FORUM

Nutrient limitation along the Jurien Bay dune chronosequence: response to Uren & Parsons (2013)

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Summary

1. Uren & Parsons (2013) criticize our nutrient addition experiment and question the integrity of the Jurien Bay dune chronosequence. Their primary criticisms relate to (i) inconsistencies in parent material along the chronosequence and (ii) the lack of consideration of micronutrients in our glasshouse experiment.

2. We reaffirm that the Quindalup–Spearwood succession is a consistent Holocene–Middle (possibly Early) Pleistocene soil chronosequence in which parent material, topography, and present-day climate and vegetation type (i.e. Mediterranean shrubland) are held relatively constant. The older (Early Pleistocene–Late Pliocene) Bassendean Sand probably contained less carbonate initially, but nevertheless represents the endpoint of an exceptionally strong gradient in soil nutrient availability.

3. The claim that we did not consider the potential importance of micronutrients is unfounded. We included a micronutrient treatment in our experiment and discussed the importance of micronutrient availability in young calcareous substrates.

4. *Synthesis.* We restate that our experimental results support predictions about changes in nutrient limitation during long-term pedogenesis, and affirm that the Jurien Bay chronosequence is a valuable model system for addressing ecological questions related to pedogenesis, plant diversity and plant–soil interactions.

Key-words: calcareous dune, calcifuge, chronosequence, micronutrients, nutrient limitation, parent material, pedogenesis, plant–soil (below-ground) interactions

Introduction

We recently published results of a bioassay that evaluated nutrient constraints on plant growth during long-term soil and ecosystem development (Laliberté *et al.* 2012). We used three crop species (canola, wheat and white lupin) as phytometers in the glasshouse on different soils collected along a dune chronosequence in south-western Australia. We used nutrient addition treatments to determine which nutrient(s) most probably limited plant growth on soils of different ages.

Uren & Parsons (2013) criticize our study by claiming that (i) parent material was inconsistent among chronosequence stages and (ii) we overlooked the potential importance of micronutrients on young calcareous soils. Here, we provide more details on the chronosequence to address the first criticism, explain why the second criticism is baseless, and address other minor criticisms.

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Inconsistencies in parent material

Uren & Parsons (2013) argue that the older Spearwood and Bassendean dunes (Pleistocene) are not comparable to the younger Quindalup dunes (Holocene) because of differences in parent material, particularly carbonate content. As Uren & Parsons (2013) mention, we acknowledged in our article that the Bassendean sands probably contained less carbonate initially than the younger Spearwood or Quindalup sands (Kendrick, Wyrwoll & Szabo 1991). We recognize that we did not fully justify our decision to include the Bassendean dunes in the chronosequence, and now do so below. First, however, we address the erroneous claim by Uren & Parsons (2013) that the Spearwood sands might not have been calcareous at all.

ORIGIN OF SILICEOUS SAND IN THE SPEARWOOD DUNES

The Spearwood dune system is underlain by limestone (Tamala Limestone), which crops out occasionally at the

ground surface (McArthur & Bettenay 1974; Playford, Cockbain & Low 1976). The limestone is the product of calcium carbonate cementation (calcarenite) with marine bioclastic material providing the source of calcium carbonate (Bastian 1996; McArthur 2004; Hearty & O'Leary 2008).

Uren & Parsons' (2013) criticism that the Spearwood sands might not have been calcareous stems from the 'desert extension' hypothesis (Glassford & Killigrew 1976; Killigrew & Glassford 1976; Semeniuk & Glassford 1988), resurrected recently by Hearty & O'Leary (2008). The desert extension hypothesis disputes a residual origin for the Spearwood sands that overlie the Tamala Limestone (Fig. 1) and instead proposes that the coastal sands originated from inland dunes that expanded onto the coastal plain during periods of aridity. This hypothesis has been refuted on several grounds:

1 The complete absence of 'desert sand' in the vast intervening areas between the purported desert source and the Swan Coastal Plain destination (Lowry 1977; Bastian 1996);

2 a clear west-to-east trend of increased weathering of the Spearwood sands (Bastian 1996), which matches a west-to-east increase in age of the underlying limestone (Price, Brooke & Woodroffe 2001; Hearty & O'Leary 2008);

3 the match in particle size distribution and mineralogy between the Spearwood sand and sand embedded in the underlying limestone (Wyrwoll & King 1984; Tapsell, Newsome & Bastian 2003).

