SUSAN WALKER

Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.
E-mail: susie@phyton.otago.ac.nz

MODELS OF VEGETATION DYNAMICS IN SEMI-ARID VEGETATION: APPLICATION TO LOWLAND CENTRAL OTAGO, NEW ZEALAND

Summary: Predictions from three conceptual models of the dynamics of semi-arid vegetation (Clementsian succession, alternative stable states and annuation/pulse phenomena) are used to review the available evidence on changes in the vegetation of semi-arid lowland Central Otago, New Zealand. Evidence is presented from Central Otago that corresponds with Clementsian succession and with annuation/pulse phenomena, although there is so far no formal evidence of alternative stable states. A declining-productivity model, which combines aspects of the other models, is also shown to fit the process of vegetation change in Central Otago. Present data on vegetation dynamics in Central Otago are insufficient for the employment of management frameworks such as degradation gradient assessment and the state-and-transition model.

Keywords: alternative stable states, Central Otago, declining productivity, degradation gradient, equilibrium, fluctuation, grassland, semi-arid, succession, vegetation models.

Introduction

Semi-arid communities have been an inspiration for new models of plant community dynamics and a testing ground for competing models, perhaps because they are known to fluctuate widely from year to year in terms of productivity, species composition and structure (Walker and Noy-Meir, 1982).

To date, most discussion of semi-arid vegetation arises from studies in the rangelands of Africa, Australia and the Americas, where the bioclimatic zone is widespread. None of the current models of semi-arid vegetation dynamics have yet been applied to semi-arid vegetation in New Zealand.

Three conceptual models are examined: Clementsian succession, alternative stable states, and annuation/pulse phenomena. The features of these models that are recognisable in historical accounts of the vegetation of semi-arid lowland Central Otago, as well as in published studies of the present-day vegetation, are discussed. Relatively narrow views of these models are presented, in order to emphasise their distinctive features and predictions. However, these conceptual extremes should be seen as being endpoints of a range of possible situations, and not as discrete alternatives. It is therefore unlikely that an observed field situation would be completely described by any one of the models alone.

More recently developed models use the conceptual extremes as components: they interpret the concepts more broadly, and combine them to produce integrative models that better describe observed data. The Declining-productivity model is an example of one such general model that has been applied to semi-arid rangelands worldwide. This model is examined, and its applicability to vegetation dynamics in Central Otago is discussed. Finally, the present state of knowledge of the vegetation dynamics of Central Otago is considered with reference to two frameworks for the management of semi-arid lands: degradation gradient assessment and the state-and-transition model.

Central Otago: climate and the history of the vegetation

The intermontane rainshadow basin of Central Otago, in the southern South Island of New Zealand, experiences an "almost continental" (Maunder, 1965), semi-arid climate, with large variations

---

Nomenclature: Native species: Cheeseman (1925), Allan (1961), Connor and Edgar (1987), Connor (1994). Exotic species: Webb, Sykes and Garnock-Jones (1988), Stace (1991).

New Zealand Journal of Ecology (1997) *21(2):* 129-140 ©New Zealand Ecological Society

within and between seasons in temperature and rainfall (Garnier, 1951), which are characteristic of semi-arid regions worldwide (Westoby, 1980; Walker, 1981). In this paper, the term 'Central Otago' refers specifically to the semi-arid lowlands below 750 m in altitude, whose climate and vegetation contrast with those of the mountain ranges of the region. The Thornthwaite (1948) moisture index of the valley floors is as low as -31, and annual rainfall is between 300 and 550 mm. Soil moisture in the weakly structured brown-gray earth soils may be at or below wilting point for periods of up to seven months over the summer (Gibbs, 1980), when moisture depletion is exacerbated by prevailing dry north-west winds. Diurnal temperature ranges are large, and nocturnal cooling rates are rapid, due to high insolation: daily maximum temperatures of 25 to 35°C are common in the summer, while light frosts may occur in any month. Frosts may be extreme from early autumn to late spring, and mean daily temperatures in July are typically below 5°C.

Aridity, frost and occasional natural fires probably excluded forest from most of lowland Central Otago, even in pre-Polynesian times (Molloy, Burrows, Cox, Johnston and Wardle, 1963), when mammalian herbivores were absent (Wardle, 1991). Analyses of pollen remains suggest that the vegetation comprised "dense scrub with local stands of podocarps" (Clark, Petchey, McGlone and Bristow, 1996). Occupation by Polynesian people some time after 1000 AD (Anderson, 1991) brought about some increase in fire frequency, which would have reduced the woody component of the vegetation (McGlone, 1989). European explorers in 1857 found "country all open, well grassed and watered, sufficient scrub for fuel for many years, but no bush or timber...a very land of promise" (W. Shennan, quoted in Beattie, 1947), and the region was rapidly settled by pastoralists (Beattie, 1947; Mather, 1982). However, after less than a decade of pastoralism, the "well grassed" valley floors became "but a poor pasture of very few species...of a remarkably sparse growth" , and only "a little scrub" remained, while richer pasture was still to be found on hill slopes and in small valleys, from which scrub had been recently cleared (Buchanan, 1968). The primary causes of the deterioration were frequent burning of the land (which was undertaken to promote palatability and to reduce scrub - Zotov, 1939), and high stocking rates, which exceeded the rapidly declining carrying capacity of the pasture. In 1870, rabbits (*Oryctolagus cuniculus*) were introduced to New Zealand, and by 1876 had reached plague proportions in Central Otago (Parcell, 1951). The sudden rabbit eruption induced an awareness of a serious environmental crisis. However, "the problem of declining carrying capacity was perceived as one of rabbit control" (Mather, 1982), and stocking and burning rates were not reduced sufficiently to arrest the degradation (Petrie, 1912; O'Connor, 1986). Over the next three decades, not less than 2000 sq. km of grassland in the driest areas reached a state described as "practically desert land" (Petrie, 1883; 1912), destitute of vegetation but for patches of "scabweeds" (*Raoulia* spp.).

The European settlers also introduced many exotic plant species which have become naturalised in Central Otago (Hubbard and Wilson, 1988). This, and the degradation caused by grazing and burning, has given rise to an induced vegetation, dominated by exotic species, which today bears little resemblance to that of pre-European times. Some improvement of the pastoral productivity of the region was achieved with the advent of aerial topdressing and a reduction in the rabbit population in the 1950s (O'Connor, 1986), although this period also saw the spread of weed species (Morgan, 1989). Over this century, rabbits populations in Central Otago have resurged repeatedly despite eradication efforts, and although irrigation has allowed vegetation improvement in some areas, there is otherwise little evidence of the reversal of the degradation.

