

Use of Reciprocal Averaging Ordination for the Study of Range Condition Gradients

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Abstract

The use of a multivariate ordination procedure, Reciprocal Averaging, to study species responses to grazing along range condition gradients was investigated using both artificial and field data. Results suggest that the technique should be a useful aid in the elucidation of such responses and in the study of plant-environment relationships generally in grazed ecosystems.

The assessment of range condition and the manipulation of grazing pressure based on trend assessment demands a clear understanding of the role of individual species in the grazing-induced succession. Much of the relevant information currently available has been derived through observations made over long time periods in grazing trials, exclosures, or the landscape generally. This is essentially the "dynamic" approach to the study of ecological succession (Austin 1977). The alternative "static" approach seeks to understand successional changes by study of the ecosystem at one point in time over a set of sites which may be considered to represent a series of successional stages. Both approaches have advantages and disadvantages. Changes in ecological condition often occur slowly and may be masked by short-term seasonal fluctuations. The dynamic approach may thus yield useful information only in the long term. A major difficulty with the static approach, as Austin (1977) notes, is the uncertainty of whether a true succession rather than an environmental zonation is represented. Similar comment has been made by Daubenmire (1940).

Nevertheless, sites may be selected in the field across which habitat conditions are reasonably constant and within which floristic variation is associated mainly with prior grazing history. The study of such gradients can reveal useful insights into the role of species in the grazing-induced succession (e.g. Tueller and Blackburn 1974).

In the present study, the use of an ordination technique, Reciprocal Averaging (RA), to study range condition gradients is investigated on both artificial and field data. The use of RA ordination in this context is appealing since the mathematical model employed has affinities with the quantitative climax approach to range condition assessment (Dyksterhuis 1949) and thus conforms to the "psychological" model of range condition held by many ecologists.

Reciprocal Averaging as an Ordination Procedure

Reciprocal Averaging in its simplest form (Hill 1973) represents an extension of the "weighted averages" ordination of Whittaker (1956, 1960, 1967). In this procedure sites may be ranked along an environmental gradient on the basis of a score calculated as $q_i = (\sum_j x_{ij}s_j) / x_i$, where q_i represents the score of site i , s_j is a score assigned to species j based on its optimum position for growth in relation to the gradient, x_{ij} is the abundance of species j in the i th site, and x_i is the total of all species in the i th site.

From these "weighted averages", however, a new set of scores for species may be obtained, viz, $S_j = (\sum_i x_{ij}q_i) / x_j$ and these new species scores may in turn be used to derive a second set of site scores and so on. Hill (1973) has shown that if the derived scores are rescaled

to a fixed range (say 0-100) between successive iterations, this process will eventually stabilize to produce a unique one-dimensional ordination for both species and sites. If 0/1 data are used, the final site scores are averages of the scores of species they contain while species scores are averages of the scores for sites in which they occur, hence Reciprocal Averaging. A similar approach had earlier been suggested by Goff and Cottam (1967).

Although this procedure produces a unique set of scores for both sites and species (i.e., it produces simultaneous "dual ordinations"), other solutions also exist which possess the reciprocal averaging property and which may be ecologically informative. Hill (1973, 1974) and Hatheway (1971) have shown that the complete set of such solutions can be obtained by formulating RA as a eigenvector problem. Mathematical descriptions of this procedure may be found in the above papers and also in Hacker (1979, p. 171-184). In this form RA has distinct similarities to Principal Component Analysis (PCA). It may be considered a variant of PCA distinguished from more usual forms of this procedure by the use of noncentered data (as opposed to the usual species-centered approach of PCA), double standardisation of the original sites \times species matrix and a particular poststandardisation of eigenvectors to achieve the final scores. Further discussion of data centering and standardisation in PCA may be found in Noy-Meir (1970, 1974) and Noy-Meir et al. (1975).

Formulated in this way, RA has generally proved to be less sensitive to nonlinearity problems in ecological data than (unstandardised) PCA, thus producing more readily interpretable ordinations when axes are plotted in pair-wise fashion (Austin 1976, Fasham 1977, Gauch and Whittaker 1976, Gauch et al. 1977). As in PCA, axes are ordered on the basis of descending eigenvalues which provide a measure of the efficiency of each axis in summarising the information content of the original data.