These separate lines of evidence confirm that the Spearwood sand is residual and originates from *in situ* weathering of the Tamala Limestone, with some local remobilization but no long-range transport. Therefore, the Quindalup–Spearwood dune succession represents a genuine soil chronosequence with consistent parent material whose soils range in age from present day to the Middle Pleistocene (and possibly Early Pleistocene).

WHY DID WE INCLUDE THE BASSENDEAN SAND?

The Bassendean Sand is indisputably associated with a marine unit (the Ascot Formation) that has a pervasive presence in the subsurface (Kendrick, Wyrwoll & Szabo 1991). As acknowledged in our paper (Laliberté *et al.* 2012), the Bassendean sands probably contained less carbonate than the Spearwood or Quindalup sands (Kendrick, Wyrwoll & Szabo 1991), although the deduction of chemical properties in the initial Bassendean parent material is complicated by the extreme degree of weathering.

Our decision to include the Bassendean dune system in the Jurien Bay dune chronosequence alongside the Quindalup and Spearwood dune systems was based on the clear marine origin and indisputable older age of the Bassendean dunes (Playford, Cockbain & Low 1976; Kendrick, Wyrwoll & Szabo 1991). We did not consider the lower initial carbonate content of the parent material to be a major concern for our study, since carbonate loss from soils can be relatively rapid (Salisbury 1925; Burges & Drover 1953). The younger Spearwood dunes can contain many metres of completely decalcified sand over limestone concretions (Fig. 1). Therefore, our rationale was that any carbonates initially present in the older Bassendean sands would have long disappeared from the soil profile to great depth – at least from the upper horizons where most nutrients are taken up by plants. We believe that the Bassendean dunes can, at the very least, be used as the endpoint of an exceptionally strong natural soil nutrient gradient for studies where slight differences in parent material can be neglected.

Importance of micronutrients on young calcareous soils

The second of the two main criticisms to our study made by Uren & Parsons (2013) is that we overlooked the importance of some micronutrients (e.g. Fe, Mn, Cu, Zn), especially on young calcareous soils. This criticism is baseless. As described in our Materials and methods section, our study included a weekly nutrient addition treatment in which all nutrients except nitrogen (N), phosphorus (P) and potassium (K) were supplied to plants – referred to as the '+Other' treatment. This +Other treatment included the micronutrients Fe,
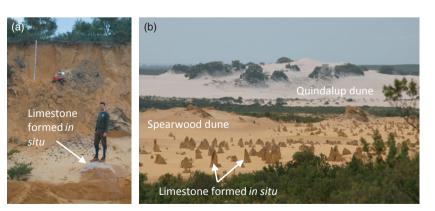

Fig. 1. (a) Quarry in the Spearwood dune system, showing approximately 5 m of residual sand over limestone formed *in situ*. (b) Foreground: in a few locations such as Nambung National Park (near Cervantes, Western Australia), residual sand on Spearwood dunes has been locally remobilized to expose limestone concretions known as 'The Pinnacles'. Background: young Quindalup (Holocene) mobile dune composed of calcareous sand. Over time, calcium carbonate in this young dune will dissolve from the upper soil horizons and precipitate lower down the profile to form *in situ* limestone, as can be seen in the older Spearwood (Pleistocene) dune in the foreground. Photo credits: Etienne Laliberté.

Mn, Cu and Zn (Laliberté *et al.* 2012; Table S2) at concentrations considered to be non-limiting, based on previous pot experiments involving canola and white lupin (Pearse *et al.* 2006).