The models

Model 1: Clementsian succession and the Range Succession Model

Traditionally, grassland ecosystems have been interpreted in terms of Clements' (1916) concept of succession (Fig. 1a), which was first applied to range management by Sampson (1919) as the 'Range Succession model'. The principles of range succession imply that in the absence of grazing, or on release from grazing, the vegetation and its habitat will follow an innate tendency to move forward along a single continuum of 'condition' towards a 'climatic climax' of perennial grasses or shrubs. Overgrazing, or other disturbance, will lead to a backward movement along this same continuum, with reduction in overall species diversity but an increased component of annual plants, reduction in soil organic content, slower nutrient cycling, less rainfall infiltration and increased temperature fluctuations at the soil surface

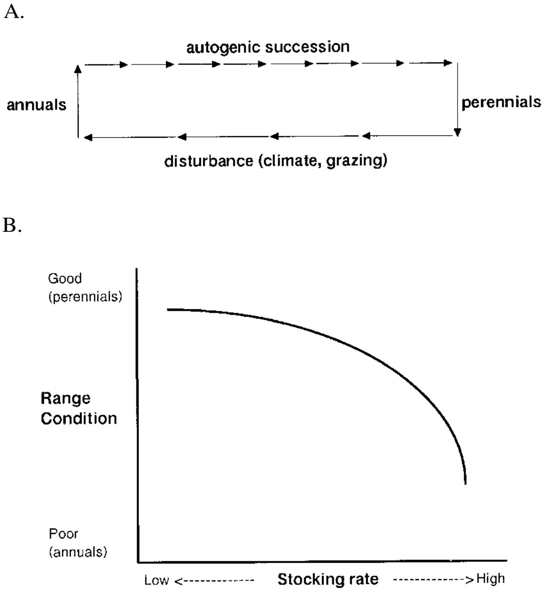

Figure 1: *(a) The principles of the Clementsian succession model. The slower autogenic succession and rapid retrogression due to disturbance are seen as opposite, potentially balanced, forces. (b) The range succession model. Range condition is supposed to increase and decrease smoothly in response to changes in stocking rate.*

(Dyksterhuis, 1949; Heady, 1975). Thus, grazing pressure and succession are 'opposite, potentially balanced forces', which may be manipulated by range management, and in particular by adjusting stocking rates (Fig. 1b) (Ellison, 1960). The model supposes that this balance, or equilibrium, is also affected by rainfall variation: drought affects vegetation in a similar way to grazing, while above-average rainfall accelerates the successional tendency (Westoby, Walker and Noy-Meir, 1989).

Evidence in support of the range succession model would be a progressive change in vegetation towards the climax (such as a decrease in annual, and an increase in perennial species) in response to the cessation of grazing. In Central Otago, Petrie (1912) and Cockayne (1920) reported that the removal of sheep and rabbits from depleted scabweed vegetation resulted in rapid transformation to a perennial grass sward, which the latter interpreted as 'recovery' stages of Clementsian succession. More recently, Allen, Wilson and Mason (1995) found that removal of grazing at five Central Otago sites led to increases in the abundance of exotic palatable perennial grasses, and decreases in the proportion of annuals. The ordination trajectories of the ungrazed treatments at these sites over time show a relatively continuous directional change (Fig. 2a) (Walker, Wilson and King, unpublished data). Similar directional vegetation change, involving an increase in perennial species, has been shown, following exclosure, on glacial outwash terraces at Luggate (Fig. 2b) (King, 1995; Walker *et al.*, unpublished data).

Model 2: Alternative stable states

Many authors have concluded that although Clementsian succession may be an appropriate model in moist grasslands, it is unsuitable for semi-arid grasslands, where vegetation change in response to rainfall and grazing is discontinuous and shows hysteresis effects (Westoby, 1980; Westoby *et al.*, 1989; Friedel, 1991; Laycock, 1991). Indeed, semi-arid vegetation released from grazing may change very little, or it may change in ways other than those predicted under the range succession model. A number of mechanisms (demographic inertia, grazing catastrophe, priority in competition, fire positive feedback and persistent change in soil conditions) have been identified which produce states in semi-arid vegetation that are not simply reversible (Westoby *et al.*, 1989). Recent literature stresses that infrequent and unpredictable events, such as drought or fire, 'drive' and 'determine' rangeland dynamics, while incremental changes are de-emphasised (Watson, Burnside and Holm, 1996).

A theoretical alternative to Clementsian succession has been the concept of multiple stable states in ecological communities, as introduced by Sutherland (1974), in which vegetation dynamics are described as a non-linear set of alternative stable states, which differ markedly in species composition and are separated by abrupt transitions in space or time. These states are likely to be maintained by positive feedback between vegetation and environment - a vegetation switch (Wilson and Agnew, 1992). The concept of thresholds (boundaries in space and time between two domains of relative stability, the crossing of which requires substantial intervention by management or some natural 'event') is compatible with the concept of alternative stable states (Friedel, 1991), and the ball and trough model, which depicts basins of attraction separated by thresholds of different size (Friedel, 1991; Laycock, 1991) may be used as an analogy (Fig. 3). Situations that conform to mathematical models of alternative stable states have been

