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ELEMENTS OF A THEORY OF VEGETATION DYNAMICS IN ARID RANGELANDS

MARK WESTOBY

*School of Biological Sciences, Macquarie University,
North Ryde, N.S.W. 2113 Australia*

ABSTRACT

Under grazing pressure the vegetation of rangelands is often altered. Range managers traditionally have thought of these changes as retrogression or disturbance, setting climax vegetation back to a seral stage. Unfortunately, removing the grazing pressure often does not reverse the changes in the way the succession model would predict. Here four elements are sketched out of a theory which can deal with these exceptions. First, which plant growth-forms win competition often depends not only on the growth-forms but also on which is present as established adults, or on which is most abundant. Second, vegetation changes can sometimes induce soil changes. The extent to which reversing a vegetation change depends on soil restoration varies greatly, and the speed with which soil structure can be restored varies from rapid to negligible. Third, the impact of grazing on different life-forms varies greatly in different situations; in particular, the nature of and scope for selectivity is very different in dense grasslands, where much of the primary production is being removed, compared to open arid vegetation. Fourth, a new model is outlined for the adaptation of plant growth-forms to different arid climates. This model shows that different growth-forms can coexist stably in arid regions because they use different growth opportunities in complex weather sequences. Climates with the same general level of aridity can offer very different mixtures of growth opportunities, because of patterning of rainfall in time; accordingly different mixtures of growth-forms are found. These growth-forms are adapted demographically, not just physiologically. After particular weather sequences, some species may be present only as seeds or seedlings, while others are present as adults; thus above-ground vegetation can vary even while the mixture of populations present is stable. One growth-form, such as annuals, can include several distinct demographic strategies, with different responses both to drought and to grazing. These four elements of a theory, taken in different combinations, can explain both classical cases of range succession and the important exceptions.

Insofar as range management has a theoretical basis, it is the concept of range succession. This concept has imperfections from two points of view. First, it has not changed to reflect recent changes in our understanding of successions generally, and of the processes that drive them (e.g., Drury & Nisbet, 1973; Connell & Slatyer, 1977). Second, there are a number of important range types, particularly in climates where rainfall is limiting, whose dynamics cannot be interpreted with the classical concepts of range succession.

Received April 15, 1980 and August 25, 1980

In this paper I sketch the outlines of a broader theory of vegetation dynamics on rangelands. The theory has four elements. The first two can be called the asymmetry of plant competition and vegetation-soil linkage; these can be described briefly. The third is the impact of grazing on the competitive advantage of different life-forms; this is straightforward, but will need to be discussed at greater length. The fourth element is a new model for what plant life-histories and growth-forms are favoured by different climates and weather sequences. This model is not immediately obvious, and so will take some space to explain, even though I shall only outline it rather than treating in depth and with rigour.

First I shall describe the concept of range succession as it now exists, and list some of the situations which it does not deal with satisfactorily. Then I shall outline the four elements of a new approach listed above. Finally I shall indicate how the four elements can be articulated in different combinations to explain both cases which do follow classical range succession and also the exceptions.

RANGE SUCCESSION

Historically, range management developed in the U.S. between 1910 and 1950, at a time when plant ecology was much concerned with the idea of succession. The concern took two forms which were particularly important for the development of range management. First, methods for classifying vegetation were based on identifying climax types, and then on describing seral stages as variants of these. Second, there was a vigorous debate (e.g. Clements, 1916; Tansley, 1935; Phillips, 1935; Weaver & Clements, 1938) which led to an acceptance that vegetation could be in equilibrium not only with climate, but also with soil conditions and with "disturbances" such as grazing. These two aspects of the plant ecology of the day led naturally to a management system which classified rangelands first as to their type (climax condition) and then as to their condition (seral stage).

The essential concepts of range succession are therefore as follows: (a) A given piece of land has a climax condition, determined by the regional or local climate and soil conditions. (b) Grazing pressure diverts this to a "disturbance climax" or disclimax. At the disclimax a given grazing pressure is in balance with the intrinsic tendency of the vegetation to change towards climax. (c) The most basic decision in range management is to set the stocking rate. The manager in choosing a stocking rate also chooses the disclimax which will result at equilibrium. Range science is occupied with characterizing the equilibrium vegetation which will result from different stocking rates, and the economic yield to be expected per animal at each possible equilibrium. Given these two kinds of information, the most profitable sustainable stocking rate can be calculated for any given pasture.

This successional approach to range management was suggested very early (Sampson, 1917, 1919), was developed into a practical system of range classification by U.S. government agencies and in the 1940s and 1950s became firmly established as the consensus of the range management profession, expressed in the first two editions of Stoddart and Smith (1943, 1955), and in a series of conceptual papers in the

journals of the profession (Humphrey, 1945; Dyksterhuis, 1949, 1958; Parker, 1954; Hanson, 1957).

This approach to management remains the core of modern range management (e.g., Heady, 1975; Stoddart, Smith & Box, 1975). It involves a number of assumptions, not always explicitly stated. Two, which are important for predicting the dynamics of grazed vegetation are (a) the response of the vegetation to a stocking rate at which it is not in equilibrium is continuous, and begins promptly, so that stocking provides a tool which can be used to adjust vegetation progressively; (b) the responses of plant life-histories and growth-forms to competition and to grazing are opposite — i.e., the most successful competitors are also the most susceptible to grazing — so that grazing pressure and succession in the absence of grazing are opposite, potentially balanced forces. For instance, vegetation dominated by annuals is interpreted as the result of overgrazing, and it is expected that the release of grazing pressure will cause the vegetation to revert to a climax of perennial grasses or shrubs.

Several other attitudes, which are widespread in range management, can be traced to the development of range succession concepts from the classical ideas of succession. These are not critical to the management system outlined above; any of them could be dropped without forcing an alternative approach. Nevertheless, they do colour the approach taken by range managers. For example, the ungrazed climax is expected to be also the most productive and most palatable vegetation (excluding succession beyond grassland to forest). A related idea is that the responses of plant types to drought are parallel to their responses to competition and to grazing, so that overgrazed vegetation is typically like the vegetation of more xeric sites. Both these ideas evidently have roots in the Clementsian concepts of the climatic climax and of succession as analogous to the ontogenetic development of an organism. These roots are reflected in the use of the term "range condition" (sometimes even "range health") to refer both to the stage in the grazing succession and to the quality of rangelands for livestock.

PROBLEM SITUATIONS

It should be recognized that the concepts of range succession, described above, apply quite well to some important rangeland ecosystems, notably the mixed-grass and short-grass prairies of North America, the vegetation most familiar to Clements and to many developers of early rangeland theory.

However, the theory does not cope well with many phenomena in rangeland dynamics. Some examples are:

(a) There are a number of vegetation types where annuals continue to dominate if grazing pressure is removed. Temperate examples include *Avena* grasslands in central California (Biswell, 1956; Heady, 1958), some areas in northern Africa and the middle east (Naveh, 1967; Le Houerou, 1972) and areas in the Intermountain of the U.S., dominated by *Bromus tectorum* under shrubs (Tueller, 1973). In the grassy woodlands of the seasonally dry tropics, certain soil types also are dominated by annuals (e.g., *Sorghum* spp. in northern Australia, Shaw & Norman, 1970) in a way which does not seem to result from overgrazing.

