



## VEGETATION: CONTINUUM OR DISCRETE STATES?

Brian Tunstall

### Abstract

Environmental legislation treats vegetation similarly to species when they have very different attributes. A key issue is whether vegetation forms discrete states, as with species, or a continuum. This issue is addressed by way vegetation survey results for central Queensland, central Sweden, and SW Queensland. The conservation implications of the conclusions are discussed.

### Introduction

Legislation on the conservation of biota initially addressed species and their environments. Recent legislation greatly expands the entities provided protection, often identifying intent to preserve. Vegetation is one such entity and it is treated similarly to species. It is assumed there are distinct forms of vegetation and, given the desire for preservation, that these forms are invariant over time. This attempt to preserve particular forms of vegetation has occurred without consideration of whether distinct forms of vegetation exist, and whether existing stands regarded as important can be preserved.

There is no logical basis for assigning attributes of species to the assemblages of species that comprise vegetation. The genetic base of species restricts the nature and speed of evolutionary change and this constraint does not arise with vegetation. Vegetation does not have the attributes of species other than being composed of individuals that eventually die. Addressing vegetation conservation requires addressing its characteristics rather than applying inapplicable criteria developed for species.

This equating of species with vegetation is not explicit in legislation as traditional vegetation descriptions usually identify discrete forms of plant communities. This has continued despite the failure of numerous attempts to statistically demonstrate their existence. The forms of plant communities identified using statistical analyses depend on how the vegetation was sampled and the weightings used in analysis.

Landscape based approaches to vegetation mapping identify relationships between discrete forms of plant communities and position in the landscape. While landscape related vegetation patterns undoubtedly exist the reliability of extrapolation of results has not been properly tested. The landscape approach to mapping has unknown reliability and, as with mapping of discrete forms of vegetation, the results vary with the practitioner.

The notion of the existence of distinct forms of vegetation similarly to species is usually linked with the successional theory of Clements (1916). While this theory has vegetation changing over time through seral stages, it centres on the premise that vegetation develops to a maximum (the climax) commensurate with the environment. Clements suggests there are distinct forms of vegetation that reflect stable and maximal levels of vegetation development.

The Clementsian theory was widely adopted and applied because of its simplicity and practicality. However, it was strongly questioned and commonly rejected by those conducting research. The alternate individualistic concept (Gleason 1927) has



vegetation changing in response to the environment. While undisputedly correct this addresses process but does not define outcomes. Theoretically a continuum of environment would produce a continuum of vegetation but this was not demonstrated. The continuum concept (McIntosh 1967, Whittaker 1975) explicitly suggests there should be an intergrade of vegetation along an environmental gradient; a continuum of vegetation in response to a continuum of environmental conditions.

Neither the theoretical considerations nor observations used in the development of the concepts resolve the issue of whether vegetation occurs as a continuum or discrete states. Even if vegetation does tend to a continuum there will be discrete states given disjuncts in the environment. That is, there must be a continuum in environment to be able to observe a continuum in vegetation. The difficulty lies in reliably identifying and characterising a continuum in environment.

These issues were addressed by Tunstall (1987). They are further addressed here providing new information on vegetation mapping and identifying general conservation implications. The issue of preservation is not addressed as it is impossible to maintain a constant form of vegetation. Even Clementsian theory invokes change through seral stages as temporal change is inevitable with biology. Moreover, results by Walker et al. 1981 and Tunstall (2007) demonstrate that vegetation does not remain at a stable maximum.

## **Vegetation Mapping SWBTA**

Results from vegetation mapping in the Shoalwater Bay Training Area (SWBTA) in central coastal Queensland are used to examine spatial relationships in largely undisturbed native vegetation. The 2,700 km<sup>2</sup> land area of SWBTA was heritage listed in the 1970s due to the condition of the native vegetation. It was previously grazed, firstly by sheep and then cattle, with 7% previously being cleared and around 50% selectively logged. Commercial grazing was removed in 1964, forestry in 1972, and feral livestock around 1990.

The vegetation is floristically complex with around 1000 vascular species. Most of the vegetation is in good condition and much is pristine. However, the mapped area includes some surrounding agricultural land much of which has been cleared and grazed by cattle.

The species diversity is associated with edaphic and climatic differences. The east west annual rainfall gradient from 1750 to 800 mm is large. The broad environments include coastal systems and western plains separated by a range. The coastal vegetation includes extensive mangroves and sand dune systems. The western vegetation is typically paperbark and/or eucalypt woodland.

