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STRATEGIC ISSUES ARTICLE

Restoration ecophysiology: an ecophysiological approach to improve restoration strategies and outcomes in severely disturbed landscapes

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As human activities destroy and degrade the world's ecosystems at unprecedented scales, there is a growing need for evidence-based methods for ecological restoration if we are to preserve biodiversity and ecosystem services. Mining represents one of the most severe anthropogenic disturbances, often necessitating intensive intervention to restore the most basic attributes of native ecosystems. Despite examples of successful mine-site restoration, re-establishing native vegetation in these degraded landscapes remains a significant challenge. Plant ecophysiology—the study of the interactions between plants and the environment—can provide a useful framework for evaluating and guiding mine-site restoration. By understanding the physiological mechanisms that allow plants to establish and persist in these highly disturbed environments, practitioners may be able to improve restoration outcomes. Specifically, methods in plant ecophysiology can inform site preparation and the selection of plant material for restoration projects, aid in monitoring restoration progress by providing additional insight into plant performance, and ultimately improve our ability to predict restoration trajectories. Here, we review the challenges and benefits of integrating an ecophysiological perspective to mine-site restoration in Western Australia, a global hotspot of biodiversity and mining operations. Using case studies and examples from the region's diverse ecosystems, we illustrate how an ecophysiological approach can guide the restoration of some of the world's most severely disturbed landscapes. With careful selection of study species and traits and consideration of the specific environmental conditions and stressors within a site, the restoration ecophysiology framework outlined here has the potential to inform restoration strategies across ecosystems.

Key words: adaptive management, conservation physiology, environmental stress, mine-site restoration, plant physiology, rehabilitation

Implications for Practice

- Restoration ecophysiology provides a conceptual foundation and mechanistic tools to inform restoration strategies for disturbed sites.
- Understanding species' ecophysiological requirements and stress tolerances can ensure more suitable site preparation and appropriate selection of plant material.
- Allowing time and resources for monitoring to also include physiological measurements, particularly in the early stages of restoration, could allow for more effective or efficient intervention and adaptive management.
- Long-term, integrated measures of ecophysiological plant traits in restored and native reference sites could allow for the identification of key attributes that can serve as indicators and predictors of restoration outcomes.

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Introduction

The severe ecological impacts of human activities worldwide have dire consequences for biodiversity and ecosystem functioning (Johnson et al. 2017). To reverse this global degradation, evidence-based approaches for ecological restoration are essential to conserve species, communities, and the ecosystem services that underpin human wellbeing (Cooke et al. 2018). Mechanistic understanding of how plant species will respond to the effects of anthropogenic environmental change is critical to the restoration of diverse, resilient, and sustainable ecosystems (Madliger et al. 2017). Plant ecophysiology aims to provide insight into the ability of plants to persist in a given environment (Lambers et al. 2008), including novel or changing ones. The integration of ecophysiology and ecological restoration is, therefore, logical (Cooke & Suski 2008).

Ecophysiological evaluation of plant responses to environmental conditions and stressors provides mechanistic insight into the capability of restoration sites to support plant establishment and persistence (Cooke & Suski 2008; Kimball et al. 2016). A variety of methods (Table 1) can be used to characterize plant traits and responses and to infer tolerance thresholds (Lambers et al. 2008). These tools may be especially useful for planning and monitoring restoration in severely disturbed landscapes, such as those impacted by mining. Mining radically transforms the landscape, often resulting in sites completely devoid of natural vegetation and soils (Cooke & Johnson 2002). Restoring degraded sites to diverse, self-sustaining, and functioning ecosystems is challenging and resource-intensive; landforms must be reshaped, soil profiles reconstructed, and plants re-established (Cooke & Johnson 2002). Furthermore, mining operations increasingly exploit ore deposits in areas of high conservation value, increasing the imperatives for successful, and adaptable restoration strategies (Miller et al. 2017). The extreme degree of disturbance, coupled with legislated mandates to restore disturbed sites in many jurisdictions suggests that these sites may serve as important natural experiments for evaluating science-based restoration techniques.

Western Australia (WA) is one of the most productive mining regions in the world, and mining contributes substantially to land cover change and habitat destruction (Lloyd et al. 2002; Brueckner et al. 2013). WA harbors unique, ancient, and many biodiverse ecosystems with high levels of endemism (Beard et al. 2000), many of which are threatened by mining. Consequently, ecological restoration is a pressing environmental concern and has become an important component of mining operations in WA (Brueckner et al. 2013). Underpinning these efforts is an appreciation of the key role that science plays in developing best practices for restoration (Koch & Hobbs 2007; Rokich 2016). Yet, only a fraction of the land area disturbed by mining has been restored

Table 1. Selected physiological plant traits, typical units of measure, the method and/or equipment required, and selected examples of implications for plant performance and ecological restoration. The most informative traits and their interpretation will depend on the study species selected and the specific environmental conditions and stressors within the ecosystem being investigated.

Trait (Units)	*Methodology*	*Implication*
Maximum photosynthetic rate ($A_{\max}$) (μmol CO_2 m^{-2} s^{-1})	Gas exchange system with infrared gas analyzer	High photosynthetic rates may indicate favorable site/environmental conditions or that a given species is suitable for the site
Transpiration (E) (mmol H_2O m^{-2} s^{-1})	Gas exchange system with infrared gas analyzer, or porometer	High rates of transpiration may indicate favorable plant water status or access to soil moisture. Transpiration rates may be used to compare plant water use across species or environmental conditions
Water-use efficiency (WUE) (µmol/mol)	Gas exchange system with infrared gas analyzer	Across species/individuals, greater WUE is associated with drought tolerance. Across sites or over time, greater WUE may indicate increasing water deficit
Stomatal conductance (g_s) (mmol m^{-2} s^{-1})	Leaf porometer, or gas exchange system with infrared gas analyzer	A measure of the degree of stomatal opening which can be used as an indicator of plant water status
Pre-dawn leaf water potential (Ψ_{pd}) (MPa)	Pressure chamber	Provides an indication of soil water availability, where lower Ψ_{pd} indicates increasing water deficit
Midday leaf water potential (Ψ_{md}) (MPa)	Pressure chamber	Useful for assessing drought strategies across species; drought avoiders will maintain a constant Ψ_{md} while drought tolerators will exhibit a drop in Ψ_{md}
Chlorophyll fluorescence (F_v/F_m), quantum yield (Φ) (ratio)	Chlorophyll fluorometer	Provides a measure of photosynthetic performance and can be used to assess levels of plant stress (e.g. photoinhibition due to high light)
Carbon isotope ratio ($\delta^{13}C$) of leaves (‰)	Isotope-ratio mass spectrometry	Can indicate plant water availability and intrinsic water-use efficiency
Nitrogen isotope ratio ($\delta^{15}N$) of leaves (‰)	Isotope-ratio mass spectrometry	Can be used to evaluate levels of N-fixation by soil microbes, associations with mycorrhizal fungi, and N cycling
Oxygen isotope ratio ($\delta^{18}O$) and deuterium (^2H) in plant water (‰)	Isotope-ratio mass spectrometry	Can be used to understand depth of water sources utilized by plants (surface water vs. groundwater)
Leaf mineral element concentrations (mg/g)	Atomic absorption spectrometry or similar	Provides insight into nutrient availability (esp. deficiencies) and potential toxicities (including non-nutrient elements such as Al and Cl)

(Brueckner et al. 2013), and more effective restoration strategies are required, particularly as climate change increasingly complicates these efforts (Harris et al. 2006).

