DOI: 10.1016/j.scitotenv.2017.07.005

Young calcareous soil chronosequences as a model for ecological restoration on alkaline mine tailings

Adam T. Cross[1,2,3,4], Hans Lambers[2]

[1]- *Centre for Mine Site Restoration, Department of Environment and Agriculture, Curtin University, GPO Box U1987, Bentley WA 6102, Perth, Australia*

[2]- *School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Perth, Australia*

[3]- *Kings Park and Botanic Garden, Kings Park, WA 6005, Perth, Australia*

[4]- *Corresponding author, adam.cross@curtin.edu.au*

Running head: Accelerating soil development on alkaline tailings

Keywords: pedogenesis; mine tailings; soil acidification; soil weathering; plant mineral nutrition

Abstract

Tailings are artificial soil-forming substrates that have not been created by the natural processes of soil formation and weathering. The extreme pH environment and corresponding low availability of some macro- and micronutrients in alkaline tailings, coupled with hostile physical and geochemical conditions, present a challenging environment to native biota. Some significant nutritional constraints to ecosystem reconstruction on alkaline tailings include i) predominant or complete absence of combined nitrogen (N) and poor soil N retention; ii) the limited bioavailability of some micronutrients at high soil pH (e.g., Mn, Fe, Zn and Cu); and iii) potentially toxic levels of biologically available soil phosphorus (P) for P-sensitive plants. The short regulatory time frames (years) for mine closure on tailings landforms are at odds with the long time required for natural pedogenic processes to ameliorate these factors (thousands of years). However, there are similarities between the chemical composition and nutrient status of alkaline tailings and the poorly-developed, very young calcareous soils of biodiverse regions such as south-western Australia. We propose that basic knowledge of chronosequences that start with calcareous soils may provide an informative model for understanding the pedogenic processes required to accelerate soil formation on tailings. Development of a functional, stable root zone is crucial to successful ecological restoration on tailings, and three major processes should be facilitated as early as possible during processing or in the early stages of restoration to accelerate soil development on alkaline tailings: i) acidification

of the upper tailings profile; ii) establishment of appropriate and resilient microbial communities; and iii) the early development of appropriate pioneer vegetation. Achieving successful ecological restoration outcomes on tailings landforms is likely one of the greatest challenges faced by restoration ecologists and the mining industry, and successful restoration on alkaline tailings likely depends upon careful management of substrate chemical conditions by targeted amendments.

Introduction

The restoration of vegetation on mine tailings, the fine-particulate residue wastes of ore processing, represents one of the greatest challenges faced by the mining industry and restoration practitioners in the 21st century (Jamieson 2011). The successful reinstatement within reasonable time scales of biodiverse, representative and self-sustaining communities on tailings landforms is a stringent closure requirement of many mine sites in biodiverse regions such as Western Australia (e.g., EPA 2009a,b), and is an aspiration of newly-formulated international standards for the practice of ecological restoration (McDonald *et al.* 2016). However, the global increase in tailings production in recent decades has occurred asynchronously with our understanding of the processes by which vegetation on tailings landforms can be effectively restored. Though the accumulative footprint of tailings storage facilities is already estimated to cover millions of hectares and continues to rise (Huang *et al.* 2012), successful ecological restoration to full ecosystem recovery (the point at which all ecosystem attributes closely resemble those of a reference ecosystem; McDonald *et al.* 2016) on a tailings landform has not yet been achieved anywhere in the world. A lack of practical, cost-effective restoration solutions impacts upon biodiversity, jeopardises the economic viability of mining, and compromises the social and environmental license of industry to mine.

Tailings are commonly produced as a byproduct of the extraction and processing of primary minerals such as iron, gold, aluminium, copper, lead and zinc (Jamieson 2011). These minerals are often associated with geologically ancient landforms in very old, climatically-stable, low-rainfall landscapes such as South Africa, south-western Australia, Brazil, and southern North America (e.g., Gordon *et al.* 1958; Beukes 1973; Sadleir and Gilkes 1976; Schidlowski *et al.* 1976; Anand and Paine 2002; Hopper 2009). Annual tailings production in south-western Australia, for example, a global biodiversity hotspot supporting a mining industry worth approximately $100 billion employing over 100,000 people (DMP 2016), is now estimated to significantly exceed a billion tonnes (Mudd 2009; Geoscience Australia 2013). Tailings production is frequently associated with unique novel landforms in geologically-ancient regions such as Western Australia, and the vegetation assemblages of ecosystems in old and climatically stable landscapes often comprise diverse suites of well-adapted plant and microbial communities on shallow, acidic and deeply-weathered soils (Anand and Paine 2002; Hopper 2009; Hopper *et al.* 2016). These communities often comprise many endemic, range-restricted, and highly-specialised taxa, to which unweathered tailings represents a very different, challenging, and potentially hostile substrate (Fig. 1). Though previous studies have examined the geochemical factors limiting plant establishment and growth in acidic tailings (e.g., Shu *et al.* 2001; Jurjovec *et al.* 2002; Paradis *et al.* 2007; Huang *et al.* 2011, 2012), many mining operations are producing extremely large volumes of highly-alkaline material that poses a different yet equally hostile environment to native biota (Jamieson 2011; Santini and Banning 2016; Santini and Fey 2016).

Organisms are sometimes naturally exposed to the challenge of recolonising new substrates following catastrophic disturbance events such as landslides, glacial retreat, volcanic activity or tsunamis (Sousa 1984; Łaska 2001). The physical and geochemical characteristics of newly formed substrates following disturbances such as these can contrast starkly with the surrounding undisturbed landscape, but the geochemical environment is affected over time by natural weathering processes resulting in soil chronosequences: a sequence of soils derived from the same parent material and developed on similar relief under the effect of constant climatic and biotic factors (Stevens and Walker 1970). Analysis of nutrient dynamics during pedogenesis along chronosequences in many regions of the world indicates that pedogenesis follows a general pattern in a dynamic process closely linked with vegetation dynamics (Walker and Syers 1976; Wardle *et al.* 2004; Laliberté *et al.* 2012; Turner and Laliberté 2015). However, natural shifts in nutrient dynamics during pedogenesis occur over hundreds, thousands or even millions of years (Walker and Syers 1976; Wardle *et al.* 2004; Laliberté *et al.* 2012; Turner and Laliberté 2015); time scales that contrast starkly with the mandated expectations of mine-site restoration projects (5–7 years) provided by regulatory bodies (e.g., EPA 2009a,b). So, how might thousands of years of pedogenesis and vegetation development on alkaline tailings be achieved in under a decade, taking advantage of the basic knowledge available on soil chronosequences? We propose that soil chronosequences, particularly those of marine origin along the coast of Western Australia, provide guidance for a methodological approach towards achieving this challenging target.

Pedogenesis on young alkaline soils

The biogeochemical changes in soils during pedogenesis follow a relatively predictable pattern over long geological time scales, with a shift in nutrient status from nitrogen (N) limitation of primary productivity on young soils to extreme phosphorus (P) limitation on old soils (Walker and Syers 1976; Lambers *et al.* 2008a; Turner and Condron 2013). Pedogenesis is mainly driven by changes in pH, organic matter and nutrient availability resulting from chemical and biological transformations (Turner and Laliberté 2015; Turner *et al.* 2017). Chronosequences of soils along coastal sand dunes in old and climatically-buffered landscapes in south-western Australia indicate that soils develop slowly from calcareous sand (<6500 years old) to deeply weathered decalcified sand (>2 million years old), although the rate of soil development depends on parent material and processes such as erosion, root metabolism and microbial activity, which are influenced primarily by rainfall and temperature (Laliberté *et al.* 2013; Turner and Laliberté 2015; Turner *et al.* 2017). Young soils are generally high in P but low in organic carbon and N (Lambers *et al.* 2008a; Laliberté *et al.* 2012; Turner and Laliberté 2015; Turner *et al.* 2017). The stoichiometry of major soil elements (particularly N, P and organic carbon) appear to be important drivers of vegetation composition and species diversity (Sykora *et al.* 2004; Wardle 2004; Laliberté *et al.* 2013), as the nutrient-acquisition strategies of plants shift in response to the changes in nutrient status from N limited to P limited (Fig. 1; Lambers *et al.* 2008b; Hayes *et al.* 2015; Zemunik *et al.* 2016, 2017).

