Bot. Bull. Acad. Sin. (1997) 38: 183-190

Determination of the coprophilous fungal fruit body successional phases and the delimitation of species association classes on dung substrates of African game animals

Colleen Ebersohn[1] and Albert Eicker[2,3]

[1]*Department of Nature Conservation, Technikon Pretoria, Private bag X680, Pretoria 0001, Republic of South Africa*
[2]*Department of Botany, University of Pretoria, Pretoria 0002, Republic of South Africa*

(Received October 13, 1993; Accepted March 28, 1997)

Abstract. The fungal fruit body succession on different dung substrates of African game animals was investigated and the successional phases determined by means of the computer analysis programmes TWINSPAN and DECORANA. The successional patterns exhibited could in all probability be attributed to a number of environmentally limiting factors and biotic pressures as well as to the existence of inherited physiological characteristics. The species association classes delimited can, in general, be explained by the overlapping of, or the joint absences of, species during the peak ecological periods. Alternatively it may be the result of interrelated species combinations with regard to the presence/absence patterns exhibited by these species combinations within the specific association classes during the peak ecological periods.

Keywords: Coprohilous fungi; Dung substrates; Fungal succession; Fungal ecology; Peak ecological periods; Species associations.

Introduction

Fungal succession on dung has been investigated, and the classical successional pattern has been established by a number of authors. A quantitative method for determining the succession of fungal fruit bodies on dung was first described by Harper and Webster (1964). Their research indicated that several of the fungi tested needed a characteristic minimum time to fruit, which corresponded closely to the observed successional sequence. Subsequently evidence was obtained by Ikediugwu and Webster (1970a) that inter-species competition plays a role in limiting the period of fungal fructification on dung. These authors illustrated that antagonism between fungi accounted for at least some of the replacements during the observed successional sequence (1970b). Characteristic species patterns with regard to the duration and profuseness of coprophilous species, based on the reproductive output, on different dung types were compiled by Nagy and Harrower (1979). Kuthubutheen and Webster (1986a,b) investigated the influence of the availability of water on the fungal succession as well as the effect hereof on the germination, growth, and sporulation of coprophilous fungi. Various other authors have researched some aspects of fungal succession on dung, including Bell (1975), Dickinson and Underhay (1977), Mitchell (1970), and Morinaga et al. (1980).

[3]Corresponding author. Fax: 27 12 432 184; Email: eicker@scientia.up.ac.za

Succession involves a change in the species composition and species abundance values over a period of time. The succession phenomenon in nature can be ascribed to the influence of any of a number of factors or, in most cases, to the combined influences of a number of factors. The importance of any one factor, in bringing about succession, can change as a result of the influences of the other factors present (Odum, 1983). These factors can be of an ecological or of a genetical nature, and in the case of the coprophilous fungi the following factors could possibly play a role in determining the species composition and species diversity of a substrate at any time.

Ecological Factors

Environmental factors such as temperature fluctuations, photoperiodicities, water potential of the substrates, the availability of nutrients in the substrates, the role of other dung-inhabiting organisms, and interspecific fungal species competition, will definitely influence the species composition of any substrate (Webster, 1970).

Fungal species interactions comprise different interactions between the coprophilous fungal species and can be of a positive or negative nature. Competition effects and interference phenomena can play an important role in limiting the time of appearance, as well as the duration and intensity of fruiting (Harper and Webster, 1964). Antagonistic interactions amongst fungi in the form of hyphal interference play an important role in the determination of the coprophilous species composition and species diversity of a substrate (Ikediugwu and Webster, 1970 a,b) and (Singh and Webster, 1973).

The food preferences and feeding habits of the animals play a definite role in the determination of the fungal species composition and diversity of the dung substrates (Ebersohn and Eicker, 1992).

Genetical Factors

Periodicities with regard to spore germination, maturation, and fructification also play a role in determining the specific species composition at any given moment (Webster, 1970).

The present research was aimed at the objective determination of the specific successional phases and the delimitation of species association classes using the computer analysis programmes, Twinspan (Two-way Indicator Species Analysis) and Decorana (Detrended correspondence Analysis) (Hill, 1979a and 1979b). The fungal fruit body succession on different dung substrates of various African game animals was investigated, the successional phases determined, and certain species associations were delimited by means of these computer programmes.

