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INTERACTIONS AND COEXISTENCE OF SPECIES IN PASTURE COMMUNITY EVOLUTION

by

LONNIE WILLIAM AARSSEN

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Department of BOTANY

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date January 16, 1983

"IT IS GENERALLY ACCEPTED THAT IN ORDER TO COEXIST MORE THAN TRANSIENTLY SPECIES MUST DIFFER - THEY MUST SHOW NICHE SEPARATION. IF SPECIES ARE TOO SIMILAR ALL BUT ONE WILL BE ELIMINATED IN COMPETITION "

NEWMAN (1982)

"IF NOTHING IN BIOLOGY HAS MEANING EXCEPT IN THE LIGHT OF EVOLUTION AND IF EVOLUTION IS ABOUT INDIVIDUALS AND THEIR DESCENDENTS - I.E. FITNESS - WE SHOULD NOT EXPECT TO REACH ANY DEPTH OF UNDERSTANDING FROM STUDIES THAT ARE BASED AT THE LEVEL OF THE SUPER-INDIVIDUAL, ... WHAT WE SEE AS THE ORGANIZED BEHAVIOUR OF SYSTEMS IS THE RESULT OF THE FATE OF INDIVIDUALS"

HARPER (1977a)

ABSTRACT

Recent studies have demonstrated intraspecific differentiation in plants associated with specialization in response to biotic interactions (e.g. competition), but the selection mechanisms involved remain largely undetermined. The common assumption that species coexistence in nature can be generally explained by processes of natural selection for niche divergence does not have strong empirical support for plants. This problem is addressed in a study of vegetation patterns and species interactions in three different aged pastures. Ordination of time-series percentage cover surveys showed a trend of increasing community 'constancy' in older pastures and suggested a developmental relationship amongst the pastures. Soil analyses showed little correlation with species cover. Temporal patterns of fine-scale association between species was studied using contact sampling. Interspecific associations in younger communities were predominantly temporary in nature, and older communities had more associations which persisted essentially unchanged. This data formed the basis of a qualitative model of pasture community evolution which attributes within-community temporal changes to the selective forces accruing from biotic interactions.

Competition experiments were set up for investigating reciprocal responses between clones of individuals which were in immediate proximity to one another as actual neighbours in the fields. For each of the 3 pastures, five of the most abundant species were used in a diallel design and three different

species pairs were studied in a replacement series design. Results suggested that competitive relations between particular species may change with increasing pasture age either in the direction of increasing niche differentiation, more balanced competitive abilities, or towards competitive exclusion. Samples of Lolium perenne and Trifolium repens clones collected as neighbouring pairs from different localities in the oldest pasture were tested for their ability to grow in the presence of each other in a reciprocal transplant design. Natural neighbouring genet pairs had the most equitable component contribution to the total yield (i.e. highest combining ability) but did not differ in total yield from pairs of non-natural neighbours.

Results from these studies suggest that selection in response to competition and other interactions among neighbours (e.g. beneficence) may result in two alternative types of 'combining ability' in plants: 1) ecological combining ability (niche differentiation), and 2) competitive combining ability (balanced competitive abilities). Most evidence was found for 2). In this mechanism, selection reduces the differential in competitive abilities of inferior and superior components for resources on which they both make demands. These findings are discussed in relation to contemporary theoretical considerations of natural selection operating in systems of competition. A general evolutionary theory of coexistence is offered based on a proposed distinction between the concepts of fundamental niche and competitive ability.

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CHAPTER 1

GENERAL INTRODUCTION

PROBLEM

The coexistence of species which interact competitively has long interested ecologists and the question of what permits so many competitors to coexist in some communities has continued largely unresolved (Hutchinson 1959, 1961, Miller 1969, Grubb 1977, Werner 1979). The notion of coexistence has been so coupled with the concept of competition that it may be aptly defined as the 'absence of competitive exclusion', much like health is the absence of disease. In general, efforts have been concerned with establishing what factors or mechanisms prevent competitive exclusion of one species by another in a resource limited environment. Gause's principle has formed the theoretical basis and has been regarded as "... perhaps the only specific principle or law of nature ever to be proposed in ecology" (Vandermeer 1972a). The common notion of identical ecologies reduces the principle to a 'trite maxim' (Cole 1960) but recent perspectives have abandoned this and are more concerned with what is the limit of niche overlap beyond which competitive exclusion of one of the species is imminent. This more operational view embodies the theory of species packing and 'limiting similarity of species' (MacArthur & Levins 1967, MacArthur & Wilson 1967, MacArthur 1972, Newman 1982) and interestingly, recapitulates one of the earliest statements of the competitive exclusion principle: "Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other" (Grinnell 1904) (italics added).

Most of the support for Gause's principle comes from observations of niche differences in animals (e.g. see extensive review by Schoener (1974)). The idea of the 'food niche' of animals was central to the early theoretical development of the niche concept. Plant ecologists however must deal with the fact that plants have virtually nothing comparable to the food niche (Harper 1977b). The coexistence of animals can be explained in part by their mobility, but more importantly by the diversity of foods available to them, especially plants. We are still left however with the problem of explaining plant species coexistence. Willson (1973) and Antonovics (1978) have drawn attention to the scarcity of clear empirical evidence for within-community niche differentiation in plants. This is particularly true in herbaceous plant communities. Some recent studies have shown that co-occurring plant species may show differences, for example, in depth and placement of roots (Wieland & Bazzaz 1975, Parrish & Bazzaz 1976, Yeaton et al . 1977, Berendse 1979, 1981a, Fitter 1982), differences in response to microtopography (Bratton 1976, Silvertown 1981), partitioning of pollinators (Reader 1975, Parrish & Bazzaz 1978, 1979, Waser 1978) and separation along soil moisture gradients (Pickett & Bazzaz 1976, 1978, Werner & Platt 1976, Platt & Weis 1977). Yet, because higher plants are relatively immobile, lack any real choice in energy supply , and make demands on essentially the same resources (of light, water and nutrients) (Harper 1968), it is difficult to imagine how there could not be considerable niche overlap and enormous opportunity for competition in many plant communities. This has raised serious

doubts concerning any predominant or widespread importance of niche differentiation as a mechanism for coexistence of plants (Grubb 1977, Fagerstrom & Agren 1979, Pickett 1980).

The study of species coexistence is an evolutionary problem and is at the interface of population and community ecology. It concerns population interactions and community organization and diversity. It embodies a 'Darwinian view' of nature which places strong emphasis on the selection pressures which accrue from competitive interactions as opposed to a 'Wallacian view' which emphasizes more the selection pressures from abiotic factors (Harper 1977b). Darwin refers to the practice of some in making,

> .... the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; whereas it cannot, I think, be disputed that the nature of the other inhabitants, with which each has to compete, is ... generally a far more important element of success (Darwin 1859, p. 400).

Bock (1972) has emphasized that biotic interactions provide a "constant modification of selection forces" exerted by each species on other interacting species , and that this stands in sharp contrast to the highly "static selection" exerted by the physical environment. These two types of selection are not mutually exclusive; the effect of abiotic selection pressure may influence the response to biotic selection pressure and vice versa. Pigott (1982, p.402) draws attention to the frequent observation in vegetation studies that plants "respond to changes in their natural environment within the context of the vegetation of which they are a part", i.e. that the reaction of many individual species may result from, and give rise to,

responses of other species. Glesener & Tilman (1978) stress that under benign physical conditions, the major selection pressures related to environmental uncertainty will be of biotic origin and suggest that the changing genotypes of the organisms with which an individual interacts are the major source of this biotic uncertainty.

Central to much of community ecology is the view that species coexistence and community diversity reflects biological accommodation among species (e.g. Sanders 1968). This is the process of evolutionary adjustment of species to their biotic environment. McNaughton & Wolf (1979) point out that no empirical attempt seems to have been made to estimate the extent of biological accommodation or its role in community organization. Antonovics (1978, p.246) writes "... genetic changes in competitive relations have rarely been studied, either in established communities , during invasions or during ecological succession. Such changes are very pertinent to any discussion of communities as coevolved systems, and in need of investigation.... Even the conflict between convergent adaptation to a common environment, and divergent adaptation to other members of the community has never been explicitly investigated".

To understand the nature of biological accommodation is to understand the evolutionary mechanisms for coexistence. To approach this problem it is necessary to recognize the most basic components of the question at hand, components which have generally been neglected. If competitive exclusion is to take place between two interacting species (besides the requirement

that resources be in sufficiently limited supply) two essential conditions must exist: 1) their resource requirements (or the number of niche dimensions in which they interact) must overlap beyond a certain critical point, and 2) one of them must be a superior competitor for these common resource requirements. A comprehensive evolutionary theory of coexistence for potential competitors must therefore encompass two distinct components: 1) fundamental niche requirements and 2) relative competitive abilities. The first component has received widespread theoretical and empirical attention (e.g. Collwell & Futuyma 1971, Pianka 1974, 1976, Schoener 1974, Collwell & Fuentes 1975, Whittaker & Levin 1975, Roughgarden 1976, Armstrong & McGehee 1976, 1980, Fenchel & Christiansen 1977, van den Bergh & Braakhekke 1978, Newman 1982). The second component by comparison has received almost none.

Langford and Buell (1969) suggest that in the study of the evolution of biotic communities, investigations of the processes involved in the interaction among organisms should yield rich rewards. Evolution of biological accommodation in interacting species will affect community organization and direct the evolution of community characteristics (Whittaker & Woodwell 1971, Whittaker 1975). Recent work has found evidence for differentiation of single populations into specialized 'biotic ecotypes' produced in response to differing selection pressures exerted by different neighbours (Watson 1969, Linhart 1974, Turkington & Harper 1979c). The results of these recent developments have led some to advance a view for the plant community which focuses on the individual genotype as the

principal unit of community diversity (Antonovics 1976a, Harper 1977b, 1982). This merges the objectives of both population and community ecology into a common goal of understanding the consequences of selective forces operating on individuals. Efforts are now needed to characterize the precise manner in which selection produces biotic specialization of genotypes within single populations and its role in the evolution of coexistence and hence, of communities.

The system under study in this thesis is the pasture community. Pastures are generally regarded as systems in which competition is an important interaction (see extensive reviews by Donald (1963) and Risser (1969)) and where genetic variation in constituent species is abundant and highly susceptible to change in response to physical and biotic factors of the environment (see review by Snaydon (1978)). The aim of this study is to investigate the qualities of biotic interactions important in evolutionary mechanisms of specialization and accommodation amongst coexisting plant species and how these contribute to the structure and evolution of the pasture community. The problem under investigation is primarily concept-oriented rather than system-oriented. Objectives are not so much to understand more about pasture ecology as to study a system in which a high intensity of neighbour interactions is predicted and in which different stages of community development are available for investigating evolutionary changes in species in response to their biotic environment. Emphasis is centered on the following questions:

1) How do interspecific competitive relations change as a

community ages?

2) Is there greater biotic specialization in populations from older communities?

3) Is specialization reciprocal between species?

4) Does biotic specialization occur at both the species and genotype levels?

5) What is the evolutionary mechanism of biotic specialization?

6) What role does the evolution of biotic specialization, permitting coexistence, have in community evolution?

TERMS AND CONCEPTS

The terminology related to niche, competition and coexistence has been used in many varied ways in the literature. To avoid ambiguity it is necessary to define the terms as they are used in this thesis. The choice of meanings for terms and concepts in ecology often reflects the biases and objectives of the practitioner. The same is true here. It is proposed however that the semantic confusion surrounding the concepts of niche and competition is related to the fact that an attempt to characterize one is often embedded in a characterization of the other, with the result that neither is clearly understood. In what follows, an attempt is made to elucidate operational meanings for, and a distinction between, fundamental niche and competitive ability in particular reference to plants.

A) INTERACTION AND COEXISTENCE

If two species in nature interact, this implies in the most general sense that one (or both) species in some way enter(s) into the sphere of influence of the other at some time during their life cycles. Types of interaction recognized by ecologists include competition, predation, parisitism, mutualism, amensalism and commensalism. If a certain interaction between the members of two populations occurs repeatedly (not necessarily continually but at least periodically) in a given area, then the two species may be regarded as 'coexisting'. In plants for example, a competitive interaction between two species populations may never occur

between vegetative individuals, but may repeatedly occur between seeds for sites suitable for germination and establishment, or competition may occur for pollinators or dispersal agents. If neither species however has the potential to continuously enter into the sphere of influence of the other in any way, either due to limitations imposed by dispersal or by genetically determined site requirements, then the two species do not coexist. Coexistence then is continuous interaction, and interaction is an event in which the activity of one organism affects the activity of another.

In this thesis, the term coexist will be used in the above context, although Harper et al. (1961) use the term cohabit in a similar sense, i.e. "individuals (or their products) ... come into such proximity that a struggle for existence could reasonably be considered possible". Werner (1979) suggests a distinction of terminology based on differences in temporal and/or spatial scale: 'coexistence' implies a stable equilibrium, incorporating the notion of continuous interaction detailed above; 'cohabitation' implies a sharing of habitat or resources without interaction (or at least without continuous interaction); and 'cooccurrence' or 'occurring together' implies only a mutual presence in which no particular assumption is made regarding any incidence of impact by one organism on another.

B) FUNDAMENTAL NICHE REQUIREMENTS

The different meanings of the term 'niche' have been reviewed by several authors (MacArthur 1968, Vandermeer 1972, Whittaker et al. 1973, Hurlbert 1981). Elton's (1927) 'all-inclusive' notion of the niche has found common usage (e.g. Krebs 1979, Ricklefs 1979) and is regarded as the species' 'position', 'role' or 'profession' in nature, including its competitive relationships with other species. Where the basic niche concept has been used interpretatively however, competitive ability has rarely ever been regarded as part of the niche of a species. The most consistent usage of the term niche recognizes its earliest connotation (Grinnell 1924, 1928) as the idealized distribution of individuals in the absence of interactions with other species. Grinnell's conception of the niche was "pre-interactive - the potential area within which a species can live as opposed to the area where one actually finds it" (Vandermeer 1972). This general view is reflected in the later more specific conceptions of 'fundamental' versus 'realized' niche (Hutchinson 1957), 'pre-competitive' versus 'post-competitive' niche (Levins 1968, Colwell & Futuyma 1971), and 'potential' versus 'actual' niche (MacMahon et al. 1981).

That competitive ability is not part of the characterization of a species niche is further evident from the competitive exclusion principle. Variously stated, the principle essentially means that two species with very similar niches cannot coexist - one will out-compete the other. According to Gause's principle, common niche results in competitive exclusion which necessarily means different

competitive abilities; this categorically precludes competitive ability from the definition of the niche. Evidently then, most ecologists have implicitly regarded competitive ability as exclusive of the principal idea of the 'niche' in spite of contradictory claims (following an Eltonian view) that the niche represents all the relationships of the organism with its environment, which includes its competitors. This raises the question of the relationship between fundamental niche and biotic interaction in general.

It is proposed here that fundamental niche (or fundamental niche requirements) be considered as all possible sets of resources (e.g. energy, chemicals, conditions of site) and resource states (e.g. quantity, quality, intensity, renewability, periodicity, etc.) that meet minimal requirements for a species (individual or population) to leave descendents. The activities of other species affects the availability of required resources to a reference species through effects on one or more of these resource states. These effects translate into biotic interactions - the activity of one organism influences the well-being of another. Other organisms therefore affect the availability of niche requirements (and in turn affect fitness) but it is crucial to recognize that they themselves are not part of the niche requirements (with the exception of obligate symbionts as in lichens, or obligate benefactors such as pollinators or individuals of the opposite gender in dioecious species). This parallels a recent view from Hurlbert (1981, p.177):

> As a consequence of its resource-using activities, an organism has many influences on the surrounding community or ecosystem. If the totality of these influences or impacts is regarded as the 'functional role' of the organism, then 'role' is not equivalent to niche, as many authors would have it, but rather 'role' is a consequence of the niche.

Biotic interactions then are consequences of the niches of species. In particular, they are consequences of niche overlap between species. Organisms interact only if they have at least some resource requirements in common. Taking this one step further, the coexistence of organisms depends not only on their having some resouces requirements (niche) in common, but also on the impact that each has on the availability of resources required by the other. This two-component perspective for coexistence applies to all biotic interactions and has been generally recognized in predator/prey and host/parasite systems for example, but largely neglected in systems of competition because the notion of competitive ability has been infused into the precept of niche.

Following above arguments, it is proposed that fundamental niche requirements be regarded as a distinct concept from competitive ability and will be defined in this thesis in a pre-interactive sense most closely resembling the hyper-volume view of Hutchinson (1957), i.e. a multidimensional description of the whole range of resource requirements encompassing all environmental limitations of a species (population or individual) within which it is potentially capable of leaving descendents - "... primarily without reference to competitors, but merely in terms of requirements and tolerances ..." (Hutchinson 1978).

A habitat in which a species is capable of living, represents an actual proportion of the species' fundamental niche that is available for occupation. In practice however, the presence of other species may deny occupation of certain portions of available niche space, or they may expand the available niche space, and hence delineates a 'post-interactive' realized niche within the habitat. Accordingly, biotic interaction is a consequence of fundamental niche and realized niche is a consequence of biotic interaction.

C) RELATIVE COMPETITIVE ABILITY

The term 'competition' has come to have a variety of meanings in ecology. In this thesis the strictest definition of the word will be used following proposals in reviews by Birch (1957) and Milne (1961). Competition will be defined as an interaction between two (or more) organisms in which each reduces the availability of resource units to the other from a limited supply on which they both make demands. Tinnin (1972) points to the variable and confusing relationship between 'competition' and 'interference' in the literature. A further variation in terminology was introduced by Hall (1974a) who regards interference as any effect, detrimental or beneficial, of one organism on another, the context in which the term 'interaction' is used presently. In underlying mechanisms to be considered later, the more traditional view that competition can be divided into two types - 'exploitation' and 'interference' - (Park 1954, Birch 1957, Miller 1967, 1969, Berendse 1981b) will be adopted here.

An even more confusing term in the literature than 'competition' is 'competitive ability'. Competitive ability alone is misleading as it is not an absolute characteristic of an individual; it has meaning only in a relative context to others. Competitive ability is manifested only within (and characterized entirely by) the prevailing neighbourhood of interacting individuals making demands on the same limiting resource(s). Competitive ability may be regarded as a combined measure of: 1) the ability of an individual to reduce the availability of limited resources to another, and 2) the ability to tolerate reduction in resource availability by another. Attributes of a plant which confer competitive ability may in the first case be considered 'offensive' characteristics, and in the second case, 'defensive' characteristics.

Offensive Characteristics Conferring Competitive Ability

Numerous characteristics of a plant will in concert determine its overall ability to reduce the availability of resources to another. Offensive characteristics important to competitive ability fall into two categories and define two types of relative competitive ability: 1) relative exploitation ability - the relative efficiency of exploitation of resources, and 2) relative interference ability - the relative level of interference with access to resources (Table 1). Exploitation competition reduces the availability of limited resources to another by reducing the quantity of those resources by removal through uptake from the site. This requires attributes related solely to effective procurement of resources. Interference

TABLE 1. Possible characters which confer competitive ability in plants in contexts of a) relative exploitation ability, and b) relative interference ability.

a) EXPLOITATION COMPETITION

1. Rapid growth rate (i.e. effective photosynthetic metabolism and/or effective or rapid uptake/storage of nutrients and/or water).

2. Tall plant height, long hypocotyls stems, petioles (Black 1960).

3. Large leaf area (Black 1960).

4. Leaf orientation for effective capture of light (Monsi et al. 1973).

5. Deep and/or extensive root system.

6. Large embryonic capital (seed size) (Black 1958).

7. Effective timing (e.g. early arrival at a site, early germination and/or early establishment) (e.g. Sagar 1959, Harper 1961).

8. Attractive flowers, pollen, seeds, or fruits for effective pollination and/or dispersal (Donald 1963, Levin & Anderson 1980, Davidson & Morton 1981).

9. General adaptation, resistence, or plasticity to 'adverse' environmental conditions other than those imposed by competitors (Daubenmire 1968).

b) INTERFERENCE COMPETITION

1. Encouraging, sheltering or carrying pests, disease organisms or predators which affect other species (Janzen 1966, Sandfaer 1968, 1970a, 1970b).

2. Encouraging/producing rhizosphere components or soil reactions unfavourable to other species (Trenbath 1976).

3. Altering the ability of the environment to provide specialized trigger mechanisms (e.g. for the breakage of dormancy (Harper 1964)).

4. Depositing a dense layer of litter on the ground surface (Grime 1973).

5. Releasing substances which are directly toxic to other species (i.e. allelopathy) (Rice 1974).

6. Interfering with pollination (e.g. "pollen allelopathy") (Kanchan 1980).

competition, in contrast, reduces the accessibility of those resouces (i.e. without resource removal). This involves attributes directly or indirectly related to preventing a competitor from getting a resource. Grime (1979, p.20) argues that an ability to maximize dry matter production is a "general feature" of competitive ability in plants. From Table 1 however, it can be seen that a superior plant competitor will not necessarily be the 'biggest', 'strongest', 'most aggressive', or 'highest yielding' (Harper 1965) and this is supported by evidence from competition experiments with plants (de Wit 1970).

It is important to note that interference effects may occur regardless of niche overlap or resource limitation, and as detrimental effects may only be incurred by one species, such an interaction may be more suitably referred to as 'amensalism'. (Harper (1961) has preferred to use the term interference to encompass both competition and amensalism, i.e. "... those hardships which are caused by the proximity of neighbours ..."). Interference phenomena however are usually thought to be evolved responses to resource shortage imposed by competition (e.g. Gill 1974, Roughgarden 1979).

Defensive Characteristics Conferring Competitive Ability

In some species, higher relative competitive ability may be conferred by a higher tolerance during periods when resources are limited by competition (for example by delaying or forgoing reproduction in that year, varying the number or size of different organs, or by dying back above ground parts but

avoiding total death). This will be particularly important in plants, where tolerance ability will be a reflection of such characteristics as seed dormancy, life forms with sustaining underground parts (e.g. as in hemicryptophytes and geophytes), indeterminate growth and modular construction (Harper 1964, 1977b). Immunity to toxic allelopathic substances produced by others would also be a type of defensive characteristic conferring competitive ability.

PROGRAMME

The studies described in this thesis are centered on a system of three coexistent stages of pasture community development. The approach to the problem under investigation is two-fold: 1) time-series surveys of vegetational patterns; 2) experimental analyses of biotic interactions. The two approaches complement one another and each contributes information not available from the other.

Percentage cover surveys of the three pastures were carried out periodically over a 33-month period to obtain quantitative data for characterizing the developmental features of pasture community evolution. The principal aim was to obtain an empirical basis for referring to the developmental relationship of the three communities. Important assumptions however are recognized concerning the unlikelihood that the three pastures experienced identical environmental conditions (e.g. of climate or grazing) at any given stage of development.

Quadrat sampling serves to reveal gross vegetational patterns but it is not wholly sensitive to the individual plant's experience of its immediate neighbours. The sessile habit of terrestrial plants and the high sward density in pastures means that a recording of the number of above ground physical contacts between individuals reflects a parameter of fine-scale interaction. If monitored over time this procedure represents a quantitative basis for discussing patterns of local coexistence at the level of individual experience, i.e. the "plant's experience of community diversity" (Harper 1977b).

This sampling method, known as 'contact sampling', is used in the present study for this purpose. It was designed originally by Yarranton (1966) and has been used in recent studies in pastures (Turkington et al. 1977, Aarssen et al. 1979, Turkington & Harper 1979a, 1979b, Saulei 1981). Alternatives in methodology and data analysis as well as its versatility and value as a method of vegetation sampling have recently been presented in detail by de Jong et al. (in press).

A variety of experimental methods were employed to investigate the biotic interactions occurring between clones of individuals which were in immediate proximity to one another as actual neighbours in the fields and differences in interactions for the same species in pastures of different age. Use is made of the mixture diallel (e.g Trenbath 1978) and replacement series (de Wit 1960) designs. A further method of reciprocal phytometer transplanting is devised and used to investigate reciprocal biotic specialization in two species in response to different neighbouring genotypes of the same species collected from different neighbourhoods in the oldest pasture (i.e. biotic specialization at the genotype level).

Where appropriate, results are interpreted by placing them into a theoretical and evolutionary context. This is pursued at length in the final chapter which explores the implications of natural selection operating in systems of competition. A general evolutionary theory of coexistence is proposed and discussed in relation to other theories of coexistence in contexts of competition.

CHAPTER 2

THE STUDY SITE: VARIABLES AND PATTERNS

INTRODUCTION

The study site consists of three pastures located on the dairy farm owned by William and Mary Chard, 25704 Fraser Highway, Aldergrove (SW 1/4 Sec. 25, Twp. 10) in the Fraser Valley of British Columbia (49° 03' 45" N Lat.; 122° 30' 45" W Long.). The farm is situated in the Coastal Douglas-fir biogeoclimatic zone of B.C. (Krajina 1965), but has been managed as grazing land since the turn of the century. The three pastures were last ploughed and seeded in 1939, 1958, and 1977 and hereinafter the fields will be named after these dates or will be referred to as the 40, 21 and 2 year-old pastures (respectively) indicating the ages of the fields when clones were collected for competition experiments. The fields were also used as pastures prior to the above most recent planting dates. Details are summarized in Table 2.

TABLE 2. Details on the three study fields.

Approx. date of clearing (from scrub/brush) and first ploughing	Date of last ploughing and seeding	Age when reseach commenced (years since last ploughed)	Size (ha)
1942	1977	2	1.04
1930	1958	21	1.44
1900	1939	40	0.99

The pastures have always been either grazed by cattle or occasionally cut for hay. Grazing in all three fields involves on average, 20 to 30 cows present intermittently from May until

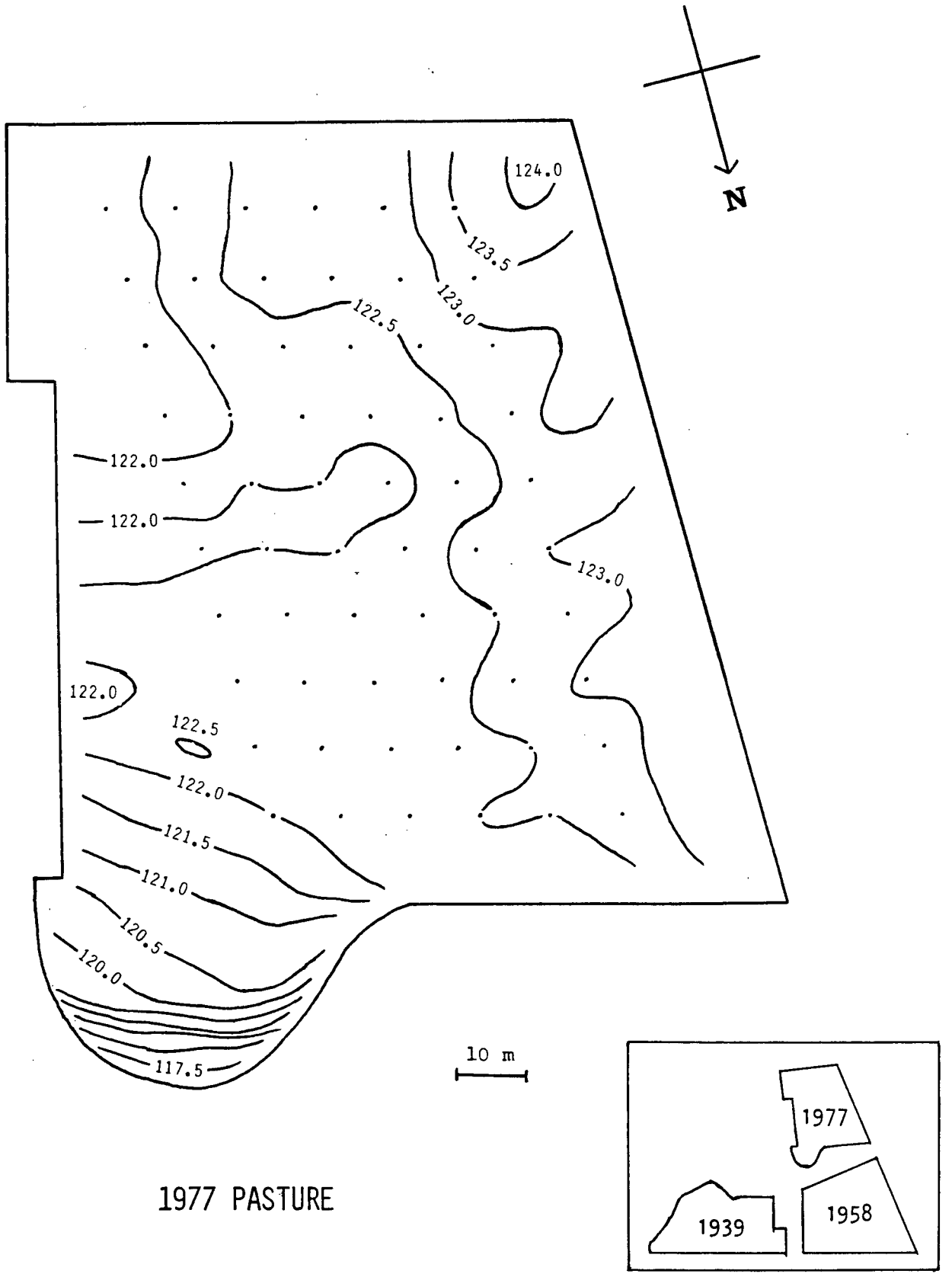
November. Weather conditions rarely permit grazing between December and April. None of the fields have been reseeded since the stated dates, nor have they ever received any chemical treatment (fertilizers or pesticides). Barnyard manure is mechanically spread periodically.

The 1939 and 1977 pastures are generally flat with a slight slope in the 1977 field. The 1958 field is gently rolling. The elevation of the site varies from 110 to 122 m above sea level. Contour maps of the fields are shown in Figure 1. The pastures are contiguous (Fig. 1) but separated from one another by rows of trees. The entire site is enclosed by wire fencing and bordered by drainage ditches and laneways, and in some places, trees.

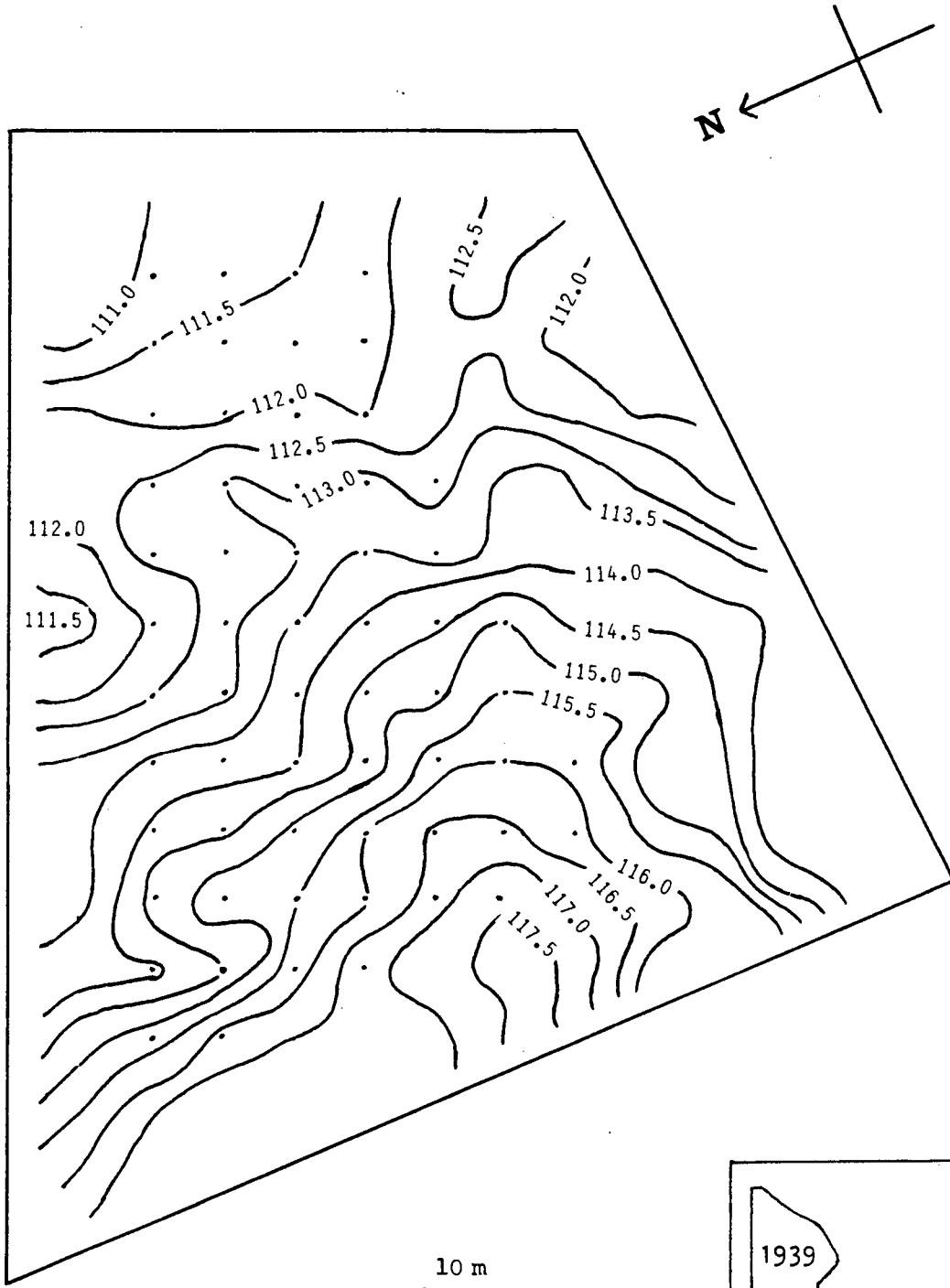
THE GEOLOGY

The general area is underlain by truncated strata of Eocene sediments upon which lie a parent material of glaciomarine deposits of latest Pleistocene age (11,000 - 12,000 years B.P.). The study site specifically has moderately to fine-textured clay loam, is generally non-stoney and poor to moderately well drained. The soil is Luvisolic Humo-Ferric Podzol and Orthic Humic Gleysol (Canada Soil Survey Committee 1978). Average top soil depth (down to the top of the 'C' horizon) is 80 - 100 cm.

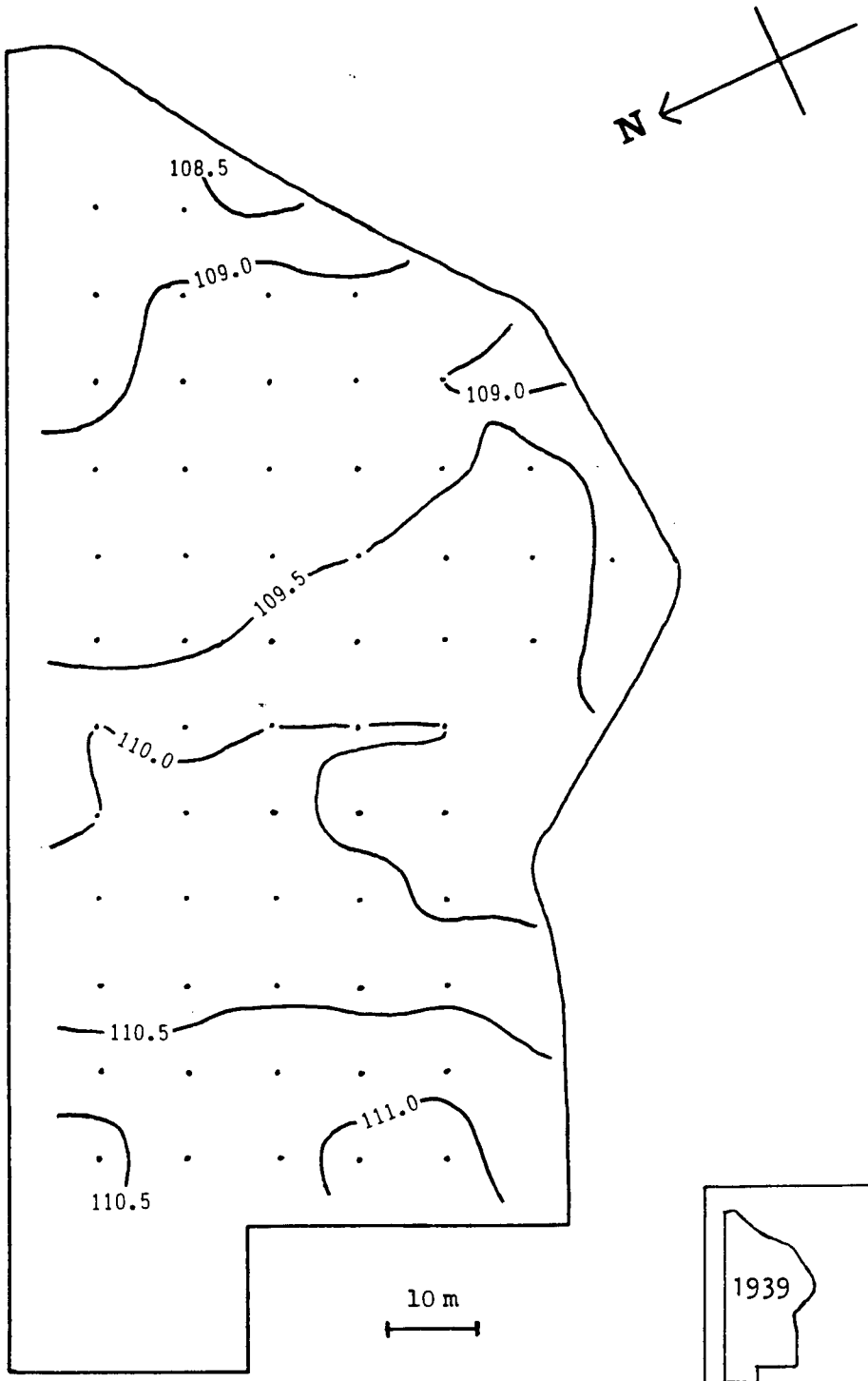
FIGURE 1. Contour maps of the study fields. Elevations are given in meters above sea level. Points represent the locations of 60 quadrats in each field used in the vegetation surveys. Insets show the positional relationship of the three pastures.

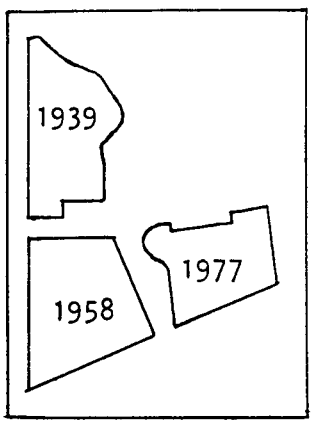


1977 PASTURE



1958 PASTURE





1939 PASTURE

THE CLIMATE

Most climatic data were recorded at Aldergrove, 2.4 km east of the study site. The study area features a relatively mild winter with heavy precipitation, mostly in the form of rainfall, averaging 164.3 cm per annum (1953-1970). In winter the area is usually not covered by snow for periods lasting longer than 1 or 2 weeks. The mean monthly distributions of rainfall, snowfall and total precipitation are shown in Table 3.

TABLE 3. The monthly distributions of a) rainfall (cm), b) snowfall (cm) and c) total precipitation (cm) (means for 1953-1970, Aldergrove).

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
a)	18.7	16.5	14.6	10.9	7.2	6.6	4.3	5.2	9.4	18.5	20.7	22.0
b)	41.9	12.4	10.4	0.5	0.3	0.0	0.0	0.0	0.0	0.0	5.1	25.4
c)	22.9	17.8	15.6	10.9	7.2	6.6	4.3	5.2	9.4	18.5	21.2	24.5

The area is exposed to predominantly north and north-easterly winds in the fall and winter months. Winds are mostly from the south and south-west in spring and summer. For the years 1953 to 1970 the maximum summer air temperature recorded was 36°C while the minimum winter temperature was -20 °C. Monthly distributions of climatic variables related to temperature and hours of sunshine are shown in Table 4.

TABLE 4. The monthly distributions of: a) mean daily temperature (°C), b) mean daily maximum temperature (°C), c) mean daily minimum temperature (°C); d) number of days with frost (daily minimum below 0 °C) (means for 1953-1970, Aldergrove); e) number of hours of sunshine (means for 1970-1980, Pacific Regional Atmospheric Environment Service).

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
a)	0.8	3.3	4.9	7.6	11.5	14.2	16.1	16.0	13.6	9.3	4.9	2.5
b)	4.1	7.6	9.8	13.3	17.8	20.2	23.2	22.9	20.3	14.6	8.8	5.7
c)	-2.4	-0.9	0.0	1.9	5.2	8.2	8.9	9.1	6.9	4.1	1.1	-0.7
d)	21	15	17	9	3	0	0	0	1	5	13	17
e)	68	77	112	164	209	217	291	245	174	137	72	54

THE SPECIES

A total of 28 naturalized herbaceous species are present in the 3 pastures, 11 of which are grasses (Table 5). All three fields were last sown with a seed mixture comprising 5-10% *Trifolium repens*, 15-20% *Dactylis glomerata* and 70-80% 'Highland' forage mixture (Table 6). The same species were present in this mixture at all three seeding times (Richardson Seed Co., pers. comm.) but information on their relative proportions is available only for the mixture used in planting the 1977 pasture (Table 6).

TABLE 5. A species list for the study site.

GRASSES	NON-GRASSES
Agropyron repens (L.) Beauv.	Achillea millefolium L.
Agrostis alba L.	Carex sp.
Anthoxanthum odoratum L.	Cerastium vulgatum L.
Dactylis glomerata L.	Cirsium arvense (L.) Scop.
Festuca rubra L.	Hypochoeris radicata L.
Holcus lanatus L.	Juncus sp.
Lolium multiflorum Lam.	Medicago lupulina L.
Lolium perenne L.	Plantago lanceolata L.
Phleum pratense L.	Plantago major L.
Poa compressa L.	Ranunculus acris L.
Poa trivialis L.	Rumex acetosella L.
	Rumex crispus L.
	Rumex obtusifolius L.
	Stellaria media (L.) Vill.
	Taraxacum officinale Weber
	Trifolium repens L.
	Trifolium pratense L.

A) PATTERNS IN THE VEGETATION

Each of the three pastures was surveyed for percentage cover of species on 9 occassions over a 33-month period. Three spring (March), three summer (June) and three fall (September) surveys were carried out. The surveys were conducted in order to test two hypotheses: 1) Species composition is the least similar between the youngest and oldest pastures; 2) Species

composition is the most variable throughout the 33-month period in the youngest community and the least variable in the oldest community.

TABLE 6. Species composition of the 'High-land' forage mixture used in sowing the three pastures. Proportions shown are for the 1977 mixture only. Lolium perenne was a tetraploid variety in the 1977 mixture.

