State and transition models for rangelands.
1. Successional theory and vegetation change

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Abstract

Traditional views of successional change in vegetation envisage orderly sequences of vegetation types leading from bare rock or water etc. through to stable climax vegetation. Disturbances are seen as discrete events involving the destruction or removal of plant biomass followed by secondary succession leading back to the original, stable, climax vegetation.

The idea that only one stable type of climax vegetation exists for each climatic zone was seriously questioned during the middle of this century, leading to the polyclimax and climax pattern hypotheses. The factorial approach to vegetation dynamics also led to serious questions being raised about the validity of the monoclimax theory.

If vegetation is assumed to be inherently unstable, and if the definition of disturbance is extended to include a change over time in any of the state factors controlling the plant species composition at any location, then a vegetation dynamics paradigm more appropriate to a highly variable environment can be constructed. The state and transition model fulfils these requirements and leads to a more pro-active approach to vegetation management than is possible with the traditional plant succession model.

Introduction

Even the most casual observer is aware that vegetation is not homogeneous in space and time. I will mostly concern myself with temporal changes in vegetation in this paper although the mechanisms producing temporal and spatial variation are often identical. Temporal variations consist of changes in the relative abundance of individuals of the different species occurring in a plant community. Variations which lead to structural changes are always the most obvious, although a species composition change without change in structure might be very important to the end-user or the land manager. In addition, the perception of change by an observer may depend upon the relationship between the life spans of the individual species in the community and the life span of the observer. In other words, the rates of change in communities comprising annual species are very rapid and easily observed whereas changes in communities comprising perennials with an average life span of many years may be much more difficult to observe and record.

A further problem which has bedevilled considerations of vegetation change is the question of how big a change in species composition must be, in order to be considered a change. Some ecologists may be more interested in the dominants and yet changes in the abundance of minor species may be of vital importance in manipulations to preserve rare and endangered species or in the maintenance of biodiversity. Therefore, any change in the relative abundance of any species in an assemblage must be considered a vegetation change if any coherent theory is to be developed.

If no vegetation change is to occur over time, then the number of individuals of each species in a community must remain constant. In other words, each individual in its lifetime, on average, can produce only one offspring (Harper 1977). One would suggest, therefore, that vegetation changes, as defined above, will continually occur in most plant communities and vegetation stability is very rare.

Disturbance

Sousa (1984) defined disturbance as: "a discrete, punctuated killing, displacement or damaging of

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one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established".

This definition is restrictive in the context of vegetation change because:

(1) It excludes gradual changes over time of factors of the environment which affect the relative abundance of different species.

(2) It implicitly assumes that new individuals need a disturbance, as defined above, to become established. However, non-catastrophic changes which lead to an increase in resources (such as a period of increased rainfall in a semi-arid environment) (Harrington and Hodgkinson 1986) can also result in new individuals becoming established.

Plant succession

The following ideas on plant succession were first formalised by Clements (1916; 1936) and have had an enormous impact on plant ecological thought over the last 75 years or so. In fact, they are still taught in Australian high schools and at university level in the eastern United States with really little change from Clements' original ideas. I will briefly outline them here, then deal with some other approaches to plant succession which I find much more satisfactory.

Primary successions (Priseres)

Primary succession involves the colonisation of a bare area by organisms and the successive replacement of one community by another, usually with an increase in the biomass and complexity of the system. The final stage in the succession is the climax. Concomitant with the development of the climax vegetation is the development of soil profiles characteristic of the climate and soil parent material of the area. The time required for the completion of a succession is very variable and in some cases is much greater than the human life span.

The climax

The term "climax" has been used in the preceding paragraph as the final stage in plant succession. Some comments on the climax concept are in order.

According to the monoclimax concept (Clements 1916; 1936), there can be only one climatic climax in any region. In North America, these are essentially the "Formations", such as Coniferous Forest, Deciduous Woodland, Grassland, etc. Communities which have not reached the climax are seral (immature), but in time, these communities will be replaced by the climatic climax for that region. This implies, or even necessitates, a convergence of all seres into the climax of that region, i.e. the lithosere, commencing with bare rock, passes through its various stages to give, finally, a woodland or forest community; the hydrosere, commencing with open water, proceeds through its own quite different stages culminating in the same forest or woodland. Furthermore, communities which were arrested in their development for long periods by one or other of the environmental factors, were regarded as "temporal climaxes" and designated by the limiting factor, e.g. edaphic climax or topographic climax. Lastly, when additional water (or more favourable climatic conditions) occurred locally in an area, the community developed was designated "post climax", i.e. the community which would be climax in a more favourable climate. It is unfortunate that "post" was used to describe these communities, as this term connotes time and implies that the course of the succession had proceeded beyond the climax.

