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Evolutionary biology

Soil alkalinity and salt tolerance: adapting to multiple stresses

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Bui's commentary [1] arises from an observation made in our paper on the evolution of salt tolerance in grasses. We described the 'paradox' of salt tolerance; that it evolves often in nature but is hard to breed into crops [2], although there has been recent success in increasing the tolerance of wheat on salt-affected soils in Australia [3]. Bui suggests that one reason for lack of success in breeding salt-tolerant crops is that researchers have focused primarily on sodium chloride in soil and have paid less attention to the effect of alkalinity. This important issue should be explored more fully, particularly with reference to Australian soils with their transient and complex salt contents [4]. However, while soils in Australia are predominantly sodic, many soils throughout the world are saline and dominated by chloride, reflecting the ion balance in seawater [5]. Screening for tolerance to sodic soils is difficult in a laboratory [6]. It requires a soil-based system [7], although the use of tanks can make this a practical proposition [8].

We agree that, given the overlap of salinity and alkalinity on the landscape [1,9], it would be interesting to ask whether there has been co-adaptation to salinity and alkalinity. Although clear differences in tolerance to salinity and alkalinity exist for some species (e.g. rice [7]), shared underlying mechanisms in salinity and alkalinity tolerance have been suggested for some taxa, such as *Eucalyptus* [10] and *Chloris* [1]. This leads to a broader question of whether some lineages have characteristics that make them better able to adapt to a range of environmental stresses. There may be a suite of stress-related traits that allow plants to survive in different stressful environments by switching from high-resource strategies to stress-tolerant strategies [11].

The stress resistance syndrome hypothesis [11] could explain, at least in part, the striking pattern which emerged from our study that salt tolerance has evolved often in a wide range of grasses [2]. C₄ photosynthesis has also evolved independently many times in grasses [12]. Because C₄ leads to improved water use efficiency, it is often associated with open, arid environments [12], which are also more likely to be affected by salinity and alkalinity [13]. Alkaline soils often have poor soil structure, which affects their hydraulic conductivity and water uptake by plants [14]. Furthermore, accumulation of sodium ions may interfere with normal stomatal closure, exacerbating water loss in plants growing in sodic soils [14]. Halophytes arise more often than expected in C₄ lineages, possibly because the greater water use efficiency of C₄ photosynthesis reduces the negative impact of osmotic stress and ion toxicity imposed by saline conditions [15]. Therefore, we might consider C₄ photosynthesis and salt tolerance as aspects of a broader stress resistance syndrome linked to aridity, which might also confer alkali tolerance. If this were the case, then selecting for salt tolerance in crops may incidentally confer a degree of tolerance to alkalinity or drought stress. Ideally, rather than investigating the phylogenetic distribution of tolerance to one particular stress, such as salinity [2], we should consider the distribution of tolerance to a range of environmental stresses. This may permit us to identify lineages that can

readily adapt to a variety of harsh environments or traits that confer multiple stress tolerances.

We agree that the investigation of evolutionary patterns of plant adaptations to harsh environments should incorporate

more data on geochemistry, combined with climatic data. Interaction between soil and plant scientists is vital for the development of salt-resistant crops, especially given the difficulties in reproducing field conditions in the laboratory.

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