Materials and Methods

Sample Methods

Fresh dung samples were collected in the Kruger National Park, South Africa. These samples were collected within minutes of being voided, to restrict insect interference and to limit aerial and contact contamination by fungus spores other than that of the coprophilous species. The samples were collected, wrapped in paper towels, and placed in sterile containers, which were then sealed. Samples were collected every two to three months for a period of three years from *Connochaetes taurinus* (Blue wildebeest), *Loxodonta africana* (African elephant), *Giraffa camelopardalis* (Giraffe), and *Equus burchelli* (Zebra). Occasional collections of *Raphicerus campestris* (Steenbok) and *Geochelone pardalis* (Leopard tortoise) dung samples were also made.

Incubation of Dung Substrates

All samples collected were placed in sterile petri dishes on sterile filter paper and covered by sterile glass beakers. Depending on the size of the samples, a certain amount of sterile water was added to the substrate. The substrates were then placed in an incubator, at various temperatures corresponding with the average seasonal temperatures of the collection sites in the Kruger National Park, and kept moist for the duration of the investigation.

Microscopic Examination of the Dung Substrates

Two microscopes were used throughout the investigation, a binocular low magnification type stereo microscope to scan the substrate surfaces and to aid in the removal of the fungal fruit-bodies that occurred, as well as a high power compound Nikon microscope with interference contrast for identification purposes. During the stereo-microscope examinations the abundance of each species present was noted. For this purpose the following scale, based on the number of fruit bodies observed on the substrate, was implemented: 1/4 + for 1–5, 1/2 + for 6–10, + for 11–20, ++ for 21–40, +++ for 41–60, ++++ for 61–100, and +++++ for over 100 fruit bodies (Ebersohn and Eicker, 1992). All the species that occurred on the various dung substrates were thus noted, and the data therefore reflect the ecological values both of the obligatory coprophiles as well as the facultative coprophiles that were present during the study period.

From an ecological point of view it was important to determine the abundance value of each species over a specific period of time, as this could give a reliable indication of the ecological importance of the species in question. Furthermore the duration of all species on the different substrates was also noted, as were the dates of first appearances and the dates of disappearances or obvious inactivity. All of the fungal species present on the different dung substrates exhibited periods of peak activity. These peak periods were determined by the abundance values and obvious vigour of the species. As a result it was possible to calculate a peak importance value for each species present.

FORMULAE USED

$$\text{Peak importance value (PIV)} = \frac{2(A+B)+C}{3}$$

$$A = \text{Relative \% peak duration} = \frac{\text{No. of peak days / species}}{\text{Total no. of peak days of all species}} \times 100/1$$

$$B = \text{Relative \% peak abundance} = \frac{\text{No. of peak plus's / species}}{\text{Total no. of peak plus's of all species}} \times 100/1$$

$$C = \text{Relative \% peak occurrences} = \frac{\text{No. of peak occurrences / species}}{\text{Total no. of peak occurrences of all species}} \times 100/1$$

More weight is given to the relative % duration and the relative % abundance than to the relative % occurrence, as the duration and abundance of a species are considered more important than the mere presence or absence of a species (occurrence). The duration and abundance of a species will determine the rate and extent of metabolic activity and thus strongly influence its ecological peak importance value.

Using these formulae, with slight modifications, it was possible to also determine the following importance values:

- Substrate importance values
- Seasonal importance values
- Successional importance values

Calculation of overall importance values were made using the following formulae:

Overall substrate importance value (O SUB IV)=

$$\frac{\text{Sum of the substrate importance values / species}}{\text{6 [number of substrates investigated]}}$$

Overall seasonal importance values / (0 SEA IV) =

$$\frac{\text{Sum of the seasonal importance values / species}}{\text{3 [number of seasons recognized in the study area]}}$$

Overall successional importance value (0 SUC IV) =

$$\frac{\text{Sum of the successional importance values / species}}{\text{6 [number of successional phases determined]}}$$

Total overall ecological importance value (TOEIV) =

$$\frac{\text{O SUB IV} + \text{SEA IV} + \text{O SUC IV}}{3}$$

Delimitation of the Species Association Classes

The association of different coprophilous fungal species could be ascribed to the ability of the species involved to tolerate the presence of each other or actually to benefit from the presence of each other, as opposed to antagonistic interactions as reported by Harper and Webster (1964).