Secondary successions (Pedoseres)

A secondary succession is one which occurs on a previously formed soil from which the vegetation has been partially or completely removed. Catastrophic natural events which initiate secondary successions include fire produced by lightning, earth movements induced by landslides, strong winds uprooting patches of vegetation, or the destructive effects of native animals.

Human activities have greatly altered the biota in most areas, sometimes with devastating results initiating secondary succession. These activities include the felling of timber and the clearing of land for agriculture, the introduction of new species, both plant and animal, firing, and the movement of earth and rock. Succession after cropping is a common form of secondary succession.

The outcome of a secondary succession is the stable, regional climax vegetation. However, the pathway of the secondary succession will usually vary from that of primary successions in the same region because of the different starting points and the fact that the soil profile is already developed.

Alternative views of the climax

Clements' (1916) view of succession as proceeding through a number of intermediate stages to a climax vegetation that was unique to each climatic region was enthusiastically welcomed by a large number of American ecologists (e.g. Sampson 1917; Weaver and Clements 1938; Odum 1969) and extensively applied to different vegetation over the next 35 years. The fact that the successional stages did not always correspond exactly to the classical format was recognised in the early stages but the basis of the successional approach was not seriously questioned by many ecologists. The importance of chance events in determining which species were present at intermediate stages was well recognised, and by the early 1950s, there were essentially 3 schools of thought concerning climax vegetation.

One school happily accepted successional convergence on a monoclimax for each climatic region and a second view was the polyclimax theory. The proponents of this second view (e.g. Tansley 1935) did not accept that vegetation convergence always occurred during succession but that a number of different stable climaxes could occur in each climatic region and the determinants of which climax was present were sometimes random events during the course of the succession. According to the polyclimax theory, different climaxes within a region were separated by ecotones, or transitional zones, which could be gradual or quite sharp discontinuities.

Whittaker (1953) recognised that a number of factors of the environment varied spatially producing environmental gradients within climatic zones. These environmental gradients could be produced by topography, changes in parent material or aspect etc. and consequently produced vegetation gradients. Whittaker (1953) completely rejected the monoclimax theory and proposed the third, his climax pattern hypothesis which stated that: "a pattern of climax vegetation in a steady state of community productivity, structure and population could exist at a particular site". In this hypothesis, he accepted that the vegetation gradients between different climaxes could be so gradual that it could be almost impossible to distinguish the boundaries between them.

Whittaker's (1953) climax pattern hypothesis was essentially based on 3 propositions and a number of corollaries. These initial propositions were as follows:

(1) Climax vegetation represents a steady state where community productivity, structure and floristics fluctuate about a mean over time.
(2) The balance of floristics shifts with changes in the environment, so that the climax vegetation represents a pattern of communities corresponding with environmental gradients. These patterns are more or less diverse depending on the diversity of the environments and the steepness of the gradients within a region.
(3) The characteristics of the vegetation at each point within the pattern are determined by a number of factors of the environment including the properties of the species involved, the climate, the soil and other aspects of the site, biotic interrelations, floristic and faunistic availability, chances of dispersal and interaction etc. The result is that there is no absolute climax for any area and the vegetation at any point within the region is relative to environmental gradients and a number of other factors.

Whittaker (1953) also proposed a number of secondary propositions (corollaries) under 3 broad headings:
• those concerning the determination of climax vegetation;
• those concerning the relationship between climax and seral vegetation; and
• those concerning how climax vegetation can be recognised.

The environmental factors concerned with the climax determination are essentially those factors proposed by Jenny (1961), which will be dealt with in more detail later. Whittaker (1953) described them in slightly different terms from Jenny (1961), but they are essentially the same. The only addition is the recognition given by Whittaker (1953) that chance events, such as dispersal and successful establishment of the dispersed propagules, can be determinants of climax vegetation.