(b) Vegetation, even in the absence of grazing, may have alternative stable states. Following a particular weather sequence, one species may dominate for decades, to be replaced by another following some different weather pattern (Williams & Roe, 1975).

(c) Woody perennials sometimes increase due to a reduction in grazing, and sometimes due to an increase.

(d) Some changes cannot be reversed by changing the stocking rate — e.g., if woody perennials increase under heavy grazing, removal of the grazing typically does not reverse the process, and sometimes the increase actually continues.

(e) When grazing has affected vegetation enough to allow soil erosion, recovery rates of soil and vegetation vary from substantial to undetectable.

My point in raising these cases is not to imply that range managers have failed to recognize them. On the contrary, most are to be found in introductory texts. In many cases, the mechanisms underlying the phenomena have been well investigated. The point is that range management as a discipline has to treat them on an ad hoc basis as special cases, not fitting the "typical" pattern of range succession.

Expecting classical succession, range managers have consistently tried to create perennial grasslands from vegetations dominated by annuals, or with increasing shrub populations, by destocking. In many cases, decades have been lost before the ineffectiveness of this approach has reluctantly been recognized. In the less-investigated rangelands of the tropics, annual grasses are often still treated automatically as evidence of overgrazing (e.g., Whyte, 1974).

ELEMENTS OF A THEORY

Asymmetry of Plant Competition

The asymmetry of plant competition refers to the fact that the outcome of competition between two plant species is often determined not by the species, or even by the life history or growth-form of each, but by which is an adult and which is a seedling. For example, perennial grasses which can outcompete shrub seedlings (e.g., Humphrey, 1949; Litav, Kupernick & Orshan, 1962; Scifres, Brock & Hahn, 1971) lose to adult shrubs. Similarly, annual grasses which can outcompete seedlings of perennial grasses or shrubs (e.g., Holmgren, 1956) are often defeated by adult shrubs or by the tillers of established perennial grasses.

The most important source of this asymmetry is that light descends from above. Where competition for light is important, adult plants of any species have a great advantage over seedlings. Also, an accumulation of mulch favours the tillers of perennials over seedlings supported by seed reserves only. There are, however, two more subtle forms of positive frequency-dependence in plant competition which should be mentioned here. First, when shrubs rather than grasses dominate the vegetation, the fuel load in the ground layer may be changed so that fires are less frequent. Since adult shrubs can often survive fires where their seedlings cannot, the effect of establishing a cohort of adult shrubs can be to shift the competitive balance in favour of shrubs at recruitment stage as well. This effect is best known in desert grassland (e.g., Brown,

1950; Glendening, 1952; Humphrey, 1958). Second, it seems that herbivores will sometimes take a plant species as a minor component of the diet, but not take more when more is available (Westoby, 1974, 1978, 1980). The result is that grazing can have a serious impact on a species present as a minor element in a pasture, but no real impact when the species is more abundant (e.g., Frishknecht & Harris, 1973), unless the livestock are deliberately introduced at very high stocking rates (e.g., the use of goats to control brush regrowth, Stoddart, Smith & Box, 1975).

Vegetation-Soil Linkage

Vegetation-soil linkage is the idea that vegetation affects soil and soil affects vegetation. A grazing-induced change in vegetation can sometimes change soil properties. The reversal of the effects of grazing pressure then requires a soil change, which can be much slower than would be the working out of competition between plant population strategies in a given climate and soil environment. However, we have no coherent account of how long we expect soil restoration to take under different circumstances. Some examples will indicate how variable the situation can be.

The first is the soil developed on fairly nutrient-rich materials under perennial grasslands, characterized by a dense mat of live and dead roots. This mat holds the soil against wind and water erosion, increases infiltration and hence the effectiveness of rain, and buffers soil temperature (Johnson, Dormaar & Smoliak, 1971). This is one reason why the assumption that the climax is the most productive vegetation holds true in these grasslands. If overgrazing shifts the vegetation to one of ephemerals, these binding roots decompose to small lengths and can be blown or washed away, along with mineral soil. With erosion continuing, perennials, establishing when grazing pressure is removed, tend to be left on pedestals and killed. Nevertheless, a run of wet years can accumulate enough biomass of ephemerals to hold the soil while perennials establish. The soil change is therefore likely to delay the reversal of grazing effects by decades at the most, and by proper management it is feasible to reduce this delay.

In contrast to this are (for example) the skeletal soils of erosional slopes in deserts. These have negligible organic matter, and their properties are hardly affected by the vegetation which occupies them. There is no time-delay needed for them to recover after overgrazing.

A third situation is found in many arid shrublands on poor soils. Here nutrient uptake and litter fall have concentrated most nutrients very near the surface; Australian *Atriplex* shrublands are of this type (Charley & Cowling, 1968; Charley, 1972). The spacing of the shrubs controls wind-speed at the soil surface. When grazing thins them to more than about 6 diameters apart (Marshall, 1970; 1971; Wooding, Bradley & Marshall, 1973), this nutrient-rich surface is lost, and the surface left behind may be "scalded" (Beadle, 1948) — smooth and hard. Reversal of this situation is almost undetectably slow, although mechanical disturbance of the surface in conjunction with a seed supply and adequate rains can overcome the scalding (Cunningham, Walker & Green, 1976). The shrubs and the distribution of nutrients may actually be phenomena able to survive by mutual support from a period of wetter climate, in which case the effects of grazing cannot be reversed without a return to the earlier climate.

A fourth situation is where soils are more saline at depth than near the surface, for example, the many areas formerly occupied by *Kochia americana* in the U.S. Intermountain region (Kearney et al., 1914; Cook, 1961). When overgrazed before 1914, these were reoccupied by *Kochia* (Kearney et al., 1914), but since its introduction the exotic salt-pumping annual *Halogeton glomeratus* has often occupied overgrazed *Kochia* areas (Clarke & West, 1969). This seems to be a permanent situation in the continued presence of *Halogeton*. Even if *Halogeton* could be removed, it is not certain that the present climate would leach the salts back to depth; their former position could have resulted from an earlier climate.

A fifth situation is where sand-dunes previously stabilized by vegetation are mobilized by its removal. Seedlings establishing on mobile dunes are liable either to have their roots exposed or their shoots buried. The damage may be self-enhancing, as even established plants on what had been areas between or outside the dunes are overwhelmed. The existence of fossil dunes now fixed by vegetation (Mabbutt, 1977) shows that vegetation can re-establish on dunes given time and an appropriate climate; the time can be shortened by management which stops movement of surface sand.

Impact of Grazing on Life-Forms

The subject of how well individual plants of different life-forms tolerate having biomass removed is treated at length in texts (Heady, 1975; Stoddart, Smith & Box, 1975). Here I am concerned rather with how a given grazing pressure (total biomass removal) is distributed over different plant species in different ecosystems. Two major kinds of ecological situation can be distinguished: those in which primary production is large and a large proportion of it is regularly dissipated by grazing or fire; and those in which primary production is smaller, and most of it either accumulates as wood or is decomposed.

In what follows I will restrict myself for the sake of simplicity to grazers which mainly take green material within 50 cm of the ground, bringing the mouth down on it from above (i.e., cattle and sheep, also various wildlife species).