From the eigenvector formulation of RA it may be easily shown that for any site i and species j , ordination scores on axis k may be represented as

$$q_{ik} = \frac{\sum_{j=1}^m x_{ij}s_{jk}}{\rho_k \sum_{j=1}^m x_{ij}} \quad \text{and} \quad s_{jk} = \frac{\sum_{i=1}^n x_{ij}q_{ik}}{\rho_k \sum_{i=1}^n x_{ij}}$$

where q_{ik} , s_{jk} and x_{ij} have their usual meanings and summations are over the n sites or m species in the sample. The term ρ represents the square root of the k th eigenvalue.

These formulae indicate that site scores are adjusted for site "richness" while species scores are adjusted for total species abundance. In the present context, this model implies that information concerning the range condition of a site resides primarily in its botanical composition rather than in the total amount of vegetation present while information regarding the response of species to grazing resides mainly in their distribution among sites rather than in their abundance.

Such a model has affinities with the quantitative climax approach to range condition assessment based on departure from climax in terms of relative floristic composition. It is likely to be inadequate, as is the quantitative climax method, in situations in which a reduction in absolute abundance rather than change in composition is the primary indicator of degradation.

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Development of the Model Data Sets

The RA procedure was tested on a series of artificial data sets designed to represent a particular range site in a series of condition states from ungrazed or excellent condition to very poor condition. Each data set consisted of 9 sites and either 10 or 15 species.

Consistent with the classification of Smith (1940) four types of species response to increasing grazing pressure were incorporated in the models. These were (a) a progressive decrease in abundance with grazing pressure, (b) a temporary increase followed by a decrease, (c) a progressive increase in abundance with grazing pressure, and (d) no response.

The models are thus based on the conventional decreaser, increaser, invader classification of range species (response types a, b, and c respectively) although species abundances are represented in absolute rather than relative terms. Poulton's (1959) division of both increaser and invader groups into type I and type II categories is not specifically reflected in the models. However, Poulton's divisions have their effective counterparts in responses (b) and (c) above.

Basic data for response types (a) and (c) were generated by a simple linear procedure; i.e., species abundance increased or decreased linearly across the range condition gradient. Basic data for response type (b) were generated on the basis of a linear rise to maximum abundance followed by a linear decline across the remainder of the gradient. The abundance of type (d) species remained unchanged across the gradient. Between-site heterogeneity in a sampled ecosystem was simulated by superimposing a degree of random variation on these basic data.

This approach was used to generate 2 series of model data sets. In Series 1, consisting of 8 data sets, no random variation between sites within a set was imposed. Each model thus represented 9 sites, spaced equidistant along a range condition gradient, across which floristic variation was associated only with the grazing effect. The mixture of species response types was varied between models.

In series 2, 4 of these original models were altered by the imposition of random variation. Each cell entry in the original site \times species matrix was allowed to increase, decrease, or remain unchanged, the probability of any outcome being set at 0.33. The magnitude of any change was determined as a random percentage on the range 0–20%. This series of models thus represented ecosystems with between-site heterogeneity, but in which such heterogeneity was small relative to the grazing effect.

In a third series, "pristine state" models incorporating between-site heterogeneity were generated first and grazing responses were imposed subsequently. Each model contained 6 decreasers, 2 increasers, 2 invaders, and 5 unresponsive species. Three levels of between-site heterogeneity were achieved by allowing each species to fluctuate, in the "pristine state" models, by 20, 30 or 40% of its maximum value. In developing the "pristine state" models, maximum and minimum values for each species were assigned at random to 2 of the 9 sites; and values for all other sites were then calculated by reducing the maximum value by a random percentage on the range 1–20, 1–30 or 1–40 for the 3 models developed. "Grazed" models were then developed from the "pristine state" models by imposing a fixed grazing trend based on the response forms described earlier but applied in percentage terms; e.g., the abundance of decreaser species declined linearly from 100% to 20% of the pristine state values across the gradient. Since invader species are not present in the pristine state models, data for these were taken direct from one of the models used in series 2. This set of 3 models thus represented ecosystems in which the effect of between-site heterogeneity on floristic composition became progressively more important relative to the effect of grazing. An example of one of the models analysed in this series, that for 40% between-site heterogeneity, is given in Table 1.

