Soil Factors Affecting the Competition between Trees and Grasses

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Abstract

Soil factors affecting the competition between trees and grasses are examined by way of the proposals that outcomes derive from the high grass root density promoting nutrient uptake directly by increasing contact with soil particles and indirectly by reducing the build up of salt around roots. The significance of these effects varies with soil texture and is greatest with clay soils. However, the occurrence of grasslands usually depends additionally on other environmental constraints that affect the ability of plants to take up nutrients. The nature and implication of the interactions are examined by reference to natural patterns of plant communities.

Introduction

Trees and grasses have very different life forms (Table 1) but typically coexist in native plant communities. Even where grasses are large, as with bamboo, they represent an understory species. Trees always have the potential to suppress grasses by shading hence to co-exist grasses must have attributes that limit their suppression by trees. Grasses have attributes that can provide an advantage over trees, as with the basal leaf meristem being beneficial with grazing by ungulates.

Situations exist where grasses are effectively excluded by trees, as in rainforests. However, situations also exist where grasses occur without trees or other woody plants. Some of these occurrences of grasslands are ascribed to fire regimes, often involving interactions with grazing, but there are many natural occurrences of grasslands surrounded by woodlands or forests where fire and/or grazing do not determine the patterns of vegetation.

Grasslands typically occur on soils with appreciable clay content but for complete grass dominance other factors may also be required. While fire and grazing are often implicated factors such as intermittent waterlogging and the occurrence of salt spray can also combine with the soil properties to produce grasslands.

Mutual exclusion between grasses and trees represents an extreme outcome in the balance of trees and grasses. The broad pattern of plant communities in the east of Australia is forests along the coast and ranges grading westwards through grassy woodlands, shrub woodlands and shrublands. Grasslands naturally occur in all of these environments but they are most common in the western areas. There is an interaction between soil type and climate in determining the relative abundance of the different plant life forms in natural plant communities.

The association between grasses and clay soils is usually attributed to the characteristics of soil water storage. The depth of penetration of a rainfall event is appreciably less in clays than sands because of differences in soil water holding capacity. The effect of this difference is greatest in drier regions where sporadic rainfall events seldom saturated soil profiles. This is said to confer a competitive advantage to grasses because their high density of roots in the surface soil allows rapid exploitation of water in the surficial soil.

This suggested effect of the depth of water penetration may be of consequence but it does not account for the situation where soils are seasonally inundated. Moreover, it does not take account of the reality that virtually all terrestrial plants have most of their roots in the surface soil and that trees tend to maintain their capacity for growth longer than grasses when conditions become dry. Grasses often senesce when conditions are dry while woody plants tend to maintain physiologically active leaf. Trees can therefore have a greater potential to use sporadic rainfalls than grasses.

Another issue with the suggested importance of root density in accessing soil water is that grasses could extract water at the potential rates with around one hundredth of the roots that they possess. This represents an over capacity of 10,000%. With natural systems a 10% difference is usually significant and an excess capacity of even 100% in plant design is highly unlikely. The large disparity in root characteristics between trees and grasses is likely significant but it is difficult to ascribe the importance directly to the capacity to take up water.

This paper examines the characteristics of trees and grasses to identify which factors are important in determining their relative competitive advantage in different environments. It examines how differences in morphology and physiology can produce differences in the composition of plants communities in different environments.

Table 1. Comparative morphological attributes of trees and grasses.

Attributes	**Trees**	**Grasses**
Size	Big	Small
Height	Moderate to tall	Short to moderate
Life span	Moderate to long	Annual to moderate
Root diameter	Big and small	Small
Root/shoot ratio	<1	>1
Leaf / stem ratio	Low	High
Leaf meristem	Apical	Basal

Context

The general context is that realised vegetation patterns represent an interaction between plants having disparate characteristics and a number of environmental factors. These environmental factors are not constant but vary with space and time. With interactions between multiple factors there can be many optimal solutions. Situations may arise where one combination is obviously superior but more commonly there are multiple optima that are equally viable. Different combinations of plants can provide equally viable solutions. The viability of a solution by way of a particular form of plant community does not depend on it being the best adapted to the environment.

It is normal for most species of plants to be excluded from a particular environment. The existing vegetation could therefore be said to arise by default through the environment excluding others. However, the number of species that exists in a particular environment, and the different combinations, are much less than is physiologically possible. Many species are effectively excluded by the occurrence of others and this interaction between species results in distinct forms of plant communities.

The occurrence of interactions means that outcomes cannot be reliably predicted from individual processes. Reliable conclusions can only be obtained by analysing the system as a whole. This involves examining the relative significance of different factors by way of how they operate and interact to produce outcomes. Outcomes are probabilistic rather than deterministic.

Methods and Results

The approach taken is to present a conceptual model and examine its applicability, which equates with hypothesis testing. The proposals are:

- A high density of plant roots significantly reduces the accumulation of salts around the root surfaces in clay soils where this benefits the uptake of nutrients.
- Nutrient uptake in clay soils is promoted by a high root density as it depends on ion exchange between roots and soil colloids.