Soil P is lost from the biosphere over long time periods during pedogenesis, predominantly through erosion and leaching, but also as a result of chemical and biological transformations that convert primary mineral phosphate into occluded forms (Walker and Syers 1976; Turner *et al.* 2007). However, the availability of N is driven predominantly by biological processes, most importantly biological N_2-fixation, and that of some micronutrients by a gradual acidification of the soil (Lambers *et al.* 2008a; Baumann *et al.* 2009). Soil N accumulates rapidly in young soils through biological N_2 fixation (Menge and Hedin 2009), primarily by free-living soil microbes (Nemergut *et al.* 2007; Van Der Heijden *et al.* 2008) and symbiotic N_2 fixation (Cleveland *et al.* 1999; Lambers *et al.* 2008a). Plant roots exhibit a diverse range of mechanisms by which they alter the biogeochemistry of their rhizosphere (Hinsinger *et al.* 2003, 2009), and in addition to contributing to rhizosphere acidification, the exudation of C compounds by plant roots significantly enhances soil microbial activity (Hinsinger 2001). Soil microbial communities are also important drivers of decomposition processes and play a major role in determining nutrient bioavailability (Wardle 2004). Natural soils support significantly greater microbial diversity, functional composition and biomass than do tailings (and these factors are likely to also vary between tailings created from different parent materials with different physical, hydrological, and geochemical properties). However, a degree of functional redundancy has been observed in tailings inoculated with even small amounts of stored topsoil (Kumerasan *et al.* 2017).

Young soils of marine origin may be highly alkaline (pH 8–9) and contain abundant carbonate and iron oxides which are leached from the profile over several thousands of years (Laliberté *et al.* 2012; Turner and Laliberté 2015; Turner *et al.* 2017). However, numerous studies present evidence for pH gradients from alkaline to acidic as soil age increases along chronosequences (Jobbágy and Jackson 2003; Nierop *et al.* 2003; Laliberté *et al.* 2012, 2013; Turner and Laliberté 2015). Acidification occurs through H^+ transfer processes, mainly including nitrogen transformations, pyrite oxidation, mineral weathering, the assimilation of more cations than anions by vegetation, and acidic atmospheric deposition (van Breemen *et al.* 1983; Hinsinger *et al.* 2003; Prakongkep *et al.* 2012). It appears feasible, therefore, that similar biogeochemical changes could be achieved in alkaline tailings (perhaps even at markedly accelerated pace) through the use of targeted soil amendments.

Geochemical characteristics of unweathered alkaline tailings

Although the specific mineralogy and dominant chemical composition of tailings is a reflection of ore type, processing method and parent rock (Jamieson 2011), tailings materials generally share a number of physicochemical characteristics. Tailings often exhibit a dysfunctional physical structure, altered or inadequate hydrological functioning, and unstable geochemistry (Cooke and Johnson 2002; Huang *et al.* 2012; Santini and Banning 2016). They comprise predominantly ultrafine material (ca. 95–100% of particles <2 mm, up to 50% <0.02 mm), mainly SiO_2 or $CaCO_3$ (50–70% by mass) with unweathered primary and secondary mineral oxides, sulfides, oxyhydroxides, sulfates, carbonates and silicates (Parviainen 2009; Sracek *et al.* 2010, 2014; Jamieson

2011; Lindsay *et al.* 2015; AT Cross unpubl.). Processing in some operations results in hyper-salinity or an accumulation of potentially toxic or radioactive substances, and hydraulic conductivity and water infiltration are often poor (Huang *et al.* 2012). Alkaline tailings are produced in large volumes by operations targeting minerals such as magnetite and bauxite (e.g., Jamieson 2011; Santini and Banning 2016; Santini and Fey 2016; A.T. Cross unpubl.). However, it must be noted that the processing of other minerals produces acidic tailings that present a suite of additional and quite different challenges to biota (e.g., Huang *et al.* 2012).

Unweathered alkaline tailings are essentially biologically inert (Kumerasan *et al.* 2017), fine-particulate, mineral-rich artificial substrates that have not been created by the natural processes of soil formation and weathering (Table 1). However, in chemical composition and nutrient status, they are somewhat similar to the poorly-developed, very young calcareous soils studied in biodiverse regions such as south-western Australia (Laliberté *et al.* 2012; Turner *et al.* 2017). Alkaline tailings usually have a pH in the range of pH 8–10, are depauperate in N and organic C, and contain high concentrations of inorganic P and minerals such as calcium (Ca), iron (Fe), potassium (K), magnesium (Mg) and sodium (Na) (Sracek *et al.* 2010; Santini and Fey 2016; AT Cross unpubl.). The chemical and physical properties of tailings make them significant soil-forming substrates conducive to rapid soil formation (Santini and Banning 2016). It has been proposed that the processes of soil formation on tailings can be accelerated through careful manipulation of substrate chemical conditions by targeted amendments (Li *et al.* 2015; Li and Huang 2015).

Table 1. Chemical composition of alkaline tailings, created from an operation processing magnetite ore from a Banded Ironstone Formation in southwest Western Australia (Mt Karara), compared with young calcareous sand from a chronosequence of soils along coastal sand dunes and undisturbed soil from the ridgeline of Mt Karara. All soil samples were collected in March 2016, with five replicates of 100 g collected from the top 2 cm of freshly deposited dry stacked tailings (*Alkaline tailings;* see Kumerasan *et al.* 2017), soil beneath undisturbed vegetation on the Quindalup dune system, south-western Australia (*Young calcareous soil*; see Hayes *et al.* 2014), and soil beneath undisturbed vegetation on Mt Karara (*Banded Ironstone Formation soil;* see Kumerasan *et al.* 2017). Soil samples were stored dry at ambient temperature (ca. 22ºC) prior to analytical determination of chemical factors in April 2017. Analyses undertaken by ChemCentre (Bentley, Western Australia) following the methods of Rayment and Lyons (2011). n.d.- not detected.

Factor	Method	Unit	**Alkaline tailings**	**Young calcareous soil**	**Banded Ironstone Formation soil**
pH	H_2O		9.7 ± 0.1	9.5 ± 0.1	5.5 ± 0.5
EC	1:5 Water	mS/m	27.2 ± 3.0	5.4 ± 0.2	20.8 ± 5.0
OrgC	Walkley-Black	%	0.23 ± 0.01	0.20 ± 0.01	0.72 ± 0.01
K	Mehlich-3	mg/kg	>550	2 ± 1	174 ± 51
Total N	Total	mg/kg	n.d.	0.25 ± 0.03	0.49 ± 0.01
Total P	Total	mg/kg	1020 ± 58	378 ± 7	250 ± 20
Avail. P	Olsen	mg/kg	8.2 ± 2.0	1.4 ± 0.2	5.6 ± 2.6