Dactylis glomerata	45%
Trifolium pratense	20
Lolium perenne	15
Lolium multiflorum	10
Phleum pratense	5
Trifolium repens	2
Ladino Clover (T. repens) (1977 only)	3

Methods

Each survey was based on data collected from 25 systematically positioned points (5 rows of 5) within each of 60 systematically arranged 'permanent' quadrats, each 0.5 m x 0.5 m, giving a total of 1500 points per field. Relative cover results for an initial survey of 2000 points (in 80 quadrats) per field were not substantially changed after randomly discarding up to 500 points from the data. To minimize field effort, all subsequent surveys were therefore based on 1500 points per field. Each quadrat was approximately 10 m from each neighbouring quadrat and a border of at least 10 m was avoided

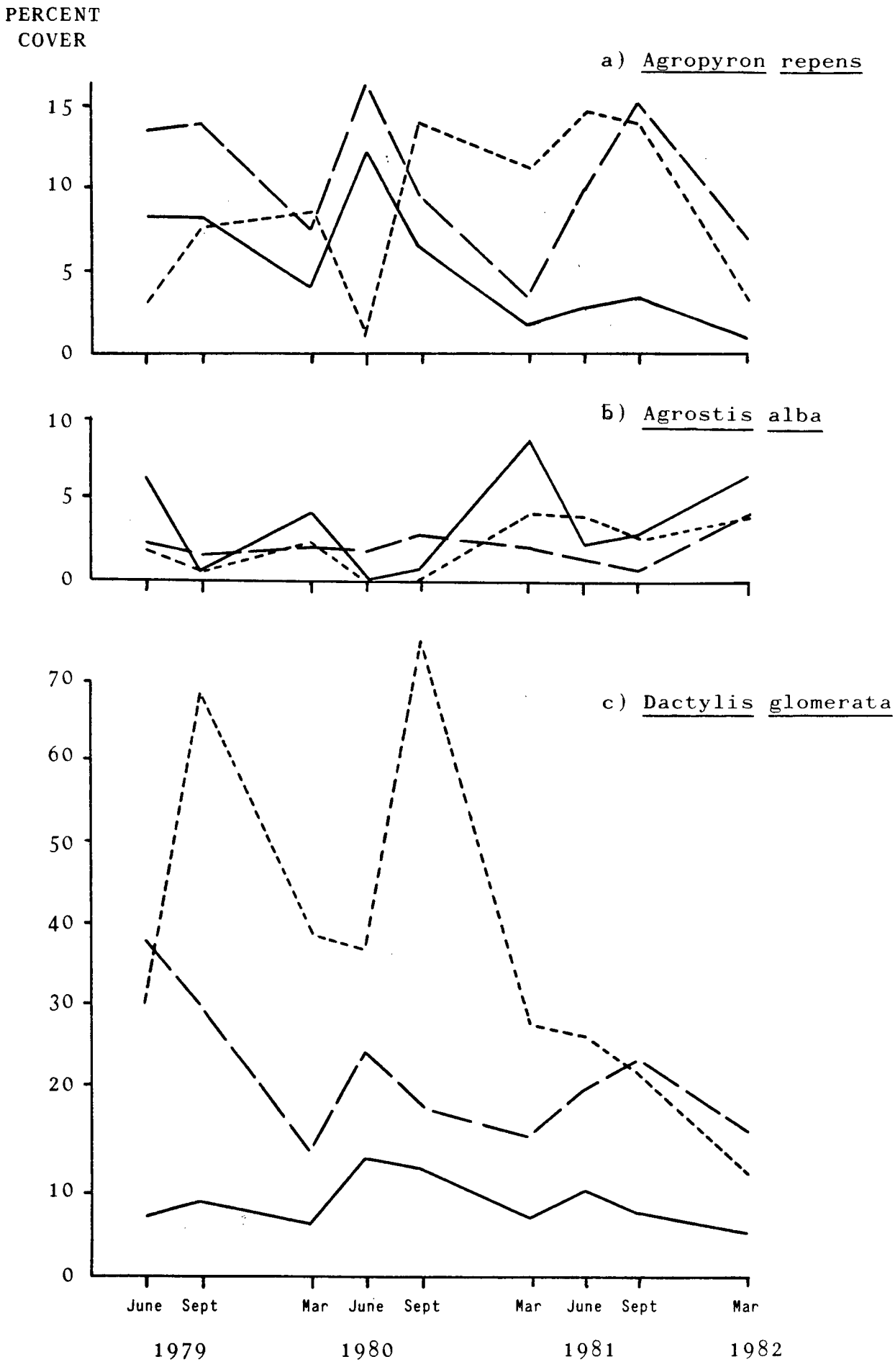
as a buffer zone around the perimeter of each pasture (Fig. 1). Estimates of percentage cover were obtained by recording all different species encountered in a downward (vertical) projection at each point and expressing these in terms of percentage cover for every 25 points examined. The total percentage of ground covered by the species in any one quadrat will exceed 100% because the leaves of more than one species may cover the same point on the ground. Due to difficulty of quick differentiation between Lolium multiflorum and Lolium perenne and because they are known to hybridize readily in nature (Hubbard 1968), the two species were lumped together and recorded as one species. Upon careful inspection, specimens of Lolium multiflorum were only identified in the 1977 field; all occurrences of Lolium spp. were therefore recorded as Lolium perenne .

To analyze the percentage cover data, a reciprocal averaging, eigenvector method of ordination was employed using a program written by Dr. Gary Bradfield developed after the algorithm outlined in Orloci (1978).

Results

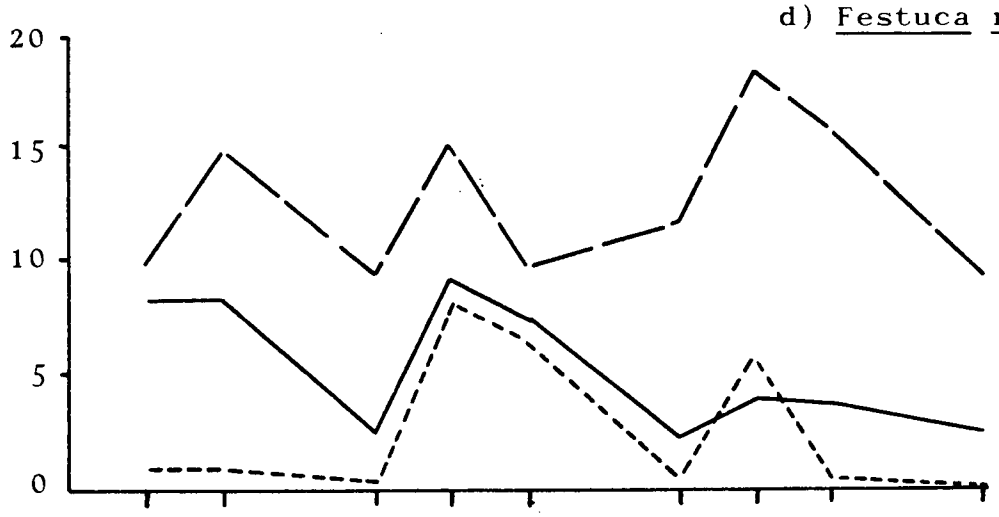
The mean total percentage cover over the study period for the 1977, 1958 and 1939 pastures was 159%, 186% and 212% respectively. The relative representations of the most abundant species in the 3 fields are shown for each survey in Figure 2, and as means over the study period in Figure 3. Some trends are notable. With increasing field age, Dactylis glomerata shows a general decline in percentage cover while Holcus lanatus , Poa compressa and Trifolium repens show an increase in cover.

FIGURE 2. Total percentage cover of the 14 most abundant species present in the three pasture communities over the 33-month sampling period;
--------1977 field; —— —— 1958 field; ———— 1939 field.

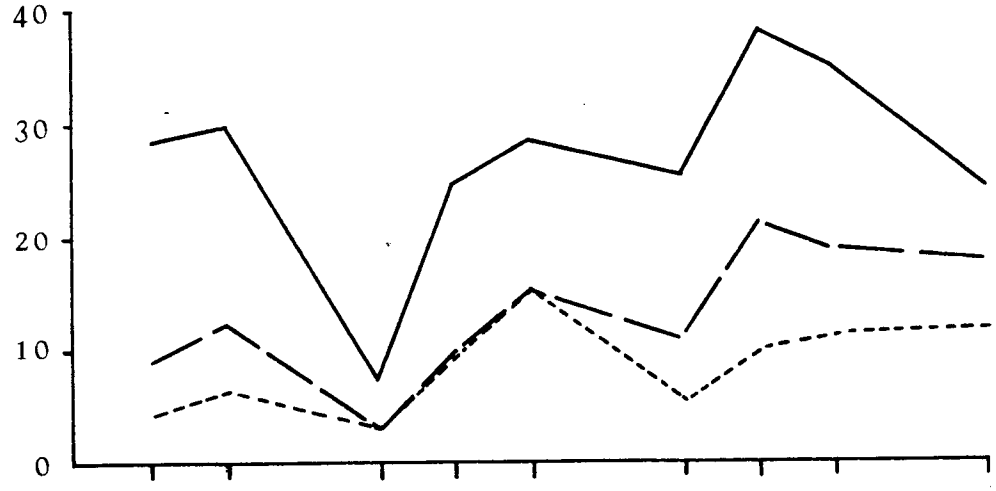

PERCENT COVER
a) Agropyron repens
15
10
5
0
b) Agrostis alba
10
5
0
c) Dactylis glomerata
70
60
50
40
30
20
10
0
June
Sept
Mar
June
Sept
Mar
June
Sept
Mar
1979
1980
1981
1982

PERCENT
COVER

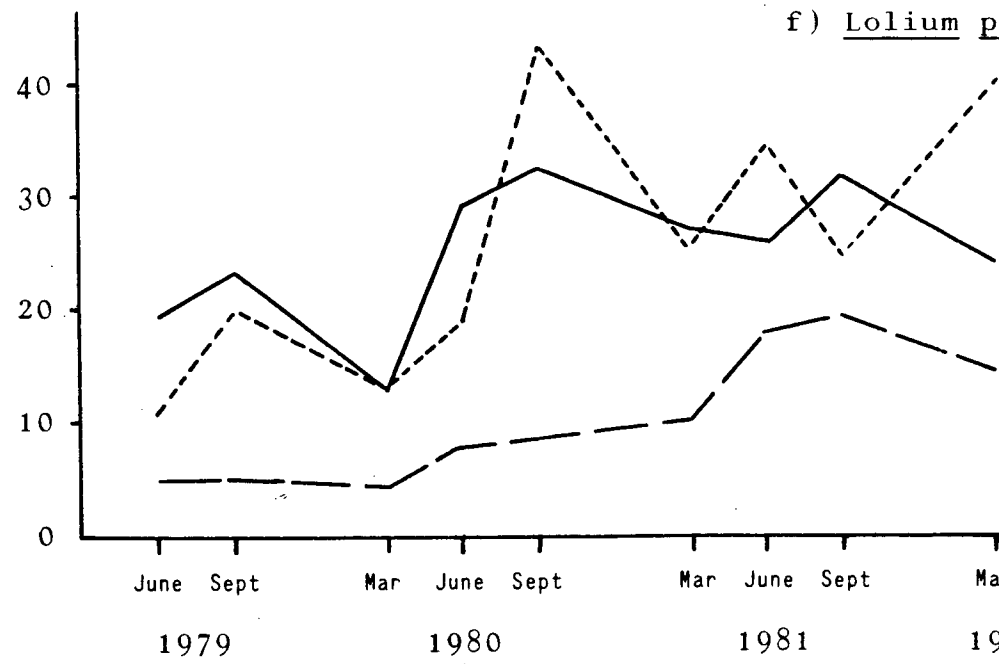
d) Festuca rubra

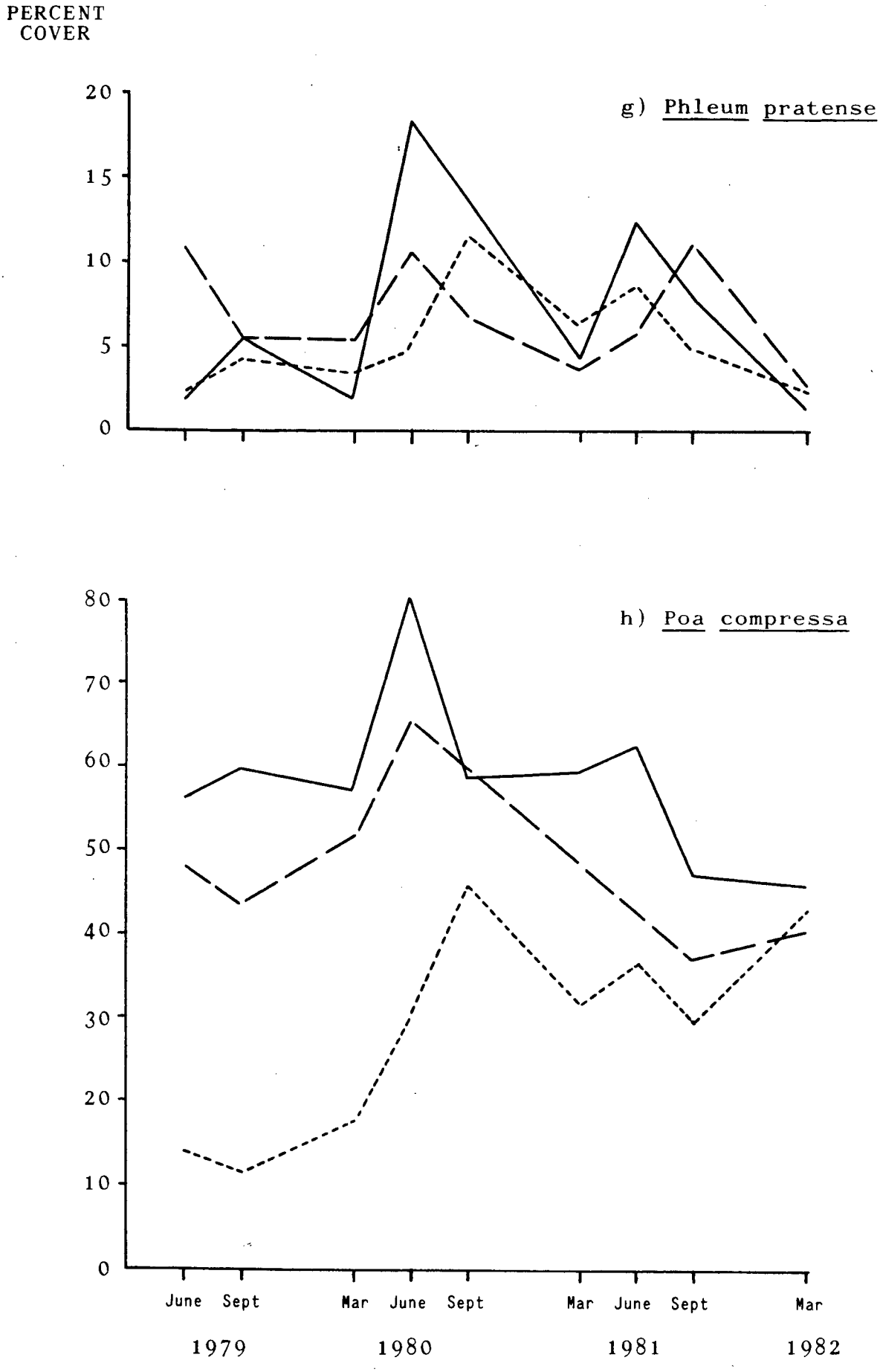


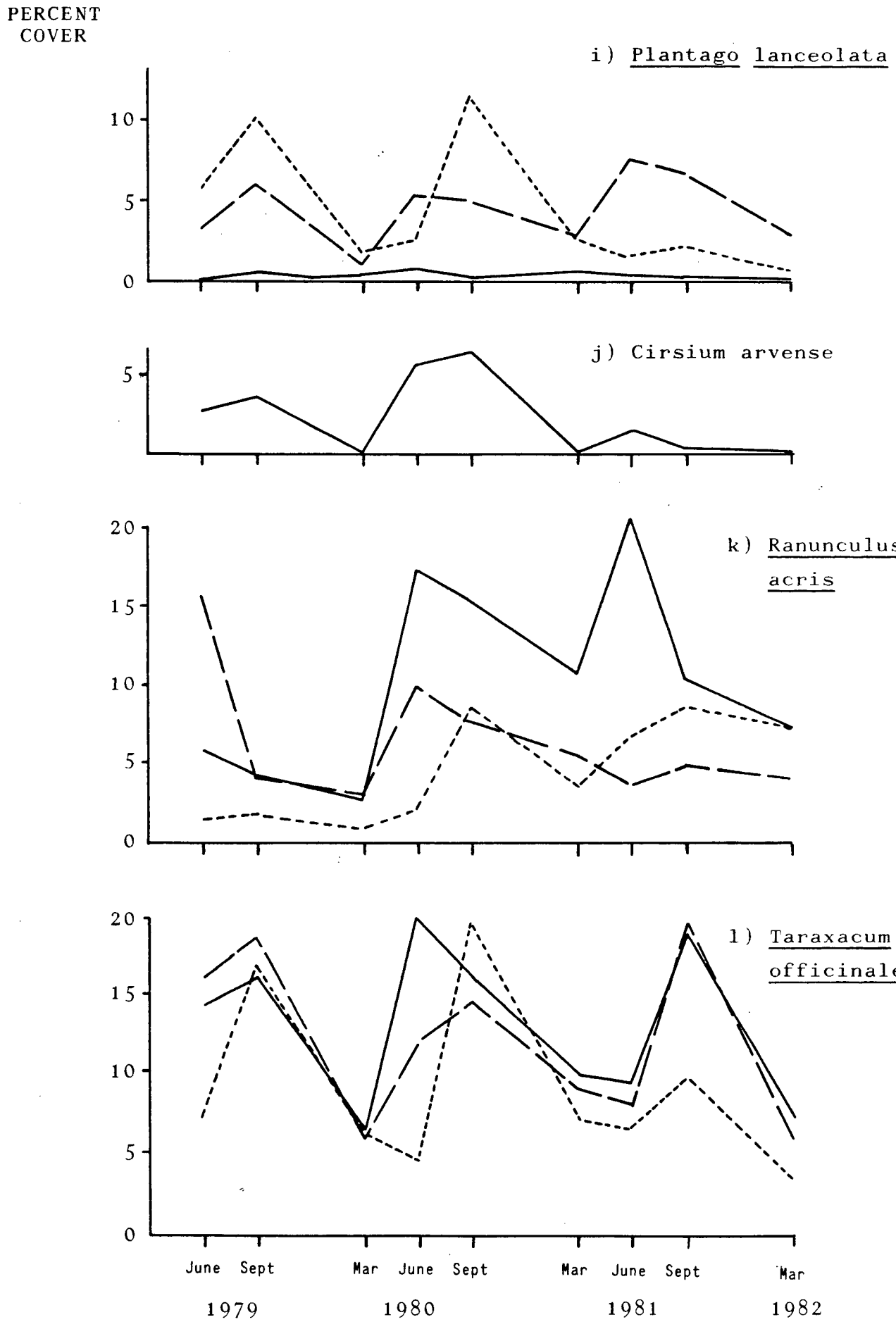
e) Holcus lanatus



f) Lolium perenne




PERCENT COVER
g) Phleum pratense
20
15
10
5
0
h) Poa compressa
80
70
60
50
40
30
20
10
0
June
Sept
Mar
June
Sept
Mar
June
Sept
Mar
1979
1980
1981
1982


PERCENT COVER
i) Plantago lanceolata
10
5
0
j) Cirsium arvense
5
k) Ranunculus acris
20
15
10
5
0
l) Taraxacum officinale
20
15
10
5
0
June Sept Mar June Sept Mar June Sept Mar
1979 1980 1981 1982

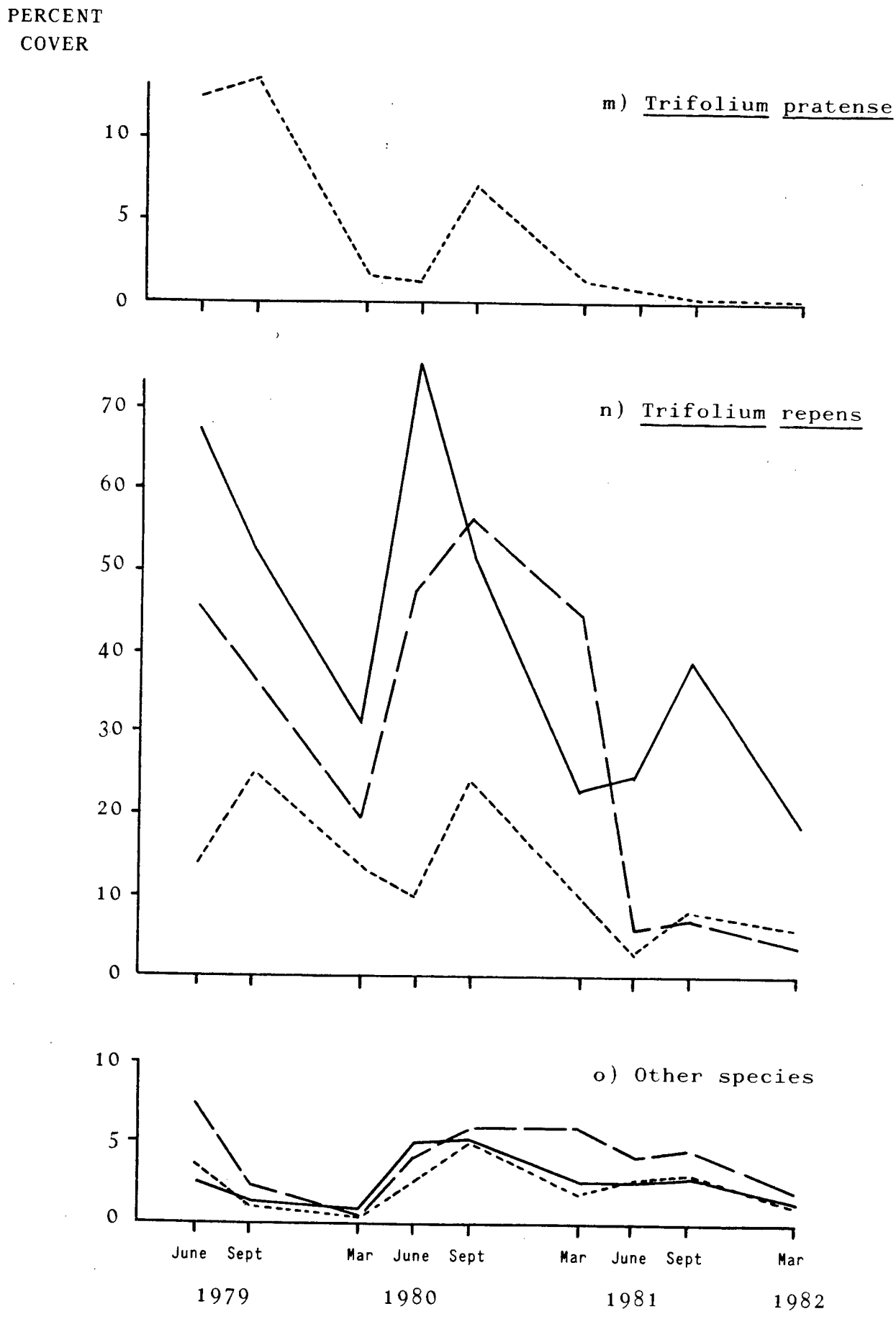

PERCENT
COVER
m) Trifolium pratense
10
5
0
n) Trifolium repens
70
60
50
40
30
20
10
0
o) Other species
10
5
0
June
Sept
Mar
June
Sept
Mar
June
Sept
Mar
1979
1980
1981
1982

FIGURE 3. The 10 most abundant species present in each study field based on mean percentage cover over the study period. Standard errors are indicated by vertical bars. The 5 species collected and cloned for competition experiments are shown by cross-hatching and stippling. Differences in percentage cover of these 5 species depending on field age are significant at $P<0.05$ from an analysis of variance using a MIDAS program (Fox & Guire 1976). Analysis was based on log-transformed data wherever an F-test indicated unequal variances in the raw data.

Ar - Agropyron repens

Dg - Dactylis glomerata

Fr - Festuca rubra

Hl - Holcus lanatus

Lp - Lolium perenne

Pp - Phleum pratense

Pl - Plantago lanceolata

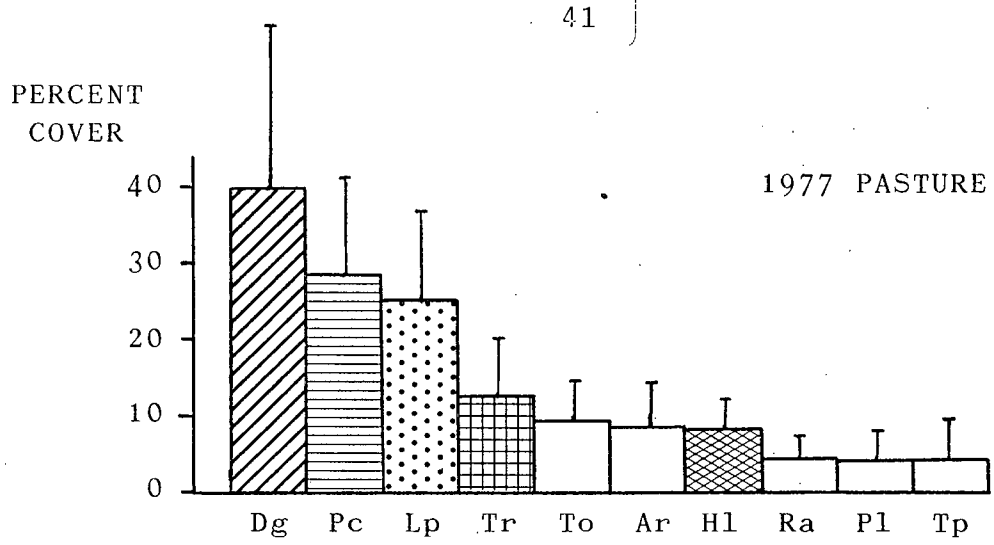
Pc - Poa compressa

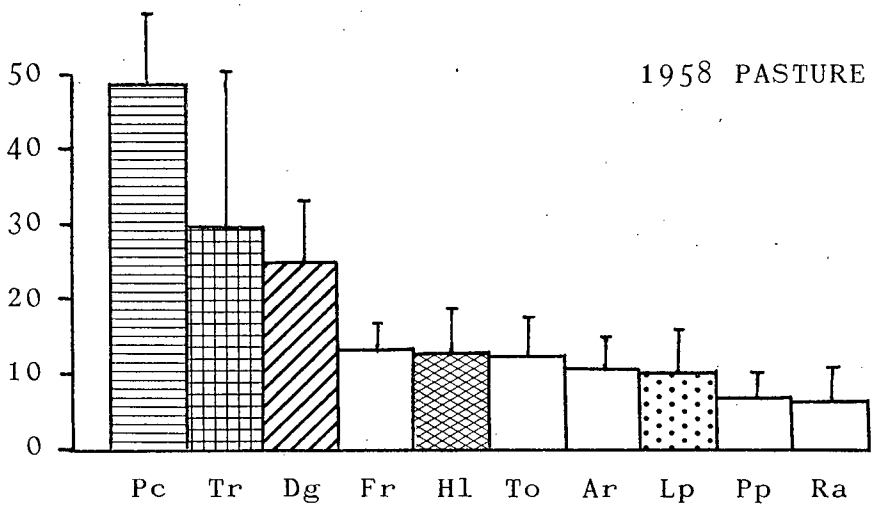
Ra - Ranunculus acris

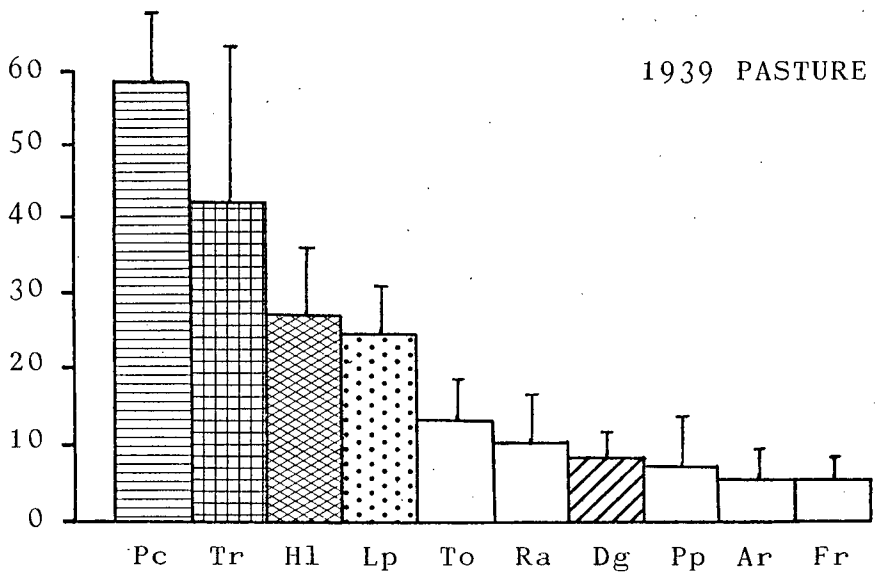
To - Taraxacum officinale

Tp - Trifolium pratense

Tr - Trifolium repens


PERCENT
COVER
1977 PASTURE
40
30
20
10
0
Dg Pc Lp Tr To Ar Hl Ra Pl Tp


1958 PASTURE
50
40
30
20
10
0
Pc Tr Dg Fr Hl To Ar Lp Pp Ra


1939 PASTURE
60
50
40
30
20
10
0
Pc Tr Hl Lp To Ra Dg Pp Ar Fr

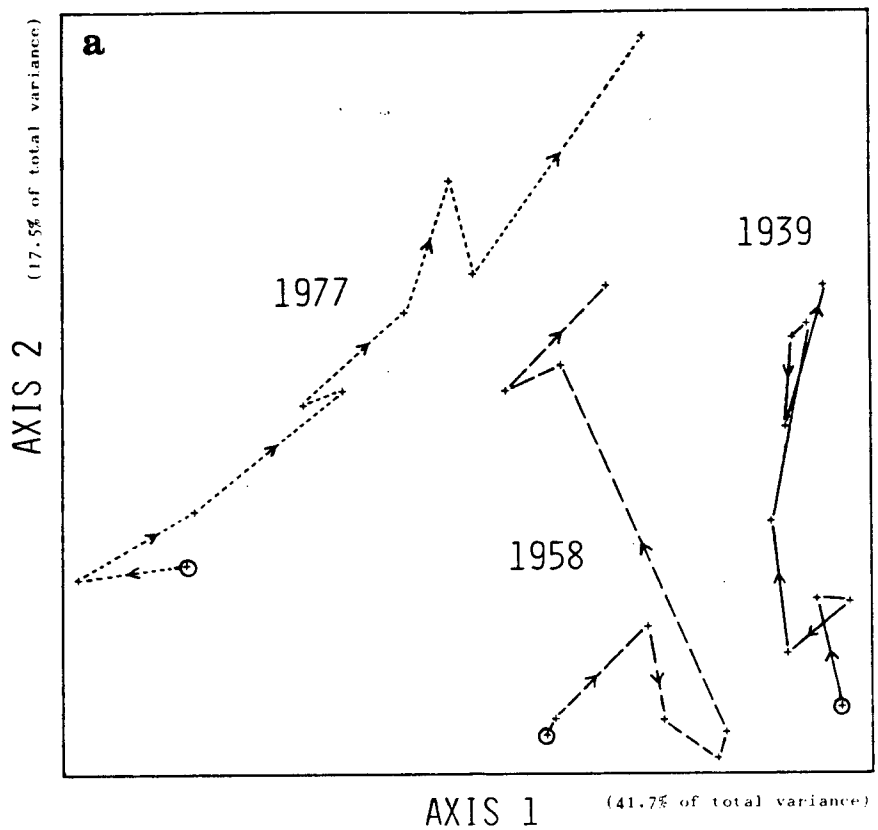
Festuca rubra has the highest cover in the middle-aged (1958) pasture compared to its cover in the other pastures.

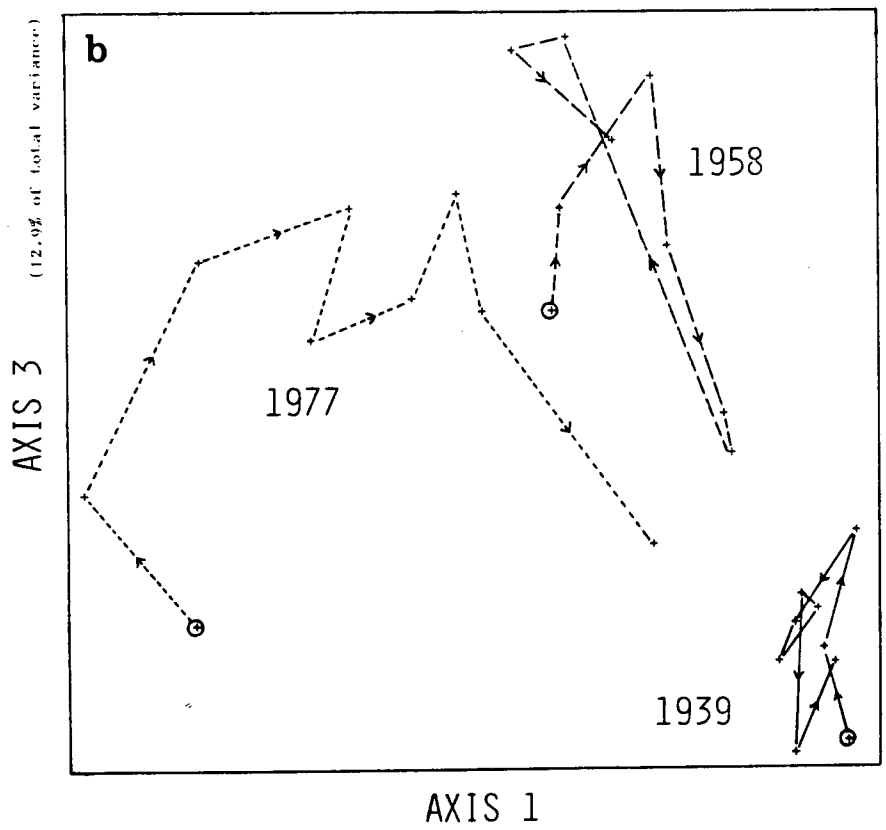
These overall vegetational differences among the 3 pastures are summarized in an ordination of the 27 surveys (3 pastures x 9 sampling events) based on total percentage cover for each species over the 60 quadrats in each field (Fig. 4). The three pastures are readily distinguished along the axis 1 plane which accounts for 42% of the variation in the data. The results show that the quantity of variation accounted for by the first 3 axes of the ordination generally declines with increasing field age. Axis 2 accounts for appreciable variation in all three pastures. For axes 1 and 3 however, the quantity of variation accounted for decreases with increasing pasture age; an F-test for the equality of variances of axis scores for the three pastures was significant at $P<0.05$ for both axes 1 and 3. Time-series course lines showing successive sampling events follow the same direction in all three fields along the axis 2 plane. The course line for the 1977 field is the most directional proceeding towards the positioning of the 1958 pasture surveys on axis 1. In contrast, the course line for the 1939 pasture on the axis 3 versus axis 1 plot appears as an 'oscillation around a mean'.

B) COLLECTION AND PROPAGATION OF CLONES

In order to investigate fine-scale competitive relations, several pairs of naturally neighbouring 'genets' (or clones) (growing in physical contact above ground in the field) were collected from locations in all 3 pastures where there was the

FIGURE 4. Ordination results of the 27 surveys. a) axis 2 vs. axis 1. b) axis 3 vs. axis 1. Time-series course lines are drawn for each pasture showing the progression from the first (circled point) to the ninth sampling event;
------- 1977 field; —— —— 1958 field; ———— 1939 field.


a
1977
1939
1958
AXIS 2
(17.5% of total variance)
AXIS 1
(41.7% of total variance)


b
1958
1977
1939
AXIS 3
(12.9% of total variance)
AXIS 1

greatest overlap in their respective percentage cover frequencies in the first survey (June, 1979). Clones were collected in all possible pairs for 5 of the most abundant species common to all three pastures; they were Dactylis glomerata, Holcus lanatus , Lolium perenne , Poa compressa and Trifolium repens (Fig. 3). Each genet was given a 'type' name X/Y, where X is its species name and Y is the species name of its natural neighbour (and X does not equal Y) Hence, X/Y and Y/X would be a natural neighbouring genet pair. The pairs were collected as two whole plants (including root material) and each genet type was propagated separately under glasshouse conditions by periodic separation of tillers or cutting of stolon pieces followed by replanting as 'ramets' (physiologically independent individuals) of the original clone. Each such population of ramets provided a stock supply of cloned individuals of the genet type. In experimental setups, a 'ramet' was designated as one 8-10 cm tiller from a grass clone with all root material removed, or an approximately 2.5 cm section of white clover stolon with one trifoliate leaf and an associated axillary bud.

SOIL SAMPLING AND ANALYSES

Soil samples from all three fields were analyzed for the following variables: pH (in water), total phosphorus, total nitrogen, total carbon, total cation exchange capacity, and exchangable calcium, magnesium, potassium and sodium.

Methods

A reciprocal averaging ordination of quadrats (based on species cover) from the March (1981) survey (the most recent survey before soil sampling) was carried out for all three fields. From the axis 2 vs axis 1 plot of these ordinations, 20 stands from each of the three fields were subjectively chosen to represent the range of variation present within each field. These 20 stands were then subjected to re-ordination. The ordinations so produced formed the basis of the environmental ordinations shown in Figure 9 used to test the hypothesis that vegetation differences within a given field can be accounted for by underlying edaphic variation.

At each of the 20 selected sites in each field, soil samples were taken in May 1981 by the composite method (e.g. Chapman et al . 1940) as follows: 12 soil cores, each 15 cm deep by 2 cm diameter, were extracted from around the outside perimeter of the positioned quadrat so as not to disturb the interior of the quadrat. These 12 independent samples were amalgamated into the composite sample which gave a mean analytical value representative of the entire soil sampling volume at the quadrat site. Each composite sample was air dried for 14 days, sifted through a 2 mm sieve and thoroughly mixed in preparation for soil analyses.

All analyses were carried out on the 2 mm fraction by procedures outlined in Lavkulich (1978). Phosphorus was extracted using the ammonium fluoride method. A colourimetric procedure by auto-analyzer was used for total nitrogen determination. Total carbon analysis was obtained using a 'Leco

FIGURE 5. Mean values for chemical analyses of soil from 20 selected stands from each pasture (4, 23 and 42 years old). Total cation exchange capacity (CEC) and all exchangeable cations are expressed as meq per 100 g soil.