Most soils are infertile but there are localised occurrences of reasonably fertile geologies. Pockets of broad leafed (rainforest) vegetation exist in the ranges and on coastal plains.

### **Mapping method**

The vegetation was mapped using numerical classification of a 1979 Landsat MSS image. The procedure involved generating a large number of classes and iteratively grouping classes taking account of spatial association and spectral similarity as well as class labels. Class labels describe the vegetation associated with classes and were identified through field observation.

The mapping was checked using ground and aerial observations. Numerous low level helicopter sorties were used to identify the form of vegetation in inaccessible locations, most initiated for other purposes but some conducted specifically for vegetation survey. Ground

observations were accurately matched to the satellite mapping pre the availability of GPS and georegistration of the image by transferring the satellite vegetation patterns to 1:25,000 colour aerial photography.

The analysis spanned more than 5 years from 1981 and involved the development of the co-occurrence statistic to incorporate spatial association in the analysis (Tunstall et al. 1984). The co-occurrence analysis derives a normalised probability of a pixel in class **i** occurring alongside one in class **j**. The **i - i** comparison indicates the cohesiveness of classes. The **i - j** comparison indicates the level of spatial association between different classes. The statistic is normalised to take account of the number of pixels in the classes.

The spatial associations between the 77 base classes across the entire mapped area identify that all classes were spatially coherent (Fig.1). All classes are distinct. It also identifies that most classes are only spatially associated (linked) with few other classes. Classes that are spectrally similar tend to be spatially associated.

A final 27 class classification was produced by aggregating the base classes (Fig. 2). This aggregation was zoned according to major environmental regions to eliminate the main ambiguities. The base classification differentiated different forms of vegetation within general environments such as hills, dry plains and wetlands but did not always discriminate between distinct vegetation forms in the different environments. For example, mangroves in littoral zone had the same spectral characteristics as *Lysicarpus* forest on the coastal plain and were associated with the same base classes.

The zones used to stratify the base classification were sand dunes, coastal plain, marine plain, ranges, and western plain. Different aggregations of classes were used for each zone.

### **Spatial associations on the western plains**

Results for the western plains are used to illustrate the nature of spatial associations between forms of vegetation. Most of the western plain is geologically reasonably uniform in being derived from Pyri Pyri Granite. Old marine sediments occur at the south (Wandilla Formation below Tilpal Creek). Recent sediments in the NW were associated with higher sea levels and Herbert Creek draining the Fitzroy River. The localised volcanic Pine Mountain occurs in the north

The spatial associations between the base and final classes are given in Fig. 3. The coloured boxes identifying the final classes encompass aggregated base classes and so identify the relationship between the base and final classifications.

The most open vegetation is grassland which links with paperbark woodland. In one direction (down) the paperbark woodland links with wet paperbark communities. In the other direction the sequence of vegetation is eucalypt / paperbark woodland, open eucalypt forest with paperbark, and dense or open eucalypt forest (Fig 4). That is, regionally there is a sequence from grassland through paperbark to eucalypt forest where paperbark is initially dominant and then forms an understory under eucalypts that decreases as the eucalypts increase.

While statistically discrete classes can be recognised, the results indicate that the vegetation tends to form a continuum. For drained areas the sequence is from grassland through increasing cover of paper bark to increasing cover of eucalypts, with the paperbarks decreasing as the eucalypts increase.

The results identify spatial relationships that occur across a region of around 1,000 square kilometres. The regional patterns relate to water supply by way of rainfall and drainage where

drainage is linked with fertility. Only a few localised patterns relate to the occurrence of more fertile parent materials (geology / lithology). The patterns are landscape related but at a number of scales.

The general floristic composition of the trees is 3 species of *Melaleuca* (*nervosa*, *viridiflora*, *leucodendra*), 14 species in the *Eucalyptus* – *Corymbia* – *Lophostemon* complex (*E tereticornis*, *E alba*, *E exerta*, *E tracyphloia*, *E populnea*, *E mollucana*, *E crebra*, *E tessellaris*, *E papuana*, *C intermedia*, *C polycarpa*, *C dichromophloia*, *L suaveolens*, *L conferta*), *Lysicarpus augustifolius* and *Allocasuarina leuhmanii*. The number of species allows for diverse combinations given the subtle variations in environments and wide overlap in environmental limits for the species.