Al	Mehlich-3	mg/kg	53 ± 5	n.d	532 ± 18
B	Mehlich-3	mg/kg	0.4 ± 0.1	2.4 ± 0.5	0.9 ± 0.1
Ca	Mehlich-3	mg/kg	3694 ± 531	>5500	408 ± 82
Cu	Mehlich-3	mg/kg	1.8 ± 0.2	n.d.	1.8 ± 0.2
Fe	Mehlich-3	mg/kg	>550	8 ± 1	41 ± 6
Mg	Mehlich-3	mg/kg	158 ± 5	>1000	75 ± 9
Mn	Mehlich-3	mg/kg	46.8 ± 1.8	1.5 ± 0.1	60.8 ± 15.7
Na	Mehlich-3	mg/kg	98 ± 14	190 ± 14	74 ± 14
S	Mehlich-3	mg/kg	83 ± 18	152 ± 12	38 ± 6
Se	Mehlich-3	mg/kg	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Zn	Mehlich-3	mg/kg	3.1 ± 0.1	n.d.	0.1 ± 0.1
	Mehlich-3				
As	Mehlich-3	mg/kg	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.1
Cd	Mehlich-3	mg/kg	0.06 ± 0.01	0.05 ± 0.01	0.01 ± 0.01
Co	Mehlich-3	mg/kg	0.27 ± 0.04	0.01 ± 0.01	0.49 ± 0.13
Mo	Mehlich-3	mg/kg	n.d.	0.02 ± 0.01	0.01 ± 0.01
Ni	Mehlich-3	mg/kg	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.1
Pb	Mehlich-3	mg/kg	5.1 ± 0.7	0.2 ± 0.1	0.9 ± 0.1

Vegetation development along soil chronosequences

Nutrient dynamics along soil chronosequences are a major edaphic control of plant species diversity and vegetation development (Laliberté *et al.* 2012, 2013; Turner and Laliberté 2015; Zemunik *et al.* 2015, 2016), and the type of nutrient limitation influences plant competitive interaction and coexistence (McKane *et al.* 2002; Richardson *et al.* 2004, 2008; Turner 2008; Olde Venterink and Güsewell 2010). As soils age and the ratios between N, P and organic C shift (as well as the bioavailability of various micronutrients), the functional composition of the supported plant community changes (Laliberté *et al.* 2013; Hayes *et al.* 2014; Zemunik *et al.* 2016, 2017). Generally speaking, both the biological diversity and functional complexity of ecosystems increases dramatically along chronosequences from young to old soils (Lambers *et al.* 2008a), reflective of the efficacy of various nutrient-acquisition strategies as soils age (Fig. 2). Vegetation richness, functional composition and structure therefore reflects a long history of soil development and biogeochemical change, contrasting rather starkly with the regulatory conditions placed upon industry that often mandate the rapid return of functional, biodiverse plant communities to tailings landforms that are representative of vegetation on the pre-mining landform (e.g., EPA 2009a,b).

The natural soils of regions supporting significant tailings production are generally highly weathered and extremely P-impoverished (Lambers *et al.* 2008a; Hopper 2009; Turner and Laliberté 2015). They often support vegetation assemblages that are hyperdiverse, comprise many highly-specialised species, and harbour high degrees of endemism (Hopper *et al.* 2016). The nutrient-acquisition strategies of species on P-limited soils differ markedly from those of species inhabiting very young soils where P availability is relatively high. Many species adapted to severely P-impoverished soils do not strongly down-regulate their P-uptake capacity, and, consequently, are highly sensitive to elevated P availability, showing severe symptoms of P toxicity (Handreck 1997; Shane and Lambers 2006). Subsequently, plant communities on young calcareous soils exhibit a strong convergence from selection toward species with higher N-use efficiency on N-poor young soils to selection for species with highly conservative P-use strategies and a highl P-resorption proficiency and efficiency on older soils where P is limiting (Mason *et al.* 2012; Hayes *et al.* 2014). Plant growth on young calcareous soils may also be co-limited by potassium (K), and by micronutrients that are poorly soluble at high pH including Fe, Mn, Cu and Zn (Laliberté *et al.* 2013).

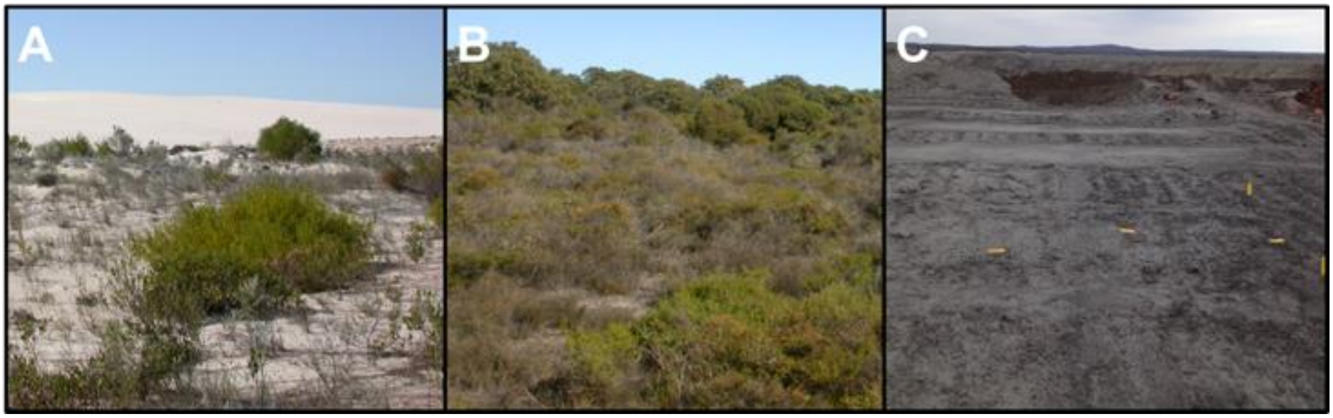

Figure 1. Native vegetation on young calcareous primary (A) and secondary (B) dunes of the Quindalup dunes along a 2-million year old dune chronosequence, Jurien Bay, Western Australia, and unweathered dry stacked tailings produced during the processing of magnetite ore from Banded Ironstone Formations in the Midwest region of Western Australia (C). The Quindalup dunes are the youngest dunes along the chronosequences (Hayes *et al.* 2014). Photos by Hans Lambers (A, B) and Adam T. Cross (C).

Vegetation along soil chronosequences exhibit a diverse range of nutrient-acquisition strategies (Fig. 2), with plant communities on younger soils comprising principally primary mycorrhizal colonisers, species with arbuscular, ericoid or ectomycorrhizal strategies, N_2-fixing species (Fig. 3), and species with no special nutrient-acquisition strategies (Lambers *et al.* 2008b; Hayes *et al.* 2014). These strategies all allow the effective acquisition of both P and N (Hodge *et al.* 2001, 2010; Krüger *et al.* 2015). It has been proposed that the arbuscular mycorrhizal strategy (increasing the volume of soil explored) is highly successful in young soils where P availability is relatively high (Lambers *et al.* 2008b). Here, both N_2-fixing species of various types (representatives of Fabaceae and Casuarinaceae) and rapid-growing species with no specialised strategy for P or N acquisition (e.g., Brassicaceae, Chenopodiaceae, respectively) are common and successful colonisers of disturbed and N-limited soils (Virginia and Delwiche 1982; Francis and Read 1994; Lambers *et al.* 2008b). Mycorrhizal fungal diversity in soils is closely linked to plant biodiversity and vegetation productivity (Van der Heijden *et al.* 1998), and at least some families of arbuscular mycorrhizal fungi (e.g., Glomeraceae) occur in even the youngest calcareous sandy soils in dune chronosequences (Shi *et al.* 2012; Krüger *et al.* 2015). As soils age, there is a gradual change to strategies such as scavenging from large soil volumes (Lambers *et al.* 2008a,b), chemical alteration of the mycorrhizosphere (Subramanian and Charest 1999; Lambers *et al.* 2008a,b), and facilitative interactions where species with a mining strategy make nutrients available for those that lack this trait (Muler *et al.* 2014). Occasionally, however, species occurring on the youngest soils along a chronosequence may be present in, and are sometimes still dominant components of, the vegetation assemblages supported by older soils (Lambers *et al.* 2008b; Hayes *et al.* 2014). It therefore seems likely that at least some elements of a regional flora and microflora should display a capacity to establish on unweathered alkaline tailings in the absence of phytotoxicity or significant physical/hydrological constraints. Indeed, several pioneer species with wind-dispersed seeds have been observed to naturally establish, set seed, and begin colonising areas of a tailings storage facility in the semi-arid Midwest of Western Australia (A.T.Cross, unpubl.), although only in areas where the incorporation of rocky material into the surface layer has increased surface heterogeneity (Fig. 4).

