

COMPONENT REPLACEMENT OF TREES, SHRUBS AND GRASS IN A POPLAR BOX WOODLAND INTERPRETED FROM THE SPATIAL VARIABILITY

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date

Abstract.

The relative amounts of foliage of the components of *Eucalyptus populnea* woodland systems were measured using rapid survey techniques. The systems were stratified into trees, shrubs, and grasses, with the shrubs further divided into *Acacia deanii*, *Cassia nemophila*, and others. The data were interpreted as points in a replacement series, however, analysis using plant population models was not readily possible because the requirement for mutual exclusion was not satisfied. This condition was attributed to incomplete resource utilisation rather than variation in resource availability. It is suggested that incomplete resource utilisation occurs through both insufficient germination/establishment and the natural cyclical development of the plant components. The inference is that in woodland systems environmental variation is confounded with temporal variation resulting in mean or average definitions of the systems being difficult to interpret as they do not represent states of full utilisation of resource.

Introduction

In the *Eucalyptus populnea* (poplar box) woodlands of south-western Queensland the trees are often killed by injection of chemical herbicides or removed by mechanical means to increase herbage production. This method of improving pastures has mainly relied on the growth of native grasses and has rarely been associated with either cropping or the introduction of exotic species. Grasses respond rapidly following killing of trees due to an increase in both water and nitrogen availability (Tunstall et al. 1979), but the subsequent growth of shrubs reduces herbage yields and generates problems in animal husbandry. Walker et al. (1972) demonstrate that for the first two years following tree killing the magnitude of the herbage response is strongly dependent on the level of tree thinning. Virtually all trees must be killed to obtain maximum herbage production. However, even after 10 years a shrub response, which was expected to follow the herbage response, could not be demonstrated (Torssell 1979).

This study was instigated to explain why after 10 years an expected shrub response to the thinning of trees could not be demonstrated. As the design of the initial experiment was derived from studies on crops and pastures, the objective of this study was to ascertain what aspects of the woodland system limited the usefulness of conventional statistical analyses. The approach used draws on concepts embodied in plant competition theory (de Wit 1960; van den Bergh 1968; Torssell and Nicholls 1976) and the results are interpreted in terms of plant succession (Clements 1916, 1936; Gleason 1917, 1926, 1927; Horn 1976; Connell and Slatyer 1977) and the related life cycles of the components of the vegetation (Harper 1977).

Methods

The experimental site was at the Wycanna Woodland Experiment Centre (lat. 28°50'S, long. 149°50'E) near Talwood in southern Queensland. The measurements were obtained during September 1977 in a woodland dominated by *Eucalyptus populnea* (poplar box) with 300-500

stems per hectare in natural stands. The soil was a red solodic and the area has an average annual rainfall of 500 mm which, while summer dominant, is highly variable.

The main experimental area was part of an earlier experiment initiated in June 1967 to investigate the responses of grasses, forbs and shrubs following tree killing without grazing. The experiment had a non-orthogonal replicated factorial design with the treatments of 0, 50, 90 and 100% trees killed by chemical injection, 100% shrubs, and 100% trees and shrubs killed. The plot size was 100 x 40 m. Parameters measured at roughly yearly intervals over 9 years were shrub, grass and forb density, and herbage (grass and forb) standing biomass. Grass and forb distribution were recorded in permanent quadrats. Some of the results were reported by Walker et al. (1972).

The treatments were imposed 10 years prior to this study when, as a consequence of both recruitment and growth of plants, the plots contained various proportions of trees, shrubs and grasses. Most results relate to this area, but additional observations were made in adjacent areas of the property to provide information on the regeneration of trees and the replacement of grass by shrubs. These latter data were not included in the primary analysis.

Within each of the 12 experimental plots, twelve 5 x 5 m plots were selected to encompass the full range of variation in vegetation. For recording the vegetation was divided into trees, shrubs, and herbage, and the shrubs subdivided into *Acacia deanii*, *Cassia nemophila*, and other shrubs. The only tree present was *Eucalyptus populnea* and *Eremophila mitchellii* was the main component of the 'other shrubs'.

The projected foliage cover of the components was measured as follows.

Trees. The crown ratio (the ratio of the distance between crowns to the diameter of crowns) and the percentage foliage cover of the crowns (100 - gap) were estimated (Walker and Hopkins in McDonald et al. 1984). These measures allow calculation of the projected foliage cover on a plot basis. To adjust the plot average for each sample a measure of effective basal area was taken from the centre of each quadrat. The mean basal area for the 12 samples within a plot was taken to equal the estimated projected foliage cover for that plot. For interpolation a yield - density curve (rectangular hyperbola, Torrsell and Nicholls 1976) was fitted to the points at 100, 50 and 0 tree thinning.

Shrubs. The product of estimates of the projected crown cover and projected cover of the crowns give an estimate of the projected cover for each element.

