Pergamon
www.elsevier.nl/locate/asr

Adv. Space Res. Vol. 24, No. 3, pp. 297–302, 1999
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Printed in Great Britain
0273-1177/99 $20.00 + 0.00

PII: S0273-1177(99)00317-8

THE USE OF MICROCOSMS AS AN EXPERIMENTAL APPROACH TO UNDERSTANDING TERRESTRIAL ECOSYSTEM FUNCTIONING

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ABSTRACT

Since 1986, a series of microcosm experiments has been conducted at the Unit of Comparative Plant Ecology (UCPE) in an attempt to test our understanding of the principles controlling the structure and dynamics of plant communities and ecosystems. In each experiment microcosms have been seeded with a common pool of organisms, and systems have been allowed to assemble under replicated controlled conditions. Experiment variables have included mineral nutrient supply, temperature, moisture supply, soil depth, carbon dioxide concentration, mycorrhizas, rhizobia, herbivores and carnivores. Results from these experiments are presented to illustrate the value of synthesised ecosystems in ecological research.

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INTRODUCTION

Microcosms are basically small ecosystems in containers. There is a huge range of microcosm studies from simple experimentally sown mixtures of two species of plants (for example DeWit's replacement series 1960) to sophisticated controlled environments housing entire terrestrial ecosystems such as the Ecotron facility at Silwood Park (Naeem *et al.* 1994). Microcosms also vary in size from test tube studies (eg. Fish and Principe (1994) to the vast multi-ecosystem complex found in Arizona - the Biosphere 2. Many disciplines have utilised microcosms as a powerful research tool, most notably limnologists and toxicologists (Beyers and Odum 1993), because the independent variables can be relatively easily manipulated. But, the use of microcosms has been significantly neglected in terrestrial ecology.

The main role of microcosms is that they act as a bridge between theory and nature. They do not mirror nature but they can increase our understanding of natural processes by simplifying the complexities of our natural environment. Microcosm experiments have played an important role in developing and testing ecological theories (Gause 1934; Huffaker 1958; Park 1962; Grime *et al.* 1987; Weiher and Keddy 1995) and investigating current global change scenarios (Bazzaz 1990; Diaz *et al.* 1993; Lucas et al. 1993). The advantages of using microcosms include the ease of replication and manipulation of the parameters and treatments involved. However, there are limitations and disadvantages as well when using microcosms, the major one being restricted space. Otherwise, each microcosm experiment will have their own specific advantages and disadvantages according to the researcher's design.

The main purpose of this paper is to demonstrate the application of microcosms as a research tool in testing and developing ecological theories. The Natural Environment Research Council (NERC) Unit of Comparative Plant Ecology at the University of Sheffield, England is the UK pioneer in synthesising terrestrial communities and ecosystems in microcosms. One of the main emphases of these microcosm studies has been the assembly of large plant species pools and how each species, and functional groups of species (see Grime 1974, 1977, 1979), are effected by biotic and abiotic factors. In order to meet the objective outlined above, examples of published

experiments from the Unit of Comparative Plant Ecology will be reviewed, as well as presenting results from a recently completed experiment conducted in closed outdoor microcosms.

EXAMPLES OF MICROCOSM STUDIES

1) Mycorrhiza, soil structure and grazing effects on floristic diversity

One of the first microcosm experiments conducted at the Unit of Comparative Plant Ecology exposed the functional significance of mycorrhizal infection, soil structure, and razing to floristic diversity (Table 1). Grime *et al.* (1987) found that mycorrhizas can increase diversity markedly by raising the biomass of the subordinate plant species relative to that of the canopy dominant. The results suggested that the transfer of mineral nutrients and assimilate through mycorrhizas may be one of the factors which reduce the intensity of competition and encourage species co-existence on infertile soils. Progress in the field had been limited because important factors, such as mycorrhizal infection and soil structure, were not amenable to precise field measurement or manipulation, whereas the use of microcosms allowed such fine-scale manipulations.

Table 1. Influence of soil heterogeneity, grazing and mycorrhizal infection on floristic diversity of turf microcosms. Diversity indices are based on shoot dry weights measured at the end of the experiment. Each value is the mean of five replicates. Confidence limits (95%) are presented in brackets. Reproduced with permission from Grime *et al.* (1987).

