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Introduction

Soil chemistry is an important environmental filter driving the ecology of plants (Laliberte et al. 2014). Soil conditions can restrict establishment and distribution of plant species, leading to strong phenotypic selection for edaphically endemic plants—species that only grow on specific soil types. These plants are spatially limited to the distributions of a particular soil system and are highly specialized to their habitats (Anacker 2011). The patchy distributions of unusual soils, in combination with the highly specialized endemics that inhabit these regions, make them biodiversity hotspots (Escudero et al. 2014). Edaphic endemics contribute to a large portion of the world's biodiversity despite their limited distribution (Damschen et al. 2011). Such communities are vulnerable to the effects of disturbance because unusual soils are spatially patchy and isolated, endemics are highly specialized, and the resources present in arid soil environments where such soils commonly exist are limited (Damschen et al. 2011).

Soils rich in gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) epitomize these biodiverse plant communities. Although gypsum deposits occur globally, gypsum soils are almost completely restricted to arid and semiarid regions, as evaporative demand creates capillary uplift of gypsum to surface soil layers, creating gypsum crusts; in more mesic or humid environments, water infiltration and percolation prevents gypsum crust development (Escudero et al. 2014, Parsons 1976). Compared to saline soils, gypsum's solubility impacts plant species in a different way from soils high in soluble ions (Herrero and Porta 2000; Escudero et al. 2014). Because gypsum soils have a less negative osmotic potential than saline soils, ion toxicity is not as significant on gypsum

soils as saline or sodic soils (Herrero and Porta 2000). In fact, gypsum can act as a dispersive agent in saline or sodic soils, minimizing ionic stress (Escudero et al. 2014). However, other characteristics of gypsum soils may limit plant nutrient availability. High sulfate may induce nutrient deficiencies due to ion competition at the root surface (Marschner 2012), and its high Ca/Mg ratio may limit availability of some macro- and micronutrients, due to precipitation and complexation with calcium ions (e.g., precipitation of insoluble Ca-P phases), and the potential for high Ca^{2+} to limit uptake of K^{+} and Mg^{2+} due to similarity in size and charge (Marschner 2012). Additionally, as gypsum concentration increases in soils, cation exchange capacity decreases, further limiting nutrient availability (Escudero et al. 2014, Castillejo et al. 2011). The effects of the unique soil properties of gypsum, compounded by the deficiency of nutrient and water resources of arid environments, present a challenge for plant establishment and success.

Understanding the specific drivers of gypsum endemism is an area of focused research currently, particularly in Europe. Early work from the Mojave Desert suggested soil physical factors appeared to drive patterns of distribution and abundance of plants on and off gypsum soils more than differences in soil chemistry (Meyer 1986). In general, species able to penetrate the gypsum surface crust were able to grow and establish in these soils, although they also were capable of growing in non-gypsum soils. As a result, the author concluded that rather than chemical soil features, physical features were a main driver of plant distribution and abundance in these soils. However, drought-imposed nutrient deficiencies in these Mojave species may mask any gypsum-specific effects of soil chemistry on plant distribution and abundance (Parsons 1976), and therefore, this site may not be optimal for testing hypotheses regarding plant-soil chemical feedbacks. More current work from Europe suggests that gypsophiles are adapted to the unique chemistry of gypsum soils, as indicated by the unique leaf nutrient signatures in

gypsophiles versus gypsovags (i.e., plants growing both on and off gypsum soils) (Palacio et al. 2007, 2014). In general, regionally dominant gypsophiles have higher concentrations of inorganic compounds than gypsovags, and in some cases accumulate calcium oxalate crystals. The unique leaf nutrient signatures of gypsophiles are strong evidence of physiological specialization in the gypsum flora of Spain.

