

ACACIA – EUCALYPT STRATEGIES FOR WATER & NUTRIENTS

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Introduction

The general distribution of vegetation across Australia has been related to water availability by way of annual deficits (Specht, 1970) and seasonal distributions (Fitzpatrick and Nix, 1970). Their focus on water reflects the large variation in water availability across the continent and the almost universal occurrence of water deficits. Evaporative demand exceeds rainfall for a substantial part of the year with winter and summer deficits in the north and south respectively. Between these extremes the deficits can occur at any time of year and are characterised by high variability resulting from temporal variations in rainfall patterns.

The role of nutrients in determining continental patterns of vegetation has been little explored by comparison with water. Nutrient availability has mainly been examined at local or regional scales by reference to geomorphology. For example, coastal sands generally support heath whereas adjacent areas on fine sediments or weathered rock support forest. On the Lamington Plateau rainforest occurs on basalt while wet sclerophyll occurs on granites. Such large local variations tend to mask regional and continental patterns.

This paper examines implications of nutrient availability at continental scales where consideration of continental patterns requires a higher level of generalisation than when addressing local patterns. It also requires multi-factorial analysis as effects of factors other than nutrients must be accounted for to determine the effects of nutrients. Rainfall is the prime determinant of continental patterns of vegetation in Australia and nutrient effects arise through interactions with water.

Given the masking and confounding of nutrient effects by other factors the approach used it to compare the water use and nutrient strategies of eucalypts and acacias and relate these to observed distributions of communities dominated by species from these genera.

Community Distribution and Structure

Communities dominated by eucalypts and acacias occur across Australia. While acacias have a broad distribution they tend only to dominate on clay soils between the 20 and 30^o S latitudes. Outside these latitudes, and on non-clay soils within these latitudes, acacias tend to either be understory species or a minor component of the upper story vegetation.

Where acacias comprise the largest life form in a community they often tend to develop monospecific tree layers. They also tend to exclude other plant forms such as shrubs and grasses. While extensive communities with a monospecific eucalypt tree layer occur on inland plains eucalypt communities tend to contain several tree species. Different eucalypt species tend to coexist such that eucalypt dominated communities tend to contain several eucalypt species. Moreover, eucalypt communities almost invariably have well-developed understories of either grasses (woodland) or shrubs (forest). There is a tendency for mono-specificity in acacia dominated vegetation and species mixtures in eucalypt dominated vegetation.

Some of the acacia species that tend to form monospecific stands are brigalow (*Acacia harpophylla*), gidgee (*A. cambagei*), and mulga (*A. aneura*). The distribution of these species reflects water availability. Progressing west from Brisbane brigalow first occurs in the

Lockyer Valley and extends to around St George. Mulga first occurs just west of Goondiwindi and extends across Australia. Gidgee is generally to the west/north west of brigalow. Additionally, myall (*A. pendula*) commonly dominates the tree layer on heavy clay soils along the southern edge of this belt from the Great Dividing Range to around St George. Heavy infestations of the introduced prickly acacia (*A. nilotica*) have developed on heavy clay soils to the east of the gidgee.

Isbell (1962) identifies that the strong association between brigalow and clay soils is not invariant. Brigalow occurs on coarser textured soils in some lower rainfall areas and does not occur on shallow clay soils within its climatic range. These exceptions reflect the moderation of water availability by soils. While these conditions do not account for all situations where brigalow is unexpectedly absent from clay soils they do not invalidate the general conclusion of a strong association between brigalow and clay soils.

Several considerations are critical when addressing relationships between soils and vegetation. There is no reason to expect close relationships between classifications of vegetation and soils, particularly where the soil classification incorporates an interpretation of pedogenesis. Plants respond to soil properties and relationships between soil properties and soil types identified by classifications such as The Australian Soil Classification are usually poor. The association between vegetation and soils is by way of properties such as depth, texture, fertility and salinity.

Such analyses are also affected by the nature of the vegetation classification. The situation is straightforward when communities are dominated by a single species, as with many acacia communities, but is complicated by the occurrence of a complex of tree species. This is addressed here by addressing eucalypts generically where they are dominants.

Additionally, the environment experienced by plants depends on the interaction between climate and soils thus relationships between soil properties and vegetation would be expected to vary with climate. For example, Cunningham et al. (1981) identify a change in the relative occurrence of poplar box (*Eucalyptus populnea*) on different soils across a rainfall gradient. Taking the relative occurrence of soil types into account, poplar box preferentially occurs on coarser textured soils in areas of low rainfall and finer textured soils in areas with high rainfall as identified above for brigalow.