The amount of biomass removed is nearly all that is within reach of the biomass-removing agent. This is achieved by (i) fires (ii) the grazing period of some rotational-grazing schemes (iii) grazing by herds which for reasons not to do with the supply of forage are concentrated in space – e.g., wildebeest in the Serengeti (McNaughton, 1979) concentrated for predator-saturation (Estes, 1976); bison before 1800 in the U.S. (Larson, 1940; Roe, 1970); and perhaps some effects around watering-points (Osborn, Wood & Paltridge, 1932; Lange, 1969).

Biomass-removal of this sort gives no scope for species to escape by being less palatable than others. It favours species which keep their meristems at or under the ground surface, and do not commit too much of their biomass to the zone from which all biomass is removed. It also favours individuals with woody trunks resistant to the biomass removal and with foliage above the zone of removal. An extended period free from biomass-removal is necessary for such individuals to be recruited. However, once established, such emergent trees are probably very long-lived, even under heavy grazing or frequent fire.

Biomass-removal of this type is responsible for the maintenance of grasslands and savanna-grasslands in relatively well-watered regions, climatically able to maintain a vegetation largely of woody perennials that succeed in competition over grasses.

Within such regions, the ground-layer is dense enough so that biomass lower in it is concealed or protected by biomass above it. Between incidents of nearly complete biomass-removal, grazing at lower intensity removes biomass predominantly from the species which are overtopping, i.e. outcompeting, the others. Thus grazing pressure of this kind does operate in precisely the opposite direction from succession after release of grazing. This situation, found in prairies of the U.S., fits the assumptions of the classical range succession model well.

The vegetation is open enough so that grazers choose food because they prefer it, not because it is all they can reach or see. This situation is usually found towards the arid end of the spectrum of rangelands. Fires are at most rare events, and grazers do not remove a large proportion of the small primary production. Under these circumstances preferred species are disfavoured. The relations between a species' life history or growth form and whether it is preferred or not are complex here. Several kinds of factors can be listed:

(1) Grazers prefer species with little dead foliage among the live. This can lead them to choose annual over perennial grasses until the annual's tillers flower. Also, previously grazed individuals are preferred over ungrazed individuals.

(2) (producing opposite tendencies from 1) Grazers prefer species from which more material can be obtained in a single bite (Stobbs, 1973; Belovsky, 1978). This can lead them to prefer perennial tussock-grasses over ephemerals or shrubs.

(3) Individual woody perennials with foliage above about 2 m are protected. The response of their populations to grazing pressure depends on whether their juveniles are preferred; if they are not, such species are potential woody weeds.

(4) The supply of vegetation varies in time, but the amount being removed by grazing does not (e.g., under set stocking) or at least varies less. This sort of grazing pressure favours species which are actively growing at times when others are also growing, and disfavours perennials – for example, those which continue photosynthesis long into drought. Its effects are therefore superficially similar to those of grazing in more mesic grasslands (see above) in that grazing advantages ephemerals compared to perennials. Whether perennial shrubs or grasses are most disadvantaged seems to depend on whether the grazer selects mostly for protein content (sheep – disadvantages shrubs, particularly in winter) or for bite size (cattle – disadvantages grasses). However, the situation differs from more mesic grasslands, in that the ability of perennials to overtop annuals and grow through a dense mulch is not necessarily critical to the outcome of competition between them. Therefore when grazing pressure is removed, its effects are not promptly reversed.

(5) Species may vary in their nutritional usefulness to herbivores, or in their mechanical (e.g., thorns), chemical or symbiotic (e.g., ants, Bentley, 1977) defenses against livestock. Of the five listed, only this idea corresponds at all closely to the concept of palatability with which range managers currently interpret grazing preferences.

In range plants, the nutritional content seems to depend more on the phenology of different tissues than on which species is in question. However, there may well be some patterns in the incidence of defensive (so-called secondary) chemicals in species with different life-forms. A coherent body of ideas (Feeny, 1976; Rhoades & Cates, 1976; Rhoades, 1979) is just beginning to emerge from work on insect-plant coevolution. This predicts, for instance, that ephemeral tissues can be defended against insect attack by toxins such as alkaloids. Persistent tissues defended this way would be too susceptible to attack by insects with specialized detoxifying mechanisms, and are instead defended at much greater cost by digestibility-reducing substances such as tannins. The implications of these ideas for diet selection by ruminants with complex digestive ecosystems in their gut are too large a subject to develop here.

As far as the impact of livestock on vegetation dynamics is concerned, the key question is: how does consumption of a plant species change as its abundance changes? Does consumption decline sharply as a species declines, so that species which have been driven to low abundance then have the pressure of grazing lifted from them? Or do herbivores keep it in their diet in response to some nutritional need (Westoby, 1974), so that overgrazed species suffer increasing pressure? All five of the factors influencing preference, listed above, are clearly likely to produce nonlinear responses of consumption to abundance. Range managers recognize that preference depends not only on the plant species and the herbivore, but on factors such as the other plant species present and their relative abundance (Heady, 1975; Stoddart, Smith & Box, 1975).

Unfortunately, range and wildlife management's near-universal method of analyzing diet data (e.g., Heady, 1975) is to calculate a preference index p_i for species i as a ratio of consumption c_i to availability a_i . If p_i has any predictive power at all, it predicts that c_i/a_i , the grazing pressure on the species, is a constant. This method of analysing data obscures the answer to the key question about functional response.

Impact of Climate and Weather on Growth-Forms

The three elements of a theory of vegetation dynamics on arid rangelands, outlined above, contain nothing new, although I have ordered available information in new ways, and have treated as general propositions situations previously regarded as special cases. In this section, on the other hand, I outline a new model which in principle can predict the mixture of growth-forms and life-histories (and to that extent the vegetation composition) found in a given climatic regime, and also the response of their populations to particular weather sequences.

The orthodox approach to understanding how vegetation changes as one travels from grassland into progressively more arid climates is to focus on two changes. First, as water becomes harder to get, shrubs with extensive root systems are favoured over grasses. Second, as rain becomes more unpredictable, ephemerals are favoured over perennials. These ideas are manifestly inadequate to explain many features of growth-form distribution. For example: Why are there some vegetations dominated by annuals in areas with relatively good (e.g., 200–400 mm) rainfall, while some more extreme deserts (e.g., Sonoran with 50 mm) are dominated by perennials (Shreve & Wiggins,

1964)? Why are there many desert shrubs without extensive root systems? What accounts for the distribution of stem-succulents, which are not by any means consistently found below some level of aridity? How can some deserts (e.g., upper Sonoran) contain such a wide variety of growth-forms (Whittaker & Niering, 1965) — why is there not a single best growth-form?

Growing conditions for plants in arid areas cannot be characterized by an average degree of dryness, even with a measure of variation attached. Rather there occur sequences of excellent growing conditions, difficult but usable conditions and drought. Different life-histories and growth-forms use these sequences in different ways. The viability of a given life-history in a given climate is determined, not by some general measure of dryness, but by the incidence of growing conditions that it is able to use and by the success of its growth-form in using them relative to the success of others. This is the basic idea of the model which follows.

The model is intended to apply to arid regions, defined as those where the highest growth rate during good (i.e. moist) growing conditions is achieved by species efficient at photosynthesis when well hydrated, and without heavy investment in roots or stems. It does not apply where more biomass is accumulated, and the maximal growth rates of different plant growth-forms relative to each other are determined more by their ability to overtop others, so that taller perennials will win. It happens that this distinction roughly corresponds to that made when considering the impact of grazing on life-forms, between situations with larger production of biomass (maintained as grasslands only by fire or intense grazing) and those in which primary production is less and grazers are more able to exercise preference between the different growth-forms and species.