Some combinations of species effectively do not occur. While some omissions relate to obvious environmental limits, as with eucalypts being intolerant to waterlogging, some are without obvious explanation. For example, *E populnea* and *E mollucana* effectively do not occur together despite occurring on similar soils in the same part of the landscape. Their occurrence in SWBTA is lithology related, and *E mollucana* tends to be associated with *C citriodora* on the hills and *E populnea* with *E crebra*. The only coexistence of *E populnea* and *E mollucana* observed in central Queensland was a small patch on recent sediments in the north west of the mapped area where *E populnea* was suppressed.

## Conclusions SWBTA

The vegetation mapping involved the identification of discrete vegetation classes and was needed to reduce the complexity to something that could be comprehended. While distinct classes were identified the spatial associations indicate a continuous spatial progression through classes. The results indicate that vegetation occurs as a continuum

An issue that arises with this conclusion is whether the result could derive from the analytical method. The classification is broad, the imagery has a nominal 80m pixel (sample area of 60 x 80m), and the pixels are serially correlated. However, the appropriate pixel size for woody vegetation is around 50m as the large size provides a reliable average. Also, while pixels are serially correlated the aggregated pixels in classes are not.

While the pixel size may be appropriate the regular grid imposed by the satellite imager results in some pixels being positioned on the overlap between vegetation forms. Pixels can be composed of a number of vegetation forms (mixed pixels or mixels) and this introduces a tendency to identify gradients rather than disjunct states. However, the classification identifies the existence of classes where the spatial links between pixels within classes is much stronger than between. The classes are statistically distinct.

While the classes are statistically distinct they are not homogeneous. The vegetation occurring within a class includes forms that occur in spatially linked classes. That is, a sequence of vegetation occurs within classes similarly to within the entire classification, as identified in Fig.3. While the method may have a bias towards identifying gradients it cannot identify gradients where they do not exist.

The broad classification does not include all vegetation forms that exist in the area. For example, while *Lysicarpus augustifolius* (budgeroo) generally co-occurs with eucalypts and paperbarks it can occur as monospecific stands. Within the study area this arose on a relict beach ridge previously associated with Herbert Creek. However, as for the mix of eucalypts and paperbarks, the composition of communities containing budgeroo comprises a continuum

from sparse individual to monospecific stands depending on the sandiness of the soil. There is no apparent basis for identifying that the occurrence of a gradient derives from the method.

### **Vegetation patterns with simple floristics**

Observations obtained in pine forests in central Sweden are reported in Tunstall and Torssell (2004b). The climate, while severe, has little gradient and recent glaciation has produced geologically and floristically simple systems. Most of the area is dominated by a single tree species *Pinus sylvestrus* growing on sandy soils, with spruce (*Picea abies*) and birch (*Betula alba*) being the only other tree species. Essentially only 6 understory 'species' occur under pines, lichen, moss, and the shrubs *Vaccinium myrtillus*, *Vaccinium vitis idaeus*, *Caluna vulgaris*, and *Rubus idaeus*

Sample sites were selected to encompass the full range of variation in vegetation. Results identify that, while there are limits to what is observed, within those limits there is a full spectrum of combinations (Fig 5). As the sampling was non-random the results cannot identify any tendency for the preferential occurrence of particular forms of vegetation but they do identify that all forms can occur.

The considerations of Clements centred on vegetation developing to a stable maximum commensurate with the environment. The temporal development of pine illustrates that, while there is a maximal level of development, it declines with time after it has been achieved. (Fig. 6). Moreover, the maximum is seldom achieved

While the coexisting species have distinct environmental preferences the vegetation does not develop into distinct forms or states as the physical environment contains gradations. Also, further gradations arise from the inevitable mortality of plants. The existence of a gradations in vegetation arises from the life cycle of plants as well as gradations in the environment.

### **Vegetation patterns in a Poplar Box Woodland**

Variations in the composition of vegetation within a poplar box woodland are identified by Tunstall & Torssell (2004a), and Tunstall & Reece (2005) show how these patterns affect tree recruitment. While these observations relate to part of a paddock rather than a region the results are equivalent to those for Sweden. The results identify there are limits to what vegetation can occur but within those limits most combinations can be observed (Figs. 7, 8). Even at a fine scale the vegetation represents a continuum.