Whittaker (1953) made some interesting comments concerning the relationship between climax vegetation and seral stages and noted that there is no essential difference between them except for their relative stability and instability and the relative significance of directional change in seral communities. He also commented that there is no reason why some of the species should not occur in both seral and climax communities and that types, associations or various stratal groups of species may also occur in both seral and climax vegetation types. Whittaker (1953)

included substantial discussion of the difficulties involved in the recognition of climax communities, leading one to wonder whether it is all worthwhile! One might be forgiven for asking whether the climax has any reality, if climax communities are so difficult to recognise.

Change and the climax

So far I have spent time discussing the concept of climax vegetation but have spent little time on the mechanisms of succession itself. Clements (1916) and many subsequent American ecologists considered succession as essentially "relay floristics" (Figure 1). With a primary or secondary succession, relay floristics occurs when each species assemblage replaces the one previously in occupation of the area, and in turn, makes the site uninhabitable for its own species and is replaced by subsequent groups until the self-sustaining climax vegetation becomes established. This

approach is essentially the basis for the convergence of different types of succession to the monoclimax which was proposed by Clements (1916; 1936).

Egler (1954) suggested that, in many situations, particularly with succession on abandoned farmland whether grazing or cropping land, relay floristics was not so common. He suggested that trees and shrubs, which appeared in later parts of the succession, actually became established much earlier in the sequence but grew slowly and became apparent only after a number of years. He suggested that whether a particular species became established in the early stages was largely a matter of chance and that, therefore, these chance events determined the ultimate climax vegetation composition. Egler's (1954) model, therefore, was different from relay floristics and is illustrated in Figure 2. Note that, in this model, manipulation in the early stages of the succession with respect to either removal or addition of dif-
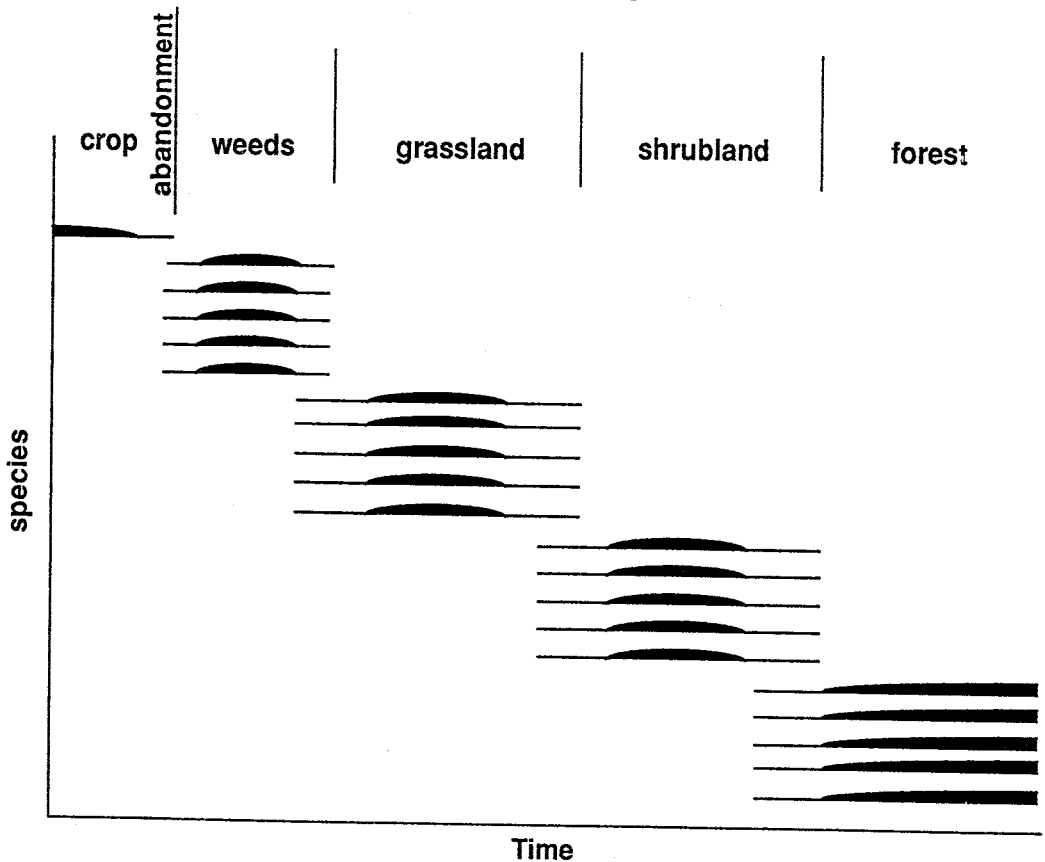

Figure 1. Relay floristics in which a succession of plant communities occurs after the abandonment of cropland (after Egler 1954).

ferent species, can have marked effects on the species composition of the ultimate climax vegetation. The significance of Egler's (1954) contribution is in his questioning of the validity of relay floristics.

