studies for both plant and animal communities (Laughlin 2014), we are unaware of any management projects that are actively restoring communities for future climatic conditions. Extreme events are likely to

increase in frequency along with climate change, and this suggests careful selection of restoration sites (chap. 17). Steep slopes, for example, present challenges to plant growth due to continual erosion, but such slopes may become even more difficult to restore during years with large rain events (Bochet et al. 2009).

Soil Nutrients

Most plants take up nutrients through their roots, specifically through root hairs that probe the aqueous soil environment surrounding a root. A common practice in restoration settings is to supply some of the critical macronutrients for plant growth—particularly calcium, iron, magnesium, nitrogen, phosphorus, and sulfur —as fertilizer (Bloomfield et al. 1982; 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 such as rain forests (Paul et al. 2010; Marschner 2012). Of the mineral elements extracted from the soil, nitrogen is the element needed in highest concentration within leaves as an essential component of proteins (particularly the photosynthetic enzyme rubisco), pigments, and nucleic acids, which explains why high additions of nitrogen are particularly important (Bradshaw 1983, 1984). Many pioneer species that establish readily in restoration settings are nitrogen-fixers, including rhizobial and actinorhizal plant species (Macedo et al. 2008). These plants have evolved mutually beneficial relationships with soil bacteria that convert atmospheric nitrogen into ammonium, which the plant uses in exchange for carbon. While some restoration efforts use nitrogen-fixing plant species to help replenish soil nutrient availability following disturbance (Griscom and Ashton 2011), they can be problematic invaders that impede restoration efforts, particularly in nutrient-poor soil (Funk 2013).

Often the root surface area and lateral extension of root hairs are inadequate to provide sufficient uptake of 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, associations with mycorrhizal fungi are essential to establishment and nutrient (especially P) uptake by most higher plants (Bolan 1991; Jeffries et al. 2003). Fungal hyphae are able to extend up to several orders of magnitude farther away from the root than can root hairs, creating such a wider effective mineral-uptake domain that many plants fail to grow or have significantly reduced growth rates in the absence of their symbiotic mycorrhizal partners (Allen et al. 2003). Disturbance processes (e.g., strip-mining activities,

atmospheric nitrogen deposition, or desertification) often disrupt plant-microbe symbioses, requiring that seeds or transplanted seedlings on restoration sites be provided a fungal or bacterial inoculum (Egerton-Warburton and Allen 2000; Requena et al. 2001; Siguenza et al. 2006). Areas dominated by nonnative species show decreased numbers of the mycorrhizae required by natives. The reduction may be due to weaker associations between mutualists and nonnative plants or due to exudation of allelopathic chemicals by the nonnatives that are toxic to the soil micro-biota (Callaway and Ridenour 2004; Vogelsang and Bever 2009). In many restoration cases the microbial symbionts can be provided to the system by collecting and reserving the surface soils during the initial disturbance process, then adding back this soil during restoration. If pre-disturbance soils are not available, mycorrhizal inoculum may be collected from nearby sites dominated by natives and added to the restoration site along with native seeds or plants (Renker et al. 2004). Using local innocula results in higher increases in mycorrhizal colonization than inocula from commercial sources (Maltz and Treseder 2015).

In contrast to nutrient limitations, many ecosystems are receiving excessive nutrient additions through fertilizer runoff and atmospheric deposition (Vitousek et al. 1997). Increased soil fertility can cause problems for some restoration efforts because nutrients stimulate the growth of invasive species (chaps. 8, 12) with more competitive resource acquisition traits such as high SLA and A_{max} (table 6-1). In addition, increased soil nitrogen may limit the growth of native pioneer species that associate with N-fixing bacteria (Kimball, Goulden et al., 2014). Many studies have attempted, with some success, to reduce soil N availability by adding carbon, typically in the form of sugar or sawdust, to the soil (Zink and Allen 1998; Corbin and D'Antonio 2004; Suding, LeJeune, and Seastedt. 2004). Adding carbon stimulates microbial activity and N immobilization, and has been demonstrated to suppress the growth of fast-growing invaders and promote the growth of stress-tolerant natives. For example, sugar addition to a California desert system invaded by the annual grass *Schismus barbatus* reduced biomass of the invader relative to natives when applied in years where rainfall patterns stimulated early germination of the invader (Steers et al. 2011). However, when a large, early-season rainfall event stimulated the germination of both *S. barbatus* and native species, N immobilization resulting from sugar addition suppressed the growth of all species, including natives. Additionally, these treatments may need to be applied every year as the microbial population turns over and N is returned to the soil (Steers et al. 2011), making this application most effective under certain conditions (e.g., dry years) and for restoration of small areas.