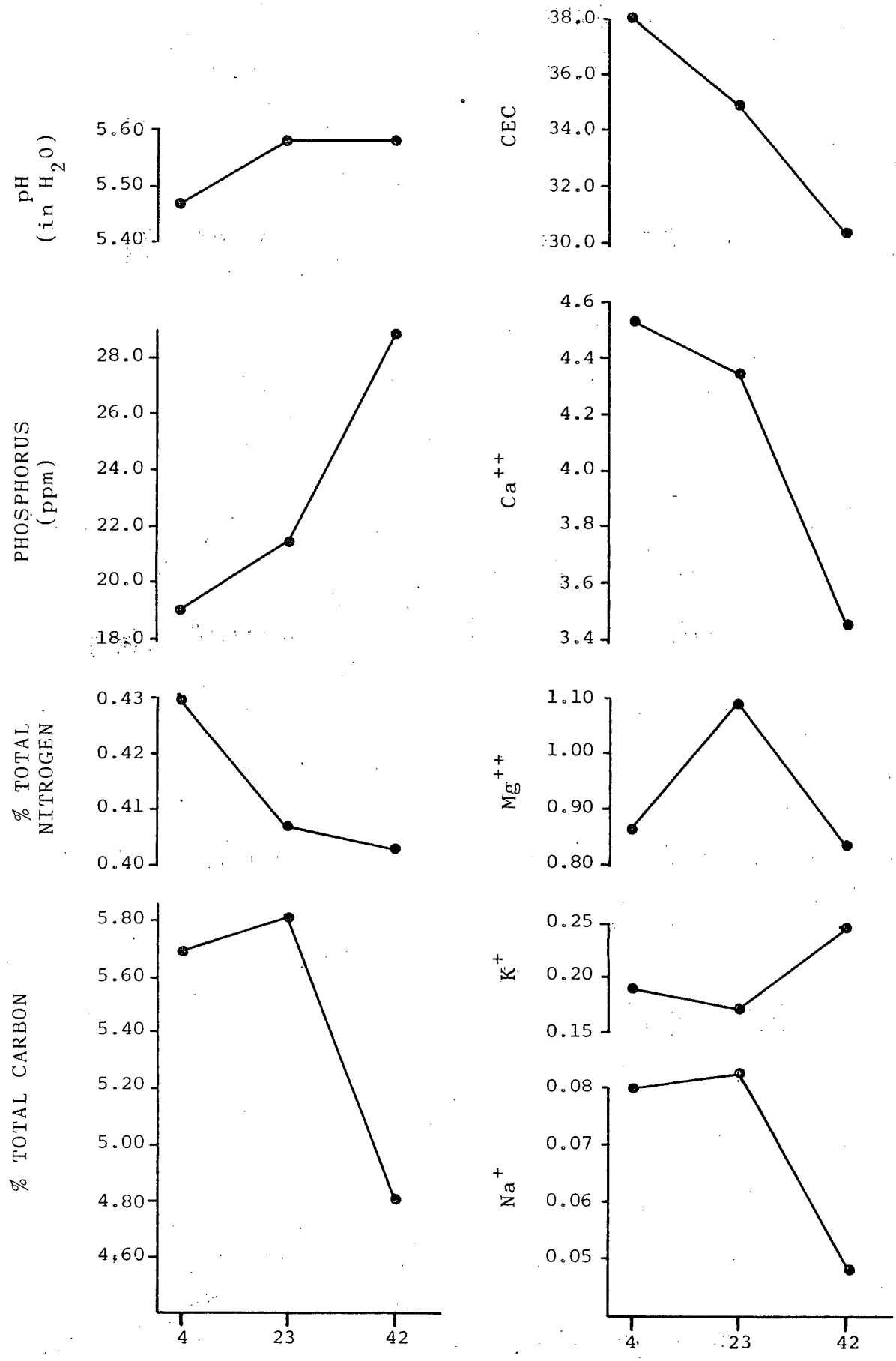
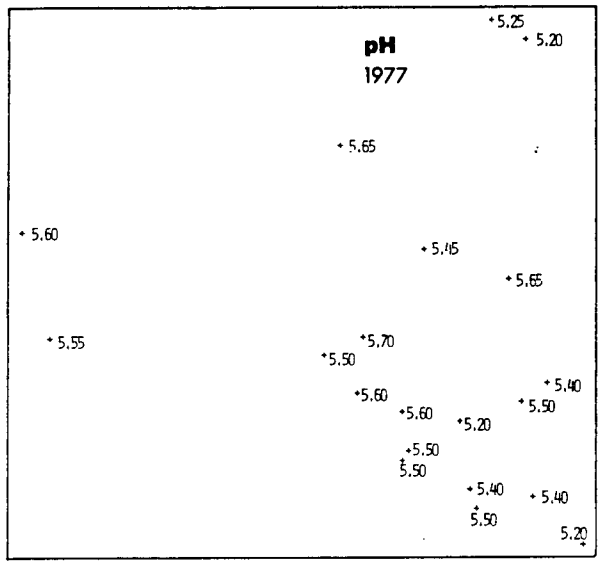
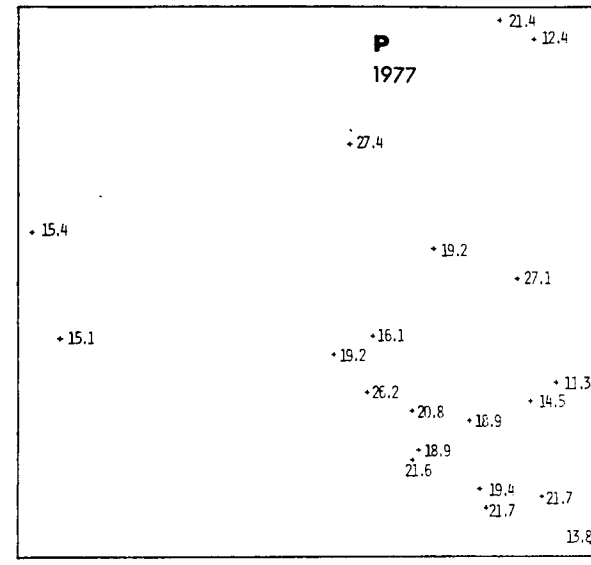
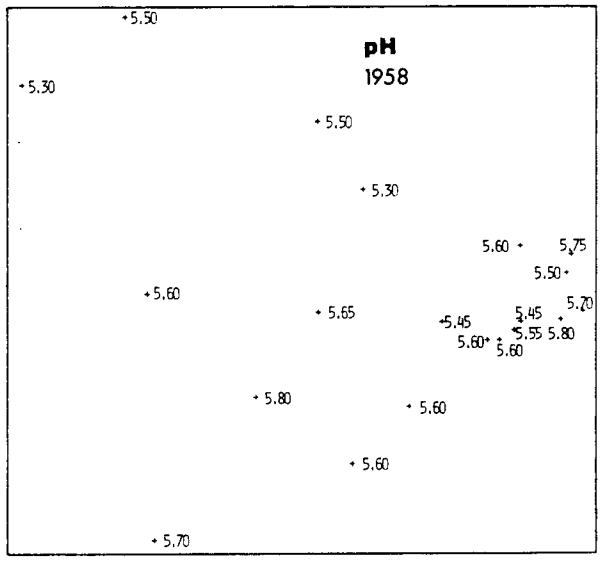
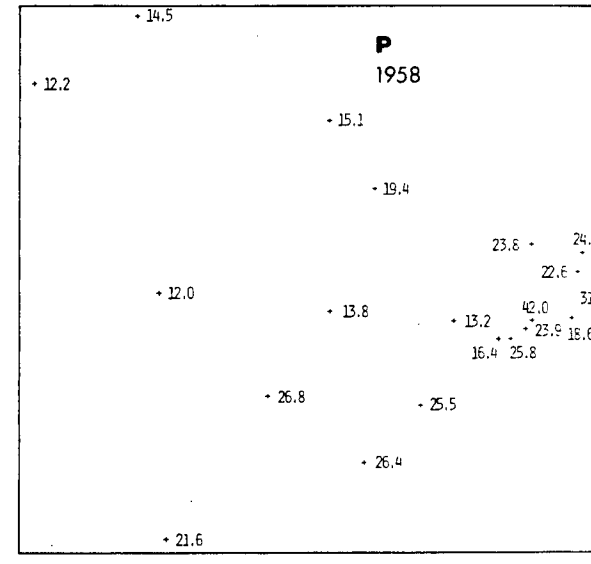

pH (in H_2O)
5.60
5.50
5.40
CEC
38.0
36.0
34.0
32.0
30.0
PHOSPHORUS (ppm)
28.0
26.0
24.0
22.0
20.0
18.0
Ca^{++}
4.6
4.4
4.2
4.0
3.8
3.6
3.4
% TOTAL NITROGEN
0.43
0.42
0.41
0.40
Mg^{++}
1.10
1.00
0.90
0.80
% TOTAL CARBON
5.80
5.60
5.40
5.20
5.00
4.80
4.60
K^{+}
0.25
0.20
0.15
Na^{+}
0.08
0.07
0.06
0.05
4
23
42
4
23
42
YEARS SINCE PLANTING

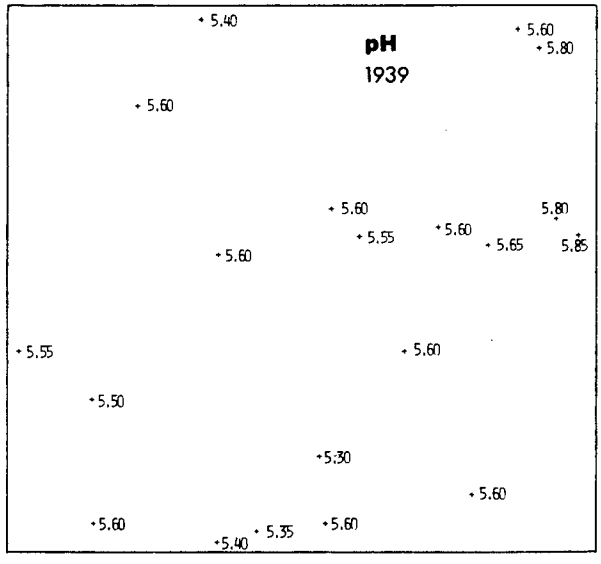
FIGURE 6. Distributional patterns of the 9 soil variables on the axis 2 versus axis 1 plane of the stand ordination of 20 selected quadrats from each pasture. Values for exchangable cations are in meq per 100 g of soil.

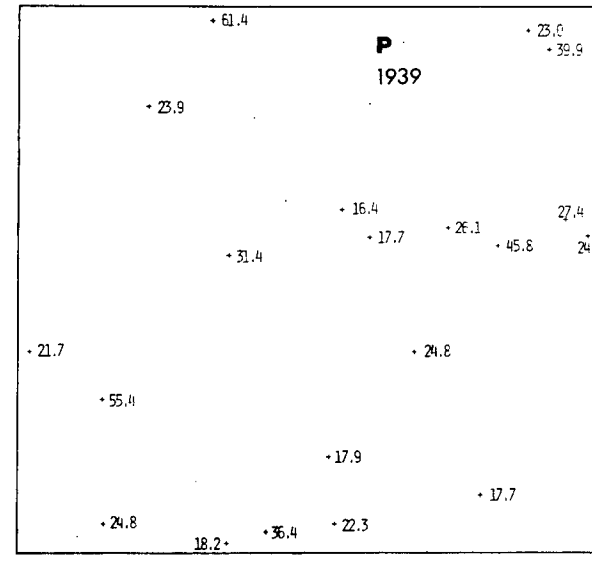

pH
1977
5.25
5.20
5.65
5.60
5.45
5.65
5.55
5.70
5.50
5.60
5.40
5.50
5.60
5.20
5.50
5.50
5.40
5.40
5.50
5.20

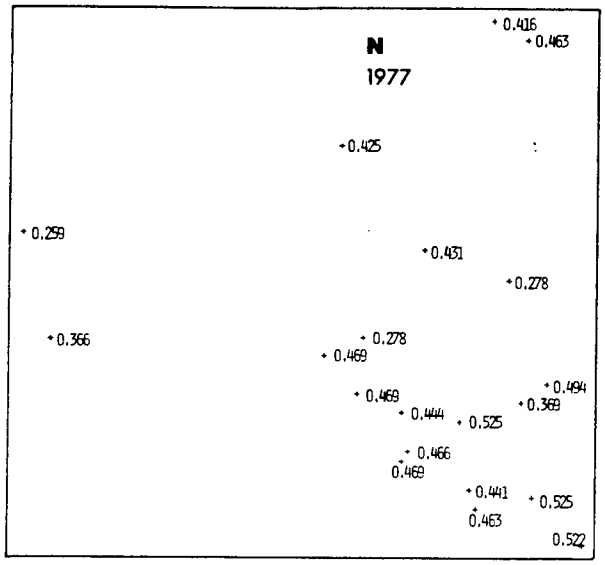

P
1977
21.4
12.4
27.4
15.4
19.2
27.1
15.1
16.1
19.2
11.3
26.2
14.5
20.8
18.9
18.9
21.6
19.4
21.7
21.7
13.8

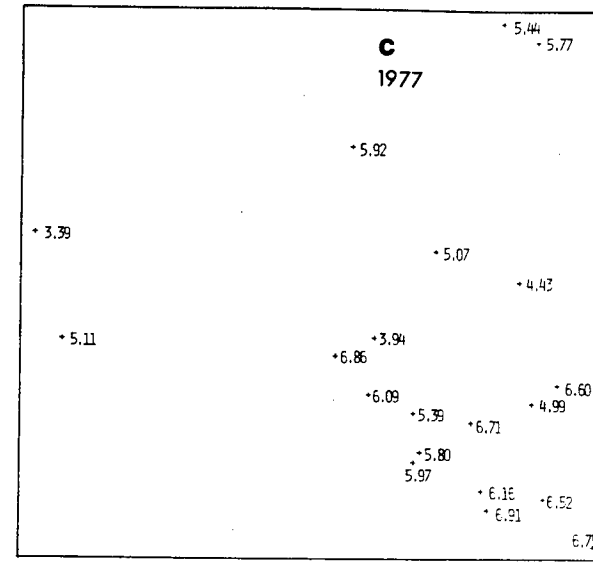

pH
1958
5.50
5.30
5.50
5.30
5.60
5.75
5.50
5.60
5.70
5.65
5.45
5.45
5.55
5.80
5.60
5.60
5.80
5.60
5.60
5.70

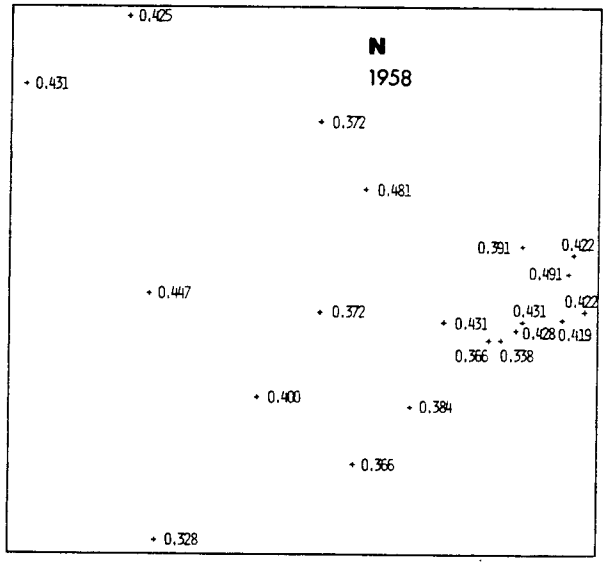

P
1958
14.5
12.2
15.1
19.4
23.8
24.5
22.6
12.0
42.0
31.1
13.8
13.2
23.9
18.6
16.4
25.8
26.8
25.5
26.4
21.6

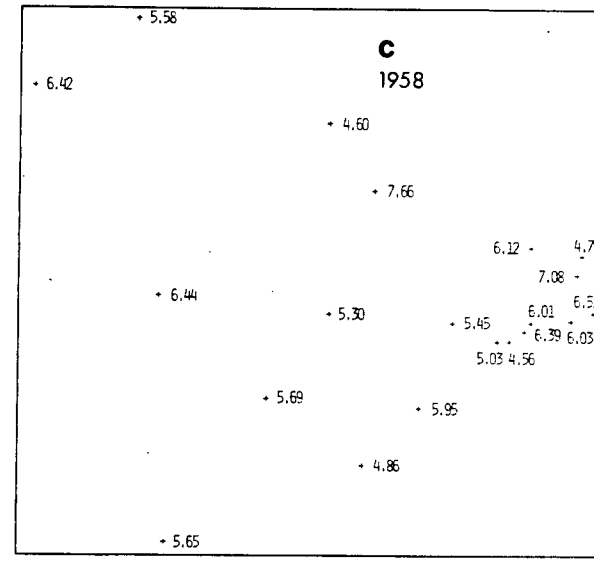

pH
1939
5.40
5.60
5.80
5.60
5.60
5.80
5.55
5.60
5.65
5.60
5.85
5.55
5.60
5.50
5.30
5.60
5.60
5.40
5.35
5.60

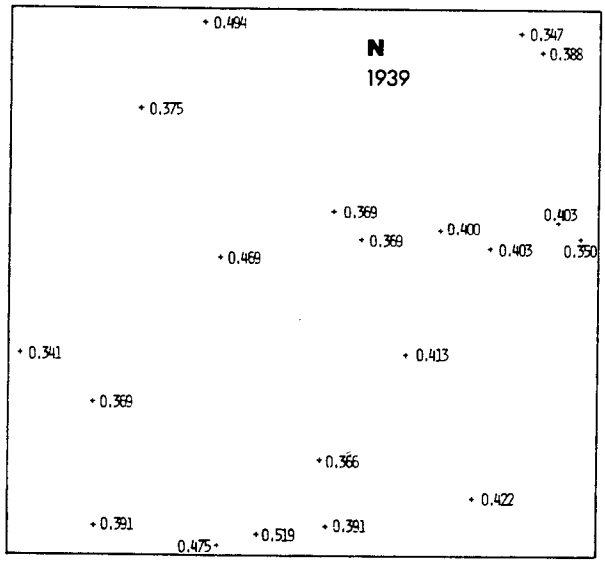

P
1939
61.4
23.0
39.9
23.9
16.4
27.4
17.7
28.1
45.8
24.6
31.4
21.7
24.8
55.4
17.9
17.7
24.8
36.4
22.3
18.2

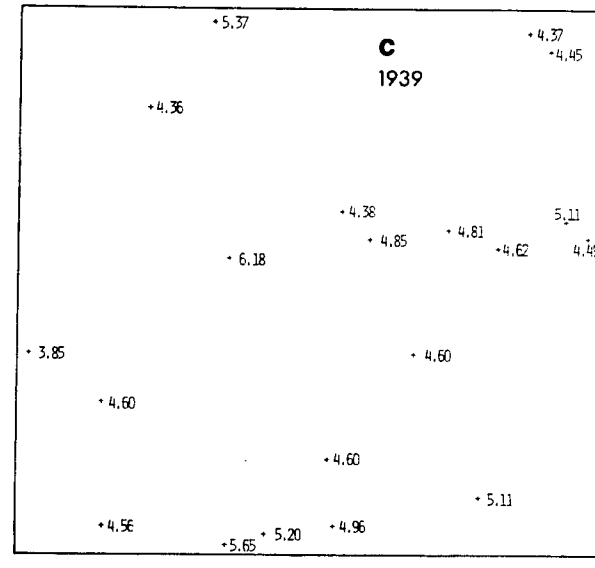

N
1977
0.416
0.463
0.425
0.259
0.431
0.278
0.366
0.278
0.469
0.494
0.469
0.369
0.444
0.525
0.466
0.469
0.441
0.525
0.463
0.522

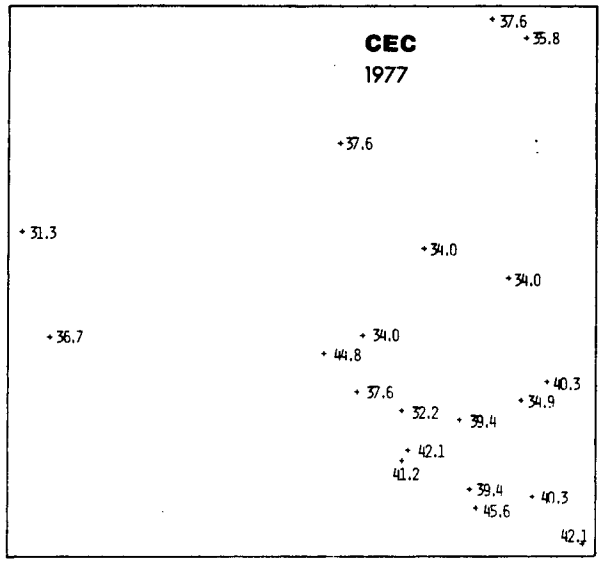

C
1977
5.44
5.77
5.92
3.39
5.07
4.43
5.11
3.94
6.86
6.09
6.60
4.99
5.39
6.71
5.80
5.97
6.18
6.52
6.91
6.75

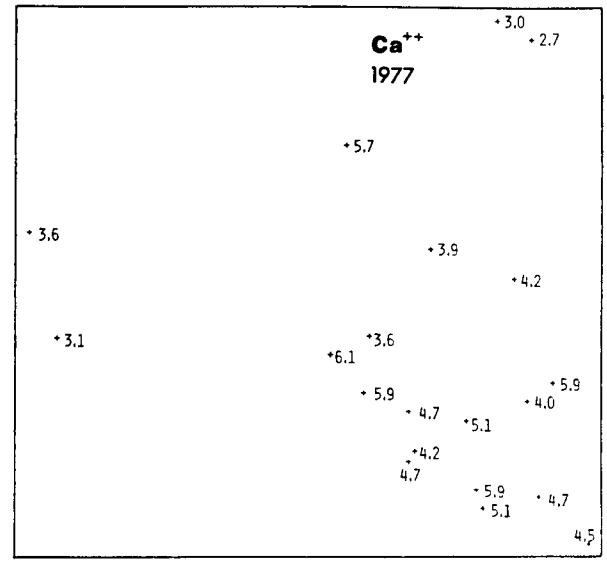

N
1958
0.425
0.431
0.372
0.481
0.391
0.422
0.491
0.447
0.372
0.431
0.431
0.422
0.428
0.419
0.366
0.338
0.400
0.384
0.366
0.328

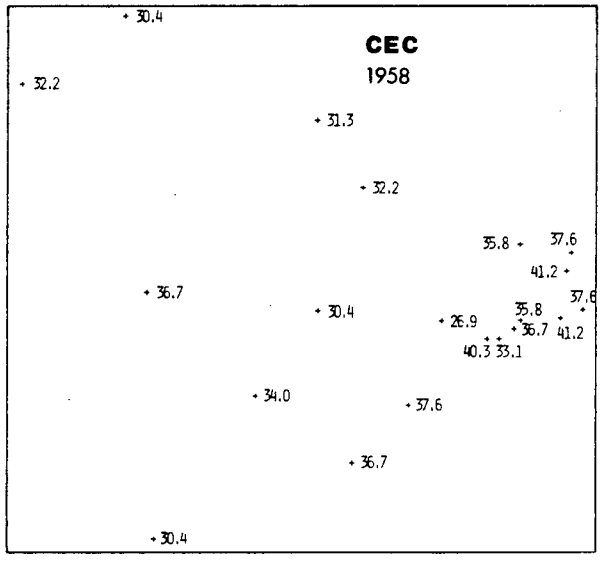

C
1958
5.58
6.42
4.60
7.66
6.12
4.79
7.08
6.44
6.52
5.30
6.01
5.45
6.39
6.03
5.03
4.56
5.69
5.95
4.86
5.65

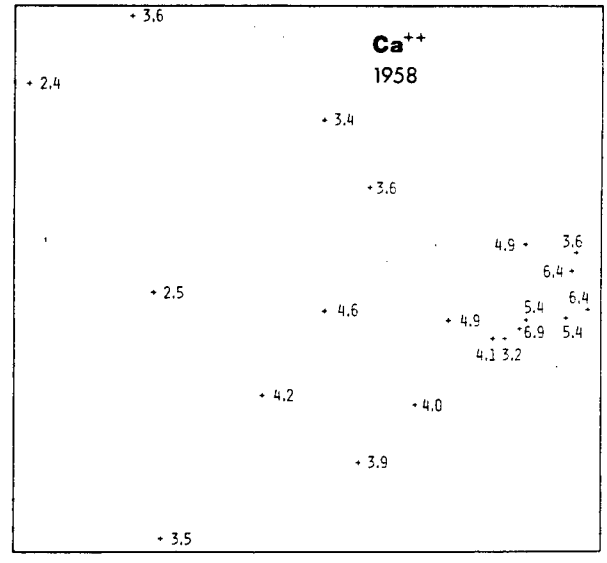

N
1939
0.494
0.347
0.388
0.375
0.369
0.403
0.400
0.369
0.403
0.350
0.469
0.341
0.413
0.369
0.366
0.422
0.391
0.475
0.519
0.391

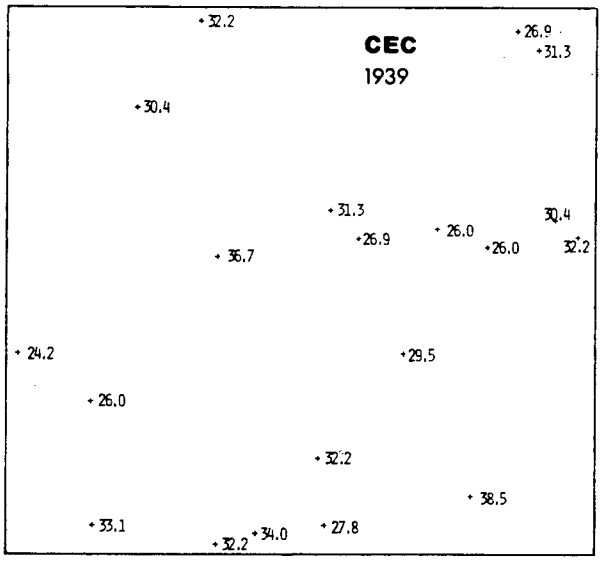

C
1939
5.37
4.37
4.45
4.36
4.38
5.11
4.81
4.85
4.62
4.49
6.18
3.85
4.60
4.60
4.60
5.11
4.56
5.65
5.20
4.96

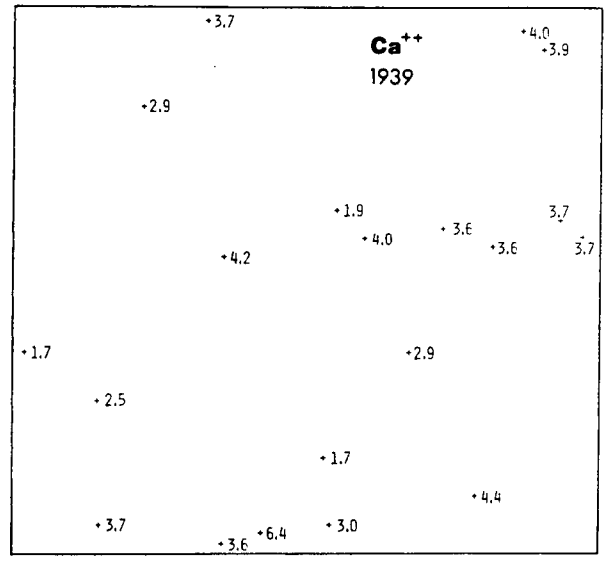

CEC
1977
37.6
35.8
37.6
31.3
34.0
34.0
36.7
34.0
44.8
40.3
37.6
34.9
32.2
39.4
42.1
41.2
39.4
40.3
45.6
42.1

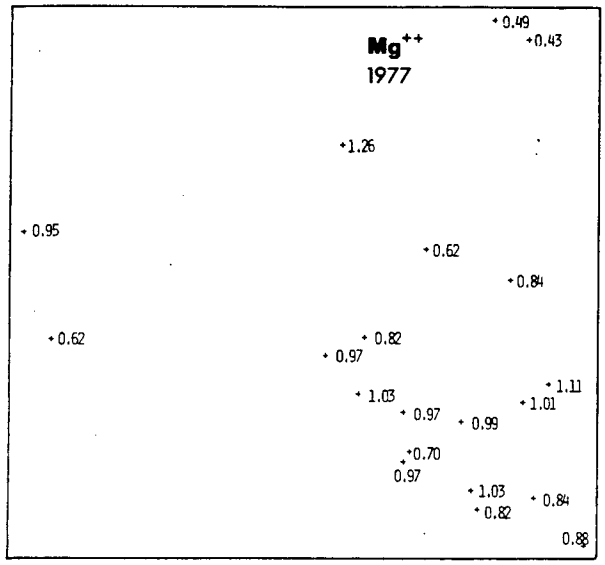

Ca++
1977
3.0
2.7
5.7
3.6
3.9
4.2
3.1
3.6
6.1
5.9
5.9
4.0
4.7
5.1
4.2
4.7
5.9
5.1
4.7
4.5

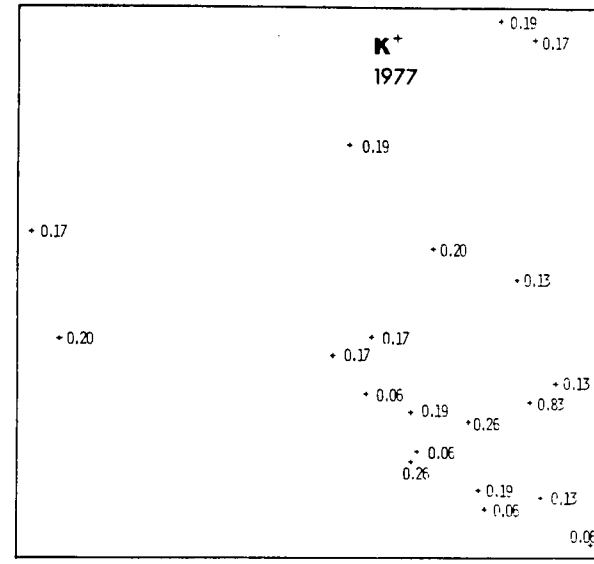

CEC
1958
30.4
32.2
31.3
32.2
35.8
37.6
41.2
36.7
37.6
30.4
35.8
26.9
36.7
41.2
40.3
33.1
34.0
37.6
36.7
30.4

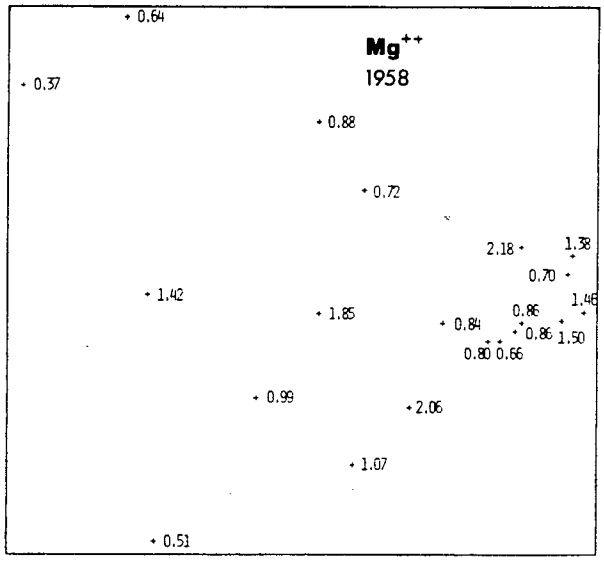

Ca++
1958
3.6
2.4
3.4
3.6
4.9
3.6
6.4
2.5
4.6
4.9
5.4
6.4
6.9
5.4
4.1
3.2
4.2
4.0
3.9
3.5

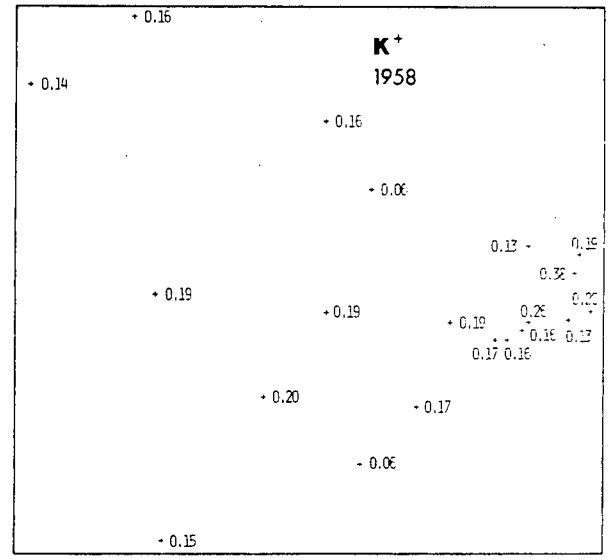

CEC
1939
32.2
26.9
31.3
30.4
31.3
26.9
26.0
30.4
26.0
32.2
36.7
24.2
29.5
26.0
32.2
38.5
33.1
32.2
34.0
27.8

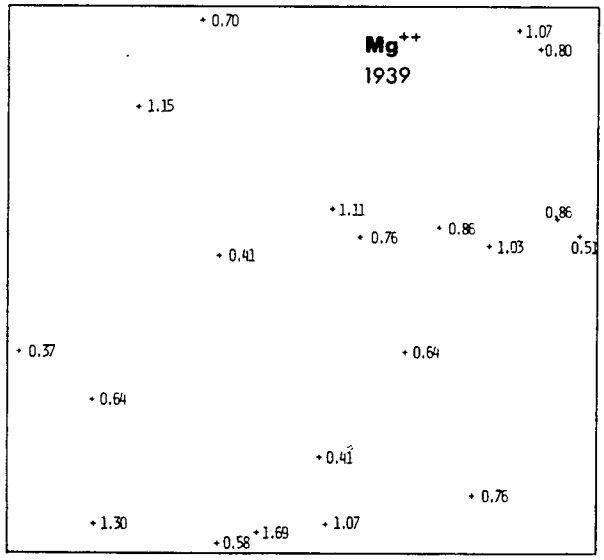

Ca++
1939
3.7
4.0
3.9
2.9
1.9
3.7
3.6
4.0
3.6
3.7
4.2
1.7
2.9
2.5
1.7
4.4
3.7
6.4
3.0
3.6

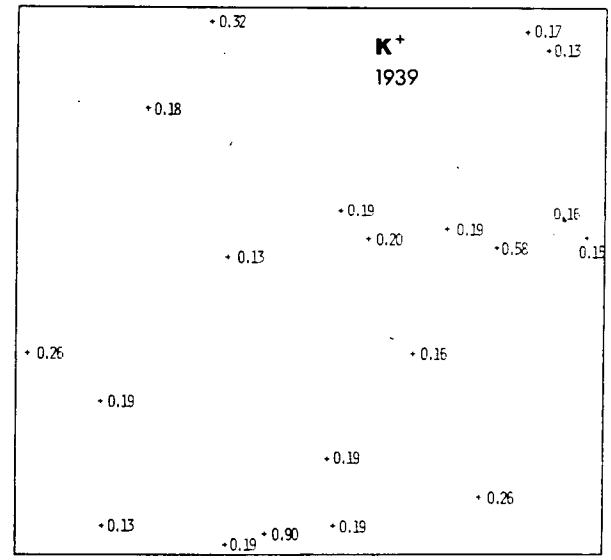

Mg++
1977
0.49
0.43
1.26
0.95
0.62
0.84
0.62
0.82
0.97
1.11
1.03
1.01
0.97
0.99
0.70
0.97
1.03
0.84
0.82
0.88

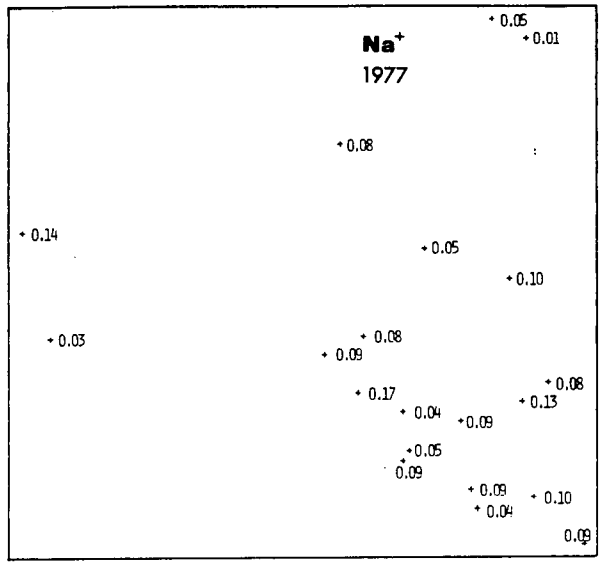

K+
1977
0.19
0.17
0.19
0.17
0.20
0.13
0.20
0.17
0.17
0.13
0.06
0.83
0.19
0.26
0.06
0.26
0.19
0.13
0.06
0.06

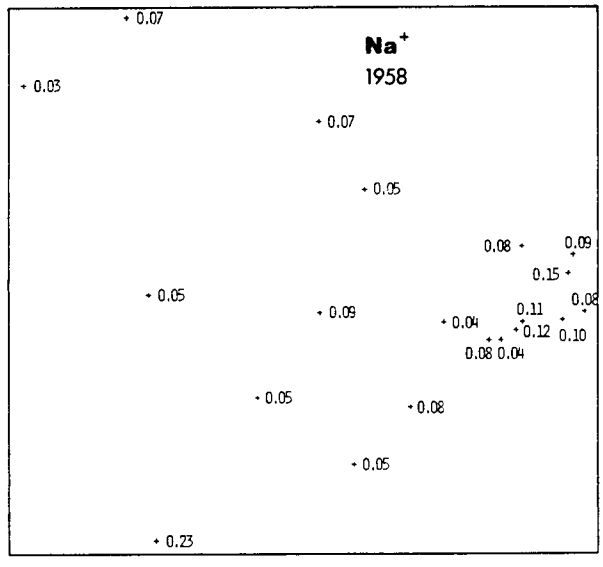

Mg++
1958
0.64
0.37
0.88
0.72
2.18
1.38
0.70
1.42
1.46
1.85
0.84
0.86
0.86
1.50
0.80
0.66
0.99
2.06
1.07
0.51

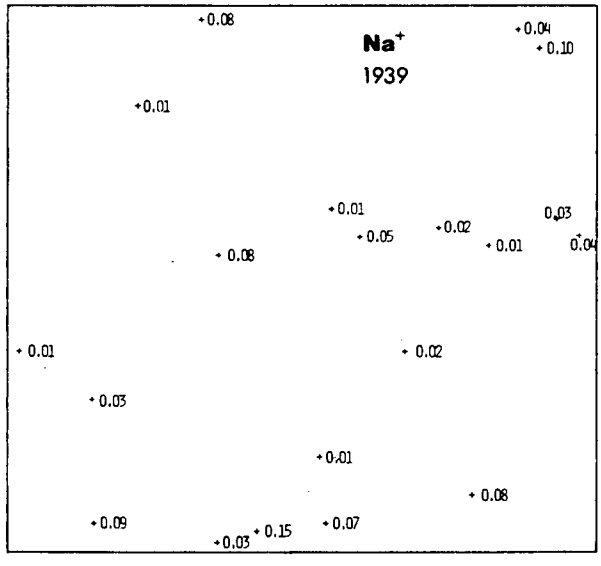

K+
1958
0.16
0.14
0.16
0.06
0.19
0.19
0.19
0.17
0.16
0.20
0.17
0.06
0.15


Mg++
1939
0.70
1.07
0.80
1.15
1.11
0.86
0.76
0.86
0.41
1.03
0.51
0.37
0.64
0.64
0.41
0.76
1.30
1.07
0.58
1.69


K+
1939
0.32
0.17
0.13
0.18
0.19
0.19
0.20
0.58
0.13
0.26
0.16
0.19
0.19
0.26
0.13
0.19
0.90
0.19


Na+
1977
0.05
0.01
0.08
0.14
0.05
0.10
0.03
0.08
0.09
0.08
0.17
0.13
0.04
0.09
0.05
0.09
0.09
0.10
0.04
0.09


Na+
1958
0.07
0.03
0.07
0.05
0.08
0.09
0.15
0.05
0.09
0.11
0.08
0.04
0.12
0.10
0.08
0.04
0.05
0.08
0.05
0.23


Na+
1939
0.08
0.04
0.10
0.01
0.01
0.03
0.02
0.05
0.01
0.04
0.08
0.01
0.02
0.03
0.01
0.08
0.09
0.03
0.15
0.07

analyzer'. The ammonium acetate method was used for exchangable cations and total cation exchange capacity (CEC).

Results

The mean results are summarized in Figure 5. A test of significant differences in mean values for soil variables between fields was not possible as soil samples were not collected randomly. Figure 6 illustrates the distributional patterns of the measured soil variables on the stand ordinations for each field. Each diagram is based on the axis 2 versus axis 1 plane of the ordination of the 20 selected quadrats mentioned previously. Correlation coefficients for the different soil variables with the percentage cover of 10 species and with the axis scores for the first 3 axes of the above ordination of 20 quadrats are shown in Table 7. A few significant correlations were found suggesting that gross vegetation differences within a given field may to some extent be accounted for by underlying edaphic variation.

DISCUSSION

The unique management history of this series of three different aged pastures provides an approximation of different coexistent stages of community evolution belonging to the same natural sequence of development. This is corroborated by the time-series survey results for percentage cover. Time of planting (i.e. age) is assummed therefore to be a major variable distinguishing the vegetation structure of the three pastures. It must be recognized however that environmental conditions (e.g. climate, grazing intensity) at particular

TABLE 7. Product moment correlation coefficients for the 9 measured soil variables with quadrat percentage cover for 10 of the most abundant species overall at the study site and with axis scores for the first 3 axes of the ordination of 20 selected quadrats (Fig. 6). a) 1977 pasture; b) 1958 pasture; c) 1939 pasture. (* significant at the 5% level; ** significant at the 1% level).

a) 1977 PASTURE

	pH	P	N	C	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Agropyron repens	.345	-.179	-.460*	-.451*	-.261	-.251	-.048	-.072	.128
Dactylis glomerata	.059	.502*	.212	.266	.170	.364	.276	.361	.276
Festuca rubra	.455*	.185	-.642**	-.524*	-.345	-.207	-.061	-.087	.088
Holcus lanatus	-.240	-.258	-.109	-.107	-.149	-.406	-.505*	-.085	-.368
Lolium perenne	.212	.138	-.009	.075	.305	.193	.070	.064	-.036
Phleum pratense	.244	.342	-.105	-.147	-.267	.092	.244	-.016	-.059
Poa compressa	-.362	-.474*	.295	.164	-.069	.030	.225	.173	.137
Trifolium repens	-.299	-.221	.325	.379	.451*	.216	.111	-.187	.130
Ranunculus acris	-.076	-.333	.025	.027	.001	.026	.084	.490*	.130
Taraxacum officinale	.371	.268	-.411	-.376	-.159	-.062	-.202	-.224	-.071
Axis 1	-.505*	.022	.512*	.503*	.320	.185	-.026	.073	-.108
Axis 2	-.048	.042	-.374	-.421	-.477	-.506*	-.419	.029	-.270
Axis 3	.216	.382	.127	.074	-.125	.359	.507*	.075	.109

b) 1958 PASTURE

	pH	P	N	C	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{++}
Agropyron repens	.063	.120	-.196	-.020	.141	.044	.483*	-.099	-.001
Dactylis glomerata	.261	.261	.086	-.142	.310	.298	.341	.342	.164
Festuca rubra	.372	-.043	-.388	-.092	-.201	-.365	-.031	-.096	.214
Holcus lanatus	-.468*	-.615**	.172	.059	-.530*	-.565**	-.295	-.206	-.406
Lolium perenne	-.149	.395	.138	.029	-.167	.336	-.334	.385	-.097
Phleum pratense	-.048	.117	.577**	.585**	.513*	.661**	-.068	.547*	.361
Poa compressa	.161	.489*	.251	.201	.506*	.367	.347	.003	-.047
Trifolium repens	.356	.478*	-.160	-.221	.349	.646**	.387	.199	.114
Ranunculus acris	-.609**	.298	.210	.361	-.342	-.529*	-.251	-.404	-.244
Taraxacum officinale	.306	.030	-.163	-.285	.292	.232	.010	.201	-.180
Axis 1	.280	.526*	.115	-.012	.557*	.702**	.340	.283	.130
Axis 2	-.540*	-.419	.458	.166	-.218	-.207	-.185	-.002	-.414
Axis 3	-.234	.174	-.264	-.266	-.440	-.004	-.172	-.242	-.035

c) 1939 PASTURE

	pH	P	N	C	CEC	Ca^{++}	Mg^{++}	K^{+}	Na^{+}
Agropyron repens	.346	.016	-.134	-.110	.037	.117	.100	-.178	.376
Dactylis glomerata	.500*	-.132	-.390	-.303	-.035	-.128	.097	-.308	.050
Festuca rubra	.051	-.222	.105	.083	.438	.135	-.112	-.030	.100
Holcus lanatus	-.562**	-.013	.296	.230	.249	-.079	.083	.146	.199
Lolium perenne	.307	-.334	-.141	-.016	.224	.078	.034	.165	-.056
Phleum pratense	-.194	.407	.156	.159	.113	-.110	.038	-.133	-.015
Poa compressa	.329	.036	-.023	.089	-.242	.203	-.050	.012	-.173
Trifolium repens	.453*	.368	.032	.017	.170	.193	-.111	-.045	.031
Ranunculus acris	-.336	.080	.221	.197	-.092	.159	.031	.149	.260
Taraxacum officinale	.214	-.349	-.172	-.146	.043	.142	.245	-.060	-.128
Axis 1	.569**	-.147	-.167	-.029	.042	.278	.034	-.056	-.024
Axis 2	.404	.312	-.210	-.195	-.231	-.042	-.070	-.228	-.183
Axis 3	.096	-.197	.045	.189	-.243	.270	-.017	.092	.054

times (e.g. during and immediately following planting), as well as the relative proportions of the species in the planting mixture (Table 6) are likely to have been different in the three fields. The cover of various species changes within each field over the study period and this, not surprisingly, is at least partially reflective of seasonal growth patterns. More importantly, the representation of various species differs substantially among different aged fields (Fig. 3). Some species show trends of increasing relative abundance, and others decreasing relative abundance with increasing field age. Poa compressa and Trifolium repens, the second and fourth most abundant species in the 1977 pasture, are the two most dominant species in both older pastures. There are no species (with the exception of Trifolium pratense and perhaps Lolium multiflorum) that show a declining trend to total extinction with increasing field age. The implication is that after 43 years since the establishment of the 1939 pasture there have been no major species (now present in the 1977 pasture) that have been totally eliminated.