Nineteen different species association classes were recognized as delimited by a computer cluster analysis programme, according to the peak ecological importance values of the individual species.

Two of the original associations delimited by the programme were discounted and moved to another species association class. In both cases the original "associations" consisted of a single species that could easily be accomodated in another existing association class as both share the essential delimiting characteristics of species association class No. 15.

One of the original association classes (No 9) was subdivided into three subclasses (No 9A, No. 9B, and No. 9C) on account of distinct subclass characteristics. As a result of the formation of these three subclasses, *Leuconeurospora pulcherrima*, which originally belonged to species association class No. 10 was moved to species association subclass No. 9A, as it now clearly belongs to the subclass in question, sharing the same distinct characteristic exhibited by this subclass.

Results

The results indicated a gradual change of the species composition and importance values of the fungi on the dung substrates over time. The presence of the different fungal species and even fungal classes leads to overlap. It is therefore not possible to easily distinguish clear cut successional phases by mere observation on the presence and absence patterns of the fungi occurring on the dung substrates.

The peak importance values were thus used to determine the successional position of each species. This lead to a subjective determination of the following successional phases:

Phase 1: Day 1–4
Phase 2: Day 5–14
Phase 3: Day 15–32
Phase 4: Day 33–48
Phase 5: Day 49–67
Phase 6: Day 68–104
Phase 7: Day 105–112

These findings were then tested using the objective computer cluster analysis programmes which resulted in the construction of a dendrogram (Figure 1). The following results were thus obtained:

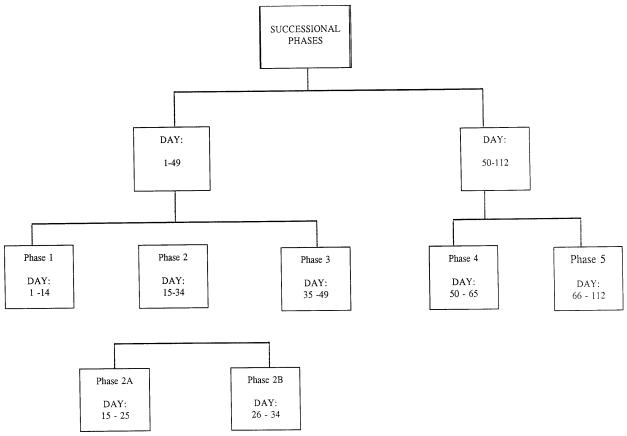

Figure 1. Dendrogram - successional phases.

Phase 1: Day 1–4
Phase 2: Day 5–14
Phase 3: Day 15–34
Phase 4: Day 35–49
Phase 5: Day 50–65
Phase 6: Day 66–104
Phase 7: Day 105–112

After analysis of the dendrogram the following final successional phases and respective class sequences were identified:

Phase 1: Day 1–14, Zygomycetes

Phase 2A: Day 15–25, Hyphomycetes, Pyrenomycetes, Discomycetes gr. 1

Phase 2B: Day 26–34, Plectomycetes, Basidiomycetes

Phase 3: Day 35–49, Coelomycetes, Loculoascomycetes, Discomycetes gr. 2, Basidiomycetes

Phase 4: Day 50–65, Coelomycetes

Phase 5: Day 66–112

No dominant fungal class was discernible, and only 2.11% of all the species observed exhibited any peak ecological activity during this period.

Phase 2 was divided into phases 2A and 2B as these divisions occurred on a lower level in the dendrogram than all the other phases, yet clearly constituted separate identifiable phase entities.