Using mine-site restoration in WA as an example, we provide an overview of the ways in which plant ecophysiology can be used to guide the ecological restoration of severely degraded lands. We outline the ways in which ecophysiology can (1) guide site preparation; (2) inform the selection of plant material; (3) improve plant establishment and survival; (4) aid in monitoring restoration outcomes; and (5) potentially improve our ability to predict restoration trajectories (Fig. 1). Highlighting case studies and examples from across multiple unique ecosystems in WA representing a diversity of species, climates, and edaphic conditions, we aim to illustrate how this restoration ecophysiology framework can benefit restoration initiatives more broadly, including in other similarly biodiverse ecosystems worldwide.

Guiding Site Preparation to Promote Successful Restoration

The Inhospitable Nature of Mine Sites for Restoration

The biotic and abiotic environments of mine sites are radically different from those of undisturbed, native vegetation. Mine sites therefore impose challenging conditions for plant growth which may severely hinder restoration efforts (Cooke & Johnson 2002). Important considerations for designing and implementing mine-site restoration include substrates, hydrology, water availability, and (micro)climatic conditions. Understanding how these environmental factors impact plant ecophysiology can improve restoration strategies and outcomes (Kimball et al. 2016).

Reconstructed Substrates

Following mine closure, entire soil profiles may be reconstructed using topsoil, subsoil, and waste materials. These substrates may be dramatically different in structure and function compared to natural systems (Bradshaw 1997; Duncan et al. 2020). Altered soil properties may cause significant declines in plant performance, including low nutrient availability (Cross et al. 2019), reduced soil biological activity (Birnbaum et al. 2017), soil contamination by heavy metals (Bradshaw 1997), compaction (Rokich et al. 2001), and altered hydrology (Enright & Lamont 1992). Understanding how plants will respond to novel substrates in mine sites is critical for developing best practices for revegetation. Successful establishment early in restoration either from seed or outplanted seedlings is imperative to avoid losing windows of opportunity for recruitment and for plants to attain a minimum size (especially belowground) to survive subsequent heat waves, seasonal droughts, or other stressors. Physiological measurements in the field and under controlled conditions can provide insight into these important plant-substrate-climate interactions and inform management approaches.

The ways in which soil profiles are reconstructed can have important implications for plant-water relations and survival (Enright & Lamont 1992; Lamoureux et al. 2016*a*; Lison et al. 2021). In water-limited ecosystems, such as those of

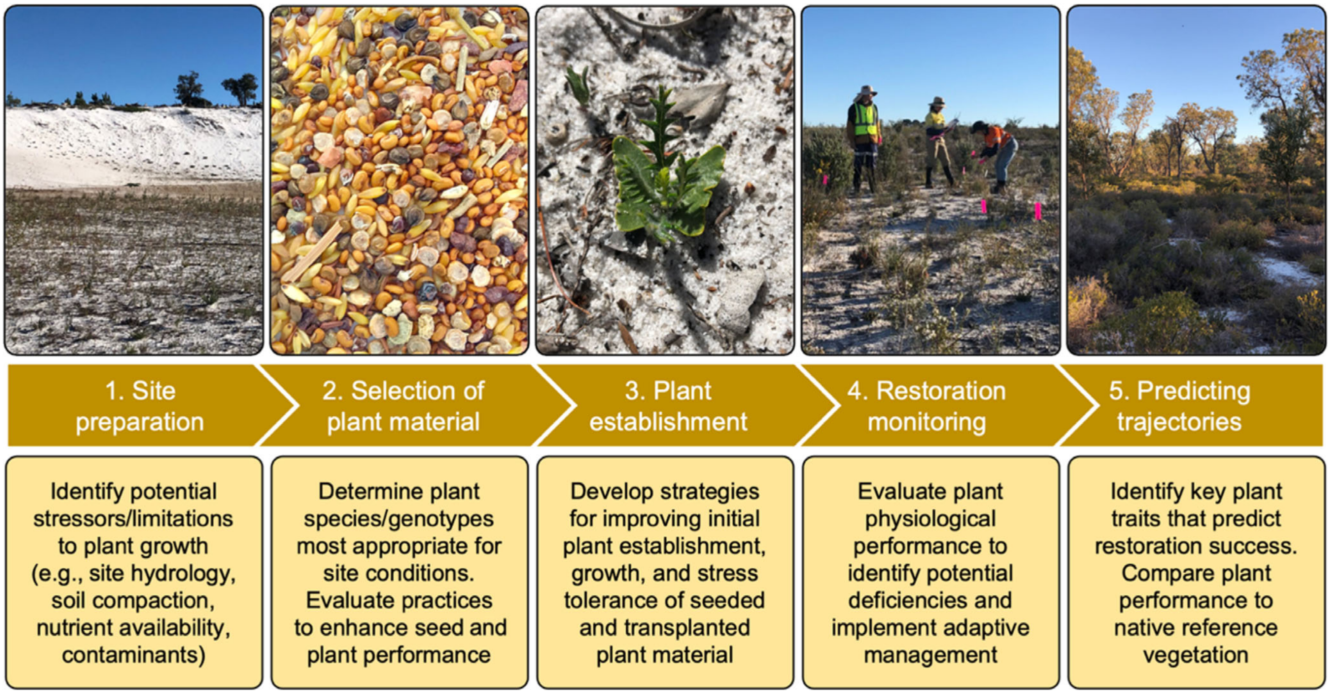

Figure 1. Overview of the ways in which an ecophysiological approach can guide mine-site restoration planning, implementation, and monitoring and ultimately improve restoration outcomes, including (1) guiding site preparation; (2) informing the selection of plant material; (3) optimizing plant establishment and survival; (4) aiding monitoring of restoration outcomes; and (5) advancing our ability to predict restoration trajectories.