Types of time. The sequence of events in the growth of arid vegetation is as follows. A drought is broken by rain. Different growth forms deploy their photosynthetic tissue with varying promptness: instantaneously for evergreens, bark-photosynthesizers or stem-succulents; quickly for deciduous shrubs, geophytes and perennial grasses or forbs; more slowly for ephemerals starting from seed. There follows a period during which soil moisture is adequate for growth of all the life-forms; its duration depends on the size of the initial rains or on follow-up rains. The soil dries out progressively, and plants have increasing difficulty in maintaining tissue hydration. Ephemerals abandon the effort early and convert their accumulated photosynthate into seeds; perennials adjust their water budgets, by closing stomates or shedding leaves to reduce transpiration, by obtaining more water through deep or extensive root systems or by some combination of the two. As the drought progresses, perennials which have not taken steps sufficient to maintain a water column between their meristems and the soil are killed. Rains may fall which allow some kinds of perennials to increase photosynthesis, but are not adequate to make it worthwhile for perennials to deploy new photosynthetic tissue or for ephemeral seeds to germinate. Finally a heavy rain falls and the sequence begins again.

I will formalize the different growth opportunities available during this sequence by speaking of three types of time. Type II time represents good growing conditions for all life-forms. It is defined as a time during which different growth-forms have

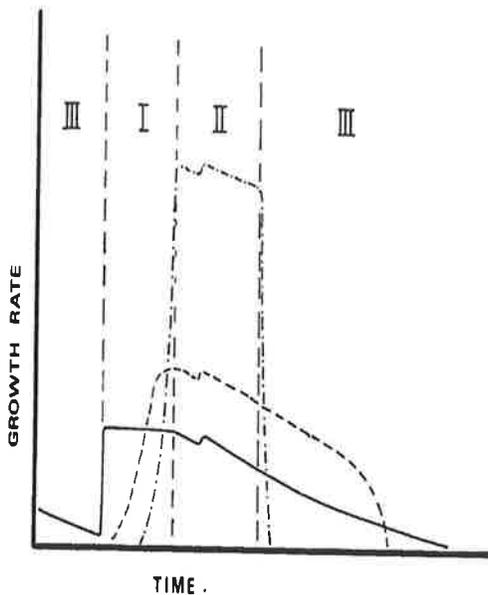


Fig. 1. Scheme of the time courses of growth-rates in three contrasting growth-forms (ephemerals – solid line; drought-deciduous – dashed line; stem-succulents – dot-and-dashed line) over a sequence of types of time, to illustrate the definitions of types of time (see text). There is initiating rain at the beginning of type I time and a follow-up rain is shown during type II time.

growth-rates which are fixed relative to each other – e.g., if mesophylls with little stem or root investment achieve 100 units of growth-rate, woody perennials with xeromorphic leaves may achieve 40 units. Type III time begins at the end of type II time, as soil dries out and the relativities of growth rates break down. Type III time ends with germinating rains, at the beginning of type I time. Type I time is “start-up” time, lasting from germinating rains until photosynthetic tissue is well deployed, at the beginning of type II time.

The growth-rates of three representative growth-forms during this sequence of events are schematized in Fig. 1. Type I and type II time have been defined with a particular purpose in mind – that the ranking of total growth made by different growth forms during an incident of either type of time will be fixed. The rankings will be fixed for different reasons in the two types of time. During type II time, the ranking is the same at any moment, so that the ranking of growth over the whole period will be unaffected by the duration of the incident of type II time. During type I time, on the other hand, the time-courses of increase of growth rate are characteristically-shaped for each growth-form. The total growth over the period of type I time, equivalent to the area under each curve, should be in a fixed ranking when growth-forms are compared.

Clearly the three types of time are abstractions of more complicated variation in the growth opportunities available to plants in arid zones. Actual boundaries between time bands could well be unclear in a field situation. However, for the purposes of the arguments which follow, it is sufficient that the types capture some of the variation

which exists; it need not be possible to attribute any given day unambiguously to a type of time.

Niche separation and coexistence of life-forms. Plants with different life-histories and growth-forms are able to exploit the different types of time to different degrees. The patterning in time of growth opportunities is a niche axis which can be subdivided by species with different population strategies.

During type I time the relative success of different growth-forms depends partly on their maximum growth-rates, but more importantly on how fast they deploy photosynthetic tissue. Evergreens and stem-succulents will do best, followed by perennials which have the reserves and the buds to deploy a large leaf area quickly, followed by those plants which have to grow from seed. During type II time, on the other hand, species with mesophyll foliage and with minimal investment in stems or roots will do best. Perennials and species with xerophyll photosynthetic tissue will have lower growth rates.

Type III time is rather heterogeneous, and no one growth-form has a clear advantage in using it. The soil dries out progressively, but plants have no information on the length and severity of the impending drought. In this context they face a trade-off between the probability of survival should the drought prove to be a long one, and higher growth rate (Orians & Solbrig, 1977; Chabot & Bunce, 1979; Mooney & Gulmon, 1979). To survive a plant must maintain a water column in the xylem leading to each meristem. This is not because meristem tissues could not in principle evolve to tolerate desiccation – after all, the embryos in seeds are reduced to very low water contents – but because meristems depend on passive uptake of water to rehydrate after drought. Therefore if a perennial is to obtain the advantage during type I time of leafing out rapidly from buds distributed along branches, it must bear the cost of maintaining a water column in the xylem leading to each of them.

This cost can appear either as the cost of reducing transpiration (either from each leaf or by shedding leaves – Orshan, 1972), with a correspondingly lower rate of photosynthesis, or as the cost of investing in roots to acquire water, that is the opportunity cost of foregoing investment in foliage and the respiration cost of maintaining roots.

Perennials in deserts typically do not acquire adaptations which fit them to survive all droughts; most are sometimes killed. There is no clear distinction between ephemerals and perennials, but rather a continuum from species which are killed by a few days of type III time to those which have not been observed to be killed by drought, i.e. they are killed less than once every 100 years or so. Generally, selection will favour genotypes which distribute their limited resources so as to ensure their own persistence, or so as to establish their progeny by means of more, larger or better-dispersed seeds, in proportions which depend on the probabilities that each will be successful in producing an individual after a drought. The cost of being killed is of three sorts: (a) progeny must start as seedlings in the type I time following the lethal drought, and so use that time much less efficiently; (b) seedlings may be put at great competitive disadvantage relative to those which survived as adults; (c) a larger reserve of seed progeny must be maintained, only some of which are able to germinate on any one

occasion. The important point here is that these are not disadvantages to be avoided by perennials at all costs. They will be avoided only when they, multiplied by the frequency with which they are incurred, exceed the benefits of a higher growth rate obtained during type II and early type III time.

The growth-rates which probably can be achieved by some different plant types relative to each other during different types of time are indicated in Table I. The table shows that one of the essential conditions for several life-history strategies and growth-forms to coexist with each other is present; there are several resources (types of time), and the competitive winner on each resource ought to be different. Thus we expect mesophyll ephemerals to win competition for type II time, and either evergreen or deciduous perennials to win competition for type I time, depending on the frequency with which each is killed in late type III time.

