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The Ecotron: a controlled environmental facility for the investigation of population and ecosystem processes

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SUMMARY

This paper reports on aspects of the design and philosophy of the Ecotron, an integrated series of 16 controlled environmental chambers at the NERC Centre for Population Biology. The Ecotron serves as an experimental means for analysing population and community dynamics and ecosystem processes under controlled physical conditions. Within the chambers, terrestrial experimental communities are assembled into foodwebs of desired complexity from a pool of species selected for their preadaptations to the physical conditions of the Ecotron. These species include decomposers (earthworms, snails, microarthropods and microbes), primary producers (16 species of plants), primary consumers (four species of herbivorous arthropods), and secondary consumers (four species of parasitoids).

The design of the Ecotron is unique in several aspects with respect to its blend of biology and technology. It supports small, dynamic communities of up to 30 plant and metazoan species, thereby making it among the more biologically complex controlled environmental systems currently in use. Its architecture permits replication and variation of spatial scale in experimental design. Its artificial climate simulates natural environmental conditions within chambers allowing experimental control over light, water, temperature, humidity, and in the near future CO_2 and UV-B radiation. Sensors monitor both macro- and micro-environmental conditions of a number of physical factors within the chambers.

Preliminary experiments show the Ecotron to be an excellent facility for long-term population and community-level experiments. We discuss the results of one of these early experiments and briefly consider ongoing and future experiments.

1. INTRODUCTION

Recent rapid increases in the sophistication of ecological experiments have paved the way for attempts to study the population dynamics and ecosystem processes of an entire community under specified environmental conditions. (In this paper we use the term 'ecosystem' as defined by Odum (1971) to mean a community of organisms plus the physical and chemical environments with which the community interacts.) Such an attempt is being conducted by the Natural Environment Research Council (NERC) Centre for Population Biology as part of its overall research programme into the ecology of populations and communities. These whole-community studies are being conducted in the Ecotron, a system of 16 physically and electronically integrated environmental chambers.

This major facility took three and a half years from conception, through consultation, design, and construction to proven functioning, and it is still undergoing development and improvement with experience. In total, the facility and its machinery occupies approximately 200 m^2 and two levels of a building (figure 1).

The Ecotron is unique among controlled environmental facilities (CEFS) in that it attempts to construct, maintain and manipulate entire model ecosystems and simultaneously monitor population dynamics and ecosystem processes. Outdoor CEFS typically examine intact communities (see, for example, Rogers *et al.* 1983; Drake *et al.* 1989; Hendrey & Kimball 1990; Strain *et al.* 1991; Oechel *et al.* 1992). Such systems allow measurement of the effect of changing physical conditions on natural communities, but because community structure is not manipulated in these systems they provide little insight into the importance of this structure in determining ecosystem responses. Indoor CEFS typically focus on the response of one or a few species to environmental change (see, for example,

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Figure 1. The Ecotron. Anticlockwise, from top, left; view of one bank of Ecotron units; view of vegetation in an ecosystem container from an early experiment; internal view of an Ecotron unit prior to loading an ecosystem container.

Bazzaz & Carlson 1984; Grime *et al.* 1987; Fajer *et al.* 1989; Lechowicz & Romer 1990; Korner & Arnone 1992), but such studies generally lack the complexity of real systems. They have low biodiversity (see Ecological considerations. (d). Biodiversity, below); lack a decomposer fauna; generally have only one or at most two trophic levels; and the plants within them usually have no population dynamics, i.e. no seedling establishment or turnover of individuals. The Ecotron can examine and manipulate relative abundances of up to 30 species of terrestrial plants and metazoans among four trophic levels, over several generations.

This paper describes the ecological basis for the construction of the Ecotron, its technological features, and its programme of experimental investigation. It is intended to serve as a report for those constructing similar devices, as a reference for future Ecotron research, and to provide a summary of our discoveries thus far in the construction and use of the facility. Ongoing and future research are briefly outlined.

2. ECOLOGICAL MOTIVATIONS

For historical reasons, ecology has been a collective of related but separate disciplines each with overlapping agendas. Unification of these separate disciplines and agendas, in particular population and ecosystem ecology, was inevitable, but increasing scientific and public interest in global change has recently hastened the process (see, for example, Lubchenco *et al.* 1991). The Ecotron is an example of this process of unification in that it combines the methodologies developed in several ecological subdisciplines to examine whole-community response to environmental change in a single experimental system.

The impetus for the NERC Centre for Population Biology's research programme, and the construction of the Ecotron in particular, stems from current trends in both basic and applied ecology. From the standpoint of basic research, the community remains the most difficult level at which to investigate ecological issues because of its complexity. Central issues such as the relative roles of biotic against abiotic processes in structuring communities, the determinants of community diversity, the stability of communities, the importance of historical factors in determining distribution and abundance, and the assembly rules of foodwebs have been the focus of much research in basic ecology, but still remain largely unresolved. Although there was a sense of progress towards resolution of some of these issues in the 1960s (see papers in Cody & Diamond 1975), much of that progress has been recently challenged (papers in Price *et al.* 1984; Strong *et al.* 1984; Diamond & Case 1986; Kikkawa & Anderson 1986; Gee & Giller 1987). Theory is well in advance of empirical work largely because of the practical problems of doing experimental work, especially at the level of the community. The list of theories in need of experimental confirmation is long (Karieva 1989) and the Ecotron can provide laboratory tests of several theories on this list (see Ecological considerations below).

3. ECOLOGICAL CONSIDERATIONS

The species assemblages (communities) used in the Ecotron are not intended to be *exact* analogues of any particular natural system, but they are modelled closely on temperate, British, early successional weedy fields. Rather, the Ecotron constructs replicated communities designed to contain a set of universal features of terrestrial ecosystems, features known to be important in governing ecosystem behaviour and dynamics. Some examples are as follows; the list is illustrative, not exhaustive.

(*a*) *Leaf litter dynamics*

The importance of leaf litter dynamics on the chemical and physical environment of plants is well documented (Facelli & Pickett 1991). Leaf litter has important effects on community composition and productivity (Monk & Gabrielson 1985; Fowler 1986, 1988; Knapp & Seastedt 1986; Carson & Peterson 1990). Temporal and spatial patterns of leaf litter production are also known to affect the population dynamics of simple communities (Bergelson 1990).