Jenny's factorial approach

The factorial approach has its roots in the work of the great Russian pedologist V. V. Dokuchaev, but by far the greatest contribution to its development has come from Hans Jenny (1941; 1958; 1961).

Jenny was a soil scientist and turned his attention to the development of soil profiles and the interaction between soils, animals, vegetation and the environment. It is important to realise that he developed his ideas in the context of the Clementsian monoclimax approach but his particular contribution is in the treatment of the dependent and independent variables affecting the development and maintenance of ecosystems at a particular site.

Jenny (1961) derived a state factor equation which describes an ecosystem at a point in space and time (L) composed of vegetation (v), animals (z) and soils (s) as a function of the climate (cl), the organisms present (o), the relief (r), parent material (p), time (t) and other, unspecified factors (...).

Jenny's equation is:

$$L, v, z, s, = f(cl, o, r, p, t ...)$$

All of the state factors on the right hand side of the equation can be further subdivided. Such subdivisions are essential if this equation is to be useful for the study of the effects of manipulations on vegetation or ecosystems as a whole.

Climate (cl)

This factor includes the average regional climate, the range of microclimates within a particular
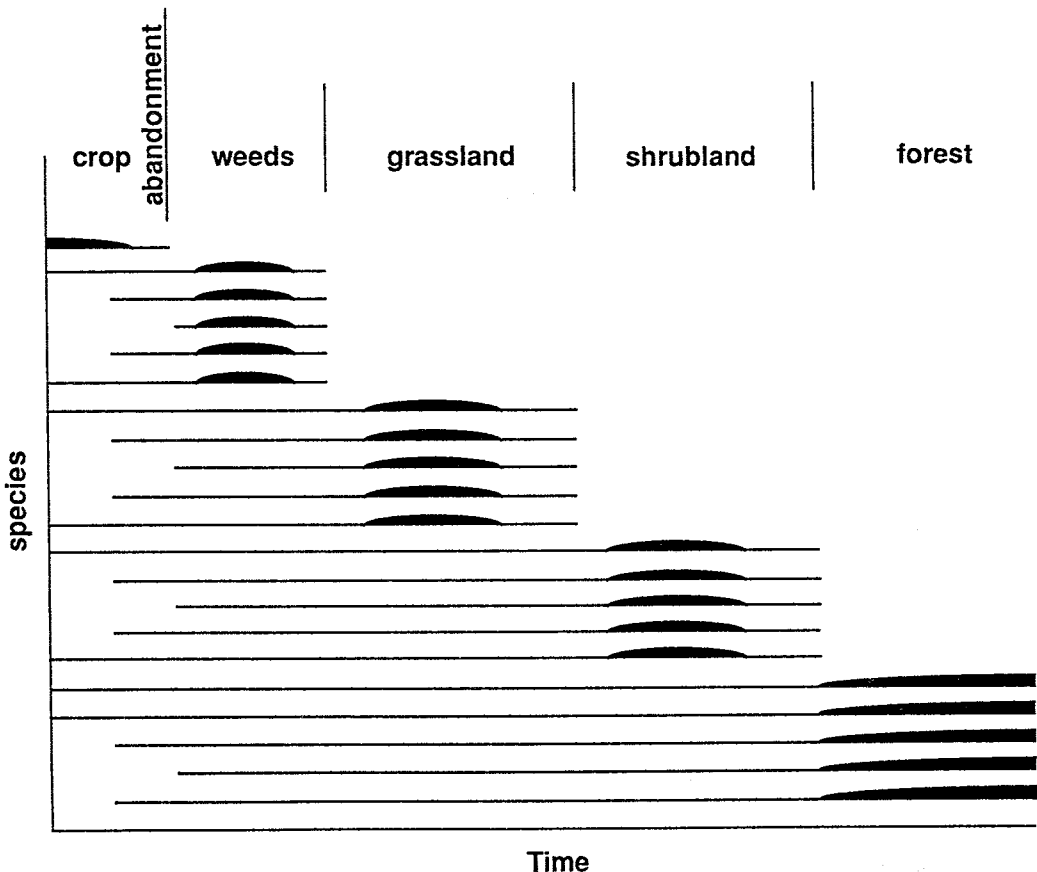