These effects are synergistic with a high density of small roots promoting nutrient uptake in clay soils.

Water from the bulk soil solution is drawn towards roots when plants transpire water. This water can contain all elements required for plant growth, mainly in ionic form. However, most elements are only required in very small amounts and concentrations of many ions, such as sodium and chloride, are much higher than needed by plants. The high concentrations of some ions can interfere with the uptake of essential and limiting ions. This can create nutrient deficiencies even where all necessary elements are present in adequate quantities. It can also necessitate the expenditure of energy by plants (ion pumps) to preferentially obtain some elements and exclude others.

The uptake of water and exclusion of ions increases the salinity of water in proximity to roots. The flow of ions to roots is via bulk water flow which is rapid. However, a return to an equilibrium condition whereby ions are evenly distributed throughout the bulk soil solution is slow as, without the addition of water, it depends on diffusion. Reducing the concentration of ions around roots therefore depends largely on the flow of water through soils associated with the infiltration of rainfall.

The mechanism for the accumulation of salt around roots is the same as in the development of a soil profile with salt accumulating in regions where plants take up water and the accumulated salt is not leached. The combination of water taken up by plants having lower salt concentrations than in the soil and the leaching of soil salts by rainfall produces the characteristic soil profile where A2 horizons become leached and ions accumulate in the B horizon. Limited accumulation of salts in the A1 horizon is promoted by the accumulation of organic matter and evaporation of water from the soil surface.

The leaching of accumulated salts away from root surfaces depends on the flow patterns of water through soils and the bonding between ions and soil particles. Sands function as a uniform or homogeneous porous medium and they have limited ability to adsorb ions, as reflected by their low cation exchange capacity (CEC). Salts that accumulate around roots in sandy soils are readily leached back into the bulk soil solution.

Clay particles typically form aggregates whereby the soil is no longer uniform. Water can flow rapidly in the spaces or voids between aggregates and this water is readily available to plants. Conversely, water associated with the surfaces of clay colloids is tightly bound, as are most cations. Movement of water and ions from inside to the outside of aggregates is slow because of the high resistances to water movement. The resistance to flow increases markedly as soils become dry hence most flow occurs when soils are close to saturation.

In their simplest form clay soils have two markedly different states and the balance between these determines the delivery of water and nutrients to plants. Most water is obtained from large voids but this contains few nutrients. Obtaining water from within aggregates has the advantage that plant roots are appropriately located to take up nutrients but that concentrates salts in locations where dispersal of salts is slow. The situation within aggregates is similar to that within soil profiles whereby salt accumulates in regions where plants extract water and which are not subject to leaching.

Several results demonstrate the applicability of the mechanism. Salt sieving by clay soil aggregates (Blackmore, 1976[1]) demonstrates that clay aggregates accumulate salts even without extraction of low salinity water by plants. The concentrations of ions in water flowing through soils were lower than expected from the general soil salinity (Peck, 1973[2]). Water flow through soils is mainly along preferred pathways and salts within aggregates are protected from leaching.

Anions tend to occur in the bulk soil solution and are therefore readily available to plants and are highly susceptible to leaching. Occurrence in the bulk soil solution means a single root can exploit anions from a large volume of soil. Cations tend to be bound onto colloids and become available to plants through ion exchange. As much of the ion exchange is between the surface of the roots and the soil colloidal particles the potential for plants to obtain cations depends on the association between plant roots and the colloidal particles. A single root has a limited ability to source cations.

A high root density is beneficial in accessing nutrients where the cations are strongly associated with colloids, as with clay soils. A high root density is then also beneficial in reducing the concentrations of salt around the root surfaces where the reduced salt concentration improves the potential for plants to take up nutrients. The uptake of water is a causal factor in the interaction between root density and soil type but its significance to plants derives from the consequent effects on the uptake of nutrients arising through the accumulation of salts around roots. There is also a synergistic direct effect with high root densities promoting the uptake of nutrients from clay soils.

Examples

General examples are given in the introduction so this details some specific occurrences. The commonality between examples is that the realised outcomes seldom represent a response to a single factor as realised outcomes usually arise through interactions.

The Shoalwater Bay Training Area in central coastal Queensland contains around 1,700 km2 of largely intact native vegetation in a wide range of environments. Natural grasslands are uncommon but occur on heavy clay soils in localised seasonally inundated areas, on frontal slopes of headlands having shallow clay soils and on saline clays some of which are intermittently inundated by seawater. Another environment where a grass effectively dominates is on the frontal dunes on sandy beaches where *Spinifex sericus* is the frontal vegetation sometimes coexisting with the prostrate herb *Ipomea pes-caprae*. The soil is fresh

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[1] Blackmore, A.V. (1976). Salt sieving within clay soil aggregates. Aust. J. Soil. Res. 14, 149-58
[2] Peck, A. J. (1973). Chloride balance of some farmed and forested catchments in southwestern Australia. Water Resour. Res. 9: 648,57

beach sand. Trees of *Casuarina equisetifolia* typically occur just inland of the *Spinifex sericus* and have an understorey of different grass species with organic matter having accumulated in the surface soil.

