CONTROLS ON THE DEVELOPMENT OF VEGETATION

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Abstract

A positive feedback mechanism is identified whereby the development of vegetation depends on its level of development. The implications for land use impacts such as global warming are identified.

Introduction

In crop experiments involving species mixtures and increase in one species produces a proportionate decline in the others. This response identifies competition between the species for a limited and set amount of resource. Some species may access resources not available to the others and/or use the resources more effectively, but there is competition for resources that are essential to all.

This simple situation of component replacement was not observed in a poplar box (Eucalyptus populnea) woodland (Tunstall & Torssell 2004 a). The total amount of vegetation in patches varied greatly, as did the relative proportions of the tree, shrub and grass components.

The variability in the composition of the poplar box woodland was interpreted in terms of plant life cycles. With crop experiments the development of the plants is synchronised such that they germinate and develop together. With native vegetation the grasses can be senescing when the shrubs are developing, and vice versa. Even with the simplified representation of the woodland as a three component system comprising trees, shrubs and grasses there can be a wide range in the absolute and relative levels of development of the vegetation and its components due to the different lengths of their life cycles and differences in the phasic relationships.

This suggested interaction between plant life cycles in the development of vegetation was confirmed by observations of tree recruitment in the poplar box woodland, but for the tree component only (Tunstall and Reece, 2004). The recruitment of trees depends on the abundance of existing trees as substantial recruitment of tree seedlings only occurs where the overstory of mature trees has declined to a low level. This indicates that the mature trees and their seedlings compete strongly where this to be expected given their genetic similarity.

While the abundance of tree seedlings depended on the abundance of trees extensive data on the abundance of shrubs and grasses in stands of poplar box of different density did not show any relationship between the abundance of the different components. The abundance of shrubs and grasses changed over time in relation to seasonal conditions and plant life cycles but there was no apparent relationship between the levels of development of the different components. This indicates independent development of the different components. To a large extent the tree, shrub and grass components are not competing.

That plant development is related to its life cycle is axiomatic. It is inevitable, but its significance for the development of vegetation had not previously been identified. With episodic recruitment the patterns of development of vegetation reflect the life cycles of component plants. However, the apparent independence between the development of the different life forms is counter intuitive given the normal assumption that all components are competing for the same finite resource.

In the poplar box woodland light would seldom be limiting. However, nutrients and water would generally be limiting, and all plants need both water and the same nutrients. Direct and strong competition between the different components of the vegetation appears to be inevitable but it is not occurring. This paper examines why.

Analysis

The assumption that the different plant life forms use the same resources is realistic. While their requirements may differ to some extent they are basically the same for nutrients, water, oxygen etc. Direct and strong competition appears inevitable even if there is only one essential resource with limited availability.

Despite and because of the fluctuating conditions it is usual in semi arid woodlands for at least one essential resource to be limiting. A very large degree of competition between the different components of the woodland would therefore be expected. The issue is how can there not be competition.

A lack of competition can arise where the components access different resource pools but this appears improbable with plants sharing the same space. However, competition can be limited where the development of plants increases the availability of resources. That is, limited competition is logically possible if the resource availability is not fixed but depends on the level of vegetation development.

Taking the level of available resource to increase with increase in vegetation is contrary to the current view that resource availability is fixed and set by the physical constraints. It suggests that the available resource depends on the biological components as well as the physical constraints. The greater the amount of vegetation the greater the potential level of resource availability.

The observed vegetation patterns in the poplar box woodland accords with the resource availability depending on the vegetation both by way of spatial variability and the patterns of change over time. However, to fully accord the different life forms must produce different resource pools. The resources produced by a component must be largely only available to that component. This arises because the maximum levels of vegetation development are greater for mixtures than for any life form on its own.

An issue of circularity deriving from a lack of independence arises with such analyses. The available resource must be defined independently of the vegetation and this is made difficult by the available resource depending on the vegetation.

The notion of fixed resource availability relates to the fixed inputs of solar radiation and rainfall and the finite amount of minerals in the soil. However, losses occur with water hence gains can be made through plants reducing losses. The issue of losses also arises with nutrients, but there is an additional issue of accession. The availability of nutrients to plants is intrinsically linked with the development of vegetation.