The second essential condition for coexistence is that the supply of one resource is affected most strongly by the number of competitors trying to use that same resource, and not by the number trying to use some other resource; or to put it another way, that plants compete most with each other when they grow at the same time. Since in this model the types of time are defined with respect to time-patterns in the supply of soil water, the model makes some assumptions about competition for soil water, and these should now be made explicit.

Soil water is the subject of competition not merely because it is both in short supply and essential to the competing plants. There is competition only if the shortness of supply to one competitor is increased by the presence of other competitors. It is often supposed that water constitutes several independent resources when it occurs at different levels in the soil (e.g., Cable, 1969), and that plants are able to coexist by virtue of having root systems which specialize in different soil levels so far as water

extraction is concerned. However, a notable feature of desert vegetation is that different life-forms (e.g., stem-succulents, perennial grasses, annual herbs and some shrubs) can coexist with their roots in the same soil volume. This is the phenomenon explained by the use of different types of time. The model in this paper in effect assumes that water diffuses quickly between different levels of soils. To the extent that this assumption is not true, a further mechanism allowing coexistence will be present; but the argument explaining coexistence of plants with roots at the same level does not depend on the assumption.

It is also often argued (e.g., Harper, 1977) that water used by one plant species at one time (e.g., type II) is not available to other species at some later time (e.g., type III). This is of course true; but the question is, how much more of it would be available to the second species if the first were not present? The answer to this question depends on the rate of evaporative loss, which in turn depends on the soil, the climate and the depth at which the water occurs (Cable, 1969). For example, in sandy or rocky soils evaporative loss is low once the surface soil has dried, so that water at depth remains available unless it is extracted by plants. In heavy-textured or shallow soils, on the other hand, water not used by plants will be greatly diminished by evaporation before later-growing plants can use it. Our knowledge of the influence of plants on the rate of decline of soil water content is still very fragmentary. More experiments involving removing plants and measuring the trend of soil water at different depths under different conditions of soil and climate are badly needed. Meantime, the model in this paper assumes that evaporation of water is substantial enough, so that competition is strongest between plants growing at the same time. The essential conclusions from the model require only this, and do not require that there be no competition at all between plants growing at different times.

It has even been argued that some plants have strategies which involve using water conservatively with a view to having it available in the soil at a later date. This is probably not an evolutionarily stable strategy, since "cheats" using water fast would not be disadvantaged (Cohen, 1970). The possibility cannot be ruled out, however, that group selection could produce this result in populations where all neighbouring plants are close kin.

The two conditions that resources are used differentially, and that competition is strongest within a resource, are sufficient to produce frequency-dependent competition. Imagine an environment which provides (say) 50 units of potential growth per decade per unit area during periods of type II time and 50 units during periods of type I time. Now suppose this is occupied by a density of ephemerals sufficient to use 100 units of type II time, but only a few perennials using 10 units of type I time. Clearly, each ephemeral will be more disadvantaged by competition than will each perennial, and in due course there will be relatively more perennials compared to ephemerals. Conversely, if the same environment were occupied by a large density of perennials compared to ephemerals, the ephemerals would have a competitive advantage. In this way we expect stable coexistence to arise between two or more plant growth-forms or life-history strategies.

Of course, different growth-forms are also able to coexist in deserts because local

TABLE I
Relative abilities, on an arbitrary 0 (low) to 5 (high) scale, of plants with different features of life-history and growth-form, to accumulate carbon during different types of time (see text)

	Types of time			
	I	II	early III	late III
Mesophyll ephemerals	1	5	0	0
Xerophyll ephemerals	1	4	1	0
Mesophyll leaves, shed early	2	4	0	0
Xerophyll leaves, shed late	2	3	2	0
Xerophyll leaves, evergreen	2	2	1	1
Stem-succulence	2	2	2	0
Investment in deep roots, relative to the above leaf types	-1	-1	+1	+1

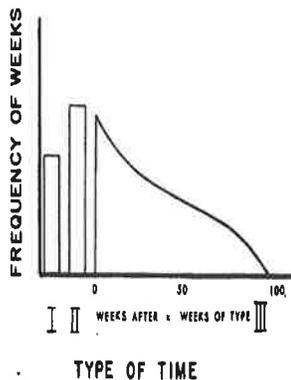


Fig. 2. Probability-distribution of kinds of growth opportunities (types of time) available in a given climatic regime. See text.

topography and soil variation, particularly in conjunction with the redistribution of water in the landscape after intense storms, produce a wide variety of degrees of soil drought at one time within a given area; also plants differ in their ability to use water at different depths in the soil, as mentioned above. Nevertheless, a notable feature of desert vegetation is that different life-forms occur with their roots in the same volume of soil; the use of different types of time offers an explanation for this.

Climatic regimes as niche axes. To interpret the impact of climate on vegetation, a given climate can best be characterized by the growth opportunities it offers plants. We are now in a position to formalize this idea by describing climates, not in terms of their average dryness and its variability, but in terms of the probability-distribution (or frequency-distribution) of types of time. Moreover, to the extent that the types of time have been defined so as to capture successfully differences between plant types in the growth opportunities they can use, each probability distribution will have associated with it a characteristic equilibrium mixture of different types of plant. We should therefore be able to make some predictions about how the growth-form mix of the vegetation will be seen to change in response to particular sorts of changes in the climatic regime.

One possible representation of the probability distribution of types of time is shown in Fig. 2. I will shortly discuss the effect of varying climatic regimes by referring to Fig. 2. Therefore I must first point out some of the figure's features, and some simplifying assumptions embodied in it. Its important feature is that type I and type II time are treated as internally homogeneous, while type III time is regarded as heterogeneous. This heterogeneity is treated as a continuum from "early" to "late" type III time, rather than by subdividing type III into further classes. This treatment reflects the variation in growth opportunity that I want to discuss. Type I time and type II time have single adaptive effects, favouring rapid start-up, and high growth rate under optimal conditions, respectively. However type III time has varied effects. Early type III time can be used by plants which can continue to transpire to some extent under fairly dry soil conditions. Late type III time represents the risk that a given period of type III time will last long enough to be lethal to a would-be perennial which

has however not taken sufficient steps to survive a drought of that intensity. Because there is a continuum of responses of plants to this trade-off, no sharp line can be drawn dividing the "opportunity" zone from the "risk" zone of type III time.

One simplifying assumption is that the intensity of drought increases steadily after the end of type II time, so that the variation within type III time can be expressed as a function of the time since it began. Another way of putting this is to say that rains falling after the beginning of type III time which are not large enough to encourage plants to invest reserves in deploying new foliage, either by seed germination or by leafing out, do not greatly change the usefulness of type III time. Since light rains falling on dry soils in the highly evaporative climate of deserts do not infiltrate far and are quickly evaporated, this may not be as unreasonable an assumption as it might appear at first glance. Nevertheless, there are two possibilities which should be noted here. The first is that succulents might use water available even in the few hours after a light rain to rehydrate their tissues, and then make that water last much longer than the soil water content is elevated. The second is that there may exist rainfalls which make it worthwhile for a deciduous perennial to deploy more leaf mass, but not for a seed to germinate. Either of these possibilities would call for time to be subdivided into further types, if they were to be treated formally. I will not deal further with them here, except to point out that some of the effects of rains of this sort can be considered as simply increasing the amount of early type III time at the expense of late type III time.