Grass. Visual estimates were obtained of grass height and percentage herbage basal cover. The product of these provided an estimate of herbage biomass which was evaluated by harvesting 20 quadrats, each 1.0 m x 0.75 m in size. The regression of best fit between estimated and measured herbage biomass accounted for 96 of the variance. For comparisons with the shrubs and trees only the basal cover estimates were used.

Because leaves are the main functional units of plants their leaf area provides a valid basis for comparisons between the different life forms. Projected cover was used in preference to absolute leaf area because of measurement difficulties associated with the latter. Confounding effects which preclude absolute comparisons arise mainly from variations in leaf angle and photosynthetic activity.

Results

When a species is grown in monoculture at varying densities the relationship between plant biomass and density at any time takes the form of a rectangular hyperbola (Torrsell and

Nicholls 1976). When two species are grown in mixtures at total densities large enough that the addition of another individual does not alter the total yield, the relationship between the yields of the components is usually linear or curvilinear and is statistically well-defined (Bergh 1968). The results of Walker et al. (1972), which characterize the herbage response following the thinning of trees in a poplar box woodland, illustrate that with experimental manipulation such results can be obtained in a natural system. The magnitude of the herbage response at any tree density varied with time, but for any sampling occasion a well-defined curvilinear relationship between herbage biomass and tree density was obtained.

The results presented in Fig. 1 are for one sampling occasion and are from the same plots as characterized by Walker et al. (1972), so although an edaphic gradient exists within the experiment this does not confound the comparison between the two sets of data. The differences between the data are that Walker et al. (1972) present treatment means for the first two years following the initiation of the experiment whereas the results in Fig. 1 are for 25 m² plots and were obtained 10 years following the tree killing.

The regression of best fit to the data in Fig. 1 accounts for 36 of the variance. As equal projected cover of trees and shrubs may have different effects on herbage, part of this variance may be due to the combining of these components in the calculation of the upper strata projected cover. From Figs 2a, b and c it can be seen that with disaggregation of the data using the model of Torssell and Nicholls (1976) does not reduce the variability, but there is an apparently greater suppression of herbage by *Cassia nemophila* than by *Acacia deanii* than by *Eucalyptus populnea*. Plant competition models such as those of Torssell and Nicholls (1976) and van den Bergh (1968) provide a means of analysing and summarising such interrelationships but these could not be successfully applied to this data because the requirement for mutual exclusion was not met. Such models require that the loss of one component be compensated for by an increase in another and so cannot accommodate the condition of virtually zero herbage at both low and high overstory projected covers.

In the initial experiment tree killing resulted in greater herbage biomass but there was no effect on grass density. The relationship between herbage biomass and grass density for selected sampling occasions is illustrated in Fig. 3. The data are presented as plot and not treatment means. The initial grass response is due to an increase in size of existing individuals (Fig. 3a, b). Maximum grass growth followed recruitment, but high herbage yields were not necessarily associated with low production (Fig. 3c). After four years there had been grass recruitment in all plots but there is considerable variation in density and little relationship between grass density and biomass (Fig. 3d). These data illustrate an independence between grass density and the amount of overstory vegetation (no effect of tree killing on grass density). Spatial variation in grass density did not preclude the characterisation of a herbage growth response following tree killing but there is spatial variation in the recruitment of grasses which appears independent of the environment (treatment and time).

An alternate means of presenting the data in Fig. 2 is in a three-dimensional replacement triangle (Fig. 4). Mutual exclusion between components is a basic requirement for such a presentation so the data are presented as relative contributions of the components in a mixture. As the relative yield of a component can be increased through an absolute increase or through a decrease in the magnitude of the other components (Fig. 1), care must be taken in the interpretation of such a figure, but valid generalisations can be made. Points are found in most areas of the triangle excepting around 100 trees. Poplar box cannot exclude all other components while monocultures of both shrubs and grasses do occur. The encircled points are from the undisturbed plots and therefore illustrate the relative proportions of the components

in the 'natural' woodland which, on the basis of projected cover, is approximately 30% herbage, 10% shrubs and 60% trees.

The balance between trees and grasses can be further illustrated using a replacement diagram (de Wit 1960). The data of Walker et al. (1972) characterise the contribution of grass relative to trees but only for relative tree contributions up to approximately 0.6. As the condition of 100% trees does not naturally occur the inference is that the relationship between grass and trees in the range of a relative tree contribution of 0.6 to 1 is of the form indicated in Fig. 5. The relationship for trees relative to grass (Fig. 5) is derived from this curve assuming a constant relative yield total of 1.

Fig. 3 illustrates the variation in the relative proportions of the tree, shrub and grass components in a number of experimental plots 10 years after treatments were applied. As the data from the undisturbed plots only occur in a small area of the triangle the disturbances have resulted in a wide range of proportions of trees, shrubs and herbage. Maximum grass biomass was recorded 2 - 4 years following treatment (Torssell 1979) and after 10 years there were areas of complete exclusion of herbage by shrubs. From poplar box trees which had regenerated from seed in these plots and in adjacent paddocks following the killing of trees the approximate time required for communities of box trees to attain maximum projected cover of foliage could be estimated. The times required for each component to reach such a maximum indicated in Fig. 6 are the approximate maximum and minimum values given adequate initial recruitment.

