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THE NATURE OF VEGETATION CHANGES IN MANAGED ECOSYSTEMS

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ABSTRACT

Vegetation changes in managed ecosystems are the result of complex interactions among the manipulations imposed by the manager and the biotic and abiotic factors of the environment. These factors operate by altering the fineness of the environmental sieves at different stages in the life cycles of the constituent species. The factors have been identified in the Jenny equation and the interactions summarised in a way that can be useful to the land manager in the State and Transition model. Data are presented illustrating how these concepts can be applied to the problem of the maintenance of woodland eucalypts in grazed pastures on the Northern Tablelands of New South Wales.

INTRODUCTION.

Australian ecosystems are subject to different intensities of human management ranging from high intensity irrigation agriculture to wilderness areas where human inputs may be confined to intermittent fire control and the accidental introduction of feral plants and animals. The model of vegetation dynamics most commonly accepted by those responsible for land management is Clementsian succession (Clements 1916). The basic assumption of this model is that, following a sequence of successional stages, some form of climax vegetation results which is essentially stable over time unless subjected to disturbance (Clements 1916; Egler 1954 and many other authors). Disturb the climax and the vegetation changes to something else but then, if the disturbance is removed, secondary succession takes place and the community returns to the stable climax. These assumptions of inherent stability in the absence of disturbance and the supposed predictability of the successional stages are the cornerstones of management methods derived from Clements' (1916) original proposals.

An alternative assumption is that vegetation is the product of a number of independent variables or factors of the environment. These factors vary with time and individual species are either advantaged or disadvantaged by the changes in these factors. Therefore, the species composition of a sample of vegetation is continually changing over time. These changes would be slow for vegetation dominated by long lived perennials or faster for communities dominated by annuals. Because of the inherent inertia of most vegetation, the actual species composition lags behind that composition which would be stable for any particular set of environmental factors should they remain constant. The result is that vegetation is always in a state of flux but the rates of change depend on the type of vegetation and the magnitude of the changes in the state factors. Vegetation appears stable if the lifetime of the dominant species is long in relation to the lifetime of ecologists, as is the case for many forest communities.

ENVIRONMENTAL FACTORS AND VEGETATION

One of the earliest workers to formalise the relationships among ecosystems and the independent factors of the environment was Hans Jenny (1961). He derived a state factor equation which described an ecosystem at a point in space and time (L) composed of vegetation (v), animals (z) and soils (s) as a function (f) of the climate (cl), the organisms present (o); the relief (r), parent material (p), additional factors (a), time (t) and any other factors not already included (....).

Jenny's equation is : $$L,v,z,s, = f(cl,o,r,p,a,t....)$$

Some of the state factors on the right hand side of the equation can be manipulated by the land manager to produce vegetation of desired structure and species composition within the limits imposed by the factors which cannot be manipulated.

Climate (cl)

This factor includes the average regional climate, the range of microclimates within a particular study site as well as the specific sequence of rainfall intensity and temperature experienced by an ecosystem since time to. Specific weather sequences are perhaps of more interest in the context of this paper because of their dramatic effects on plant recruitment and plant death (Curtis 1989). As these specific sequences vary from year to year, so the vegetation component of an ecosystem will also vary, but with the rates and amplitude of the changes depending on the longevity of the component species.

Organisms (o)

The plant species present include those actually present in the vegetation as well as those represented by propagules in the soil seed bank and which are potential components of the vegetation. Other important organisms include micro-organisms which may be mutualistic or pathogenic, as well as insects and the vast array of soil fauna. Both wild and domestic animals can have major impacts on the vegetation and may or may not be under the control of the land manager. Episodic events involving organisms other than plants can have dramatic and long lasting effects on the vegetation.

Additional factors (a)

Human activities can have deliberate and/or accidental impacts on vegetation. These include the use of fire as well as inputs such fertilisers and the application of herbicides which are designed to produce planned vegetation changes. Other impacts include soil erosion and mineral losses by leaching and the removal of agricultural products, and industrial pollutants such as SO2, oxides of nitrogen and acid rain. These effects may be dramatic or so slow and subtle that we may be unaware that they are happening.

Time (t)

Time can refer to either the age of the ecosystem which may be the time from the last catastrophic disturbance or simply from an arbitrarily chosen point in time (to).

VEGETATION CHANGES OVER TIME

Changes in the species composition of vegetation involve differential reproductive and/or death rates of the constituent species over time. If the species composition of a particular patch of vegetation is to remain constant over a time span exceeding the generation time of the constituent species, then each individual within the community can only give rise to one offspring. Of course, this exact replacement never takes place and so vegetation is inherently unstable, as discussed above.