A second simplifying assumption is that rainfall patterns are occurring in an environment without seasonal temperature variation. Actually, of course, virtually all the world's arid zones are substantially warmer in summer than in winter. At high temperatures plants can grow faster, so that a week of type II time represents a larger growth opportunity. At the same time, the rate at which a given rainfall is lost to evaporation is also greater when temperatures are high, so that a given amount of rain provides less growing time. As a first approximation, I will simply assume that these two effects compensate for each other. As a second approximation, growth opportunities could be described not by rainfall but by (for instance) precipitation $P > 0.4 \times$ evaporation E over one week for initiating rains, and $P > 0.2E$ over 4 weeks for follow-up rains (Slatyer, 1962); time could be described in (say) degree-days rather than weeks.

One other consequence of seasonal temperature variation is that two or more distinct floras of ephemerals may be developed. For an ephemeral seed, no more elaborate adaptations are needed to survive a long rather than a short time before germination, so the cost of ignoring some wet periods in order to be more highly adapted to the temperature of other wet periods is small. For perennials, on the other hand, ignoring wet periods sharply increases the costs of surviving between times of active growth. Seasonal specialization is therefore less common in perennials, although it does occur. However, this complication does not affect the basic operation of the model in predicting the partitioning of growth opportunities between different population strategies; rather it is relevant to the question (beyond the scope of this paper) of how many species can co-occur using the same population strategy.

Now, having dealt with these various complications, we can consider how some important kinds of variation in climatic regime ought to affect the mixture of plant population strategies which is found. Without attempting to compute Fig. 1 exactly for any particular climate, we can see how it might differ between different climates. I will consider three major sorts of effects: decreasing mean annual rainfall, increasing the size of individual rainstorms and concentrating the rainfall in one part of the year.

As the mean annual rainfall becomes less, fewer rains will act as follow-up to other rains, that is act to lengthen a period of type II time. There will therefore be less type II time relative both to type I time and to type III time. The effect is to favour perennials compared to ephemerals. Meanwhile, however, the incidence of late type III time, that is the probability that a given drought will be dangerously long, is increased. Reducing mean annual rainfall therefore favours perennials with a conservative approach to early type III time (to increase the ability to survive long droughts) and with rapid activation during type I time. As the mean duration of periods of type III time increases, so does the variance of the duration. This can favour ephemerals. The reduction in the ratio of type II to type I time, on the other hand, disfavours ephemerality as a way of dealing with unpredictably long droughts.

All the above is on the assumption that "wet weeks", i.e. weeks of type I or type II time, occur randomly in time. However in reality they do not. One sort of clustering of wet weeks in time is that caused by single large storms, which wet the soil for several weeks. Above some minimum size, these have the effect of increasing the proportion of type II time relative to type I time, and so of favouring ephemerals. In many arid zones most of the rain falls in quite large storms of this kind. This is to some extent confounded with the seasonality of rain, because in most arid zones summer rains are local thunderstorms due to daily heating of the ground in the presence of moist air-masses, while winter rains are predominantly frontal. Generally summer rains are larger individual events, and at any one point on the ground, less predictable from year to year. As is well known, seeds of ephemerals have a problem in deciding whether to germinate, not knowing how long wet soil conditions will last (Cohen, 1967; Beatley, 1974). The best-known strategy is to use only type II time which is wet as a result of the single rain which begins the preceding type I time. Adaptations to germinate only in response to rains of some minimum size are therefore widespread. A second strategy, appropriate to areas with a small but reliable winter wet season, is to germinate in response to light rains, but only when temperature conditions are appropriate, or only after a hot dry summer has broken dormancy.

A second sort of clustering of wet weeks in time is due to seasonal concentration of rainfall. When rain is concentrated into one part of the year, there are two effects. First, the probability that a given rain will act as follow-up, rather than to break a drought, is increased, hence there is more type II time compared to type I time. This favours ephemerals, particularly ephemerals which are to some extent xerophyll, so that they can tolerate short dry periods within the wet season. Second, the probability that a drought will last longer than a single dry season becomes small; the incidence of early type III time is increased and that of late type III time decreased. This favours

perennials which use early type III time effectively and take precautions only sufficient to survive droughts of intermediate and predictable length.

When precipitation falls as winter snow, it is effectively released in the spring thaw, and is thus even more reliably seasonal and predictable in duration than precipitation data suggest. Conceivably, this fact contributes to limiting the set of growth-forms found in the cold shrub-steppes of the world. However, other aspects of growth-form adaptation to very cold winters may also be important; they are beyond the scope of this paper.

Plant population strategies. In the light of the above discussion, we can see that the traditional classifications of plant life-histories (annual or ephemeral vs. perennial, drought-avoider vs. drought-endurer vs. drought-resister, therophyte vs. chamaephyte vs. phanerophyte, etc.) do not capture much of the important variation in plant demographics as they relate to dealing with the rainfall patterns of arid zones.

One example is the life form called ephemeral (therophyte, drought-avoider, annual). A strategy of rapidly converting all growth gains to seed should be favoured by three distinct kinds of selective pressure:

(a) Difficulty in surviving droughts except as seed, i.e. a substantial incidence of late type III time. Since this commonly goes with a high level of uncertainty that any given rain will produce a useful period of type II time, usually only a small proportion of the soil seed reserves of such species will germinate, as was shown by Cohen (1966) to be adaptive. As a result the seed reserves at any one time are often large. For example, at Fowlers Gap, western NSW, after 18 months of drought, *Dactyloctenium radulans*, *Sporobolus actinocladius* and *S. caroli* all had viable seed reserves in the order of 10^4 m^{-2} ; of these only 5% or less of seeds would germinate unless steps were taken to break dormancy (M. Westoby, J.M. Cousins & A.C. Grice, unpublished data).

(b) A large amount of type II time compared to type I time, as in the strongly seasonal rainfall pattern of dry Mediterranean areas, or dry summer monsoon areas near the tropics. Here we expect a large proportion of seeds to germinate each year, and seeds may often be large because the risk is small that a seed once germinated will not have a period of type II time ahead of it. Demographies of this sort have been found in several Mediterranean annuals (Rossiter, 1966), such as *Avena* spp. in the Central Valley of California (Marshall & Jain, 1967), and in annuals of xeric environments on the Welsh coast (Watkinson, 1978).

This strategy is not really restricted to annuals, for geophytes can be considered as an extreme case of it. Like seeds, the meristems from which they will grow when rain falls are reduced to very low water content and will initiate growth by passive uptake of water. The tendency to produce fewer seeds, each supported by larger reserves, is carried to its logical extreme in the bulb or corm of geophytes, which is moreover always 100% kin to its progenitor.

(c) Conditions where vegetative plants are frequently destroyed, or where spaces in the vegetative cover are frequently opened up for colonization. These encourage the "fugitive" or "weed" ephemeral, which in classical range succession is the strategy encouraged by overgrazing and outcompeted when grazing pressure is removed.