While all of the models analysed are extremely simple, and to some extent simplistic, they contain the basic response types that would be expected in ecosystems subjected to increasing degrees of grazing disturbance. To this extent they form a reasonable basis for

Table 1. Model data matrix for 40% between-site heterogeneity, series 3. Response types represented are (a) decreaser, (b) invader, (c) increaser, (d) unresponsive.

| | | Sites | | | | | | | | | |
|--|-----|-------|-----|-----|-----|-----|-----|-----|-----|---|----------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| | 124 | 162 | 96 | 126 | 72 | 71 | 80 | 44 | 31 | a | |
| | 120 | 113 | 72 | 96 | 88 | 74 | 60 | 42 | 27 | a | |
| | 102 | 114 | 67 | 88 | 83 | 54 | 56 | 39 | 19 | a | |
| | 55 | 65 | 38 | 55 | 41 | 27 | 32 | 19 | 14 | a | |
| | 102 | 124 | 82 | 117 | 91 | 66 | 68 | 32 | 28 | a | |
| | 85 | 78 | 53 | 58 | 40 | 51 | 44 | 26 | 21 | a | |
| | 0 | 9 | 20 | 32 | 38 | 58 | 60 | 76 | 78 | b | |
| | 0 | 24 | 45 | 60 | 86 | 85 | 100 | 140 | 134 | b | |
| | 126 | 147 | 117 | 209 | 180 | 133 | 128 | 59 | 47 | c | |
| | 59 | 90 | 70 | 80 | 102 | 79 | 72 | 37 | 28 | c | |
| | 45 | 55 | 42 | 65 | 43 | 48 | 70 | 66 | 44 | d | |
| | 106 | 90 | 69 | 104 | 81 | 74 | 115 | 91 | 95 | d | |
| | 93 | 114 | 90 | 141 | 138 | 119 | 150 | 134 | 96 | d | |
| | 79 | 77 | 54 | 70 | 54 | 57 | 90 | 81 | 62 | d | |
| | 170 | 180 | 120 | 128 | 184 | 136 | 200 | 184 | 166 | d | |
| | | | | | | | | | | | Good condition |
| | | | | | | | | | | | Poor condition |

preliminary testing of the procedure.

Results of Reciprocal Averaging Ordination of Model Data

Only the results for the third set of models will be illustrated in detail as these represent the most complex of the artificial data sets examined.

For the total of 12 data sets analysed in series 1 and 2 the first 2 axes in all cases provided a highly efficient summarisation of the original data matrix with a cumulative efficiency of at least 93%. In all cases the site ordinations produced by plotting axis 1 scores against axis 2 scores represented the gradient in the form of a distinct "arch" configuration (see Hill 1973, 1974) but despite this distortion the rank order of sites along the first axis conformed exactly with their range condition ranking except in one instance. This model was dominated by nonlinear, increaser responses (type b above) and although the first axis seriation was unsatisfactory, the ordering of sites around the "arch" was entirely consistent with their range condition so that "straightening" of the two dimensional configuration (see Noy-Meir 1974) would have produced an entirely satisfactory arrangement.

Species ordinations tended to reflect the general arched configuration of the site ordinations, but were characterized by the distinct clustering of species with identical grazing responses. Thus increaser, decreaser, invader and unresponsive species appeared as distinct groups in the ordination space. While the intensity of the clustering varied between models, depending on the particular mixture of response types present, groups were always clearly separated and defined.

Site and species ordinations in the plane of the first 2 axes are presented in Figure 1 for the models analysed in series 3. In all cases, the data summarisation provided by these axes was highly efficient, cumulative efficiencies being 97.8, 96.1, and 93.3% for the 20, 30 and 40% models, respectively.

The site ordinations of Figure 1 indicate that in all cases sites are ranked correctly along the first axis in terms of their range condition. The distortion of the gradient into a 2-dimensional arch is also illustrated.

Species ordinations demonstrate the distinct clustering of the various response types present. Increaser, decreaser, and invader species, while clustered, form a discontinuous arch which is co-ordinate with the site ordination while unresponsive species form a distinct group which is clearly separated from the arched configuration of the remainder. The intensity of clustering, particularly of unresponsive species, tends to diminish as progressively more between-site heterogeneity is introduced.

Application of Reciprocal Averaging to Field Data

The field data analysed here were compiled from a set of 9 study sites located in a mulga (*Acacia aneura*)-shrub community near Leonora (lat. 28° 52' S; long. 121° 20' E) in the arid winter rainfall zone of Western Australia. Average annual rainfall at the Glenorn station homestead, about 9 km from the study sites, is 198 mm (51 years of records) with a coefficient of variation of 58%. Winter rainfall (May–July) is the more reliable.