### **Discussion**

There are limits to what vegetation can occur but within those limits most combinations are possible. Some associations are positive (dependency) and others negative (mutual exclusion) but, despite these associations, there are no distinct states or forms of vegetation as occur with species. Vegetation forms a continuum in relation to a continuum in environment where that situation is accentuated by succession depending on the life cycles of the component species.

The existence of a continuum of vegetation in relation to a continuum of environment does not preclude the existence of distinct spatial vegetation patterns. Abrupt spatial changes in forms of vegetation obviously exist but these are generally associated with abrupt changes in the environment. The issue is whether the forms of vegetation remain constant across gradients. The evidence is they do not.

Situations arise where there is little possibility of a gradational environment, as with the transition from the sea to land. Mangroves constitute a distinct form of vegetation with very little intergrade with other vegetation forms. Freshwater inundation and fire tend to produce distinct environments similar to saltwater inundation but they are much more variable. In Australia fire tends to produce a switch between sclerophyll and 'broad leaf' vegetation but intergrades in vegetation development are common.

Not all forms of vegetation by way of species combinations need occur even where the environment appears suitable, as illustrated by *E populnea* and *E. mollucana*. However, it appears that such dichotomies reflect disjunct differences in the environment. There is no opportunity for a gradational response.

### **Conservation implications**

Protecting a particular patch of vegetation is unsound and unlikely to be effective in the long term as vegetation naturally changes due to the inevitable death of plants. Maintaining vegetation depends on maintaining the environment

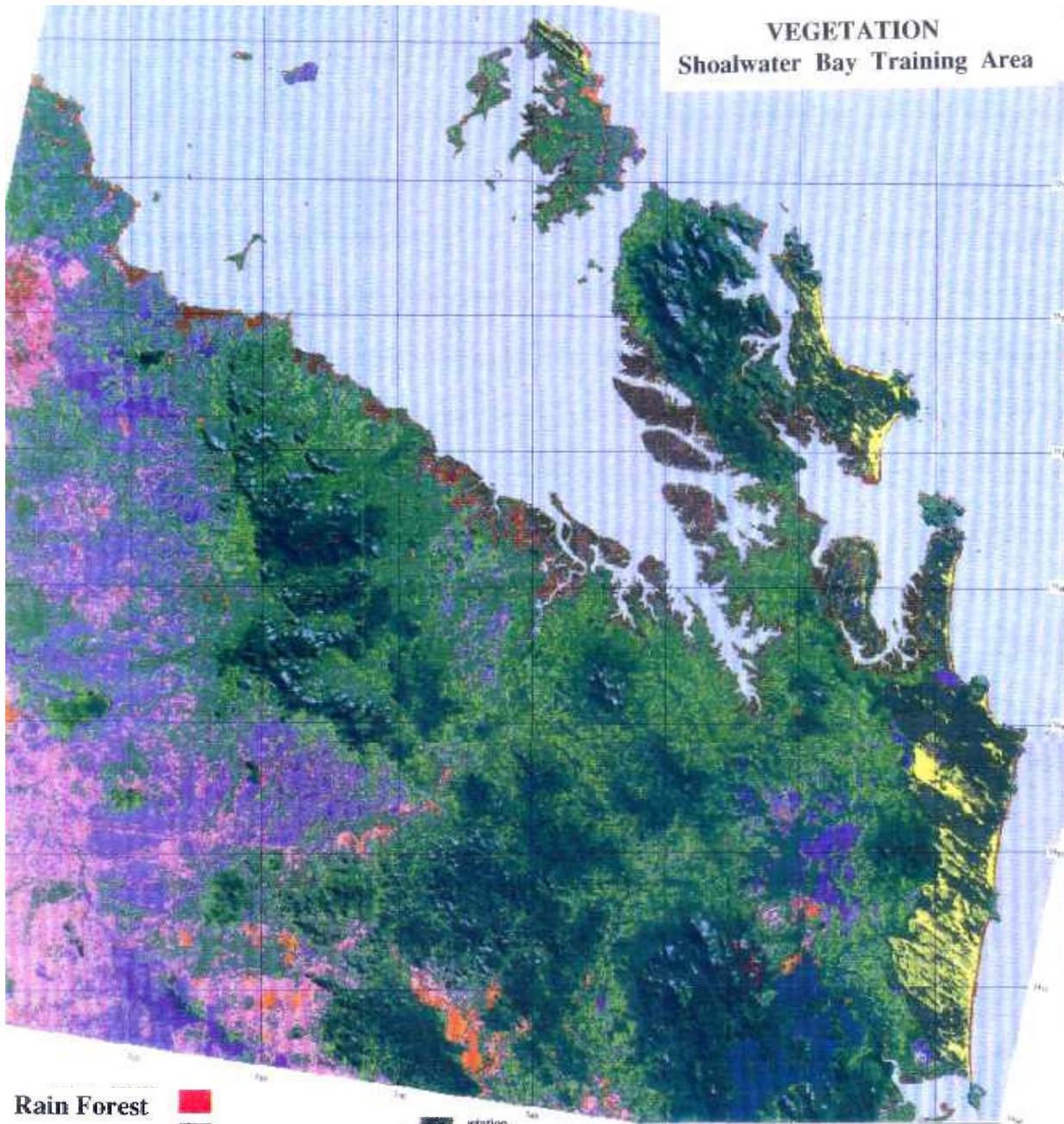
Managing the vegetation additionally involves taking account of the life cycles of the component species, the interactions between component plants, and the interactions between plants and the environment. Plants modify the physical environment, often strongly as with brigalow (Tunstall 2007).