Trends also occur in several soil variables with increasing field age (Fig. 5) which may be either responsible for, or a consequence of (or neither), the trends in species cover. Within-community correlations of species cover with the soil variables however was not greater with increasing pasture age. The oldest (1939) pasture in fact had notably the fewest significant correlations of the three fields (Table 7). Within-community vegetational patterns are therefore least accounted for by underlying edaphic variation in the oldest pasture

compared with the two younger pastures.

The ordination results indicate that the three study fields represent a sequence of pasture community development with respect to overall vegetational patterns. In particular, the youngest and oldest pastures are the most different in this respect and there is more stability over time in the vegetational patterns with increasing pasture age (Fig. 4). 'Stability' here is used in the sense of community 'constancy' (Orians 1975). The youngest pasture showed the most variability in community composition over the 33-month study period and this was represented by a directional trend in the ordination toward those quadrats in older pastures (Fig. 4).

Superficially the three study fields show no striking differences; their species compositions are virtually identical (although relative cover varies) and differences in soil variables are not large. A Simpson's diversity index (Peet 1974) was calculated for each survey based on total percentage cover of each species per field (Table 8) and no significant differences were found amongst the three pastures over the study period. In spite of this, the data presented here on vegetational patterns over time (Fig.4) exposes the three pastures as distinct 'community entities', each distinguished by its peculiar placement in a common developmental series characterized by increasing community constancy. Increasing community constancy however is not accompanied by any significant change in species diversity. This together with the lack of any clear trends with increasing pasture age for soil variables on the quadrat ordinations (Fig. 6, Table 7) points

TABLE 8. Simpson's diversity indexes (D) calculated for each survey based on total percentage cover of each species per field. ($D=1-\sum_{i=1}^{S}(p_i)^2$, where p_i is the proportion of individuals of species i in the community and S is the number of species). The mean values over the study period were not significantly different amongst the three fields (P=0.3697) based on an analysis of variance using a MIDAS program (Fox & Guire 1976). An F-test for the homogeneity of variances was not rejected and analysis was performed on untransformed data.

SURVEY NO.	SURVEY DATE	PASTURE 1977	1958	1939
1	June 1979	.859	.863	.822
2	Sept. 1979	.809	.862	.832
3	Mar. 1980	.805	.790	.755
4	June 1980	.829	.845	.845
5	Sept. 1980	.859	.842	.864
6	Mar. 1981	.854	.831	.824
7	June 1981	.854	.868	.842
8	Sept. 1981	.870	.888	.852
9	Mar. 1982	.789	.844	.818
Mean		.836	.848	.828

to the question of the importance of biotic factors (e.g. grazing and neighbour interactions) in determining the properties and development of neighbour relationships in these pastures.

It is important to bear in mind that the three pastures have been exposed to different lengths of time of grazing (i.e. since last planted). Grazing may provide an important selection pressure, e.g. in affecting plant growth habit (Kemp 1937) or species relative abundance (if grazing is preferential). It is reasonable to expect that community structure and dynamics may be affected by how long such selection has been operating. It is also reasonable that the findings presented in this chapter may be attributable to the fact that the ancestral components of older communities have had a longer history of biotic interaction and hence a longer time for subsequent selective forces to accumulate and generate biological accommodation. This focuses attention on the dynamics of interactions occurring in local neighbourhoods within the community. Such micro-scale within-community events are not adequately addressed at the traditional scale of vegetational succession. The critical events occur at the level of individual response to selective forces and involve changes in genetic constitution. These issues concerning neighbour interactions are pursued in chapters to follow. Subsequent discussion assumes however that selection pressure related to both grazing and neighbour interactions (e.g. competition) operate simultaneously and that their effects may not be readily separable.

CHAPTER 3

A QUALITATIVE MODEL FOR PASTURE COMMUNITY EVOLUTION: PRELIMINARY EVIDENCE FOR SPECIES INTERACTIONS AND COEXISTENCE USING CONTACT SAMPLING

INTRODUCTION

Species interact in nature. To the animal ecologist this is often readily observable, unprofound, and perhaps a truism. Yet between plants, species interaction in nature is often not immediately obvious. Most interest has centered on competition and ecologists even face an enigma in the virtual impossibility of empirically demonstrating that resources are really limiting in some communities. Only studies on species removals from an area and the subsequent response of those left undisturbed have provided some quantitative data (Sagar & Harper 1961, Putwain & Harper 1970, Pinder 1975, Allen & Forman 1976, Abul-Fatih & Bazzaz 1979, Fowler 1981). Some have called for more attention to be given to the role of predation and other disturbances (e.g. climatic) which are also important factors controlling populations (Connell 1975, Wiens 1977, Caswell 1978, Menge 1979). Against this however, most species have an innate capacity to produce many more offspring than is necessary for population replacement and yet remain on average fairly constant in population size. This echoed paradigm of Malthus and Darwin supports the tacit assumption that resource limitation will be common in nature and competitive interaction virtually inevitable. Dispute arises only with attempts to generalize about the importance (or unimportance) of competition in nature (e.g. Andrewartha & Birch 1954; see also Hairston *et al.* 1960 versus Murdock 1966). It is more realistic to view competition as an interaction of varying intensity determined by prevailing environmental conditions, rather than an all-or-nothing phenomenon (Pianka 1976).

A persistent interaction between two species means that they are coexisting. Spatial and temporal components are built into the notion of coexistence, both of which seem somewhat arbitrary; coexisting species must in some way be in the same place together for some length of time . The spatial component for mobile organisms is very different from that for sessile organisms. Mobile organisms interact while altering their spatial relations with respect to one another. The spatial component for sessile organisms however is more equivocal - the inherent question exists as to what degree of proximity elicits an interaction between two permanently displaced individuals. In some vegetation types such as pastures, species interactions occur in very local neighbourhoods involving plants often in physical contact and the individual rarely has any means of adjusting its proximity to neighbours. Mack & Harper (1977) found that up to 69% of the variation in plant weight and reproductive output of individual sand dune annuals can be accounted for by the neighbours present within a radius of 2 cm. Sampling which records species presence/absence in quadrats may not reflect the relevant scale of interactions, and a more appropriate perspective may be to take a "plant's-eye-view" of the vegetation (Harper 1977a, 1977b, Turkington & Harper 1979a) based on physical contacts between individuals.

A plotless method of sampling vegetation has been developed which enables investigations of community structure and variation from the "plants-eye-view" in terms of neighbour contacts. It was originally designed by Yarranton (1966) and further modified by Turkington (1975) and used recently in

grasslands as the 'contact sampling method' (Turkington et al . 1977, Turkington & Harper 1979a, 1979b, Aarssen et al . 1979). This sampling scheme defines a precise spatial component for coexistence in plants. It provides an unequivocal frame of reference because neighbours are regarded as those laterally fixed individuals which physically contact above ground. Moreover, the method embodies a neighbourhood concept of community organization, i.e. it is sensitive to the way that a plant experiences its immediate neighbours and hence, non-randomness of interspecific association is detected at the smallest possible scale - the local neighbourhood.

Plotless methods of sampling avoid the problems of scale inherent in determining appropriate quadrat size and shape for a particular vegetation type. The "species-juxtaposition" method of recording species sequence along a transect at small intervals (Stowe & Wade 1979) and the "neighbouring point analysis" of Fowler & Antonovics (1981) are similar plotless methods also offering these advantages. The latter study, carried out in two different seasons, revealed two distinct groups of associated grassland species which differed in their seasonality of growth. Using the contact sampling method in grass-legume communities, Turkington et al. (1977) found predominantly negative association amongst grasses, negative association amongst legumes and positive association between grasses and legumes. Turkington and Harper (1979b) found that in a 50-year-old pasture, all of the associations between Trifolium repens and each of eight major grasses remained either permanently positive or permanently negative over a 16-month

period.

Contact sampling goes further than any previously devised technique for providing quantitative data reflecting a measure of species coexistence in communities. Aarssen et al . (1979), using the contact sampling method, identified three categories of significant ($P<0.05$) interspecific association in pastures - stable, seasonal and temporary. Saulei (1981) reported similar types of associations in abandoned fields. A stable association is one which is constant through time. A stable positive association detected by contact sampling is interpreted as evidence that two species exist frequently within each other's sphere of influence (more often than expected by chance). A stable negative association on the other hand can be interpreted as evidence for some measure of avoidance (in a non-cognizant sense) of interaction. This however is not evidence against coexistence; there may always be some individuals that enter into one another's sphere of influence.

The present investigation uses the contact sampling method to provide a quantitative basis for constructing a preliminary picture of the nature and dynamics of fine-scale species interactions in the study site of different aged pastures. Antonovics (1978) drew attention to the lack of attempts to quantify the process of community change in pastures. Aarssen et al. (1979) and Saulei (1981) studied interspecific associations on three occassions in pastures which differed in age (since last ploughed) by a range of 18 and 8 years respectively. By comparison, the present investigation concerns three pastures of which no two are less than 20 years different

in their ages, and involves a longer term period of study encompassing surveys in 3 seasons over each of 3 years. The question of central importance is: What are the patterns of change in species associations during pasture community development? The following hypothesis will be tested: There are more 'stable' (unchanging) associations in older pastures than in younger pastures, whereas younger pastures have more associations which are relatively short-lived or 'temporary'.

On the basis of the results, a model is proposed for the role of changing patterns of interspecific association in characterizing pasture community evolution. 'Community evolution' is used here not in the sense of paleoecolgical progression (e.g. Gray et al . 1981) or community-level group selection (e.g. Wilson 1976, 1980), but rather in the sense that the properties of multi-species assemblages may be viewed as community-level products of Darwinian natural selection (Whittaker & Woodwell 1971). Data on the patterns of fine-scale neighbour relationships will also provide a foundation for the experimental work reported later, designed to identify more precisely the way(s) in which competitive relations change between species in response to neighbour interactions.

METHODS

Vegetation Sampling

Data were collected from 60 systematically arranged 0.5 m x 0.5 m quadrats in each of the three fields (Fig. 1). Within each quadrat, contact-samples were taken at each of 25

systematically arranged sampling points, i.e. 1500 contact-samples per field. There are several optional methods for data collection at each point. The method used here follows the recommended strategy of de Jong et al. (in press). At each sampling point, the individual hit by the vertical downward projection of a sampling pin is the initial sample species i ('point species'). The sampling point is subsequently removed from that location to the nearest point of contact with a neighbouring individual j ('contact mate'). If the contact mate is of identical species to the point species (i.e. j=i) then j is rejected and resampled until a contact mate of a different species from the point species is determined, or until it is established that no different species is in contact with the point species. In the former case, the interspecific contact point closest to the original sampling point is ultimately chosen. Where the point species has no interspecific contacts or no contacts whatever, or where there is no point species, the entire sample is rejected and resampling occurs for another point species.

No information is gathered on intraspecific association in this sampling strategy; the procedure selectively focuses on neighbourhoods featuring interspecific interaction. The advantage of this is that it avoids the often formidable task in grassland vegetation of trying to distinguish whether, at the point of contact, there are two different plants involved, or two different parts of the same plant.

Each of the three pasture communities was surveyed using the above method on the same dates as the surveys for the

percentage cover of species, i.e three spring (March), three summer (June) and three fall (September) surveys were carried out starting in June 1979 and terminating with the last survey in March 1982. Winter surveys were not possible due to intermittent snowfall.

Data Analysis

The hypothesis tested was that of random association amongst species. Randomness in this context means that the number of contacts between species does not deviate from random expectation. The point species and its contact mate define an ordered contact pair (i,j) where i is the species of the first selected plant, and j that of the second. Table 9 illustrates the appropriate layout of the data in a complete count matrix displaying the number of each pair (n_{ij}) observed after N samples.

Given the count matrix, previous practice has been to fold the matrix along the diagonal resulting in a triangular array where cell (i,j), $i<j$ is the aggregate number of contacts between species i and j without distinguishing between the order in which the pairs were determined. Earlier studies (Yarranton 1966, Turkington et al. 1977, Turkington & Harper 1979a, 1979b) have analyzed such data using the usual but incorrect procedure which incorporates a chi-square test of a 2 X 2 contingency table. De Jong et al . (1980) drew attention to this improper treatment of contact sampling data and presented a correct method of analysis for such folded contingency tables.

Subsequently, de Jong et al . (in press) designed a more straightforward analysis in which the distinction between the

TABLE 9. Count matrix generated by contact sampling. f and s are respectively the row and column totals for species k; n_{ij} is the number of (i,j) contact pairs; K is the total number of species; N is the total number of contact-samples taken.

First selected species (point species)	Second selected species (contact mate) 1	2	3	. . .	K	Total
1	-	n_{12}	n_{13}	. . .	n_{1K}	f_1
2	n_{21}	-	n_{23}	. . .	n_{2K}	f_2
3	n_{31}	n_{32}	-	. . .	n_{3K}	f_3
.	.	.	.	.	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
K	n_{K1}	n_{K2}	n_{K3}	. . .	-	f_K
Total	s_1	s_2	s_3	. . .	s_K	N

TABLE 10. Contingency table for (i,j) interaction; notation follows that in Table 9.

First choice	Second choice i	j	other	Total
i	-	n_{ij}	$f_i - n_{ij}$	f_i
j	n_{ji}	-	$f_j - n_{ji}$	f_j
other	$s_i - n_{ji}$	$s_j - n_{ij}$	$N - f_i - f_j - s_i - s_j + n_{ij} + n_{ji}$	$N - f_i - f_j$
Total	s_i	s_j	$N - s_i - s_j$	N

ordered pairs (i,j) and (j,i) is maintained and the data are tabulated in an unfolded matrix as in Table 9. Variations in growth forms and percentage cover amongst the different species dictate that first and second choice probabilities will be different under the above specified sampling strategy. As de Jong et al. (in press) have argued, this calls for the parameterization of the random association hypothesis in terms of two sets of parameters: the first related to the relative cover of the various species, and a second set related to growth densities at contact level. This second set of parameters accounts for vertical structure in the vegetation which may be assumed virtually negligible in some vegetation types such as lichen-bryophyte communities (e.g. Yarranton 1966) or grazed grasslands as in the present study. In such situations contacts essentially occur in a lateral plane which implies that the non-zero second choice probabilities are proportional to the first choice probabilities. This has been called the "proportionality hypothesis" after de Jong et al. (in press). Details of data analysis for random association are presented there and will only be summarized below.

The probability of selecting the ordered pair (i,j), not assuming proportionality, is given by

$$p_i q_j/(1-q_i), \quad i,j=1,2,\ldots,K;\ i\neq j$$

where p_k is the relative cover frequency of species k in the community and q_k is the relative growth density of species k at the vertical position in the canopy where contact occurs. This test is conditional on all other associations assumed random. This is often a restrictive assumption which can be avoided

under the proportionality hypothesis. This hypothesis states that $q = p$ and the probability of selecting the ordered pair (i,j) becomes

$$p_i p_j/(1-p_i).$$

The estimation of the maximum likelihood expected cell counts, e_{ij} under either random pairing model is accomplished using an iterative procedure outlined by De Jong et al. (in press). To measure the deviation from random association the Pearson goodness of fit statistic was used:

$$\hat{\chi}^2 = \Sigma\Sigma_{ij}(n_{ij}-e_{ij})^2/e_{ij}$$

Significantly large values of chi-square argues against the hypothesis used to construct the e_{ij} values, and hence is evidence for non-randomness in the data matrix as a whole. Because the chi-square technique is a 'large-sample' method, it cannot be legitimately applied in situations where there are few observations. Conventional practice has set a somewhat arbitrary limit that the expected number of counts in each cell should be at least five. Accordingly, rare species, occurring in less than 40 contact-samples in total, were excluded from the analysis.

For investigation of particular pairwise associations, the whole matrix of counts was first collapsed into cells defined by Table 10. Expected cell counts corresponding to this table were calculated using an iterative procedure which mimics that used for the overall test and again, a chi-square statistic was used to indicate departures from randomness. For certain species pairs of particular interest, an index of association was calculated as C=1-P where P is the significance probability from

the chi-square test. The sign (positive or negative) of significant associations was obtained from the sign of the 'standardized residuals', being the components of chi-square:

$$(n_{ij}-e_{ij})/\sqrt{e_{ij}}.$$

The index C therefore ranges between +1.0 (maximum positive association) and -1.0 (maximum negative association). Significant associations (at less than the 5% level) occur when $C>+0.95$ and $C<-0.95$.

RESULTS

For all 27 data sets the overall chi-square test indicated global departures from randomness. Accordingly, it was decided that an exact test for individual pairwise associations which assumes that other pairs are random was inappropriate. The proportionality hypothesis does not invoke this assumption (de Jong *et al.*, in press) and was therefore used to detect significant associations for all pairwise combinations. Significant ($P<0.05$) pairwise associations, together with their signs (positive or negative) are listed in Table 11 for all surveys.

Table 11 shows that associations between grasses are predominantly negative and this is more pronounced in older pastures. An exception is *Agropyron repens* - *Poa compressa* which shows periodic positive association. Significant positive associations typically involved a grass and a non-grass, especially *Trifolium repens* and *Taraxacum officinale*.

Most significant associations were 'temporary', occurring in only one or a few successive surveys, and then disappearing

TABLE 11. Summmary of significant ($P<0.05$) individual pairwise associations in the three pastures in each survey. Each value is the attained significance level (to 3 decimal places) when testing for individual interspecific association together with the sign (+ or -) obtained from the standardized residuals. Species names are abbreviated to their generic name only except in cases where more than one species is represented for a genus. Complete species names are available in Table 5.

A) 1977 PASTURE

SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
AGROPYRON - DACTYLIS	+.005	-.000		-.002	-.000	-.039	-.000	-.000	-.021
AGROPYRON - HOLCUS			-.030			-.006		-.001	
AGROPYRON - LOLIUM			-.034				-.000		-.001
AGROPYRON - PHLEUM			-.036						
AGROPYRON - PLANTAGO LANCEOLATA					+.038				
AGROPYRON - POA COMPRESSA		+.000			+.000			+.000	+.014
AGROPYRON - RANUNCULUS							+.043		
AGROPYRON - TARAXACUM		+.023				+.001	+.000	+.005	+.000
AGROPYRON - TRIFOLIUM PRATENSE		+.046							
AGROPYRON - TRIFOLIUM REPENS		+.000	+.007			-.034		-.004	
AGROSTIS - DACTYLIS			-.000			-.042			
AGROSTIS - LOLIUM						-.019			
AGROSTIS - POA COMPRESSA			+.018						
AGROSTIS - RANUNCULUS						+.000			+.000
AGROSTIS - TARAXACUM						+.000		+.000	
AGROSTIS - TRIFOLIUM REPENS			+.005						
DACTYLIS - FESTUCA				-.002					
DACTYLIS - HOLCUS		-.007	-.003		-.000			-.000	-.024
DACTYLIS - LOLIUM		-.000			-.001	-.000	-.004		
DACTYLIS - PHLEUM	-.004					-.000	-.000		
DACTYLIS - PLANTAGO LANCEOLATA		-.001							
DACTYLIS - POA COMPRESSA	-.050		-.001		+.000	+.000			

1977 PASTURE (CONT.) SURVEY NO. : SEASON	1 SUM	2 FALL	3 SPR	4 SUM	5 FALL	6 SPR	7 SUM	8 FALL	9 SPR
DACTYLIS - RANUNCULUS							-.043		+.000
DACTYLIS - TARAXACUM		-.003		-.009	+.000	-.005	+.000		
DACTYLIS - TRIFOLIUM PRATENSE			+.005		+.012				
DACTYLIS - TRIFOLIUM REPENS	-.002	+.000	-.000	-.001	+.015	-.000		+.003	
FESTUCA - POA COMPRESSA							+.002		
FESTUCA - TARAXACUM				+.000					
FESTUCA - TRIFOLIUM REPENS				-.009					
HOLCUS - LOLIUM						-.001	-.043		-.004
HOLCUS - POA COMPRESSA			+.038		+.000	+.000			
HOLCUS - RANUNCULUS							+.013	+.000	+.001
HOLCUS - TARAXACUM	+.036	+.000							
HOLCUS - TRIFOLIUM REPENS				+.045	+.045	+.039	+.000	+.002	+.000
LOLIUM - PHLEUM					-.005	-.005	-.000	-.035	
LOLIUM - PLANTAGO LANCEOLATA		-.017							
LOLIUM - POA COMPRESSA				-.025		-.001	-.000		-.001
LOLIUM - RANUNCULUS								+.020	-.001
LOLIUM - TARAXACUM					-.000	+.038	-.000		
LOLIUM - TRIFOLIUM REPENS		+.010	-.007			-.005	+.013		-.015
PHLEUM - PLANTAGO LANCEOLATA					+.000				
PHLEUM - POA COMPRESSA	+.005	+.001				+.019	+.000	+.003	
PHLEUM - TARAXACUM		+.003				+.000	+.000		
PHLEUM - TRIFOLIUM REPENS		+.009	+.001	+.003	+.043	+.009			

1977 PASTURE (CONT.) SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
POA COMPRESSA - PLANTAGO LANCEOLATA		+.000							
POA COMPRESSA - RANUNCULUS							+.000		+.000
POA COMPRESSA - TARAXACUM	+.028	+.000	+.000	-.027		+.001	+.001		
POA COMPRESSA - TRIFOLIUM REPENS		+.002	+.000			+.000	+.001		-.000
TRIFOLIUM REPENS - P. LANCEOLATA					+.003				
TRIFOLIUM REPENS - RANUNCULUS						+.004	+.001		+.001
TRIFOLIUM REPENS - TARAXACUM	+.019			+.006					+.009
TRIFOLIUM REPENS - T. PRATENSE		-.002							
PLANTAGO LANCEOLATA - RANUNCULUS								+.048	
PLANTAGO LANCEOLATA - TARAXACUM		+.000		+.000	+.014				

B) 1958 PASTURE SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
AGROPYRON - DACTYLIS	-.028	-.000	-.007	-.000	-.072				
AGROPYRON - FESTUCA		-.029	-.005						
AGROPYRON - HOLCUS		-.046		-.013	-.007			-.000	-.000
AGROPYRON - PHLEUM	-.026		-.022	-.006					
AGROPYRON - POA COMPRESSA	-.001				-.045		+.000	+.000	+.000
AGROPYRON - RANUNCULUS		+.043							
AGROPYRON - TARAXACUM				+.002			+.000	+.000	
AGROPYRON - TRIFOLIUM REPENS		+.000	+.000	+.009		+.002		-.047	
AGROSTIS - DACTYLIS			-.019						-.016
AGROSTIS - HOLCUS									-.002
AGROSTIS - RANUNCULUS			+.003						
AGROSTIS - TARAXACUM			+.014						
AGROSTIS - TRIFOLIUM REPENS			+.047						+.007
ANTHOXANTHUM - DACTYLIS						-.039	-.022	-.031	
ANTHOXANTHUM - FESTUCA							+.037	+.000	
ANTHOXANTHUM - PLANTAGO LANCEOLATA							+.000		
ANTHOXANTHUM - POA COMPRESSA						-.034			
ANTHOXANTHUM - RANUNCULUS						+.001			
ANTHOXANTHUM - TRIFOLIUM REPENS						+.015		+.000	
DACTYLIS - FESTUCA	-.000	-.000	-.000	-.002	-.000	-.000	-.000	-.000	-.000
DACTYLIS - HOLCUS	-.000	-.000	-.000	-.049	-.037	-.000	-.000	-.000	-.000
DACTYLIS - LOLIUM	-.034		-.000	-.001		-.000	+.001		

1958 PASTURE (CONT.) SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
DACTYLIS - PHLEUM	-.000	-.000	-.000	-.000	-.039			-.000	
DACTYLIS - PLANTAGO LANCEOLATA		-.009		-.005	-.009		-.001	-.009	-.046
DACTYLIS - POA COMPRESSA	+.000	-.000	-.000	-.000	+.001	-.000	+.000	+.000	+.000
DACTYLIS - POA TRIVIALIS	+.013								
DACTYLIS - RANUNCULUS									+.026
DACTYLIS - TARAXACUM		+.000	+.000	+.002			+.017	+.006	+.049
DACTYLIS - TRIFOLIUM REPENS	-.002	-.000	+.000	+.000		+.000			
FESTUCA - HOLCUS		-.005		+.008			+.004		+.000
FESTUCA - LOLIUM							-.002	-.008	
FESTUCA - PLANTAGO LANCEOLATA		+.000			+.012	+.015	+.000	+.000	+.000
FESTUCA - POA COMPRESSA							-.031	-.001	-.000
FESTUCA - RANUNCULUS		+.006	+.000		+.002				+.000
FESTUCA - TARAXACUM				+.000					
FESTUCA - TRIFOLIUM REPENS	+.000	+.009	+.000	+.022		-.021			+.000
HOLCUS - LOLIUM									-.012
HOLCUS - PHLEUM								-.034	
HOLCUS - POA COMPRESSA	+.000		-.011		-.023	-.004	-.005	+.002	-.000
HOLCUS - RANUNCULUS				+.007	+.001	+.013	+.000		+.000
HOLCUS - TARAXACUM			+.008					-.016	
HOLCUS - TRIFOLIUM REPENS	+.007	+.000	+.002	+.010		-.000		+.001	
LOLIUM - PHLEUM		+.007							
LOLIUM - PLANTAGO LANCEOLATA						+.006			

1958 PASTURE (CONT.) SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
LOLIUM - POA COMPRESSA					-.035	-.005			
LOLIUM - RANUNCULUS			+.007		+.018				
LOLIUM - TARAXACUM								-.024	+.000
LOLIUM - TRIFOLIUM REPENS	+.001	+.031	+.000	+.000	+.004	+.000			+.001
PHLEUM - POA COMPRESSA			-.000	-.015		+.008	+.005	+.000	+.023
PHLEUM - POA TRIVIALIS	+.000								
PHLEUM - RANUNCULUS									+.012
PHLEUM - TARAXACUM			+.001				+.012	+.017	+.004
PHLEUM - TRIFOLIUM REPENS	-.030	+.014	+.000	+.006					
POA COMPRESSA - POA TRIVIALIS	-.022								
POA COMPRESSA - P. LANCEOLATA									-.028
POA COMPRESSA - TARAXACUM	+.013	+.025	+.000	+.000		+.001	+.000	+.006	+.007
POA COMPRESSA - TRIFOLIUM REPENS	+.000	+.000	+.000	+.000	+.000	+.000	+.000	+.002	+.002
TRIFOLIUM REPENS - P. LANCEOLATA				+.047				+.000	
TRIFOLIUM REPENS - RANUCULUS					-.020				
TRIFOLIUM REPENS - TARAXACUM			+.000						
PLANTAGO LANCEOLATA - RANUNCULUS							+.013	+.036	+.000

C) 1939 PASTURE

SURVEY NO. :	1	2	3	4	5	6	7	8	9
SEASON :	SUM	FALL	SPR	SUM	FALL	SPR	SUM	FALL	SPR
AGROPYRON - CIRSIUM				+.000					
AGROPYRON - FESTUCA	+.030	+.040		+.032				+.003	
AGROPYRON - HOLCUS	-.001	-.023		-.020				-.008	-.008
AGROPYRON - LOLIUM		-.031		-.031		-.028			-.005
AGROPYRON - PHLEUM				-.005					
AGROPYRON - POA COMPRESSA	-.007							+.021	
AGROPYRON - TARAXACUM							+.000		
AGROPYRON - TRIFOLIUM REPENS	+.009	+.000	+.021	+.001	+.001	+.012	+.000		+.001
AGROSTIS - HOLCUS	-.013								
AGROSTIS - TRIFOLIUM REPENS			+.005				+.039		
DACTYLIS - CIRSIUM		+.037							
DACTYLIS - HOLCUS	-.000	-.006		-.008	-.001	-.007	-.047	-.001	-.000
DACTYLIS - LOLIUM				-.022	-.005		-.041		
DACTYLIS - PHLEUM				-.018			-.006		
DACTYLIS - POA COMPRESSA	-.011	-.002	-.000	-.018	-.018	-.006			-.039
DACTYLIS - TARAXACUM	+.043								+.046
DACTYLIS - TRIFOLIUM REPENS	+.000			+.000	+.001	+.007	+.000	+.000	+.000
FESTUCA - POA COMPRESSA	-.000		-.039						
FESTUCA - RANUNCULUS		+.000	+.014						
FESTUCA - TARAXACUM		+.037							
FESTUCA - TRIFOLIUM REPENS			+.026	+.008				+.043	
HOLCUS - LOLIUM		-.017				-.000			-.000

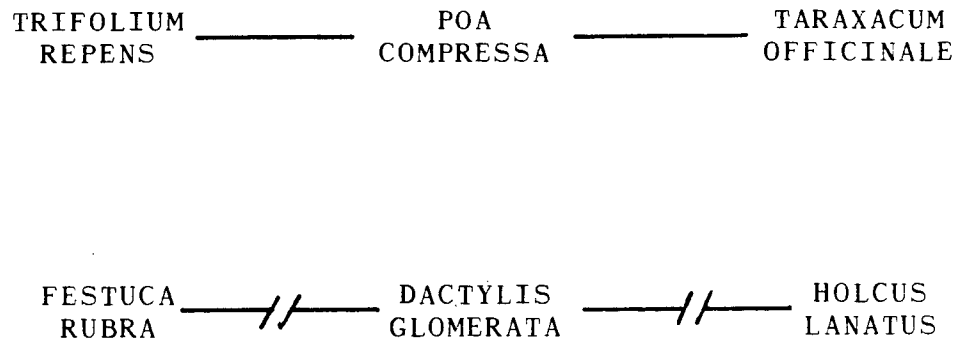
1939 PASTURE (CONT.) SURVEY NO. : / SEASON :	1 SUM	2 FALL	3 SPR	4 SUM	5 FALL	6 SPR	7 SUM	8 FALL	9 SPR
HOLCUS - PHLEUM					+.013	-.020			
HOLCUS - POA COMPRESSA		-.037	-.023			-.000	+.001	-.011	-.000
HOLCUS - RANUNCULUS							+.026		
HOLCUS - TARAXACUM				-.046					
HOLCUS - TRIFOLIUM REPENS	+.001	+.000	+.000	+.026	+.010	+.003	+.026	+.001	+.000
LOLIUM - CIRSIUM					+.022				
LOLIUM - POA COMPRESSA	-.000	-.000	-.000	-.000	-.005	-.000	-.000	-.000	-.001
LOLIUM - TARAXACUM		+.027				+.016	+.026	+.015	
LOLIUM - TRIFOLIUM REPENS	+.000	+.000	+.000	+.000	+.000	+.000	+.000	+.016	+.000
PHLEUM - POA COMPRESSA		-.012		+.012					
PHLEUM - RANUNCULUS					+.022				
PHLEUM - TARAXACUM				-.020					
PHLEUM - TRIFOLIUM REPENS		+.000			+.032	+.003	-.014		
POA COMPRESSA - RANUNCULUS					-.006				+.048
POA COMPRESSA - TARAXACUM	+.000			+.000	+.035				+.024
POA COMPRESSA - TRIFOLIUM REPENS	+.000	+.000	+.000	+.000	+.000	+.000	+.000	+.000	+.000
TRIFOLIUM REPENS - CIRSIUM				-.041	-.017				
TRIFOLIUM REPENS - RANUNCULUS				-.023	-.000	-.022			
TRIFOLIUM REPENS - TARAXACUM						-.008	+.028	+.021	+.014
RANUNCULUS - TARAXACUM						-.037			

and sometimes reappearing in later surveys. The oldest pasture had notably fewer temporary associations than the two younger pastures (Table 12). Some species pairs alternated between positive and negative association and this was especially evident in the youngest pasture. The youngest pasture had no significant paired associations which were consistently positive or negative over the 33-month study period. However, the 1958 pasture had 4 such 'stable' associations and the 1939 pasture had 6 stable associations (Fig. 7).

The occurrence of increasing stability or constancy of positive and negative association between particular species pairs with increasing pasture age is further illustrated in Figure 8. Particularly notable is the development with increasing pasture age, of stable negative association between 4 different pairs of grass species (Fig. 8 a,c,e,h) and the development of more stable positive association between Trifolium repens and 5 different grasses (Fig. 8 b,d,g,i,j). Likewise, patterns of seasonal association show a similar trend reflecting a tendency of increasing community constancy. A seasonal association can been seen developing between Holcus lanatus and Poa compressa which were significantly negative in association in all three spring surveys in the 1939 and 1958 pastures, but showed no seasonal pattern of association in the youngest pasture (Fig. 8f). In the 1977 pasture, D. glomerata and T. repens were positively associated in all three fall surveys but this seasonal pattern was not present in the two older pastures where association was progressively less variable (Fig. 8d). The same trend was found for L. perenne and T.

FIGURE 7. Stable pairwise associations (positive - solid lines, and negative - broken lines) detected in a) the 1958 pasture, and b) the 1939 pasture. Each association was significant ($P<0.05$) in all nine surveys (except *P. compressa* - *T. officinale* in a) with $P=0.070$ in survey 5, and *D. glomerata* - *H. lanatus* in b) with $P=0.083$ in survey 3).

a) 1958 PASTURE



b) 1939 PASTURE

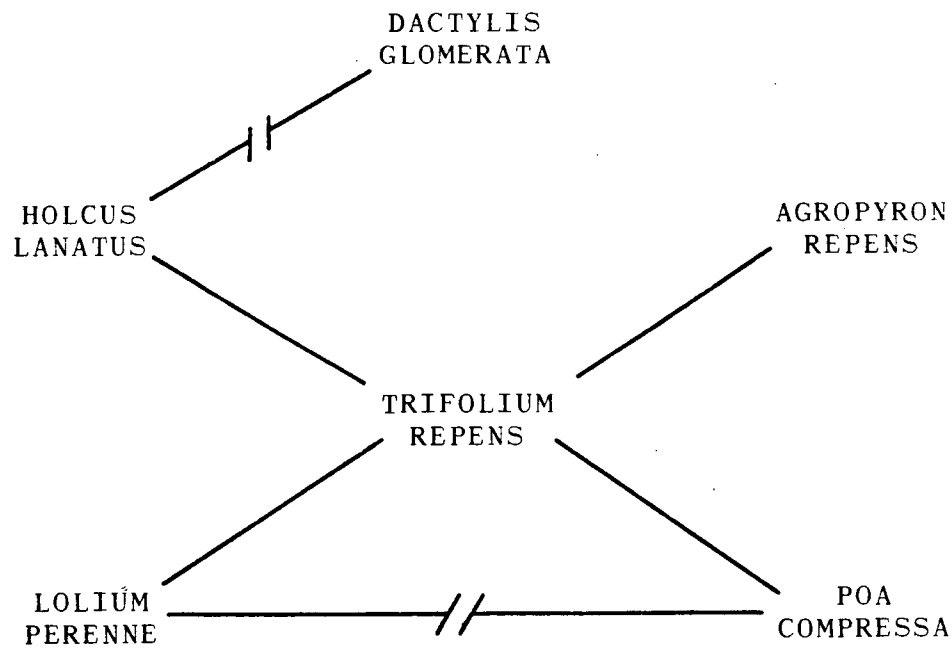
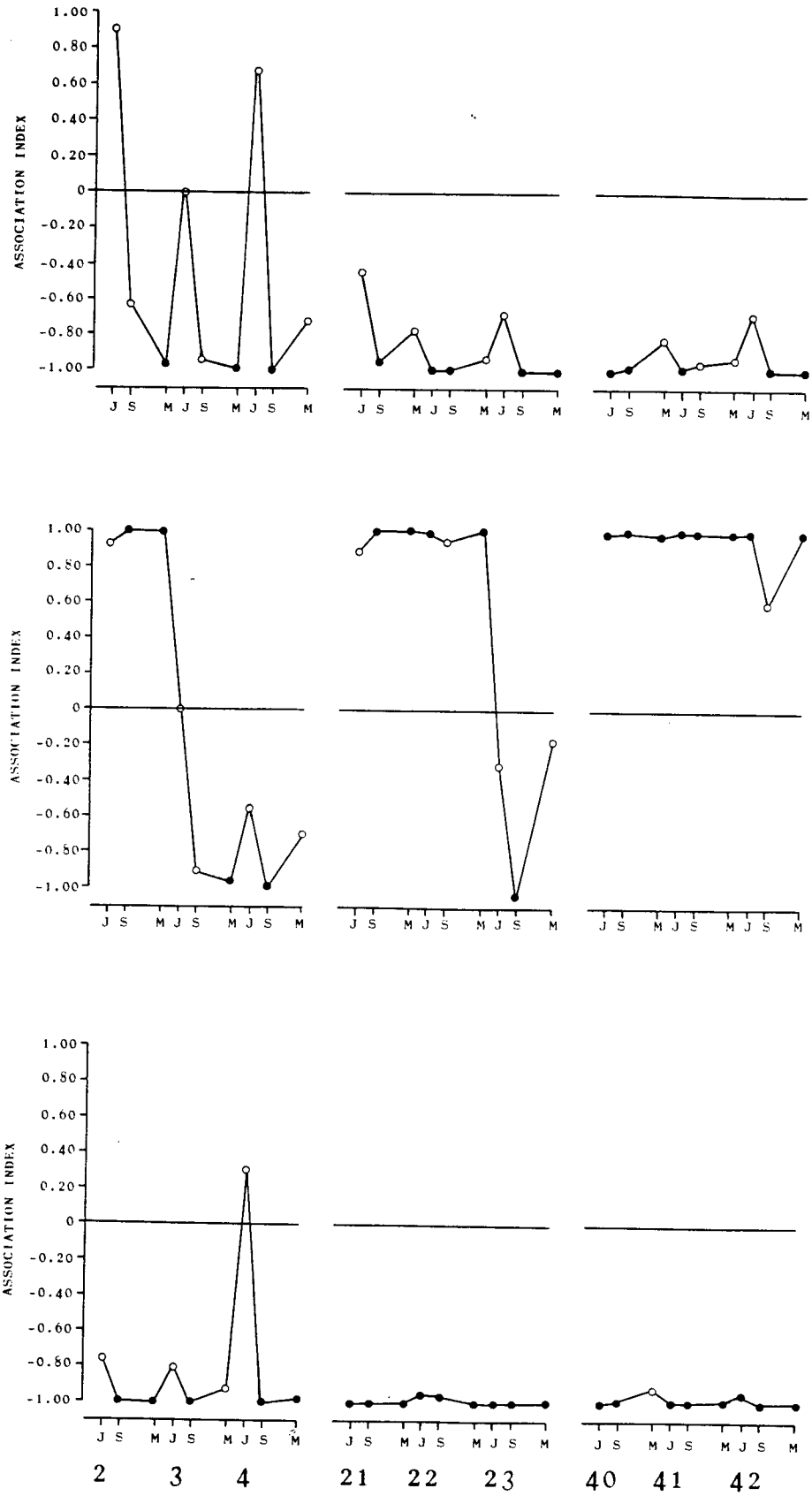


FIGURE 8. Course lines showing the degree of association for selected individual species pairs versus the number of years since the sampled field was sown. Survey data from the three study fields over a period of 33 months from June 1979 to March 1982 are represented in each graph. Plotted values are association indexes calculated as C=1-P with the appropriate sign of the standardized residual attached and where P is the significance probability level for the particular pairwise association. Closed circles represent significant associations at $P<0.05$ ($C>0.95$ or $C<-0.95$). The months in which surveys were conducted are indicated as M=March, J=June, S=September.