The vegetation consists of a sparse overstorey of mulga below which occur a mid-storey of shrubs and a ground storey of perennial grasses, mostly wire wandarrie grass (*Eragrostis xerophila*). Herbs and short lived perennial grasses are abundant following favourable seasonal conditions. This community is located on deep (generally >1 m) red loamy sands which are non-saline and of acid reaction.

Study sites were each 0.9 ha (256 m × 35 m) and were selected by the use of fenceline contrasts and distance from water to provide examples of the ecosystem in widely differing range condition states.

Although data for all layers of the vegetation have been profitably analysed by RA, only results for the upper and mid-storey species are presented here. Population inventories for these species were obtained by field annotation of large scale colour aerial photographs covering each study site.

These photographs also facilitated the partition of each species population into a number of appropriate size classes based on canopy area distribution. Seedlings, assumed to have no canopy area, were identified as such in the field. The process of data collection and size class classification is detailed further in Hacker (1978, 1979). For all species, class 1 corresponds to seedlings while larger numbers represent groups of progressively larger individuals. The number of size classes per species varied from 2 to 5.

Previous studies of 6 of these sites using the Multiple Pattern Analysis (MPA) procedure of Noy-Meir and Anderson (1970) have been reported by Hacker (1978, 1979). These studies clearly revealed that over the range of grazing intensity examined, Wilcox bush (*Eremophila leucophylla*) acted as a decreaser while both low blue bush (*Maireana planifolia*) and *Eremophila*¹ increased in more disturbed areas. Mulga regeneration appeared to be favoured by grazing disturbance while *Maireana villosa* appeared to act as a decreaser.

On the basis of this understanding of the mulga-shrub ecosystem it was possible to classify all study sites into subjective range condition classes as detailed in Table 2. These classes were used as independent evidence to evaluate the ordination results.

Data entered in the analysis consisted of densities (plants per ha.) of 13 species divided into a total of 40 size classes. Data were entered for individual size classes rather than for species *in toto* in an attempt to elucidate the presence of any secondary gradients in addition to the range condition gradient.

Since many mid- and upper-storey species probably have long life spans relative to the grazing history of the area (about 80 years) the presence of both site and grazing influences on species distribution may be reflected in the clumping or dispersion of the component (age-related) size classes in the species ordination.

Site and species ordinations in the plane of the first 2 axes are presented in Figure 2. The cumulative efficiency of the axes was 79.1%.

The arrangement of sites on the first axis clearly reflects the range condition gradient as defined in Table 2. Typically, the gradient is distorted into an arched configuration but this has not detracted seriously from the first axis seriation.

The species ordination, which is co-ordinate with the site configuration, reveals that for most species, size classes are fairly tightly grouped suggesting that grazing is the predominant factor affecting their distribution. For these species the ordination position of size class groups conforms with their response to grazing as known

¹Positive identification of this species proved impossible due to the lack of flowering material throughout the course of the study. Vegetative specimens are lodged as voucher Specimen No. 1, W.A. Herbarium Perth.