The estimates of relative proportions of the components given in Fig. 4 and summarised in Fig. 6 agree with those of Tunstall and Reece (2004) but the later results provide additional information. Tree recruitment occurs when the abundance of tree foliage is around 25% of the 'normal' level and this allows identification of the likely bounds to the relative abundances of trees, shrubs and grasses in intact woodlands. Observations in the external area, identified by the dotted lines, are associated with systems that have been impacted by clearing¹. These new observations extend the expected range of mixtures of trees, shrubs and grasses in intact woodlands.

The direction of successional change following disturbance is also illustrated in Fig. 6. This only indicates general direction and cannot be used to predict change at any given point. The sequence is from plants with the shorter to the longer life cycle. The change following tree killing of first grasses and then shrubs dominating is based on 10 years' observation of grass and shrub densities following tree killing (Torssell and Tunstall 1979). The change from shrubs to trees is based on general observation, with a woodland being the most common community in the area (Fig. 4).

Discussion

The objective of this study was to ascertain why an expected shrub response to the killing of trees was not obtained when a grass response had previously been demonstrated. The approach was to characterise the relative abundance of plants occurring in small, strongly interacting units rather than evaluate changes in terms of treatment means. The concept was that data characterising the relative abundance of species growing in mixtures could be analysed using techniques developed for studies on plant competition but success was limited

¹ The absolute level of shrubs appears to naturally remain reasonably constant hence the indicated increase in shrub abundance in Fig. 4 is an artifact of the assumed replacement in such a diagram.

because the requirement for mutual exclusion was not met. A reduction in the level of one plant component was not necessarily compensated for by an increase in another (Figs 1, 2).

In the past small-scale spatial variability in vegetation has usually been interpreted as a consequence of plant-plant interaction or a response to edaphic variation. Plant competition models are designed to analyse for plant interactions. As they were not applicable the conclusion would generally be that the observed spatial variability in the amount of vegetation (Fig. 1) is a result of edaphic variation. This would be difficult to demonstrate as in this system soil change can result from vegetation change (Tunstall and Walker 1975), and with survey data cause and effect cannot be separated. While edaphic variation exists the herbage response was characterised despite such variation and the results of other studies do not suggest a four-fold range in resource (water, nutrients, light, etc.) availability. It is unlikely that spatial variation in resource availability is of sufficient magnitude to generate the spatial variability in vegetation illustrated in Fig. 1.

If the variability in vegetation does not reflect variation in resource availability then the conclusion is that vegetation does not necessarily utilise all the available resource. The level of resource may set the limit to vegetation development but there is variation within this limit that is independent of resource availability. A basis for this can be seen in Fig. 3 which illustrates spatial variation in the recruitment of grasses which is essentially independent of the environment. Combining such environmentally independent and hence spatially variable recruitment in all vegetative components (trees, shrubs, grasses) with differences in development times (Fig. 6) and longevities, a wide range in the amount of vegetation can result. With perennials as with annuals the life cycles of the components, which within limits are relatively independent of environmental fluctuations, can generate variation in resource utilisation. With annuals this is mainly expressed as temporal variation but with perennials it is largely manifest as spatial variation.

In vegetation surveys the natural or existing native vegetation is frequently used as a measure of site potential. Vegetation is used to evaluate resource availability. While the physical system limits the development of vegetation these results suggest that this limit is rarely attained. With spatial variation in vegetation generated through plant life cycles an average or mean measure of vegetation within an area will always be less than the maximum the system can support. As the amount by which it is less is not known this generates problems in the analysis and interpretation of survey data. Aspects of this problem are discussed by Tunstall and Walker (1980).

Plant competition theory is largely based on agronomic experiments where uniform phasic development of the plants is ensured through planting all species at the one time under favourable conditions. With the herbage response following tree killing (Walker et al. 1972) the establishment of all treatments at one time established a temporal reference point, but even so there was large spatial variation in grass recruitment. It appears a herbage growth response was obtained because grass densities were not limiting and the development time for grasses is short. With shrubs and with the data collected here there is no time reference. In one area shrubs may be developing while adjacent shrubs are dying. Where shrubs die, even given establishment of grasses, it would be 2 to 4 years before the space is fully occupied (Fig. 6) and in this environment conditions favourable for grass establishment do not necessarily occur every year. Thus through variation in establishment and through the development times of the different components it is inevitable that over a large area not all the space will be fully occupied. The apparent lack of a shrub response therefore appears due to both insufficient recruitment and the long life cycle of this component.

As the requirement for mutual exclusion was not met. Figs 4 and 6 are technically incorrect. However, generalisations can be drawn which are not invalidated by the assumptions. The first is that where a community is disturbed without the addition or removal of resource the effect is to generate systems that reflect differences in time (time space equivalence). The second is that while at any time the exact temporal sequence of vegetation development cannot be predicted a general developmental sequence can be observed, the progression being from shorter to longer development times of the major component.