The fact that water as a limiting factor was excluded, as a result of the dung substrates being kept moist for the duration of the investigations, and the fact that other environmentally limiting factors such as temperature and photoperiodicity were regulated according to the seasonal changes, to a large extent cancelled the environmental impact that these factors might have had on the fungal composition of the substrates. Other environmental factors such as inter- and intra-species competition were not monitored; however, the fact that competition can play a part in determining fungal succession on dung substrates can not be discounted.

Exclusion of certain species as a result of intra-specific species competion can possibly give rise to the inclusion of other species which exhibit a certain degree of tolerance to one another. In the process, specific species associations are formed. If this is the case, then intra-specific species competition can, to a certain degree, be cancelled by intra-specific species tolerance.

Therefore, the resulting fungal composition of the different successional phases can, to a large extent, be attributed to genetic factors. The phenomenon of generic succession can possibly be ascribed to inherited genetical characteristics rather than to environmentally limiting factors.

The following species association classes were delimited as all exhibited specific species correlations with regard to the time and duration of their respective peak ecological periods:

Legend: (toeiv.* = Total overall ecological importance value.)

Species association class No. 1

Species	Toeiv.*	Peak phase
Aspergillus flavus group	0.31	1
Saccobolus beckii	0.25	2A
Podospora comata	0.12	2A
Sordaria macrospora	0.09	2A
Chaetomium robustum	0.04	2A
Trichobolus sphaerosporus	0.03	2A

All species involved reached a common peak ecological period during day 18 and were closely associated during days 17–20.

Species association class No. 2

Species	Toeiv.*	Peak phase
Pilobolus kleinii	1.96	1
Ascobolus stictoideus	1.50	1
Ascobolus immersus	1.35	1
Pilobolus crystallinus	1.19	1
Pilobolus longipes	1.11	1
Aspergillus niger	0.51	1
Rhizopus stolonifer	0.38	1
Ascobolus amoenus	0.35	1
Lasiobolus lasioboloides	0.32	2A
Aspergillus glaucus group	0.30	1
Rhopalomyces sp.	0.18	2A
Lasiobolus intermedius	0.13	1 & 2A
Saccobolus portoricensis	0.10	1
Penicillium (*monoverticillata* group)	0.05	1
Coprotus dextrinoideus	0.04	1

All species involved exhibited peak ecological periods within 14 days after the onset of incubation.

Species association class No. 3

Species	Toeiv.*	Peak phase
Sordaria brevicollis	0.54	2A
Peziza sp.	0.47	2A
Ascobolus degluptus	0.07	2A

All species involved exhibited common peak ecological periods during days 9–14 and 18–20 and were jointly absent during day 17.

Species association class No. 4

Species	Toeiv.*	Peak phase
Bahupaathra samala	0.52	2A
Sporormiella isomera	0.35	2A
Coprotus glaucellus	0.29	2A
Mucor sp.	0.27	2A

All species involved reached a common peak ecological period during days 16–17.

Species association class No. 5

Species	Toeiv.*	Peak phase
Stachybotrys chartarum	0.92	2A
Chalara sp.	0.91	2A
Sordaria fimicola	0.43	2A

All species involved reached a common peak ecological period during days 8–34.

Species association class No. 6

Species	Toeiv.*	Peak phase
Phialophora sp.	1.09	2A
Strattonia hansenii	0.28	2A
Ascobolus hawaiiensis	0.17	2A
Fusarium sp.	0.17	2A

All species involved reached common peak ecological periods during days 15–19 and 23–29.

Species association class No. 7

Species	Toeiv.*	Peak phase
Penicillium (*biverticillata* group)	0.49	1
Sporotrichum sp.	0.39	2A
Coprinus poliomalus	0.38	2A
Iodophanus carneus	0.06	2A

An interrelated species combination exists between a representative of the *Penicillium biverticillata* group and a representative of the genus *Sporotrichum* as they commonly reached peak ecological periods during days 15–20 and 43–45. The representatives of the *Penicillium (biverticillata* group), *Iodophanus carneus* and *Coprinus poliomalus*, were closely associated and reached a common peak ecological period during days 21–24.

Species association class No. 8

Species	Toeiv.*	Peak phase
Sporormiella minima	3.21	2B
Saccobolus glaber	0.75	2B
Sporormiella minimoides	0.60	2A
Thelebolus crustaceus	0.54	3

All species involved reached common peak ecological periods during days 17–20; 33–38 and 43–45.