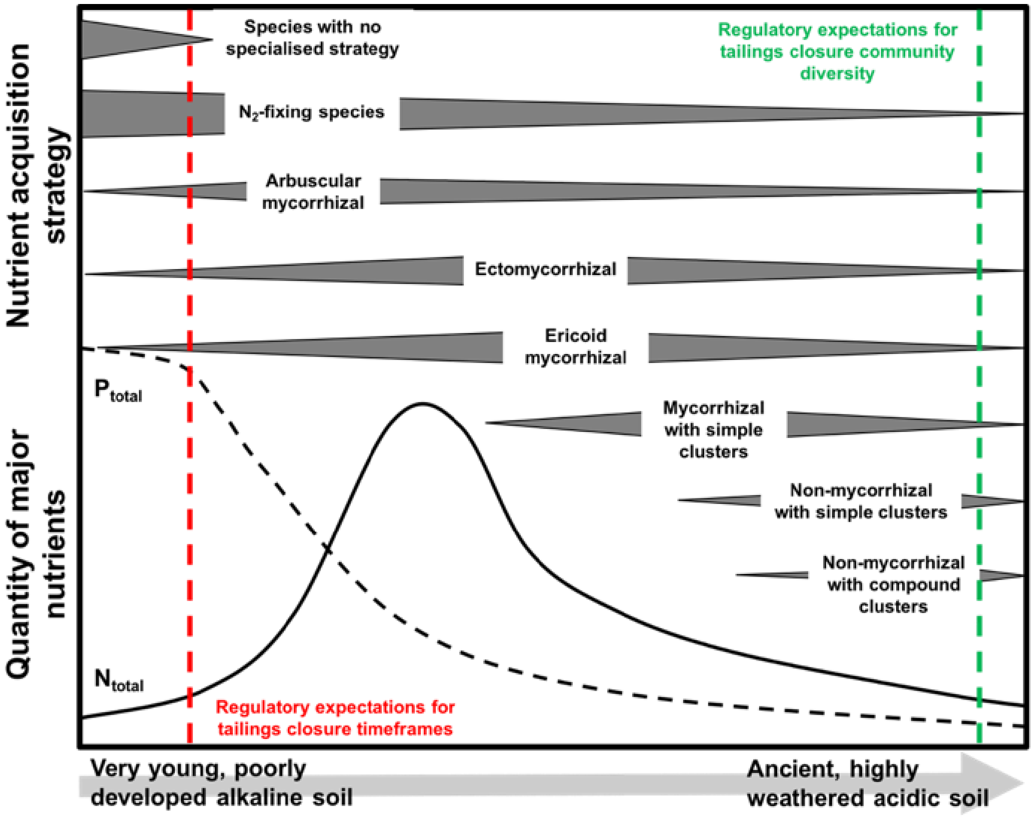

Figure 2. Changes in the relative frequency of plant nutrient-acquisition strategies in relation to changes in total soil phosphorus (P) (dashed line) and nitrogen (N) (solid line) from very young, poorly developed alkaline soils to ancient, highly weathered acidic soils, adapted from Lambers *et al.* (2008b). Though Lambers *et al.* (2008b) discuss young soils as those originating from recent volcanic eruptions and glacial retreats, and ancient soils as those that have remained above sea-level and unglaciated for millions of years, the same biogeochemical changes during pedogenesis (including shifts in macro- and micronutrient availability) can be expected to occur in alkaline tailings. This theoretical model provides a conceptual framework of the potential diversity in plant functional groups that may be achievable at different stages of soil development on tailings landforms. Clearly the regulatory expectations of required time frame (dashed red line) and community diversity (dashed green line) for ecological restoration projects following mine closure are incompatible with current regulatory conditions often requiring the return of biodiverse, representative, and functional native plant communities on tailings landforms in time frames of less than a decade (e.g., EPA 2009a,b).

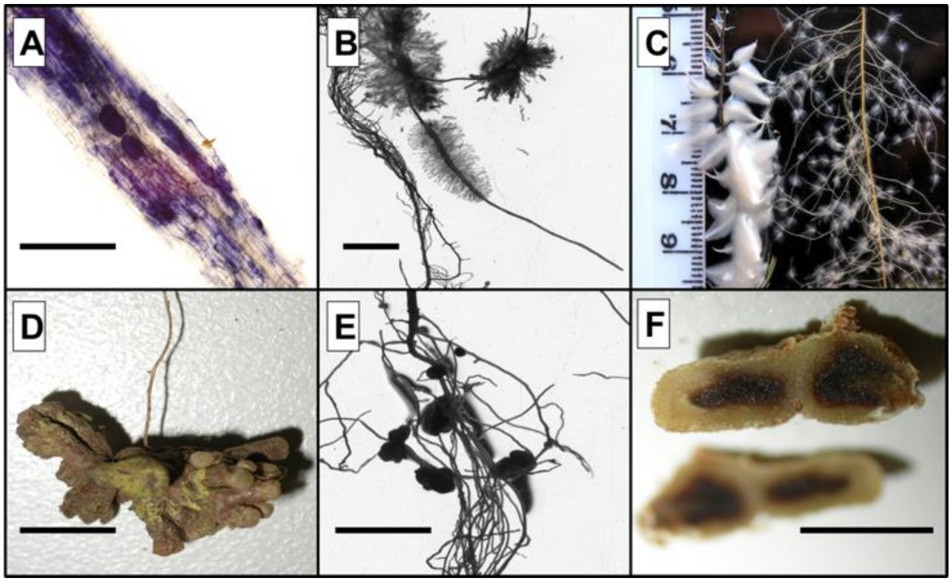

Figure 3. Some examples of root structures associated with nutrient acquisition in the flora of young calcareous soils. A- Arbuscular mycorrhizal fungal hyphae in the root of *Spyridium globulosum* (Rhamnaceae) (image by Francois P. Teste). B- Cluster roots of two-month old *Hakea trifurcata* (Proteaceae) seedling (image by Dmitri Ivanov). C- Dauciform roots of *Schoenus* (left) and *Carex* (right) spp. (Cyperaceae) grown hydroponically (image by Michael W Shane). D- Rhizothamnia of *Allocasuarina humilis* (Casuarinaceae) from Lesueur National Park (image by Hans Lambers). E- Root nodules of two-month old *Acacia cyclops* (Fabaceae) seedling (image by Dmitri Ivanov). F- Cross-section of *Acacia* sp. root nodule displaying the leghemoglobin (red oxygen-transferring pigment, similar to myoglobin in human muscles; Lambers *et al.* 2008a) evidencing active nodules (image by Hans Lambers).

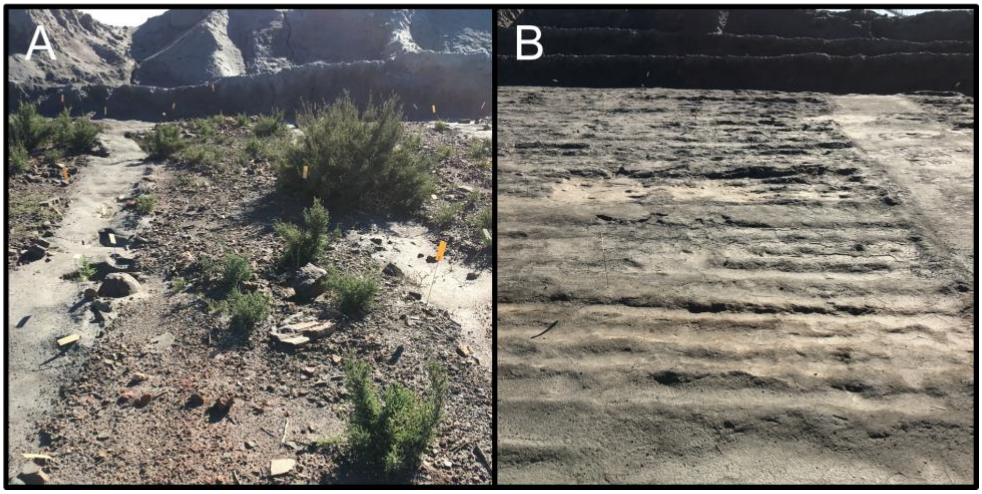

Figure 4. Improving soil surface heterogeneity appears to facilitate the unassisted establishment of some native pioneer species on unweathered alkaline tailings in the semi-arid Midwest of Western Australia. Up to 54 individuals of seven Chenopodiaceous species (*Atriplex semibaccata*, *Maireana brevifolia*, *M. carnosa, Salsola australis*, *Sclerolaena diacantha, S. fusiformis*) were recorded after 18 months from unirrigated and unseeded 10

m × 2 m plots prepared by incorporating a 300 mm layer of waste rock into the uppermost 400 mm of the tailings soil surface (A), compared with no establishment in neighbouring (10 m distant) unamended tailings plots with low surface heterogeneity (B). Photos by Adam T. Cross.