ENVIRONMENTAL SIEVES

If we have a cohort of say, 10,000 ovules produced at flowering time in a population of a particular species, then say 10% or only 1,000 of them may be fertilised to form zygotes. This proportion may vary from season to season depending on the interaction between the particular species and the appropriate state factors each year. These state factors therefore operate as environmental sieves (Harper 1977). If the sieve is fine, then only a small proportion of the ovules is fertilised and if coarse then a larger proportion. The factor in this case might be the abundance of pollination vectors.

As the cohort of ovules moves through its life cycle, a whole sequence of environmental sieves may operate (Fig. 1) which collectively determine how many ovules are produced in the next generations. The size of the population of a monocarpic species will obviously fluctuate more from year to year than that of a polycarpic species. On the other hand, a year in which critical environmental sieves for a long lived polycarpic species are particularly coarse might have dramatic and long lasting effects on the vegetation. The state factors of Jenny (1961) therefore operate on the species composition of vegetation by altering the coarseness of the environmental sieves on an individual species basis.

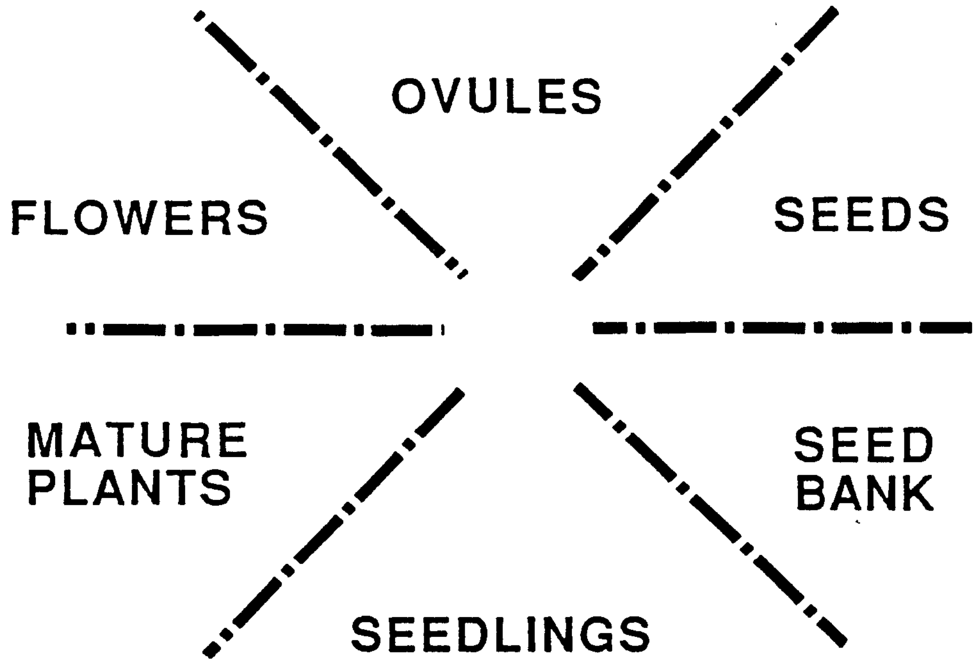

Figure 1. Life stages of a plant showing some of the environmental sieves (___ _ ___ _ ___) between the stages.

STATE AND TRANSITION MODEL

Westoby **et al.** (1989) described rangeland vegetation as a series of catalogues of alternative states with transitions between them. A particular set of state factors (Jenny 1961) must occur in order for a transition to result and, provided enough is known about the states and transitions, whether such a transition is likely to occur or not can be predicted. If these changes are undesirable from the point of view of the land manager, then this particular set of transitions would represent a management hazard and if desirable, an opportunity. The art of land management consists of recognising and avoiding the hazards and taking the opportunities.

WOODLANDS AND GRASSLANDS

The last 160 years of grazing on the Northern Tablelands has seen extensive clearing of the original grassy forests and grassy woodlands with the aim of producing eucalypt woodlands with varying tree densities suitable for sheep and cattle grazing. Unfortunately, there have been episodic occurrences of abnormally extensive debilitation and death of the eucalypts (dieback) at least since the late 1850s. The latest episode during the 1970s was by far the worst on record, affecting more species and a much larger area than any previously recorded outbreaks (Nadolny 1984).

Flowering of eucalypts commences with the formation of tiny inflorescence buds in the axils of young leaves. Shedding of the two bracts covering the inflorescence buds reveals a tiny cluster of pin buds which slowly develop into flower buds borne on a single stalk in clusters of 3-11 or more, depending on the species. After flowering, the young capsules develop slowly with wide differences in the rate of development among different species. Mature fruit remain on the trees of some species for relatively long periods of time and the capsules slowly open and shed the seed or simply fall from the tree (Curtis 1989).