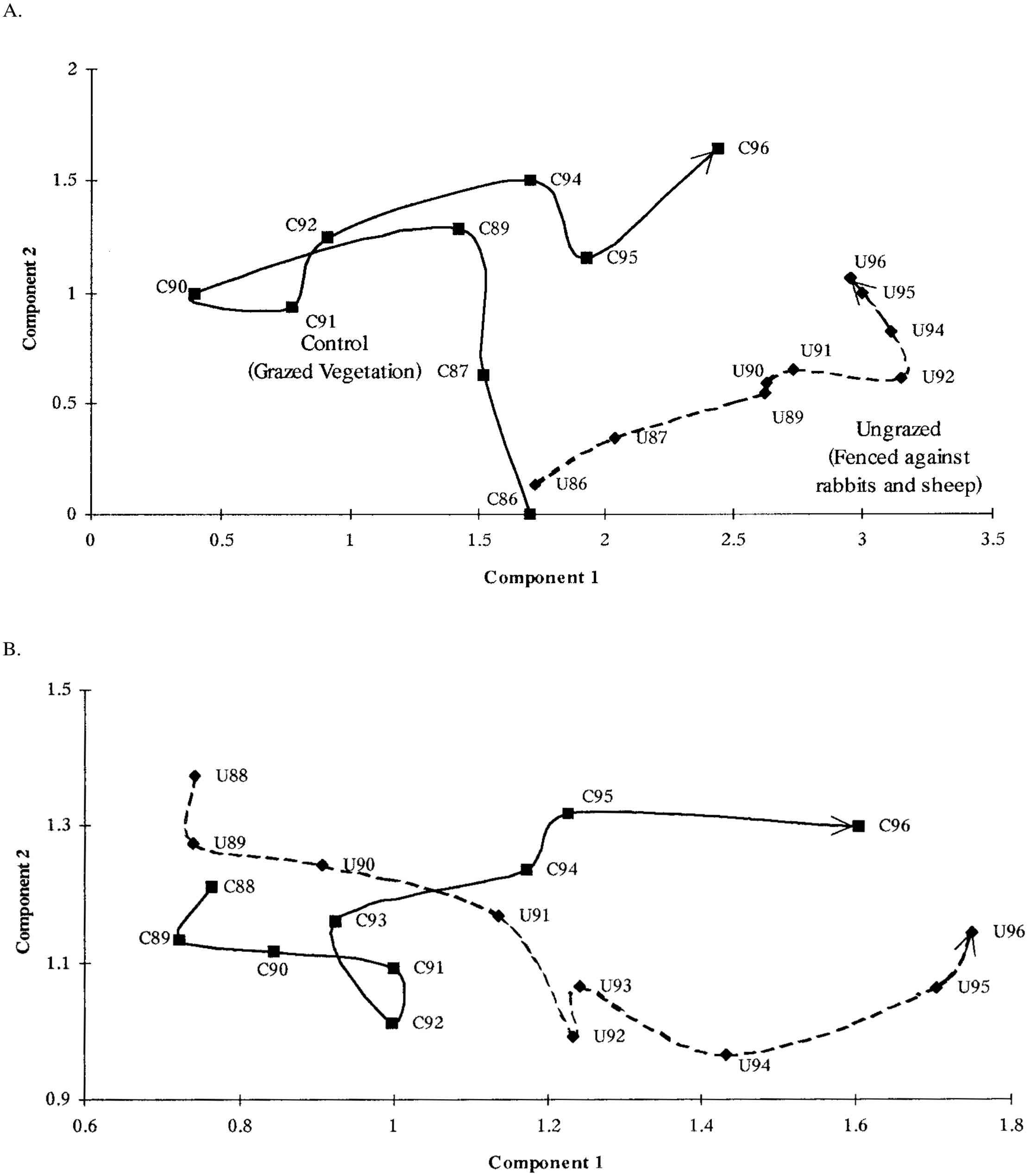

Figure 2: *Plot of the first two component axes from Detrended Correspondence Analysis, showing the trajectories of vegetation change in grazed control plots and ungrazed vegetation on the first two components of the ordination. At both sites, the position of the control plots on Component 1 was related to rainfall (P<0.01 by regression). Data point labels refer to treatment: C = control, U = Ungrazed, and year of sampling (19)86 to 96. Axis units are standard deviations. (a) Earnscleugh Station (Earnscleugh Site 1 - Allen* et al., *1995; Walker* et al., *unpublished data). Vegetation was sampled each spring over the ten years from 1986 to 1996, with the exceptions of 1988 and 1993. (b) Luggate experimental site (King, 1995; Walker* et al., *unpublished data). The plots were sampled in the spring over the eight years from 1988 to 1996.*

described in mesic New Zealand pastures (Noy-Meir, 1975; see also May, 1977) and in grazed semi-arid regions by Walker *et al.* (1981).

If a vegetation state is stable, then relief from grazing may not necessarily cause any directional change from a degraded condition. For example, in northern Utah, Rice and Westoby (1978) showed that protection of overgrazed semi-desert communities from herbivores did not cause the communities to move to a different vegetation condition or state, nor did it cause annual species to decrease, at least in 15 years. They concluded that overgrazing had moved the vegetation and its habitat into an alternative stable state. Friedel (1991) and Laycock (1991) provide further examples from Australian and North American rangelands.

Similar evidence for alternative stable states has not yet been found in the vegetation of Central Otago. Rather, it has long been observed that the scabweed (*Raoulia* spp.) "deserts" created in the 1880s, which persist under present-day grazing regimes, are rapidly converted to a cover of perennial grasses on the removal of herbivores. Cockayne (1920) reported this process at numerous sites around Central Otago, and his observations are supported by the recent studies of Allen *et al* (1995), King (1995) and Walker *et al.* (unpublished data). However, Petrie (1912) predicted that soil desiccation and erosion would prevent recolonisation by native grasses, and a recent study (Hewitt, 1996) has confirmed local loss of topsoil from sunny faces in Central Otago. Such an environmental change would almost certainly prevent the return of the vegetation to its undisturbed "climax" for decades, or even centuries. However, the length of time over which monitoring has been carried out (<10 years; Figs. 2a and b) is probably insufficient for such barriers to succession (thresholds) to have become apparent.

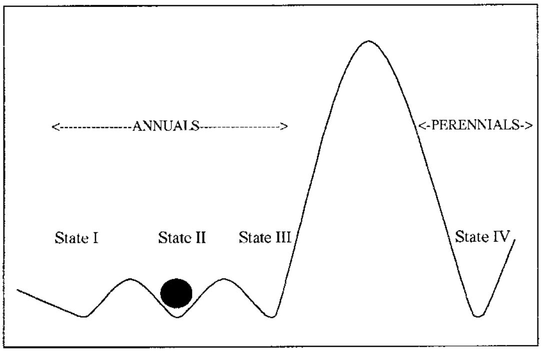

Figure 3: *The ball-and-trough analogy of alternative stable sites. In this cross-section of a hypothetical surface, basins are stable states of attraction for the vegetation, which represented by the ball, and the humps are thresholds of differing magnitudes. If a disturbance is too small to force the vegetation across the threshold, it will return to the state it came from.*

There are no data which provide formal evidence of stability, under present grazing and climatic regimes, in the vegetation of Central Otago: i.e. evidence of whether the vegetation returns to its original composition following perturbation (although work is in process). However, there has been some debate as to whether the vegetation of Central Otago has yet reached any equilibrium, subsequent to the changes brought about by European settlement, fire, mammalian herbivory, and the introduction of exotic plant species (e.g. Wilson, Williams and Lee, 1989). Partridge, Allen, Johnson and Lee (1989) argued that the strong relationships between species distributions and the environment are evidence for equilibrium. However, Wilson (1989) showed that exotic species were continuing to invade plant communities. If the vegetation of Central Otago has indeed not yet reached equilibrium, we could not expect stability in the present plant communities.