The occurrence of grasslands on heavy clay soils is common, particularly where additional factors help suppress other plant life forms. Waterlogging suppresses the ability of plants to selectively take up nutrients and waterlogging of clay soils promotes grasses. Local patterns of grasslands developing around drainage lines are common and are associated with the accumulation of clay and intermittent waterlogging.

The accumulation of salt also suppresses the ability of plants to take up nutrients and saline clays promote the occurrence of grassland. Three factors affect nutrient uptake with salt-water or marine couch (*Sporobolus virginicus*), clay, waterlogging and salinity.

Salt spray on headlands suppresses many tree species that might otherwise occur but several tree species occur locally in environments exposed to salt laden winds, such as *Casuarina equisetifolia* and *Araucaria cunninghamii*. *Casuarina equisetifolia* occurs on sands while *Araucaria cunninghamii* occurs on areas of sands and fractured rock that are protected from fire. Exposed headlands with sandy soils have woody vegetation with shrublands dominated by *Grevillia banksii* being common. The grass *Themeda triandra* forms extensive grasslands on shallow clay soils on headlands that receive aeolian accessions of salt.

The dominance of *Spinifex sericus* on frontal sand dunes is an apparent exception to the proposed mechanism as the sand contains no clay. It could be that the high levels of salt accessions impose equivalent constraints on nutrient uptake in such sands as occurs in clays. Nutrients are exceedingly restricted in beach sands and only become available through microbial activity of the surface of sand grains. Once in solution the nutrients are readily leached and have to be extracted from a solution containing abundant sodium chloride. Obtaining nutrients requires good affinity between plant roots and sand grains.

Experimental evidence of the significance of soil salinity in competition between grasses and woody vegetation is given by artificial flooding of subarctic communities with salt water[3]. Woody plants were reduced by 83% and this loss was compensated for by the growth of grasses.

Acacias

Acacias dominate on heavy clay soils in a broad belt across the middle of Australia where they tend to form monospecific communities. Grasses, shrubs and other tree species tend to be excluded from these communities. A prime difference between the acacias and the eucalypts that usually dominate Australian vegetation is the occurrence of endogenous mycorrhiza where these increase the availability of nutrients to the acacias.

The general dominance of acacias on clay soils in this belt is reversed in *Astrebla pectinata* grasslands (Mitchell grass). Acacias can readily occur in the Mitchell grass environment as evidenced by the invasion of the exotic *Acacia nilotica* (prickly acacia). However, this invasion is associated with disturbance with heaviest infestations along drainage lines. The development of *Acacia nilotica* on flat ground relates to paddock boundaries indicating a pronounced effect of grazing. While acacias can thrive in the environment they were naturally excluded by grasses.

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[3] Person, B. T. & Ruess, R. W. (2003) Stability of a subarctic saltmarsh: Plant resistance to tidal inundation. Ecoscience 10 (3) 351, 360

Climate Interactions

Grasslands naturally occur in very diverse climates across Australia from the monsoonal tropics to Tasmania and on cold elevated plains and deserts in between. There is no absolute climatic constraint but there are interactions that determine their relative occurrence. Grasses are most abundant in the woodland belt where rainfall is less than the potential evaporation but still sufficient to support trees.

The beneficial effect of fluctuating soil water availability for grasses is logically linked with the accumulation of salt around roots. The mechanisms identified above do not arise where water is always readily available.

The large areas of natural grasslands occur on clay soils in the woodland belt. The most extensive are the Mitchell grass plains in Queensland and the Monaro grasslands on a basaltic plain in southern NSW. While the occurrence of clay is important there are no obvious additional factors that promote the occurrence of these grasslands.

An additional factor that may be significant on the Monaro plains is the occurrence of severe frosts. Trees naturally occur on the plains but only on rock outcrops. Trees around the perimeter of the plains similarly occur on slopes where there is drainage of cold air.

One suggestion is that trees are precluded from heavy clay soils by the cracking clay damaging their roots. This explanation is commonly applied to open grassy woodlands of bimble or poplar box (*Eucalyptus populnea*) on the Darling Downs in southern Queensland and myall (*Acacia pendula*) in central northern NSW. However, extensive brigalow forests naturally occurred on the heaviest cracking clays and prickly acacia has invaded the Mitchell grass plains.

Conclusions

The preferential occurrence of grasses on clay soils appears to arise from the very high density of small roots providing extensive contact between plant roots and colloidal surfaces. This reduces the volume of soil water extracted per unit root length and thereby reduces the accumulation of salt around roots. The extensive contact between the plant roots and soil colloids, and the limited accumulation of salts around roots promote the uptake of nutrients.

The relative root density is likely important in determining the relative abundance of trees, grasses and shrubs in different environments. Most grasslands occur on clay soils so clay is most important. However, grasslands can occur in sandy soils and grasslands typically occur where several factors combine to restrict the ability of plants to obtain nutrients. The combinations identified that promote grasses relative to trees are:

- High clay, salinity
- High clay, intermittent waterlogging
- High clay, salinity, intermittent waterlogging
- No clay, extremely low nutrient availability, salinity