Although extensive work on the systematics of the Chihuahuan Desert gypsum flora has been conducted (Moore and Jansen 2007, Moore et al. 2014), no previous research, to our knowledge, has investigated the potential physiological adaptations of the gypsum flora of this region. The Chihuahuan Desert provides an excellent study system for questions of adaptation to gypsum soil. This area is known for some of the largest outcrops of gypsum in North America (Parsons 1976). Additionally, summer monsoon precipitation reduces the strength of summer drought, potentially reducing the severity of drought-induced nutrient limitation across soil types and making it more possible to investigate gypsum-related plant nutrient signatures. The Chihuahuan Desert also is highly diverse, with closely related taxa (either congeners or confamilials) being found in the mosaic of gypsum and non-gypsum soils, allowing for phylogenetic control in studies of physiological adaptation. The gypsum flora of the Chihuahuan Desert also provides interesting contrasts to the well-researched flora of Spain, particularly in relation to plant phenology. The Spanish flora experiences a Mediterranean climate with cool, wet winters and hot, dry summers, with most plant growth and reproduction occurring during spring. In contrast, most plants of the Chihuahuan Desert preferentially grow and flower during the hottest months of the year, which coincide with the summer monsoon. The distinct environmental drivers may uniquely influence the physiology of these species.

Objective and Hypothesis

The overall objective of this study is to determine whether the chemical properties of gypsum soils are linked to unique plant tissue nutrient signatures in gypsum endemics compared to congeners or confamilials growing off of gypsum. We expected that plants endemic to gypsum will have higher leaf ion concentrations than their taxonomic partners growing on calcareous soils in the same locality. We expected that gypsum soils would be enriched in calcium and sulfur compared to non-gypsum soils. Due to high Ca^{2+} and SO_4^{2-} in gypsum soils, we predicted gypsum endemics would be enriched in both calcium and sulfur in leaf tissue relative to plants growing off gypsum, whereas uptake of other nutrients (e.g., leaf P and Mg) may be lower in gypsum endemics compared to plants growing off gypsum.

Methods

Study Site and Species Selection

This study was conducted at four sites in Eddy County, New Mexico in the northern Chihuahuan Desert: Yeso Hills ($32^{\circ} 02' 23''$ N, $-104^{\circ} 27' 38''$ W), Seven Rivers Hills ($32^{\circ} 33' 18.4''$ N, $-104^{\circ} 27' 06.1''$ W), north of Carlsbad near US 285 ($32^{\circ} 28' 33.6''$ N, $-104^{\circ} 17' 31.5''$ W), and near NM 128 ($32^{\circ} 18' 36.4''$ N, $-103^{\circ} 48' 55.2''$ W). Sampling was also conducted at the northern edge of Culberson County, Texas near TX 54 ($31^{\circ} 35' 36.1''$ N, $-104^{\circ} 51' 19.3''$ W). Mean annual temperature in Eddy County, NM is 61° C, and mean annual precipitation is 330 mm (averages represent 30 years of data obtained from Carlsbad NM station, National Climate Data Center, ncdc.noaa.gov). This area encompasses large outcrops of Permian-aged gypsum, as well as areas dominated by limestone and alluvial soils. Soil complexes are commonly of the Reeves, Cottonwood, and Gypsum-Cottonwood series, among others. The Reeves and

Cottonwood series are characterized by having shallow soils, loamy textures, and little rock/gravel cover. Gypsum soils have gypsum bedrock, very shallow soils, and sometimes hard surface crusts (Chugg et al. 1971). Dominant plant species on the gypsum soil sites are perennial forbs rather than larger shrubs (Parsons 1976) and are endemic to gypsum. Hardier gypsovags are less common than endemics.

Sampling Design and Field Measurements

Soil samples and plant leaf tissue were collected from areas on and off gypsum soils. At each location, samples were collected from an area 1 m by 1 m and at least 20 m from roadsides for all species except *Acleisanthes* spp., to limit disturbance. Twenty-two plant species both on and off gypsum soils were sampled, with at least five replicate plants per species. Where possible, we collected congeners or confamilials growing on and off gypsum soils to account for potential phylogenetic patterns in the data. In total, of the 22 species, there were six congener pairs (12 species total; *Oenothera hartwegii*, *O. gayleana*, *Acleisanthes lanceolata*, *A. longiflora*, *Sporobolus nealleyi*, an unknown *Sporobolus* species, *Bouteloua brevisita*, *B. curtipendula*, *Tiquilia hispidissima*, *T. canescens*, *Mentzelia strictissima*, and *M. humilis*). These replicate plants were randomly selected from within the sampling area at least 10 m away from the nearest sampled individual of the same species. From each plant, we collected approximately 1-3 g of leaf tissue (dry weight) from the youngest, fully mature, green sun leaves.