Conclusions

The descriptions of a woodland in terms of its variability rather than a mean state has demonstrated that the assumptions underlying agronomically based plant competition models currently limit application to woodlands. It is concluded that much of the spatial variability in vegetation in woodlands arises from the life cycles of the components and is thus equivalent to temporal variation. This leads to spatial variation in resource utilisation and the statement that plants occupy all available space must be modified to that plants tend to occupy the available space. This, combined with uncertain germination and establishment, means that the successional sequence at any point cannot be predicted and only general directions of, and times for, successional changes can be given. This uncertainty, which stems from lack of understanding of the demography of treed systems, leads to difficulties in interpreting mean or survey data on woodland systems.

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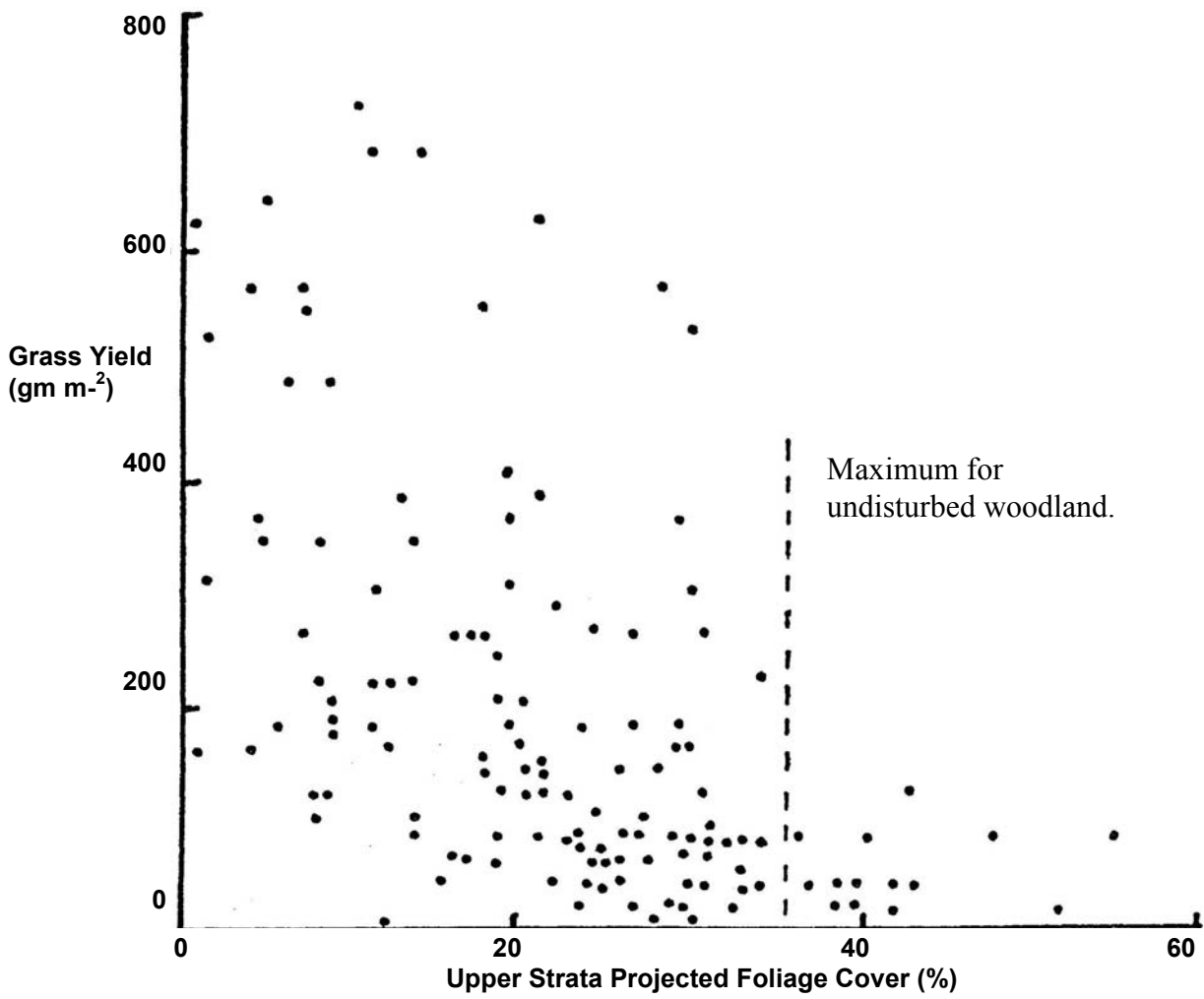


Fig. 1. The relative yield of grass versus the combined projected foliage cover of shrubs and trees in *Eucalyptus populnea* woodland systems.