Soil heterogeneity	Grazing	VA mycorrhizas	Mean no. species per microcosm	Mean Shannon diversity index
-	-	-	15.2 (1.0)	0.23 (0.07)
+	-	-	15.8 (2.8)	0.20 (0.03)
-	+	-	14.4 (1.7)	0.59 (0.14)
-	-	+	15.0 (2.5)	0.43 (0.15)
+	+	-	16.0 (2.2)	0.61 (0.13)
+	-	+	16.2 (1.8)	0.44 (0.23)
-	+	+	14.2 (2.0)	0.68 (0.16)
+	+	+	17.2 (1.0)	0.78 (0.14)

2) Elevated CO_2 effects on a plant community

Microcosms were used in one of the first experiments designed to test the community level response of plants to elevated CO_2 (Diaz *et al.* 1993). The data presented (Fig. 1) indicate that there may be a feedback mechanism in which elevated carbon dioxide causes an increase in substrate release into the rhizosphere by non-mycorrhizal plants (*Rumex obtusifolius* and *Cardamine flexuosa*), leading to mineral nutrient sequestration by the expanded microflora and a consequent nutritional limitation on plant growth. As a result, slow-growing mycorrhizal plants (*Agrostis capillaris* and *Calluna vulgaris*) are shown to dominate after 112 days (Fig. 1b). Once again, factors which were very difficult to control and measure in the field have been shown to be important through the use of microcosms. Marked differences were observed in the responsiveness of native British plant species to CO_2 concentration. However, the pattern of response differed substantially from that recorded for plants grown in the laboratory as isolated individuals. Therefore, this experiment also highlighted the need to examine the broad community level responses to independent abiotic factors.