Managing for sustainability involves managing for the future. For vegetation this involves addressing recruitment and not simply managing what is there. Addressing sustainable management of woodlands without addressing the recruitment of trees is not a viable option. Neither the precautionary principle nor any other such perverse generalisation can compensate for a lack of knowledge of how the systems function.

## References

- Clements, F.E. (1916) Plant succession. An analysis of the development of vegetation. Carnegie Inst. Washington Publ. 242. Washington D.C.
- Gleason, H.A. (1927) Further views on the succession-concept. *Ecol.* 8: 299-326.
- Whittaker, R.H. (1978). Direct gradient analysis. 2 nd. ed. In 'Ordination of Plant Communities'. (Ed. R.H. Whittaker). Junk, The Hague, pp 7-51.
- McIntosh, R.P. (1967) The continuum concept of vegetation. *Bot. Rev.* 33: 130-87.
- Tunstall, B.R. (1987) On the Relationship Between Vegetation Classification and Environmental Association. On [www.eric.com.au](http://www.eric.com.au) 16 pp.
- Tunstall, B.R. (2007) The Natural Development of Nutrients in Soils. On [www.eric.com.au](http://www.eric.com.au) 12 pp.
- Tunstall, B. R., Jupp, D. L. B. and Mayo, K. K. (1984) The use of co-occurrence in land cover classification for the investigation of ecological landscape patterns. In 'Landsat 84', Proc. 3rd Australasian Remote Sensing Conf., Gold Coast, Queensland, 147-54. (Organising Committee, Brisbane).
- Tunstall, B.R. & Reece, P.H. (2005) Tree Recruitment in a Poplar Box Woodland. On [www.eric.com.au](http://www.eric.com.au) 8 pp.
- Tunstall, B.R. and Torrsell, B. (2004a) An interpretation of spatial variability in vegetation in a *Eucalyptus populnea* woodland. On [www.eric.com.au](http://www.eric.com.au) 13 pp.
- Tunstall, B.R. & Torrsell, B. (2004b) Analysis of competition in spruce-pine-birch communities in Central Sweden. . On [www.eric.com.au](http://www.eric.com.au) 13 pp.
- Walker, J., Thompson, C. H., Fergus, I. F. and Tunstall, B. R. (1981) Plant succession and soil development in coastal dunes of subtropical eastern Australia. In *Forest Succession Concepts and Applications*, pp 107, 131. Eds. D. E. West, H. H. Shugart and D. B. Botkin. Springer-Verlag, New York.