The length of time from inflorescence bud formation to the completion of seed fall of a cohort of fruits varies widely among species being of the order of three and a half years for *Eucalyptus blakelyi* and five and half years for *E. caliginosa*. During this time, a cohort of ovules formed at flowering is subject to a number of environmental sieves. Stress on the trees at any time can cause the complete loss of several cohorts of ovules. The percentage of trees bearing flowers or fruits and the size of the crop is strongly associated with the health of the trees (Nadolny 1984).

Seedlings appear in the late spring or early summer and the number of seedlings is strongly associated with:-

(1) the size of the seed crop

(2) the herbaceous cover under or near the parent trees

(3) the spring and summer rainfall

Most eucalypt species have a transient soil seed bank in that seeds rarely survive for more than a year following seed fall (Curtis 1989). The major storage of propagules is in the form of suppressed seedlings beneath the trees. These seedlings may survive for over 20 years before being released by the death of the trees above. Suppressed seedlings can also survive for relatively long periods in some grazing land until released by appropriate environmental conditions. Released seedlings usually grow quite rapidly in the absence of further stresses (Curtis 1989).

Two states and a transition can therefore be recognised for woodlands and grasslands on the Northern Tablelands (**Fig.** 2). State 1 consists of woodland with an adequate population of suppressed seedlings below and between the mature trees. Such a state is relatively stable because if the adult trees die for any reason (e.g. dieback) then they will be replaced from the suppressed seedling population.

Should the suppressed seedlings be eliminated, then the vegetation is in a transition (**Fig.** 2). The elimination of the suppressed seedlings may result from cultivation or from heavy grazing associated with heavy superphosphate applications over many years. The factors affecting the death of suppressed seedlings require further study.

While the adult trees remain healthy, appropriate manipulation during years when weather sequences provide opportunities for regeneration can perhaps return the vegetation to State 1. These conditions are the existence of a heavy seed crop at the end of winter followed by above average spring and summer rainfall. Under these conditions, the herbaceous cover beneath the trees must be reduced by heavy grazing or herbicide aplications to reduce the fineness of the environmental sieves associated with seed germination, seedling establishment and seedling survival (Curtis 1989).

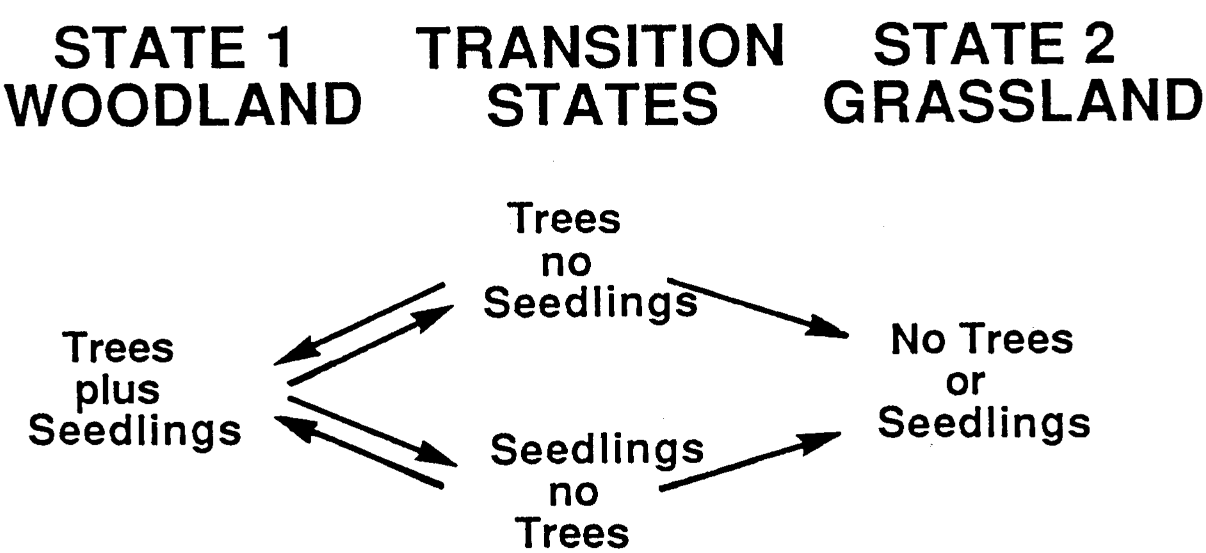

Figure 2. Woodland and grassland states with two intermediate transition states.

If the adult trees in the transition state (**Fig.** 2) die for any reason then the vegetation is inevitably converted to the undesirable treeless grassland of State 2 (**Fig.** 2). Return to State 1 is now very difficult because woodland eucalypts lack a soil seed bank (Curtis 1989). The transition state therefore represents a management hazard in that it may suddenly change to grassland, and the land manager can do nothing about it. A return to State 1 must involve artificial seeding or planting of established seedlings (Curtis 1989).

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