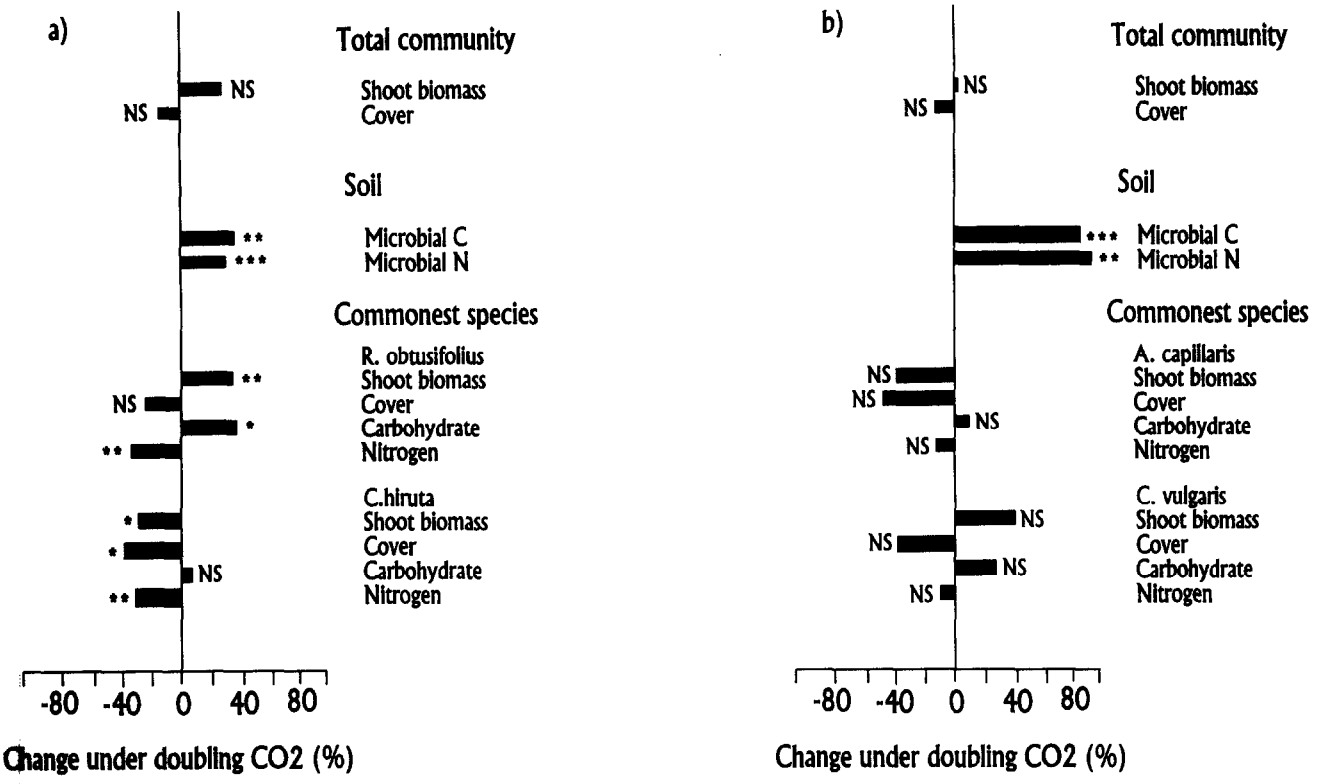

Figure 1. Responses of commonest consituents and soil microflora grown in 2,400 ml microcosms (six replicates per combination) to a doubling of atmospheric CO_2 (700 v.p.m.) as compared with controls at 350 v.p.m. Vegetation was allowed to develop for (a) 84 days, and (b) 112 days by natural recruitment from the seed bands. Shoot biomass was measured as mg dry weight, cover using point-quadrat analysis, carbohydrate as mg g^{-1} fresh weight, and nitrogen as mg g^{-1} dry weight of fully expanded young leaves, soil microbial biomass C and N as mg g^{-1} dry soil (fumigation techniques); NS, not significant; *P≤0.05; **P≤0.01; ***P≤0.001 (ANOVA). Key to species: R. obtusifolius = *Rumex obtusifolius*; C. hirsuta = *Cardamine flexuosa*; A. capillaris = *Agrostis capillaris*; C. vulgaris = *Calluna vulgaris*. Reproduced with permission from (Diaz *et al.* 1993).

3) Herbivory and soil fertility effects on secondary plant succession

Thirty six closed outdoor microcosms were used to study the effects of herbivory and soil fertility on plant succession (Fraser and Grime 1996). Closed microcosms were required in order to contain the herbivores added (land snails (*Helix aspersa*, *Arianta arbustorum*, and *Cepaea hortensis*) and aphids (*Sitobion avenae*)), and to exclude all other animals from the microcosms where herbivores were absent, and present. The microcosms were outdoors because it was necessary to have seasonal and diurnal changes for studying plant succession. Of course, this could be simulated in the laboratory but the cost would have been considerable. Because the microcosms were economical many could be made, which allowed for good replication. No attempt was made to exclude bacteria and fungi; indeed, the most sophisticated systems would not be able do that. Each point in Fig. 2 represents each plant species included in the experiment. Points falling below the line performed better in the absence of herbivores, points falling above the line performed better in the presence of herbivores. The results show that herbivory at medium and high soil fertility suppressed fast-growing plants (circles) and promoted slow-growing plants (diamonds). Plant succession usually begins with fast-growing species, followed by slow-growing species (Feeny 1976; Rhoades and Cates 1976; Grime 1977, 1979; Coley *et al.* 1985), therefore it can be inferred from these results that herbivores increase the rate of secondary succession by preferentially feeding on fast-growing plants, even at high soil fertility. The obvious advantage of using closed microcosms in this study was the absolute exclusion of the third trophic level, which is virtually impossible to accomplish in the field without also eliminating the second trophic level (herbivores).