WA, explicit consideration of soil compaction, site hydrology, and soil water availability is critical for restoration planning. For example, in *Banksia* woodlands, which grow on deep dunal sands, many species have distinct ecohydrological niches in regard to depth to groundwater (Fig. 2). Subsurface soil hardening constrains plant establishment following sand extraction by impeding seedling emergence, root growth, and penetration (Rokich 2016), culminating in increased drought stress and

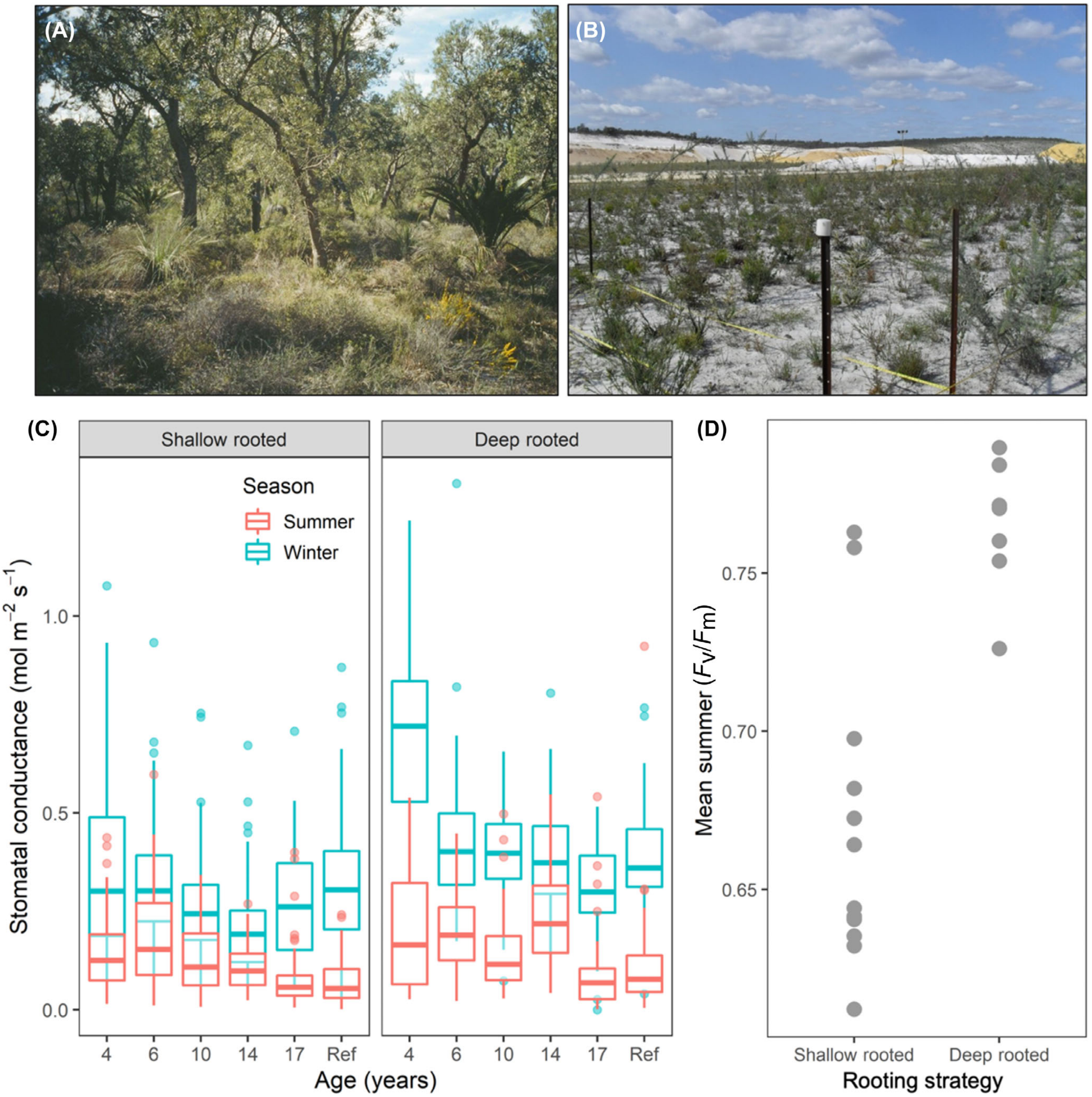

Figure 2. At a sand mine site in Southwest Australia, where Banksia woodland vegetation (A) is being restored (B), the dry summer of the Mediterranean-type climate represents a severe stress for plants, compared to the cool moist winter. Stomatal conductance (C) can be used as an indicator of plants' access to water to sustain transpiration. Nineteen species, representing trees, shrubs, and perennial herbs, were measured in 2020–2021 at restoration sites of different ages as well as reference sites (labeled "Ref"). The species are classified as shallow rooted (<2 m) or deep rooted (>2 m) based on Pate and Bell (1999) and Veneklaas and Poot (2003). Deep-rooted species showed evidence of better access to water; however, stomatal conductance tends to decline with age of the restoration site, which may indicate gradual depletion of water stored in the profile and increasing competition between plants. Poor access to water makes shallow-rooted plants prone to photoinhibition during the hot and sunny summer, which is expressed as low photochemical efficiency (F_v/F_m) (D).

higher mortality. Amelioration through ripping and/or the use of more favorable material may be possible, but these measures do not always cause permanent solutions (Rokich 2016). Similarly, in the semi-arid Pilbara, post-mining seedling establishment is strongly influenced by interactions between substrate type and water availability (Muñoz-Rojas et al. 2016), and ecophysiological studies have proven useful for evaluating the effect of different substrates on seedling establishment, water use, and drought sensitivity (Bateman et al. 2018).

Many aspects of reconstructed substrates (e.g. depth and texture) are permanent, but other soil properties may be manipulated following reconstruction to improve plant performance. Ecophysiological data can be used to identify potential belowground obstacles for restoration and determine appropriate post-reconstruction treatments. Practitioners may be able to improve establishment and drought tolerance through the creation of more micro-topographically and micro-climatically complex soil surfaces, achieved through the incorporation of litter, mulch, waste rock, or surface ripping into cover designs (Szota et al. 2007; Benigno et al. 2013). For example, Ruthrof et al. (2016) found that soil ripping resulted in higher stomatal conductance and more favorable leaf water potentials in *Eucalyptus gomphocephala* seedlings, suggesting this method improves plant access to soil moisture.

Other Climate Factors

Other climate variables (e.g. light, temperature, humidity, and wind) in mine sites could exert a strong influence on germination, growth, and survival. In mine sites, these factors may differ substantially from those of natural areas due to the absence of microclimate amelioration from vegetation or differences in landforms. For example, in some ecosystems impacted by mining, solar radiation may be higher in young restoration sites compared to undisturbed systems, which may impose a major stressor on establishing seedlings by reducing photosynthetic capacity via photoinhibition (Lambers et al. 2008). This could be detrimental to species that typically regenerate under some level of canopy cover (McChesney et al. 1995). Increased solar radiation and a lack of vegetation will also lead to higher temperatures in mine sites, resulting in thermal stress, and exacerbating water stress. These climatic factors may produce interactive responses, where the combined effect of coincident high temperatures and solar irradiation may be more stressful than the effects of either factor alone (Valladares & Pearcy 1997). Investigating multivariate drivers of ecophysiological stress—and methods for alleviation—is a critical endeavor in restoration science.