Soil samples were collected near plants growing on gypsum soils and non-gypsum soils. Soils were sampled near the plant replicates for eight species. Two subsamples were collected at the canopy drip-line using soil corers up to 20 cm depth. Soils that were moist when collected

were allowed to air dry. Soils were then sieved (<2 mm), weighing both the gravel and fine fractions.

Soil and Plant Analyses

Soil soluble salts (Ca^{2+} and Mg^{2+}), phosphorus, sulfur, electrical conductivity, and pH were determined using saturated soil paste extractions as described in Pietrasiak (2013) and ICP-OES (Plasma 400; Perkin-Elmer). Leaf tissues were prepared by microwave digestion, using concentrated nitric acid, and analyzed using ICP-OES for the elements P, S, Ca, and Mg.

Statistical Analysis

Principal Components Analysis (PCA) was used to compare patterns in leaf chemistry between gypsum endemics and plants growing off gypsum or whether congeners/confamilials have related elemental patterns. A separate PCA was run on all soil chemical variables to assess patterns in soil properties between the soil types. PCA is a linear, multivariate method that be used to help describe patterns in data. As a linear method, predictor variables are plotted as vectors indicating the direction of increase for each variable. Samples are plotted as centroids, and those plotting closer to one another in multivariate space are more similar in their chemical signatures than samples plotting further from each other. Axes are orthogonal to each other; therefore, the first axis describes the greatest amount of variation in the data. Descriptive statistics (means \pm SE) were calculated for individual elements for soil and leaf chemistry.

Results

Soil chemistry differed strongly between gypsum and non-gypsum soils (Figure 1). Gypsum soils had much higher Ca and S than non-gypsum soils (Figure 2). Gypsum soils also had higher electrical conductivity than non-gypsum soils, reflecting greater concentrations of charged ions. However, extractable Mg, P, and pH did not drive separation between soil types. Mean soil Mg was slightly lower in gypsum soils, and mean soil P was slightly higher in gypsum soils.

Plants growing on gypsum showed a distinct leaf chemical signature, driven primarily by calcium and sulfur (Figure 3). Gypsophilic plants had much higher Ca and S than plants growing off gypsum, including close relatives (Figure 4). Some close relatives like *Acleisanthes lanceolata* and *A. longiflora* and *Tiquilia hispidissima* and *T. canescens* had notable differences in leaf Mg between plants growing on gypsum and non-gypsum soils (Figure 3). Mean leaf Mg of all plants growing on gypsum was slightly reduced from plants growing off gypsum (Figure 4). Phosphorus did not create major separation between plants from the two soil types (Figure 3). Mean leaf P from plants on gypsum was slightly higher than plants growing off gypsum (Figure 4).

Discussion

As predicted, leaf chemical signatures were reflective of the soils in which plants grow, with gypsophilic plants having higher leaf Ca and S than their close relatives from other soil types. Because plants are sensitive to their soil environments, they often have relative nutrient concentrations comparable to their associated soils. As a result, leaves from gypsophiles are more enriched in Ca and S in comparison to plants growing off gypsum. In the plants we sampled growing on gypsum, leaf Ca and S averaged 72.56 g kg^{-1} and 19.99 g kg^{-1} , respectively.