The paper on the global implications of soil organic matter (Tunstall 2008) outlines the mutualistic association between plants and microbes whereby the availability of nutrients to plants depends on microbes, and the food for microbes comes from plants. By providing food to microbes plants directly increase their access to nutrients as microbes essentially supply all nutrients. However, there are also indirect gains that arise by microbes expending some of their resources on producing long lived humic compounds that greatly improve soil structure and the retention of water and nutrients. The development of microbes through plants greatly increases the supply of resources and reduces losses. As the level of microbial development in this mutualistic association depends on the level of plant development, the amount of resources available to plants depends on their level of development.

Feedbacks

The availability of resources is based on a positive feedback wherein the availability of resources to plants increases with plant development. Without the imposition of constraints such positive feedback produces unlimited exponential growth. While the development of vegetation is initially somewhat exponential in mirroring the development of plants it is constrained within limits. There are limits to the development of vegetation as implied by the earth's surface not being buried by vegetation and illustrated by data from central Sweden and Australia (Tunstall & Torssell 2004 a, b).

A limit to vegetation development will arise where only one of the essential resources is limiting and its availability is not subject to positive feedback. Radiation is one such resource, hence the level of radiation sets an absolute limit to the level of vegetation development. While some of the resource availability is not subject to competition some definitely is. The observed patterns of vegetation therefore reflect the balance/interaction between the supply of resources that are and are not subject to competition.

The degree to which a resource is subject to competition is not constant but varies with the level of vegetation development and the availabilities of other resources. For example, radiation is effectively non-limiting in open woodlands but becomes increasingly limiting as the density of the trees increases. The limitations of water availability similarly increase as the density of vegetation increases.

Life Cycles

The system described above develops through positive feedbacks within a constrained maximum. Models simulating such development produce a function of the form in Fig.1 where the level of development asymptotes to a maximum. Models addressing the development indicate a build up to a maximum where the rate of increase in development decreases as the maximum is approached.

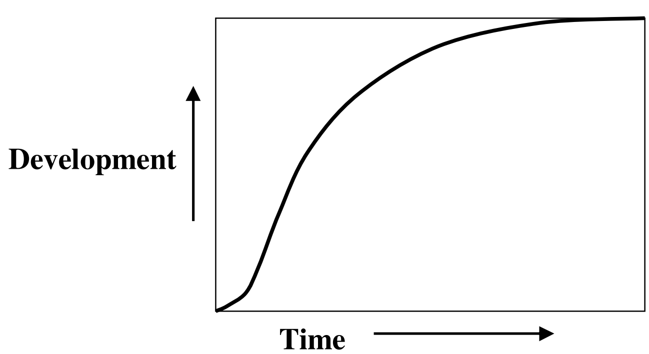

Fig. 1 Indicative pattern of development of vegetation from bare ground.

This pattern of development is not observed in vegetation. While there are limits to the level of development of vegetation these limits are seldom observed (Tunstall & Torssell 2004 a, b). Even where a maxim is attained it is not sustained. This is an inevitable consequence of plant life cycles where both resource availability and plant recruitment depend on the level of the existing vegetation.

Plants have a finite life span and in populations individuals live to different ages. With episodic recruitment there is loss of individuals throughout the existence of that cohort with replacement only occurring when the numbers, and hence level of development of that component of the vegetation have declined to a low level. This produces large fluctuations in the level of resource availability within natural systems related to the life cycles of the component plants.

Land Use Impacts

The realisation of the positive feedback in the availability of resources arose when glancing at a bare patch in an unkempt and long unmown household lawn. The bare patches had persisted for several years, along with distinct vegetation patterns in the remainder of the lawn. It was apparent that the level of resource availability in the bare patches was lower than elsewhere despite the soils initially being spatially uniform.

The same pattern of bare ground interspersed with vegetation is pronounced in grazed poplar box woodlands. Indeed, the realisation that shrub encroachments reflected desertification caused by grazing arose through the observation that grasses occurred under trees but not in the bare patches between them when trees were being cleared to promote grasses. The same pattern also occurs in the regenerating native vegetation around Cobar in NW NSW. Large patches of bare ground persist between copses of degraded woody native vegetation. However, when the bare patches are ploughed, seeded and fertilised the grasses flourish (Fig. 2).