Informing the Selection and Preparation of Plant Material

Plant Ecophysiological Traits and Environmental Tolerances

A key determinant of restoration success is the selection of appropriate plant material (Herman et al. 2014). Species palettes are often dictated by the composition of native reference sites. However, within a plant community, species exhibit a range of resource requirements and stress tolerances (Lambers et al. 2008) that are determined by physiological mechanisms. Understanding the traits and tolerances of target species is critical for restoration; if site conditions do not meet species' resource requirements or exceed tolerance thresholds, restoration attempts are destined to fail. Furthermore, failure to reinstate sustainable populations can result from sub-lethal stressors that compromise demographic processes (James et al. 2013). Studies exploring plant traits (e.g. root growth, nutrition, and plant-water relations) across a diversity of species and environmental conditions (Lamoureux et al. 2016*b*; Bateman et al. 2018; Cross et al. 2021) will allow practitioners to determine those species that are most likely to succeed at a given site. For example, post-mining substrates are often nutrient-poor or contaminated by heavy metals. Evaluating growth and physiological performance under controlled conditions could aid in the identification of species that are most likely to persist under such conditions. Zhong et al. (2021) found that multiple species in the genus *Maireana* are highly efficient at nitrogen (N) resorption, and this trait may allow them to survive in mine tailings. Such pioneer species could be particularly useful for restoration in substrates that are inhospitable to other species.

Functional Traits and Groups

In the absence of empirical data on species' physiology and environmental responses, known functional traits or groups may also be good predictors of plant performance during mine-site restoration (Pywell et al. 2003), and characterizing plant functional types that represent different ecological strategies may also be useful in designing plant palettes (Navarro-Cano et al. 2019). Such classifications are based on physiological, morphological, biochemical, and phenological traits, and may aid practitioners in identifying appropriate species for specific site conditions. For example, in a study that included 40 different native plant species Cross et al. (2019) found some calcicole plant species, N-fixers, and those with cluster roots outperformed calcifuge species, species dependent on mycorrhizal associations, and species without specialized nutrient acquisition strategies in alkaline mine tailings. Functional groups based on rooting and water-use strategies may also be useful for predicting how species will respond to different edaphic conditions and climate scenarios during restoration (Muler et al. 2018).

Intraspecific Trait Variation

Intraspecific trait variation is another important ecophysiological consideration for the selection of plant material (Hufford & Mazer 2003). Populations of the same species can exhibit very different ecophysiological traits which govern how they respond to site conditions. Ecophysiology can be used to link population genetics with environmental responses, thereby guiding the selection of source populations and improving restoration outcomes. The prevailing paradigm has been the idea that "local is best" when choosing plant material, based on the assumption that populations are locally adapted (McKay et al. 2005). However, source populations may also be selected to match plant traits with unique site conditions. For example, Farrell et al. (1996) evaluated plant growth and water use in populations of *Eucalyptus camaldulensis* in response to soil waterlogging, alkalinity, and salinity. The authors found a wide range of tolerances to these extreme conditions and suggested more stress-tolerant genotypes could be used to restore areas impacted by mining. Climate-adjusted provenancing could also aid in establishing plant communities resilient to future climate change (Breed et al. 2013), for example, by selecting genotypes from more arid regions of a species range, as these are more likely to possess physiological traits that confer greater stress tolerance (Prober et al. 2016).

Optimizing Seed Germination and Establishment

Seed-based approaches remain the most commonly employed method of revegetation worldwide (Pedrini & Dixon 2020). The transition from seed to established plants is the largest bottleneck in ecological restoration, with over 90% of establishment failure associated with seed dormancy, germination, and emergence failure (Chambers & MacMahon 1994). Careful consideration of seed ecophysiology may aid practitioners in making every seed count in mine-site restoration (Long et al. 2015; Kildisheva et al. 2020). For example, targeted manipulations and enhancements of seed accessions may be used to break dormancy and improve germination (Cross et al. 2017; Lewandrowski et al. 2017; Turner et al. 2017). Lewandrowski et al. (2017) alleviated seed dormancy of keystone *Triodia* grass species through wet–dry cycling treatments prior to seeding, thereby improving germination success in the field (Fig. 3). Similarly, Turner et al. (2017) demonstrated improved germination in the threatened species *Ricinocarpos brevis* under drought after treating seeds with the stimulant karrikinolide. By quantifying tolerance thresholds to environmental and edaphic factors, the identification of suitable germination niches can also be used to guide appropriate site selection (Rajapakshe et al. 2020) and preparation (Merino-Martín et al. 2017) to maximize seedling establishment. A greater understanding of seed functional traits will aid in these endeavors (Saatkamp et al. 2019).

As seed germination is driven by metabolic processes (Bewley et al. 2012), future directions for seed ecophysiology