Model 3: Annuation and pulse phenomena

Within-year variation in weather on a scale of days, weeks and months, may result in dramatic community fluctuations (i.e. reversible changes in dominance within a stable species assemblage - Rabotnov, 1974) in mesic grasslands (Grime, Willis, Hunt and Dunnett, 1994; Silvertown, Dodd, McConway, Potts and Crawley, 1994). Community fluctuations are particularly marked in grazed semi-arid systems, which experience extremely variable climatic conditions within and between seasons (Coupland, 1974; Sims, Singh and Lauenroth, 1978; Collins, Bradford and Sims 1987; Bartolome, 1989; Peco, 1989). Clements (1934 pp 41-42) referred to "the striking difference from year to year in consequence of the effect of plus and minus phases of the climatic cycle" as 'annuation'.

Annuation may be found where vegetation composition tracks environmental variation over time, without apparent directional change, and without crossing thresholds. For example, Collins *et al.* (1987), in their study of an Oklahoma sage-brush grassland, recorded simultaneous fluctuations in growth-form composition over 39 years in two grazed communities, which could be related to climate. In the grazed control plots at Luggate (Walker *et al.*, unpublished data; Fig. 2b) and on

Earnscleugh Station (Allen *et al*., 1995; Fig. 2a), annual fluctuations were related to rainfall patterns over the study periods, and might be interpreted as annuation.

Model 3 is not necessarily incompatible with the concept of alternative stable states, since vegetation fluctuations may occur within stable states, and indeed Friedel (1991) seems to envisage this. In fact, the continuation of erratic, 'non-directional' climate-driven fluctuations over long time periods (in the order of several decades) may be informal evidence for the stability of a state, because climatic fluctuations constitute a 'natural perturbation experiment' (Silvertown, 1987). However, the <10-year records from sites in Central Otago (Figs. 2a and b) are insufficient to demonstrate that there is no overall directional change in the grazed vegetation.

Penfould (1964) referred to instances of unpredictable and short-lived increases in abundance of particular species in semi-arid grasslands as the 'pulse phenomenon'. The probable cause of the pulse phenomenon is individualistic responses of different species to particular combinations of climatic conditions (Peco, 1989; Houle and Phillips, 1989). Observations have been made in Central Otago of eruptions of particular exotic species, which have declined some years later to become minor components of the vegetation (e.g. *Vittidinia gracilis*: Williams, 1985). However, published data are scarce: the eruption and decline of *Poa pratensis* in grazed vegetation on Earnscleugh Station (Allen *et al*., 1995) may be one of the few documented instances of the pulse phenomenon in Central Otago.

Overlap between the models

Although I have contrasted the three models, there is in fact some overlap between them. For example, the difference between the succession and alternative stable states models is that in the latter, the vegetation will remain in one state for a considerable length of time (time-scales of one to several decades are considered appropriate in semi-arid grasslands, e.g. Westoby *et al*., 1989; Weigand and Milton, 1996) with some fluctuation around that state, whereas trends in succession will comprise steady movement towards the climax, with rapid reversals due to disturbance. Clements did envisage that succession could be stayed for a "long period" (Clements 1916 p 145), although it is not clear that he attributed this to resistance to change at particular points along the succession continuum.

Clementsian succession shares with annuation the concept that when the climate changes, the vegetation will change too. The difference is that the succession model distinguishes between change in two directions: continued succession when the climate becomes more mesic, versus the resetting of the vegetation to an earlier seral stage when the climate becomes less mesic. Annuation envisages that changes occur on the time scales down to single years, and that the direction of change is more unpredictable, but the distinction may be far from clear in a field situation.

The models I have described might be seen as components that may be used in constructing new models that more adequately fit observed data (Joyce, 1993), rather than as alternatives. One model that attempts to utilise and integrate some of the concepts is the Declining-productivity model of Milton, Dean, du Plessis and Seigfried (1994).

Model 4: The Declining-productivity model

The Declining-productivity model is a generalised model that is distilled from conceptual models of progressive desertification and productivity-reduction in semi-arid rangelands worldwide. The model comprises a sequence of retrogressive 'steps', and each step may comprise a number of vegetation 'states'. These are not alternative stable states, because they are not necessarily discrete, or stable, and it is envisaged that various cyclic process will occur within them (Milton *et al*., 1994). The model resembles the classical succession model in that it is essentially linear and invokes the same mechanisms: it supposes that the highest productivity is found in undisturbed vegetation, and that there is a loss of productivity in heavily grazed vegetation. Effective reversal of the steps of the model becomes more improbable as desertification progresses (Table 1).

I ask whether this model fits change in the vegetation of Central Otago, which has been described as "one of the most dramatic examples" of "severe land degradation resulting form the expansion of European-type farming overseas during the nineteenth century" (Mather, 1982). I use both historical and recent vegetation descriptions, and draw especially on the description of Flat Top Hill (Walker, Wilson and Mark, 1995), an area which lies close to the driest part of the region.

Step 0

Vegetation in Step 0 was suggested by Milton *et al*. (1994) to produce "maximal stable yield", or to sustain a "diverse indigenous fauna", while its species composition varied in response to climatic oscillations (Table 1).