Species association class No. 9

Species	Toeiv.*	Peak phase
Coprinus stellatus	0.53	3
Phoma sp.	0.46	5
Graphium calicioides	0.37	3
Leuconeurospora pulcherrima	0.31	3
Saccobolus minimus	0.24	3
Coprotus marginatus	0.19	3
Sporormiella subtilis	0.19	3
Chaetomium tortile	0.16	4
Podospora pleiospora	0.14	3
Coprotus winteri	0.06	3
Epicoccum purpurascens	0.04	4

In this species association class the following three subclasses can be distinguished by common presences and joint absences during the peak ecological periods.

Species association subclass No. 9A

Species	Toeiv.*	Peak phase
Graphium calicioides	0.37	3
Leuconeurospora pulcherrima	0.31	3
Saccobolus minimus	0.24	3
Podospora pleiospora	0.14	3
Coprotus winteri	0.06	3

All species involved reached a common peak ecological period during day 46.

Species association subclass No. 9B

Species	Toeiv.*	Peak phase
Phoma sp.	0.46	5
Chaetomium tortile	0.16	4
Epicoccum purpurascens	0.04	4

All species involved reached a common peak ecological period during days 52–55.

Species association subclass No. 9C

Species	Toeiv.*	Peak phase
Coprinus stellatus	0.53	3
Coprotus marginatus	0.19	3
Sporormiella subtilis	0.19	3

All the species involved reached a common peak ecological period during days 48–55. This subclass thus partly overlaps with association subclass 9B. *Coprotus marginatus* and *Coprinus stellatus* also partly overlap with association subclass 9A. This association subclass therefore forms a transitional group between the other two subclasses involved.

Species association class No. 10

Species	Toeiv.*	Peak phase
Podospora curvuloides	0.93	3
Podospora communis	0.96	3
Coprotus lacteus	0.34	3

All species involved reached a common peak ecological period during days 46–48. Because of the overlapping of day 46 this species association is closely related to association subclass 9A.

Species association class No. 11

Species	Toeiv.*	Peak phase
Cercophora coprophila	0.35	3
Trichurus spiralis	0.22	3
Trichodelitschia microspora	0.10	3
Fimaria hepatica	0.06	3
Saccobolus verrucisporus	0.06	3
Botryosphaeria sp.	0.05	3

All species involved reached a common peak ecological period during day 40.

Species association class No. 12

Species	Toeiv.*	Peak phase
Coprinus heptemerus	2.01	3
Kernia nitida	0.61	3
Arthrobotrys oligospora	0.36	3
Coprinus niveus	0.34	3
Podospora similis	0.30	2B
Coprotus aurora	0.17	4
Chaetomium concinnum	0.09	3

All species involved reached a common peak ecological period during days 27–42. The competitive interference of *C. heptemerus* is well documented (Ikediugwu and Webster 1970a,b). It would therefore be interesting to test the ability of the other species belonging to this association to withstand the competition of *C. heptemerus.*

Species association class No. 13

Species	Toeiv.*	Peak phase
Coprotus leucopocillium	0.36	2B
Kernia sp. 1.	0.31	3
Chaetomium bostrychodes	0.11	2A
Coemansia sp.	0.10	2B
Kernia sp. 2	0.08	2B
Cheilymenia sp.	0.04	2B

All species involved reached a common peak ecological period during days 33 and 34.

Species association class No. 14

Species	Toeiv.*	Peak phase
Coprotus disculus	0.22	2B
Chaetomium atterimum	0.16	3

Both species involved reached a common peak ecological period during days 17–26.

Species association class No. 15

Species	Toeiv.*	Peak phase
Geotrichum candidum	0.66	1
Cercophora californica	0.60	3
Coprinus miser	0.53	3
Cercophora mirabilis	0.45	3
Podospora ostlingospora	0.27	3
Sporormiella australis	0.17	4

Two distinctly separable peak ecological periods are exhibited by all the species involved. An early peak period starts as early as day 5 and lasts up to day 49, depending on the particular species involved. A late peak period starts as late as day 41 and lasts up to day 68, again depending on the particular species involved. The distinct association characteristic is the two separable peak periods exhibited by all species involved.