It should be noted that nearly all plant species produce seeds for the purpose of

dispersal to some extent. In those perennials where the probability of being killed by drought is negligible, all seed production can be regarded in this light. At the other extreme, most of the seeds of ephemerals of type (b) above can be regarded as devices for surviving drought in situ. In some cases this dichotomy of seed function has generated two seed morphs; as would be expected, this outcome is most common in environments favouring ephemerals of type (b) above, as in *Gymnarrhena micrantha* in the Negev (Koller, 1969; Evenari, Shanan & Tadmor, 1971).

Another example of variation in demographic strategy is within the class of woody perennials, or phanerophytes. There is a continuum of variation in how quickly the transpiring body is reduced as type III time begins, from those with very mesophyll leaves, shed quickly, to those with xerophyll leaves, retained until death. In many cases in the Middle East perennials convert from relatively mesophyll to relatively xerophyll leaves as they enter on type III time (Orshan, 1972); this of course involves costs in energy and nutrients in the discarded leaves, in exchange for the improved growth rate during type II time. Also, the seedlings of many perennials with xerophyll leaves have relatively mesophyll leaves for use during the plant's first type II time, e.g., the phyllodineous *Acacias* in Australia.

There is also in woody perennials a continuum of ability to survive drought. For example in Australian chenopod shrublands, perennials of the genus *Maireana* have not suffered extensive death in any recorded drought; Crisp (1978) found that only 8–14% of *M. sedifolia* died on permanent plots at Koonamore between 1931 and 1972. *Maireana* does not maintain a reserve of dormant seeds; after rains, no ungerminated seeds are viable (Burbidge, 1946). The other widespread dominant of these shrublands, *Atriplex vesicaria*, on the other hand, suffers extensive death in droughts of a severity which recurs probably in the range 1 in 20 to 1 in 100 years. Osborn, Wood and Paltridge (1932) observed extensive mortality in South Australia in 1929; Crisp (1978) found that 10 out of 10 established plants died on the Koonamore plots in 1959; and there was extensive mortality at Fowlers Gap in 1976–1978 during a 26-month drought that was an event of between 50-year and 100-year return time (M. Westoby and B. Rice, unpublished data). *Atriplex vesicaria* maintains a reserve of viable but dormant seeds, although a larger proportion of its seeds are germinable than are those of annual *Atriplex* species (Beadle, 1952); after the drought at Fowlers Gap seedling populations have reestablished.

Somewhat similar differences exist at Fowlers Gap between *Acacia victoriae* and *Cassia nemophila*. In the glasshouse well-watered *Acacia* seedlings have a higher growth rate and a smaller root-shoot ratio, but die more quickly when droughted (A.C. Grice, unpublished data). Judging from revisiting photo-sites established by N.C.W. Beadle in 1954, *Acacia* grows faster and recruits seedling cohorts more often in the field. Both species have soil seed reserves a large proportion of which are hard (A.C. Grice, unpublished data). *Acacia* tends to occur on less well-drained soils than *Cassia*, but mixed stands exist, as is the case with *Atriplex* relative to *Maireana* (Carrodus & Specht, 1965).

Thus at least under Australian conditions, with a high probability of very long droughts, there are perennials which have adapted to survive in perhaps 95–99% of all

years, but rely on seed reserves to reestablish after the more exceptional events. One consequence which should be pointed out of a demography of this kind is that populations using it may often be dominated by a single cohort, as is often the case with *Cassia* at Fowlers Gap.

The above examples show that categories such as annual and phanerophyte conceal within them several different population strategies. This is important because the population strategies respond differently both to drought and to grazing. Only confusion can result from attempting to generalize about the responses of all three types of annuals (for instance) to overgrazing.

Dynamics during particular weather sequences. The above model predicts that a climate characterized by a given Fig. 1 should favour a given mix of plant growth-forms and life-histories. This mixture is however the equilibrium vegetation only in a long-term and statistical sense. All the elements of the mix are present at all times, but which are present as adults, which as juveniles and which as seed depends on the recent weather. An obvious case of this is that during any type III time ephemerals are present only as seeds. Less obvious is that incidents of late type III time can reduce dominant populations of some perennials (see above) to seed populations. While such populations are expected to include seed reserves allowing them to reestablish after the killing drought, there may be a sizeable delay before the seedlings grow to dominance. Moreover, if a coexisting perennial species survived the drought as adults, the seedlings could be at a competitive disadvantage with respect to it.

In this context it is important to distinguish occasions when a population is reestablishing from soil seed reserves, from occasions when the propagules of a species are arriving from elsewhere and establishing. These tend both to be called "invasion" in the literature, but this confusing usage should be avoided.

Recapitulation. Since the above discussion has been fairly long, it will be useful here to recapitulate briefly those conclusions from the model which are most important to understanding the dynamical behaviour of arid rangelands under different permutations of drought and grazing sequences. These are:

- (a) A growth-form or life-history (e.g., "annual") can include several quite different demographies which correspondingly are affected differently by weather and grazing.
- (b) A given mean annual level of aridity (net deficit of rainfall relative to evaporation) can favour vegetations with widely varying growth-form mixtures, depending on the clustering in time of the periods of moist soil.
- (c) The equilibrium mixture of growth-forms in a given climate is a mixture of populations, not a mixture of vegetative plants only. Within this equilibrium, fluctuations in the mixture to be observed above-ground are expected not merely on the time-scale of fluctuations in rainfall income, but with time-lags decades long after particular rare droughts or establishment events.

USE OF THE ELEMENTS TO EXPLAIN PROBLEM SITUATIONS

Here I will indicate how the four elements of a theory which were outlined above can be used, singly or in combinations, to understand both classical range succession and also the situations which pose a problem for the classical theory.

Of the five situations listed earlier in this paper as examples of problems for the classical theory, two [(c) and (e)] can be understood with single elements of the theory. The variable recovery rate of vegetation when it is dependent on soil recovery calls for a knowledge of the vegetation-soil linkage. The fact that woody perennials in some situations increase under grazing, in others decrease and in yet others increase if grazing is removed, can be understood in terms of the different situations described under "Impact of Grazing on Life-Forms". Some relatively mesic grasslands are restrained from becoming forests only by regular "mowing" by grazing (or fire). In some semi-arid areas, such as Australian chenopod shrublands, under set-stocking by sheep, species which remain green during drought (i.e. shrubs) are disfavoured; these tend to become grasslands under grazing (Moore, 1953). In other semi-arid areas, where shrubs are taller and where grazing is by cattle, grazing disfavours perennial grasses and can lead to an increase in shrubs or ephemerals or both.

The classical range succession, and the three remaining problem situations, all need to be understood in terms of different combinations of the elements of a theory. The combinations which are needed are summarized in Table II.

The classical range succession proceeds from bare ground, to ephemerals, to perennial grasses. It is found in environments where the biomass produced is such that perennial grasses competitively defeat ephemerals. Grazing pressure opens up the dense accumulation of biomass, removing the competitive advantage of perennial grasses. Important features of the soil, such as water-holding capacity and buffering of surface temperature fluctuations, are determined by the vegetative cover. However, if over-grazing leads to substantial changes in the soil, these can be reversed simply by accumulation of organic matter in and on the soil, which can follow quite quickly if grazing pressure is removed.