Young calcareous soils as a model for ecosystem restoration on alkaline tailings

Current regulatory expectations of closure time frames for tailings landforms are misaligned with the time frames required for natural processes to alleviate substrate hostility. Finding cost-effective and scalable methods of addressing this issue represents perhaps the only opportunity for the mining industry to deliver native plant communities within short periods that are self-sustaining and representative of pre-disturbance vegetation. A lack of restoration capability is likely to jeopardise the long-term economic viability of the mining industry through the delay or rejection of future projects, and impacts upon both the industry's social and environmental license to mine (Mudd 2009; McDonald *et al.* 2016). Tailings experience the same drivers of weathering and soil development that shape pedogenesis on natural landforms (Santini and Banning 2016), and there is a clear need for research to explore methods to accelerate biogeochemical changes to drive soil formation in tailings. We believe that the application of soil developmental theory from calcareous-soil chronosequences may prove to be of significant utility in improving the outcomes of ecosystem restoration on alkaline tailings landforms.

The major biogeochemical limitations to the establishment of representative, locally native microbial and plant communities on unweathered alkaline tailings include the same major constraints identified for very young and poorly-developed calcareous soils: i) predominant or complete absence of combined N and poor soil N retention; ii) limited bioavailability of some micronutrients at high pH; and iii) high levels of soil P that may result in P toxicity for some species that are capable of mobilising P and poorly capable of down-regulating P uptake, especially at high Ca concentrations (Grundon 1972). These limitations should be addressed as early as possible during processing or in the early stages of restoration to accelerate soil development and alleviate the limitations to plant community establishment. However, we also acknowledge that additional factors such as the accumulation of phytotoxic compounds (Jamieson 2011), the oxidation of metallic sulfides (Kelly 1995; Lindsay *et al.* 2015), and a lack of competent surface material leading to high potential for erosion (e.g. Wray 1998) may impact upon restoration success in specific situations; in such cases translation research is required to adapt and improve restoration technologies on a case-by-case basis. It should also be noted that many tailings operations are situated in arid and semi-arid regions, and that in these regions natural recruitment often occurs opportunistically and unpredictably in years of above-average rainfall or after significant weather events (e.g., Weltzin *et al.* 2003; Schwinning *et al.* 2004; Holmgren *et al.* 2006). The geophysical characteristics (often poorly competent, structureless and fine-particulate material) and topographical design (either water-shedding or internally draining) of tailings landforms result in stark differences in hydrological function compared with natural soil systems (Jamieson 2011; Huang *et al.* 2011, 2012), and the performance and resilience of restored ecosystems on unweathered and unamended tailings substrates may be further compromised by severe water-limitation in areas characterised by limited or capricious rainfall. Pedogenesis occurs more rapidly (at least initially) in regions of high rainfall or where irrigation is available (Webb *et al.* 1986; Stewart *et al.* 2001; Santini and Fey 2013), enabling more rapid dissolution of minerals and leaching of alkaline compounds, greater loss of P by erosion and leaching, and faster organic matter turnover and breakdown (Huang *et al.* 2012; Santini and Fey 2013). These processes occur much more slowly in arid and semiarid regions where soil moisture can be a limiting factor for plant growth and microbial activity (Lambers *et al.* 2008a), and regulatory time frames should take this into account.

Simple remediation of the rhizosphere on tailings by tillage, topsoil capping, organic matter amendment, fertiliser addition, the establishment of tolerant plant species (e.g., metallophytes), or microbial inoculation does not result in the development of functional soils capable of supporting diverse native plant communities (Clemens *et al.* 2002; Huang *et al.* 2011; Mulligan *et al.* 2006; Wehr *et al.* 2006; Mendez and Maier 2008; Santini and Fey 2013). The establishment of appropriate communities on tailings landforms requires a functional, stable root zone (Huang *et al.* 2012), the development of which in tailings can only be achieved by managed long-term alteration of the chemical, physical, and biological properties of the substrate (Santini and Banning 2016). Early intervention in the alteration of the tailings soil profile likely significantly reduces the time frame for soil development compared with that of conventional restoration methods (e.g., topsoil and overburden capping and broadcast seeding of predisturbance species; Santini and Fey 2015). We propose that the following three processes are considered central to early ecological restoration projects on alkaline tailings:

Acidification of the top layer of the soil profile. Fundamentally, all three of the significant constraints identified are linked to the interaction between an extreme pH environment and a highly reactive unweathered substrate of unstable geochemistry. The N-retention capacity of soils is very poor at high pH and in the absence of organic matter (Huang *et al.* 2012), limiting the efficacy of N-fertiliser application. The bioavailability of some micronutrients such as Mn, Fe, Zn and Cu is greatly reduced at high pH (Hinsinger 2001; Lambers *et al.* 2008a), and pH is a major factor controlling the solubility of numerous metals, metalloids and other ions in pore water (Huang *et al.* 2012). Soil P is poorly available in highly alkaline and highly acidic soils (Lambers *et al.* 2008a), and the biological and chemical transformations influencing the biological availability of P increase at neutral pH allowing for faster rates of P loss through leaching and erosion (Walker and Syers 1976; Turner *et al.* 2007). The stabilisation and long-term control of pH in the rhizosphere is considered a priority requirement in tailings remediation (Huang *et al.* 2012), and accelerated acidification of the soil profile is likely foundational to soil formation on alkaline tailings. Additional methods of more rapid acidification could include acidifying fertiliser inputs (Barak *et al.,* 1997), or the incorporation of acid-forming minerals derived from the tailings production process such as pyrite (Nordstrom 1982; Huang *et al.* 2012).