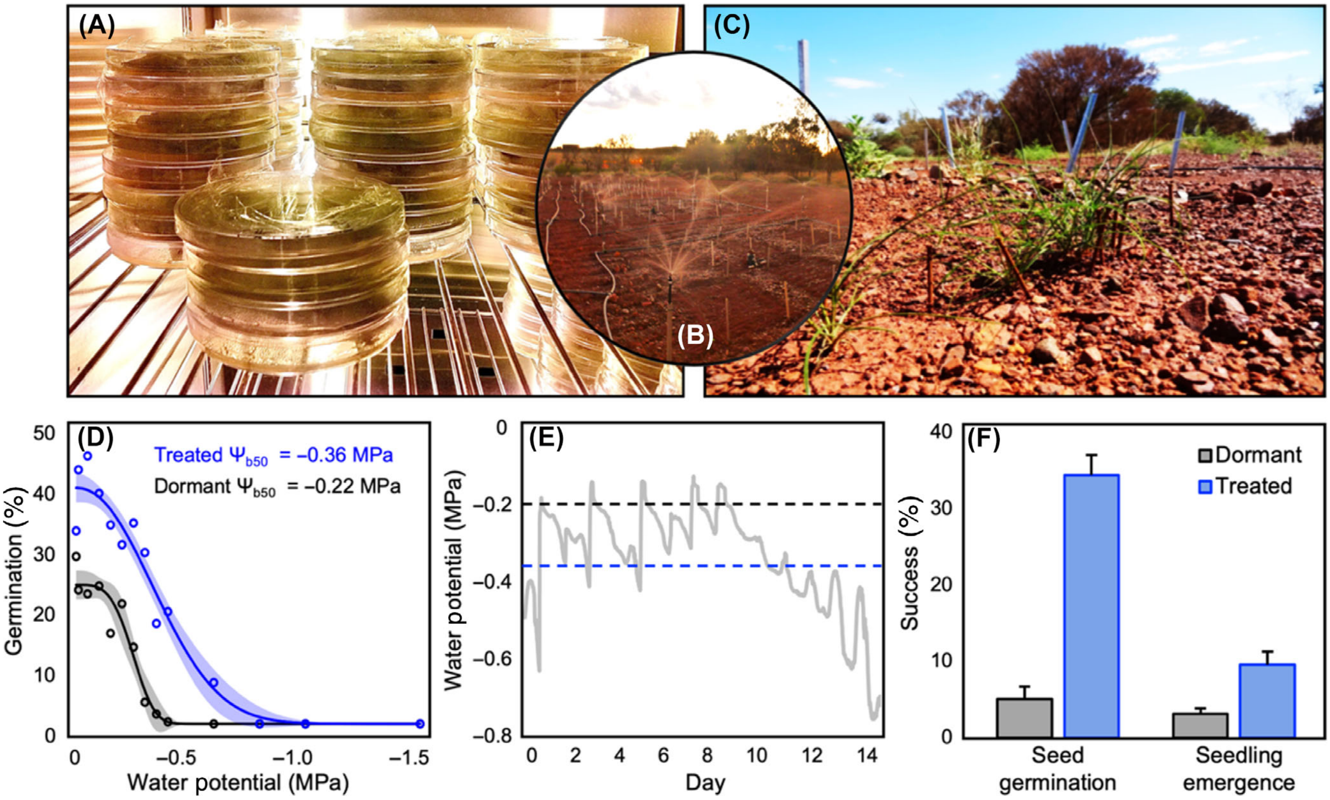

Figure 3. Case study demonstrating how ecophysiological studies in the laboratory and field informed seed treatments in *Triodia epactia* for arid-zone restoration in the Pilbara, Northwest Western Australia (adapted from Lewandrowski et al. 2017). A series of controlled laboratory (A) and field (B,C) studies were conducted to manipulate seed dormancy and understand germination potential under drought conditions. After treating seeds for dormancy, seed germination envelopes widened into more negative water potentials, indicating that seeds were able to tolerate lower water availabilities (D). Treated (blue) and untreated dormant (black) seeds were exposed to a gradient of rainfall regimes in the field (B), mimicking precipitation events varying in different amounts and frequencies (E). At a 4 × 24 mm rainfall regime, treated seeds with a more negative germination threshold could take advantage of lower soil water availability (E), which promoted greater recruitment success (C) by increasing germination and emergence proportions in sown seeds (F).

should include measuring seed metabolic rate to optimize seed storage and utilization. For example, Dalziell and Tomlinson (2017) demonstrated a strong linear relationship between seed respiration and the percentage of viable seed in stored cohorts, and (Tomlinson et al. 2018) showed that dormant seeds have lower seed metabolic rates compared to non-dormant or dormancy-alleviated seeds. Greater accessibility of these tools to restoration practitioners and seed collectors/suppliers could prove useful for seed-based revegetation efforts.

Developing Strategies to Optimize Plant Establishment

Environmental Manipulations

Ecophysiological tools can be used to evaluate how plants respond to management strategies and develop best practices to facilitate establishment. Outplanting nursery-grown plants is often more expensive and resource-intensive than sowing seed, and typically restricted to rare, endangered, or keystone species. Physiological assessment of transplanted individuals could be particularly useful for detecting and ameliorating drivers of plant stress before these result in mortality (Fig. 4), thereby improving outplanting success and cost effectiveness. Such interventions could include irrigation (Elliott & Turner 2021), fertilization (Tibbett et al. 2020), and soil covers or amendments (Lamoureux et al. 2016*a*). Microbial inoculations of transplants, including soil bacteria or mycorrhizal fungi, may also be a useful strategy for overcoming the negative impacts of soil disturbance on belowground biota and improving plant performance and stress tolerance (Wubs et al. 2016; Valliere et al. 2020). Conversely, some practices can be detrimental, such as the greater mortality rates from thermal stress induced by the use of plastic tree guards in WA's *Banksia* woodlands (Close et al. 2009). Guards constructed from shade cloth, however, did not have these negative effects and also improved plant photosynthesis, growth, and survival (Close et al. 2009; Rokich 2016).

Plant Conditioning

In addition to choosing appropriate plant palettes for restoration projects, practitioners may also consider how methods of propagation may influence plant establishment following outplanting. In some instances, it may be possible to condition nursery-grown seedlings prior to outplanting to improve stress tolerance in the field (Valliere et al. 2019). For example, Valliere et al. (2019) found that in some species, plants that had previously experienced a drought event exhibited improved growth and higher water-use efficiency and specific leaf area compared to seedlings that were well-watered prior to transplanting. However, such stress conditioning cannot be assumed, and multiple stress events could also lead to reduced plant performance or death; Benigno et al. (2014) found biphasic drought reduced physiological resilience and led to high levels of mortality in multiple native tree species from WA.

Rare Species Translocation

Mining sometimes impacts rare or threatened species, necessitating translocation to other sites. However, translocation efforts often fail to establish self-sustaining populations, in part due to a lack of knowledge on species' ecophysiological requirements and selection of unsuitable recipient sites (Silcock et al. 2019). For example, the high microclimatic variability of banded ironstone formations (BIF) in WA probably contributes to their high plant diversity and endemism (Gibson et al. 2010; Byrne et al. 2019), but this also makes identifying suitable translocation sites for BIF species challenging. Understanding species' niche requirements can help guide site selection and optimize plant establishment. High-resolution species distribution modeling and fine-scale habitat assessments have been used to identify areas in these landscapes that meet species' microclimatic and edaphic requirements (Miller et al. 2015; Tomlinson et al. 2020). By linking germination profiles with long-term climate averages, windows of opportunity for establishing populations of range-restricted species from seed in areas with variable precipitation can be identified. For example, the correlation between time required for germination and soil moisture residence following rainfall was reported for six threatened BIF species (Elliott et al. 2019), suggesting supplementary irrigation at translocation sites may be required. Ultimately, translocations guided by theoretical expectations should be tested by long-term monitoring of translocated individuals, and physiological assessments could be an important tool for understanding drivers of translocation success (Fig. 4).

Using Ecophysiology to Monitor Restoration Outcomes

Moving beyond Traditional Restoration Monitoring

Monitoring activities, while a critical element of restoration, typically evaluate community-level metrics, such as plant cover, richness, and abundance (Ruiz-Jaen & Mitchell Aide 2005). Although these parameters are useful for quantifying restoration progress, deficiencies in plant performance may not be detected until plants are visibly dead or dying, and stress-induced demographic constraints will only become apparent as intergenerational recruitment failure. Physiological measurements may reveal such deficiencies before they manifest at the community level and provide the opportunity for adaptive management (Cooke & Suski 2008). Multiple laboratory and field-based techniques can provide a mechanistic understanding of plant performance during restoration (Table 1), enhancing the value of traditional monitoring by identifying sources of plant stress or limitations to growth and survival (Kimball et al. 2016). For example, measures of leaf water potential, stomatal conductance, and gas exchange can yield valuable information on plant water use, access to soil water, and drought tolerance. Nutrient and isotopic analysis of leaf tissue can also provide insight into multiple facets of plant physiological performance and be used to compare plant health among sites of different ages or with different management histories; carbon (C) isotope ratios ($\delta^{13}C$) can be used to assess plant water use, N isotope ratios ($\delta^{15}N$)