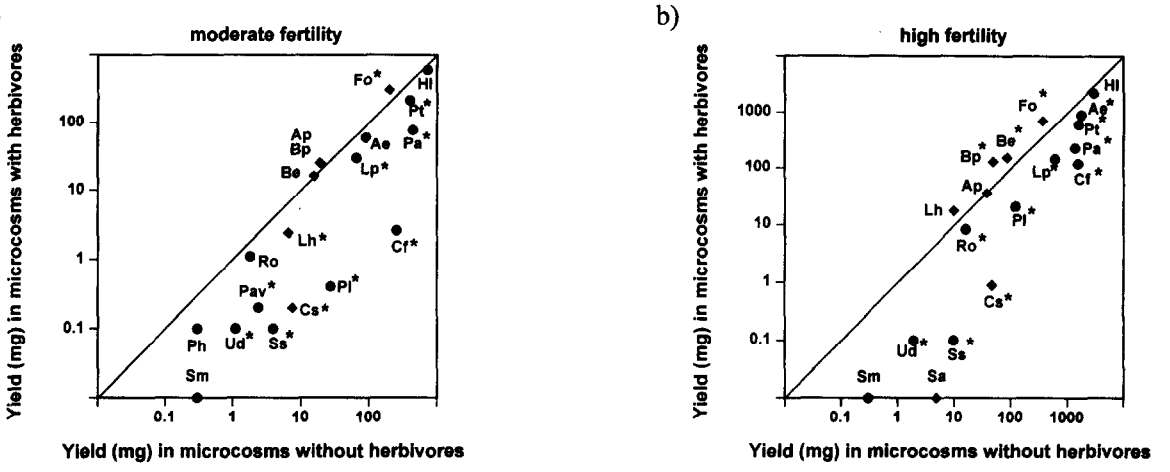

Figure 2. Effects of herbivory on the mean shoot biomass of individuals of various species grown together for two growing seasons in closed outdoor microcosms (six replicates per combination) at **(a)** moderate soil fertility (100 mL full Rorison's/week), and **(b)** high soil fertility (1000 mL full Rorison's/week)(see Fraser and Grime 1996). The outdoor microcosms measured 1.5-m high x 1.2-m long x 1-m wide and were constructed from a reinforced clear polythene fabric on an angle iron frame. The statistical significance of changes in weight associated with herbivory is indicated as follows: *P<0.05; **P<0.01; ***P<0.001 (standard t-test). Squares represent fast-growing plants, diamonds represent slow-growing plants (Grime *et al.* 1988). Key to species: Ae = *Arrhenatherum elatius*; Ap = *Avenula pratensis*; Bp = *Brachypodium pinnatum*; Be = *Bromopsis erecta*; Cs = *Centaurea scabiosa*; Cf = *Cerastium fontanum*; Fo = *Festuca ovina*; Hl = *Holcus lanatus*; Lh = *Leontodon hispidus*; Lp = *Lolium perenne*; Ph = *Petasites hybridus*; Pl = *Plantago lanceolata*; Pa = *Poa annua*; Pt = *Poa trivialis*; Pav = *Polygonum aviculare*; Ro = *Rumex obtusifolius*; Sa = *Sedum acre*; Ss = *Stachys sylvatica*; Sm = *Stellaria media*; Ud = *Urtica dioica*.

4) Future developments

The closed outdoor microcosms are being used for further experiments. The obvious direction proceeding the first outdoor microcosm experiment described above (3) is to include a third trophic level as an experimental variable. In so doing, hypotheses regarding the control from the top trophic layer (top-down (Hairston *et al.* 1960)) or from the bottom trophic layer (bottom-up (White 1978)) can be tested.

Another experiment underway in the closed outdoor microcosms involves controlling the level of CO_2 in the microcosms, in relation to herbivory and soil fertility. Recent studies have shown that some plants grown under enhanced CO_2 produced more biomass than plants grown under ambient levels of CO_2, but their foliar nutrient concentrations were less (Hunt *et al.* 1991, 1995). These results pose a number of interesting questions: (1) is this result consistent for all plant species? (2) how would herbivores respond to such a change in vegetation? (3) what influence would soil fertility levels have on this outcome?

SUMMARY

Clearly, there is a very wide range of possibilities for experimental research that can be conducted in microcosms. Advantages of microcosm research include ease of replication and repetition, precise control over independent variables, exclusion of most foreign material, and trophic level manipulation. Disadvantages

include restrictions of space and working with an 'unnatural' environment. At the Unit of Comparative Plant Ecology the emphasis has been on the assembly of large sets of species and their consequent responses to various independent factors. However, this level of research and hypothesis testing is only one step towards the scientific goal of theory and prediction. Furthermore, it's not the first step. In order to gain the most information from such a study, it is important to begin with an understanding of the traits of the species being used. Ultimately, a model may be constructed that borrows on all aspects of the experimental approach: trait screening, hypothesis formulation, testing in the field, and testing in the laboratory. The experiments described in this paper demonstrate that microcosms are an important and useful tool in ecological research.

ACKNOWLEDGMENTS

This work was funded by NERC and a University of Sheffield post-graduate scholarship. I thank J.P. Grime for helpful comments.

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