Not only was the average for Ca high compared to values typically reported in the literature (1-50 g kg⁻¹, Marschner 2012), it was also at the high end of the range reported for plants dominant in gypsum soils (Moore et al. 2014). Average leaf S for plants we sampled was also quite high compared to typically reported values (1-5 g kg⁻¹, Marschner 2012) and was mid-range for values reported for dominant gypsophiles (Moore et al. 2014). Given these high levels, how do gypsum endemics prevent toxicity? Some plants are capable of sequestering toxic levels of elements in non-harmful crystalline forms (e.g., sodium; Parida and Das 2004, Munns 2002). Some data suggest that widespread gypsophiles are capable of sequestering excess Ca as calcium oxalate crystals, which can be stored or excreted through their leaves (Palacio et al. 2014). Other work suggests gypsophiles can secrete crystal forms of gypsum through their leaves (He et al. 2015). Although we do not currently know the mechanisms used to prevent elemental toxicity in our suite of species, current work in our research laboratories is using Fourier transform infrared spectroscopy (FTIR) to determine which forms of calcium and sulfate are stored in our focal species.

Despite high leaf Ca, plants growing on gypsum had similar levels of Mg compared to plants growing off gypsum. This is contrary to our expectation that high soil Ca would compete with Mg uptake at the root surface, due to the similarity in charge and size of these two cations (Marschner 2012). The similar leaf concentrations between plants growing on and off gypsum soils indicates strong selectivity for Mg in gypsum endemics, potentially due to transport proteins with greater Mg specificity (Marschner 2012) and may provide support for adaptation in these species to gypsum soils. Other studies have shown how selectivity for ions with reduced relative soil concentrations is an indication of adaptation. For example, the salt-tolerant shrub *Sarcobatus vermiculatus* was able to maintain sufficient levels of leaf Mg throughout the

growing season, despite increasing soil and leaf Na over time (Donovan et al. 1997). *Sarcobatus* showed increased selectivity for uptake of Mg and other nutrients as concentrations of Na increased, compensating for the added stress. The study concluded that *Sarcobatus* was adapted to select for essential nutrients during saline toxic stress (Donovan et al. 1997). Similarly, serpentine and non-serpentine ecotypes of the sunflower, *Helianthus exilis* differed in their leaf nutrient profiles when grown in reciprocal soil types (Sambatti and Rice 2007). Serpentine soils are enriched in Mg relative to Ca, and ecotypes growing in serpentine soils successfully excluded excess Mg uptake at the root surface to maintain favorable leaf Ca:Mg, while non-serpentine ecotypes lacked this ability. As a consequence, biomass production (a proxy for fitness) was higher for serpentine vs. non-serpentine plants growing in serpentine soils, suggesting adaptation to this soil type.

In our study, leaf chemistry in *Acleisanthes* species is suggestive of a phylogenetic influence. Leaf Mg was quite high in both *Acleisanthes longiflora*, growing off of gypsum, and *Acleisanthes lanceolata*, a gypsophile, possibly as a result of adaptation for Mg selectivity. Although these species differ in their concentrations of Ca and S, due to their different associated soils, they were much higher in leaf Mg than other species included in our analysis. Nearly all other confamilials and congeners produced similar leaf P and Mg, but differed in Ca and S, as in *Bouteloua* (Figure 3). Future work will include more congener and confamilial pairs to investigate potential phylogenetic effects on leaf chemical signatures and explicitly include these relationships in statistical analyses.

Future directions for this work seek to better understand how responsive the plants in this study are to their associated soils. A reciprocal transplant study comparing gypsum endemics and their congeners and confamilials growing off gypsum and their associated soils would

provide a more explicit test of plant adaptation to these soils, including the roles of nutrient selectivity and potential phylogenetic constraints on tolerance. Likewise, competition studies, using a target plant-neighbor model would help explore potential biotic influences on plant distribution on these soil types. Understanding the environmental and biotic filters on plant distribution will help reveal selective forces in these unique soil systems.

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Figure Legends

Figure 1. PCA of soil chemistry. Gypsum soils are open circles, non-gypsum soils are closed circles. 93.01% of the variation is explained by the first two axes.

Figure 2. Mean soil nutrient concentrations for gypsum and non-gypsum soils, averaged across species. Error bars are SE (n=23 for gypsum soils, n=14 for non-gypsum soils).