It is unlikely that any Step 0 vegetation remains in Central Otago today. Clark *et al*. (1996) suggest

Table 1: *The step-wise Declining Productivity Model and symptoms recognisable in the present-day vegetation of Central Otago*

Step	Symptom	Central Otago Vegetation
0	Undisturbed state: diverse indigenous communities	Pre-Polynesian and/or pre-European vegetation, probably survived only until the late 1850s
1	Loss of palatable species, increase in unpalatable species	"Remnant" shrub and tussock vegetation, surviving in fire and herbivore-sheltered pockets
2	Reduced carrying capacity, low productivity vegetation	Most of Central Otago today: species-poor "scabweed" and grassland communities
3	Perennial plants lost, annuals and year-to-year fluctuations increase	Local areas of ephemeral vegetation, e.g. Flat Top Hill and on saline soils throughout Central Otago
4	Complete denudation: bare ground, erosion, aridification	Not extensive: patches on exposed ridge crests and in saline areas

that a complex vegetation mosaic, supporting a rich fauna, was destroyed by fire early in the Polynesian settlement of Central Otago, around 800 years ago. Following European settlement in 1857, large areas of the resulting native shrubland were cleared by burning to make way for pasture (O'Connor, 1986), and many grasses (e.g. *Trisetum*, *Rytidosperma* and *Agrostis* spp.) and palatable herbs (e.g. *Gingidia* and *Anisotome* spp.) were rapidly reduced to scarcity, leaving only three species (the tussock grasses *Festuca novae-zelandiae*, *Poa cita* and *Elymus apricus*) to account for much of the vegetation cover of the area (Buchanan, 1868, 1880; Petrie, 1912).

Step 1

The age structure of plant populations is altered in this step, as the recruitment of palatable species is reduced and unpalatable components of the vegetation increase (Milton *et al.*, 1994).

There are several anecdotal records of a decrease in finer, matrix species, and the increased dominance of less palatable tussock growth forms, in Central Otago grasslands over the decades following pastoral establishment (e.g. Buchanan, 1868, 1880; Petrie, 1912; Cockayne, 1921). The hard tussock *Festuca novae-zelandiae* became "by far the most abundant grass" in the driest areas between 1875 and 1894 (Petrie, 1912), while there was a substantial decline in the more palatable *Elymus apricus*, which had survived the initial round of elimination (Wardle, 1985).

In Central Otago, 'Step 1' vegetation presently exists in sites protected from grazing and fire, such as in gully-bottoms or around rock outcrops, and has been loosely described as 'remnant'. Three such communities have been described on Flat Top Hill (Communities I, J and K - Walker *et al.* 1995). They comprise relatively species-rich communities, dominated by native tussock species (*Festuca novae-zelandiae* or *Poa cita*) or retaining native shrubs such as *Discaria toumatou*, *Olearia*, *Coprosma* and *Carmichaelia* spp., which were listed as present in the early-European vegetation by Buchanan (1868). Similar communities to those described by Cockayne (1921) as "remnant shrubland" have been documented in the Kawarau Gorge by Partridge *et al.* (1991), and Hubbard and Wilson (1988) described "remnants of *Kunzea ericoides* woodland" along the Clutha River. Wilson *et al.* (1989) referred to native shrub species in the Luggate area as "relics".

Step 2

The second step of desertification in the Declining-productivity model is caused by chronic grazing: plant cover becomes depleted, and this leads to soil surface crusting and reduced rainfall infiltration.

Petrie (1883, 1912) and Cockayne (1910) described this sequence of events relatively early in Central Otago, while McQueen and Hewitt (un prep.) recently confirmed by measurement that these soil changes have occurred.

According to the model, species diversity and ecosystem productivity are reduced in this step, leading to a diminished stock-carrying capacity.

The simultaneous loss of native pasture species and levelling off of stock numbers that occurred in New Zealand's semi-arid grasslands in the 1870s (Buchanan, 1868; Petrie, 1883, 1912; O'Connor, 1982) clearly match these criteria. The early literature holds many reports of decreasing species diversity, and of the replacement of grassland by xerophytic native species, such as *Raoulia* spp., *Colobanthus brevisepalus*, *Poa maniototo* and *Stellaria gracilenta*, forming "induced steppe" (Cockayne, 1919; 1920; 1921), "semi-desert" (Zotov, 1938) or "*Raoulia* deserts" (Petrie, 1883; 1912).

Vegetation that has undergone a transition to 'Step 2' today covers most of undeveloped lowland

Central Otago: plant cover has been reduced to occasional tussocks of native grasses and sparse, low-growing and mainly unpalatable herbs. Much of the vegetation of Flat Top Hill (Communities C to I - Walker *et al.*, 1995) falls into this category. Early development of 'Step-2' vegetation on Flat Top Hill might be represented by Community H, where native grasses have been replaced by the exotic grasses *Anthoxanthum odoratum* and *Festuca rubra*, the unpalatable *Sedum acre*, sub-shrubs of *Thymus vulgaris* and occasional mats of the native *Raoulia australis*. More advanced stages may be mixtures of *Sedum acre* and mat-forming xerophytes (Community C) or near-monocultures of *T. vulgaris* (Communities F and G). Most of the communities described by Hubbard and Wilson (1988) (Communities C to G) and Wilson *et al.* (1989) (Formations A and B), also fit the criteria of Step 2 vegetation. However only one 'Step 2' community (Community XIII) has been described in the more mesic Kawarau Gorge (Partridge *et al.* 1991).

Petrie (1912) stated the opinion, shared by Milton *et al.* (1994), that reversal of degradation at this stage is unlikely to be achievable, and that it would involve the removal of all herbivores as well as vegetation manipulation (e.g. reseeding).

Step 3

The third step in the Declining-productivity model incorporates accelerated erosion and increasingly extreme fluctuations of temperature at the soil surface.

The former was described by Petrie (1883) and Cockayne (1910), while the latter was confirmed, along a present-day degradation sequence in Central Otago, by Hewitt (1996) and McQueen and Hewitt (un prep.).

A decrease in perennial plant cover occurs in this step, accompanied by an increase in ephemeral and short-lived weedy species.

Cockayne (1921, 1922) first described a "vernal florula" in Central Otago, with ephemerals germinating in transient spring moisture amid a "desert-like" vegetation of *Raoulia* species and much bare ground.

Vegetation similar to that described by Cockayne (op cit.) - a sparse, species-poor mixture of ephemerals, annuals and short-lived perennials, and a component of unpalatable native perennials - occurs today on Flat Top Hill (Communities A and B, Walker *et al.*, 1995) but is restricted to sunny, heavily rabbit-grazed areas that are exposed to desiccating winds. The presence of senescent *Raoulia australis* cushions, suggests that these communities may have been induced by continued grazing from 'Step 2' type vegetation. Similar vegetation, with a component of spring annual species, is described by Hubbard and Wilson (1988) as Community H.