Eco-physiological characteristics of acacias and eucalypts

Rates of water use

The potential for water use by plants is, to a first approximation, related to leaf area and in the same climate brigalow communities maintain around twice the leaf area as adjacent eucalypt communities. Most Australian plants tend to drop old leaf following the onset of new leaf growth as this promotes recycling of nutrients within the plant. Most species, including eucalypts, also drop leaf during drought but brigalow only drops leaf in association with new leaf growth. Neither acacia nor eucalypt communities maintain a constant leaf area but acacia communities tend to¹. The leaf area of brigalow communities only declines when leaf shed at the commencement of growth is not replaced because of the suppression of new growth by drought or insects.

¹ The exotic *A. nilotica* tends to drop its pinnate leaves during drought in contrast with the native species that have phyllodes which are retained during drought.

Maintaining leaf regardless of drought maximises the potential for water use. The penalty relates to the need to maintain leaf during extended rainless periods. Plants must be capable of restricting water loss and maintaining physiological activity when water is highly limiting.

Leaf dehiscence associated with drought provides a means of conserving water but reduces the potential for growth following rain. The associated slow uptake of water allows for considerable loss of water to the eucalypts through direct evaporation from the soil and its use by other plant species.

Brigalow communities tend to use water rapidly when it is available and survive extended periods of restricted water availability. Eucalypt communities tend to use water conservatively and hence limit the period and severity of water stress. Even where the communities utilise the same amount of water they differ in how rapidly it is used.

Most plants lose water even when the stomata are fully closed due to leakage from the stomata and the surrounding leaf surface. However, water loss from brigalow can be too small to be measured due to the small stomata and heavy wax coating on the phyllodes. The ability to prevent the loss of water makes plant survival during drought dependent on the use of food reserves to maintain physiological activity rather than the availability of water.

Nutrient implications

The benefits of leaf dehiscence versus retention reflect the energetic cost of maintaining leaf under unfavourable conditions compared with the cost of extracting nutrients from the soil and building new leaf structures. The energetic costs of acquiring soil nutrients by way of root growth and ion exchange are low in fertile soils but high in infertile soils. Also, there is a considerable risk that nutrient availability will be limiting in infertile soils regardless of the level of root growth. The significance of this can be seen in the forests of central Sweden where evergreen trees are most abundant despite the extended adverse conditions over winter. The only deciduous tree species, Birch (*Betula alba*) only occurs on fertile soils and the same pattern occurs with shrubs (Tunstall & Torssell, 2004).

Leaf structure

Eucalypts have leaves whereas the Australian acacias that form monospecific stands have phyllodes. Cells in phyllodes tend to be small and thick walled and this allows the development of the low water potentials needed to extract water from dry soils. Field water potentials for brigalow can be lower than -6 MPa when the highest soil water potentials are around -3.5 MPa (Tunstall & Connor, 1975, 1981). The nominal wilting point for crops is -1.5 MPa.

Nitrogen fixation

Nitrogen fixation represents the primary nutritional difference between acacias and eucalypts. Acacias expend energy maintaining microbial populations which has the long term advantage of making nitrogen levels non-limiting to growth. The disadvantage is that accumulation in the soil makes the nitrogen potentially available to other species.

The lack of nitrogen fixation by eucalypts results in a delay in the plant obtaining adequate nutrition following rainfall. Soil nitrogen levels take several days to develop following rainfall and this creates a time lag between water becoming available and the development of a potential for plant growth. This delay makes rapid use of water by plants undesirable where they depend on mineralisation for nutrient availability.

SOIL INTERACTIONS

The main soil interactions relate to the effects of soil properties on temporal patterns of water availability and the mineralisation of soil organic matter.

Water availability

Coarse textured soils release most water at high water potentials with little water being stored in what could be termed the survival range between water potentials where growth begins to be suppressed and where the plant can no longer extract water. By comparison, clay restricts the availability of water in the water potential range that supports active growth (leaf extension) and makes more water available within the survival range. Clay limits the rate of water use and, together with the water storage at low potentials, this extends the period when water is available to sustain life.

Nutrient availability

Tunstall (2001) identifies that nitrogen mineralisation is low in undisturbed brigalow clay soils hence they have the potential to accumulate organic matter and build the soil nutrient availability. Conversely, organic matter is rapidly mineralised in adjacent coarse textured soils supporting eucalypts thereby limiting the development of high levels of soil nutrient.

The rapid rate of nitrogen mineralisation in coarser textured soils makes feasible the strategy of waiting for release of nutrients through mineralisation following rain. The slow mineralisation in clay soils would negate such a strategy by limiting the release of nitrogen and hence its utilisation by plants.