Figure 3. PCA of leaf tissue chemistry for 131 individuals. 93.52% of the variation is explained by the first two axes. + symbols are unpaired plants growing on gypsum soils, × symbols are unpaired plants growing on non-gypsum soils. All other symbols represent congener species pairs. Unfilled symbols are plant species growing on gypsum. Filled symbols are plants growing off gypsum. Stars represent *Bouteloua* spp., rectangles are *Acleisanthes* spp., and diamonds are *Tiquilia* spp., all of which are grouped with ellipses. Squares are *Oenothera* spp., triangles are *Mentzelia* spp., and circles are *Sporobolus* spp.

Figure 4. Mean leaf nutrient concentrations for plants growing on gypsum and non-gypsum soils, averaged across species. Error bars are SE (n=77 for plants growing on gypsum soils, n=41 for plants growing on non-gypsum soils).

Figure 1

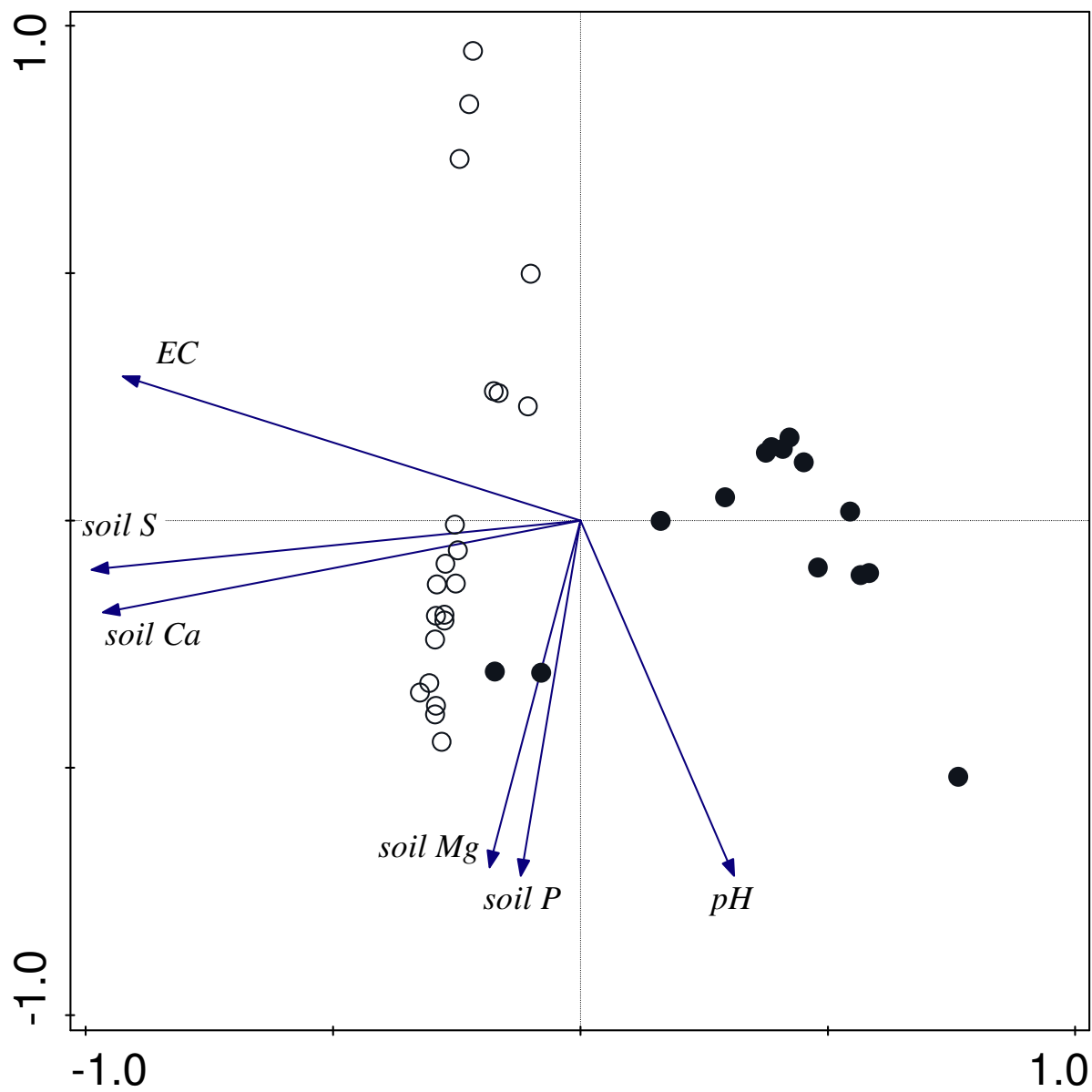


Figure 2

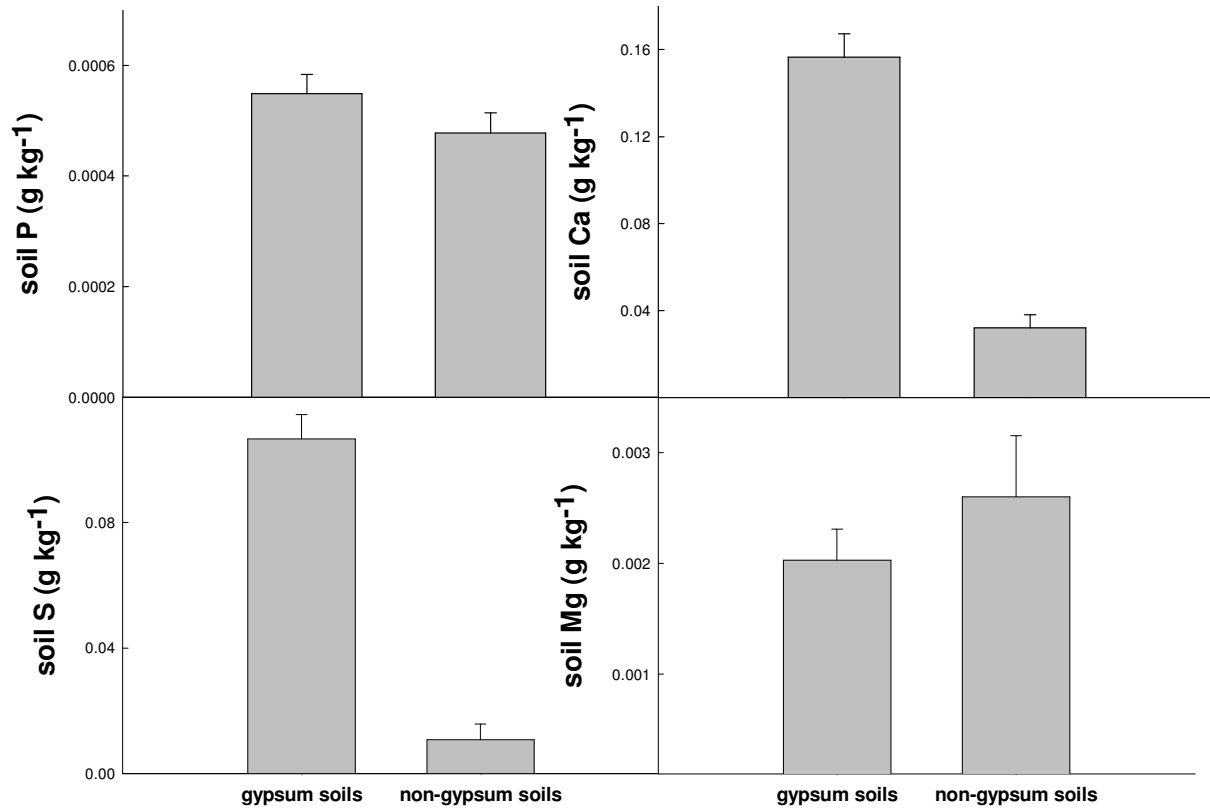


Figure 3

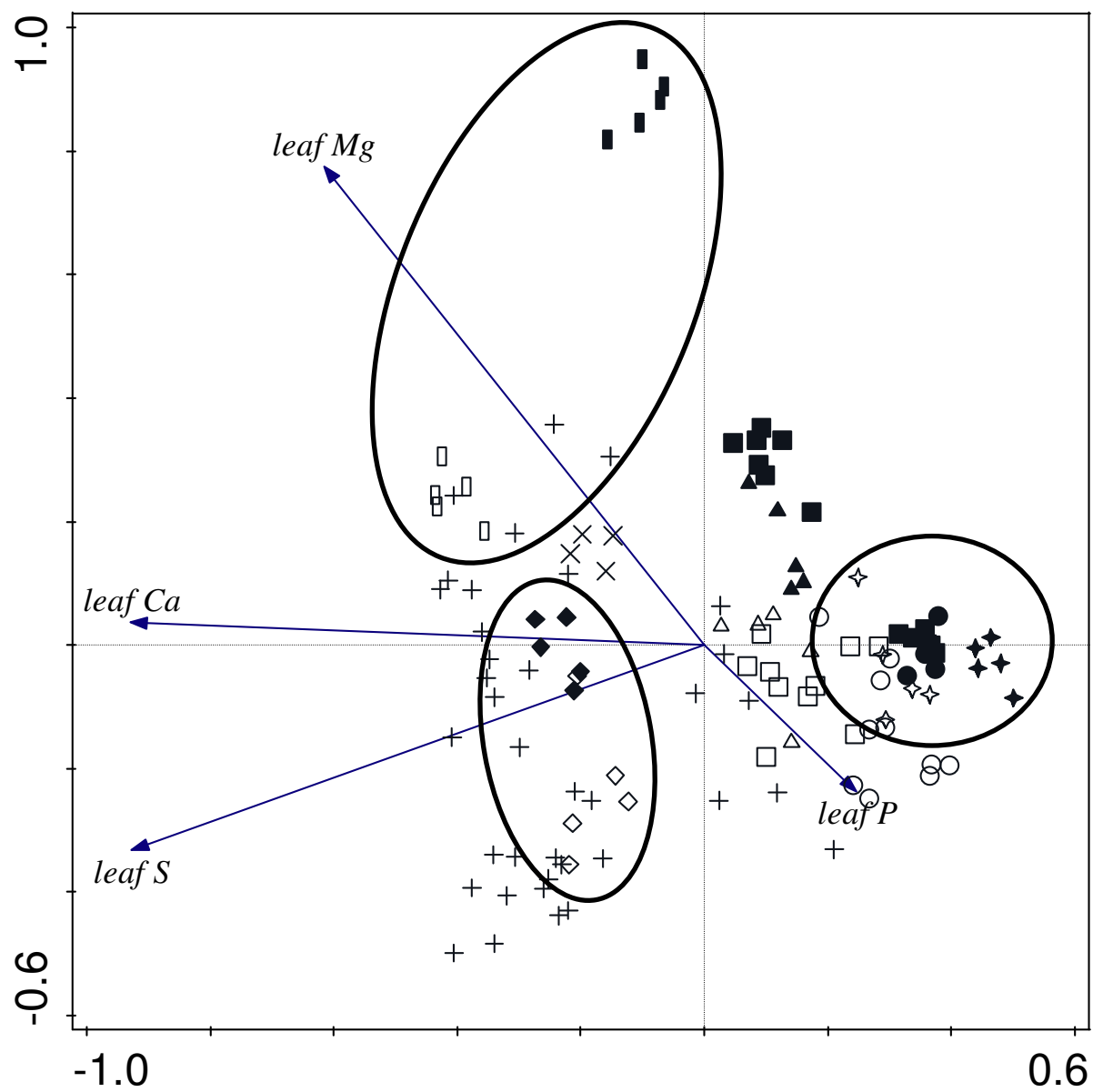


Figure 4