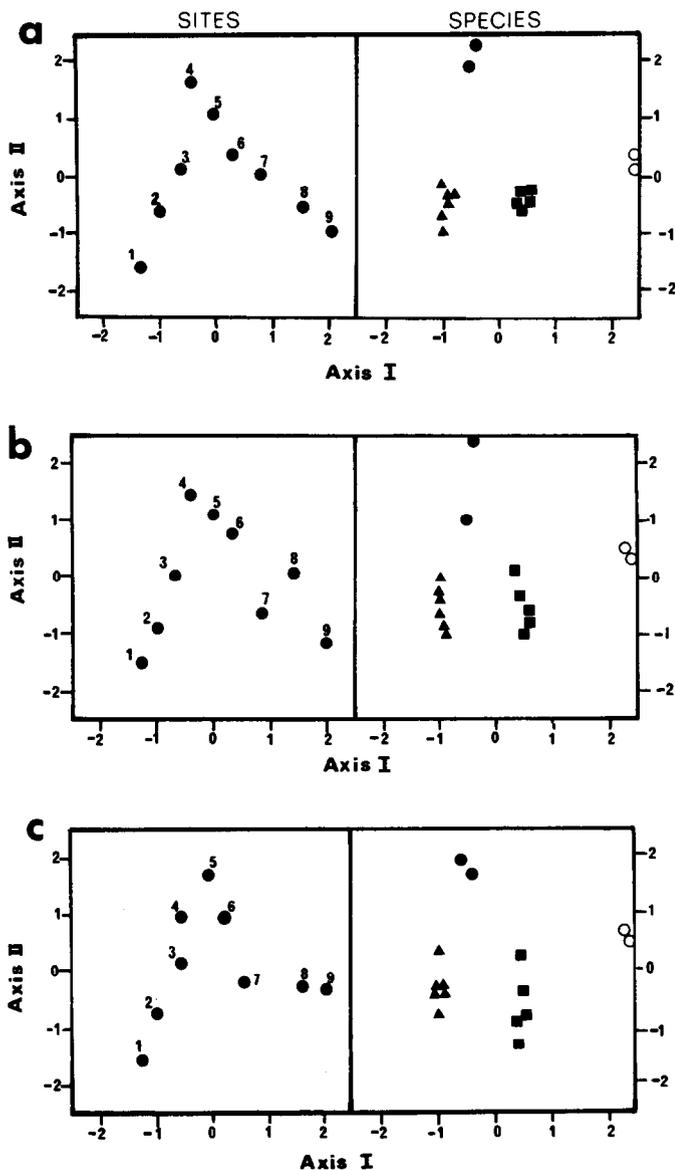


Fig. 1. Ordination diagrams for series 3 models (a) 20% between-site variation (b) 30% between-site variation (c) 40% between-site variation.

Species symbols: Δ decreaser; \bullet increaser; \circ invader; \square unresponsive

from field experience or previous studies. The role of such species in the grazing-induced succession can be readily interpreted although such interpretations must be accepted with caution in the case of species with low overall densities (e.g., *Mirbelia*) since sampling error may be high in such cases.

Table 2. Key species populations and range condition classification for mulga-shrub study sites.

| Site No. | <i>Eremophila leucophylla</i> | <i>Maireana planifolia</i> | <i>Eremophila</i> | Range condition |
|----------|-------------------------------|----------------------------|-------------------|-----------------|
| 1 | 1067 | 115 | 30 | Good |
| 2 | 915 | 129 | 9 | Good |
| 3 | 630 | 125 | 194 | Fair-Good |
| 4 | 34 | 17 | 0 | Very poor |
| 5 | 19 | 26 | 1 | Very poor |
| 6 | 18 | 14 | 6 | Very poor |
| 7 | 796 | 67 | 145 | Fair-Good |
| 8 | 307 | 486 | 1095 | Fair-Poor |
| 9 | 646 | 428 | 875 | Fair |