1977 PASTURE 1958 PASTURE 1939 PASTURE



a)

Agropyron repens – Holcus lanatus

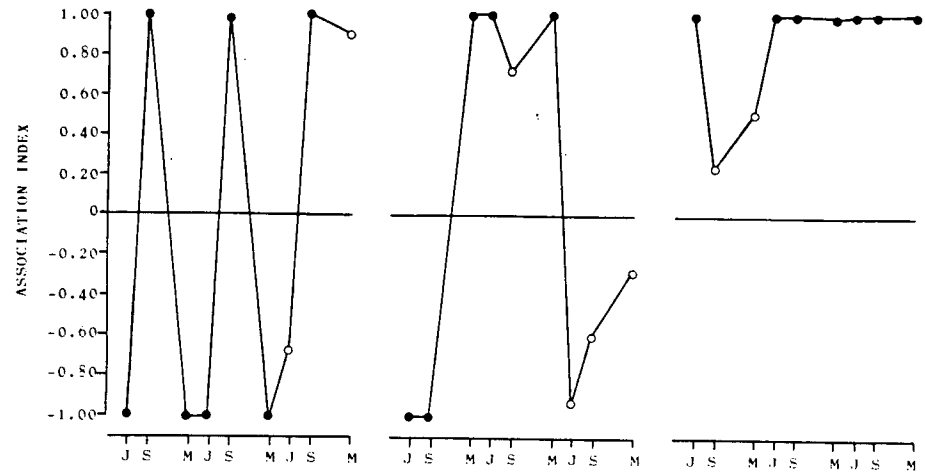
b)

Agropyron repens – Trifolium repens

c)

Dactylis glomerata – Holcus lanatus

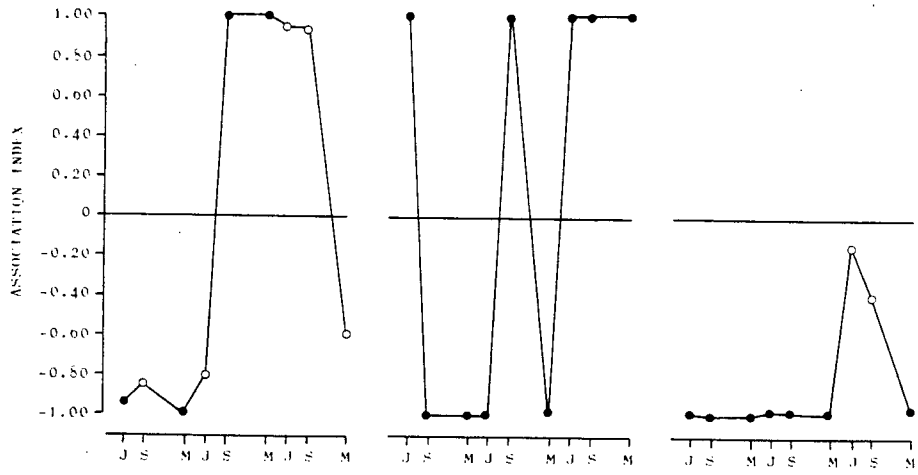
1977 PASTURE 1958 PASTURE 1939 PASTURE



d)

Dactylis glomerata

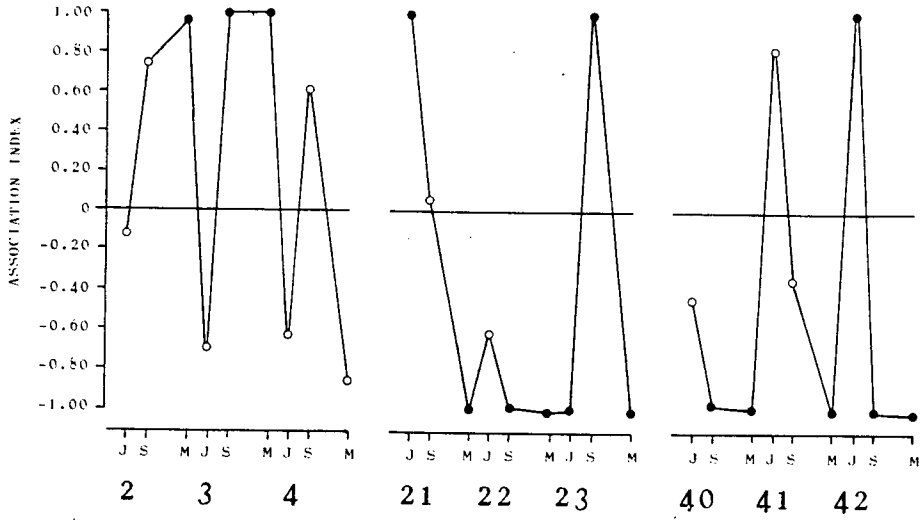
Trifolium repens



e)

Dactylis glomerata

Poa compressa



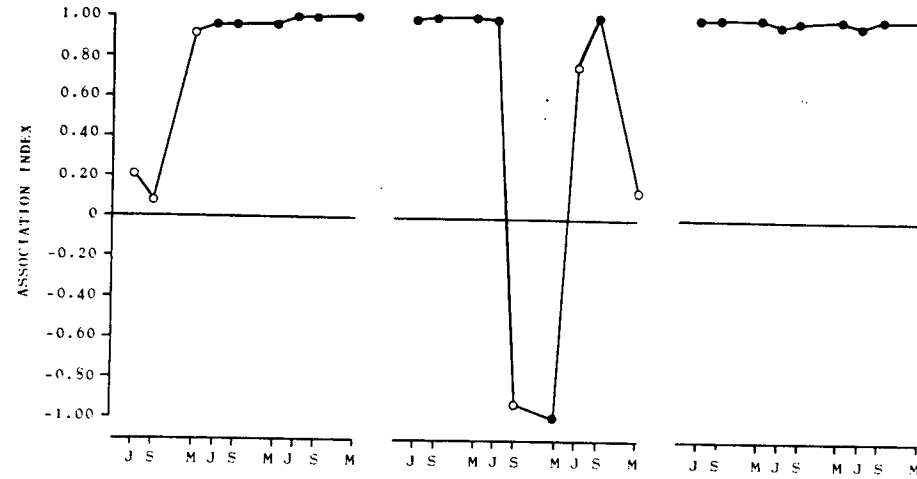
f)

Holcus lanatus -

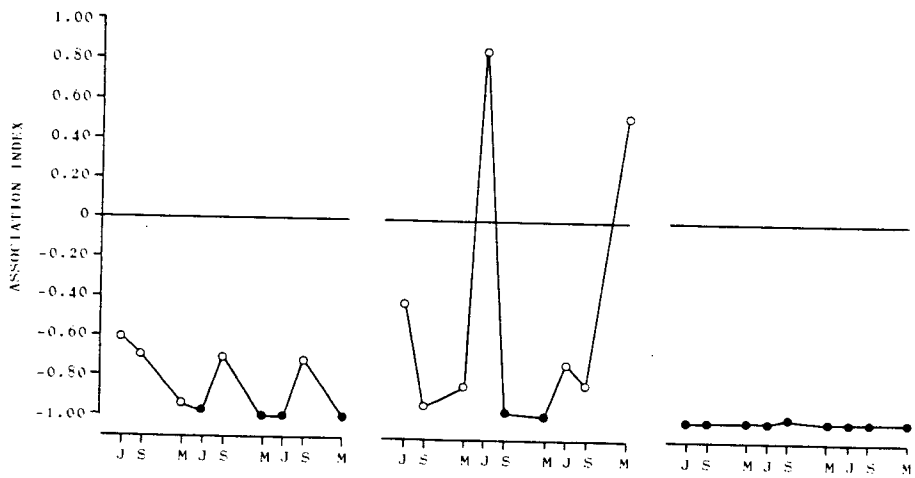
Poa compressa

YEARS SINCE PLANTING

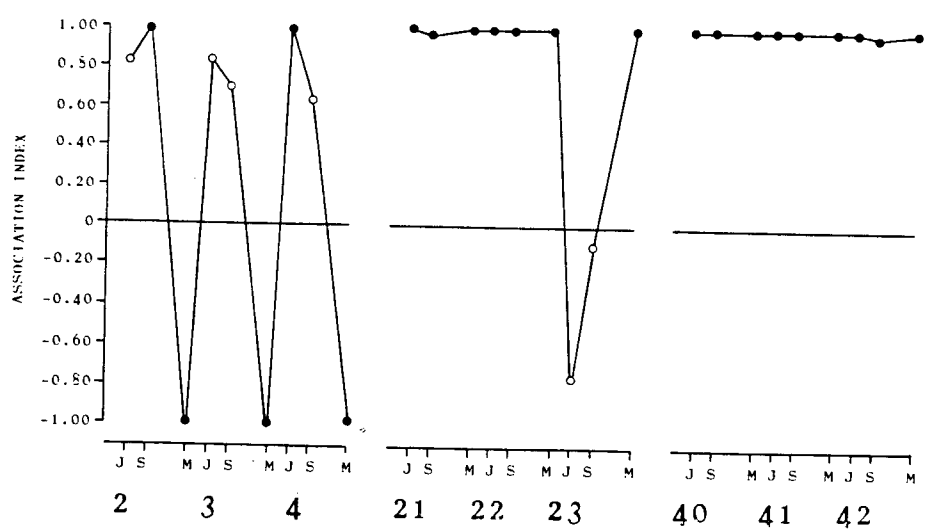
1977 PASTURE 1958 PASTURE 1939 PASTURE



g) Holcus lanatus - Trifolium repens

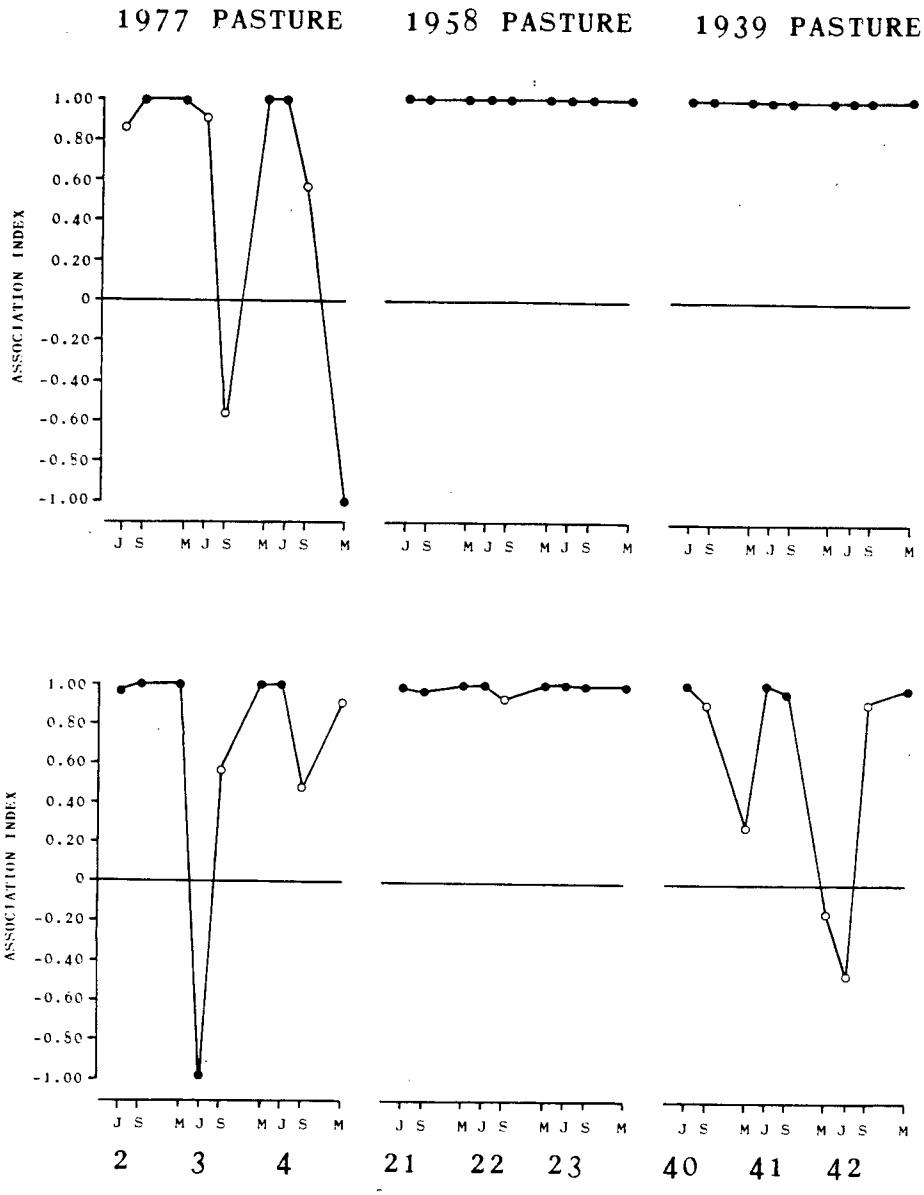


h) Lolium perenne - Poa compressa



i) Lolium perenne - Trifolium repens

YEARS SINCE PLANTING



j) Poa compressa - Trifolium repens

k) Poa compressa - Taraxacum officinale

repens which were significantly negative in association in the three spring surveys for the 1977 pasture, but association was less variable in the two older pastures and was positive and stable in the 1939 pasture. P. compressa and Taraxacum officinale showed a stable behaviour of positive association in the 1958 pasture but a temporary pattern of association in the other two pastures (Fig. 8k). The overall trend is one of increasing stability of associations between species in progressively older fields.

DISCUSSION

The reaction of individuals to the presence of other organisms is crucial to the understanding of the ecology of both populations and communities. The manner of coping with the biotic environment consititutes a major part of the environmentally-induced genetic changes in many species (Cantlon 1968). In referring to species assemblages over broad spatial and temporal scales, Whittaker (1975) commented, "Species associations with other species are predominantly loose and changeable, and community evolution is net-like in the sense that species are variously combined and recombined into communities in evolutionary time". No special distinction of duration need be imposed however for 'evolutionary time'; evolutionary changes may occur on almost any time scale (Antonovics 1976a).

The results presented provide evidence for the transient nature of interspecific association discussed by Whittaker, on a very local scale. Detailed studies of developmental changes in

local patterns of association in communities, from the "plant's-eye-view", have been recent and few in number (Aarssen et al. 1979, Turkington & Cavers 1979, Saulei 1981). The present study involves more intensive sampling over a longer period of investigation in pastures which differ more widely in age than in previous studies. The results are consistent with the findings in earlier work, i.e. younger communities have a preponderance of interspecific associations which are temporary in nature during the study period and older communities have more associations which persist essentially unchanged over the same time period than do younger communities. Table 12 summarizes the temporal patterns of associations in the three pastures.

TABLE 12. Numbers of significant temporary, seasonal and stable associations (both positive and negative) detected in the three different aged pastures.

YEAR OF	NUMBER OF SIGNIFICANT ASSOCIATIONS (P<0.05)		
PLANTING	Temporary	Seasonal	Stable
1977	52	2	0
1958	57	0	4
1939	35	1	6

Apparently, associations between species become less 'loose and changeable' and pasture community evolution tends toward a stability in species interrelationships. The developmental trends toward stability in interspecific associations (Fig. 11)

parallel those directional trends in the ordination of quadrat percentage cover data (Fig. 4, Chapter 2). The data on neighbour contacts however translates the gross vegetational patterns from quadrat sampling into an identification of the particular neighbours representing the individual plant's experience of its immediate biotic environment. The general picture is that of a transition from an essentially random assemblage of neighbourhoods in which the positional relationship of consituent members is in a constant state of flux, to a more fixed community matrix in which the most proximate interspecific neighbours (i.e. in physical contact) share a more or less permanent address.

The results may be best interpreted by placing them into a theoretical and evolutionary context for the pasture community. A popular view of community evolution was propounded by Whittaker and Woodwell (1971, p. 137): "The community is the context of species evolution ... the evolution of a community must entail 'parallel' or coadaptive evolution of the community's species. The community is an assemblage of interacting and coevolving species.... Through this evolution there will appear adaptation to environment for the community as well as the species.... Community level characteristics also will evolve". Community evolution in this perspective means that community-level characteristics (e.g. diversity, dominance, physiognomy, trophic structure, stability, spatial pattern, coadaptive associations or networks, etc.) will tend to follow certain deducible and recognizable trends through time dictated by the fact that they are community-level products of

evolution and interaction at the species level (Whittaker & Woodwell 1971). Cody & Diamond (1975) echoed a similar sentiment arguing that "... the observed patterns in community structure are products of natural selection ...." The central community characteristic here is that of 'coadaptive associations or networks' and changes in this characteristic are reflected by changes in all the others. In this context, the results from the present study may be used to fashion a qualitative model for community evolution.

Ultimately, the model set forth below is concerned with interspecific interaction and coexistence, but the premise of the model considers the community primarily as a collection of genotypes. This is in keeping with the fact that the contact sampling method focuses on interspecific interactions from the perspective of the individual. In addition, Harper (1977b) has stressed how conventional descriptions of diversity based on the taxonomic species unit may not be entirely adequate and that a major part of the functional diversity of a plant community exists at the intraspecific level. The proposed model treats genetic and species diversity as integral and interdependent components of community diversity rather than as separate phenomena. Hypothetical events are traced from the initial 'colonization' (sowing of the pasture) to some future state of the community which may be defined arbitrarily as a 'subclimax' maintained by grazing animals, although it is not intended that the model be cast as a description of succession in the traditional sense of replacement of 'community types'. Attention is focused on finer-scale events occurring in local

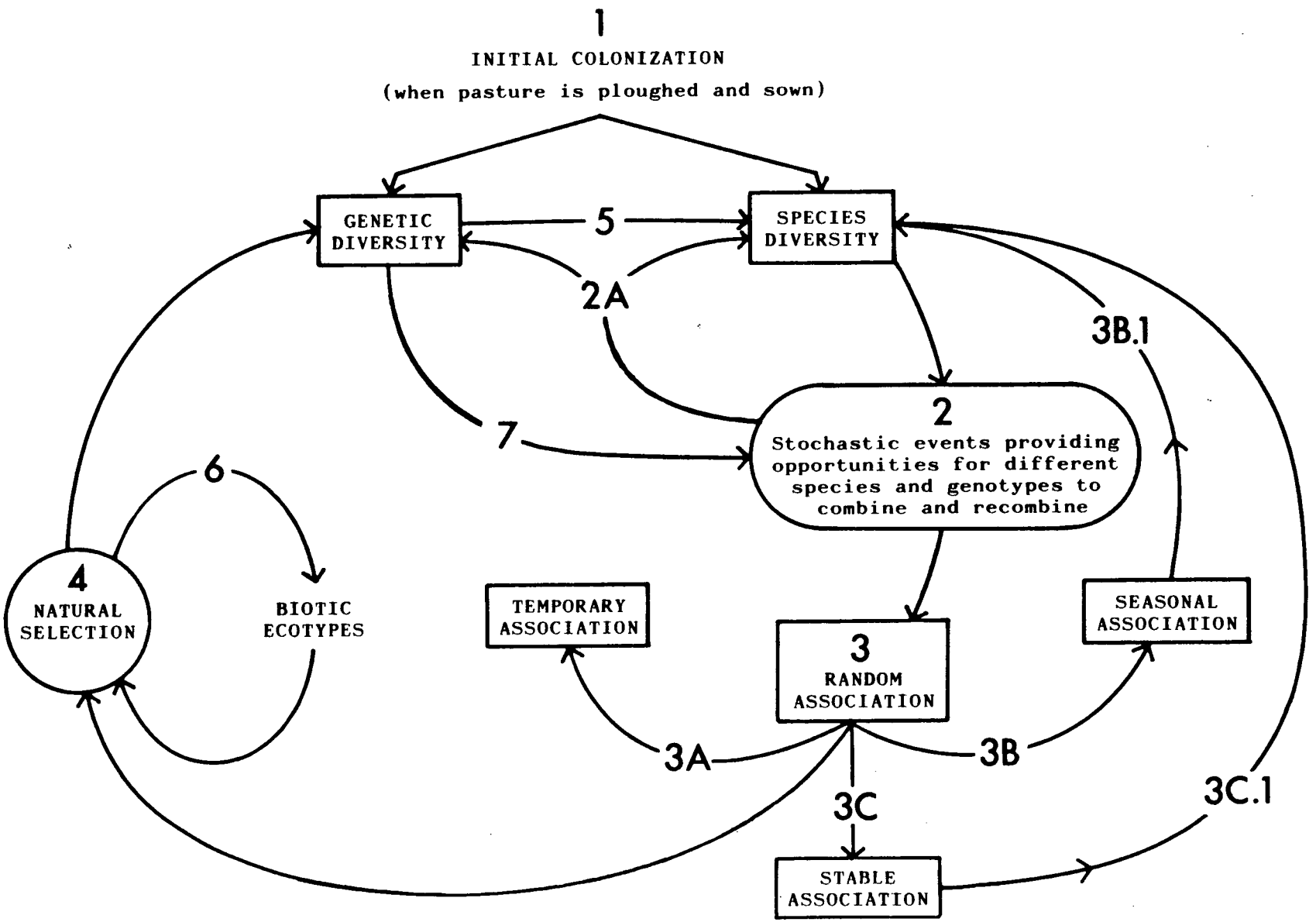
neighbourhoods within the pasture community. The model is displayed in Figure 9 and described by the following stages:

1) When the pasture is initially ploughed and sown, a degree of both genetic and species diversity is imparted on the community which together with the diversity represented in the seed bank comprises the total 'initial' diversity, genetic and species, in the community.

2) Local disturbances (e.g. grazing, mole hills, hoof marks), management practices, variations in climate, emigration and immigration (gene flow), natural death of plants or plant parts (and subsequent newly available space), and other chance events (local dispersal patterns, mutations, genetic drift, etc.) represent the stochastic factors responsible for affecting community change. Species and genetic diversity in the community will be affected (2A). These events provide opportunities for different species and genotypes to combine and recombine with one another - to 'sample' their neighbours in a random and unpredictable manner.

3) The higher the diversity (species and genetic), the more opportunities there will be for new 'random association', i.e. the greater the probability of different species and genotypes meeting randomly. Growth form will also influence the number of opportunities for species to 'sample' their neighbours. Stoloniferous species such as Trifolium repens (and to a lesser extent rhizomatous species such as Poa compressa) are able to

FIGURE 9. A qualitative model for pasture community evolution. Steps in the model are described in the text.


1
INITIAL COLONIZATION
(when pasture is ploughed and sown)
GENETIC DIVERSITY
5
SPECIES DIVERSITY
2A
3B.1
7
2
Stochastic events providing opportunities for different species and genotypes to combine and recombine
6
4
NATURAL SELECTION
BIOTIC ECOTYPES
TEMPORARY ASSOCIATION
3
RANDOM ASSOCIATION
SEASONAL ASSOCIATION
3A
3B
3C
3C.1
STABLE ASSOCIATION

migrate within the community, perhaps escape from inhospitable neighbourhoods, and eventually happen upon compatible ones. In this context, the stoloniferous species may be regarded as an itinerant species and one which greatly influences the propensity of initial random associations. In the present study, T. repens was involved in more significant associations ($P<0.05$) (most of which were 'temporary') during the study period than any other species (Table 11). This influential role played by stoloniferous species has been suggested by Turkington & Harper (1979c) and has been developed by Aarssen et al . (1979).

Depending on the compatibility of the species involved in these random associations, three different events may be predicted as follows (Aarssen et al . 1979):

3A) The association may be significant but transient. An association (either positive or negative) may break down (and perhaps reform) because of recurring disturbances. Species which respond to disturbance in similar ways may tend to occur together and those which respond differently may become mutually exclusive. A significant negative association may result during competitive exclusion and may be temporary if disturbance halts the exclusion process and periodically restores random association. This interpretation applies to the vast majority of associations listed in Table 11.

3B) The association may be significant only on a seasonal basis. Seasonal compatibility may result if two species have

asynchronous life cycles (temporal partitioning). Species which have some difference in their ecologies that permits their coexistence, have "ecological combining ability" (Harper 1964, 1967). Mechanisms permitting coexistence contribute to the maintenance of diversity in the community (3B.1). Such seasonal differences may be mediated by short term fluctuations in environment. In the present study, two seasonal associations were detected in the 1977 pasture (Fig. 8d,i) and one in the 1939 pasture (Fig. 8f).

3C) The association may be significant and persistent, i.e. a stable association. Stable significant associations are an important developmental feature of the pastures in the present study (Figs. 7 and 8). On a grand scale, species are 'found together' because they are 'adapted' to a common type of habitat. The contact sampling method however reveals fine-scale association at the critical level of individual experience. Such an association which is significantly positive may also be due to common site requirements on a local scale. If this association is stable however it means that something is preventing competitive exclusion. Species which coexist are usually thought to differ in some way(s) in which they exploit the environment (e.g see reviews by Grubb (1977) and Werner (1979)). Ecological combining ability may take on several forms based on the notion that two species of contrasting habit with respect to some morphological or physiological character, will together be able to exploit the total environment more effectively than both species growing alone. A resource-based

selective advantage may be afforded by such an association and their complementarity dictates that they may be found growing in proximity to one another more often than expected by chance. Positive association may also be encouraged by a beneficial interaction between species such as mutualism or commensalism. Stable (and significant) negative association may be a result of some differentiation on a horizontal spatial scale with the consequence that the two species rarely enter into each other's immediate sphere of influence. This may confer an advantage in terms of fitness if it serves to quell threats of competitive exclusion. Harper (1967) has stressed that an understanding of the critical differences between species will presumably provide the 'explanation' of stable diversity in nature (3C.1).

4) Many associations will remain random (i.e. found together as often as expected by chance). Within each population there will be a range of genetic variability reflecting a range of individual abilities to persist in a random association (with perhaps any one of many different species or genotypes). Selection acting on this existing genetic variability will oust from the community or from certain neighbourhoods within the community, those genotypes which do not 'fit in', i.e. are incompatible. A reduction in genetic diversity may result. Those genotypes which do 'fit in' are those capable of residing in neighbourhoods in which immediate neighbours do not impose overbearing constraints on fitness - neighbourhoods where superior rivals are not residents.

5) The above selection process leaves genotypes which are more compatible within local neighbourhoods than the resident genotypes before selection. This may permit coexistence and hence further contributes to the maintenance of species diversity. Having come full circle in the model demonstrates its feedback potential; The steps 2 through 5 occur continuously during the evolution of the community. The result is that some random associations remain random, but others may become significantly stable (positive or negative) if selection involves niche differentiation or beneficence (see 3C above).

6) As selection results in members of a population adapted to different segments of the community, 'biotic ecotypes' (Turesson 1922, Turkington & Harper 1979c) may evolve. Biotic specialization may evolve between species regardless of whether they are found in association more often than expected by chance. Species which develop a more persistent association deviating significantly from random expectation (e.g. Fig. 8) however attract particular attention and may exhibit the most recognizable biotic ecotypes. Harper (1977b) has proposed that the pattern of associations in old permanent pastures is likely to be the result of a close evolutionary coadaptation involving all the species.

7) As more and more biotic specialization is evolved, the community is continually approaching the 'subclimax' which should theoretically be characterized more and more by a 'fixed' community matrix of unchanging interspecific associations (some

of which will be significantly stable) - a stage which is never fully realized because of step 2. The net result may be a decrease in genetic diversity (in terms of coexisting genotypes, not genes). After several iterations, the model predicts that the number of opportunities for species and genotypes to combine and recombine in association is restricted because the community is transfigured from an essentially random and diverse collection of genotypes into an assemblage of largely specialized biotic ecotypes which may also be superimposed on abiotic ecotypes. In older communities then, threats of competitive exclusion are less severe and the response to disturbance in local neighbourhoods is more predictable. Hence, there are fewer significant temporary associations than in younger communties.

Placing the results into a broad theoretical context leads next to a consideration of particular species interactions. Only in this way can insight be gained into the mechanisms which may drive the model. The prominence of Trifolium repens in stable positive associations and the prominence of stable negative associations between grasses is noteworthy (Fig. 8). Negative association may be expected amongst species such as grasses with similar growth forms and hence perhaps similar ways of exploiting the environment. Negative association may also result if species have different site requirements in a heterogeneous habitat. Results from the soil analyses (Chapter 2) however showed very little variation within fields and very little correlation with species cover (Table 7).

Turkington & Harper (1979b) attribute a stable positive association between T. repens and Lolium perenne to an asynchrony of their growth cycles. No clear evidence of this was found in the present study and of particular interest is the development of stable positive association between T. repens and 5 different grasses (Fig. 8 b,d,g,i,j). These positive associations involving T. repens may be related to selection for some form of 'combining ability' and generated by a complex of factors involving the 'wandering' habit of the stoloniferous T. repens, 'seeking out' compatible neighbourhoods of grass genotypes, and a beneficence afforded to the grasses by a close association with the nitrogen-rich environment provided by the legume. Turkington & Harper (1979c) found that each of four different clones of T. repens exhibited precise biotic specialization to four respectively different species of neighbouring grass in an old pasture.

Very little can be said about the nature of species interactions from contact sampling data alone. Contact sampling serves to detect departures from random association of species i and j - it does not permit decisions to be made concerning the relative natural hostility or affinity of i for j, versus j for i. Interpretations of patterns in terms of processes are only possible using controlled experimental procedures. This poses the question as to what are the mechanisms producing associations and permitting coexistence in these pastures? This forms the line of inquiry in subsequent chapters.

CHAPTER 4

COMPETITIVE RELATIONS IN DIFFERENT AGED PASTURES: A MIXTURE DIALLEL OF FIVE SPECIES

INTRODUCTION

> "The fact that organisms living in different places are different is easy to explain by Wallacian forces. The question of how so many sorts of organisms are able to persist together in the same 'place' is much more difficult to answer, is much more interesting; it demands biotic interpretation and a Darwinian solution" (Harper 1977b).

Traditional studies of intraspecific differentiation within plant species have been dominated by a 'Wallacian' perspective concentrating on local and large-scale differences amongst populations in relation to different qualities of abiotic environmental factors (e.g. Turesson 1922, Clausen Keck & Hiesey 1948, Kruckeberg 1951, Jain & Bradshaw 1966, Snaydon 1970, 1971, Davies & Snaydon 1973, Teramura & Strain 1979, Snaydon & Davies 1982). Other studies have shown ecotypic differentiation between populations in relation to grazing (Kemp 1937), other forms of disturbance from human activities (Solbirg & Simpson 1974, Warwick & Briggs 1980), changes in overall habitat conditions in different stages of abandonment of agricultural fields (Hancock & Wilson 1976), and in the conversion of a woodland to a grassland (Lovett Doust 1981). Questions concerning species coexistence however center attention on the role of competitive interactions as selectional forces and this represents the focal point of a 'Darwinian' perspective of intraspecific differentiation.

Only recently have efforts been made to search for and document intraspecific differentiation associated with biotic

specialization in response to competition. Some studies have reported population differentiation in a single plant species that appeared to be associated with the particular constitution of the surrounding vegetation (Watson 1969, Linhart 1974, Watson 1974 - in Antonovics 1978). Other studies have attempted to pinpoint more precisely the biotic elements involved. Remison and Snaydon (in Snaydon 1978) demonstrated ecotypic differentiation in populations of Anthoxanthum odoratum, Dactylis glomerata , Holcus lanatus and Lolium perenne ; pairs of populations collected from the same site had a higher combined yield when grown in experiment together than did populations collected from different sites. Turkington & Harper (1979c) demonstrated fine-scale population specialization in Trifolium repens in response to different specified neighbouring species within a single pasture less than 1 ha in size. Martin & Harding (1981) also showed evidence for biotic specialization in sympatric versus allopatric populations of Erodium obtusiplicatum and E. cicutarium. The implication of these findings is that such differentiation is a consequence of genetic changes reflecting local adjustment (specialization) to the biotic environment. Moreover, such intraspecific differentiation may exist not only between populations, but also within a single population (e.g. Turkington & Harper 1979c). Some studies have indicated that a specific pair of genotypes may be specialized to each other in relation to other genotypes of the same two species (Allard & Adams 1969, Remison & Snaydon - in Snaydon 1978, Joy & Laitinen 1980). In the context of multispecies interactions, this underscores the modus operandi

of "biological accommodation" (Saunders 1968, McNaughton & Wolf 1979) in communities - the nucleus of an evolutionary perspective of species coexistence.

The crucial question left unanswered by previous studies of biotic specialization concerns the precise selection mechansism(s) by which species adjust to their environment of neighbours, resulting in more compatible behaviour in their presence. Previous interpretations of biotic specialization concern 'ecological combining ability' (Harper 1964, 1977b) implying an evolved niche displacement. This confers some measure of escape from competition with the result that species yield higher together in mixture. This interpretation seems to apply for example to the data of Remison & Snaydon (in Snaydon 1978). Biotic specialization in the pasture population of Trifolium repens described above has been interpreted as evidence for local 'coadaptation' between white clover and grasses involving a process of selection for ecological combining ability (Harper 1977b). There was no attempt however in the study to test for reciprocal specialization in the grasses, so it is not certain whether this is evidence for coadaptation or simply one-way adaptation (specialization) by the clover. Furthermore, without information about the reciprocal effects of competitors, it is not possible to distinguish whether such local specialization is a consequence of selection for ecological combining ability (niche shift), or selection which improves relative fitness through an improvement in the relative capacity to reduce the availability of resources to a competitor.

The best reflection of the way(s) in which neighbours respond reciprocally to each other must come from investigations involving individuals which actually interact in nature, yet no former attempt at this has been made. Insight into the selection mechanisms producing biotic specialization is only possible through studying how the reciprocal responses between natural neighbours in a community change through time or in different aged communities with an established ontogenetic relationship. Furthermore, no previous efforts have been made to elucidate the process of biological accommodation in a community-wide framework. This requires a study of the changes in reciprocal responses between natural neighbours for several of the most dominant species in a community. These are the objectives of the present investigation.

One approach to understanding the relationships amongst the members of a community is to isolate the members and combine them in all possible pairs. In this experimental design, called a 'diallel analysis', a number of species are grown in all possible combinations of pairs and their yields as mixtures are contrasted with their yields as pure stands (Norrington-Davies 1967, 1968, Trenbath 1975, 1978). Both the yield differential between the two component species and their total yield provide information for the analysis of reciprocal effects of competition. It is also interesting to ask whether a particular population exhibits a stable or sensitive behaviour in response to different associates. Such information on the 'sociological homeostasis' of mixtures can be obtained from the analysis of mixture diallels (Jaquard & Caputa 1970, Rousvoal & Gallais

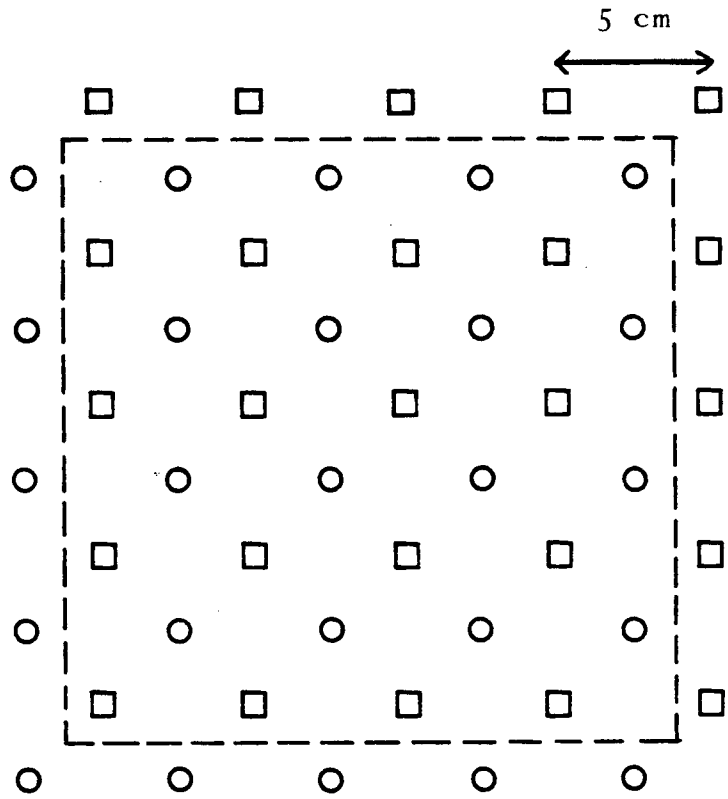
1973). The above information is sought in the present study using a variation of the diallel set-up involving 5 of the most dominant species in the different aged pastures under study. The principal aim is to test for the occurrence of developing biological accommodation during pasture community evolution, and to characterize the possible mechanisms that may be involved.

METHODS

All possible 2-species pairs of natural neighbouring genets were collected from each of the three different aged pastures and cloned, as outlined in Chapter 2, for the following five species: Dactylis glomerata , Holcus lanatus , Lolium perenne , Poa compressa and Trifolium repens . In the first week of May 1980, 25 ramets of each genet were planted with 25 ramets of its natural neighbouring genet in 25 cm x 25 cm field plots in the arrangement shown in Figure 10. Since each genet type was defined by a specific natural neighbouring species, there was no basis for deciding upon the genotypic composition for monoculture plots; these were therefore omitted. Ramets of each of the above species were also obtained from a stock source of plants derived from a commercial seed supply (Richardson's Seed Co., Burnaby, B.C.) and planted in all possible species pairs of 25 ramets each, as above. This represented 'natural neighbours' from a pasture of age 'zero'. All mixtures were replicated 3 times. Plots were set up 1.5 m apart and arranged randomly in the field at the experimental field station, University of British Columbia.

Successive harvests were taken by placing a square

FIGURE 10. Planting arrangement in the mixture diallel showing positions for 25 ramets of each of two species. The dashed lines indicate the size and positioning of the harvesting frame placed over the plot within which the vegetation was clipped and collected at each harvest.


5 cm

harvesting frame over each plot (Fig. 10) and clipping the vegetation inside the frame to approximately 3 cm. The clippings were collected, separated according to species, dried and weighed. The first harvest was taken 10 weeks after planting the ramets. Four more harvests were taken at approximately 3-4 week intervals until November. Negligible growth occurred over winter and harvesting resumed in the first week of April 1981 and continued at 3-4 week intervals until mid-July 1981, one year after the first harvest. In the final harvest, the total above ground parts within each plot were collected, dried and weighed and the total cummulative dry weights for each of the two components over the one year period were determined. Analysis of variance used in data analysis involved a MIDAS program (Fox & Guire 1976).

RESULTS

It is first interesting to compare the mean performance and variability in performance of each species with their different associates (Table 13). The variability of performance for a species from a given field age is measured by the coefficient of variation in Table 13 and reflects the sensitivity of that species to the nature of its associates in its community. Holcus lanatus generally showed the lowest sensitivity to the nature of its associates (except in the 21 year pasture where it was second lowest). Trifolium repens generally showed the highest sensitivity to the nature of its associates (except in the 0 year pasture where it was second highest). Statistical analysis showed that for each species (and for all species

TABLE 13. 5 x 5 matrices of per-species yields (g) (means of 3 replicates) from the mixture diallel involving 5 species planted as ramets. In a) all ramets were derived from a commercial seed source (pasture age 'zero'). In b), c) and d) all ramets were clones of 2 natural neighbouring genets collected from the 2, 21 and 40 year old pastures respectively. Probability levels are given from the analysis of variance of mean yields, and from an F-test for the equality of variances for each species with all associates from a given field age. Attained P levels when all species from a given field age are averaged (*) are also shown. C.V. = coefficient of variation. D.g. = Dactylis glomerata ; H.l. = Holcus lanatus ; L.p. = Lolium perenne ; P.c. = Poa compressa ; T.r. = Trifolium repens .

ASSOCIATES		PRODUCERS					
		D.g.	H.l.	L.p.	P.c.	T.r.	Mean (*)
a)	D.g.	-	121.6	113.0	2.2	35.8	
	H.l.	116.0	-	101.3	1.0	21.8	
	L.p.	109.4	116.7	-	1.6	46.5	
	P.c.	257.8	179.1	181.5	-	91.6	
	T.r.	181.3	166.2	180.0	17.7	-	
	mean	166.1	145.9	144.0	5.6	48.9	102.1
	st. dev.	69.2	31.4	42.8	8.1	30.2	36.3
	C.V.	0.42	0.22	0.30	1.45	0.62	
b)	D.g.	-	76.3	106.7	9.7	1.7	
	H.l.	223.1	-	35.7	16.4	29.5	
	L.p.	179.9	212.9	-	11.4	70.8	
	P.c.	369.9	143.6	187.6	-	81.2	
	T.r.	448.3	144.7	108.6	26.4	-	
	mean	305.3	144.4	109.7	16.0	45.8	124.2
	st. dev.	125.3	55.8	62.1	7.5	36.9	57.5
	C.V.	0.41	0.39	0.57	0.47	0.81	
c)	D.g.	-	84.6	70.3	12.3	3.3	
	H.l.	226.6	-	58.5	7.3	2.2	
	L.p.	273.3	182.9	-	5.2	11.4	
	P.c.	270.6	242.3	180.2	-	59.4	
	T.r.	419.6	225.2	162.4	24.1	-	
	mean	297.5	183.8	117.9	12.2	19.1	126.1
	st. dev	84.2	70.7	62.3	8.5	27.2	50.6
	C.V.	0.28	0.38	0.53	0.70	1.42	
d)	D.g.	-	150.5	33.1	10.5	5.4	
	H.l.	221.4	-	73.3	13.8	16.2	
	L.p.	291.4	128.5	-	11.2	72.0	
	P.c.	346.9	211.3	163.0	-	54.3	
	T.r.	408.6	172.5	61.3	36.6	-	
	mean	317.1	165.7	82.7	18.0	37.0	124.1
	st. dev.	79.8	35.5	56.1	12.5	31.4	43.0
	C.V.	0.25	0.21	0.68	0.69	0.85	
P (analysis of variance)		0.1230	0.6662	0.5167	0.3007	0.5596	0.9823
P (equality of variances)		0.7743	0.5271	0.9313	0.8254	0.9677	0.7431

averaged), there was a remarkable consistency amongst plants from the different aged pastures in their mean yields and variances with all associates.

Attention now turns to the differences in reciprocal responses between particular neighbouring species from different aged pastures. An index of 'combining ability' was devised as a reflection of the reciprocity of competitive effects between neighbours. Combining ability is calculated as

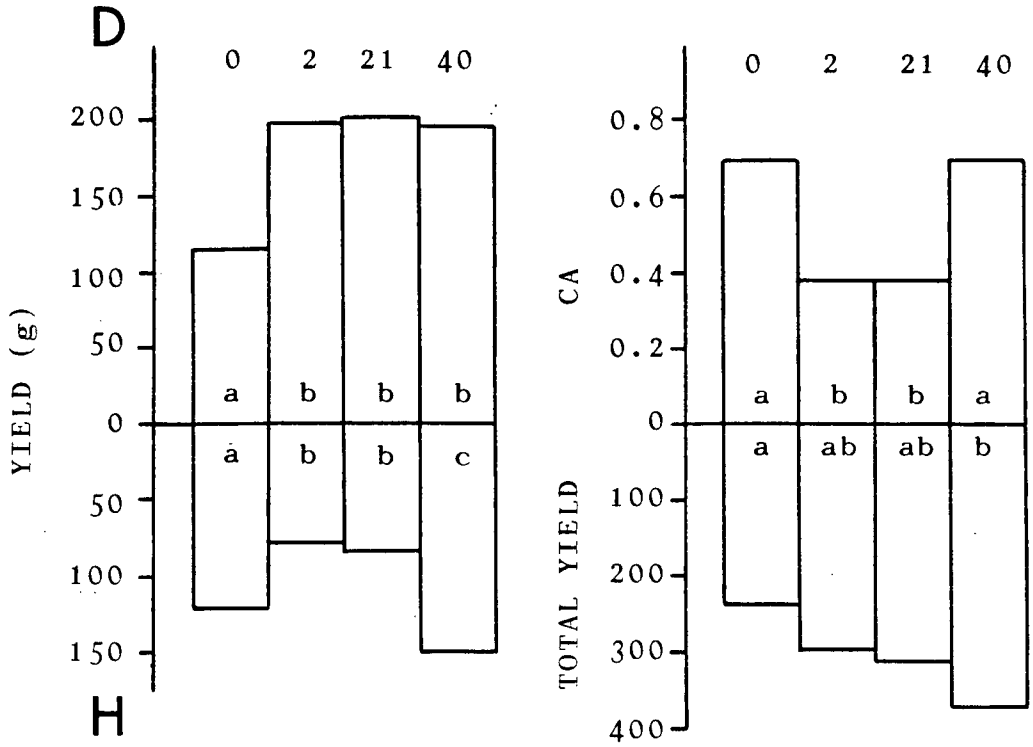
$$CA = Y/Y'$$

where Y and Y' are the recorded dry weight yields (g) of the lower and higher yielding components of a mixture respectively. CA indices have strictly relative value in comparing combinations of a given neighbouring genet pair type (i.e. of the same two species) from different aged pastures. Values of CA closer to 1.0 indicate that the two components are more balanced in their yields in mixtures than are combinations having a value closer to zero.