Species association class No. 16

Species	Toeiv.*	Peak phase
Podospora anserina	0.60	2A
Paneolus fimicola	0.05	4

Both species involved reached a common peak ecological period during days 52–58.

Species association class No. 17

Species	Toeiv.*	Peak phase
Coprinus cinereus	2.13	2A
Coprotus luteus	0.27	4
Coprinus curtus	0.06	4
Pseudoeurotium sp.	0.04	4

All species involved reached a common peak ecological period during days 55–60.

*S*pecies association class No. 18

Species	Toeiv.*	Peak phase
Cheilymenia theleboloides	0.38	5
Myrothecium verrucaria	0.22	5
Gliomastix sp.	0.15	5

All species involved reached a common peak ecological period during days 76–98.

Species association No. 19

Species	Toeiv.*	Peak phase
Acremonium sp.	1.75	2B & 3
Chaetomium brevipilum	0.05	5

Both species involved reached a common peak ecological period on day 112.

Discussion

In total, representatives of 23 genera were observed during the investigation period. Of these, 14 genera were represented by more than one species, all of which, to some degree, exhibited similar species successional phase correlations.

The minimum association factor in all cases was a 33% species successional phase correlation, and the maximum association factor in 50% of the cases was a 100% species successional phase correlation, with regard to those genera with more than one representative species (common genera).

Percentage of common genera with a 100% species successional phase correlation = 50%

Percentage of common genera with > 57% species successional phase correlation = 71%

Percentage of common genera with > 40% species successional phase correlation = 86%

Percentage of common genera with > 33% species successional phase correlation = 100%

Thus 61% of all species present on all dung substrates and during all seasons and successional phases exhibited some degree of positive species association within the particular genus involved. The other 39% of the species present were the only representatives of the particular genus and as such, contributed to the generic diversity rather than to the generic dominance pattern.

Fungal succession on dung substrates can not merely be ascribed to a single environmental or genetic factor—or even to a simple combination of factors. However, it seems possible, that at the very least, 60% of the successional occurrences in the common genera, as observed during the laboratory investigations, can be attributed to some degree (50%) to inherited genetical characteristics.

Consequently, it is highly probable that a combination of both environmental and genetical factors could determine the phenomenon of fungal fruit body succession on dung substrates and can account for the majority of the successional phase positions occupied by the more common coprophilous genera and their respective representatives.

The degree to which any specific factor or combination of factors influences the succession of fungi on dung substrates will probably vary within the distribution range of the specific fungus and with the prevalent conditions of existence, as the coprophilous fungi has in all probability developed locally adapted ecotypes as is the case in most ecological groups (Lundqvist, 1972).

If this is the case, the coprophilous fungi are genetically adapted in either morphological and/or physiological aspects to cope with the complex environmental conditions and biotic pressures they have to deal with, in order to be successful on any given substrate at any time, in a specific area of their distribution.

This phenomenon could thus give a possible explanation for the morphological differences, within a given species, as reported by some authors from different countries and regions within the distribution area of the fungus.

The highest species diversity was observed during phase 2A, closely followed by phases 3 and 2B. The next highest species diversity was exhibited by phase 1 followed by phases 4 and 5, respectively.

The classification of the successional phases according to their respective species diversities and compositions is summarized in the following table:

Position	Phase	Duration
1	2A	Day 15–25
2	3	Day 35–49
3	2B	Day 26–34
4	1	Day 01–14
5	4	Day 50–65
6	5	Day 66–112

The total overall ecological importance values (TOEIV) as quoted in the species association tables indicate the dominance hierarchy in the respective classes and is at the same time indicative of the ecological role of the specific fungus on the dung of African game animals.

Conclusion

When investigating incubated substrates the highest species diversity on all substrates can be observed between days 15–25 after the onset of incubation.

Fungal succession on dung can be attributed to the concurrent influences of a number of environmental factors, biotic pressures, and inherited genetical characteristics.