Disturbed sites in need of restoration often also differ from more natural habitats by an abundance of toxic elements in the soil (Antonovics and Bradshaw 1970; Bradshaw 1984; Wong 2003). The three most common mineral-related challenges

to restoration are highly saline soils, 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 restoration. Altered soil pH levels have multiple effects on plant roots. 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. Heavy-metal tolerance in plants is often fairly specific and limited to a single metal instead of 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 hyperaccumulate 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 (De la Fuente-Martinez and Herrera-Estrella 1999). Zinc, cadmium, copper, iron and other metals can also have negative effects on plant metabolism when present in the soil in high concentrations (Shaw 1990; Rout and Das 2003). Plants with physiological traits that resist or tolerate soils with high metal concentrations, or metallophytes, are typically endemic to areas with high metals in the soils, and are often the best species to use in restoration of such sites (Whiting et al. 2004). For example, *Stanleya pinnata* and *Astragalus bisulcatus* both accumulate selenium when grown in soils that are toxic to most plant species (Freeman et al. 2006).

Traits and Restoration

Early in this chapter, we introduced commonly measured ecophysiological traits and described what they tell us about tolerances to environmental conditions and rates of nutrient cycling (table 6-1). These traits, and their combinations, are particularly useful predictors for restoration success, and provide valuable information for planning. For example, in a Ponderosa pine forest, old growth trees were subjected to thinning and burning treatments in an attempt to return the forest to pre-fire-suppression conditions. Measurements of leaf gas exchange, leaf nutrient content, water potential, and resin flow were used to assess the success of these methods, and indicated that restoration treatments increased the health of old growth trees (Feeney et al. 1998). Comparing traits of native and nonnative species can reveal useful methods of controlling invasions. For example, measurements of several traits in a Hawaiian system demonstrated that natives were more shade-tolerant than nonnatives, indicating the possibility of planting taller natives or adding artificial shade structures to prevent invasion (Funk and McDaniel 2010). Recognizing trait combinations of common natives and nonnatives in a system can also be useful when deciding the plant palette to use in active restoration. This is based on the hypothesis of limiting similarity, and the concept of competitive ex-

clusion, which state that no two species that occupy the same ecological niche can coexist indefinitely (Macarthur and Levins 1967; Abrams 1983). In natural systems, there is evidence that communities are more resistant to invasion when they contain natives that have traits similar to potential nonnative invaders (Fargione et al. 2003; Emery 2007), suggesting that restoration practitioners should consider planting natives with traits similar to the most common invasive species (Funk et al. 2008; Drenovsky et al. 2012). There are problems in practice, however, since planting diverse natives can limit establishment through increased competition among fast- and slow-growing native species (Kimball, Lulow et al. 2014). Additionally, planting different types of natives together prevents the use of selective herbicides to control nonnative species following planting (Kimball, Lulow et al. 2014). Nonetheless, there is strong support of the limiting similarity hypothesis from experimentally assembled communities, suggesting that the theory shows promising applicability to restoration contexts (Price and Partel 2013).

Ecophysiological traits may also be useful to assess the success of restoration projects in terms of the ecosystem functions or services provided by the restored system. With billions of dollars spent annually on restoration, there is an increasing need to define metrics for success. Rates of carbon, water, and nutrient cycles have been proposed as a preferred metric in restoration (Palmer et al. 2005), and these processes may be determined through measuring ecophysiological traits of all species in the community and calculating community-weighted trait mean and functional diversity (FD) values (Diaz et al. 2007). FD values provide information regarding community-level processes, such as community assembly and function, and are valuable for assessing the health of restored communities (Cadotte et al. 2011). Other measurements taken at the community level, such as net primary productivity, and measurements of functional diversity across multiple trophic levels would further aid in assessments of ecosystem processes as indicators of restoration success (Lavorel 2013).

Closing Remarks

In the most idealized study design, plant ecophysiological performance and metrics of system functioning (such as net primary production) in a restored setting should be compared to measurements in a reference system (Morgan and Short 2002). Such studies provide the best opportunities for identifying performance expectations and ultimately attaining restoration goals (Feeney et al. 1998; Ruiz-Jaen and Aide 2005). 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 technological capabilities over the past three decades,

such as lightweight portable gas-exchange systems and compact data loggers, have made field ecophysiological assessments much more rapid and tractable (table 6-1). 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 (Adams and Kolb 2004; Roden et al. 2005; McDowell et al. 2010). Careful selection of which ecophysiological variables to monitor, and on which species, also helps to refine such studies; 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 high light environments) 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 all plant species do not exhibit the same sets of physiological response curves or stress tolerances, because these responses reflect the evolved species niche space (Sultan et al. 1998; Reich et al. 2003; Kimball et al. 2012; Gianoli and Saldana 2013). 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 traits of the key species are characterized. Restoration involves not only understanding 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. In this context, the restoration of plant communities may benefit from ecophysiological research on animal and microbe communities (Reynolds et al. 2003; Tylianakis et al. 2008). An understanding 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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