Step 4

The fourth step of the Declining-productivity model involves complete denudation of the soil, accelerated erosion, and salinisation. Although Petrie (1912) and Zotov (1938) claimed that the soil was rarely completely stripped of vegetation in Central Otago, even following severe overgrazing, Cockayne (1919, 1922) described a "final stage of depletion" on the Dunstan Mountains, "the scabweed having been eroded and blown away" leaving "desert pure and simple" following the death of the *Raoulia* cushions. Although 'Step 4' vegetation is not represented in other recent published descriptions, small patches of completely bare soil occur on Flat Top Hill, where scabweed has been abraded on exposed ridge crests and saline toeslopes (Walker *et al.*, 1995).

A declining-productivity gradient in Central Otago

The first two component axes of the a DCA ordination of the vegetation of Flat Top Hill (eigenvalues 0.642 and 0.489) are related to soil moisture and soil depth, respectively (Walker *et al.*, 1995). However the third component axis (which also represents considerable variation: eigenvalue 0.424) represents a gradient from sheltered, herbivore and fire-protected sites with relatively moist soils and high native and total species-richness on the left, to open, sparsely-vegetated, heavily rabbit-grazed and species-poor habitats on the right, i.e. a degradation gradient. When the plant communities of Flat Top Hill are categorised according to the criteria of the Declining-productivity model, the three steps appear in order along the third axis, showing a convincing fit with the model (Fig. 4).

Most of the points on the ordination plot are clustered, and there is considerable overlap between steps, suggesting that the steps are not discrete (Fig. 4). One prominent discontinuity occurs at the extreme right of the third axis, between the Step 3 samples of Community A (extremely sparse vegetation which occurs in particularly disturbed, dry sites), and Community B (which occupies dry and saline sites) (Walker *et al.*, 1995). Disturbance by rabbit grazing has been substantially reduced on Flat Top Hill since sampling was carried out in 1994. Monitoring of the vegetation following the reduction of grazing might indicate whether

Community A recovers to a state more similar Community B, or whether this gap represents a threshold, with ‘domains of attraction’ on either side, as envisaged by Friedel (1991).

Discussion

The current state of knowledge of vegetation dynamics in Central Otago

It may take several decades for vegetation trends to become apparent in semi-arid grasslands (Jones, Jones and McDonald, 1995; Weigand and Milton, 1996). Central Otago has been poorly studied, compared with semi-arid rangelands overseas: reliable records from fenced exclosure plots extend back only 10 years, and our knowledge of historical change relies heavily upon anecdotal accounts. This appraisal of semi-arid Central Otago in relation to current theories of vegetation dynamics is therefore preliminary and tentative.

There is some evidence from Central Otago for vegetation dynamics corresponding with the concepts of Clementsian succession and with annuation/pulse dynamics. However, there is as yet no quantitative evidence that alternative stable states exist in the present vegetation, and it has been disputed whether the vegetation has reached equilibrium since European settlement. Changes in the vegetation over the last 150 years correspond with Milton’s (1994) Declining-productivity model, and steps of the model are represented along degradation gradients in parts of the region today.

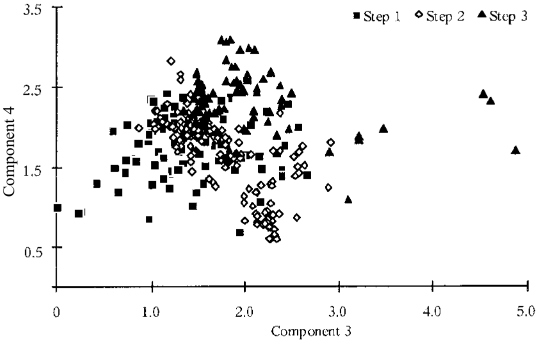

Figure 4: *Distribution of vegetation samples along the third and fourth components axes of the Detrended Correspondence Analysis ordination of the vegetation of Flat Top Hill (Walker* et al. *1995). The third axis was identified as a degradation gradient. The different symbols are assigned to vegetation conforming to the features described in the first three steps in the Declining-productivity model of Milton* et al. *(1994). Axis units are standard deviations.*

Can we apply management frameworks for semi-arid lands to Central Otago?

Sustainable management of grazed semi-arid regions requires the organisation of theoretical knowledge of vegetation processes within an appropriate framework. Two such frameworks for the management of semi-arid vegetation are degradation gradient assessment and the state-and-transition model.

Bosch and Kellner (1991) describe the use of degradation gradients as a basis for condition assessments in rangelands. In their method, multivariate ordination is used to arrange vegetation samples along a gradient, which they interpret as a gradient of degradation, employing a technique similar to that used above for Flat Top Hill (Walker *et al.*, 1995; Fig. 4). Processes along the gradient resemble those proposed by Milton *et al.* (1994) (Table 1). The movement of sites along the gradient over time, combined with specific information on management variables at each site, should enable thresholds and stable states to be identified, and could provide managers with information about the recovery potential of the vegetation and its response to events. However, with the possible exception of the small area of Flat Top Hill, the number and distribution of long-term monitoring sites in Central Otago is presently inadequate to provide the data required for this method.

The ‘state-and-transition’ model (Westoby *et al.*, 1989) resembles Sutherland’s (1974) concept of alternative stable states, in that rangelands are perceived as a set of alternative states separated by transitions (Fig. 5). However, the model claims not to follow from theoretical models of dynamics, but to offer merely “a practicable way to organise information for management”. Under the state-and-transition model, states are distinguished on management criteria, and may be ‘persistent’ (within a management-meaningful time frame of up to several decades) rather than formally stable. Any critical point in the vegetation composition, at which management or climatic intervention may cause particular outcomes, may be also regarded as a state, so that the ball and trough analogy does not necessarily apply to this model. Transitions between different states are triggered either by rare natural events, or by management actions, or a combination of both, and, as with alternative stable states, the transitions are not necessarily reversible.

management, or both.