The mechanistic underpinnings of these effects on community dynamics, however, have received less attention. This is a difficult issue to address because of the complexity of the leaf litter cycle. For example, herbivores affect rates and quality of litter production (Choudry 1988) while quantity and quality of litter produced affects decomposer communities which in turn affect rates of litter breakdown (Richards 1987). Further, rates of litter breakdown affect plant population and community dynamics (Carson & Peterson 1990; Facelli & Pickett 1991) which in turn affects herbivore dynamics. Add to this picture predator–prey dynamics among herbivores and their predators and even a simple community becomes a complex network of interacting entities that is difficult to study. Each of these relationships, however, can be monitored closely in the Ecotron. This close examination of the various links in the cycles of leaf litter dynamics will shed light on the mechanisms behind changes in the composition of plant and animal communities associated with leaf litter dynamics.

(*b*) *Spatial distributions and population dynamics*

The importance of spatial distributions of organisms to population and community dynamics has generated considerable empirical and theoretical work and several recent volumes review this literature (Pickett & White 1985; Shorrocks & Swingland 1990; Kolasa & Pickett 1991). However, the way in which the aggregation of individuals into subpopulations affects population and community dynamics is still the subject of much debate (reviewed in Chesson 1986, 1991). Differences among competing schools of theory remain unresolved.

Within the Ecotron, seedling arrangements are established according to specific spatial distributions to create arrangements suitable for testing theory. We can vary spatial distributions both within and among plant species and examine the effects of this variation within and among trophic levels. Plant spatial dynamics are recorded by an overhead camera and pin sampling methods. Changes in climatic, chemical, hydric, faunal, and microbial conditions can be monitored at a microscale level within chambers. With this information the predictions of plant (see, for example, Bergelson & Karieva 1987), plant–herbivore (reviewed in Karieva 1986), and parasitoid–host community dynamics (reviewed in Hassell & May 1989; Hassell *et al.* 1991; Pacala & Hassell 1991; Stiling *et al.* 1992) in response to spatial distributions can be directly tested.

(*c*) *Food web structure*

The analysis of patterns in food web architecture has led to a number of predictions about community assembly, stability and dynamics (see, for example, Cohen 1989; Sugihara *et al.* 1989; Pimm 1982; Lawton 1989; Pimm *et al.* 1991; De Angelis 1992; Martinez 1992). Food webs, however, are difficult to manipulate and, in spite of considerable theoretical and observational work, and considerable promise for the utility of food web theory, little manipulative experimental work has been done.

The Ecotron can provide several tests of food web theory using assemblages of terrestrial organisms. Ecotron food webs can also be used to test predictions about ecosystem processes and food web architecture (reviewed in DeAngelis 1992) through monitoring of nutrient and energy dynamics.

(*d*) *Biodiversity*

The Ecotron will be useful for addressing several issues in biodiversity (we use 'biodiversity' as convenient shorthand for several interrelated phenomena, including species richness, species evenness, trophic diversity, lifestyle diversity, and phylogenetic diversity). What governs the patterns that we see in biodiversity? How critical is biodiversity for the stability of communities and ecosystem processes? These are major topics of basic and applied ecology (papers in Wilson & Peter 1988; Hawksworth 1991; see also Andow 1991; Ehrlich & Wilson 1991; Soulé 1991; Groombridge 1992; Lawton & Brown 1993). The issues surrounding the maintenance of biodiversity are still unresolved in basic ecology (reviewed in Iwasa *et* *al.* 1993). The role of biotic diversity in ecosystem processes, a potentially important issue in the face of anthropogenic global change (see Global change below), is still controversial. Three different views exist: (i) the biocentric view (*sensu* Andrewartha & Birch 1984) holds that the loss of each species incrementally and predictably alters ecosystem processes; (ii) the redundant-species view (*sensu* Lawton & Brown 1993) holds that many species perform similar roles in ecosystem processes providing that biomass is maintained; and (iii) a third view holds that the effect of loss of a species on ecosystem processes defies reduction or easy generalization. Determining which of these views better describes ecosystems will be important for designing and implementing strategies for conservation and management.

Biodiversity can be manipulated within or among all trophic levels in the Ecotron. The effects of these manipulations, and the effects of manipulations of physical factors on biodiversity, can be readily conducted in this system. Thus, the importance of biodiversity to ecosystem stability, resilience and performance can be directly tested.

(*e*) *Global change*

The rapidity of global climate change caused by anthropogenic production of greenhouse gases has caused considerable concern about how the biosphere will respond (see, for example, papers in Houghton *et al.* 1990 and in Woodward 1992). Global atmospheric models vary considerably in the details of their predictions of global temperature change (Goodes & Palutikof 1992) and there is little consensus on global hydrological changes (Rind *et al.* 1992). They agree, however, that with the 'business as usual' scenario the Earth's temperature will indeed rise and that this rise can have dramatic effects on global weather patterns, natural ecosystem processes, agriculture and forestry. These effects will in turn affect the political and economical well-being of nations (Houghton *et al.* 1990; Rubin *et al.* 1992).

Ecological analyses of the consequences of global change have been necessarily constrained by the overwhelming complexity of the phenomenon. Minimally, at least five interacting factors, CO_2, UV-B, H_2O, temperature and community composition, are potentially important to global change. For example, even at only three levels of each factor, this produces a full experimental design involving 243 treatments plus one control treatment! With a minimal replication of two per treatment, a full experiment would require 488 experimental units. Most studies have therefore been limited in the possibilities for experimental design and set out to examine only one or two factors (e.g. temperature alone (van Cleve *et al.* 1983); CO_2 alone (Fajer *et al.* 1989); CO_2 and temperature (Idso *et al.* 1987); CO_2 and H_2O (Bazzaz & Carlson 1984)). The Ecotron, with only 16 chambers, is similarly constrained to the manipulation of two or three factors but stands out among other systems in that it specifically focuses on community response and food web architecture (see Ecological motivations, above).

The Ecotron is controlled in two blocks (although the design allows adaptation to four) that can be each independently programmed to produce different atmospheric conditions. Constructing replicate communities within these blocks allows experimental examination of population and community theory under the environmental conditions of global change.