Canola did not respond to the +Other treatment in any soil (Laliberté *et al.* 2012; fig. 4), showing that micronutrients did not limit the growth of that species. Similarly, wheat also generally did not respond to the +Other treatment, except for a small but significant growth increase in the youngest calcareous soil (Laliberté *et al.* 2012; fig. 4). We explicitly acknowledged this result in our article, highlighting the potential importance of micronutrients in young calcareous soils. The criticism that we did not consider the potential importance of micronutrients on young calcareous soils is therefore unfounded.

Uren & Parsons (2013) also criticize us for not discussing in more detail why white lupin showed severe leaf chlorosis in the young calcareous dunes. As discussed in our paper, white lupin was selected because it has a nutrient acquisition strategy similar to Proteaceae species (i.e. cluster roots; Lambers, Clements & Nelson 2013), which are abundant in later stages of the Jurien Bay chronosequence. However, it was not well suited to our bioassay, because (i) it grew poorly in all of the soils, even in the full fertilizer (+All) treatment (Laliberté *et al.* 2012; Fig. S3), and (ii) contrary to canola and wheat, its pH tolerance was too narrow to make it useful in the context of our study, in which soils varied from alkaline to acidic (Laliberté *et al.* 2012; fig. 2e). Therefore, we decided that results for white lupin did not warrant detailed discussion in our article, except to briefly mention that the severe leaf chlorosis observed on the youngest calcareous soils was likely related to the fact that white lupin had been identified as a calcifuge species (Liu & Tang 1999). Uren & Parsons (2013) state that we should have provided additional discussion on the potential role of Fe and Zn deficiency in leaf chlorosis; this was unnecessary since it is widely known that calcifuge species do poorly on alkaline soils because of their inability to acquire (or transport internally) sufficient Fe, Zn and other micronutrients (Lambers, Chapin & Pons 2008).

Other criticisms

CROP SPECIES AS PHYTOMETERS

Uren & Parsons (2013) criticize the choice of crop species as phytometers for our nutrient addition experiment. While it is clear that crop species have different nutrient requirements than native species, crop species can nonetheless provide useful indicators of nutrient limitation. For example, Beadle (1954) used tomato seedlings in a similar nutrient addition experiment to show that P was the key limiting nutrient on soils around Sydney, Australia, which has been supported subsequently by other lines of evidence (Beadle 1962; Clements 1983; Leishman *et al.* 2007).

From a pragmatic point of view, crop plants generally grow much faster than native plants and therefore greatly reduce the efforts of a glasshouse experiment. Importantly, native plant species from infertile habitats often show little response to nutrient addition (or even negative responses, e.g. Heddle & Specht 1975; Thomson & Leishman 2004), such that nutrient limitation only becomes apparent following replacement by faster-growing species (Chapin, Vitousek & Cleve 1986). Finally, plant species turnover along the Jurien Bay dune chronosequence is high and no species occurs across all stages (G. Zemunik, unpublished data), thus complicating the choice of 'appropriate' native phytometers. Consequently, using native species would not have necessarily improved our study. That said, we agree with Uren & Parsons (2013) that leaf nutrient status from native plant species growing in the field can provide valuable additional information on nutrient limitation. Accordingly, a comprehensive survey of leaf nutrient (i.e. macro- and micronutrients) concentration and resorption for a wide range of native plant species along the dune chronosequence has recently been conducted (Hayes 2012). The results obtained from that field survey support those from our glasshouse experiment, that is, a shift from N to P limitation with increasing soil age.

PARALLEL BEACH RIDGES

Uren & Parsons (2013) suggest that our work on the Jurien Bay dune chronosequence is problematic when compared with other sequences of regular, parallel beach ridges, such as those described by Burges & Drover (1953) in eastern Australia. However, we should not dismiss dune chronosequences that are not laid out as clear sequences of parallel dunes simply because they are more complex to study, as they can represent powerful natural experiments once properly characterized. For example, the large overlapping parabolic Cooloola dunes in Queensland, Australia (Thompson 1981), have been central to our understanding of long-term podzol development (McKenzie *et al.* 2004).