Inoculation of tailings with appropriate and resilient microbial communities. The inoculation of alkaline tailings with suitable local microbial communities comprising N_2-fixing microbes and mycorrhizal fungi should rapidly increase the availability of soil N and P and increase plant productivity (Van der Heijden *et al.* 1998; 2008; Nemergut *et al.* 2007; Menge and Hedin 2009; Huang *et al.* 2012; Krüger *et al.* 2015; Li *et al.* 2015). Free-living cyanobacteria are an important component of N-cycling (Pate *et al.* 1998), with many species being lithotrophic and extracting mineral nutrients from rocky substrates, while obtaining C and N from photosynthesis and biological N_2 fixation (Eldridge and Greene 1994). Cyanobacteria, in combination with fungi and other microbes, are key elements of microbiotic crusts in many arid and semiarid regions (West 1990; Eldridge and Greene 1994; Harris 2009). Microbiotic crusts can be activated by even small rainfall events, are successful in systems where rainfall unpredictability or episodicity is a limitation to plant growth, and fix large amounts of N (Eldridge and Greene 1994). Plant biodiversity and vegetation productivity are both positively associated with mycorrhizal fungal diversity (Van der Heijden *et al.* 1998), and free-living bacteria and mycorrhizal fungi significantly enhance plant growth by alleviating stress factors and influencing phytohormone production (Glick 1995; Parniske 2008; Farrar *et al.* 2014; Pozo *et al.* 2015). Numerous cyanobacteria species and some groups of mycorrhizal fungi (e.g., Glomeraceae) occur in calcareous soils from Mediterranean-climate and semi-arid regions (Wynn-Williams 2000; Seckbach 2007; Shi *et al.* 2012; Krüger *et al.* 2015), and may be able to tolerate the pH and moisture conditions presented by alkaline tailings. Key focus points of all ecological restoration programs should be the identification and isolation of any locally-native microbial species (particularly N_2-fixing cyanobacteria and mycorrhizal fungi) that possess the capacity for survival in unweathered tailings, and an assessment of the degree to which the functional capacity of these microbial communities is preserved in engineered restoration substrates (Kumerasan *et al.* 2017). The establishment of N_2-fixing microbes may also assist in soil acidification through N-transformations (Haynes 1983; Helyar and Porter 1989; Ulrich 1991), and a biological N contribution from N_2-fixing microbes and the establishment of N_2-fixing plants likely yields a higher and more sustainable rate of soil acidification compared with fertiliser amendments alone (Helyar and Porter 1989; Ulrich 1991; Tang and Rengel 2003). Additionally, termites may contribute significantly to N_2 fixation in semiarid regions (Collins 1981; Pate *et al.* 1998), due to their gut flora containing N_2-fixing bacteria (Collins 1981; Prestwich and Bentley 1981). The incorporation of woody debris onto tailings landforms and the establishment of termite populations if termites are locally present likely improves both N_2-fixation and carbon cycling.

The early establishment of appropriate pioneer vegetation. The geochemistry and nutrient status of unweathered alkaline tailings suggests that the immediate establishment of biodiverse native plant communities is not feasible. However, the early establishment of functionally-appropriate locally-native pioneer vegetation and species that facilitate the growth of their neighbours may assist in developing rhizosphere processes, increase N availability, and begin nutrient cycles and organic C (litter) accumulation (Cleveland *et al.* 1999; Lambers *et al.* 2008a,b; Hayes *et al.* 2014). Although specific genera and species will depend on local floras, pioneer communities likely comprise species that are rapid-growing with no special strategy for N or P acquisition (e.g., Brassicaceae, Chenopodiaceae), N_2-fixing species (e.g., Fabaceae, Casuarinaceae), rapid-growing species with an arbuscular mycorrhizal strategy (e.g., Asteraceae, Poaceae), and possibly species harbouring endophytic N_2-fixing microbes (Reinhold-Hurek and Hurek 2011). Further floristic elements to enrich biodiversity could then be introduced further along the restoration trajectory as soil monitoring activities indicate that biogeochemical conditions are suitable to their establishment. Carefully-targeted species selection from appropriate functional groups, enhanced by the development of appropriate soil microbial communities, may not only assist in improving early vegetation establishment along an ecosystem function trajectory but also reduce restoration costs by minimising seed and greenstock wastage.

Conclusions

The timely restoration of functional, biodiverse, representative, and self-sustaining native ecosystems on alkaline tailings undoubtedly represents an enormous challenge to the mining industry and restoration practitioners. The attitudes to tailings production and storage must experience a shift in perspective from simple waste management to the production of artificial substrates capable of being developed into functional soils (Santini and Banning 2016). As tailings production globally continues to increase, a new paradigm of collaborative and multidisciplinary science-driven innovation is required to ensure our ability to effectively restore ecosystems on tailings increases in parallel. The regulatory expectations of tailings-closure time frames are clearly incompatible with the time frames required for natural biogeochemical processes to facilitate pedogenesis on these landforms, and methods of accelerating these processes represent perhaps the only opportunity to achieve timely restoration success (Huang *et al.* 2012; Li and Huang 2015; Santini and Banning 2016). The processes of soil development, nutrient dynamics and vegetation succession in young alkaline soils offer a valuable model to examine the underlying mechanisms by which the restoration of native ecosystems on alkaline tailings might be accelerated. Though significant further study is required to demonstrate the practical applicability and scalability of these processes on tailings landforms, this model represents a potentially effective method of improving the success, timeliness, and cost-effectiveness of future restoration efforts.

Acknowledgements

This research was funded by the Australian Government through the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (project number ICI150100041) and by an ARC Linkage Project (project number LP160100598), and builds upon conceptual discussion with the lead investigators of both these grants. The authors thank Longbin Huang and Hongtao Zhong for comments on the manuscript draft, and Patrick Hayes for providing soil samples from the Quindalup dune system for chemical analyses.

References

Aplet, G.H., Vitousek, P.M. (1994). An age-altitude matrix analysis of Hawaiian rain-forest succession. *Journal of Ecology* 82, 137–147

Anand, R.R., Payne, M. (2002). Regolith geology of the Yilgarn Craton, Western Australia: implications for exploration. *Australian Journal of Earth Sciences* 49, 3–162.

Barak, P., Jobe, B.O., Krueger, A.R., Peterson, L.A., Laird, D.A. (1997). Effects of long-term soil acidification due to nitrogen fertilizer inputs in Wisconsin. *Plant and Soil* 197, 61–69.

Baumann, F., He, J., Schmidt, K., Kühn, P., Scholten, T. (2009). Pedogenesis, permafrost, and soil moisture as controlling factors for soil nitrogen and carbon contents across the Tibetan Plateau. *Global Change Biology* 15, 3001–3017.

Beukes, N.J. (1973). Precambrian iron-formations of southern Africa. *Economic Geology* 68, 960–1004.

Cleveland, C.C., Townsend, A.R., Schimel, D.S., Fisher, H., Howarth, R.W., Hedin, L.O., Perakis, S.S., Latty, E.F., Von Fischer, J.C., Elseroad, A., Wasson, M.F. (1999). Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems. *Global biogeochemical cycles* 13, 623–645.

Collins, N.M. (1981). The utilization of nitrogen resources by termites (Isoptera). In *Nitrogen as an Ecological Factor* (eds J. A. Lee, S. McNeill & I. H. Rorison) pp. 381– 412. Blackwell Scientific Publications, Oxford, UK.

Cooke, J.A., Johnson, M.S. (2002). Ecological restoration of land with particular reference to the mining of metals and industrial minerals: a review of theory and practice. *Environmental Reviews* 10, 41–71.

Eldridge, D.J., Greene, R.S.B. (1994). Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* 32, 389.

EPA (2009a). Karara Iron Ore Project. Report and recommendations of the Environmental Protection Authority, Report 1321, Government of Western Australia, Perth, AU.

EPA (2009b). Koolanooka/Blue Hills Direct Shipping Ore Mining Project Shires of Morawa and Perenjori. Report of the Environmental Protection Authority, Report 1328, Government of Western Australia, Perth, AU.

Farrar, K., Bryant, D., Cope-Selby, N. (2014). Understanding and engineering beneficial plant–microbe interactions: plant growth promotion in energy crops. *Plant Biotechnology Journal* 12, 1193–1206.

Francis, R., Read, D. (1994) The contributions of mycorrhizal fungi to the determination of plant community structure. *Plant and Soil* 159, 11– 25

Geoscience Australia. (2013). *Australia's mineral resource assessment 2013*. Australian Government, Canberra.

Glick, B.R. (1995). The enhancement of plant growth by free-living bacteria. *Canadian Journal of Microbiology* 4, 109–117.

Gordon Jr, M., Tracey Jr, J.I., Ellis, M.W. (1958). *Geology of the Arkansas bauxite region* (United States Geological Survey Professional Paper 299). United States Government Printing Office, Washington, USA.

Grundon, N.J. (1972). Mineral nutrition of some Queensland heath plants. *Journal of Ecology*, 60, 171-181.

Handreck, K.A. (1997). Phosphorus requirements of Australian native plants. *Australian Journal of Soil Research* 35, 241–290.