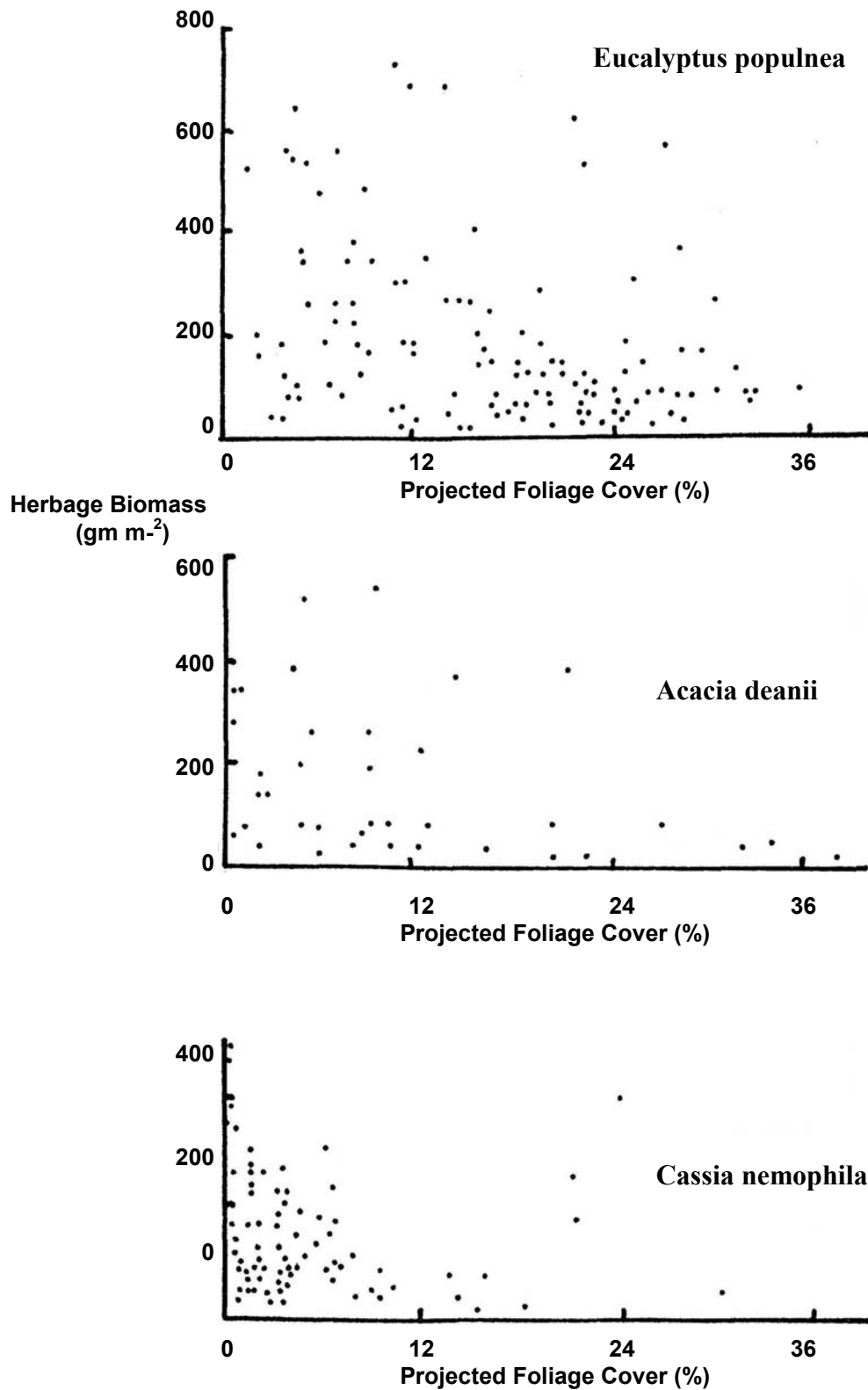


Fig. 2. The yield of herbage versus projected foliage cover trees (a); *Acacia deanii* and (b); *Cassia nemophila* (c) in *Eucalyptus populnea* woodland systems.