4. BIOLOGICAL CONSIDERATIONS

The terrestrial communities used in the Ecotron are constructed from species preadapted to conditions in the chambers. Although these communities are artificial, they are modelled on real, early successional communities and embody the essential features of most communities: the species are found in similar environments, overlap in resource use, and interact with one another.

We chose communities that are not tightly coevolved assemblages and unlikely ever to be at or near equilibrium. This method of community construction reflects current trends in contemporary ecology that have shifted away from the paradigm that views species assemblages as coevolved equilibrium communities (Caswell 1978; Murdoch 1979; Connell & Sousa 1983; Weins 1984; DeAngelis & Waterhouse 1987). This choice of construction also reflects the fact that most communities in northern temperate systems are only recently derived since the last glaciation period (see, for example, Davis 1986, 1988; Collinson & Scott 1987) and that pristine (i.e. undisturbed long enough to potentially be near equilibrium) systems are rare in the face of expanding human populations and the disturbance this creates.

To amplify the effects of interactions and physical conditions on community dynamics, the system will primarily be run without seasons. Without seasons, all organisms selected for use in the Ecotron reproduce continuously at the environmental settings we have chosen, allowing more generations than in seasonal environments. The Ecotron functions like a biological accelerator that allows a rapid expression of any predicted effect of an experimentally manipulated factor on community dynamics. Such experiments are not possible in the field where the majority of habitats are seasonal either in photoperiod, temperature or rainfall. Seasonal environmental conditions, however, can be readily created in the Ecotron should we wish to focus more specifically on modelling seasonal communities.

(*a*) *Soil and soil fauna*

The soil composition is 56% loam and 44% sand on a 15 cm washed gravel base, all sterilized by methyl bromylation before use. Microbial communities are reintroduced by the addition of a soil wash, paper filtered for the removal of larger organisms. In preliminary experiments (Thompson *et al.* 1993), we re-introduced soil microbes by burying a thin layer of soil 15 cm down. Filtered soil-water provides a more reliable method, reducing the risk of contamination by soil animals. Nutrient levels are thus within a typical

Table 1. *Summary of biological characteristics of annual plants used in Ecotron experiments*

(Family, family that contains species; life form, summer or winter annual; canopy struct, 'L' if leafy species with no basal rosette and leaves equal in length, 'S' if semi-rosette species with leafy stems but with large basal leaves (Clapham *et al.* 1962); canopy height = 1 if < 100 mm, 2 if 101–299 mm, 3 if 300–599 mm, 4 if 600–999 mm, and 5 if 1000–3000 mm; max height, maximum height attained in the field; lat spread = 1 if therophytes, 3 if rhizomes/tussocks diameter 100–250 mm, and 4 if diameter 251–1000 mm; diam, stem diameter as measured after one month in the field; pH, pH range in which the species is most widely distributed. Note these data were largely compiled from Grime *et al.* (1988).)

	family	life form	canopy struct	canopy height	max height	lat spread	diam/mm	pH
Aphanes arvensis	Rosacea	winter/summer	L	2	80	3	—	—
Arabidopsis thaliana	Cruciferae	winter	S	1	500	3	66	6.0–8.0
Capsella bursa-pastoris	Cruciferae	winter/summer	S	1	400	4	163	> 5.0
Cardamine hirsuta	Cruciferae	winter/summer	S	2	300	1	—	7.0–8.0
Chenopodium album	Chenopodiacae	summer	L	5	1000	4	67	—
Conyza canadensis	Compositae	summer	L	—	1000	—	—	—
Lamium purpureum	Labiatae	summer	S	3	—	1	450	6.0–8.0
Poa annua	Graminae	winter/summer	S	2	300	1	526	5.0–8.0
Senecio vulgaris	Compositae	winter/summer	L	3	450	1	—	> 6.0
Sinapsis arvensis	Cruciferae	winter/summer	S	3	750	1	240	> 6.0
Sonchus oleraceus	Compositae	winter/summer	S	5	1500	1	—	> 6.0
Spergula arvensis	Caryophyllacea	summer	L	2	300	1	662	5.0–7.0
Stellaria media	Caryophyllacea	winter	L	2	300	1	425	> 5.0
Tripleurospermum inodorum	Compositae	winter/summer	S	3	600	1	—	—
Veronica arvensis	Scrophulariaceae	winter/summer	S	1	250	1	200	6.0–8.0
Veronica persica	Scrophulariaceae	winter/summer	L	1	50	1	450	6.0–8.0

range of field conditions, although plants experience competition relatively quickly. The soil has an average pH of 6.4.

The soil fauna consists primarily of earthworms and microarthropods. Earthworms were chosen as important soil organisms for which a considerable amount of biology is known (see, for example, Lee 1985). Earthworms have large and complex effects on the physical, chemical and biotic structure of soil (see, for example, Russell 1973; Edwards & Lofty 1978; review, Brown 1988) and are therefore necessary to achieve proper leaf litter dynamics within the Ecotron. The earthworm assemblage includes both *Lumbricus terrestris* and *Aporrectodea* spp. (Thompson *et al.* 1993).

Microarthropods, such as mites and Collembola, are important contributers to the decomposition of litter and the cycling of nutrients in soil (see, for example, Engelmann 1968; Heal & MacLean 1975; Anderson & MacFadyen 1976; Hanlon & Anderson 1979; Swift *et al.* 1979; Usher *et al.* 1979; Seastedt 1984; Moore *et al.* 1988; Hagvar 1988). We chose Collembola for their ease of culturing and known importance in decomposition processes (Butcher *et al.* 1971; Hanlon & Anderson 1979; van Amelsvoort *et al.* 1988; Leonard & Anderson 1991). Currently, we have four species of Collembola, all decomposer species, and a predatory mite (table 1) that were cultured as contaminants from Ecotron soils in preliminary experiments and are therefore known to survive and reproduce in the Ecotron.

(*b*) *Study organisms*

(*i*) Plant–herbivore communities. The majority of described animal species are herbivorous insects (Strong *et al.* 1984). Historically (see, for example, Hairston *et al.* 1960; Slobodkin *et al.* 1967) and to date (see, for example, Sih *et al.* 1985; Hairston 1991; Sih 1991), plant–herbivore systems form the basis for much of the conceptual synthesis in community ecology. Experiments on these systems yield results that apply to a vast number of organisms in the terrestrial portion of the biosphere and an important component of terrestrial ecosystem processes. From an applied perspective, results from plant–herbivore systems apply directly to pest management in agro-ecosystems and managed forests.