Harris J. (2009). Soil microbial communities and restoration ecology: facilitators or followers? *Science* 325, 573–574.

Haynes, R.J. (1983). Soil acidification induced by leguminous crops. *Grass and Forage Science* 38, 1–11.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* 237, 173–195.

Hinsinger, P., Plassard, C., Tang, C. Jaillard, B. (2003). Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. *Plant and Soil* 248, 43–59.

Hinsinger, P., Bengough, A.G., Vetterlein, D., Young, A.M. (2009). Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil* 321, 117–152.

Helyar, K.R., Porter, W.M. (1989). Soil acidification, its measurement and the processes involved. In (Robson A.D) *Soil Acidity and Plant Growth* (pp 61-101), Academic Press Australia, Marrickville.

Hodge, A., Campbell, C.D., Fitter, A.H. (2001). An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* 413, 297–299.

Hodge, A., Fitter, A.H. (2010). Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences* 107, 13754–13759.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M. (2006). Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment* 4, 87–95.

Hopper, S.D. (2009). OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* 322, 49–86.

Hopper, S.D., Silveira, F.A., Fiedler, P.L. (2016). Biodiversity hotspots and Ocbil theory. *Plant and Soil 403*, 167-216.

Huang, L., Baumgartl, T., Mulligan, D. (2011). Organic matter amendment in copper mine tailings improving primary physical structure, water storage and native grass growth. In: Sanchez M, Mulligan D, Wilertz J. eds. Enviromine 2011, 2nd International Seminar on Environmental Issues in the Mining Industry, Santiago, Chile.

Huang, L., Baumgartl, T., Mulligan, D. (2012). Is rhizosphere remediation sufficient for sustainable revegetation of mine tailings? *Annals of Botany* 110, 223–238.

Jamieson, H.E. (2011). Geochemistry and mineralogy of solid mine waste: essential knowledge for predicting environmental impact. *Elements* 7, 381–386.

Jobbágy, E.G., Jackson, R.B. (2003). Patterns and mechanisms of soil acidification in the conversion of grasslands to forests. *Biogeochemistry* 64, 205–229.

Jurjovec, J., Ptacek, C.J., Blowes, D.W. (2002). Acid neutralization mechanisms and metal release in mine tailings: a laboratory column experiment. *Geochimica et Cosmochimica Acta* 66, 1511–1523.

Kelly, D.P. (1995). Sulfur and its Doppelgänger. *Archives of Microbiology* 163, 157-158.

Krüger, M., Teste, F.P., Laliberté, E., Lambers, H., Coghlan, M., Zemunik, G., Bunce, M. (2015). The rise and fall of arbuscular mycorrhizal fungal diversity during ecosystem retrogression. *Molecular Ecology* 24, 4912–4930.

Kumaresan, D., Cross, A.T., Moreira-Grez, B., Kariman, K., Nevill, P., Stevens, J., Allcock, R.J.N., O’Donnell, A.G., Dixon, K.W., Whiteley, A.S. 2017. Microbial functional capacity is preserved within engineered soil formulations used in mine site restoration. *Scientific Reports*, doi:10.1038/s41598-017-00650-6.

Lambers, H., Chapin, F.S., Pons, T.L. (2008a) *Plant Physiological Ecology*. Springer, New York, NY.

Lambers, H., Raven, J.A., Shaver, G.R., Smith, S.E. (2008b). Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution* 23, 95–103.

Łaska, G. (2001). The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecology* 157, 7799.

Li, X., You, F., Bond, P.L., Huang, L. (2015). Establishing microbial diversity and functions in weathered and neutral Cu–Pb–Zn tailings with native soil addition. *Geoderma* 247, 108–116.

Li, X., Huang, L. (2015). Toward a new paradigm for tailings phytostabilization - nature of the substrates, amendment options, and anthropogenic pedogenesis. *Critical Reviews in Environmental Science and Technology* 45, 813–839.

Lindsay, M.B., Moncur, M.C., Bain, J.G., Jambor, J.L., Ptacek, C.J., Blowes, D.W. (2015). Geochemical and mineralogical aspects of sulfide mine tailings. *Applied Geochemistry* 57, 157–177.

Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A., Allen, R.B. (2012) Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology* 100, 678–689.

McDonald, T., Gann, G., Jonson, J., Dixon, K.W. (2016) *International Standards for the Practice of Ecological Restoration*. Society for Ecological Restoration, Washington, USA.

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A. & Murray, G. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415, 68–71.

Mendez, M., Maier, R. (2008). Phytoremediation of mine tailings in temperate and arid environments. *Reviews in Environmental Science and Biotec*hnology 7, 47–59.

Menge, D.N.L., Hedin, L.O. (2009). Nitrogen fixation in different biogeochemical niches along as 120 000-year chronosequence in New Zealand. *Ecology* 90, 2190–201.

Mudd, G.M. (2009). *The Sustainability of Mining in Australia: Key Production Trends and Their Environmental Implications for the Future*. Research Report No. RR5. Department of Civil Engineering, Monash University and Mineral Policy Institute, Perth, Australia.

Muler A.L., Oliveira R.S., Lambers H., Veneklaas E.J. (2014). Does cluster-root activity of Banksia attenuata (Proteaceae) benefit phosphorus or micronutrient uptake and growth of neighbouring shrubs? *Oecologia* 174, 23–31.

Mulligan, D.R., Gillespie, M.J., Gravina, A.J., Currey, A. (2006). An assessment of the direct revegetation strategy on the tailings storage facility at Kidston gold mine, North Queensland, Australia. In: Fourie A, Tibbett M. eds. Mine closure 2006. pp 371–381. Australian Centre for Geomechanics, Perth, AU.

Nemergut, D.R., Anderson, S.P., Cleveland, C.C., Martin, A.P., Miller, A.E., Seimon, A., Schmidt, S.K. (2007). Microbial community succession in an unvegetated, recently deglaciated soil. *Microbial ecology* 53, 110–122.

Nierop, K.G., Naafs, D.F., Verstraten, J.M. (2003). Occurrence and distribution of ester-bound lipids in Dutch coastal dune soils along a pH gradient. *Organic Geochemistry* 34, 719–729.

Nordstrom, D.K. (1982). Aqueous pyrite oxidation and the consequent formation of secondary iron minerals. In: J.A. Kittrick, D.S. Fanning and L.R. Hossner (eds.) *Acid Sulfate Weathering.* Soil Science Society of America Special Publication 10. (pp. 37-56) Soil Science Society of America, Madison, USA.

Olde Venterink, H., Güsewell, S. (2010). Competitive interactions between two meadow grasses under nitrogen and phosphorus limitation. *Functional Ecology* 24, 877–886.

Pate, J.S., Unkovich, M.J., Erskine, P.D., Stewart, G.R. (1998). Australian mulga ecosystems – ^{13}C and ^{15}N natural abundances of biota components and their ecophysiological significance. *Plant, Cell and Environment* 21, 1231–1242.

Paradis, M., Duchesne, J., Lamontagne, A., Isabel, D. (2007). Long-term neutralisation potential of red mud bauxite with brine amendment for the neutralisation of acidic mine tailings. *Applied Geochemistry* 22, 2326–2333.

Parniske, M. (2008). Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Reviews Microbiology* 6, 763–775.

Parviainen, A. (2009). Tailings mineralogy and geochemistry at the abandoned Haveri Au–Cu mine, SW Finland. *Mine Water and the Environment* 28, 291.

Pozo, M.J., López-Ráez, J.A., Azcón-Aguilar, C., García-Garrido, J.M. (2015). Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. *New Phytologist* 205, 1431–1436.

Prakongkep, N., Gilkes, R.J., Singh, B., Wong, S. 2011. Mineralogy and chemistry of sandy acid sulfate soils in the Perth metropolitan area of the Swan Coastal Plain. Department of Environment and Conservation, Perth, AU.

Prakongkep, N., Gilkes, R.J., Singh, B., Wong, S. (2012). Pyrite and other sulphur minerals in giant aquic spodosols, Western Australia. *Geoderma* 181–182, 78–90.