Figure 2. An example where the initial floristic composition alters the final plant community after the abandonment of cropland (after Egler 1954).

study site as well as specific sequences of rainfall events and temperatures which can have dramatic and long-lasting effects on ecosystems. Specific weather sequences are, perhaps, of more interest in the context of this paper because of their effects on vegetation such as the specific rainfall sequences necessary for eucalypt establishment on the Northern Tablelands of NSW (Curtis 1989). As these specific sequences vary from year to year, so the vegetation component of an ecosystem can be expected to vary, but with an amplitude which depends upon the longevity of the component species.

Organisms (o)

There are 2 aspects to this variable, which are particularly relevant to this paper. The first is the plants whose propagules (seeds, seedlings etc.) are present in the community (either active or in the soil seed-bank) and which are actual or potential components of the vegetation. Of particular interest is invasions by alien plants. These often remain minor components of the vegetation for substantial periods of time and then the population suddenly explodes. *Mimosa nigra* was introduced into Darwin some 100 years before the population suddenly escalated (Humphries *et al.* 1991) and *Chrysanthemoides monilifera* ssp. *rotunda* was present for some 30 years before it became a problem on Lord Howe Island (Humphries *et al.* 1991). It is very difficult to predict which introduced plant will become a problem and which will not.

The second aspect is organisms which interact with these actual or potential plant components. These may be micro-organisms which may be mutualistic or pathogenic, insects or large grazing animals. Grazing animals, of course, are particularly relevant to this paper. In some cases, the organisms may be other plants (e.g. mistletoe). The important point is that numbers of organisms can often fluctuate widely from time to time, which can have dramatic and long-lasting effects on vegetation (e.g. insect grazing and eucalypt dieback) (Landsberg 1990).

Relief (r)

This factor includes aspect, slope and position on the slope. Erosion can gradually change relief as can uplift. Any change to relief produced by natural agencies is usually very gradual.

Parent material (p)

Parent material generally refers to the rock type from which the soil of the ecosystem was derived. However, in some cases the parent material may be an alluvium and further material may be deposited by flood waters, therefore affecting the vegetation.

Time (t)

Time can refer to either the age of the ecosystem from the commencement of primary succession or to the period from an arbitrarily chosen point in time. The time from introduction can be important in studying alien, environmental weeds.

Other factors (...)

There are always other inputs to and losses from ecosystems which can affect the vegetation. For instance, with respect to mineral nutrients, vegetation can be affected by inputs from fertilisers and redistribution of nutrients by grazing animals (Taylor 1980), and losses by leaching, volatilisation, and the removal of agricultural products. Industrial pollutants such as SO_2, oxides of nitrogen and acid rain also have effects on vegetation. These effects may be dramatic or so slow and subtle that we may be unaware that they are happening. These other factors include most of the options for human manipulation of vegetation such as the use of fire and the manipulation of grazing pressure etc.

More recent models of succession and disturbance

Connell and Slatyer (1977) described 3 pathways of succession, calling the classical concept the "facilitation pathway", where early occupants "facilitate" the entry of later occupants of a site. The second was the "tolerance pathway", where later entrants were successful irrespective of the presence of earlier species. In other words, later entrants to an established community can grow to maturity at a lower level of resources. The "inhibition pathway" described the situation where later species cannot grow to maturity in the presence of earlier ones. Therefore, unless they are early entrants to a site after disturbance, their entry may be inhibited by the early entrants, and what would normally be considered the climax dominants may be excluded.

Noble and Slatyer (1980) assumed that disturbances are usually frequent relative to the lifespan of individual species, particularly in forest communities. The sequence of events following a disturbance is critical in determining the floristics and structure of vegetation at any particular site. The nature and severity of the disturbance can also strongly influence this sequence of events. These authors have developed principles to come up with theoretical methods for predicting the path of a secondary succession following a disturbance and based on a knowledge of certain attributes of the species present or potentially present.