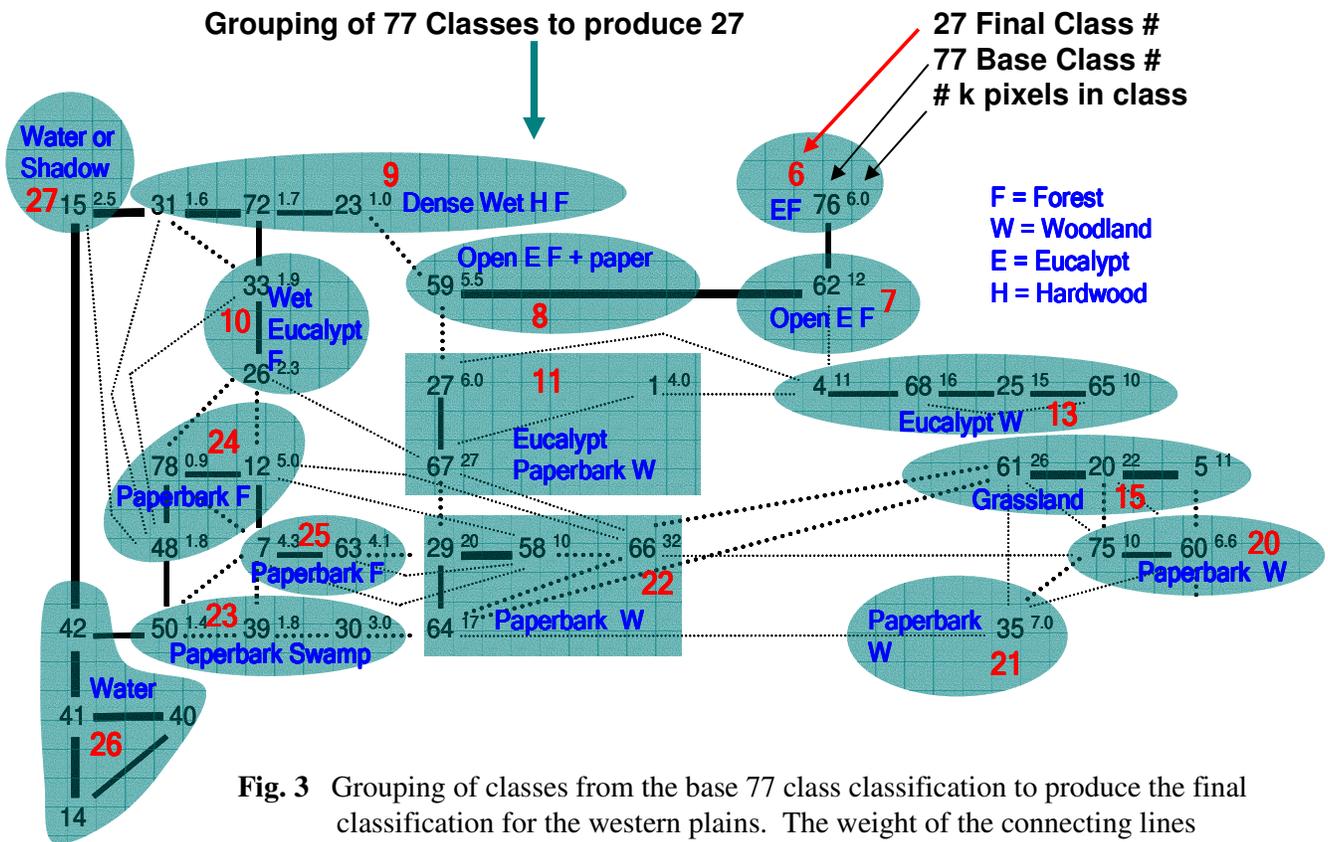




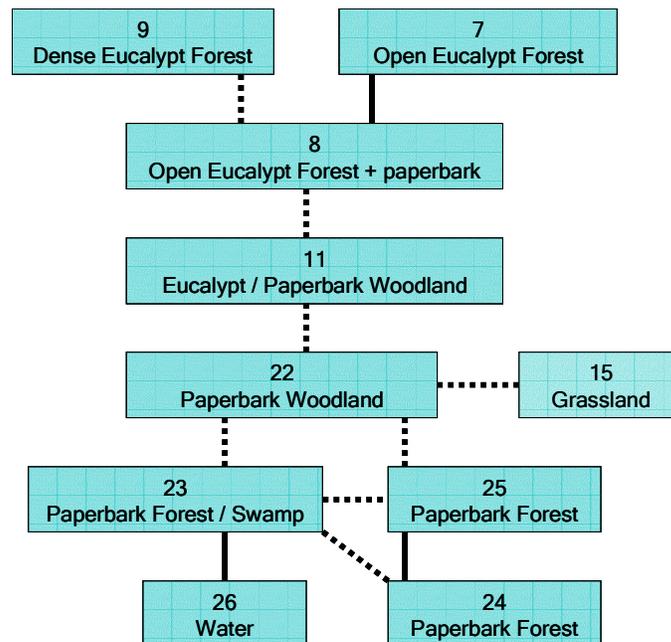
**VEGETATION**  
Shoalwater Bay Training Area