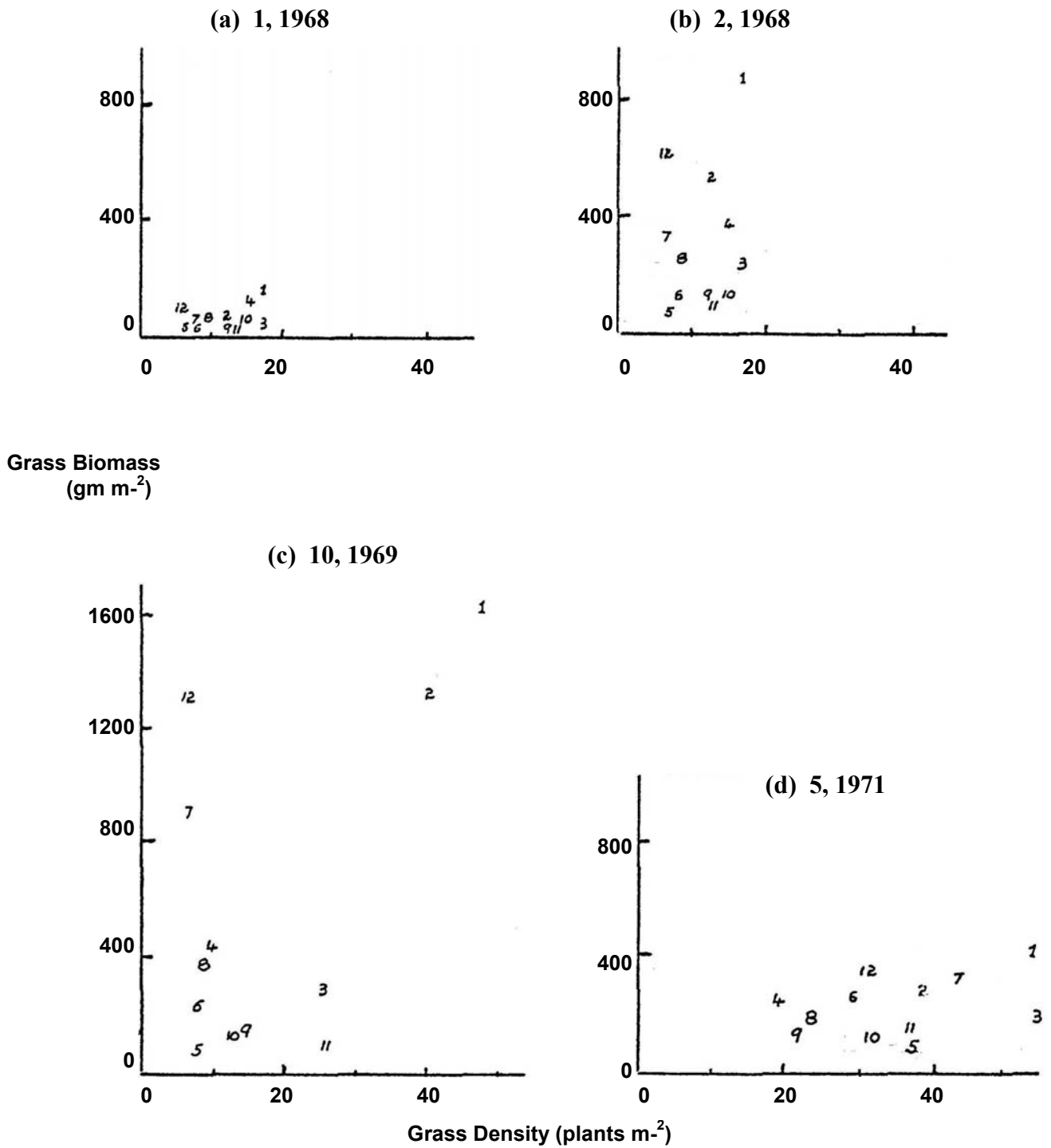


Fig. 3. The relationship between grass biomass and grass density in plots following the killing of different proportions of trees and shrubs.