TABLE II

Elements of a theory which must be used to understand classical range succession and various situations which are a problem for the classical model. See text for further explanation

Situation	Elements			
	Asymmetry of competition	Vegetation-soil linkage	Impact of grazing on life-forms	Climate as a probability-distribution of growth opportunities
Classical range succession		X	X	
Stable vegetations of annuals	X		X	X
Alternative steady states of vegetation	X			X
Woody perennial increase initiated under grazing but not reversed on removal of grazing	X		X	

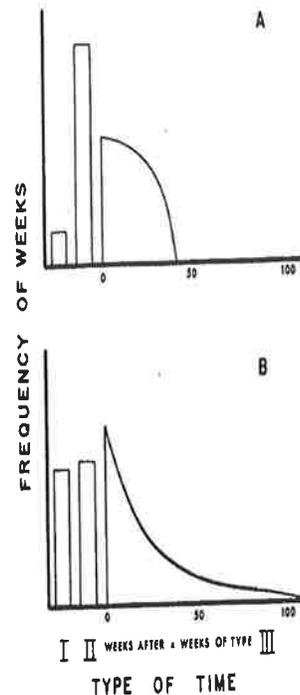


Fig. 3. Differences in probability-distributions of growth opportunities available in two climates of similar aridity but contrasting type. (a) Semi-arid Mediterranean. (b) Semi-arid south-central Australia. See text.

Stable vegetations of annuals are to be found in semi-arid climates with a reliable growing season and a drought in the remainder of the year. Under these circumstances, annuals often with large seeds, most or all of which germinate each year, are very competitive with perennials. In particular, the annuals are capable of outcompeting the seedlings of perennials, even though they may have been marginally inferior to adult perennials. Grazing can therefore shift a vegetation of perennial grasses to one of annuals, particularly if the grazing is continued through the dry season. Once this has happened removal of grazing will not reverse the change. This sequence has been recorded in recent history in the central valley of California, in many areas of the northern Great Basin now occupied by *Bromus tectorum*, and may have happened at an earlier date in Central Asia and in the Negev and Africa north of the Sahara (Evans & Young, 1972). The sort of probability-distribution which should favour such vegetations of annuals is shown in Fig. 3(a). There is a lot of type III time compared to type I time, and the probability that substantial growth opportunities will arise after the beginning of type III time, but before the next rainy season begins, is low. The only advantage of being a perennial is a slightly faster start in type I time.

In contrast to this is the sort of climatic regime depicted in Fig. 3(b). Conditions of this second kind are found in (for instance) inland Australia at about 200 mm of rain annually on average, falling both in winter and in summer. Under these conditions substantial opportunities may be lost by plants which become inactive too quickly at

the beginning of type III time. However there is also a substantial incidence of late type III time. These conflicting demands have selected perennials with a mixed strategy, remaining quite active during early part III time, but maintaining a reserve of dormant seed from which to establish after the occasional lethal drought. In conjunction with the competitive advantage of adults over seedlings, rare droughts operating on such perennials can produce switches in dominance which last well beyond the drought itself (Williams & Roe, 1975). These processes may be operating in several cases reported as fluctuations in response to climate (e.g., Blake, 1938; Jameson, 1970).

The best-studied case where an increase in woody perennial populations is initiated by grazing pressure, but is not reversed by the removal of grazing, is that of *Prosopis* spp. in desert grassland in the southwest USA. The elements of the situation are that a good perennial grass cover outcompetes *Prosopis* seedlings and probably also carries fires that kill them (Humphrey, 1949, 1958). Grazing opens up this grass cover, allowing *Prosopis* to establish; competition from *Prosopis* adults then keeps the grass cover open even in the absence of grazing, allowing continued establishment of *Prosopis* seedlings. A very similar situation is found in the understorey of some *Callitris* and *Eucalyptus* woodlands in about the 400 mm rainfall zone in temperate Australia, where grazing of the original (and very likely fire-maintained) grass understorey has encouraged dense populations of shrubs in the genera *Cassia* and *Eremophila*, which do not decline when stocking rates are reduced (Anon., 1969).

IMPLICATIONS FOR RANGE MANAGEMENT

The classical model of range succession thinks of vegetation, at any given stocking rate, as in a stable equilibrium, held in place by the balance of two steadily-applied opposing forces, grazing pressure and the tendency of the vegetation to change towards climax. Correspondingly, range management has set as its first task to determine the equilibrium condition, and hence the stocking rate, appropriate to each area of rangeland.

However the forces of intrinsic change and of grazing pressure in arid vegetation do not operate steadily, and not necessarily in opposing directions. Changes in one direction often cannot be reversed by changing the pressure. Given grazing pressures may have no significant impact on vegetation much of the time, but in conjunction with a particular weather event may quickly produce radical changes. Range management has handled these problems by continuing to set equilibrium stocking rates, but making them conservative. Aside from using vegetation inefficiently, this policy can cause range problems of its own; it allows stock to select the most palatable species, so that mean palatability of the vegetation decreases.

Basically an equilibrium approach to stocking is ill-adapted to arid vegetation. Changes in the vegetation are often responses to exceptional events, rather than to average conditions. To remove undesired species it may be necessary to apply very high stocking rates briefly at any times when the plant is susceptible, due to being the only species available, or for other reasons. Conversely, in vegetation where the

establishment of cohorts of desired perennials is a rare event, destocking during the early type III time following germination may establish a stand which can be stocked much more heavily for decades into the future. In short, grazing pressure needs to be thrown in either to help or to obstruct those transitions in the state of the vegetation which are produced by low-frequency weather sequences. It may be that research should be directed to recognizing these rare events in different kinds of vegetation, and to investigating the effect of grazing during them, rather than to determining a steady stocking rate.

ACKNOWLEDGMENTS

The ideas in this paper were developed in discussion with G.H. Orians and B. Rice, while I was on leave in the Department of Zoology, University of Washington; I thank them, I. Noy-Meir and an anonymous reviewer for very helpful comments on the drafts of the manuscript.

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GERMINATION AND GROWTH MODELS OF FORB POPULATIONS BASED ON LONG TERM RECORDS AT KOONAMORE, SOUTH AUSTRALIA

I.R. NOBLE

Research School of Biological Sciences, Australian
Canberra City, A.C.T. 260

AND

M.D. CRISP

National Botanic Gardens, Canberra

ABSTRACT

Long term chart and photo records have been taken of a pod shrubland since enclosure of the Koonamore Reserve. Studies of seasonality in ephemerals at Koonamore have shown that the demography and growth of the ephemeral grasses were obtained from 3-monthly permanent plot data. Long term point records (1926-55). Neither taxon showed results of studies elsewhere. The 5 yr chart data provide an adequate sample of ephemeral growth patterns due to which a model was developed which fitted the germination data. The occurrence of a germination event is closely related to simple temperature and a soil moisture budget based on the composition of the germination pulse are much

The T.G.B. Osborn Vegetation Reserve at Koonamore is the longest running study sites in an arid region where long term records have been made; as such, it provides a unique opportunity to study the dynamics of an arid zone community. Sheep and goats have grazed 390 ha in the northeast of South Australia (32 July 1925). The reserve was established in a chevron-shaped area (Heward ex Benth. and *Maireana sedifolia* (F. Muell.) are the dominant shrubs) with a scattered tree (*Acacia* Benth., *Myoporum platycarpum* R. Br. and *Casuarina*) badly overgrazed after European settlement in 1926, and a series of 100 charted quadrats were established in 1926, and a series of black and white photographs have been taken

Received April 25, 1980 and October 5, 1980