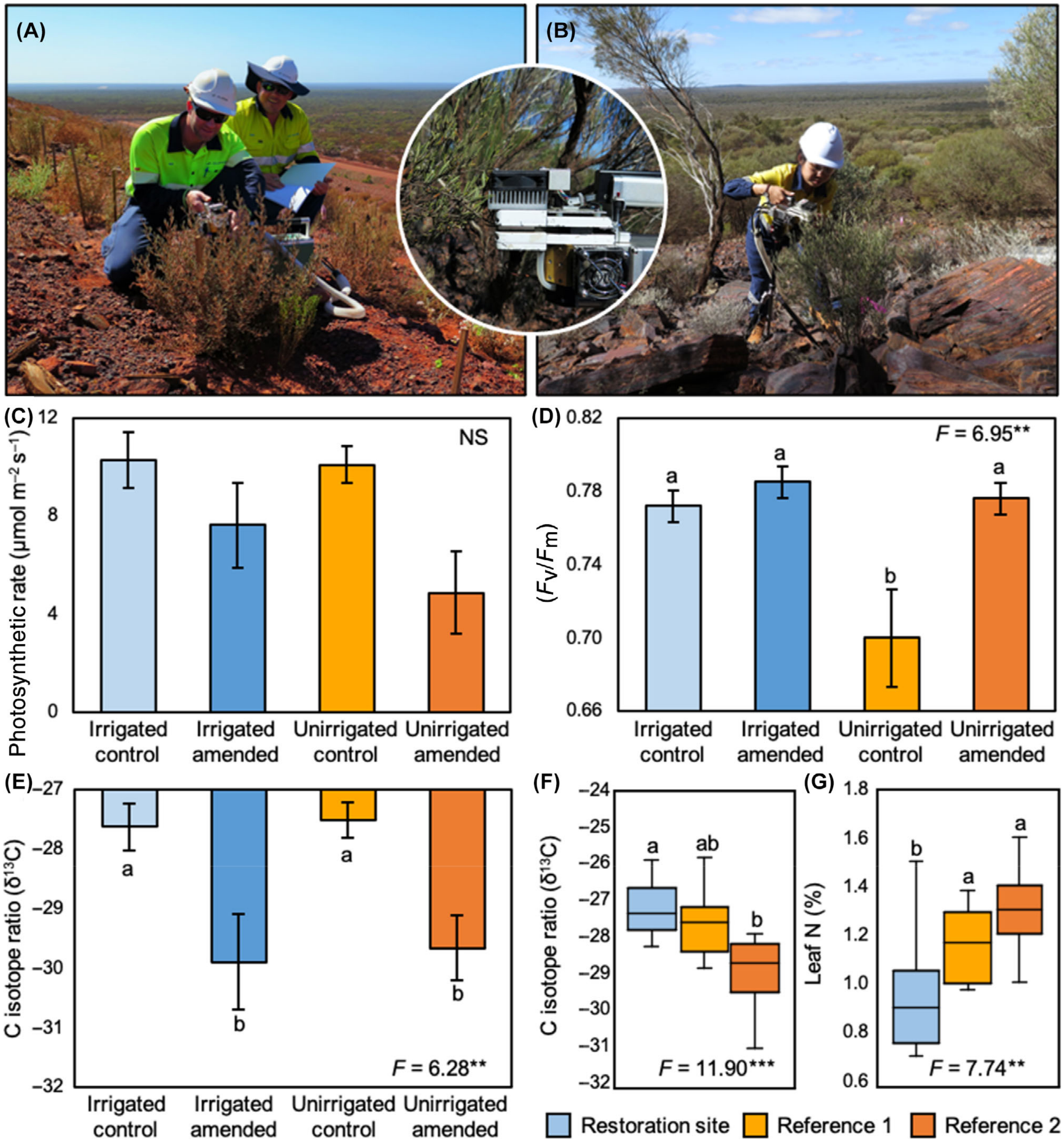

Figure 4. We recently used ecophysiological measurements to monitor restored populations of the rare endemic species *Ricinocarpos brevis* (Euphorbiaceae), which is threatened by mining in banded ironstone formations of Western Australia. Multiple measures of plant physiology were used to understand the performance of transplanted individuals at a restored waste rock site (A) and to compare the performance of these individuals to natural populations of this species in native reference vegetation (B). Based on short-term instantaneous measurements, we found no effect of irrigation (irrigated vs. unirrigated) or amending soil with water-holding crystals (amended vs. control) on photosynthetic rates (C) of plants (measured using a portable photosynthesis system; pictured center top). Measures of chlorophyll fluorescence (D) and long-term stable C isotope ratios (E) revealed that soil amendments reduced water stress; unirrigated plants that received no soil amendments exhibited the lowest chlorophyll fluorescence (D), indicating greater levels of plant stress, and stable C isotope data showed that plants that received soil amendments experienced less water stress than untreated controls (E). Complementary data on plant survival also showed that irrigation generally reduced plant mortality (Elliott & Turner 2021), and our physiological measurements highlighted that treatments that improve soil moisture could be important for promoting establishment success even in the absence of irrigation. However, comparisons of restored and natural populations also showed that restored plants may experience greater water stress (F), and these plants (grown in waste rock material) also exhibited significantly lower leaf N content. Together, these data provide important insight into the efficacy of restoration activities for this species. *F* values and significance from analysis of variance (ANOVA) are shown (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.0001$; NS, not significant). Different letters above bars indicate significant differences (from Tukey's HSD tests).

can provide insight into sources of plant N, and oxygen (O) isotope ratios ($\delta^{18}O$) can be used to understand from which soil layers (or groundwater) plants take up water (Dawson et al. 2002; Craine et al. 2015).

Instantaneous Measurements: Limitations and Alternatives

Given the complexity of plant physiological responses to their environment, isolated, and instantaneous measurements are inevitably limited in the information they can yield. Unfortunately, long-term studies that include repeated measures of physiological functioning in restored vegetation are lacking, due to the time and resources generally required for such undertakings (Cooke & Suski 2008). There are potential solutions and alternatives for overcoming this challenge. First, identifying traits that are easily measurable and can serve as indicators or proxies for key plant physiological functions or responses will increase the feasibility of ecophysiological measurements being incorporated into monitoring (Fig. 5). Alternatively, the use of chronosequences (i.e. measuring plant traits in restoration sites of different ages) may provide useful data on temporal trends in the absence of repeated measures in the same site (Fig. 2). Finally, using a functional trait framework to monitor patterns over time (either through repeated monitoring data or the use of chronosequences) could be more easily implemented than direct physiological measurements but still yield useful information on plant responses to site conditions. This could be particularly useful in hyper-diverse plant communities (such as those of WA) where high species richness complicates efforts to identify generalizable patterns (Tsakalos et al. 2019). This could allow practitioners to identify patterns of community composition over time in response to different restoration methods (Riviera 2019), potentially identifying how different management activities influence the environmental filtering of functional groups or traits.