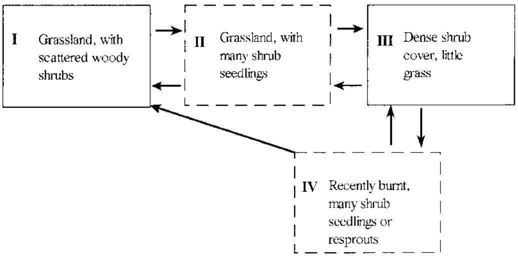

Figure 5: *A state-and-transition model diagram for a hypothetical grassland, which envisages vegetation as a set of states (represented by boxes: solid lines are persistent states, broken lines are transient states), separated by abrupt transitions (arrows), which may be triggered by natural events or management, or both.*

The state-and-transition model requires that knowledge about a given rangeland should be organised into a catalogue of possible alternative states of the system, with a catalogue of possible transitions from one state to another, and a catalogue of opportunities and hazards (Westoby *et al.*, 1989). Opportunities are climatic circumstances under which a particular management action (e.g. fire, modification of stocking rate) will produce a favourable transition, while hazards are circumstances under which actions could produce unfavourable transitions.

Although we have some idea of the broad states in Central Otago vegetation that result from degradation (see Model 4), there has been no coordinated attempt so far to catalogue the different states and transitions upon management criteria, nor have the opportunities and hazards faced by land managers been documented.

It is therefore clear that present data on vegetation dynamics in Central Otago are insufficient for the employment of these two management frameworks.

References

Allan, H.H. 1961. *Flora of New Zealand. Volume I.* Government Printer, Wellington, New Zealand. 1085 pp.

Allen, R.B. 1993. An appraisal of monitoring studies in the South Island tussock grasslands, New Zealand. *New Zealand Journal of Ecology 17:* 61-63.

Allen, R.B.; Wilson, J.B.; Mason, C.R. 1995. Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago. *Journal of Vegetation Science 6:* 615-626.

Anderson, A. 1991. The chronology of colonisation in New Zealand. *Antiquity 65:* 765-795.

Bartolome, J.W. 1989. Local, temporal and spatial structure. *In:* Huenneke, L.F.; Mooney, H. (Editors), *Grassland structure and function: California Annual Grassland*, pp. 73-80. Kluwer Academic Publishers, Dordrecht, Netherlands.

Beattie, H. 1947. *The pioneers explore Otago.* Otago Daily Times and Witness Newspapers, Dunedin, New Zealand. 160 pp.

Bosch, O.J.H; Kellner, K. 1991. The use of a degradation gradient for the ecological interpretation of condition assessments in the western grassland biome of Southern Africa. *Journal of Arid Environments 44:* 21-29.

Buchanan, J. 1868. Sketch of the botany of Otago. *Transactions of the New Zealand Institute 1(III):* 22-53.

Buchanan, J. 1880. *Manual of the indigenous grasses of New Zealand.* New Zealand Geological Survey Department, Wellington, New Zealand. 165 pp and 62 plates.

Cheeseman, T.F. 1925. *Manual of the New Zealand Flora.* 2nd Edition. Government Printer, Wellington, New Zealand. 1163 pp.

Clark, G.R.; Petchey, P.; McGlone M.S.; Bristow, P. 1996. Faunal and floral remains from Earnscleugh Cave, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand 26:* 363-380.

Clements, F.E. 1916. *Plant succession.* Publication 242, Carnegie Institute, Washington, U.S.A. 52 pp.

Clements, F.E. 1934. The relict method in dynamic ecology. *Journal of Ecology 22:* 39-68.

Cockayne, A.H. 1910. The natural pastures of New Zealand. I. The effect of burning on tussock country. *Journal of the Department of Agriculture (New Zealand) 1:* 7-15.

Cockayne, L. 1919. An economic investigation of the montane tussock-grasslands of New Zealand. III. Notes on the depletion of the grassland. *New Zealand Journal of Agriculture 19:* 129-138.

Cockayne, L. 1920. An economic investigation of the montane tussock-grassland of New Zealand. V. Regeneration of the grassland after depletion. *New Zealand Journal of Agriculture 24:* 321-334.

Cockayne, L. 1921. *The Vegetation of New Zealand.* 1st Edition. Willhelm Engelmann, Leipzig, Germany. 364 pp.

Collins, S.J.; Bradford, J.A.; Sims, P.L. 1987. Succession and fluctuation in an *Artemisia* dominated grassland. *Vegetatio 73:* 89-99.

Connor, H.E. 1994. Indigenous New Zealand Triticeae: Gramineae. *New Zealand Journal of Botany 32:* 125-154.

Connor, H.E.; Edgar E. 1987. Name changes in the indigenous New Zealand Flora 1960-1980 and Nomina Nova IV, 1963-1986. *New Zealand Journal of Botany 25:* 115-170.

Coupland, R.T. 1974. Fluctuations in North American grassland vegetation. *In:* Knapp, R. (Editors), *Vegetation dynamics,* pp. 214-226. Junk, The Hague.

Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management 2:* 104-115.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Botanical Review 26:* 1-78.

Friedel, M.H. 1991. Range condition assessment and the concept of thresholds. A viewpoint. *Journal of Range Management 44:* 422-426.

Garnier, B.J. 1951. Thornthwaite's new system of climate classification in its application to New Zealand. *Transactions of the Royal Society of New Zealand 79:* 87-103.

Gibbs, H.S. 1980. *New Zealand Soils-An Introduction.* Oxford University Press, Wellington. 115 pp.

Grime, J.P.; Willis, A.J.; Hunt, R.; Dunnett, N.P. 1994. Climate-vegetation relationships in the Bilbury road verge experiments. *In:* Leigh, R.; Johnston, A.E. (Editors) *Long-term experiments in agricultural and ecological sciences*, pp. 271-285. CAB International, Wallingford, U.K.

Heady, H.F. 1975. *Rangeland Management.* McGraw-Hill, New York, U.S.A. 460 pp.

Hewitt, A. 1996. Estimating surface erosion using ^{137}Cs at a semi-arid site in Central Otago, New Zealand. *Journal of the Royal Society of New Zealand 26:* 107-118.

Houle, G.; Phillips, D.L. 1989. Seasonal and annual fluctuation in granite outcrop plant communities. *Vegetatio 80:* 25-35.

Hubbard, J.C.E.; Wilson, J.B. 1988. A survey of the lowland vegetation of the Upper Clutha District of Otago, New Zealand. *New Zealand Journal of Botany 26:* 21-35.

Jones, R.M.; Jones, R.J.; McDonald, C.K. 1995. Some advantages of long-term grazing trials, with particular reference to changes in botanical composition. *Australian Journal of Experimental Agriculture 35:* 1029-1038.