(i) *Plants*

We (D. Magda and L. J. Thompson) screened most of the common British herbaceous annuals and selected 16 plant species whose known biologies indicated that they were pre-adapted to life in the Ecotron (table 2). These criteria included nutrient, pH, light, temperature, water and germination requirements. In the interest of simplifying the system, we elected not to use those plants that were obligate outcrossers or had any special requirements for germination.

(ii) *Animals: herbivores*

These species were similarly selected based on pre-adapted biologies suitable for the Ecotron. The herbivores are two species of aphids, a dipteran leaf miner and a white fly (table 1). These herbivores are well-studied agricultural, horticultural and common greenhouse pests and much of their biology is known (e.g. for aphids (Dixon 1985); for leaf miners (Hespenheide 1991); for whiteflies (Gerling 1990; Byrne & Bellows 1991)).

Table 2. *Communities of differing complexities*

(This table lists the nested sets of species in four types of communities of differing complexity that can be used for Ecotron experiments. Each set of species is included in the set beneath it. For example, all communities contain the basal species *Senecio vulgaris* but only community IV contains *Lamium purpurem*.)

community	plant spp.	herbivores, predators	soil fauna
I	*Senecio vulgaris* *Stellaria media*	leaf miner, *Chromatomyia syngenesia* leaf miner parasitoid, *Diglyphus isaea* snail, *Helix aspersa*	earthworms, *Lumbricus terrestris* *Aporrectodea* spp. Collembola, Onchiurus sp. predatory mite other mites
II (+I)	*Chenopodium album* *Spergula arvensis*	aphid, *Myzus persicae* aphid parasitoid, *Diaeretiella rapae*	Collembola, *Neelus* sp.
III (+I+II)	*Cardamine hirsuta* *Conyza canadensis* *Sinapsis arvensis* *Veronica persica*	aphid, *Brevicoryne brassicae* aphid parasitoid, *Aphidius matricariae*	Collembola, *Sminthurides* sp.
IV (+I+II+III)	*Lamium purpureum* *Aphanes arvensis* *Arabidopsis thaliana* *Capsella bursa-pastoris* *Poa annua* *Sonchus oleraceus* *Tripleurospermum inodorum* *Veronica arvensis*	white fly, *Trialeuroides vaporariorum* white fly parasitoid, *Encarsia formosa*	Collembola, *Proisotoma* sp.

(iii) *Animals: herbivore predators*

Four species of parasitoids have been selected for use in these experiments (table 1). Parasitoids are similarly a diverse, well studied and important group of predators (LaSalle & Gauld 1992; Godfray 1993). The physical scale of the Ecotron communities precludes the use of larger herbivore–predator systems.

5. PHYSICAL CONSIDERATIONS

(*a*) *Overview*

Environmental chambers are frequently constructed from the standpoint of electromechanical control over physical conditions within the unit, independent of the ecology of the organisms they contain. The Ecotron is unique in that it is designed with the ecology of the communities that will be maintained within it in mind. Lighting, water, air flow, temperature, humidity, and eventually UV-B and CO_2, are designed as an integrated system with performance specifications based on a consideration of the requirements of *both* the plants and animals that will be housed within the system. The following systematically reviews the various design aspects of the Ecotron.

(*b*) *Architecture*

Figures 1–3 show the general architectural layout of the Ecotron. Each chamber has a floor that averages 2 m × 2 m and is 2 m high from floor to ceiling, which is formed by the airtight, UV-transmitting, Perspex window of the lamp housing. Insulated walls are polystyrene-filled, polyester-coated, phytotoxin-free steel cold room modules. Internal, similarly constructed side walls are demountable, which gives the ability to enlarge the chambers, and the spatial scale of communities within them, but at the cost of reduced replication. Currently, the model ecosystems are housed in 1 m^2 boxes, 40 cm deep with single drainage ports located at the bottom of one side panel (figures 2 and 3).

(*c*) *Airflow*

Air (figure 3) enters the chamber from a perforated duct beneath the floor of each chamber. The air rises through a 2 mm mesh and then through the metal gridded structural floor, and leaves through a screened exit port in the top of the rear chamber wall. Two air circulation fans with adjustable, double directional diffusers are mounted on wall brackets on the front and back walls of each chamber. These fans mix chamber air and eliminate still-air patches. They also cause plants to tremble as they do in the field which is known to affect plant growth (Neel & Harris 1971; Jaffe Biro 1979; Grace *et al.* 1982; Van Gardingen & Grace 1991). The velocity of air movement is adjustable.

Chamber air pressure is slightly positive with

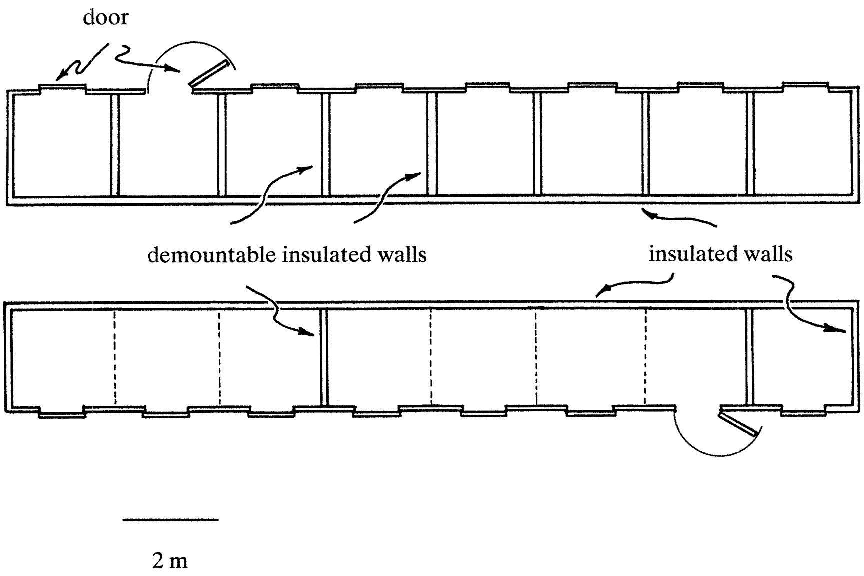

Figure 2. Ecotron plan view. This figure illustrates the overall construction of units in two banks of eight chambers each. The internal walls of each bank are demountable thereby allowing variation in unit dimensions. This feature permits conducting experiments at different scales. Broken lines show hypothetical arrangement for the purposes of illustration.

respect to air pressure of the lamp housings and air external to the chambers. This assists in preventing contaminants from entering the chamber.