Scaling up Ecophysiological Monitoring

While current techniques to assess plant physiological performance are often time-consuming and infeasible at larger spatial scales, remote sensing and drone-based technologies may enable assessment of plant physical and chemical characteristics and stress levels at spatial scales that match the growing land area undergoing restoration (Jones & Vaughan 2010). Two methods have been widely applied to obtain proxies of plant

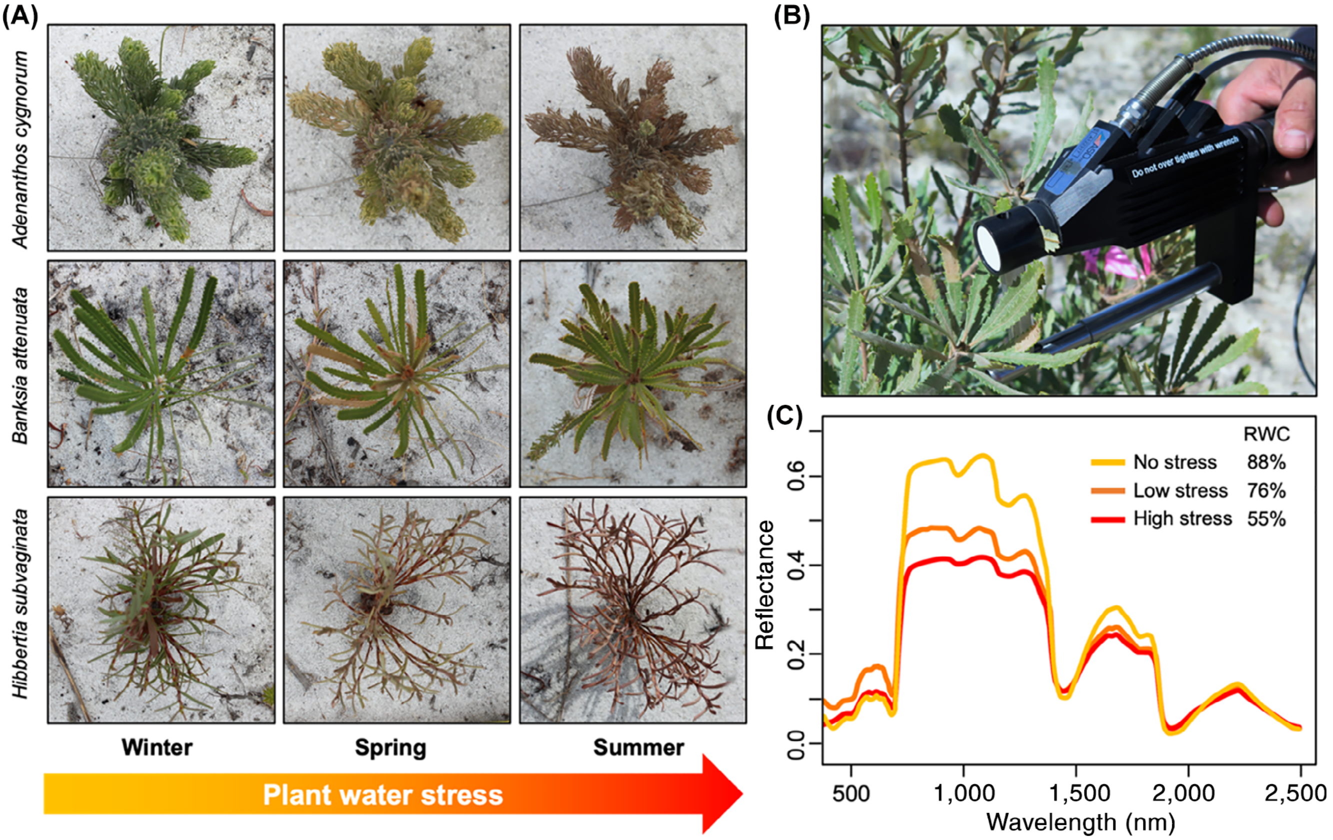

Figure 5. Case study illustrating the potential application of hyperspectral reflectance for evaluating plant water stress in a restoration context. Individual plants of native Banksia woodland species (A) including *Adenanthos cygnorum*, *Banksia attenuata*, and *Hibbertia subvaginata* were monitored using a field spectroradiometer (B) across a temporal gradient of climate stress, from winter to summer, in a 4-year old restored sand mine site in Western Australia. In some species (e.g. *Hibbertia subvaginata*), reflectance data (C) showed unique hyperspectral signatures for plants under varying levels of water stress, which can be related directly to the relative water content (RWC) of leaves. Such an approach could allow for more rapid assessments of plant water-status compared to traditional ecophysiological methods and also form the basis for remote sensing of vegetation conditions at larger spatial scales (though limitations remain).

physiological traits: hyperspectral reflectance and thermal imaging. Plant reflectance is mostly related to water content, pigment levels, and leaf and canopy structure (Chuvieco 2016), such that hyperspectral data can be directly related to leaf water potential (Rallo et al. 2014), pigment content in response to plant stress or nutrient deficiencies (Marchesini et al. 2016), and chlorophyll fluorescence (Zarco-Tejada et al. 2000). Thermal imaging allows for the estimation of plant transpiration rates based on the cooling effect of evaporation on leaf temperature (Berni et al. 2009). Despite some noted sources of measurement uncertainty (Jones et al. 2003), remote sensing of natural and restored vegetation has evolved from the basic capacities of early multi-spectral vegetation mapping into complex multi-sensor approaches, such as the combination of LiDAR and air-borne hyperspectral data for the estimation of forest canopy chemical traits (Asner et al. 2015).

Interpreting remotely sensed data from biodiverse ecosystems with complex canopies requires a detailed understanding of the relationship between sensor data and physiological processes at different stress levels and spatial resolutions (Calderón et al. 2013). Therefore, any potential application of these methods for monitoring of heterogeneous vegetation should experimentally validate relationships between remote sensing measurements and changes in plant physiology. This will be especially important for plant communities with a range of functional and structural types that show diverse responses to environmental stress. Validation can be achieved by first studying these relationships at a smaller scale to understand the potential applications and limitations of each approach (Fig. 5). Once methodological foundations are established, these may be scaled up to remote imaging platforms that allow for monitoring of larger areas in shorter periods of time, with the final goal of implementing large-scale restoration monitoring.

Comparison to Native Reference Vegetation

Although systematic physiological comparisons between restored areas and natural reference vegetation are critical for evaluating restoration trajectory, they are rarely undertaken. The few studies that have made such comparisons highlight the complexity of plant responses to restoration conditions. For example, in drought-prone sites in WA, such studies have shown that restored vegetation may experience greater (Szota et al. 2011), less (Bleby et al. 2012), or more variable stress (Benigno et al. 2013) compared to reference vegetation. Interpretation of these contrasts often requires an understanding of above- (e.g. microclimate) and belowground phenomena (e.g. soil moisture and root growth) that influence plant responses. For example, Bleby et al. (2012) found that *Eucalyptus marginata* saplings at a restored bauxite mine site exhibited four times higher transpiration per unit leaf area than those in natural forests, due to greater availability of water, light, and nutrients, and these changes were accompanied by substantial differences in biomass allocation, hydraulics, and stomatal regulation. At a nearby location, where stunted growth was observed in restored sites, these trees were shown to have lower water status and water use, which could be attributed to local subsoil constraints limiting rooting depth (Szota et al. 2011).