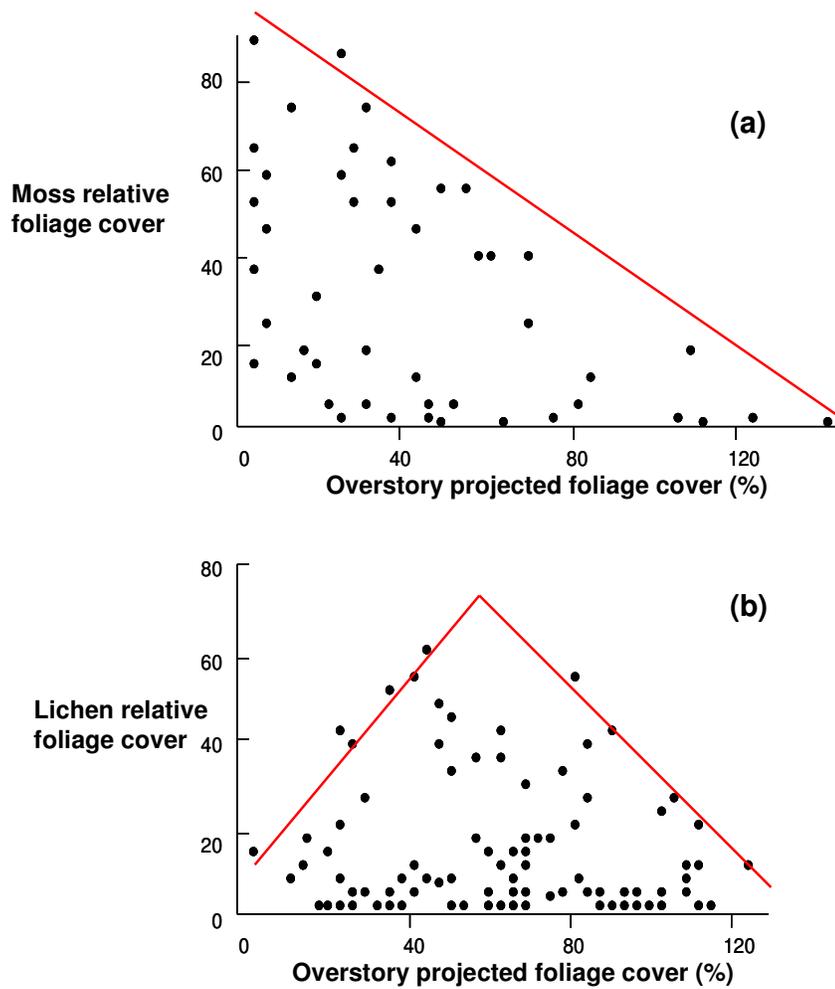
**Fig. 2** Final 27 class vegetation map for the Shoalwater Bay Training Area.



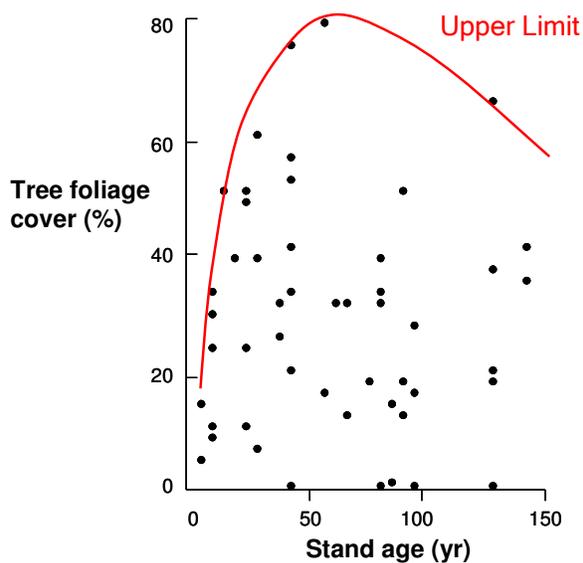
**Fig. 3** Grouping of classes from the base 77 class classification to produce the final classification for the western plains. The weight of the connecting lines indicates the strength of the spatial association.