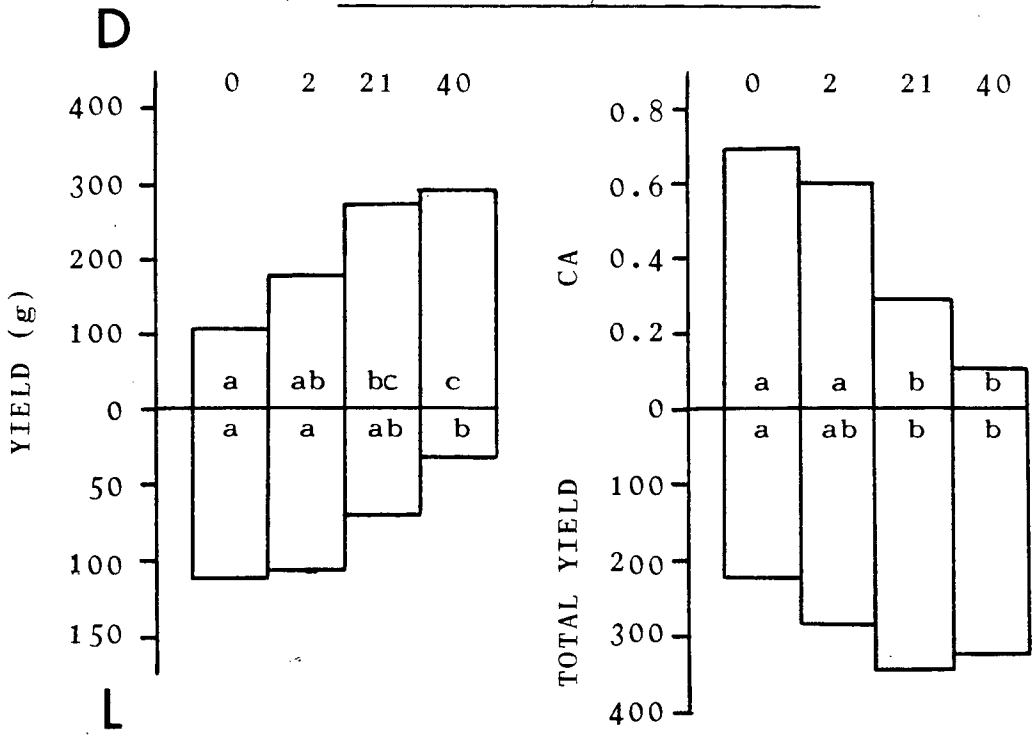
Changes in the nature of reciprocal competitive effects for a given neighbouring species pair are encompassed by two parameters: 1) changes in total yield of the combination, and 2) changes in the relative contribution to total yield from the two components as reflected by the CA index. A comparison of individual yields, total yields and CA indexes for each genet pair type from the different aged pastures is presented in Figure 11. Trends in the data with increasing pasture age are summarized in Table 14.

FIGURE 11. Comparisons of individual component yields, total yields and combining ability indices (CA) for each genet pair type collected from different aged pastures (0, 2, 21 and 40 years) and grown in competition in a mixture diallel. In each case histograms represent a mean of 3 replicates. In comparing the four field ages (with respect to component yield, total yields or CA indices), those which do not share a common code letter (a, b, c or d) are significantly different at the $P<0.05$ level based on Scheffe's multiple comparison test. F-tests for the homogeneity of variances were not rejected and all analyses were performed on untransformed data.

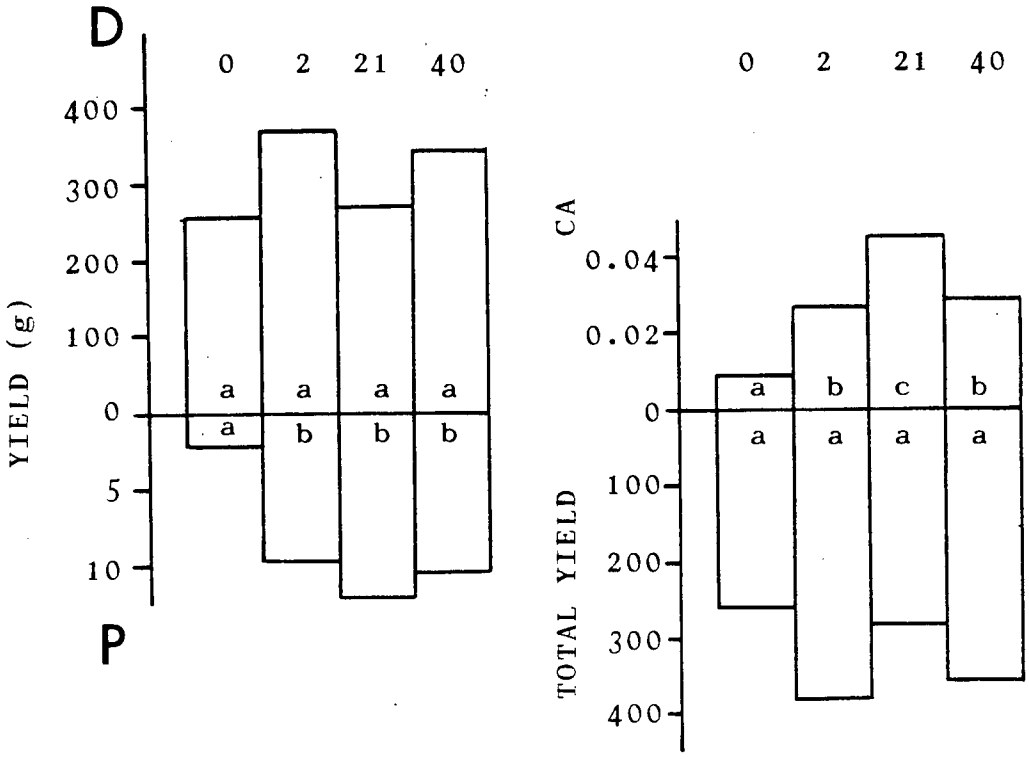
a) D. GLOMERATA / H. LANATUS



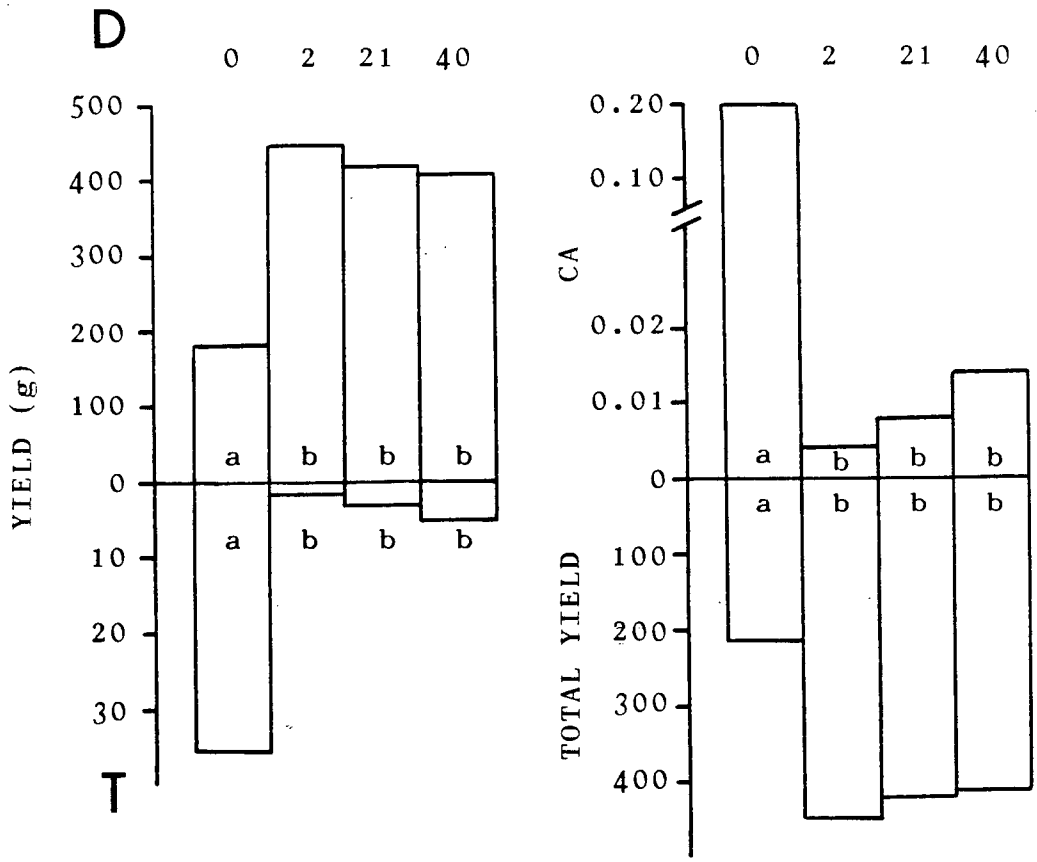
b) D. GLOMERATA / L. PERENNE



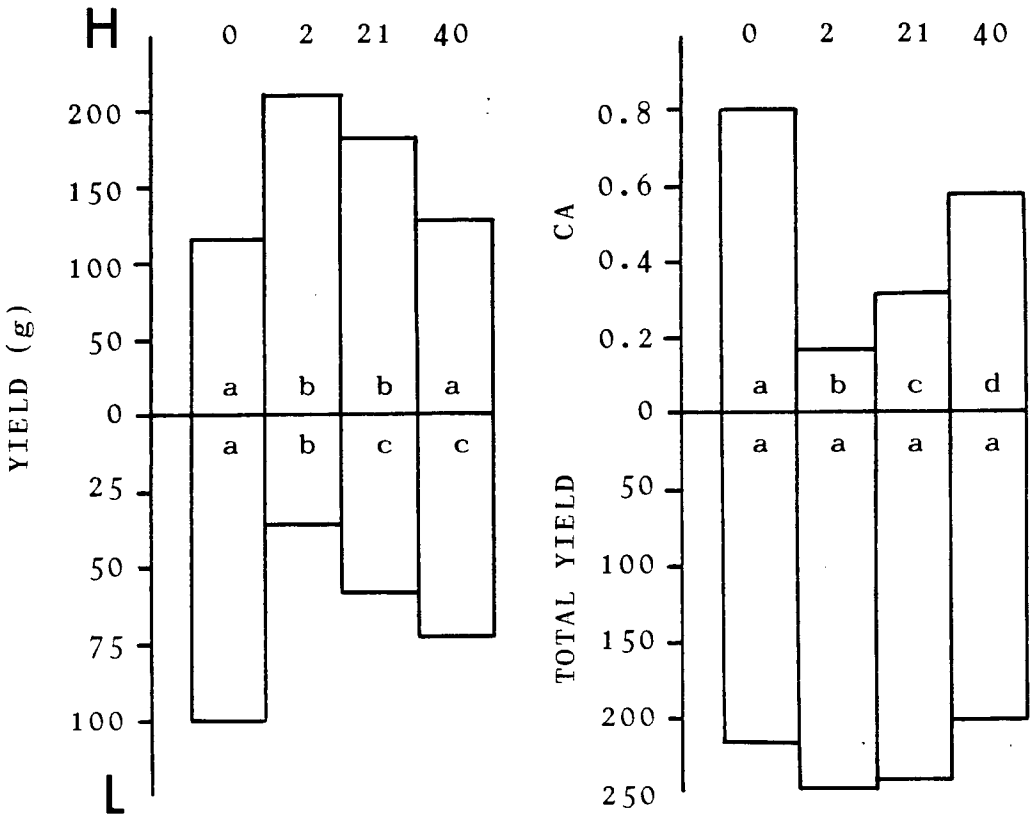
c) D. GLOMERATA / P. COMPRESSA



d) D. GLOMERATA / T. REPENS



e) H. LANATUS / L. PERENNE



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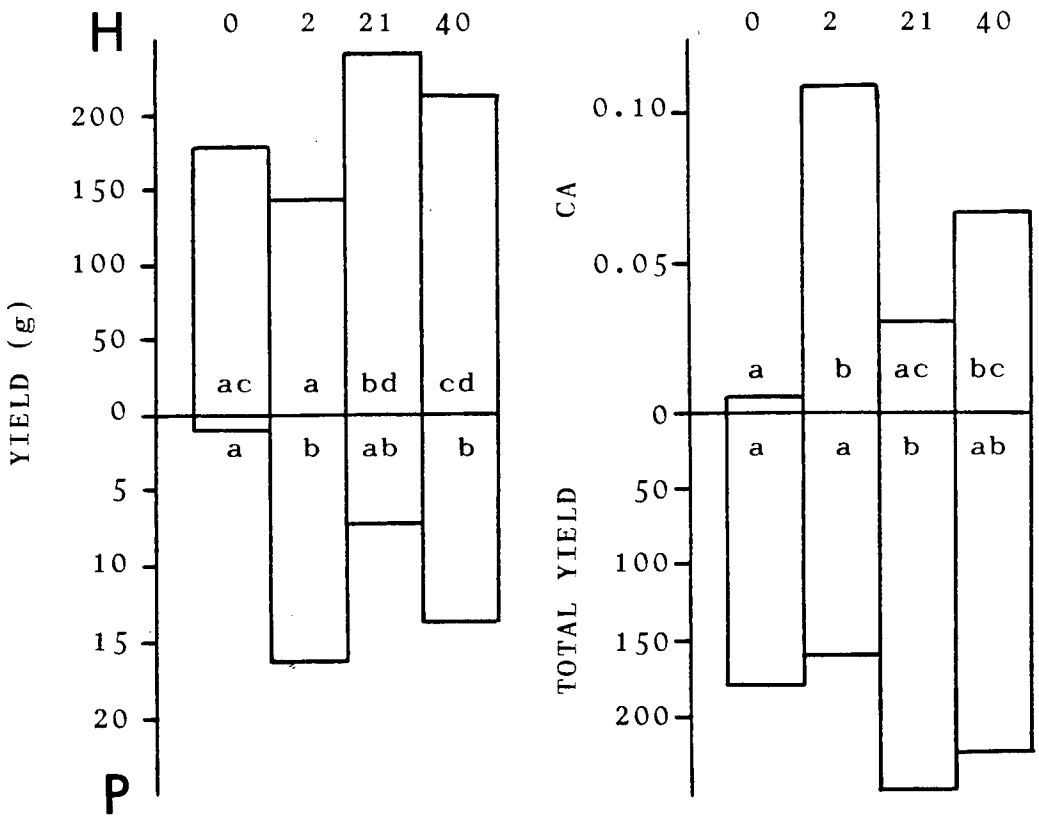
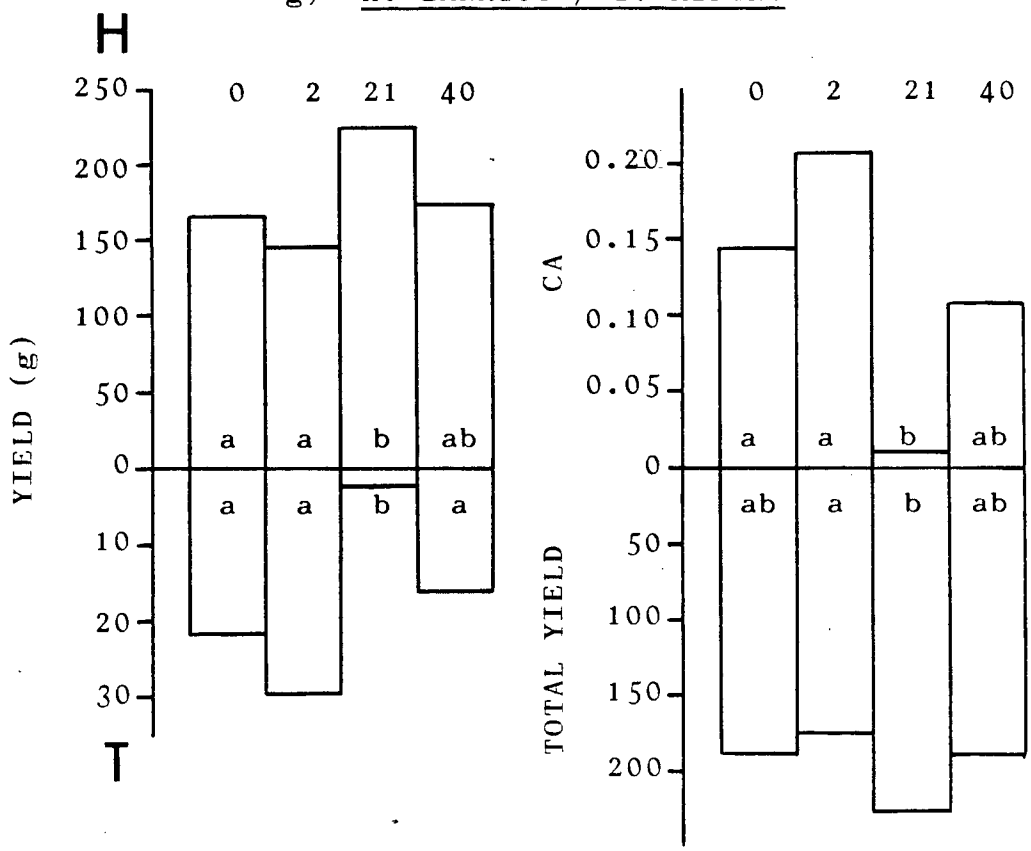
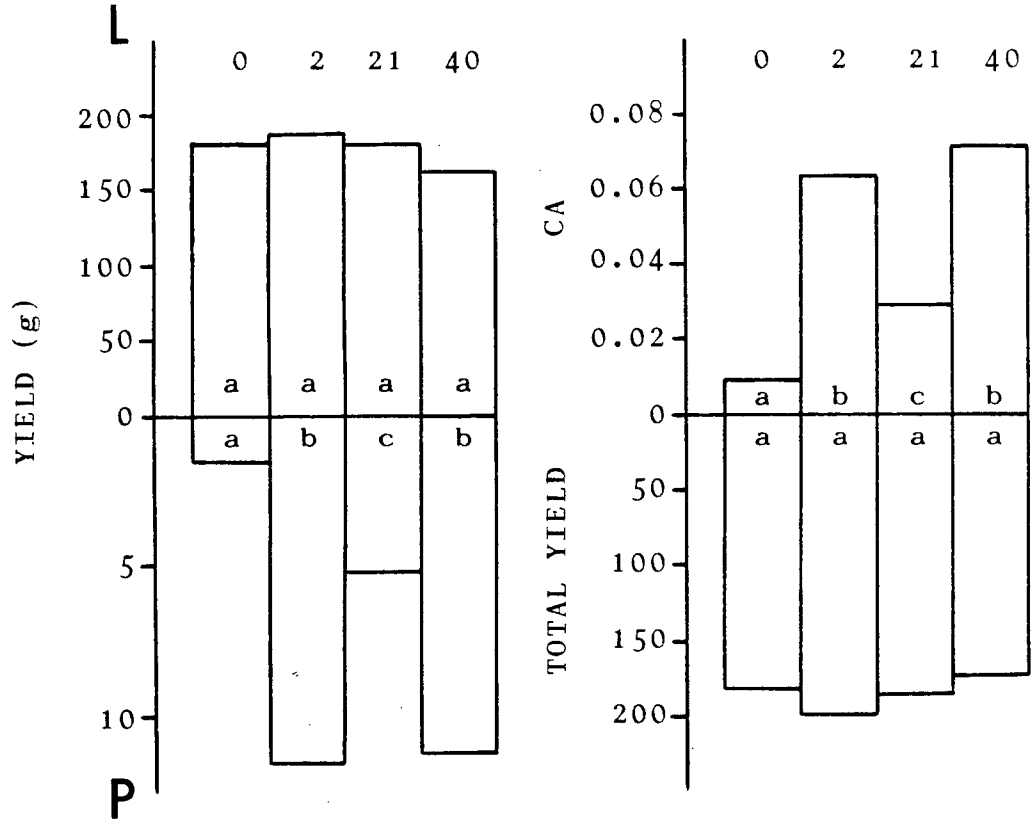


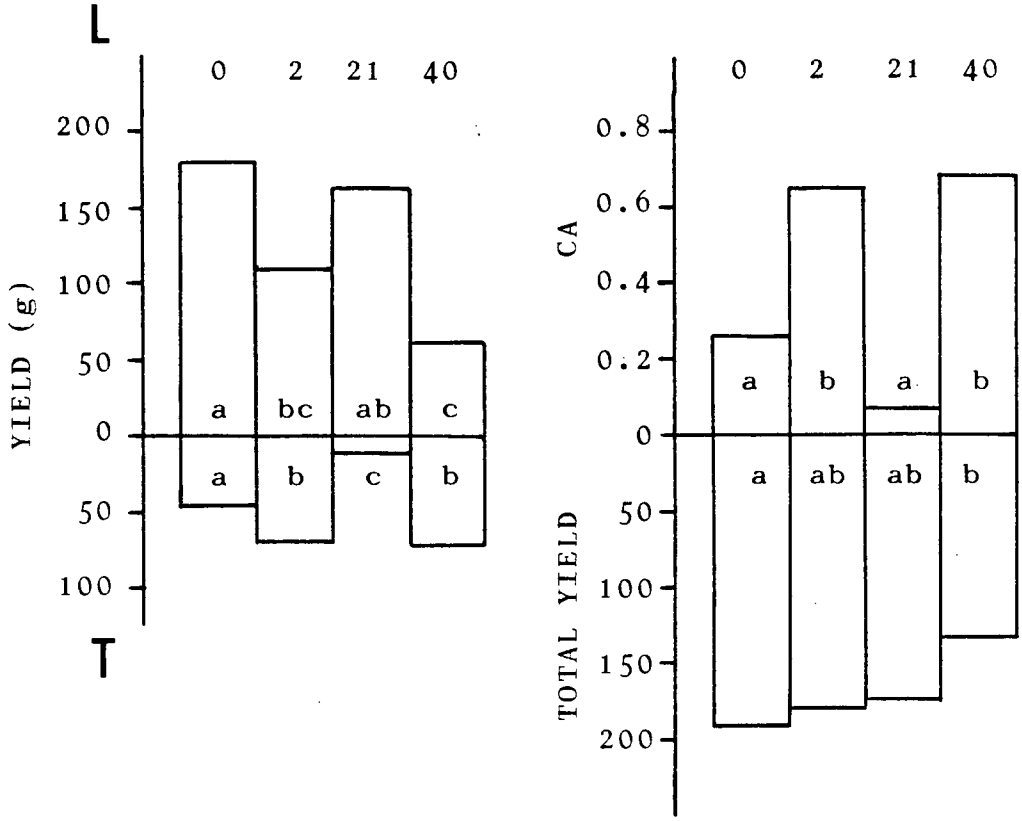
g) H. LANATUS / T. REPENS



h) L. PERENNE / P. COMPRESSA



i) L. PERENNE / T. REPENS



j) P. COMPRESSA / T. REPENS

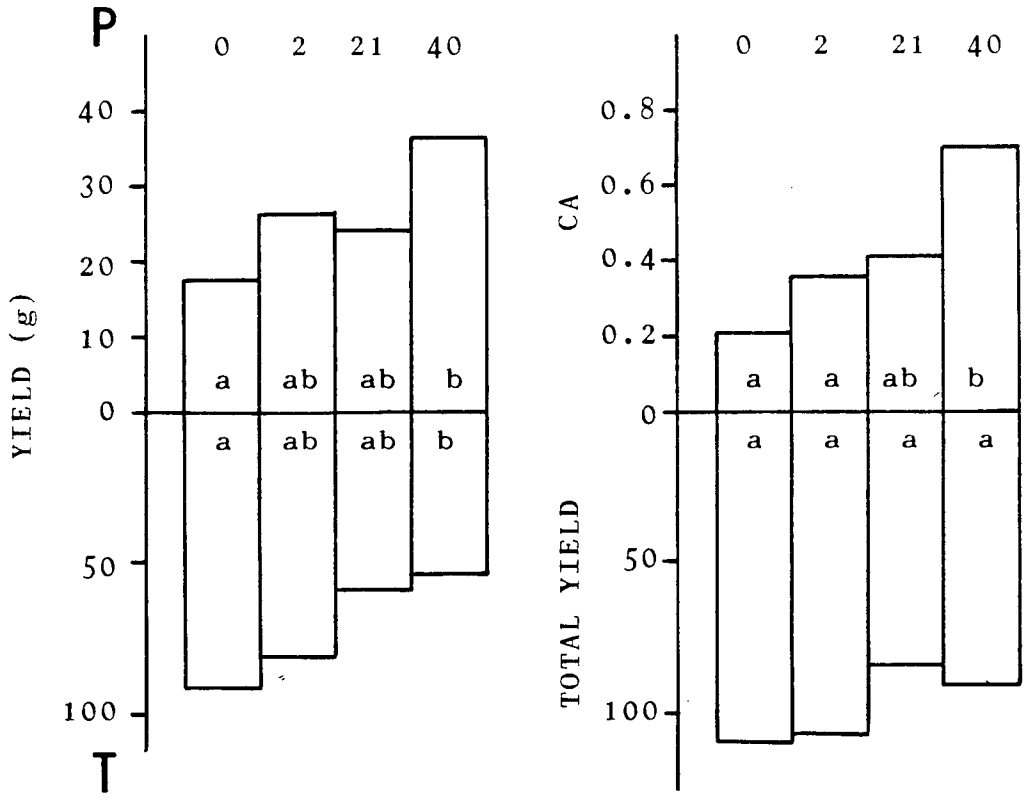


TABLE 14. A summary of significant ($P<0.05$) trends in combining ability indexes (CA) and total yields from the mixture diallel for different genet pair types as the age of the pasture from which they were collected increases (Fig. 11). An upward arrow indicates that the value increases consistently with increasing pasture age, and a downward arrow indicates a consistent decrease with increasing pasture age. Both arrows together indicate a fluctuating trend. A dash (-) indicates no significant change with increasing pasture age. An asterisk (*) means that the indicated trend occurs if the '0-year' combination is excluded.

	DACTYLIS/ HOLCUS	DACTYLIS/ LOLIUM	DACTYLIS/ POA	DACTYLIS/ TRIFOLIUM	HOLCUS/ LOLIUM	HOLCUS/ POA	HOLCUS/ TRIFOLIUM	LOLIUM/ POA	LOLIUM/ TRIFOLIUM	POA/ TRIFOLIUM
CA	↑ *	↓	↑	↓	↑ *	↑↓	↑↓	↑↓	↑↓	↑
TOTAL YIELD	↑	↓	—	↑	—	↑↓	↑↓	—	↓	—

DISCUSSION

Recent studies have demonstrated differences in niche and competitive relationships amongst species from communities of different successional maturity (Parrish & Bazzaz 1976, 1979, 1982a, 1982b). These studies have shown that species from 'late-succession' communities are more differentiated with respect to certain dimensions of niche than are species from 'early-succession' communities and this is proposed to be an evolved product of selectional forces from competition. In all of these studies, comparisons have been made between communities which differ in species composition and hence, the competitive relations of entirely different groups of species have been compared in making the above conclusions. There is also not a strong basis for considering that the different communities being compared in these studies even belong to the same successional sequence. This presents considerable uncertainty in making any inferences about the importance of past competition in the organization of a community over evolutionary time (see also Connell 1980).

There have apparently been no former attempts to answer the question of how the competitive relationship between two <u>particular</u> species changes through time in a <u>particular</u> community. Nor have previous studies been based on interactions between individuals which were known to be immediate neighbours in nature. The present study is an attempt to address these problems using a series of different aged pastures which represent a reasonable approximation of different coexistent stages in the same developmental sequence based on known

management history as well as empirical data (Chapters 2 and 3). Using this approach, interpretations concerning the role of competition as a selectional force in communities can be made with more confidence than in comparisons of communities of widely different species composition having no established ontogenetic relationship. The results showed that the overall sensitivity (variability of response) to different neighbours for any given species within a pasture did not change significantly with pasture age (Table 13). Natural neighbouring genets of a particular pair of species however, showed clear differences in their relative reponses to one another depending on their pasture age of origin (Fig. 11).

The reported data lend insight into the characterization of the development of biological accommodation in systems of competition. In order to focus attention on mechanisms, based on the operation of natural selection in relation to the attributes of organisms which confer fitness, the development of biological accommodation in a community may be translated as selection for 'combining ability' in populations. Species which have combining ability have some means of persisting in interaction with one another defined by their respective biological attributes. An explanation of competitive coexistence therefore resides in the assumption that a consequence of natural selection is increased (or stabilized) combining ability. Conversely, competitive exclusion would be reflected by a decreasing combining ability and may also be a consequence of natural selection. Three features of the data may be recognized from examining the relative changes in the

total and respective component yields of genet combinations from older pastures (i.e. 'after selection') (Fig. 11, Table 14):

1) A process of competitive exclusion is reflected by a decline in combining ability. In two species pairs, Dactylis/Lolium and Dactylis/Trifolium, combining ability decreases with increasing pasture age. This suggests that the Dactylis population has become relatively more competitive against both Lolium and Trifolium in older pastures as a result of selection. In this case, available resource units are partitioned less evenly between two populations after selection, increasing the probability that one will exclude the other.

2) Selection for ecological combining ability would be reflected by an increase in total yield after selection (accompanied by a stable or increasing combining ability). This implies a displacement in behaviour with the result that each (or one) population makes less demands on the resources needed by the other than before selection. It is remarkable that only one species combination, Dactylis/Holcus illustrated this trend.

3) The most notable feature of the data is that a change in yield for one component (e.g. an increase) is usually accompanied by an opposite change in yield (i.e. a decrease) for the other component (left-hand bar graphs in Fig. 11). The consequence of this is that combining ability changes accordingly, but that total yield rarely shows significant changes (right-hand bar graphs in Fig. 11). In two species pairs, Holcus/Lolium and Poa/Trifolium , while combining ability (CA) also increases with increasing pasture age, total yields in mixture were not significantly different with increasing pasture

age. This result does not indicate that competition has been relaxed due to niche divergence; rather, the trends suggest that selection has improved the relative ability of the inferior component to reduce the availability of resources to the superior component , thus resulting in a more balanced partitioning of resource units from a common supply on which they both make demands. The trend is similar in the Dactylis/Poa combination but combining ability declines between the 1958 and 1939 pastures.

The remaining combinations show no directional trends (Fig. 11 f,g,h,i). Neither a process of competitive exclusion nor a process of ecological combining ability is indicated. As these are traditionally the expected alternative outcomes of selection pressure from competition, it may suggest that these competitive interactions are not important forces of selection here. However, an interesting feature of these combinations suggests an alternative explanation - an increase in the yield of one component is generally accompanied by a decrease in the other and vice versa. In the two combinations involving Holcus the total yield also fluctuates but in negative relationship to the fluctuation in combining ability (Fig. 11 f & g). In the two combinations involving Lolium, combining ability fluctuates but the highest value occurs in the combination from the oldest pasture. Also, in the Lolium/Poa combination, total yield is the same with increasing pasture age (Fig. 11 h) and in the Lolium/Trifolium combination, total yield decreases (Fig. 11 i). Although none of these results are consistent with an interpretation of selection leading to either competitive

exclusion or niche differentiation, they are consistent with a selection process in which relative competitive abilities for common niche requirements are continuously adjusted so that over time a balance is maintained.

These data suggest that intraspecific differentiation associated with biotic specialization in response to competition may be related to three alternative consequences of natural selection:

a) increased combining ability resulting from niche differentiation and release from resource competition;

b) increased combining ability resulting from a 'balancing' of competitive abilities for contested resources;

c) reduced combining ability resulting from asymmetic improvement (or 'unbalancing') of competitive abilities.

Notice that in both a) and b) it is assumed that selection reduces the differential in the performance of the two components of the mixture. The implication of this is that the two populations have a greater probability of coexisting than before selection, i.e. in both cases the two populations have higher 'combining ability'. Only case a) however, where total yield increases, permits an interpretation of 'ecological' combining ability as previously defined (Harper 1977b). In c) there has been selection for biotic specialization in the superior competitor, selection which reduces combining ability. Selection operating in a) and b) then result in biological accommodation and coexistence, while selection operating in c) results in competitive exclusion.

In conclusion, the changes discovered in the combining

ability and total yields of mixtures of a given pair of naturally neighbouring species from different aged pastures, suggest that competition is an important force of natural selection in this pasture system. It is evident that a failure to study the reciprocal effects of competitors on one another does not permit a clear interpretation of the mechanisms of biotic specialization and combining ability of species. For example, the biotic specialization in Trifolium repens reported by Turkington & Harper (1979c) could be associated with any of the above 3 consequences of natural selection (a, b or c).

Very little evidence in the present study (only one species combination) (Fig. 11a) was found for the commonly assumed notion that selection pressures from competition usually result in the evolution of ecological combining ability (niche differentiation) in the component species of a community. Five out of the ten species combinations studied (Fig. 11 c, e, h, i, j) exhibited increased combining ability with increasing pasture age nonetheless, but it was of a form interpreted instead as a selectional process which reduced the differential in competitive abilities of the inferior and superior components of interactions in younger communities. As this study included several dominant species from the study site, it prescribes the role of biological accommodation in a community-wide context and lends further support to the proposed model for pasture community evolution (Fig. 9, Chapter 3).

CHAPTER 5

CHANGES IN THE NATURE OF COMPETITIVE RELATIONS AMONGST THREE SPECIES IN DIFFERENT AGED PASTURES: SUBSTITUTIVE REPLACEMENT SERIES MODEL

INTRODUCTION

In a diallel design for studying competition (Chapter 4), the performance in a 1:1 mixture can reveal a particular type of interaction between a pair of genotypes. The analysis of that interaction can however be carried further using data on mixtures having a range of proportions but maintaining density constant (i.e. a 'replacement series'). Based on these criteria, de Wit (1960, 1961) introduced experimental models which have been widely used for identifying and quantifying the properties of competitive relationships between plants (Trenbath 1978). It has been used for analyzing how competitive interactions are influenced by environment; e.g. the effect of the presence of symbiotic Rhizobium on the competitive relationship between a grass and legume (de Wit et al. 1966) and the effect of soil depth on differential root placement in species mixtures of the genus Avena (Trenbath & Harper 1973). It has also been useful for identifying limiting resources in competitive interactions (Hall 1974b).

Information on the frequency-dependence or independence of competitive interactions permits interpretation of relative competitive abilities and degree of niche overlap between genotypes or species. The competitive advantage of oats sown in a replacement series with peas was found to be independent of the proportions in mixture (de Wit 1960). In contrast, mixtures of Anthoxanthum odoratum and Phleum pratense showed frequency-dependence with a close balance in competitive ability (van den Bergh & de Wit 1960). Frequency-dependent behaviour has been shown between Trifolium repens and Lolium perenne which is

interpreted as some degree of niche differentiation in these two species (Ennik 1960, de Wit 1961).

The De Wit model provides a sensitive method for analyzing changes in the competitive relations of species in response to selection. Previous studies have shown that populations having a history of interaction generally form more stable associations demonstrated by frequency-dependent behaviour in replacement series analysis than do populations with no history of interaction (Remison & Snaydon - in Snaydon 1978, Joy & Laitinen 1980, Martin & Harding 1981). These studies present only circumstantial evidence that niche differentiation is an evolved product of past competition. No previous studies using replacement series analysis have considered how the degree of niche overlap changes in a particular pair of species in a particular site (community). This is investigated in the present study using plants collected from the study pastures belonging to a common developmental progression. Changes in competitive relations with increasing pasture age are investigated for three different pairs of species - Holcus lanatus - Trifolium repens , Lolium perenne - Trifolium repens and Holcus lanatus - Lolium perenne. The studies of evolutionary changes in competitive relations mentioned previously have used genetically non-identical individuals (products of sexual reproduction) in the replacement series. In contrast, the present study uses cloned ramets of 2 single genets collected as natural neighbours growing in immediate proximity to one another in the field. This approach was taken in an effort to detect the presence of localized biotic

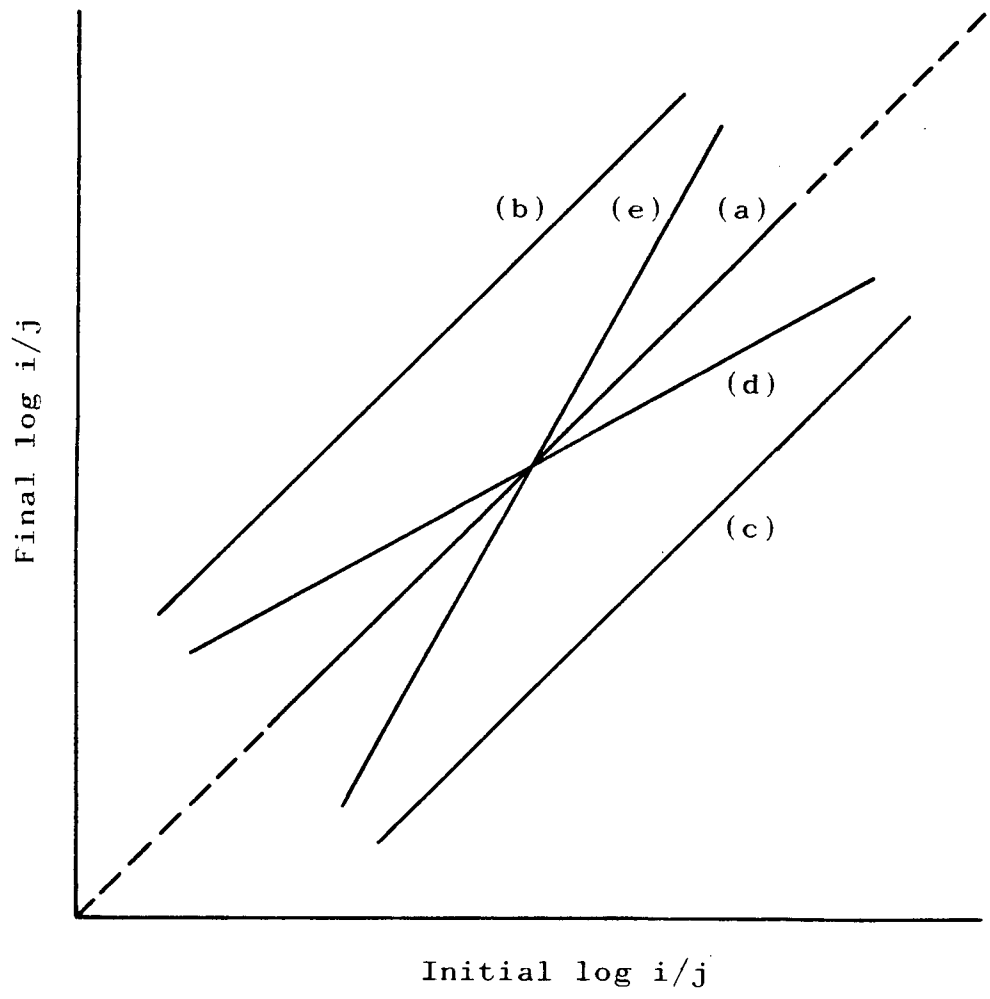
specialization of established genotypes and to investigate the developmental qualities of that specialization as the community ages. In order to set the stage for the experimental design and facilitate interpretation of the results based on accepted theory, a brief review of relevant theoretical considerations will follow.

THEORY

If mixtures of two genotypes or species are planted at a variety of proportions, the change in the ratio of those proportions after an elapsed time can be plotted against the ratio of proportions at the beginning. The plot so produced - a 'ratio diagram'- provides a sensitive figurative display for detecting the type of competitive relationship between two species. Five basic types of interaction can be interpreted (Fig. 12) (de Wit 1961, Harper 1977b):

a) (Fig. 12a). The proportion of the two species remains unchanged after a period of growth together. Since the final proportion ratio exactly equals the initial proportion ratio for all mixtures, it indicates (assuming densities are high enough) that for both species, an interspecific individual provides precisely the same intensity of competition as does an intraspecific individual, and that the two species make the same demands on environmental resources (i.e. their niches broadly overlap). In this case neither species has any 'advantage'. In all considerations below, an 'advantage' will refer to a capacity in a species to increase its frequency in the final proportion ratio relative to the initial proportion ratio.

FIGURE 12. Ratio diagrams illustrating 5 possible outcomes from a replacement series experiment reflecting 5 different types of competitive relationship between species i and j. The dashed line represents the theoretical case where all initial ratios equal all final ratios (i.e. the line of 'no advantage'). See text for description.


(b)
(e)
(a)
(d)
(c)
Final log i/j
Initial log i/j

b) (Fig. 12b). Here, species i gains an advantage in mixtures at all relative frequencies. The most intense competition for j is interspecific, whilst for i, intraspecific competition is more intense. If the slope of the line is 1.0 as shown, the advantage for i is independent of frequency; i.e. an increase in the initial proportion ratio results in a corresponding increase, by the same amount, in the final proportion ratio, once again indicating as in a) that i and j overlap in their use of available resources. Hence, the advantage possessed by i is reflected by a relatively greater capacity to reduce the availability of resources to j from a supply on which they both make demands, and that this capacity is the same regardless of relative frequency in mixture. Accordingly, the perpendicular distance of the actual ratio line from the theoretical line of 'no advantage' indicates the magnitude of the superiority of i's relative competitive ability.

c) (Fig. 12c). Here, the same principles as in b) apply except that j gains an advantage in mixtures at all relative frequencies.

d) (Fig. 12d). This result indicates a frequency-dependent competitive relationship, i.e. which species has an advantage is dependent on the initial proportion ratio. Generally, the minority component in a mixture is always at an advantage - consequently the regression slope is less than 1.0. Here, in contrast to b), each component experiences the most intense competition from an individual of its own species. Hence, the 'advantage' for the minority component of a mixture is incurred by its experience of fewer intraspecific individuals and hence

less stringent competition. With plants, this traditionally implies that resource use by the two species does not completely overlap; i and j have different niches. An equilibrium ratio occurs where the regression intersects the theoretical line of 'no advantage'. At this initial proportion ratio, an identical final proportion ratio results because, for both species, the level of intraspecific density imposes hardships of resource limitation that are equal in magnitude to those hardships imposed by interspecific competition for those elements of niche which do overlap.

e) (Fig. 12e). This result also indicates a frequency-dependent competitive relationship but in this instance, the majority component of a mixture is always at an advantage, regardless of species. Hence, the regression slope is greater than 1.0. Intraspecific competition is never stronger than interspecific competition in either species. This result predicts that either species could out-compete the other depending on which has the highest relative frequency in mixture and an unstable equilibrium point therefore exists. Such a situation would occur if each species impaired the environment of the other more than it impaired its own environment, as for example with mutual allelopathic interference (Harper 1977b). Here, the effectiveness of interference by one component on another encompasses a concerted effort amongst cohorts, and an 'advantage' for one component is entirely a consequence of higher relative numbers in the initial proportion ratio. Unlike b), the capacity to reduce the availability of resources to the other component species changes with relative frequency in

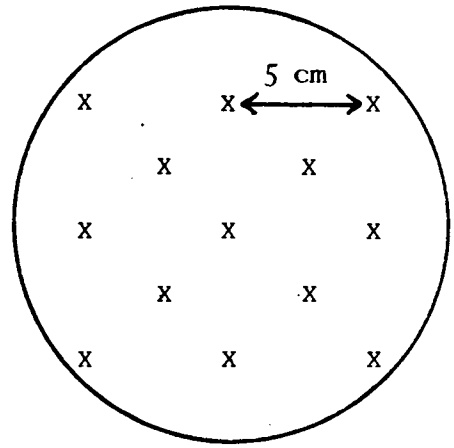
mixture, and this applies concurrently to both components. If in such an interaction, competitive exclusion was imminent (as this model predicts), it would imply that the extent of niche overlap was enough to make impossible any escape from extinction.