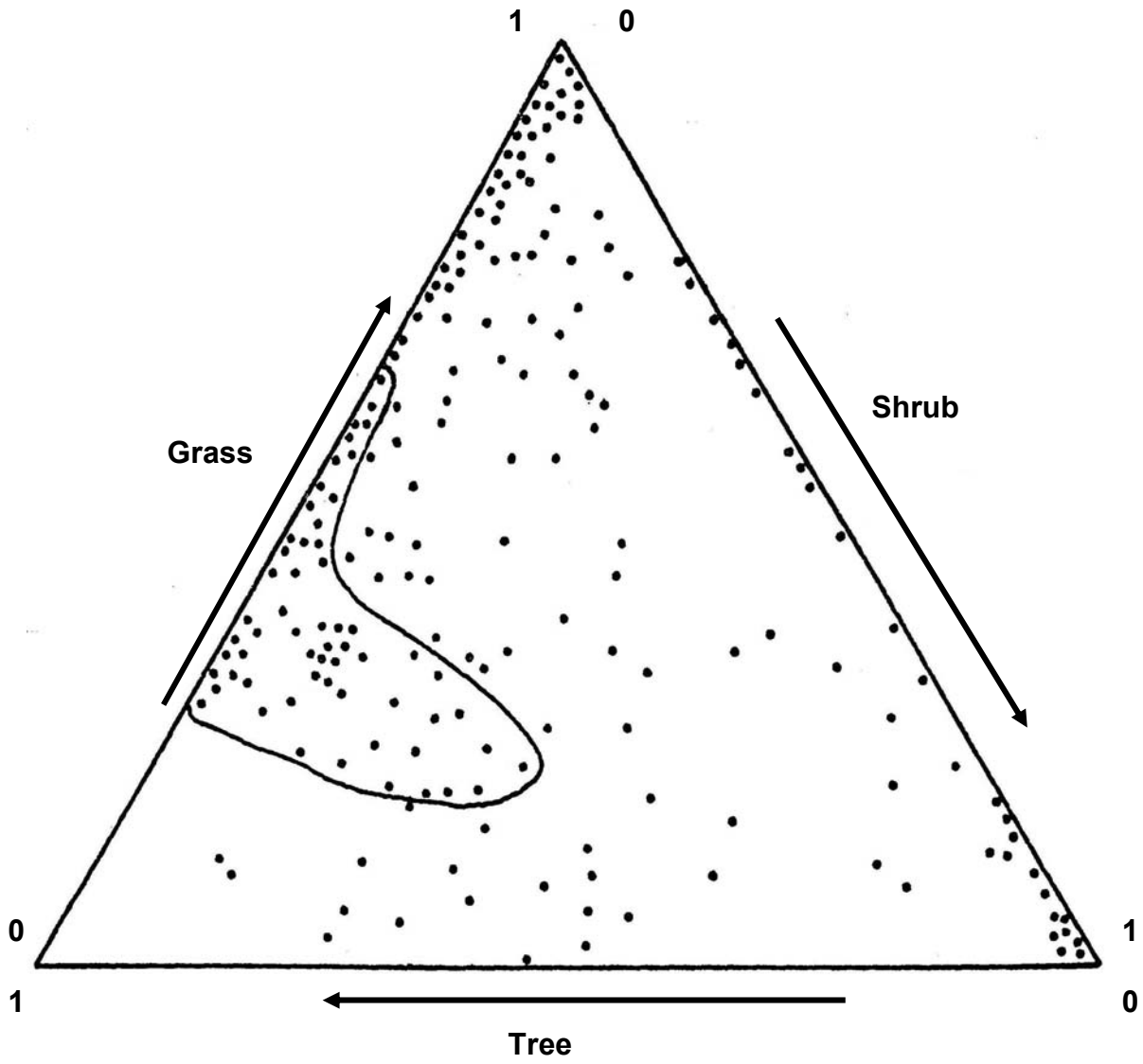


Fig. 4. The observed distribution between the projected foliage covers of the tree, shrub and grass components in *Eucalyptus populnea* woodland systems. Mutual exclusion assumed. All points for the undisturbed woodland lie within the delineated area.