Noble and Slatyer (1980) have made several generalisations about these factors affecting the pathway of succession:

(1) The presence of propagules, either dispersed from elsewhere or which survived the disturbance, determines the species composition immediately after the disturbance. Resprouting from individuals which have survived the disturbance is also important.

(2) There is a pulse of recruitment or regrowth immediately following the disturbance with little competition for resources.

(3) Recruitment slows after the initial pulse, as once a plant is established, it is difficult to displace.

(4) The initial occupants sometimes facilitate, sometimes restrict and sometimes inhibit subsequent recruitment of additional species.

(5) Long-lived species and those which can regenerate in the presence of their own adults will eventually become dominant in the absence of further disturbances.

Considerable importance is, therefore, placed on the attributes of individual species, which are important in their survival through or dispersal after a disturbance. Noble and Slatyer (1980) have called these "vital attributes" and have placed them in 3 groups:
• the method of arrival or persistence of the species at the site during and after a disturbance;
• the ability to establish and grow to maturity in the developing community; and
• the time taken for the species to reach critical life stages.

Noble and Slatyer (1980) then went on to examine a number of possible sequences following disturbances, assuming that species with different vital attributes were present before the disturbance. Ecologists have found this approach somewhat difficult to use in practice because of the qualitative nature of some of the attributes. However, it does recognise that periodic disturbance has always been an integral part of Australian ecosystems, and that there is a need for a body of successional theory which recognises this fact. Another important feature of this work was that it grouped species together which respond similarly to disturbances. Other workers such as Grime *et al.* (1988) and Leishman and Westoby (1992) have also used the functional group approach to help understand the complexities of plant community dynamics.

Vegetation stability and disturbance

It is an implicit assumption in the approaches to plant succession described above (except perhaps Jenny's), that vegetation is inherently stable unless disturbed. This assumption of stability is central to the monoclimax theory and was also accepted by Whittaker (1953). It was also central to the methods of condition assessment of rangelands based on quantitative ecology (Dyksterhuis 1949), which have been used for many years by public agencies in the USA. This assumption of stability is deeply ingrained in the minds of the public as well as many scientists, and yet it is not logical if we accept that ecosystems (and specifically vegetation) are truly functions of the Jenny (1961) factors. These factors are continually changing, particularly in Australian ecosystems, and ecosystems have resisted these changes by the evolution of long life cycles in the constituent species. Communities comprising annual species have little inertia and respond rapidly to environmental changes.

The traditional view of disturbance and resilience is best exemplified by Trudgill's (1977) description. Trudgill (1977) uses the analogy of a pool in a stream. If the stream runs into a pool and then runs out again, the level of the pool is stable. If a bucket is then dipped into the pool and a bucket of water taken out, the level of the pool will recover, depending on the relative rates of inflow and outflow of the stream and the relative sizes of the pool and the bucket. A resilient system, which is stable under perturbation, is one in which there is either a large pool or a large inflow and only a small bucket. A small pool with no inflow and a large bucket represents an unstable system, which, once disturbed (the

removal of the water), will stay in this new state until rain falls or someone else puts some water back into the puddle. The important point about this analogy is that the state of the system is represented by the level of water in the pool. The pool being full with the water level at the level of the outflow is considered the initial stable state. If there is no inflow and a large bucket, and one bucket of water is removed, the level of the pool represents another state which is likewise stable, until either more water is removed or more water is added to the puddle. Note that the states are being defined as stable unless they are perturbed by the disturbance. This view of disturbance is consistent with the traditional view of disturbances (e.g. Sousa 1984).

An alternative assumption is that vegetation is inherently unstable and is the product of a number of independent variables or factors of the environment (Jenny 1961). 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, and much 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 lifetimes of the important species are long in relation to the lifetimes of ecologists, as is the case for many forest communities.

This alternative view also requires that the concept of disturbance not be confined to isolated, sometimes catastrophic events. Disturbance is simply defined as a change over time of one of the variable Jenny (1961) factors. This change may be sudden or even catastrophic (c.f. Sousa 1984) or it may occur gradually. In grazed rangelands, it may simply be a decrease or increase in grazing pressure produced by a change in animal numbers or a change in the rate of forage production. A disturbance so defined does not necessarily result in the destruction of vegetation, but may produce dramatic changes. An example would be the addition of fertiliser, which may result in dramatic changes in the species composition of grassland vegetation simply by altering the relative competitive ability of the constituent species.