Each bank of eight chambers has a separate, overhead, central air handling unit which collects, reconditions, exchanges a portion with the external atmosphere, and recycles the air. On each 50 s cycle, 5% of the 130 kg of air in each system of the air handling unit and its associated chambers is exchanged with filtered outside air. This exchange fraction is adjustable to 15% at which point climate control becomes difficult. This exchange is necessary

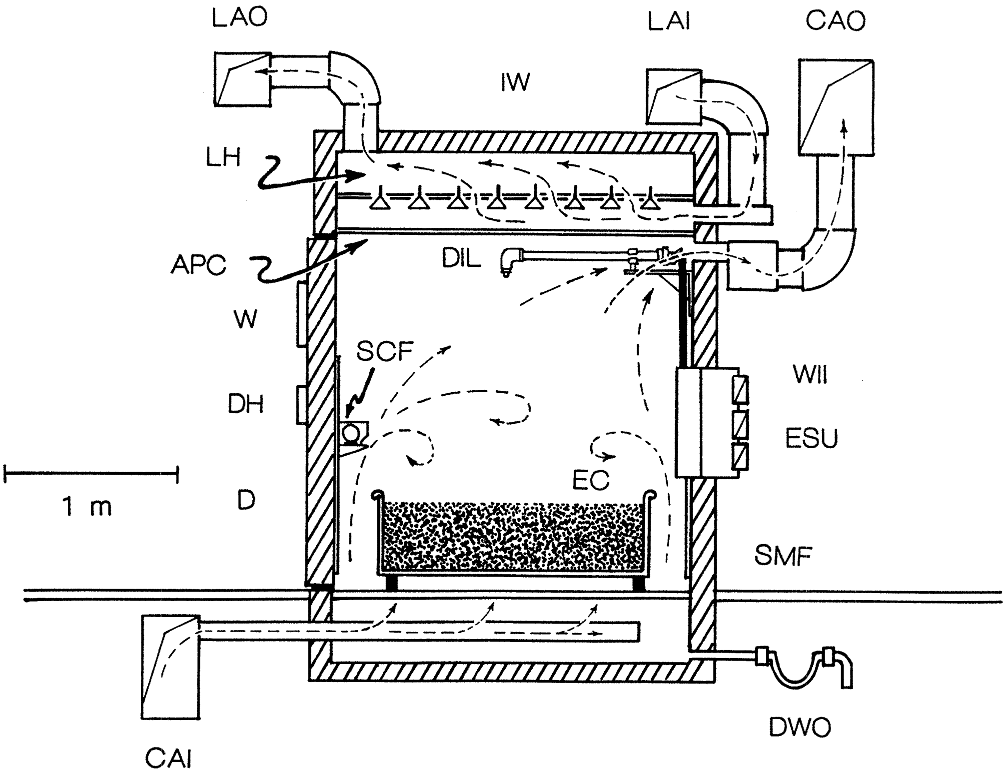

Figure 3. Single chamber diagram. Most of the features discussed in the text are illustrated in this diagram. APC, airtight Perspex ceiling; CAI, chamber air inlet; CAO, chamber air outlet; D, door, insulated and with airtight seals; DIL, demountable irrigation lance; DH, door handle; DWO, drainage water outlet; EC, ecosystem container; ESU, electronic sensors unit; IW, insulated walls (shaded regions); LAI, lamp house air inlet; LAO, lamp house air outlet; LH, lamp house with separate air flow for cooling; SCF, secondary circulation fan; SMF, stainless-steel mesh floor; W, window, shuttered and insulated; WII, water irrigation unit.

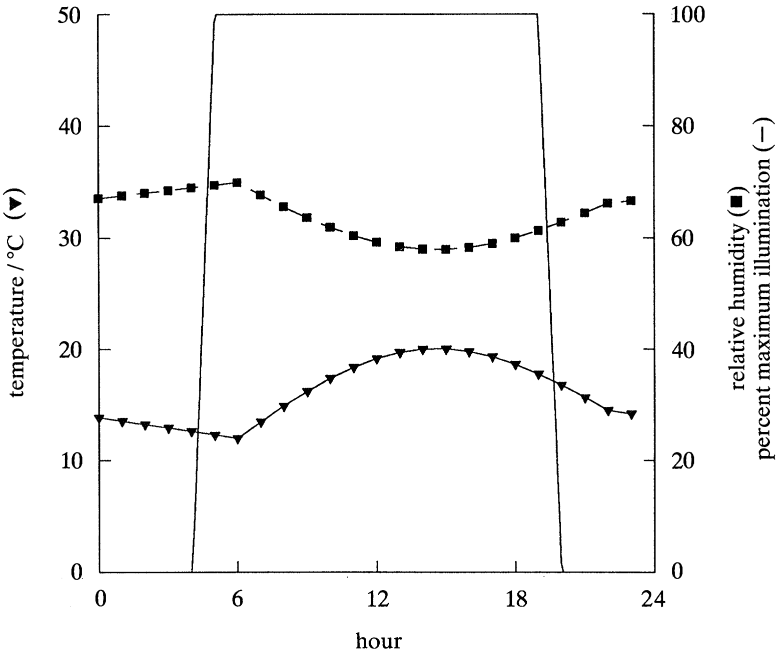

Figure 4. Temperature, humidity, and light-intensity conditions in the Ecotron during an early experiment. This figure shows how physical factors can be smoothly regulated by computer control.

to prevent buildups of contaminants. Purafil/activated carbon contaminant and microscreen filters are being added. Air cooling, heating, and relative humidity adjustments are made within the central handling units.

(*d*) *Temperature*

Thermal control of the environment is regulated by air conditioners located in the central air handling units. (The non-radiant load from the quartz-halogen lamps is cooled separately by its own air circulation facility.) Air enters each chamber at a controlled temperature, regulated by computer control with sensor input from two sensors per bank of chambers. Individual chambers have sensors that monitor temperature for information only. Temperature can be held constant or cycled smoothly over daily or longer time intervals. A typical cycle used in preliminary experiments is shown in figure 4. The system can deliver air temperatures in the range of 5°C to 30°C dry bulb (±0.5°C) and be continuously varied as required (figure 5).