Fig 2a Typical condition of native vegetation in grazed semi-arid areas of Australia

Fig 2b Single pass of a Homan plow through a patch of degraded native vegetation (www.homan.com.au)

Reasons for the persistence of the bare patches have never been elucidated other than to identify that plants do not recruit there. While sometimes referred to as scalds there are no accumulations of salt that characterise scalds. The reason could relate to resource availability. Poplar box recruitment was not observed on bare ground (Tunstall & Reece, 2004) despite floods and wind potentially providing an ample supply of seed. Given the absence of any vegetation the resource levels could be too low to sustain the development of seedlings.

It is noteworthy that occasional poplar box seedlings could usually be found at any time regardless of the climatic conditions. These always occurred in dense stands of vegetation, particularly of the tall shrub/small tree *Eremophila mitchellii* (budda / false sandalwood). Such seedlings never developed and hence were never recruited to the vegetation.

The dependence of resource availability to vegetation on the level of vegetation development identifies why the adverse impacts of land use can be severe. Denudation of vegetation through drought, clearing and/or grazing decreases the availability of resources. Where the denudation is transient the soil resource reserves are sufficient to sustain the reestablishment of vegetation. However, where the denudation is prolonged the soil resource availability declines to a level where it is insufficient to sustain the establishment of vegetation. The area therefore remains bare.

There are many areas throughout the world where this pattern of land degradation has been extensive. The resources by way of climate and soils can potentially sustain considerable vegetation, as they did in the past, but they are now effectively deserts. Left as they are they remain as deserts. Indeed, their extents will increase due to the surrounding land use. The rate of spread of the desertification increases as human population expand and attempt to survive on a declining resource.

This extensive land degradation has primarily been caused through livestock and farming (agriculture), but the collection of fuel for cooking has contributed. Such degradation is usually attributed to changes in climate, and it is certainly associated with a decrease in rainfall and increase in ambient temperatures. However, there has been no realistic assessment of the degree to which the change in climate has been caused by the change in vegetation. The change in climate is more likely to be an effect than a cause.

This dependence of desertification on vegetation provides opportunities to rehabilitate extensive areas of degraded lands by re-establishing the vegetation. It is being done in northern China and it can be done elsewhere.

Discussion

The suggestion that the physical resources available to vegetation increase with the level of vegetation is contrary to the normal assumption that they are fixed and finite. However, the suggestion explains the otherwise unexplainable occurrence of a large degree of lack of competition between the plant components in a poplar box woodland. Also, it accords with the mechanisms whereby plants obtain their resources. From a mechanistic viewpoint it is to be expected.

While a mechanism is identified that makes resource availability to vegetation dependent on its level of development it is not suggested that this is the sole mechanism by which the components of plant communities gain independent access to resources. The independent resource pools appear to be associated with life forms more than species or individuals. The knowledge is by no means complete.

The availability of resources to vegetation depending on its level of development, and the accessing of different resources by different life forms has a number of highly significant implications. Degrading vegetation is a poor option, and is disastrous where it is degraded to a level where it does not recover. In Australia and elsewhere this typically arises through a combination of land use and drought. Farmers attempt to keep livestock through droughts and in doing so completely denude the land. When the ground cover is completely denuded they even fell woody vegetation to provide food for livestock.

This degradation is promoted by technologies that allow the maintenance of livestock under conditions that would normally cause them the die, as with supplementary feeding. Based on short term economics such 'supplementary feeding' is marginally beneficial at best, but the main effect of supplementary feeding under drought is to greatly enhance land degradation. When the long term damage to the soils and environment caused by supplementary feeding are considered the practice has disastrous consequences.

Numerous land use practices can be identified that are at best poor options. Some can provide substantial short term gains but in the long term all are disadvantageous to the individual landholder, and to the entire world. The negative impact to the entire world arises through the impact on climate. While the impact of one farmer alone is not significant the combined impacts of all farmers are sufficient to change the global climate and produce global warming.

Practices that represent poor options but need not be disastrous include the development of monocultures and use of fallows in agriculture, and the shutting up of native vegetation based solely on the notion that natural is best. Old growth forests are naturally degraded and need a stimulus to initiate the cycle of regeneration. Degraded native vegetation, as occurs around Cobar, will not naturally recover to the level that it should if left alone. A stimulus is needed to repair degraded lands.

This positive feedback in the development of vegetation means that land degradation through agriculture is likely to be the cause of global warming. Grazing is well known to cause desertification and desertification represents a change in climate. Unlike theories based on levels of atmospheric CO_2 there are no observations or theoretical considerations that negate it being the cause, and the revegetation in northern China identifies that the negative impacts can be reversed.

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