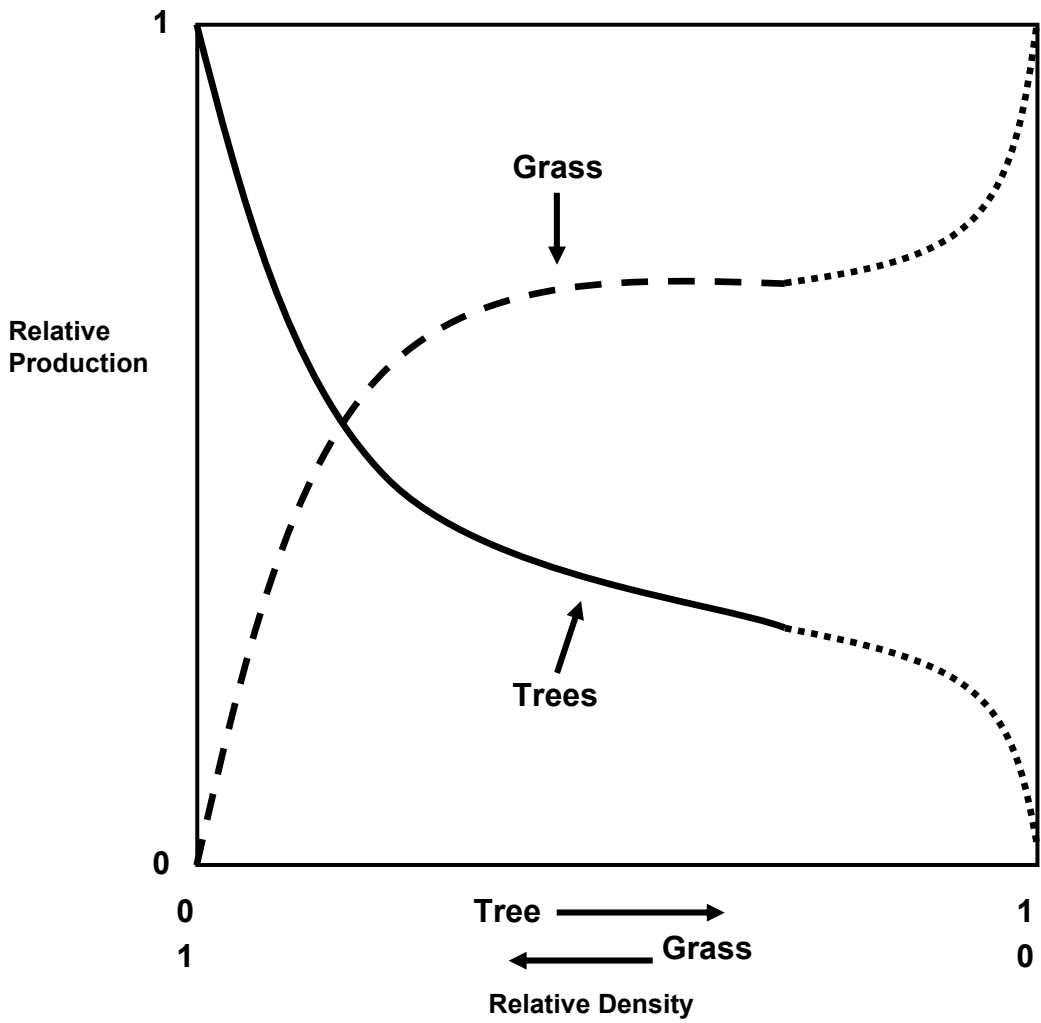


Fig. 5. A hypothetical replacement diagram for a *Eucalyptus populnea* -grass system with no shrubs.

- Field observation
- - - - - Inferred
- Not observable in the field

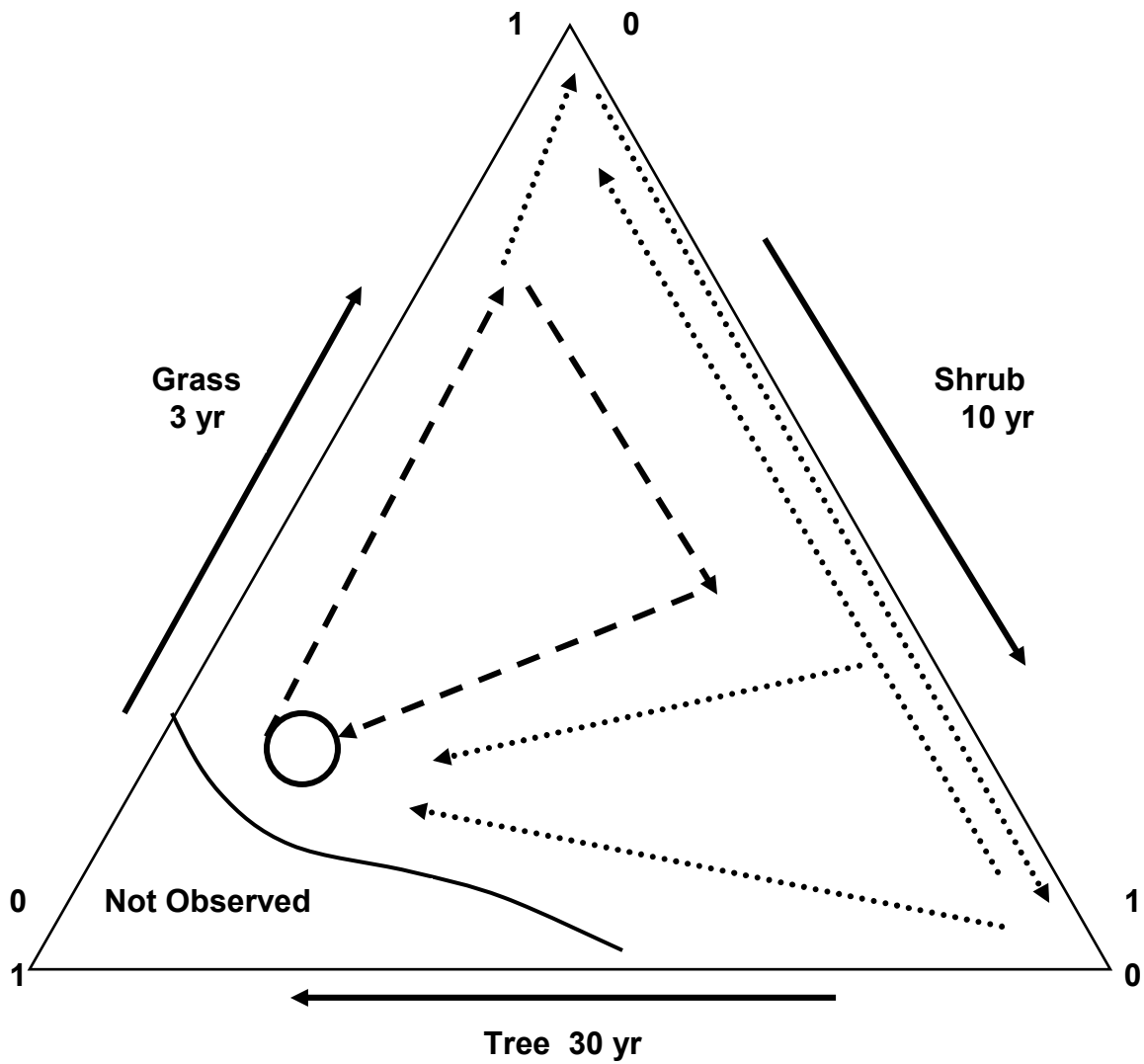


Fig. 6. Direction and approximate time scale for changes in the relative magnitude of projected foliage covers of the tree, shrub and grass components of a *Eucalyptus populnea* woodland.

- ▶ General bounds of natural change
-▶ Observed with clearing and grazing