The addressing of nutrient availability by way of soil colloids, particularly organic matter, reflects the low nutrient levels of most soil materials in Australia. Fertility largely depends on the accumulation of organic matter and the release of nutrients through mineralisation. While differences in fertility can derive from lithology the fertility of Australian soils largely depends on the accumulation of nutrients in organic matter and their release via microbial activity.

Climate Interactions

The belt across central Australia where acacias can dominate (acacia belt) tends to a seasonally neutral pattern of water availability. Rainfall in this belt tends to mirror potential evaporation hence variations in water availability reflect climatic variability more than seasonal patterns. In the seasonal north and south there is an extended period each year where plant growth is restricted by water availability.

The temperature regime in the acacia belt is most favourable for growth in spring and autumn but temperatures will support photosynthesis throughout the year. Growth by way of carbohydrate production can occur whenever water is available. The net effect is the absence of an extended period when photosynthesis and plant growth cannot occur due to either temperature or water availability.

Summary of plant and environmental characteristics

The functional differences between eucalypts and acacias mainly relate to:

- Nitrogen fixation by acacias.

- Patterns of leaf retention, particularly under water stress, whereby acacias tend to retain leaf while eucalypts dehisce.
- Potential rates of water use wherein acacias use water more rapidly than eucalypts.
- Morphological characteristics that allow acacias to develop and sustain lower water potentials than eucalypts.

The environmental differences between where acacias and eucalypts dominate plant communities are:

- Acacias usually only dominate on clay soils that, compared to coarser textured soils:
 - accumulate nutrients
 - limit the availability of nutrients following rainfall
 - limit water uptake and store more water thereby extending the period of availability of 'survival' water
- Acacias tend only to dominate in a seasonally neutral belt of water availability across Australia.

The differentiation between clay and other soils relates to fertility and water availability. Clays can accumulate large amounts of organic matter due to the fine soil texture limiting the rate of breakdown and the promotion of grasses (Tunstall, 2005). While the clay and organic colloids retain nutrients the adsorption of cations limits their availability to plants. Also, the binding of water by clays restricts water uptake by plants and, combined with the hydraulic characteristics of clay, tends to limit periods when the soil is too dry to sustain plants.

Discussion

Eucalypts and acacias have evolved distinct strategies for coping with the restricted availability of water and nutrients characteristic of the Australian environment. The relative effectiveness of these strategies depends on climate and soil properties.

Acacias build up the soil nutrient levels which, combined with their mycorrhiza, makes nutrients readily available immediately following rainfall. Rapid water use associated with the maintenance of a large leaf area is therefore effective in promoting growth of the acacia and it also suppresses other species. The main disadvantage relates to the need to maintain a high leaf area during periods without rain. Acacias have developed foliage that can effectively prevent water loss and extract water from very dry soils.

The acacia strategy expends energy in fixing nitrogen and maintains a high leaf area during unfavourable conditions. This strategy is only effective where:

- Soil properties allow a build up of nutrients.
- Soil properties regulate plant uptake of water.
- Temperatures support photosynthesis throughout the year.
- Rainfall is dominated by variability rather than seasonality (no regular extended period without rain).

These constraints result in acacias only dominating on heavy textured or clay soils in a belt across Australia that tends to a seasonally neutral pattern of water availability. The strong competitive advantage where this strategy is viable results in acacias tending to form mono-specific communities.

Eucalypts conservatively use water by limiting their leaf area. The advantages are:

- The reduced risk of having to survive without water.
- The lack of energy expenditure on nitrogen fixation.
- The promotion of nitrogen mineralisation in coarser textured soils due to the good aeration and slower utilisation of soil water.

The main disadvantages relate to the potential for other species to obtain the water and nutrients.

Despite the disadvantage of allowing other species access to water and nutrients the eucalypt strategy is obviously effective in the Australian environment. Factors associated with its success are:

- Strong seasonality in temperatures and/or water availability.
- Rapid mineralisation of soil organic matter following rainfall.

Where rapid mineralisation is associated with coarser textured soils.

With this strategy eucalypts tend to dominate outside the acacia belt where the rainfall is adequate to support trees. They are least competitive on heavy textured soils, on fertile soils in high rainfall areas where the absence of fire allows invasion by broadleaf species, and in areas subject to seasonal waterlogging. The controls by seasonal waterlogging are unclear and could be direct via root aeration and/or indirect via an effect on microbes that mineralise nitrogen and/or protect plant roots.

Within the acacia belt eucalypts tend to dominate on areas not occupied by acacias or grasses, which are essentially the coarser textured soils.

The conservative eucalypt strategy provides opportunities for other species to obtain resources. Eucalypt communities are therefore characterised by containing a mix of life forms, such as trees, shrubs and grasses, and a diversity of species.

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