(*e*) *Humidity*

Humidity (or vapour pressure deficit) control takes place in the central air-handling units and can be smoothly varied and regulated by computer control as required. Humidity is controlled on a per-bank basis. Humidity is measured on entry to and exit from each chamber. These measures can be used to estimate whole-community evapotranspiration (a function of the humidity difference between the supply air and exit air) in the chambers. A typical cycle used in preliminary experiments is shown in figure 4. The system can deliver relative humidities in the chambers varying between approximately 40% and 70% (±5%), depending on temperature. The humidifiers work by chilling the airstream to the dew point associated with the required relative humidity, saturating it with deionized water, then reheating to the required ambient temperature. This method prevents the circulating air from becoming supersaturated and avoids condensation problems. A thermal wrap-around circuit between chillers and reheaters ensures energy efficiency (figure 5).

(*f*) *Lighting*

Several considerations were taken into account in the design of the lighting system. Adequate lighting had to provide suitable intensities, a balanced spectrum, and diurnal variation in radiation reasonably comparable to natural daylight. Additional considerations included ensuring a relatively constant red to far-red radiation (R:FR) ratio during most daylight hours (Holmes & McCartney 1976; Holmes & Smith 1977), but shifting this R:FR ratio during twilight hours. It was also necessary to remove the 100 Hz fluctuations in illumination due to alternating current (AC) modulation that adversely affects arthropod behaviour and ensure that light was evenly dispersed throughout each chamber.

The Ecotron lighting system has been developed with all of the above considerations in mind (figure 3). The system consists of 60 low-voltage (50 W, 12 V, 38 degree beam), Decostar™ quartz-halogen lamps with integral dichroic reflectors. Because these lamps use direct current (DC) they eliminate fluctuation/'flicker' problems due to AC modulation. These incandescent lamps have excellent spectral properties with respect to their R:FR ratio although they are somewhat deficient in the blue end of the spectrum (figure 6).

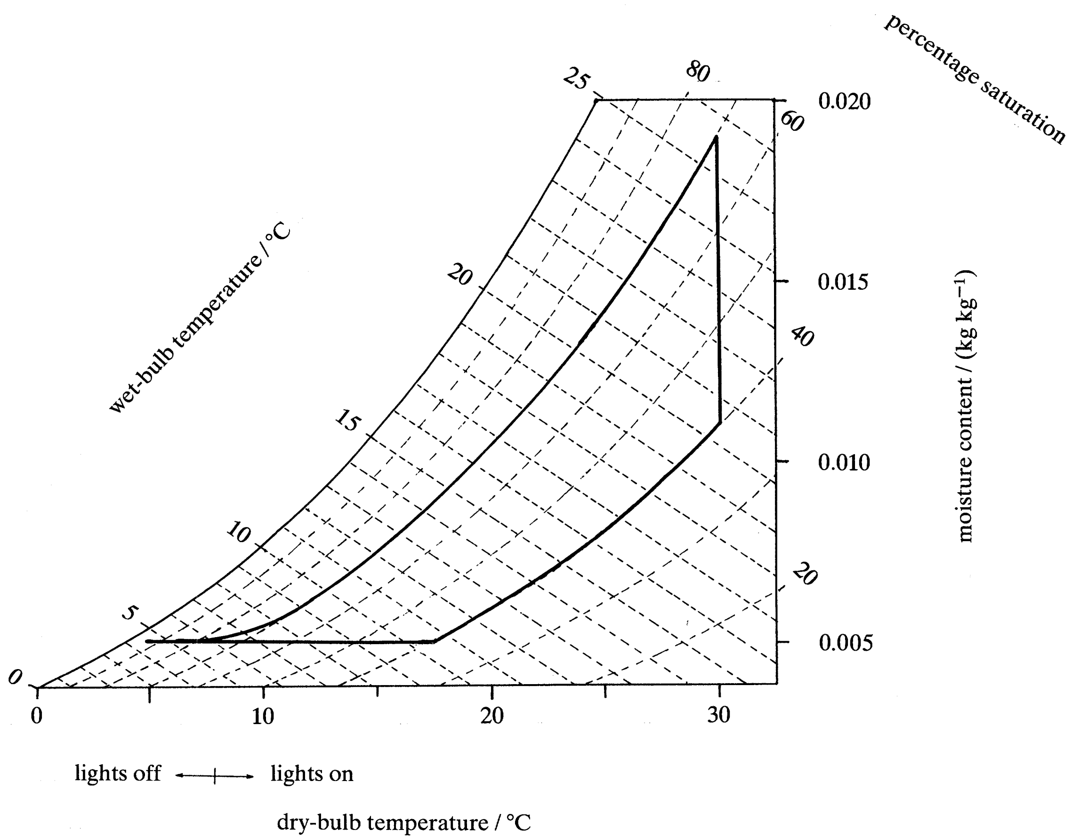

Figure 5. Psychrometer diagram of design performance specifications for the Ecotron. This figure illustrates the engineered range of temperature and humidity conditions possible in the Ecotron (shown within the region bounded by the solid line).

Gradual brightening and dimming of dawn and dusk is achieved by electronic control of the power supply voltage. This produces an R:FR shift resembling that which occurs during dawn and dusk. We intend to augment the lighting with high-frequency UV-A and blue/white fluorescents to correct for spectral deficiencies. The lamps are arranged in a regular pattern in the ceiling of each chamber. They form a grid with a 20 cm separation between lamp centres allowing the siting of fluorescent tubes between the rows. The operating frequencies of the fuorescents are well above the reception threshold of insects so fluorescent flicker is not a problem.