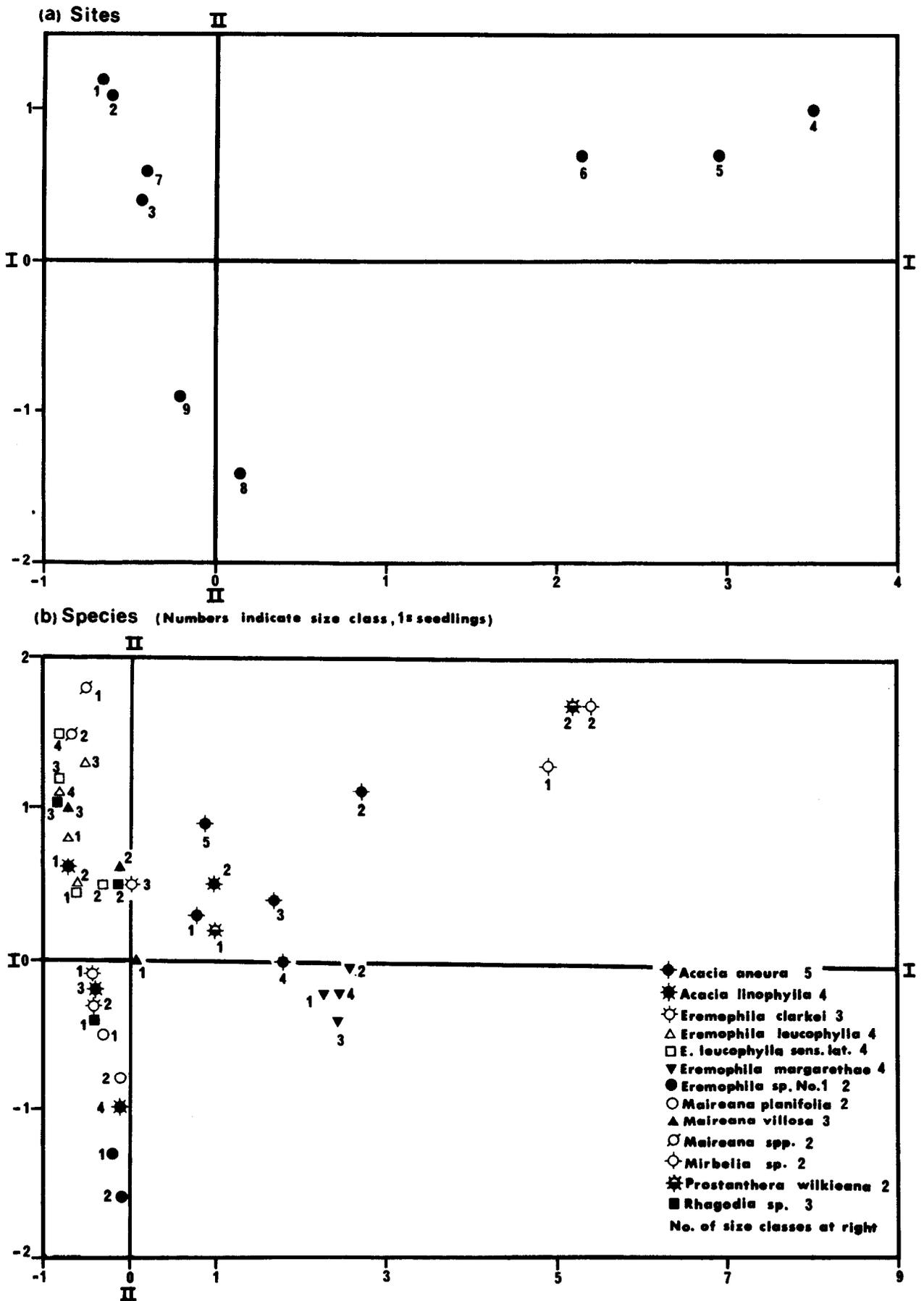


Fig. 2. Ordination diagrams for mulga-shrub study sites.

Some species, however, display a marked scatter of size class points. This is particularly obvious for mulga, bowgada (*Acacia linophylla*), and mint bush (*Prostanthera wilkieana*). The presence of mint bush seedlings at comparable (low) densities on sites 1, 4, and 9 (i.e., across the entire range condition gradient) is responsible for the marked separation of this size class from the adults and its location in a position dissociated from the general arched configuration, as would be expected for unresponsive groups. For mulga, the scatter of size class points reflects the lack of any grazing response by mature trees (class 5), as would be expected, while regenerating mulga (classes 2, 3 and 4) is more characteristic of overgrazed situations as suggested by the earlier analyses. Seedlings showed no marked trend across the gradient, as reflected by the ordination position of this size class, but were always comparatively rare.

The marked scatter of bowgada size classes suggests the possible existence of a secondary gradient influencing this species. Seedlings occurred on only one site and at very low density so the position of this group in the ordination is uninformative. The ordination position of class 2 individuals, however, suggests a lack of any grazing response while larger size classes (3 and 4) are located progressively towards the peak of the arch indicating abundance in moderately degraded sites. These larger individuals are virtually unaffected by direct grazing effects due to their tall growth habit. Re-examination of the moderately degraded sites (8 and 9) suggested that bowgada abundance may be influenced by minor soil physical and chemical differences which characterized these sites, or by a greater average depth to lateritic gravel in the soil profile.

Discussion

This evaluation of RA on both artificial and field data suggests that the technique could be a powerful tool for the study of grazing-vegetation systems. The ordinations produced in both cases have provided satisfactory rankings of sites while the simultaneous species ordinations have proved readily interpretable in terms of grazing responses or the influence of site-specific factors on species distribution.

Mathematically, the RA model is consistent with the conceptual framework in which many ecologists view range condition. Nevertheless the mathematical peculiarities of the technique should be noted. The double standardisation employed by RA tends to give particular weight to rare (i.e. uncommon rather than low density) species which occur in floristically poor sites. The presence of such species can at times severely distort the ordination and it is often preferable to eliminate them at the outset. A degree of distortion caused by such rare species (mint bush and *Mirbelia*) is evident in the ordinations of Figure 2, but in this case has not seriously detracted from the interpretability of the gradient.