Environmental sieves and vegetation changes over time

Changes in the species composition of vegetation over time involve differential reproduction and/or death rates of the constituent species. In this context, a plant can be considered as a means by which a seed produces more seeds (Harper 1977).

If we have a cohort of, for example, 10 000 ovules produced at flowering time in a population of a particular species, then only a proportion, maybe 10% or 1000, of them would 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 (Jenny 1961) each year. These state factors, therefore, operate by altering the fineness or coarseness of the 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 (Figure 3) which collectively determine how many ovules are produced in the next generation. The size of the population of a monocarpic annual species will obviously fluctuate more from year to year than that of a polycarpic perennial 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 "fortuitous co-occurrence of unlikely events, where each event has a low probability of occurring" (Noble 1986), in arid ecosystems, which can lead to the episodic reproduction of perennial species, is an example of an episodic coarsening of critical environmental sieves. 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.

State and transition model

The state and transition model (Westoby *et al.* 1989) describes vegetation (originally that of

rangelands but the principles may well apply to any form of vegetation) as a catalogue of alternative states. Primary and secondary successions following catastrophic disturbances can also be viewed as a succession of these alternative states, which merge one into another over time. The transitions between the different states and the composition of the states themselves will depend upon the state factors as described by Jenny (1961). Where environmental gradients occur in space, then gradations between different states will occur spatially. Therefore, this model appears to satisfactorily account for the complications of variations of vegetation in space and time. An important facet of this model is that the states are user-defined. For example, one user may define alternate states of a patch of vegetation in terms of its structure, while another may use the presence or absence of a rare and endangered species.

A second and important part of this model is the catalogue of possible transitions between the states. A particular set of changes in environmental factors (disturbances) 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, this particular set of conditions would represent a management hazard. If these hazards can be recognised,

appropriate action can be taken and the transition to the undesirable state prevented. Alternatively, opportunities occur when conditions are right for a transition to a more desirable state and then the appropriate manipulation can be applied. A number of states and transitions for grazing lands on the Northern Tablelands of New South Wales and the manipulations necessary to cause the transitions are illustrated in Figure 4 (Lodge and Whalley 1989). Some of the transitions are not marked on Figure 4 because we do not know enough about the vegetation to know when or even if, these particular transitions are likely to occur.

This approach to vegetation change is essentially a reductionist approach, where the whole is considered to be simply the sum of the individual plants of the constituent species. Therefore, in order to be able to catalogue the states and transitions which are valid for different patches of land in a particular region, an autecological profile of the important species or functional groups of species (Leishman and Westoby 1992) is necessary. The information required is an extension of the vital attributes described by Noble and Slatyer (1980) and is akin to the information provided in Grime *et al.* (1988).

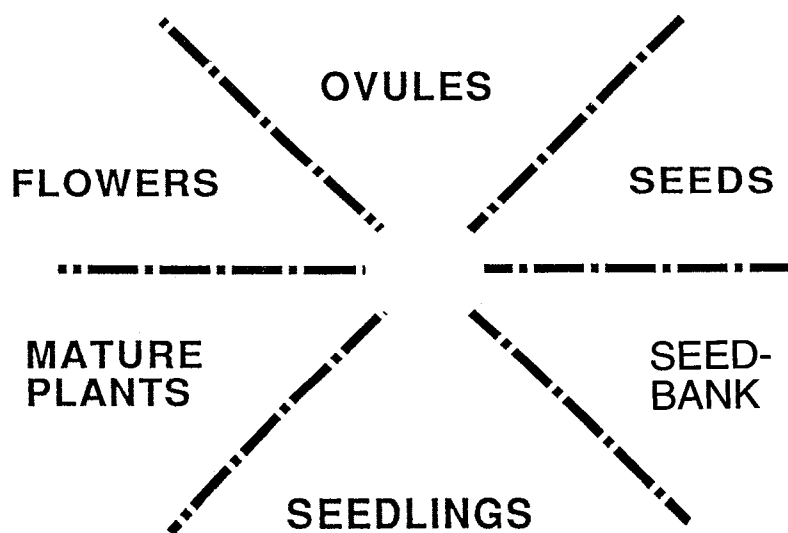Another way of looking at the state and transition model is to consider the mechanisms of