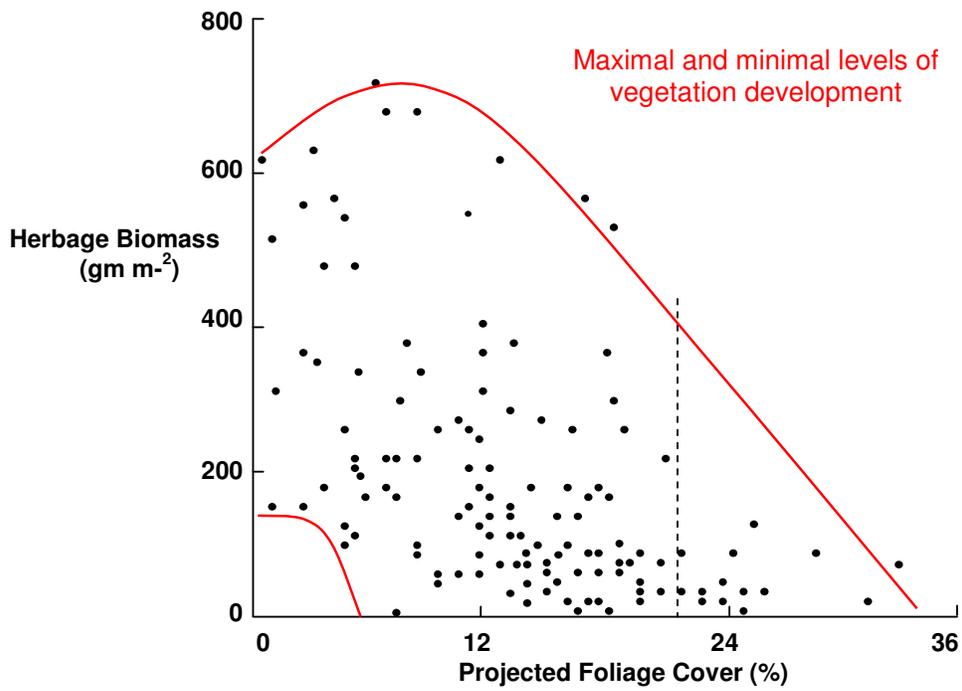
**Fig. 4** Summary of spatial associations between vegetation forms on the western plains.



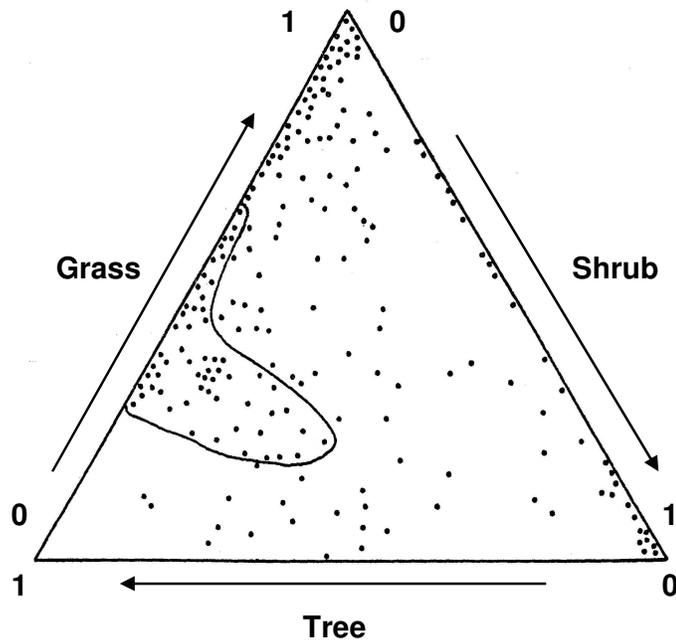
**Fig. 5** Relationships between the relative foliage cover of mosses and lichens and the cumulative projected foliage cover of all other components. Tunstall & Torrsell (2004b).  
 (a) Mosses (all systems)  
 (b) Lichens (pine systems)



**Fig. 6** Projected foliage cover of pine in relation to stand age. Tunstall & Torrsell (2004b).



**Fig. 7** Herbage biomass in relation to combined cover of the overstory vegetation. Tunstall & Torssell (2004a).



**Fig. 8** Relative abundance of tree, shrub and grass foliage in a poplar box woodland. Tunstall & Torssell (2004a).