METHODS

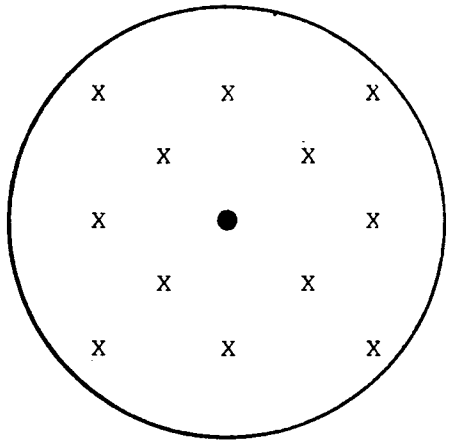
Three different genet pairs, Holcus lanatus - Trifolium repens, Lolium perenne - T. repens , and H. lanatus - L. perenne , were collected as immediately adjacent neighbours from each of the 3 different aged pasture communities (2, 21 and 40 years). Each pair was collected and propagated as outlined in Chapter 2 to obtain a population of ramets for each genet type. Plastic pots (1.75 liter - 15 cm diameter, 15 cm deep) containing a standard potting mix of 50% peat, 25% sand and 25% perlite were used. For each natural genet pair type, a constant density of 13 ramets per pot were planted in the replacement series and arrangement shown in Figure 13. The planting arrangement ensured that each ramet of the minority component type was surrounded, as much as possible, by ramets of the majority component type. Each proportion in each replacement series was replicated three times and the pots were arranged randomly in a polyethylene tunnel. Rhizobium culture was added when the ramets were planted (first week of June, 1980) and all pots received 3 applications of liquid organic fertilizer (N/P/K : 10/5/5) (after weeks 1, 5 and 9). The pots were watered whenever the soil surface became dry, about 3 times weekly on average. After 4 weeks, an 'initial' count of the total number

FIGURE 13. Planting arrangement used for 13 ramets in the replacement series:

species i / species j	0 / 13	1 / 12	2 / 11	4 / 9	5 / 8	8 / 5	9 / 4	11 / 2	12 / 1	13 / 0



0 / 13



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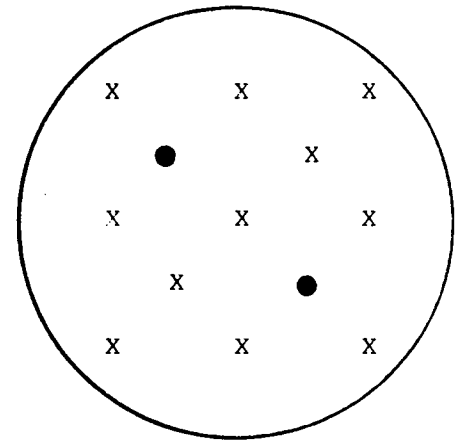

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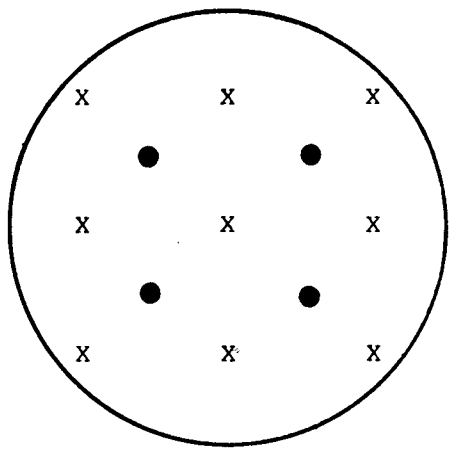
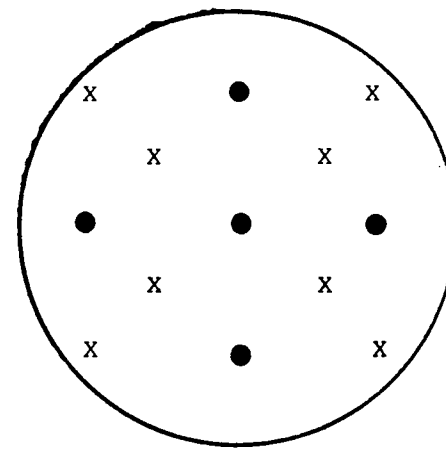


4 / 9



5 / 8

of tillers (for grasses) and measure of the total stolon length (for clover) per pot were taken. This follows Ennik (1960). After a further 12 weeks, the experiment was terminated and a 'final' tiller count and stolon measure per pot were recorded.

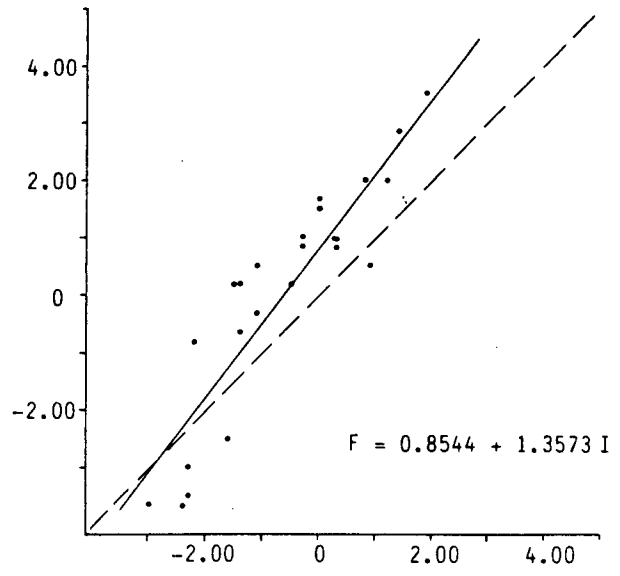
RESULTS AND DISCUSSION

For each replacement series, initial and final proportion ratios were calculated. After log transformation, the data were plotted as ratio diagrams (Fig. 14) following multiple linear regression analysis using a MIDAS program (Fox & Guire 1976). Ratio diagrams provide a convenient model for analyzing changes in interspecific competitive relations. In accordance with established theory (Fig. 12), the ratio diagrams produced from the present data may be interpreted within the context of alternative hypothetical models for changing competitive relations produced as a consequence of natural selection in component species (Fig. 15). These are considered below followed by a discussion of particular species interactions.

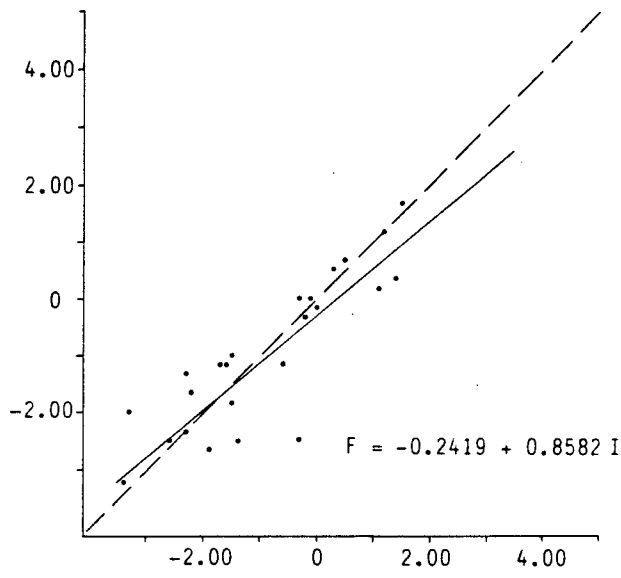
Two critical values are extracted from ratio diagrams for interpreting competitive relations: 1) Changes in the slope of the regression; 2) parallel changes in the position of the regression. A decreasing slope of the regression with a common point of rotation (Fig. 15a), reflects a process of niche differentiation. The smaller the slope, the more differentiated are the two components with respect to niche requirements. With a slope of zero, the final relative frequency is constant regardless of initial relative frequency, which implies that the two components virtually avoid one another completely. The

FIGURE 14. Ratio diagrams for the experimental results. Each point represents the value corresponding to the initial and final ratios involving total stolon length and/or total tiller number per species per pot.

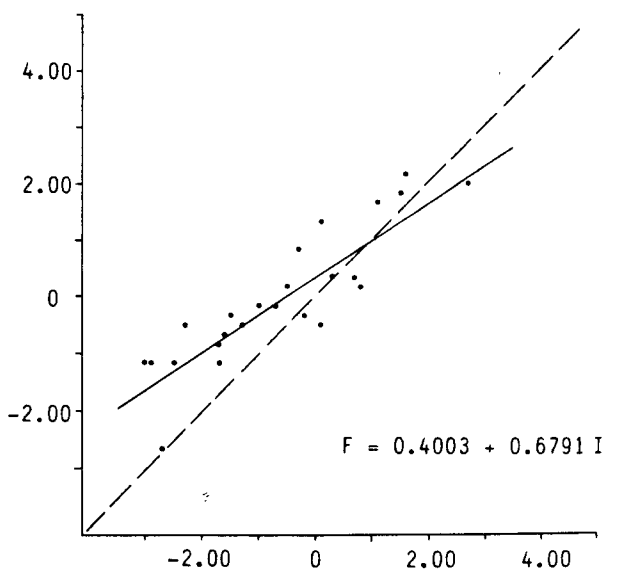
HOLCUS LANATUS - TRIFOLIUM REPENS



1977 PASTURE



1958 PASTURE

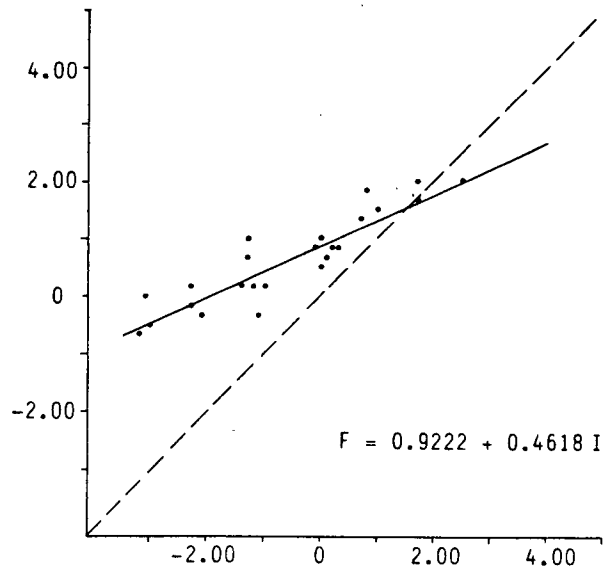


1939 PASTURE

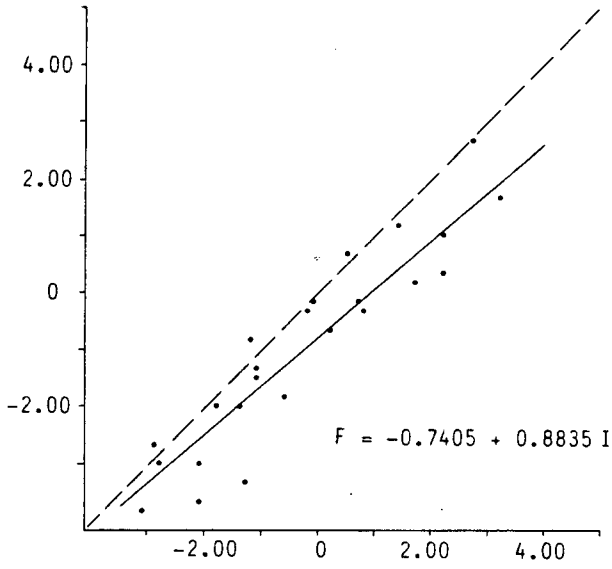
$\text{Log}_e \frac{\text{final T stolon length}}{\text{final H tiller number}}$ (F)

$\text{Log}_e \frac{\text{initial T stolon length}}{\text{initial H tiller number}}$ (I)

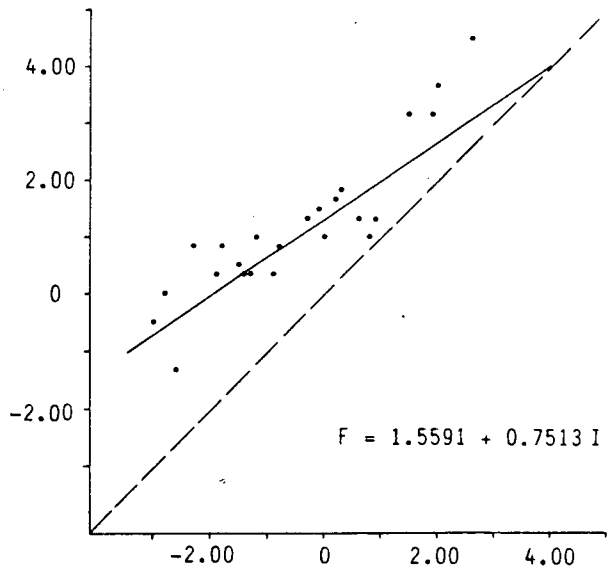
LOLIUM PERENNE - TRIFOLIUM REPENS



1977 PASTURE



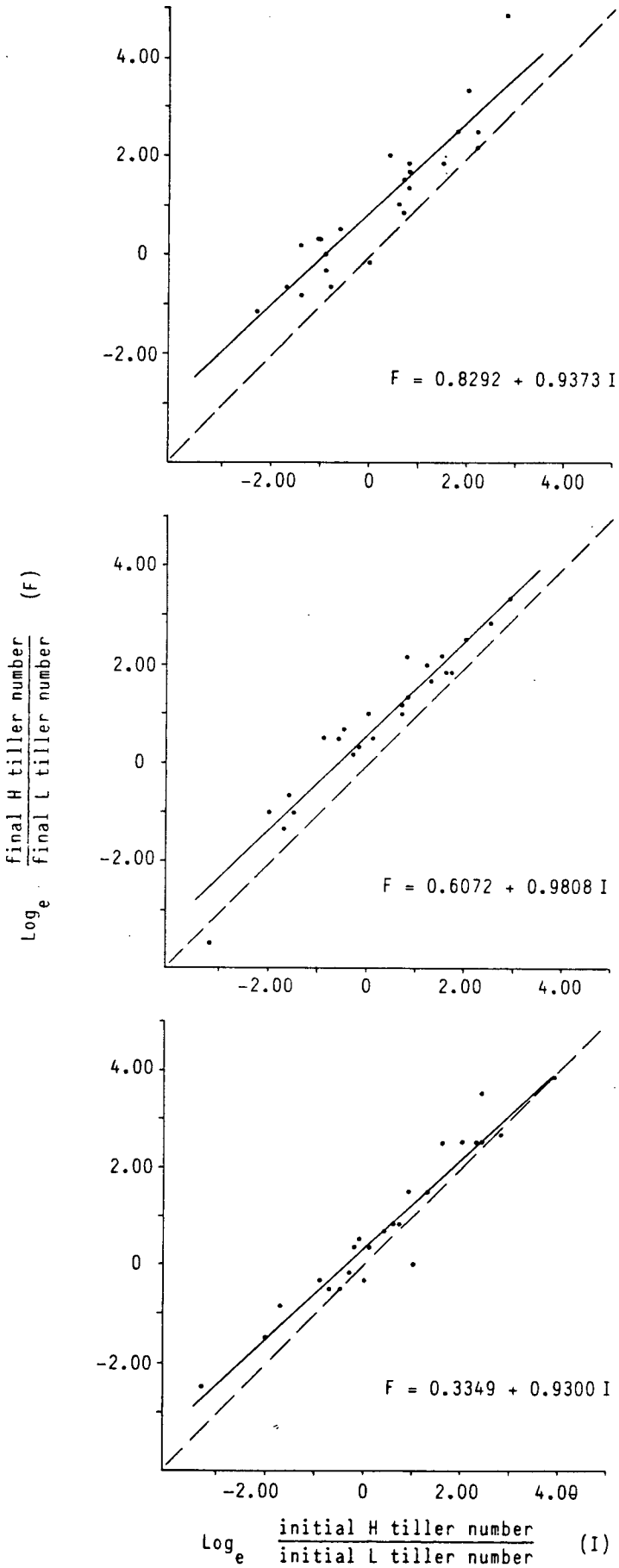
1958 PASTURE



1939 PASTURE

$\text{Log}_e \frac{\text{final T stolon length}}{\text{final L tiller number}}$ (F)

$\text{Log}_e \frac{\text{initial T stolon length}}{\text{initial L tiller number}}$ (I)



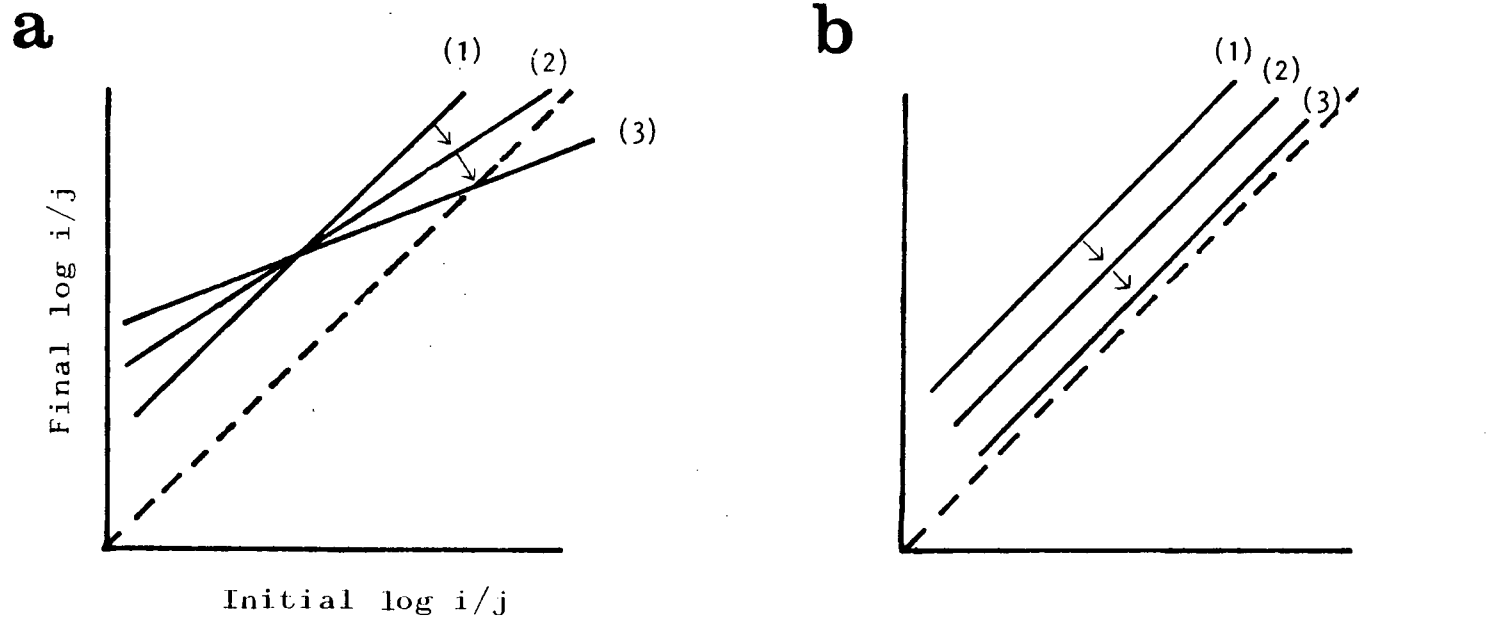
HOLCUS LANATUS - LOLIUM PERENNE

1977 PASTURE

1958 PASTURE

1939 PASTURE

FIGURE 15. Ratio diagrams showing theoretical trends for evolutionary changes in competitive relations between two species (i and j) during different stages (1, 2 and 3) of natural selection. See text for description.

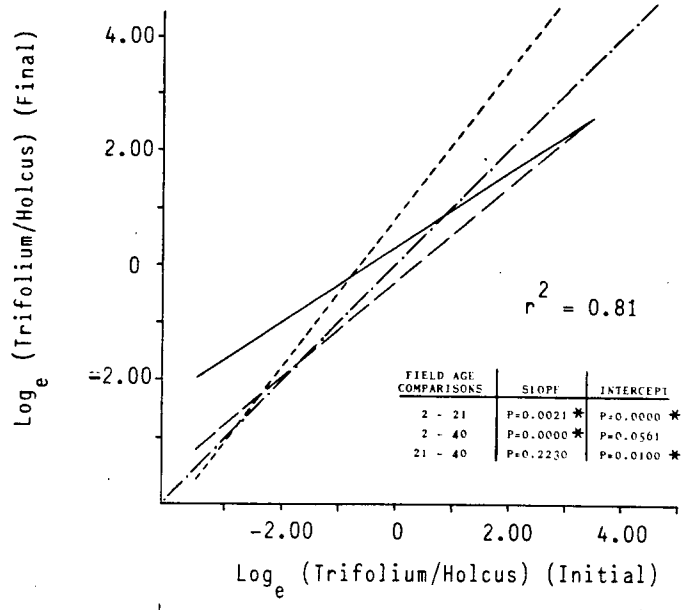

a
(1)
(2)
(3)
Final log i/j
Initial log i/j
b
(1)
(2)
(3)
c
(1)
(2)
(3)
x
y
z
d
(1)
(2)
(3)

performance of each is entirely unaffected by the presence of the other. It follows that a reverse order of increasing slope towards 1.0 would suggest selection for niche convergence where, because of interaction, the final relative frequency very much depends on the initial relative frequency. (This is not to be confused with the fact that with a slope = 1.0, an advantage for a component in mixture is independent of frequency.) An increasing slope beyond 1.0 indicates a process of selection for increasing mutual interference effects between the two components (not illustrated). Parallel shifts in the position of the regression in a frequency - independent model (Fig. 15b), or a displacement of the equilibrium point from x to y to z in a frequency dependent model (Fig. 15c), reflects changes in the relative competitive abilities of the two components. In both b) and c) the competitive ability of j relative to i is shown to be increasing through stages 1, 2 and 3. Considerations above however dictate that in b), i and j are using the same resource supply, whereas in c) their niche requirements overlap less. Neither b) nor c) implies that selection has changed the degree of niche overlap. Evolutionary changes in both niche relationship and relative competitive ability are reflected by a concomitant change in the slope of the regression and shift in its parallel position (Fig. 15d).

For each species pair studied, analysis of variance revealed the significant differences in slopes and intercepts amongst genet pairs from different aged pastures (Fig. 14). These comparisons are displayed in Figure 16 and a discussion for each species pair follows.

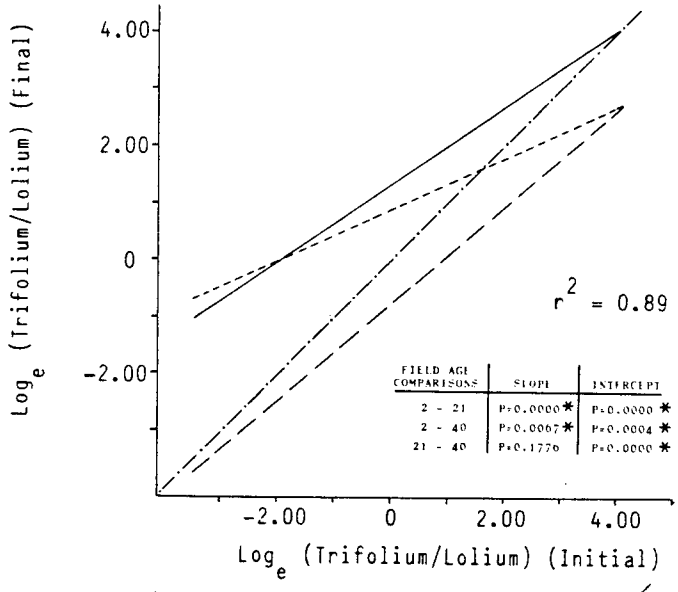
FIGURE 16. Ratio diagrams for immediately adjacent genet pairs from the three different aged pastures (2, 21 and 40 yrs) superimposed on the same graph. F-tests for the homogeneity of variances after log-transformation were not rejected. Probability levels are from an analysis of variance for significant differences in slopes and intercepts of the regressions (* significant at $P<0.05$) for all possible pairwise comparisons of field age. A coefficient of determination is given for each multiple linear regression.

Pasture age: - - - - - - 2 year; —— —— 21 year; ———— 40 year.



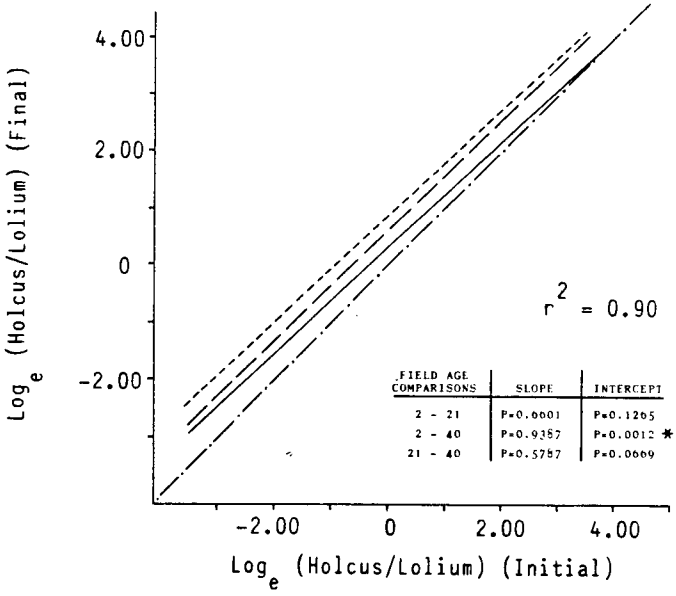
a)

HOLCUS LANATUS - TRIFOLIUM REPENS



b)

LOLIUM PERENNE - TRIFOLIUM REPENS



c)

HOLCUS LANATUS - LOLIUM PERENNE

a) Holcus lanatus - Trifolium repens (Fig. 16a).

H. lanatus and T. repens showed a trend of decreasing regression slope in the ratio diagram as well as a shift in the position of the regression (i.e. as in Figure 15d). An unstable behaviour (slope greater than 1.0) is illustrated for the two year old genet pair and this shifts to a stable behaviour (slope less than 1.0) in the pairs from the two older pastures. This is interpreted as niche divergence. The 21 year and 40 year pairs do not significantly differ in regression slope but do differ in postion (intercept). The regression shifts proportionally to favour T. repens at all relative frequencies . This indicates a higher relative competitive ability for Trifolium in the 40 year pair than in the 21 year pair but no difference in amount of niche overlap between the two components.

b) Lolium perenne - Trifolium repens (Fig. 16b).

In all cases the competitive relationship between these two species is frequency-dependent (with slope < 1.0) but the slope of the regression is higher in pairs from the two older pastures. This indicates that niche overlap is greater between genet pairs from the two older pastures than from the youngest pasture suggesting a selection process of niche convergence. The position of the regression also changes, again demonstrating an example of model d in Figure 15; i.e. the 21 year and 40 year pairs do not significantly differ in regression slope but do differ in position. As with H. lanatus and T. repens, the regression for L. perenne and T. repens shifts proportionally to favour T. repens at all relative frequencies. T. repens

evidently has a higher relative competitive ability against L. perenne for common niche requirements in the 40 year pasture than in the 21 year pasture.

c) Holcus lanatus - Lolium perenne (Fig. 16c).

These two species demonstrate largely a frequency-independent competitive relationship in all pairs. This indicates that in all 3 pastures, H. lanatus and L. perenne have widely overlapping niche requirements and this degree of overlap does not change as there is no significant difference in the three regression slopes. H. lanatus has an advantage in mixtures at all relative frequencies but this advantage diminishes with increasing pasture age; the 40 year regression approaches the theoretical line of 'no advantage' and is significantly different in intercept from the 2 year regression. This indicates that the extent to which H. lanatus is the superior competitor of the two is less in plants from older pastures (model b in Figure 15).

The traditional expectation of competitive interaction between species is divergence. Antonovics (1978) reviews the findings of experimental studies on changes in competitive performance as a result of competition, most of which involve Drosophila. Several studies have demonstrated changes, as theoretically expected, in the direction of increased differential resource utilization by one or both components and greater reproductive output of the mixture (Moore 1952, Seaton & Antonovics 1967, van Deldon 1970, Barker 1973, Chen 1973 (cited in Antonovics 1978)) . Other work has shown that competitive performance remains unchanged (Sokal et al . 1970, Hedrick

1973, Sulzbach 1980), or in some cases even declines (Futuyma 1970, Ford 1972). Variable results may be due to unpredictability associated with experimental designs, or due to lack of genetic variance or constraints on selection caused by such factors as negative correlation among fitness components or inbreeding depression (Antonovics 1978). Variable results however may also result if selection operates in a variety of different ways and the query which arises when results contradict 'traditional expectation' may simply be a consequence of an erroneous expectation.

Studies for plants comparable to the above demonstrations of the progression of change in competitive relations are unknown prior to the present investigation. Unlike previous studies, the present work addresses the question: What is the competitive relationship between established genet pairs that are actually interacting in nature and how does this relationship differ (for the same two species) in communities whose populations have had different lengths of time to respond to the competitive environment? Furthermore, in the present study, interpretation involves selection which has occurred in nature, not under artificial laboratory conditions. Individuals which interact in the experiments reported here are of identical genotype to those individuals which were actually interacting in the field. Results which do not meet traditional expectation were found and interpretations are offered which reflect different ways in which natural selection may operate (i.e. Figure 15). H. lanatus and T. repens show evidence supporting an hypothesis of niche divergence as traditionally expected, but

L. perenne and T. repens show evidence for niche convergence and all 3 species pairs show evidence suggesting that selection has changed the relative competitive abilities of the species, a non-identical event to changes in the extent of niche overlap. Results for the two grasses (Fig. 16c), H. lanatus and L. perenne , suggest that selection has resulted solely in a more balanced relative competitive power between the two species for a resource supply on which they both make demands.

The unusual result suggesting niche convergence between L. perenne and T. repens suggests the possibility of some form of beneficence between these two species. This may be related to a nitrogen-rich environment made available to the grass through close association with the clover (Wilson 1942, Vallis 1978). Evidence for a strong trend of increasing stable association between these two species with increasing pasture age was presented in Chapter 3. In respect to animal competition, MacArthur & Levins (1967) suggest that convergence may result between two species if their activity together is more effective in suppressing a third more aggressive competitor common to both. Convergence is also associated with the kinds of selection forces associated with mimicry (Sheppard 1975). Agren & Fagerstrom (1980) propose a model of niche convergence for two plant species which initially differ in their flowering times. They argue that a competitor A, which is superior to competitor B in competition for pollinators, but inferior in seedling competition , may be able to increase its relative fitness by evolving increased niche overlap with respect to flowering time, and thereby reducing seed production of competitor B. Such

considerations draw attention away from traditional preoccupation with 'divergence' as a consequence of competitive interaction, and focus instead on the role of relative competitive power and concomitant beneficial interactions in the evolutionary adjustment of species to their environment of neighbours. In this vein, a finer-scale investigation of the interaction between L. perenne and T. repens will be presented in the next chapter.

CHAPTER 6

BIOTIC SPECIALIZATION AT THE GENOTYPE LEVEL: RECIPROCAL PHYTOMETER TRANSPLANTS AMONGST FOUR NATURAL NEIGHBOURING GENET PAIRS OF *LOLIUM PERENNE* AND *TRIFOLIUM REPENS*

INTRODUCTION

Population ecology is to a large extent the study of natural selection. Genetic variation dictates that some individuals leave more descendents than others. The properties of all levels of biological organization are consequently affected and the study of ecology asks how and why of the related processes and resultant patterns. Since 1967, Harper (1967, 1978) has called attention to the need for more interaction between population genetics and population ecology and has stressed that the convergence of the two provides one of the most exciting fields of development in modern biology. Such thinking has had recent consequences at the level of community ecology. Ecologists have become dissatisfied with the taxonomists' 'typological' categorization of the species as these categories were formulated with different needs and philosophies in mind than those of ecologists (Antonovics 1976a). Interest has been aired in recent literature to regard the genotype as a relevant unit of community diversity and to view the community as a conglomerate of evolving components (Antonovics 1976a, Harper 1977b, 1982). These components may be regarded as local neighbourhoods within the community in which, not the particular species, but the particular genotypes of different neighbours dictate the events which attend biotic interaction and set the itinerary of community evolution (Fig. 9, Chapter 3).

Most demonstrations of adaptive genetic variation in plants are not community-based studies; they concern a single component population from a diverse species assemblage. Investigations

have shown that if disruptive selection is strong enough, different adaptive 'types' can arise within a single gene pool even over very short distances and in spite of the diluting effect from gene flow (Jain & Bradshaw 1966, Ehrlich & Raven 1969, Bradshaw 1972). In most studies, the environments discussed concern stringent abiotic selective forces, such as wide ranges in the degree of salinity in maritime habitats (Aston & Bradshaw 1966), or levels of heavy metals (Antonovics et al . 1971) or fertilizers (Snaydon & Davies 1972) in soils. Very little attention has been given to the role of such adaptive genetic variation in considerations of structure and evolution at the community level.

To the plant ecologist a community is essentially a group of co-occurring species on the same trophic level amongst which some degree of interaction is presumed. It is reasonable therefore to expect that the structure and evolution of plant communities will to a large extent be determined by the quantity and quality of genetic variation related to the properties of 'con-trophic' biotic interactions. In spite of this, surprisingly little work has been done to study such variation in plant communities. Any community-level interpretation of a descriptive vegetation study based on the biology of the constituent species requires an examination of the reciprocal manner in which neighbouring individuals respond to one another. Most studies which have shown micro-evolution in plant populations in response to biotic interactions however, have again been concerned with differential behaviour (responses) within a single species. For example, (Watson 1969) found that

populations of Potentilla erecta growing in neighbouring areas of Molinia - and Agrostis - dominated grassland, were different in respect to size of characters when compared as both transplant material and as seed progeny growing in an experimental garden. Linhart (1974) discovered differentiation between peripheral individuals and individuals in the central portion of a single population of Veronica peregrina over a distance of only two to five meters. The differentiation appeared to be related to intense intra-specific competition in the central region versus more intense inter-specific competition near the periphery. Watson (1974, cited in Antonovics 1978) found that with respect to several growth characters, Plantago lanceolata collected from different micro-habitats were genetically differentiated with respect to the vegetation height from which they came. Turkington & Harper (1979c) found evidence for micro-evolution in a population of Trifolium repens in response to different selection pressures exerted by different species of grass in localized regions of a permanent pasture.

Biotic ecotypes within populations are evidence of truly 'Darwinian' forces of natural selection in nature. Studies discussed above have demonstrated fine-scale genetically-based biotic specialization at the species level within single populations. A community level context for micro-evolution that focuses on the genotype as a relevant unit of diversity raises further, more elaborate questions: Does there exist local concomitant (i.e. reciprocal) biotic specialization in each of two interacting species in a community? Does specialization

occur at the genotype level? - i.e. does micro-evolution occur differentially within a single population in response to different neighbouring genotypes of a single species, and is there reciprocal specialization in the neighbouring genotypes? Allard & Adams (1969) showed that lines of barley that had persisted together in mixture over many generations on average yielded higher in mixture than in pure stands. In contrast, lines that had no history of interaction generally showed no difference in yields in mixture compared to pure stands. Joy and Laitinen (1980) discovered a higher yield advantage in mixture (over pure components) in strains of Phleum pratense and Trifolium pratense that had been cultivated in mixture for several generations than in a mixture of two other randomly chosen cultivars of the same species. In what way(s) does selection adjust the behaviour of plants in such biotic specialization at the genotype level in grass-clover combinations? Does it involve evolutionary changes in both interacting populations? What role might a possible beneficial interaction of commensalism (from the nitrogen-rich environment provided by the legume), existing concurrently with the negative interaction of competition, have in establishing the evolutionary response to neighbour interactions?

These questions underscore a view of the plant community that is centered on the coevolution of plant competitors - reciprocal evolutionary responses to competition involving mutual shifts in genetic constitutions of interacting species - a phenomenon that has received little attention in evolutionary thinking and virtually ignored in pasture ecology (Antonovics

1976b, Snaydon 1978). Information about the properties of biotic interactions and ensuing micro-evolutionary patterns is incomplete without an investigation of reciprocal responses between neighbours. Reciprocal responses of natural neighbours defines the 'combining ability' (Chapter 4) of individuals which actually interact in the community. Combining ability reflects the extent to which each component is compatible in the presence of the other; it refers to the capacity of two species or genotypes to continue interaction with one another, or to coexist (Chapter 3). Traditional theory tacitly assumes that coexistence in systems of competition requires some measure of niche differentiation. The prefixed term, 'ecological' combining ability (Harper 1964) alludes to this mechanistic interpretation; species with ecological combining ability, by definition, coexist because their niches do not broadly overlap (Harper 1977b). This does not necessarily imply that all interaction is precluded, but rather that interaction does not take place in respect to any elements or requisites of niche in either species, for which an ensuing contest would lead to the competitive exclusion of one by the other.

In the work presented here, local population differentiation at the genotype level is studied in respect to reciprocal responses between natural genotype neighbours from interacting populations of Lolium perenne and Trifolium repens . Previous studies have shown that different genotypes of a grass species differ in their response to Trifolium repens (Myers & Garber 1942, Ahlgren et al . 1945). Different clones of clover have also been shown to vary in response to a particular grass

(Turkington et al . 1979, Turkington & Harper 1979c). T. repens in the present study site showed a progression of increasing stability of association with Lolium perenne in older pastures (Fig. 8, Chapter 3). The replacement series experiment showed evidence for niche convergence between these two species and increased relative competitive ability of T. repens in older pastures (Chapter 5). The extent of specialization and the nature of the combining ability of these two species is further investigated here. The experiment was designed to test whether samples of Lolium and Trifolium clones taken as neighbouring pairs from different localities in the oldest (1939) pasture differed in their ability to grow in the presence of each other.

METHODS

Experimental Design

Four different genet pairs of Lolium perenne and Trifolium repens (designated L1-T1, L2-T2, L3-T3, L4-T4) were collected as physical neighbours from four widely separate locations in the 1939 pasture where there was abundant overlap in their percentage cover frequencies. The pairs were collected as two whole plants (including root material) and each genet 'type' was propagated separately under glasshouse conditions for 4 months by periodic separation of tillers or cutting of stolon pieces followed by replanting as ramets of the original clone. Plastic pots (26.5 cm top diameter; 30.5 cm deep) were used containing a standard potting mix of 50% peat, 25% sand and 25% perlite with

added nutrients specified in Table 15. Nutrients were added at half the recommended rate to ensure that they were not available in abundance. Each pot (Fig. 17) had a 2.5 cm border in which seeds of Dactylis glomerata were sown at a high density to serve as an outer buffer zone and to 'contain' the study plants by preventing clover stolons from growing out over the edge of the pot and keeping leaves from adjacent pots from interacting. The appropriate height to achieve this could be monitored by varying the height at which the Dactylis border was kept clipped. The Dactylis border zone was separated below ground from the central zone by a plastic 'sleeve'.

TABLE 15. Nutrient composition of potting mix used for the competition experiment between different genets of Lolium perenne and Trifolium repens . (Values are per 35 liters of potting mix).

83 g osmocote (18-6-12) (9 month slow release)

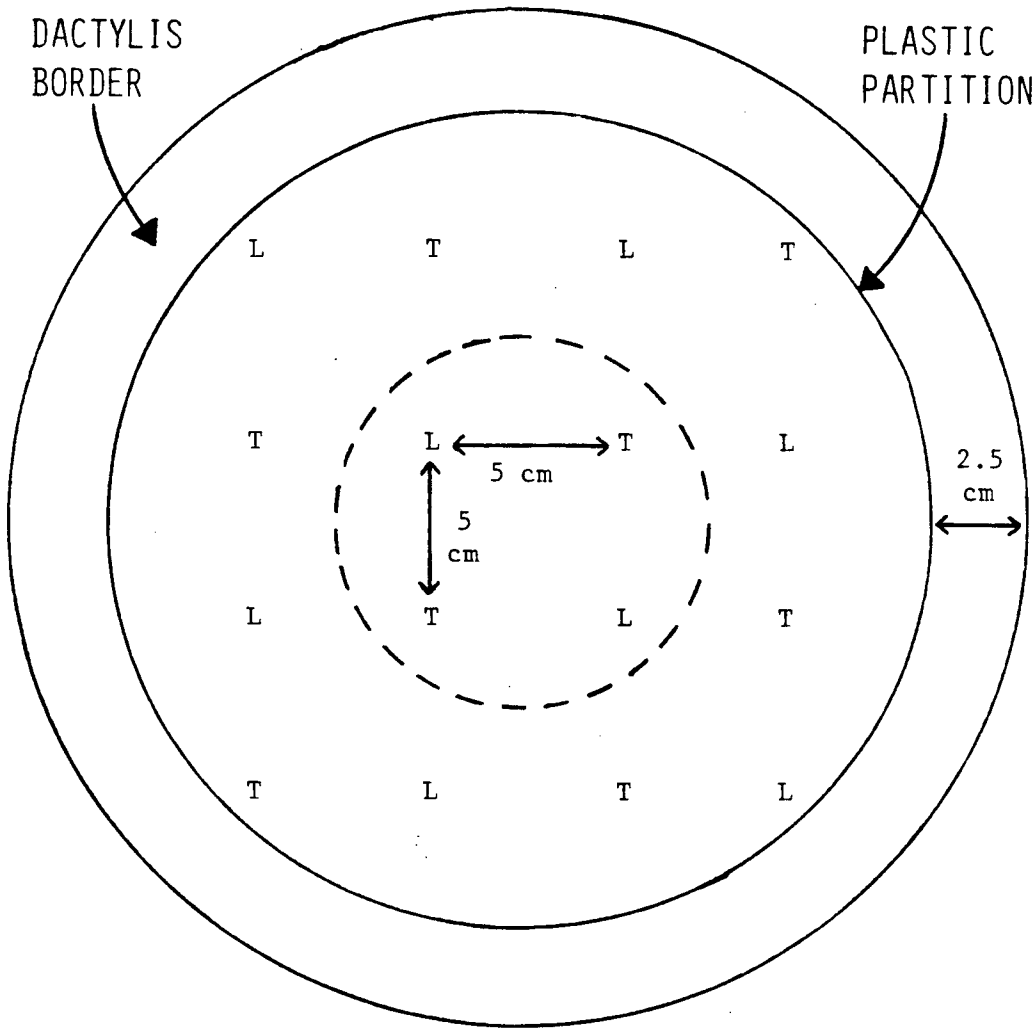
109 g dolomite lime

43 g gypsum

4.5 g fretted trace elements (boron, copper, iron, manganese, molybdenum, zinc)

Three weeks after sowing the Dactylis border, 8 ramets of each grass 'type' were planted with 8 ramets of each clover 'type' in all possible paired combinations. The planting arrangement had 4 central phytometers (2 of each species) surrounded by the remaining ramets which served as an inner buffer zone (Fig. 17). The 4 central phytometers therefore

FIGURE 17. Planting arrangement for pots containing different genet combinations of Lolium perenne (L) and Trifolium repens (T). The outer 2.5 cm border was sown with Dactylis glomerata. The cummulative yield of the 4 denoted central phytometers was followed in the experiment, each species component being recorded separately.