Energy consumption and cost constraints prevented

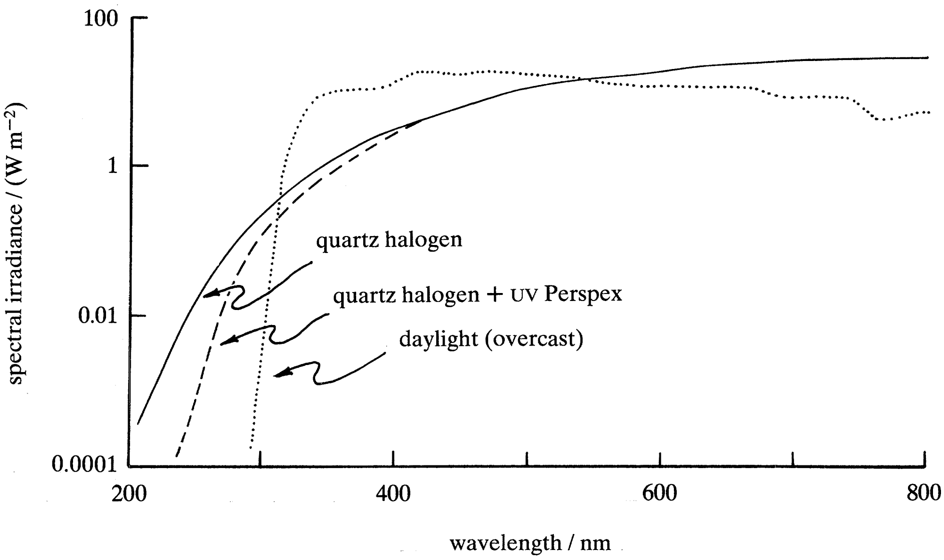

Figure 6. Spectral properties of Ecotron lighting. This figure shows the spectral output of a Decostar^{TM} quartz-halogen lamp at the voltage settings for the Ecotron (solid line). The actual light that reaches the ecosystem container is filtered through a Perspex window and is illustrated by the broken line. A typical daylight spectral reading for an overcast day for northern temperate regions is shown for comparison.

the implementation of a lighting system that could achieve the intensity of full maximum sun light (1000 W m^{-2} in the 400–700 nm spectrum). To remain within power and cost constraints, the maximum intensity of light in the Ecotron at the head of the plant canopy was chosen to be 100 W m^{-2} (photon fluence = 288 micromoles m^{-2} s^{-2}). This intensity, however, is equivalent to normal average daylight intensity for habitats in which these plants are typically found (Kendrick & Kronenberg 1986) or equivalent to daylight from overcast skies (Fitter & Hay 1987). The light intensity is computer controlled and can be smoothly varied between maximum output and darkness to mimic natural diurnal cycles (figure 4).

The lamps are situated 15 cm above a suspended 3 mm thick, UV-transmitting, Perspex window. This window seals off the lamp housing from the experimental chamber. The window consists of two panels, each demountable from within the chamber for the purposes of replacing spent lamps.

(*g*) *Water*

A reverse-osmosis deionizer supplies filtered water at 60 l h^{-1} to a 3000 l storage tank. This water is delivered to each chamber from an overhead, centrally located, demountable, irrigation lance. This lance produces a conical spray that mimics rainfall. Unlike more conventional, ground-level, drip irrigation systems, it delivers an even spread of water at a uniform flow over the entire surface of the growth area. Duration of rainfall is computer controlled and can be varied as required. Intensity of rainfall is manually controlled. Each bank of chambers has its own water delivery pump with solenoid valves servicing each individual chamber. See figure 3 for the features discussed in this paragraph.

(*h*) *Micro-environmental sensors*

Each chamber growth area contains four sets of micro-environmental sensors, one set per quadrant (figure 3). Each set is mounted on rods that insert into sockets implanted in the soil. This arrangement allows easy removal and rearrangement of sensors whenever the need arises. The sensors currently measure air temperature and photosynthetically active radiation (PAR) irradiance at different heights above the ground surface. Additionally, each set includes a resistance-based soil moisture sensor calibrated for soil matric potential and a soil temperature sensor, both situated 10 cm below the soil surface. The soil temperature sensor measures below-ground temperatures and serves as a correction sensor for the soil-water sensor.

6. CURRENT AND FUTURE EXPERIMENTS

(*a*) *Verifying ecosystem processes in the Ecotron*

Having designed and built the Ecotron as a controlled environment facility it was necessary to test the electro-mechanical system and carry out biological trials to verify that a functioning ecosystem could be maintained. Between July 1991 and April 1992, a preliminary experiment with fully operational electro-mechanical and biological systems was conducted. During this 9 month run, the facility proved to be reliable and functional in all aspects. The Ecotron maintained a controlled environment as designed and the community in all chambers cycled through two to four generations of plant growth.

These preliminary experiments in the Ecotron focused on leaf litter dynamics as potentially the most important factor in need of resolution. The importance of leaf litter community dynamics is not well understood and is currently receiving considerable attention (Sydes & Grime 1981*a*,*b*; Bergelson 1990; Facelli & Carson 1990; Facelli & Pickett 1991; Tilman & Wedin 1991). A simple detritivore and plant community was established without herbivores for these first experiments. The detritivore assemblage consisted of earthworms, snails and Collembola, the species of which are listed in table 1. The plant communities consisted of *Trifolium dubium*, *Senecio vulgaris* and *Poa annua* (see table 2 for description). Treatments consisted of manipulating the detritivore assemblage. These were: (i) with snails; (ii) with worms; (iii) with snails and worms; or (iv) with neither species. A fifth treatment consisted of cutting (into 2 cm pieces) and replacing *Poa* litter in some of the snail and earthworm replicates to hasten the cycling of leaf litter.

Results indicate that earthworms are important organisms for obtaining successful litter dynamics. Even in this 'simple' three-plant species system, however, complex interactions were apparent. Snails, for example, particularly in the absence of earthworms, reduced *Trifolium* abundance which resulted in increased *Poa* productivity and the accumulation of dead *Poa* (figure 7). The manual removal of *Poa* (treatment 5) resulted in the emergence of a second generation of *Senecio*. Additionally, earthworms had a positive effect on the abundance of *Trifolium* (figure 7); the mechanistic basis of this positive interaction appeared to be that earthworm casts provided safe sites for *Trifolium* establishment, whereas earthworm presence decreased the abundance of *Poa* litter and increased *Trifolium* nodulation. Full detail of these experiments are reported in Thompson *et al.* (1993).

This brief synopsis of the experimental results serves only to demonstrate that the Ecotron can maintain plant and animal assemblages on a continuous basis if leaf litter cycling can be successfully achieved. The degree to which leaf litter dynamics is achieved has complex and strong effects on the outcome of community dynamics.