PAST CLIMATE CHANGES, EROSION, AEOLIAN DUST DEPOSITION

Uren & Parsons (2013) argue that long-term soil chronosequences, such as the Jurien Bay chronosequence, can be problematic in that the older stages have experienced multiple climate changes. While this is undoubtedly true for all long-term chronosequences and probably affects the rates of pedogenesis at different periods, the pivotal point remains that the different soils can be reliably ranked based on relative age. Given the many glacial/interglacial cycles experienced throughout the Quaternary, such climate changes are unavoidable (Vitousek 2004).

Uren & Parsons (2013) also mention that erosion can influence soil formation over the long time-scales covered by the Jurien Bay chronosequence. This is not a problem in itself since soil formation, by definition, is the balance between the production of new soil (via weathering or deposition) and losses associated with erosion. Erosion can slow down or prevent depletion-driven P limitation where tectonic uplift is minimal (Porder *et al.* 2007; Vitousek *et al.* 2010), such as in south-western Australia. Similarly, dust deposition can slow

down depletion-driven P limitation (Eger, Almond & Condron 2013), although to our knowledge no one has identified any significant dust imprint in the stratigraphy of the Swan Coastal Plain succession. The fact that total and available P strongly decreased along the Jurien Bay chronosequence (Laliberté *et al.* 2012; fig. 2) suggests that erosion or dust deposition were not important enough to prevent the development of extreme P limitation in this system.

DIFFERENCES BETWEEN DUNE CRESTS AND SWALES

Uren & Parsons (2013) mention that there are well-known differences in nutrient and water availability between dune crests and swales and that we appear to have disregarded this issue. Although we did not acknowledge this explicitly in our paper, we avoided dune swales and collected soils on freely draining soils on dune faces where dune morphology was still relatively intact (i.e. Quindalup and Spearwood dunes). In older dunes that had lost their dune morphology (i.e. the oldest Bassendean dunes that have lost much of their relief due to their considerable age), we avoided obvious low-lying areas where water can accumulate from the surrounding landscape during the rainy season (winter).

ROLE OF WATER AVAILABILITY

Uren & Parsons (2013) suggest that water availability, rather than nutrients, could constrain primary productivity or plant species distributions along the Jurien Bay dune chronosequence. However, water constraints over primary productivity or plant species distributions were outside the scope of our study. In any case, nutrient and water constraints are not mutually exclusive. Any potential changes in water availability among the different chronosequence stages would not negate the fact that (i) there are major shifts in nutrient availability (e.g. a >30-fold decline in total P between the youngest and oldest dunes), (ii) the type of nutrient limitation varies along that dune sequence (i.e. N to P limitation) and (iii) these changes are broadly consistent with the Walker & Syers (1976) model – the main conclusion of our study.

Conclusion

We appreciate the opportunity that Uren & Parsons (2013) have given us to further clarify details about our glasshouse experiment and the Jurien Bay dune chronosequence. Our key points are that:

1 The Quindalup–Spearwood succession forms a consistent Holocene to Middle (or possibly Early) Pleistocene soil chronosequence where parent material, topography, and present-day climate and vegetation type (i.e. Mediterranean shrublands) are held relatively constant;

2 the older (Early Pleistocene–Late Pliocene) Bassendean dunes probably contained less carbonate initially, but the significance of this depends on the research question under consideration, given that carbonate loss from soils can be rapid;

3 the claim by Uren & Parsons (2013) that we did not consider the potential importance of micronutrients is baseless, as it was explicitly considered in our nutrient addition treatments and clearly mentioned in the interpretation of our results and conclusions.

We restate the validity of our experimental conclusions and affirm that the Jurien Bay dune chronosequence provides a valuable model system for understanding long-term soil and ecosystem development.

Acknowledgements

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