Prestwich, G.D., Bentley, B.L. (1981). Nitrogen fixation in intact colonies of the termite *Nasutitermes corniger*. *Oecologia* 49, 249–251.

Rayment, G.E., Lyons, D.J. (2011). *Soil chemical methods: Australasia* (Vol. 3). CSIRO publishing, Canberra, Australia.

Reinhold-Hurek, B., Hurek, T. (2011). Living inside plants: bacterial endophytes. *Current Opinion in Plant Biology* 14, 435–443.

Richardson, S., Peltzer, D., Allen, R., McGlone, M., Parfitt, R. (2004). Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. *Oecologia* 139, 267–276.

Richardson, S.J., Allen, R.B., Doherty, J.E. (2008). Shifts in leaf N:P ratio during resorption reflect soil P in temperate rainforest. *Functional Ecology* 22, 738–745.

Sadleir, S.B., Gilkes, R.J. (1976). Development of bauxite in relation to parent material near Jarrahdale, Western Australia. *Journal of the Geological Society of Australia* 23, 333-344.

Santini, T.C., Banning, N.C. (2016). Alkaline tailings as novel soil forming substrates: reframing perspectives on mining and refining wastes. *Hydrometallurgy* 164, 38–47.

Santini, T.C., Fey, M.V. (2015). Fly ash as a permeable cap for tailings management: pedogenesis in bauxite residue tailings. *Journal of Soils and Sediments* 15, 552–564.

Santini, T.C., Fey, M.V. (2016). Assessment of Technosol formation and in situ remediation in capped alkaline tailings. *Catena* 136, 17-29.

Seckbach, J. (2007). *Algae and cyanobacteria in extreme environments* (Vol. 11). Springer Science & Business Media, Berlin, DE.

Schidlowski, M., Eichmann, R., Fiebiger, W. (1976). Isotopic fractionation between organic carbon and carbonate carbon in Precambrian banded ironstone series from Brazil. *Neues Jahrbuch fuer Mineralogie, Monatshefte* 344–353.

Schwinning, S., Sala, O.E., Loik, M.E., Ehleringer, J.R. (2004). Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141, 191–193.

Shane, M.W., Lambers, H. (2006) Systemic suppression of cluster- root formation and net P-uptake rates in Grevillea crithmifolia at elevated P supply: a proteacean with resistance for developing symptoms of ‘P toxicity’. *Journal of Experimental Botany* 57, 413–423.

Shi, P., Abbott, L.K., Banning, N.C., Zhao, B. (2012). Comparison of morphological and molecular genetic quantification of relative abundance of arbuscular mycorrhizal fungi within roots. *Mycorrhiza* 22, 501–513.

Shu, W.S., Ye, Z.H., Lan, C.Y., Zhang, Z.Q., Wong, M.H. (2001). Acidification of lead/zinc mine tailings and its effect on heavy metal mobility. *Environment International* 26, 389–394.

Sousa, W.P. (1984). The role of disturbance in natural communities. *Annual review of ecology and systematics*, 15, 353–391.

Sracek, O., Mihaljevič, M., Kříbek, B., Majer, V., Veselovský, F. (2010). Geochemistry and mineralogy of Cu and Co in mine tailings at the Copperbelt, Zambia. *Journal of African Earth Sciences* 57, 14–30.

Sracek, O., Mihaljevič, M., Kříbek, B., Majer, V., Filip, J., Vaněk, A., Penížek, V., Ettler, V. and Mapani, B. (2014). Geochemistry of mine tailings and behavior of arsenic at Kombat, northeastern Namibia. *Environmental monitoring and assessment* 186, 4891–4903.

Stevens, P.R., Walker, T.W. (1970). The chronosequence concept and soil formation. *The quarterly review of biology* 45, 333–350.

Stewart, B.W., Capo, R.C., Chadwick, O.A. (2001). Effects of rainfall on weathering rate, base cation provenance, and Sr isotope composition of Hawaiian soils. *Geochimica et Cosmochimica Acta* 65, 1087–1099.

Subramanian, K.S., Charest, C. (1999). Acquisition of N by external hyphae of an arbuscular mycorrhizal fungus and its impact on physiological responses in maize under drought-stressed and well-watered conditions. *Mycorrhiza* 9, 69–75.

Sýkora, K., van den Bogert, J.C.J.M., Berendse, F. (2004). Changes in soil and vegetation during dune slack succession. *Journal of Vegetation Science* 15, 209–218.

Tang, C., Rengel, Z. (2003). Role of plant cation/anion uptake ratio in soil acidification. *Handbook of soil acidity. Marcel Dekker, New York*, pp 57–81.

Turner, B.L. (2008) Resource partitioning for soil phosphorus: a hypothesis. *Journal of Ecology* 96, 698–702.

Turner, B.L., Condron, L.M., Richardson, S.J., Peltzer, D.A., Allison, V.J. (2007). Soil organic phosphorus transformations during pedogenesis. *Ecosystems* 10, 1166–1181.

Turner B.L., Condron L.M. (2013) Pedogenesis, nutrient dynamics, and ecosystem development: the legacy of T.W. Walker and J.K. Syers. *Plant and Soil* 367, 1–10.

Turner BL, Laliberté E. (2015). Soil development and nutrient availability along a 2-million-year coastal dune chronosequence under species-rich Mediterranean shrubland in southwestern Australia. *Ecosystems* 18, 287–309.

Turner, B.L., Laliberté E., Hayes, P.E. (2017). A climosequence of chronosequences in southwestern Australia. bioRxiv, doi: 10.1101/113308

Ulrich, B. (1991). An ecosystem approach to soil acidification. In *Soil acidity* (pp. 28–79). Springer Berlin Heidelberg.

van Breemen, N., Mulder, J., Driscoll, C.T. (1983). Acidification and alkalinization of soils. *Plant and soil* 75, 283–308.

Van Der Heijden, M.G., Klironomos, J.N., Ursic, M., Moutoglis, P. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396, 69.

Van Der Heijden, M.G., Bardgett, R.D., Van Straalen, N.M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology letters* 11, 296–310.

Virginia, R.A., Delwiche, C.C. (1982). Natural 15N abundance of presumed N2-fixing and non-N2-fixing plants from selected ecosystems. *Oecologia* 54, 317–325.

Walker, T.W., Syers, J.K. (1976). The fate of phosphorus during pedogenesis. *Geoderma* 15, 1–9.

Webb, T.H., Campbell, A.S., Fox, F.B. (1986). Effect of rainfall on pedogenesis in a climosequence of soils near Lake Pukaki, New Zealand. *New Zealand Journal of Geology and Geophysics* 29, 323–334.

Wehr, J., Fulton, I., Menzies, N. (2006). Revegetation strategies for bauxite re- finery residue: a case study of

Alcan Gove in Northern Territory, Australia. *Environmental Management* 37, 297–306.

Weltzin, J.F., Tissue, D.T. (2003). Resource pulses in arid environments–patterns of rain, patterns of life. *New Phytologist* 157, 171–173.

West, N.E. (1990). Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. *Advances in Ecological Research* 20, 179–223.

Wray, D.S. (1998). The impact of unconfined mine tailings and anthropogenic pollution on a semi-arid environment–an initial study of the Rodalquilar mining district, south east Spain. *Environmental Geochemistry and Health* 20, 29–38.

Wynn-Williams, D.D. (2000). Cyanobacteria in deserts—life at the limit? In *The ecology of cyanobacteria* (Eds Whitton, B.A. & Potts, M.) (pp. 341-366). Kluwer, Netherlands.

Zemunik, G., Turner, B.L., Lambers, H., Laliberté, E. (2015). Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development. *Nature Plants* 1, doi: 10.1038/nplants.2015.1050.

Zemunik, G., Turner, B.L., Lambers, H., Laliberté, E. (2016). Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot. *Journal of Ecology* 104, 792–805.