(*b*) *Ongoing and future experiments*

The Ecotron is currently examining relationships between biotic diversity, global change and ecosystem processes. A total of 14 communities are in use, each having plants plus herbivores, predators and soil fauna as listed in table 1. Further planned experiments which require the Ecotron to be modified for

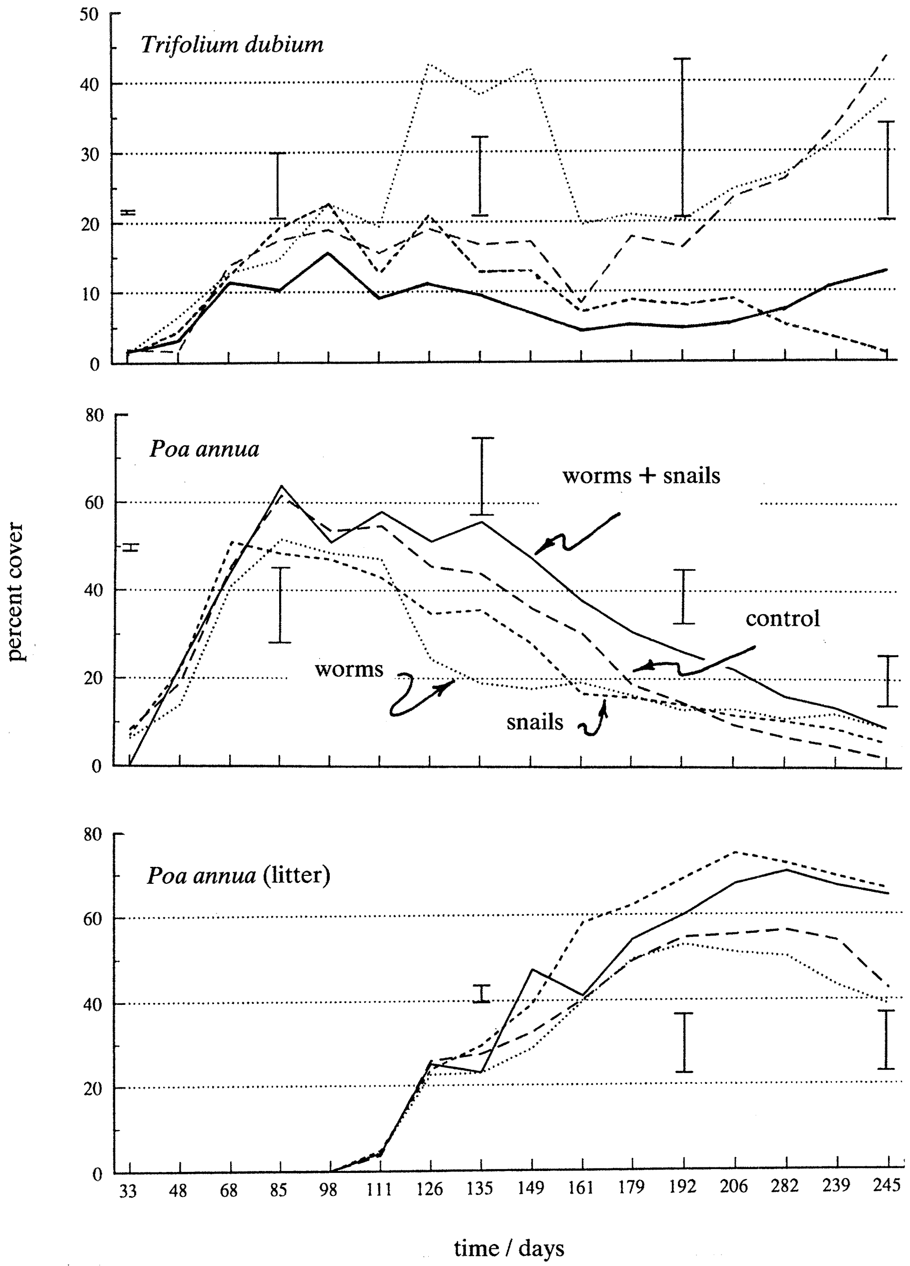

Figure 7. Plant dynamics in preliminary Ecotron experiment. Percent cover represents the percent of total area occupied by *Trifolium dubium*, *Poa annua*, and *P. annua* litter under different treatments. Treatments illustrated include worms and snails present, snails alone, worms alone, and control (without snails or worms). Results were derived from the analysis of overhead photographs, and 95% confidence intervals for significant treatment differences have been calculated for several points on the plot. These bars show distances curves must be separated by to be statistically significantly different at the 0.05 level.

work with enhanced CO_2 and UV-B will explore population and community responses to the interacting effects of rising temperature, CO_2 and UV-B.

Once sufficient experience is gained with the Ecotron, statistical issues surrounding ecological experiments will be addressed. Replication of experiments at different scales can be conducted by removing interchamber partitions to create different size compartments. Replication in time can be conducted by repeating experiments that use soil and cultures of plants, animals, and microbes generated and maintained at different times of the year. Biotic replication can be conducted by repeating experiments with similar trophic foodweb architectures but using different species. These kinds of replications, which are generally lacking in most ecological studies, will improve the robustness of our conclusions.

7. CONCLUDING REMARKS

The Ecotron aims to provide a CEF that can behave as a model or analogue of the real world, both biotically and abiotically. It is an experimental tool that fills the gap between complex field ecosystems and simplified computer models. It differs from most CEFs in that it is able to maintain multi-trophic level, terrestrial communities over many months, through several generations of plants and animals, with replication, and at different spatial scales.

From a basic research perspective, the Ecotron provides a means for tackling the burgeoning accumulation of untried ecological theories. Theories are often too complex to be tested under field conditions, but those with interesting or utilitarian predictions can be selected for preliminary trials in the Ecotron, whose aseasonal, rapid-turnover design allows relatively rapid ecological assessment of the theory's predictions. Results from the Ecotron cannot replace field work; rather, they provide guidance for future field work, may provide insights into the mechanisms explaining past results from field work, and are an essential halfway house between the relative simplicity of mathematical models and the full complexity of the field.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Figure 1. The Ecotron. Anticlockwise, from top, left; view of one bank of Ecotron units; view of vegetation in an ecosystem container from an early experiment; internal view of an Ecotron unit prior to loading an ecosystem container.