Curvilinear or polynomial relationships between lower and higher axes are characteristic of many ordinations produced by RA and have also been observed in ordinations derived by PCA (e.g., Gauch et al. 1977). Quadratic relationships between the first two axes are evident in the ordinations for both the model and field data analysed here. Such relationships distort the first axis representation of the gradient and are compounded by nonlinear species responses. Recognition of such relationships is essential to an informed interpretation of the results. Further discussion of this problem may be found in Hill (1973, 1974) in relation to RA while a considerable literature has developed on the subject of gradient distortion by PCA (e.g., Austin 1971; Orloci 1973, 1975; Whittaker and Gauch 1973; Dale 1975, 1976; Noy-Meir and Whittaker 1977). Such distortions do not necessarily mean that axes after the first are uninformative. Genuine second directions of variation may be identified and even quadratic axes, as revealed by the present study, may serve a useful purpose in clearly separating the middle of a gradient, and its characteristic species, from the ends.

In applications of the technique, an independent measure of range condition is ideally desirable to assist with interpretation.

Such a measure was available here, for the field data, from previous studies of the ecosystem in which grazing responses of some dominant species had been identified. In other situations, such independent measures could take the form of soil erosion ratings, distance from water or prior grazing history although in many cases recognition of end point states (ungrazed vs very poor condition) may suffice.

Interpretation of ordination results in conjunction with such data is probably best performed by rank correlation analysis. Since some distortion of the gradient is inevitable, intersite distances along the first axis cannot be regarded as a quantitative measure of range condition differences. An appropriate ranking of sites, however, is generally provided.

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First Call for Papers

June 1, 1983

Titles are now being solicited for papers to be presented at the 1984 Annual Meeting of the Society for Range Management in Rapid City. Papers may be submitted in the following general categories:

- I. Range Ecosystem Structure
 - A. Range plants—taxonomy, genetics, breeding, physiology, reproduction, establishment, growth and development and ecological characteristics.
 - B. Range animals—taxonomy, genetics, breeding, physiology, behavior, growth and development, nutrition and ecological characteristics of vertebrate and invertebrate range animals.
 - C. Other—soils, geology, weather, climate.
- II. Range Ecosystem Function
 - A. Succession, change.
 - B. Energy flow, nutrient cycling.
 - C. Hydrology.
- III. Range Ecosystem Utilization and Management
 - A. Managed grazing—grazing management, grazing influences.
 - B. Other animals—management, control.
 - C. Watershed management.
 - D. Outdoor recreation.
 - E. Other uses.
- IV. Range Ecosystem Improvement, Reclamation, and Associated Ecosystems
 - A. Practices—prescribed burning, tillage, seeding, plant control, fertilization, water management, erosion control.
 - B. Reclamation—mined lands, dune stabilization, etc.
 - C. Complementary forages.
 - D. Forested grazing lands.
- V. Range Ecosystem Inventory, Classification and Monitoring—measurements and surveys; classification of communities and ecosystems; monitoring ecosystem attributes, including use of remote sensing from ground, aerial and space platforms.
- VI. Range Ecosystem Planning
 - A. Ranches (livestock and game)—description, experiences, business management, simulation and optimization modeling, risk analysis, technology integration, technical assistance, loans and financing, industry and enterprise concerns.
 - B. Public lands (federal, state, tribal)—policy; the planning process; cost-benefit analyses; simulation and optimization modeling; multiple use; forage allocation; legal, social and political considerations.
- VII. Range Ecosystem Miscellaneous—research needs and funding, education and technology transfer, international programs, history.
- VIII. Range Students
 - A. Range youth forum (high school).
 - B. University student conclave.

The title of the proposed paper accompanied with 1 or 2 sentences describing the emphasis of the paper and the 1st, 2nd and 3rd choices of preferred categories (roman numeral and letter) are due on June 1. Upon receipt of titles, authors of technical papers will be furnished instructions for preparing abstracts in a standard format. Completed abstracts are due on August 1. Authors will be notified of paper acceptance or rejection by mid-September.

Presentations must be planned to conform to a 12-minute presentation. Visuals must be standard 2X2 slides or overhead transparency. Attempts will be made to place titles in categories of the author's choice. A heavy volume of titles in any one category may result in placement in an alternate category. Titles and/or abstracts received after their due date will be accepted only as space allows.

Titles should be sent to: Ben Bruce or Tex Lewis, Co-chairmen, 1984 SRM Program Committee, Department of Animal and Range Sciences, South Dakota State University, Brookings, South Dakota 57007, Phone 605/688-5165