The delimited species association classes could have specific ecological indicator values, as they are characterized by relatively strong species correlations within the respective associations classes. Consequently, the presence of at least a significant number of the species within the association class could indicate the possible presence of other species correlated with those observed.

Furthermore, the different species association classes correlate extremely well with the peak ecological periods of the different successional phases recognized, again lending credibility to the hypothesis of generic or species specific based succession and the limiting influences of interspecific competition as well as the possibility of synergistic interactions amongst fungal species, rather than environmentally dominated succession.

The species association classes indicate a certain degree of tolerance amongst the species constituting the specific association class and thus possibly a decrease in interference type competition. However, the delimited association classes should only be seen as preliminary trends, as more research of this nature is needed before definite conclusions can be drawn, especially with regard to the tolerance within and the competition amongst the different association classes.

The total overall ecological importance values (Toeiv.*) illustrate the ecological dominance hierarchy within each association class.

Acknowledgements. Financial support by the University of Pretoria, the Foundation for Research Development, and the National Parks Board is gratefully acknowledged. Prof. G.J. Bredenkamp, Dept. of Botany, University of Pretoria is thanked for his assistance with the cluster analysis computer programmes. The personnel of the National Parks Board are thanked for their kind assistance.

Literature Cited

Bell, A. 1975. Fungal succession on dung of the Brush-tailed Opossum in New Zealand. New Zealand J. Bot. **13:** 437–462.

Dickinson, C.G. and V.H.S. Underhay. 1977. Growth of fungi on cattle dung. Trans. Br. Mycol. Soc. **69**(3)**:** 473–477.

Ebersohn, C. and A. Eicker. 1992. Coprophilous fungal species composition and species diversity on various dung substrates of African game animals. Bot. Bull. Acad. Sin. **33:** 85–95.

Harper, J.E. and J. Webster. 1964. An experimental analysis of the coprophilous fungus succession. Trans. Br. Mycol. Soc. **47**(4)**:** 511–530.

Hill, M.O. 1979a. DECORANA - a Fortran program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, New York.

Hill, M.O. 1979b. TWINSPAN - a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, New York.

Ikediugwu, F.E.O. and J. Webster. 1970a. Antagonism between Coprinus heptemerus and other coprophilous fungi. Trans. Br. Mycol. Soc. **54**(2)**:** 181–204.

Ikediugwu, F.E.O. and J. Webster. 1970b. Hyphal interference in a range of coprophilous fungi. Trans. Br. Mycol. Soc. **54**(2)**:** 205–210.

Kuthubutheen, A.J. and J. Webster. 1986a. Water availability and the coprophilous fungus succession. Trans. Br. Mycol. Soc. **86**(1)**:** 63–76.

Kuthubutheen, A.J. and J. Webster. 1986b. Effects of water availability on germination, growth and sporulation of coprophilous fungi. Trans. Br. Mycol. Soc. **86**(1)**:** 77–91.

Lundqvist, N. 1972. Nordic Sordariaceae s. lat. Symbolae Botanicae Upsalienses. 20(1). Published by the University of Uppsala, Sweden. 374 pp. (+ plates).

Mitchell, D.T. 1970. Fungus succession on dung of South African Ostrich and Angora goat. J. S. Afr. Bot. **36**(3)**:** 191–198.

Morinaga, T., S. Ito, and K. Minoura. 1980. Fungal succession on deer dung-the effects of light on the development of certain fungi. Trans. Mycol. Soc. Japan. **21:** 351–357.

Nagy, L.A. and K.M. Harrower. 1979. Analysis of two Southern Hemisphere coprophilous fungal successions. Trans. Br. Mycol. Soc. **71**(1)**:** 69–74.

Odum, E.P. 1983. Basic Ecology. Saunders College Publishing, Philadelphia.

Singh, N. and J. Webster. 1973. Antagonism between Stibella erythrocephala and other coprophilous fungi. Trans. Br. Mycol. Soc. **61**(3)**:** 487–495.

Webster, J. 1970. Coprophilous Fungi. Trans. Br. Mycol. Soc. **54**(2)**:** 161–180.