Joyce, L.A. 1993. The life cycle of the range condition concept. *Journal of Range Management 46:* 132-138.

King, W.McG. 1995 (Unpublished). *Native and exotic plant guilds in the Upper Clutha catchment, Central Otago*. PhD thesis, University of Otago, Dunedin, N.Z. 188 pp.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management 44:* 427-433.

McGlone, M.S. 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology 12 (Supplement):* 115-129.

Maunder, W.J. 1965. Climatic character. *In:* Lister, R.G.; Hargreaves, R.P. (Editors), *Central Otago*, pp. 46-68. New Zealand Geographical Society, Wellington, New Zealand.

Mather, A.S. 1982. The desertification of Central Otago, New Zealand. *Environmental Conservation 9:* 209-216.

May, R.M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature 269:* 471-477.

Milton, S.J.; Dean, W.R.J.; du Plessis, M. A.; Seigfried, W.R. 1994. A conceptual model of arid rangeland degradation: the escalating cost of declining productivity. *Bioscience 44:* 70-76.

Molloy, B.P.J.; Burrows, C.J.; Cox, J.E.; Johnston, J.A.; Wardle, P. 1963. Distribution of subfossil forest remains, eastern South Island, New Zealand. *New Zealand Journal of Botany 1:* 68-77.

Morgan, R.K. 1989. Thyme in the Central Otago Landscape. *In:* Kearsley, G.; Fitzharris, B. (Editors), *Southern Landscapes. Essays in honour of Bill Brockie and Ray Hargreaves*, pp. 213-232. Department of Geography, University of Otago, Dunedin, New Zealand.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology 63:* 459-481.

O'Connor, K.F. 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology 5:* 97 -107.

O'Connor, K.F. 1986. The influence of science on the use of tussock grasslands. *Tussock Grasslands and Mountain Lands Institute Review 43:* 15-78.

Parcell, J.C. 1951. Heart of the desert: being the history of the Cromwell and Bannockburn districts of Central Otago. Otago Centennial Historical Publications, Dunedin, New Zealand. 327 pp.

Partridge, T.R.; Allen, R.B.; Johnson, P.N.; Lee, W.G. 1991. Vegetation/environment relationships in lowland and montane vegetation of the Kawarau Gorge, Central Otago, New Zealand. *New Zealand Journal of Botany 29:* 295-310.

Peco, B. 1989. Modelling mediterranean pasture dynamics. V*egetatio 83:* 269-276.

Penfould, W.T. 1964. The relation of grazing to plant succession in the tallgrass prarie. *Journal of Range Management 17:* 256-260.

Petrie, D. 1883. Some effects of the rabbit pest. *New Zealand Journal of Science 1:* 412-414.

Petrie, D. 1912. Report on the grass denuded lands of Central Otago. *New Zealand Department of Agriculture, Industries and Commerce Bulletin 23.* Government Printer, Wellington, New Zealand. 16 pp.

Rabotnov, T.A. 1974. Differences between fluctuations and successions. *In:* Knapp, R. (Editor), *Vegetation dynamics*, pp. 16-25. Junk, The Hague.

Rice, B.; Westoby, M. 1978. Vegetative responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. *Journal of Range Management 31:* 28-34.

Sampson, A.W. 1919. Plant succession in relation to range management. *United States Department of Agriculture Bulletin 791.* Department of Agriculture, Washington, USA. 76 pp.

Silvertown, J. 1987. Ecological stability: a test case. *American Naturalist 130:* 807-810.

Silvertown, J.; Dodd, M.E.; McConway, K.; Potts J.; Crawley, M. 1994. Rainfall, biomass variation, and community composition in the Park Grass Experiment. *Ecology 75:* 2340-2347.

Sims, P.L.; Singh, J.S.; Lauenroth, W.K. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology 66:* 251-286.

Stace, C.A. 1991. *New flora of the British Isles.* Cambridge: Cambridge University Press, UK. 1266 pp.

Sutherland, J.P. 1974. Multiple stable points in natural communities. *American Naturalist 108:* 859-873.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review 38:* 55-94.

Walker, B.H. 1981. Is succession a viable concept in African savanna ecosystems? *In:* West, D.C.; Shugart, H.H.; Botkin, D.B. (Editors), *Forest succession: concepts and application*, pp. 431-447. Springer, New York, U.S.A.

Walker, B.H.; Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. *In:* Huntley, B.J.; Walker, B.H. (Editors), *Ecology of Tropical Savannahs*, pp. 556-590. Springer, Berlin, Germany.

Walker, B.H.; Ludwig, D.; Holling, C.S.; Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology 69:* 473-498.

Walker, S.; Wilson, J.B.; Mark, A.F. 1995. The vegetation of Flat Top Hill: A new reserve in semi-arid Central Otago. *New Zealand Journal of Ecology 19:* 175-194.

Wardle, P. 1985. Environmental influences on the vegetation of New Zealand. *New Zealand Journal of Botany 23:* 773-788.

Wardle, P. 1991. *Vegetation of New Zealand.* Cambridge: Cambridge University Press. 672 pp.

Watson, I.W.; Burnside, D.G.; Holm, A.McR. 1996. Event-driven or continuous; which is the better model for managers? *The Rangeland Journal 18:* 351-69.

Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988. *Flora of New Zealand. Volume IV.* Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand. 1365 pp.

Weigand, A.U.; Milton, S.J. 1996. Vegetation change in semi-arid communities - simulating probabilities and time scales. *Vegetatio 125:* 169-183.

Westoby, M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany 28:* 169-194.

Westoby, M.; Walker, B.H.; Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management 42:* 266-274.

Williams, P.A. 1980. *Vittadinia triloba* and *Rumex acetosella* communities in the semi-arid regions of the South Island. *New Zealand Journal of Ecology 3:* 13-22.

Wilson, J.B. 1989: Relations between native and exotic plant guilds in the upper Clutha, New Zealand. *Journal of Ecology 77:* 223-235.

Wilson, J.B.; Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research 23:* 263-336.

Wilson, J.B.; Williams, P.A.; Lee, W.G. 1989. Vegetation composition and segregation in relation to the environment at low altitudes in the Upper Clutha Basin, New Zealand. *New Zealand Journal of Ecology 12:* 103-116.

Zotov, V.D. 1938. Survey of the tussock grasslands of the South Island of New Zealand. *New Zealand Journal of Science and Technology 20:* 212-244.