Comparisons between restored and reference vegetation are inevitably influenced by the selection of sites and plants since plant physiology dynamically adjusts to site conditions and shows ontogenetic or size-dependent patterns. Plants in restored ecosystems are faced with different climatic, edaphic, and biological challenges than plants in natural ecosystems, so physiological observations should be interpreted accordingly. Measurement of a greater number of variables provides much-improved opportunities for interpretation. For example, water status and use are best interpreted in conjunction rather than in isolation, as some species reduce transpiration to avoid dehydration, whereas others in the same environment allow a degree of dehydration to maintain transpiration rates. Researchers may use different criteria when selecting reference sites and plants to account for these differences. Bleby et al. (2012) chose trees of specified sizes in their reference sites, to control for likely size effects of the water relations of trees, considering that the trees they studied at restoration sites were of different sizes at different ages of restoration. Benigno et al. (2013) removed aboveground biomass at their reference sites to ensure that comparisons between restoration sites (with different soil amendments) and reference sites were not confounded by aboveground effects.

Ecosystem Functioning and Services

While ecosystem processes and services are increasingly appreciated and considered in mine-site restoration, they remain understudied (Prach & Tolvanen 2016). Ecophysiological tools can enhance our ability to quantify these processes, including as ecosystem-level water fluxes, nutrient pools and cycling, soil development, rates of primary production, and C sequestration (Eamus et al. 2005; Suding et al. 2008). For example, Shrestha and Lal (2006) proposed a framework for estimating ecosystem C budgets of restored coal mines, which can be directly compared to industry CO_2 emissions, and measures of evapotranspiration have been used to investigate ecohydrological feedbacks between site conditions and vegetation water use in restored mine sites (Arnold et al. 2012). Elemental and isotopic analyses of plant litter can be used to understand soil development and nutrient dynamics. These have been used to compare nutrient cycling in restored eucalypt forests following bauxite mining to undisturbed forests in WA, with results suggesting that even as vegetation recovers in restored sites, there may be impediments to decomposition (Tibbett 2010). Finally, stable isotopes of C can also be used to understand patterns of soil C sequestration. For example, the C isotope composition of soil organic matter in restored eucalypt forests has shown that soil C profiles may recover to predisturbance levels over time (George et al. 2010).

Applying Ecophysiology to Predict Restoration Outcomes

Can Ecophysiological Measurements Be Used to Predict Restoration Success?

Whether ecophysiological plant traits can predict plant community assembly and persistence, and ultimately, restoration success, remains a key question in restoration ecology (Pywell et al. 2003; Balazs et al. 2020). The practice of restoration would benefit tremendously if we could identify traits that can be measured early during restoration that provide insight into long-term trajectories. This could also allow for adaptive management to be employed more rapidly, possibly averting restoration failure. If indeed such predictors exist, they are likely to be species-specific and context dependent, highlighting the importance of selecting the most informative traits, the most significant species, and the most appropriate study sites. Isolated physiological measurements are unlikely to be very informative for restoration practitioners. Interpretation of physiological data often requires auxiliary data on environmental conditions, and such data should be considered alongside observations of plant growth and reproduction. Furthermore, restoration ecophysiologists can only study species that are present at the restoration site. The initial species composition at restoration sites is largely determined by species planted, sown, or remaining in topsoil. Since restoration sites, especially post-mining sites, are often substantially different from natural systems, initial species present may not be those that are best adapted. Future restoration trajectories may also be influenced by colonizing native and non-native species, whose success is difficult to predict. An integrative approach, repeated over time to identify temporal trends, across a diversity of species, will provide the best chance of predicting future plant performance and restoration trajectories.

Targeted Ecophysiological Measurements to Predict Restoration Outcomes

There are certainly questions about restoration success that can be answered by targeted ecophysiological research. For example, in water-limited ecosystems, the measurement of traits associated with water acquisition provides useful indicators of plant survival. For deep-rooted phreatophytes, accessing groundwater in restoration sites may be a key determinant of long-term resilience. Ecophysiological methods, such as evaluations of leaf water potential during periods of seasonal drought or stable isotope analysis, may allow practitioners to identify when and where (i.e. under which management practices) plant roots have penetrated to groundwater. Similarly, the performance of some plant species is contingent upon successful association with symbiotic soil biota (e.g. mycorrhizal fungi or N-fixing bacteria), and methods such as stable isotope analysis of N may provide a non-destructive means for evaluating if these biotic associations have been established. It may be possible to utilize indicator species that serve as bellwethers of long-term restoration success (Bal et al. 2018). The physiological performance of such species may be indicative of overall community trajectories. Potential candidates could include dominant foundation species (e.g. *Triodia* grasses in the Pilbara or *Banksia* species of coastal woodlands in WA) or pioneer species that are important for soil development and facilitation of subsequently colonizing species (e.g. N-fixing species).

Challenges and Future Directions

Ecophysiology clearly has the potential to guide ecological restoration, but challenges to its implementation remain (Cooke & Suski 2008). Since traditional metrics (e.g. plant cover) typically form the basis of restoration targets, physiological measurements may not be considered a high priority. A lack of funding, technical expertise, or specialized equipment may also prevent practitioners from implementing such an approach, and collaborations with researchers will be important for overcoming this challenge. Identifying traits that are easily measured yet still yield insight into plant health (e.g. Fig. 5) will also increase the likelihood of ecophysiology being incorporated into restoration planning and monitoring. At any given site, the value of physiological data will progressively increase when comparative approaches are used to provide understanding of temporal trends and contrasts between species with different ecological preferences. As physiological measurements are incorporated into more restoration projects and for an increasing number of species, large, open-access databases for plant trait data will also be valuable for identifying research gaps, leveraging the utility of existing data, and incorporating ecophysiological approaches into future projects (Kattge et al. 2020). Finally, partnerships between stakeholders in industry, restoration, and research, such as in the examples highlighted here, will play a critical role in the integration of plant ecophysiology and restoration.

Conclusions

As a global hotspot of biodiversity and mining activity, the restoration of ecosystems impacted by resource extraction is a pressing environmental concern in WA and has thus received considerable attention. The existing literature and case studies highlighted here illustrate how mine sites undergoing restoration in the region have served as a valuable natural laboratory for testing management strategies for severely disturbed landscapes. However, given the extreme floristic, edaphic, and climatic diversity and complexity of these ecosystems, much work remains to develop transferable, evidence-based methods for restoration. We posit that a greater integration of ecophysiological perspectives and measurements into such endeavors will further strengthen the practice and science of restoration in WA and beyond. With careful selection of study species and traits and consideration of the specific environmental conditions and stressors within a site, the restoration ecophysiology framework outlined here (Fig. 1) has the potential to inform restoration strategies in any ecosystem.

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