Figure 3. Life stages of a plant showing some of the environmental sieves between the various life stages.
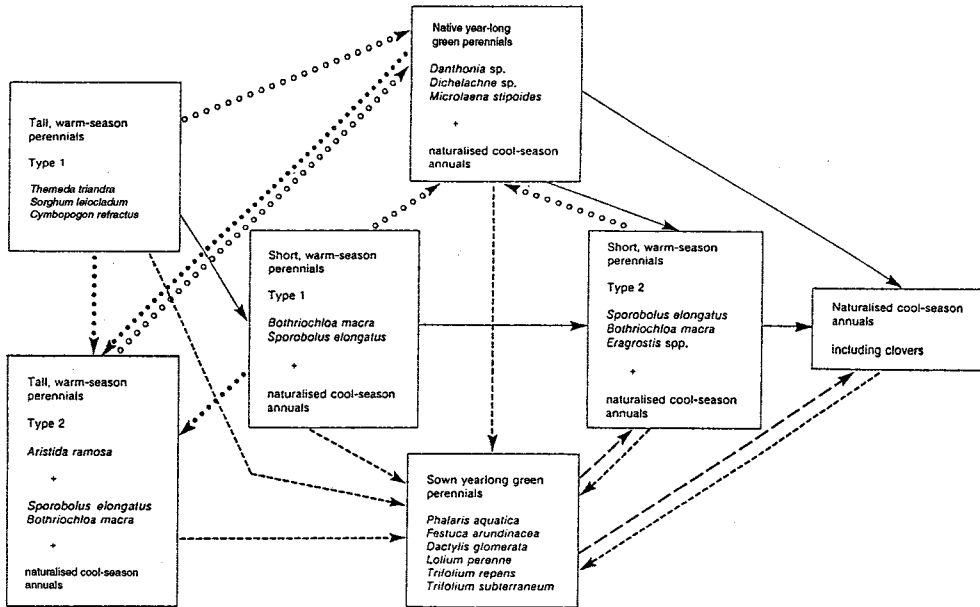
Figure 4. Some states and transitions of natural and improved pastures on the Northern Slopes and Tablelands of New South Wales. Arrows indicate transitions produced by: heavy, year-long grazing plus increased soil fertility (———); drought or improper grazing (— — —); seeding plus superphosphate addition (- - - -); regular winter or early spring burning (••••); and heavy summer grazing with or without superphosphate addition (ooooooo) (from Lodge and Whalley 1989).

change in the population size of the individual species. A population starts as a population of ovules at the flowering stage of the species in question (Figure 3). In its journey through fertilisation, development of the embryo, seed development, seed dispersal, seed germination, seedling establishment, growth to maturity, and flowering, to produce a new population of ovules, this population passes through a number of environmental sieves (Harper 1977) as described above. The fineness of these environmental sieves for each species depends upon the state factors of Jenny (1961). Some of these state factors, such as rainfall sequences, vary from time to time and from season to season, and others may be easily manipulated such as by fertiliser addition to increase soil fertility. Therefore, the hazards and opportunities represent changes in the fineness or coarseness of individual environmental sieves for individual species produced by changes in the non-manipulable environmental factors such as rainfall sequences. The reaction of the land manager can be to alter manipulable factors such as grazing pressure, soil fertility, fire etc. and so change the fineness or coarseness of particular

sieves of key species to avoid hazards or take advantage of opportunities.

Conclusions

I believe that we have come a long way from the seductive simplicity of Clements' (1916) successional model of plant community dynamics. We have now reached a stage with the state and transition model of Westoby et al. (1989) where we have a body of theory and a conceptual model which is sufficiently flexible to account for the highly variable Australian environment. This model promotes pro-active land management instead of the fatalistic approach encouraged by the Clementsian model which suggests that all we have to do to repair land degradation is to remove human disturbances and let succession take its course. Once we have enough information about the ecological profiles of a large number of Australian species or groups of species, we can apply the state and transition model to such diverse ends as maintaining the productivity of semi-arid and arid rangelands or manipulating vegetation to preserve rare and endangered species in a rainforest.

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