DACTYLIS
BORDER
PLASTIC
PARTITION
L
T
L
T
T
L
T
L
5 cm
5
cm
2.5
cm
L
T
L
T
T
L
T
L

experienced the most representative biotic environment - i.e. each central phytometer was surrounded by 4 phytometers of the other species. Each combination of clover 'type' and grass 'type' was replicated three times and the pots were arranged randomly in a temperature controlled glass house. The pots were watered whenever the soil surface became dry, about 2 to 3 times weekly on average. Once every 3 to 4 weeks the plants (including the Dactylis border) were clipped to approximately 3 cm to simulate grazing. The clippings from the 4 central phytometers were collected each time, dried and weighed separately according to species. Twelve months after planting the ramets, the total above ground parts of the 4 central phytometers were harvested, dried and weighed and the weights of the two components were added to the respective cumulative totals.

Data Analysis

An index of 'combining ability' was calculated for each L-T genet combination as follows (see Chapter 4):

$$CA = Y/Y'$$

where Y is the observed value (per pot) for the lower yielding component and Y' is the observed value for the higher yielding component. (In each combination, T. repens assumed the value of Y and L. perenne assumed the value of Y'). The CA index is compared amongst genet combinations and therefore has strictly relative value. It assumes that a measure of the relative contribution of the two components to the combined yield reflects their capacity to persist in interaction relative to the same measure for other combinations. Data were tabulated in

4 rows and 4 columns as in Table 16 for grass yields, clover yields, total yields and combining ability indexes. Each of these variables was subjected to a multiple linear regression analysis using the following linear model (Table 16):

$$y_{ijk} = \mu' + r_i + c_j + \delta_{ij} d_i + e_{ijk}$$

where, y_{ijk} is a value for the observed variable (i.e. total yield, component yield or CA index); i is the row number; j is the column number; k is the replicate number; μ is the mean of the cell in row 1, column 1 (assuming no diagonal effect); r_i is a variable for 'row effect' (i.e. component of the observation due to the effect of row i); c_j is a variable for 'column effect' (i.e. component of the observation due to the effect of column j); d_i is a variable for 'diagonal effect' (i.e. component of the observation due to the effect of principal diagonal position i); δ_{ij} has a value of 1 if i=j and a value of 0 if i≠j (i.e. incorporate a diagonal effect if the observation is in a principle diagonal cell); e_{ijk} is a random normal variate.

The overall test had the null hypothesis:

Ho: r2 = r3 = r4 = c2 = c3 = c4 = d1 = d2 = d3 = d4 = 0

(i.e. no row, column or diagonal effects). Analysis was aimed primarily to detect whether there were any significant diagonal effects in the data, allowing also for any possible row or column effects. Where the analysis revealed no significant row or column effects, an overall test was generated with the null hypothesis:

Ho: d1 = d2 = d3 = d4 = 0

(i.e. assuming row and column effects are zero). For

TABLE 16. Tabular model used in the analysis of variance (see text for description).

GRASS TYPE \ CLOVER TYPE	T1	T2	T3	T4
L1	$\mu + d_1$	$\mu + c_2$	$\mu + c_3$	$\mu + c_4$
L2	$\mu + r_2$	$\mu + r_2 + c_2 + d_2$	$\mu + r_2 + c_3$	$\mu + r_2 + c_4$
L3	$\mu + r_3$	$\mu + r_3 + c_2$	$\mu + r_3 + c_3 + d_3$	$\mu + r_3 + c_4$
L4	$\mu + r_4$	$\mu + r_4 + c_2$	$\mu + r_4 + c_3$	$\mu + r_4 + c_4 + d_4$

individual diagonal effects the following null hypotheses were tested:

Ho1: d1 = 0, Ho2: d2 = 0, Ho3: d3 = 0, Ho4: d4 = 0.

Data were analyzed using a MIDAS program (Fox & Guire 1976). F-tests for the homogeneity of variances were not rejected and all analyses were performed on untransformed data.

RESULTS

The results of dry weight production for Trifolium and Lolium in all genet-pair combinations are shown in Tables 17 and 18 respectively. The null hypothesis of no row, column or diagonal effects was rejected in both cases. For each genet-pair type Lx-Tx (Fig. 18), the yield of T (clover) in any combination involving Lx or Tx was generally highest in the natural neighbouring combination; L3-T3 and L4-T4 showed significant ($P<0.05$) diagonal effects. The converse was true for Lolium ; yield was lowest in the natural neighbouring genet combination and significant diagonal effects were found for L1-T1 and L3-T3 (Fig. 18). There was little neighbour specific pattern for total (L plus T) yields of the combinations (Table 19); the L1-T1 combination showed the only significant diagonal effect.

The fine scale nature of biotic specialization between Lolium and Trifolium genotypes is further evident from a comparison of combining ability indices (Fig. 19 and Table 20). This simultaneously incorporates the neighbour-specificity of L for T and T for L. For each genet pair type Lx-Tx, the combining ability was higher than in any other combination

TABLE 17. Yields (g) of phytometers of Trifolium repens (Tx), each collected with a natural neighbouring genet of Lolium perenne (Lx) from four sites in the 1939 pasture and planted in all combinations of clover type and grass type; the performances of the clover types with with their natural neighbouring grass types are shown on the principal diagonal; all values are means of 3 replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming row and column effects; for the overall test, P=0.0041.

		grass associate			
		L1	L2	L3	L4
clover producer	T1	3.32	2.25	1.00	0.94
	T2	2.95	3.25	1.73	0.99
	T3	1.68	1.43	3.38	1.39
	T4	2.15	1.07	1.84	2.97

P1=0.2102, P2=0.1301, P3=0.0074, P4=0.0092

TABLE 18. Yields (g) of phytometers of Lolium perenne (Lx), each collected with a natural neighbouring genet of Trifolium repens (Tx) from four sites in the 1939 pasture and planted in all combinations of clover type and grass type; the performances of the grass types with their natural neighbouring clover types are shown on the principal diagonal; all values are means of 3 replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming row and column effects; for the overall test, P=0.0126.

		clover associate			
		T1	T2	T3	T4
grass producer	L1	6.45	15.22	23.01	8.03
	L2	7.11	9.59	10.13	5.21
	L3	11.38	6.53	5.63	8.94
	L4	12.71	7.92	10.71	7.44

P1=0.0086, P2=0.2420, P3=0.0430, P4=0.6630

TABLE 19. Total combined yields (g) of phytometers of Lolium perenne (L) and Trifolium repens (T) collected as natural neighbouring pairs from four sites in the 1939 pasture and planted in all combinations of grass type and clover type; the values for the natural neighbouring pairs are shown on the principal diagonal; all values are means of 3 replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming row and column effects; for the overall test, P=0.0098.

		clover type			
		T1	T2	T3	T4
grass type	L1	9.77	18.20	24.69	10.18
	L2	9.69	12.84	11.55	6.29
	L3	12.39	7.93	9.01	10.78
	L4	13.65	8.92	12.10	10.41

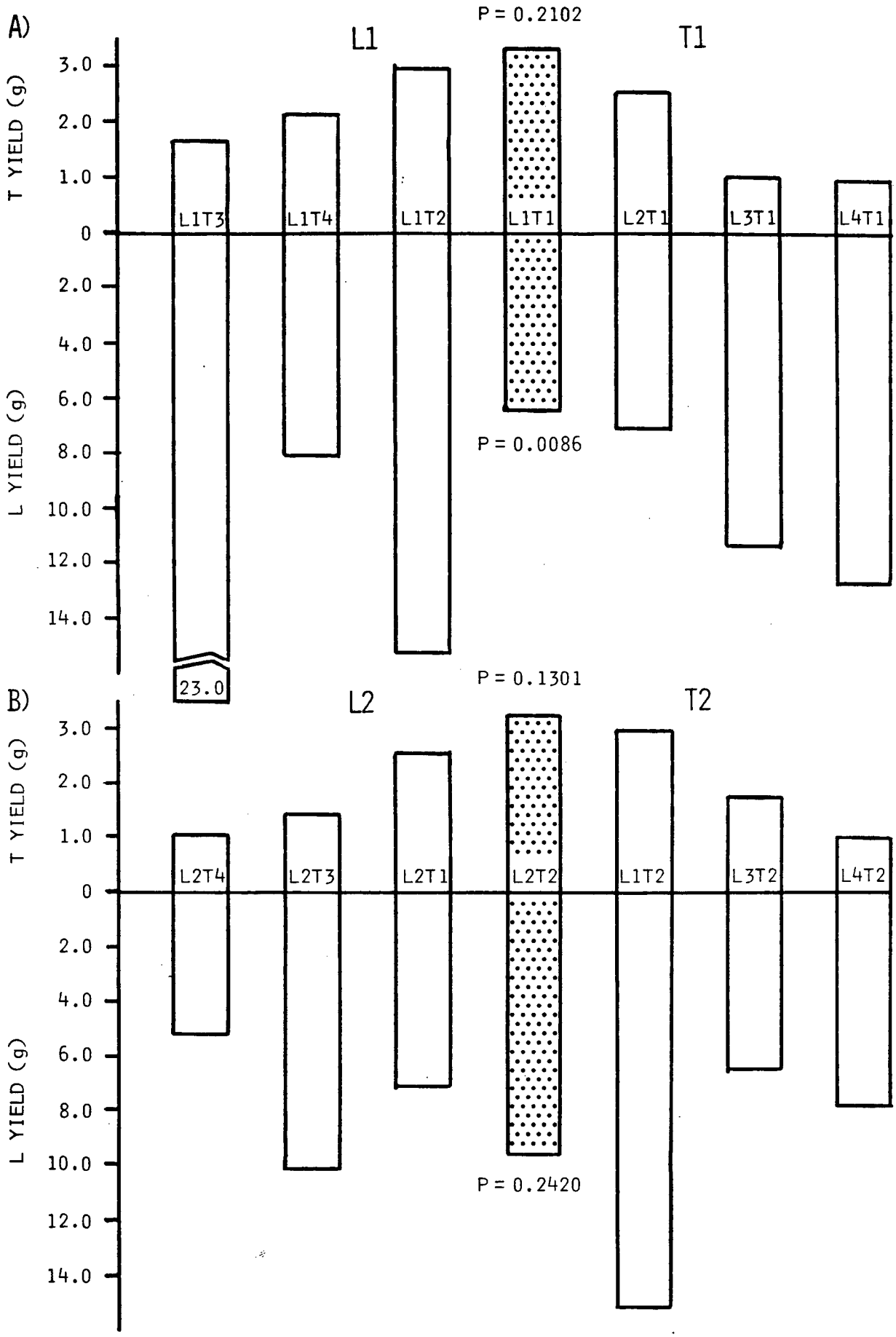
P1=0.0125, P2=0.1346, P3=0.1133, P4=0.3307

TABLE 20. Combining ability indexes for genet pairs of Lolium perenne (L) and Trifolium repens (T) collected as natural neighbouring pairs from four sites in the 1939 pasture and planted in all combinations of grass type and clover type; the values for the natural neighbouring pairs are shown on the principal diagonal; all values are means of 3 replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming no row or column effects; for the overall test, P=0.0014.

		clover type			
		T1	T2	T3	T4
grass type	L1	0.52	0.19	0.11	0.27
	L2	0.35	0.36	0.24	0.21
	L3	0.09	0.30	0.49	0.21
	L4	0.12	0.17	0.13	0.48

P1=0.0045, P2=0.1287, P3=0.0088, P4=0.0121

FIGURE 18. Yields of phytometers of Lolium perenne (L) and Trifolium repens (T) when grown together in different combinations of genet types. Graphs show the yields when in combination with natural neighbours (stippled bar graphs) compared to yields in all other combinations involving A) L1 or T1, B) L2 or T2, C) L3 or T3, D) L4 or T4. All values are means of 3 replicates.


A)
L1
T1
P = 0.2102
T YIELD (g)
3.0
2.0
1.0
0
L1T3
L1T4
L1T2
L1T1
L2T1
L3T1
L4T1
L YIELD (g)
2.0
4.0
6.0
8.0
10.0
12.0
14.0
23.0
P = 0.0086
P = 0.1301
B)
L2
T2
T YIELD (g)
3.0
2.0
1.0
0
L2T4
L2T3
L2T1
L2T2
L1T2
L3T2
L4T2
L YIELD (g)
2.0
4.0
6.0
8.0
10.0
12.0
14.0
P = 0.2420

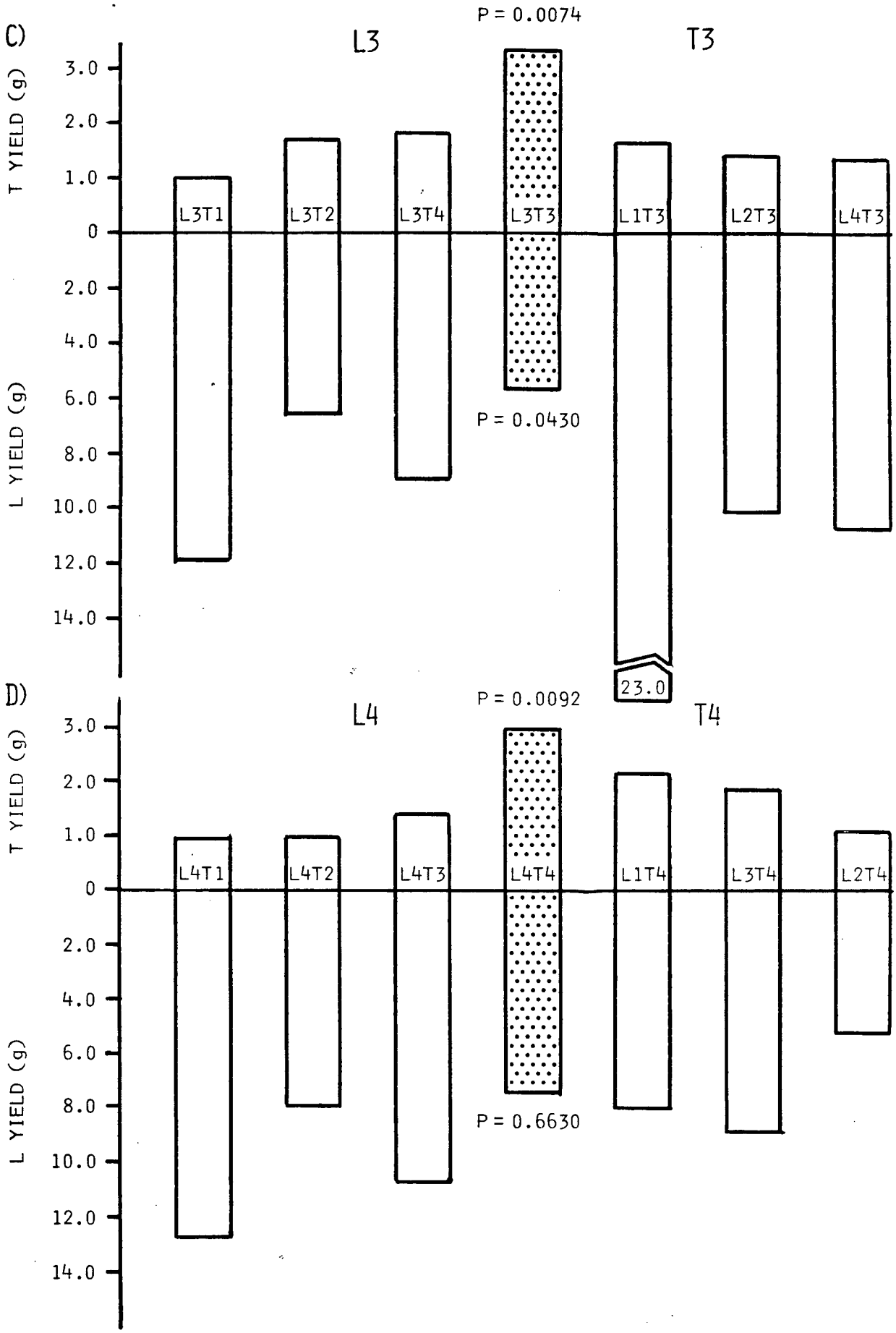
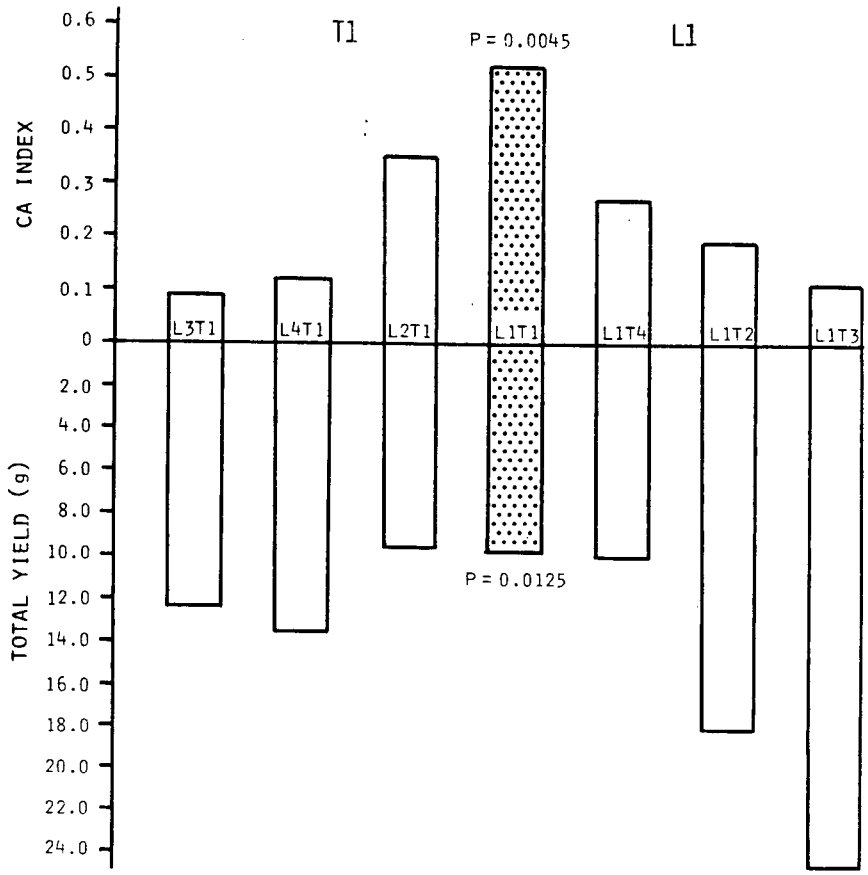
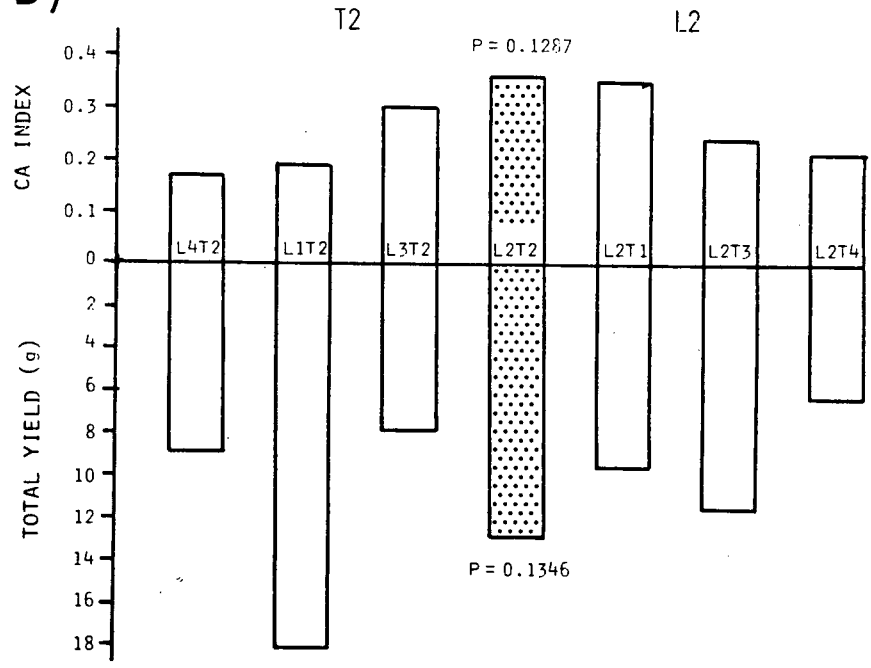

C)
P = 0.0074
L3
T3
T YIELD (g)
L YIELD (g)
3.0
2.0
1.0
0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
L3T1
L3T2
L3T4
L3T3
L1T3
L2T3
L4T3
P = 0.0430
23.0
D)
P = 0.0092
L4
T4
T YIELD (g)
L YIELD (g)
L4T1
L4T2
L4T3
L4T4
L1T4
L3T4
L2T4
P = 0.6630

FIGURE 19. Combining ability indexes and total yields for different genet type combinations of Lolium perenne and Trifolium repens . Graphs show the values for the 4 combinations of natural neighbours (stippled bar graphs) compared to all other combinations involving A) L1 or T1, B) L2 or T2, C) L3 or T3, D) L4 or T4. All values are means of 3 replicates.

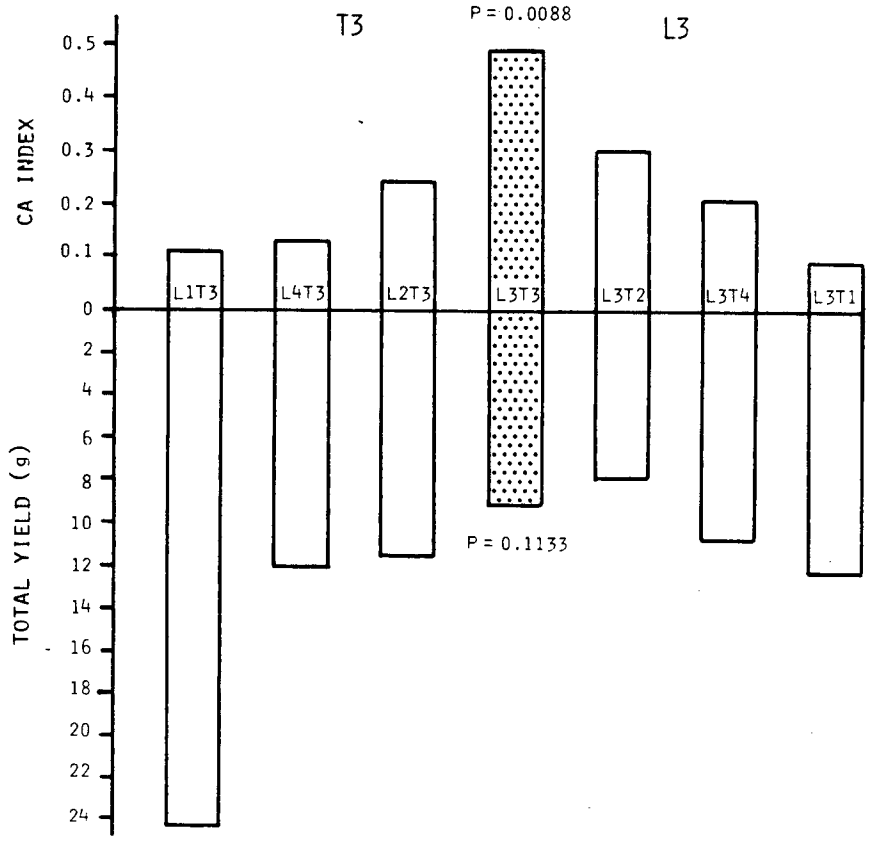
A)


T1
P = 0.0045
L1
CA INDEX
TOTAL YIELD (g)
0.6
0.5
0.4
0.3
0.2
0.1
0
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
18.0
20.0
22.0
24.0
L3T1
L4T1
L2T1
L1T1
L1T4
L1T2
L1T3
P = 0.0125

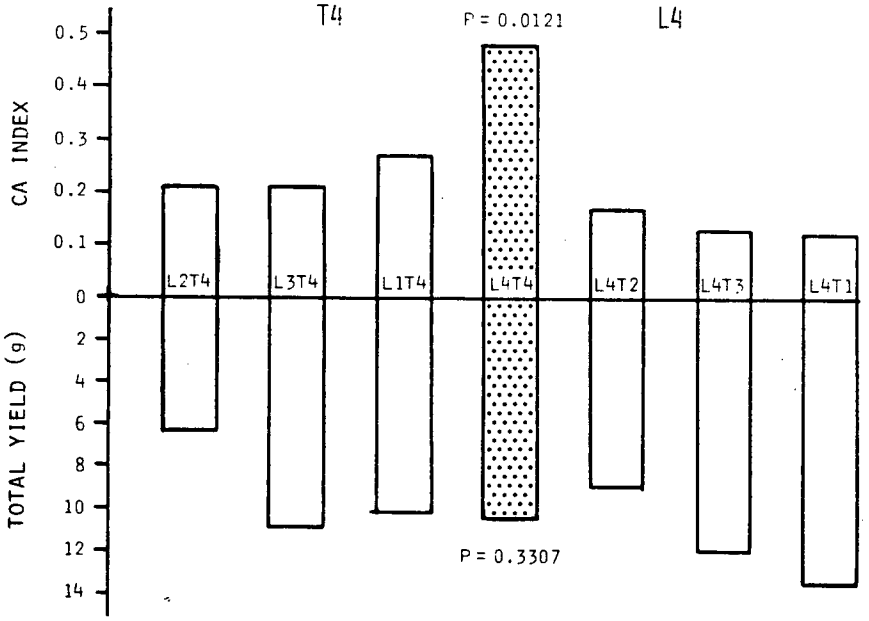
B)


T2
P = 0.1287
L2
CA INDEX
TOTAL YIELD (g)
0.4
0.3
0.2
0.1
0
2
4
6
8
10
12
14
16
18
L4T2
L1T2
L3T2
L2T2
L2T1
L2T3
L2T4
P = 0.1346

C)


T3
P = 0.0088
L3
CA INDEX
0.5
0.4
0.3
0.2
0.1
0
L1T3
L4T3
L2T3
L3T3
L3T2
L3T4
L3T1
TOTAL YIELD (g)
2
4
6
8
10
12
14
16
18
20
22
24
P = 0.1133

D)


T4
P = 0.0121
L4
CA INDEX
0.5
0.4
0.3
0.2
0.1
0
L2T4
L3T4
L1T4
L4T4
L4T2
L4T3
L4T1
TOTAL YIELD (g)
2
4
6
8
10
12
14
P = 0.3307

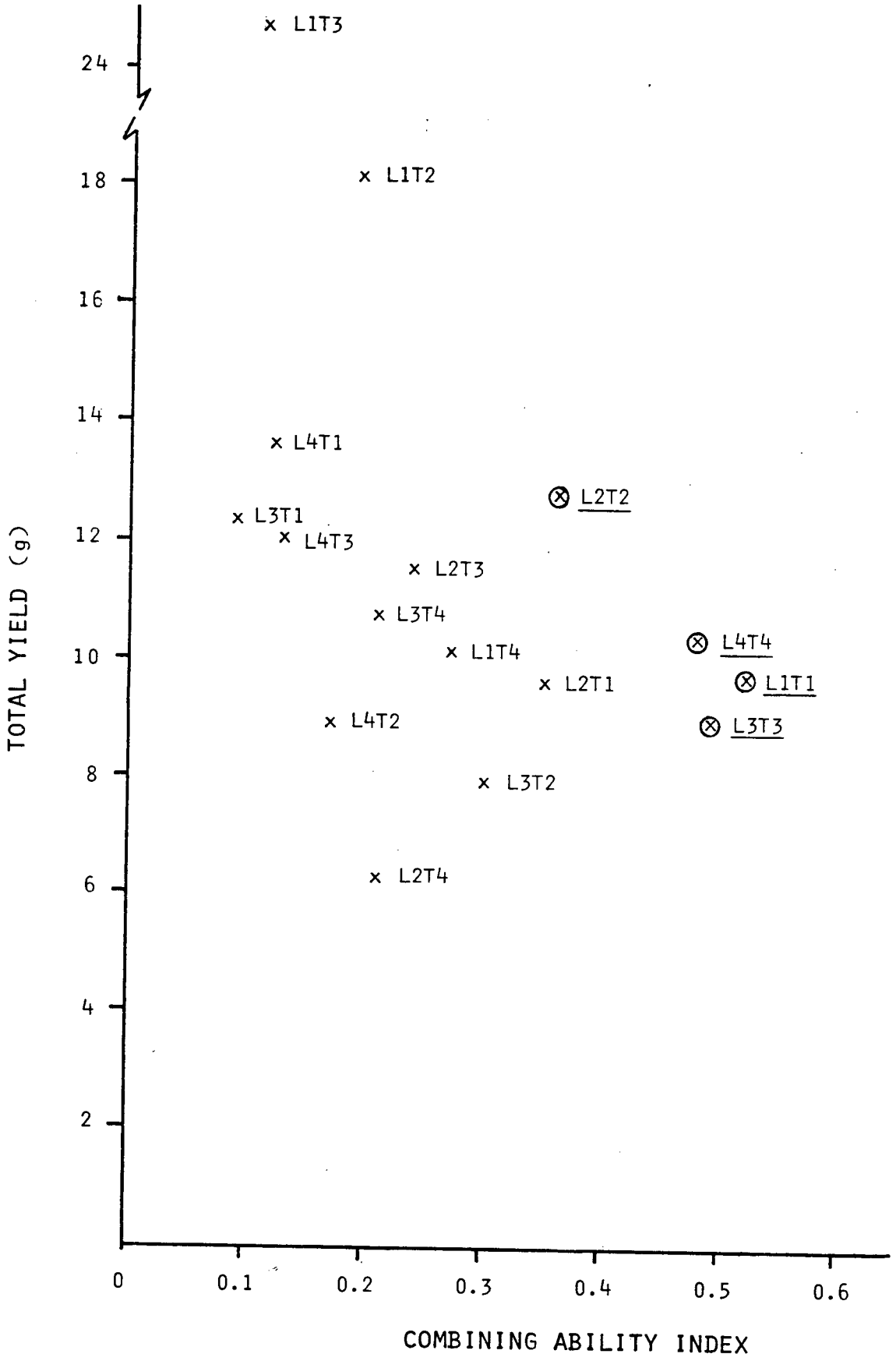
involving Lx or Tx (Fig. 19). Significant ($P<0.05$) diagonal effects were obtained for L1-T1, L3-T3 and L4-T4.

Total yields are also illustrated in Figure 19 in order to compare them with combining ability indexes. No strong trends are apparent although there appears to be some negative relationship between total yield and combining ability in combinations involving L1 or T1 (Fig. 19a) and in combinations involving L3 or T3 (Fig. 19c). Examining the data as a whole, the four natural neighbouring genet pairs had the highest combining ability indexes but did not significantly stand out from the other combinations in terms of total yield (Fig. 20).

DISCUSSION

Three out of four genet pairs of Lolium and Trifolium which were sampled together as immediate neighbours in the field had higher combining ability than those in which the two components came from different neighbourhoods. The three sets of significant results are stressed since they offer experimental indication of a potentially important organizing factor in community structure. Combining ability may be thought of as the capacity to avoid competitive exclusion or as the probability of coexistence for one genet combination relative to another. The term makes no assumption as to mechanism. Combining ability is defined in this study by the differential in the performance of the two components in the presence of each other. Those combinations in which the superior component vastly out-yielded the inferior component have a lower probability of coexistence, or lower combining ability, than combinations in which the two

FIGURE 20. Relationship between total yield and combining ability index for different genet type combinations of Lolium perenne and Trifolium repens. The values for the naturally neighbouring genet pairs collected from the four sites in the experimental field are circled. All values are means of three replicates.


TOTAL YIELD (g)
24
18
16
14
12
10
8
6
4
2
0
0.1
0.2
0.3
0.4
0.5
0.6
COMBINING ABILITY INDEX
L1T3
L1T2
L4T1
L2T2
L3T1
L4T3
L2T3
L3T4
L1T4
L4T4
L2T1
L1T1
L4T2
L3T3
L3T2
L2T4

components were more similar in their performance. Ecological combining ability implies a high probability of coexistence due to some degree of niche separation affording some measure of escape from competition (Harper 1977b). The result is that combinations with more ecological combining ability (more niche separation) have a higher total yield in combination than those with less ecological combining ability (less niche separation) (e.g. Seaton & Antonovics 1967, Allard & Adams 1969, Remison & Snaydon - in Snaydon 1978, Joy & Laitinen 1980).

The most noteworthy feature of the present results is that, as concerns the underlying mechanism for higher combining ability between naturally neighbouring genets compared to non-neighbouring genets, an interpretation of ecological combining ability is not justified. There was no indication that combinations with the highest combining ability had the highest total yield (Fig. 20). Higher combining ability of natural neighbouring genets is instead attributed to the fact that the performance of each clover genet was highest with its natural neighbouring grass genet (which parallels the findings of Turkington & Harper (1979c) with respect to clover response to natural neighbouring grass species as opposed to genets), but that the performance of each grass genet was lowest with its natural neighbouring clover genet. The result is that the differential in performance of the highest yielding component (which was always the grass) and the lowest yielding component (which was always the clover) was least in genet pairs from the same neighbourhood. The consequence of this is a higher combining ability of these genet pairs but not a higher total

yield.

Higher combining ability between natural neighbours in these results cannot be interpreted in terms of any shifts in amount of niche overlap. The interpretation instead appears to involve a form of selection which reduces the differential in relative competitive power for resource requirements that the two species have in common. Moreover, relative competitive ability appears to be genotype specific; the factors that permit high combining ability between one pair of neighbouring Lolium - Trifolium genets are not the same factors that permit a high combining ability between a different pair of neighbouring Lolium - Trifolium genets from a different neighbourhood in the community. This higher combining ability for natural neighbours may be a result of several factors most likely operating variously in concert rather than separately:

a) Differential fitness through local competitive ability and recombination

If initially the grass is generally more aggressive than the clover, it may eliminate several clover genotypes from the community. Within a local neighbourhood however, a few clover genotypes may possess challenging competitive ability against the particular resident grass genotypes. The most challenging of such clover genotypes would leave the most descendents and increase in local frequency. The exact course of selection would depend on the type of competition imposed by particular grass genotypes. (The grass population may not respond in like manner for reasons outlined in c) below). Grass genotypes would therefore face the most stringent competition from the locally

adapted clover genets that belong to the same neighbourhood and hence perform more poorly in their presence than with alien clover genets from other neighbourhoods. The converse would be true for clover genotypes. The production of genetic recombinants would facilitate tracking of local changes in the competitive environment and be important to individual fitness.

b) Differential fitness through migration ability

Some clover genotypes may have a greater capacity than others to migrate (through stolon extension) from neighbourhoods imposing stringent competition, and hence escape from impending mortality. This wandering phenotype of T. repens permits it to 'seek out' neighbourhoods of grass genotypes in which it is compatible (Chapter 3). These may be neighbourhoods in which competition is avoided through niche differentiation. The present evidence however suggests instead that they are neighbourhoods in which no member imposes an overbearing threat on the relative fitness of others through any superior ability to exploit contested resources (as in (a) above). This course of selection is especially likely if niche requirements are not readily partitionable. In the face of an adversely altered competitive environment, fitness is enhanced once again by a propensity of the genotype to migrate through lateral spread.

c) Beneficence between grass and clover

A beneficial effect on the grass may be provided by the nitrogen rich environment in the presence of the legume. This could be a sufficiently strong selective force to favour those genotypes of grass which do not exert highly stringent competitive pressures on the clover. Grass genets which

ultimately leave the most descendents in local neighborhoods may therefore be those that are competitive enough to avoid competitive exclusion by the clover but in turn, are not so competitive as to severely suppress or eliminate the source of nitrogen made available by a neighbouring clover. This may be especially important to fitness if available soil nitrogen is scarce. The genotype-specific coadaptation in local neighbourhoods may be further mediated by a complex indirect mutualism involving interaction of particular grass genotypes and particular strains of symbiotic Rhizobium in the clover (c.f. Hill 1977).

A beneficence of the above sort may place constraints on niche divergence. Niche divergence may not contribute to higher fitness if the mutualistic or commensalistic relationship is lost in the process. Selection may instead result in an equilibration of the reciprocal aggressiveness of the two competing species exploiting a broadly overlapping niche. Local selection in the present Lolium and Trifolium populations may be operating to synchronously curb and vitalize efforts respectively in the struggle to pre-empt environmental resources, and may even involve niche convergence as evidence suggests from the replacement series results (Chapter 5). Grime (1979) also advocates a phenomenon of selection for reduced competitive vigour in his theory of S-selection ("stress-tolerant" strategy). S-selection presumably brings about reduction in both vegetative and reproductive vigour, adaptations which allow endurance of continuously unproductive environments.

The relative contribution of a), b) and c) in developing the local biotic specialization reported here is a topic worthy of further inquiry. The possible role of beneficence in defining selectional forces is particularly interesting. Ecologists have tended to 'pigeonhole' species interactions into separate types, e.g. parasitism, predation, commensalism, amensalism, competition, mutualism. Competition and beneficence have generally been viewed as conflicting extremes of organism interaction and before about 1960 accounts of the evolutionary process largely dismissed cooperative phenomena as not requiring special attention (Axelrod & Hamilton 1981). Yet it is reasonable that two organisms which are competing in one respect, may be cooperating in another. Empirical and theoretical considerations to date have concerned mostly simultaneous intra - specific competition and cooperation, e.g. in Drosophila (Mather 1961) and in sessile invertebrates (Buss 1981). Possible beneficial functions in animals include cooperation between genders required for producing offspring, increased protection from weather, reduced risk of predation, increased feeding efficiency, and increased interspecific interference ability (Buss 1981). Mather (1961) argues that in so far as the cooperative function is essential to fitness, a certain minimal contribution to it may be favoured even at the risk of reduction in competitive capacity.

Evidence for concomitant positive and negative interactions between species is scarce. Thomson (1978, 1980) has described cases where two species of entomophilous annual plants compete for the same pollinators, but where they grow together,

pollination rates for both are higher than when they grow alone because the more spatially concentrated bloom attracts proportionately more visiting pollinators. Atsatt & O'Dowd (1976) cite numerous examples from the literature suggesting that the defense of a plant from herbivores and other pests may be improved in the company of specific neighbours offering some measure of protection and with whom some measure of competition can be reasonably assumed. For example, Phillips & Pfeiffer (1958) demonstrated that the grasses Agrostis and Festuca gain considerable protection from cattle when associated with the noxious buttercup Ranunculus bulbosus . Using the same species as in the present study, Radcliffe (1972 - cited in Atsatt & O'Dowd 1976) showed that susceptibility of Trifolium repens to damage from grass grubs and caterpillars was decreased in mixed stands with Lolium perenne compared to in pure stands. A further example is given in a study of the effect of removal of different components of the neighbouring vegetation on the population size of Rumex acetosa (Putwain & Harper 1970). It was found that if both dicotyledons and grasses were removed, its population increased less than if grasses alone were removed. This suggests that in some way the presence of the other dicotyledonous members of the community extends the realized niche of Rumex acetosa . Harper (1964) emphasized, "A component removed from a habitat is not only one of many species making demands on limiting light, water, and nutrient supplies; it is also a possible source of micro-environmental conditions necessary for associated species."

Because of the high nitrogen requirement of many grasses

combined with the nitrogen-rich environment provided by the legume, a natural beneficial interaction may occur together with a competitive one in pastures. Often, grasses have been found to be more competitive than white clover for other important nutrients such as potassium (see review by Robson & Loneragen 1978). This may result in what has been described as the "cycle of good and poor clover " (Blaser & Brady 1950). During 'good' clover years the soil nitrogen is increased; hence, grasses start growing very early in the spring of the subsequent year. The resultant competition for potassium may limit the growth of the leguminous associate (hence a 'poor' clover year). In the following year, clover attains more vigorous growth because the grasses face a low nitrogen supply and cannot compete as aggressively for potassium; so the cycle continues. A similar phenomenon has been described in the more detailed "grassland cycle" of Turkington & Harper (1979a). It is reasonable to consider that selection should favour those individuals in both these fluctuating populations that could establish a more 'balancing' competitive relationship. As it is possible that selection for niche differentiation with respect to potassium utilization could suppress the beneficence regarding nitrogen supply to the grass, selection may instead favour a decrease in competitive ability for potassium in the grass accompanied by an increase in this corresponding competitive ability in the legume. Those genotypes of grass which are less aggressive in this regard should be able to survive and reproduce more successively through <u>both</u> good and poor clover years along with their compatible clover neighbours and thereby may leave more

descendents.

As this selection continues during community evolution, these grassland cycles might be expected to diminish in amplitude or frequency. Evidence for such a cycle in the present study can be seen in Figure 2 (Chapter 2). T. repens in all three pastures had a higher percentage cover in the 1979 surveys than in the 1981 surveys. In contrast, L. perenne had a higher percentage cover in the three pastures in the 1981 surveys than in the 1979 surveys. The cycle seems barely to have started in the 1977 pasture, is most pronounced in the 1958 pasture and tapers off somewhat in the 1939 pasture. Poa compressa also showed this opposite cover trend to clover in the 1977 pasture and Holcus lanatus displayed the same trend in the 1958 pasture.

Biotic specialization at the genotype level as demonstrated in the present study calls for an organism - centered view of community structure and evolution (Chapter 3). The traditional view defines a community as the collection of populations occupying a given area, usually thought to affect the distribution and abundance of one another (Odum 1971). A more refined approach regards the community as a 'montage' of evolving neighbourhoods which centers on the organism as the pivotal unit of interaction (eg. MacMahon et al 1978, MacMahon et al . 1981). This view is especially suited to sessile organisms such as plants since any given individual will interact with others in only a very local neighbourhood. The present results corroborate the findings reported earlier (Chapters 4 and 5) that evolutionary changes in the combining

ability of species may be a consequence of not only niche differentiation, but also a 'balancing' of competitive abilities. The present study indicates that, given sufficient genetic variation, micro-evolutionary forces may be so precise that the properties which determine reciprocal adaptation in local neighbourhoods may be neighbour specific even at the scale of different genotypes of the same species. The interpretation exposes the need for more investigations of the occurrence and role of species interactions which integrate beneficence and opposition.

CHAPTER 7

GENERAL DISCUSSION

PROSPECTUS

The results and interpretations of the work presented in this thesis call for a general discussion of the phenomenon of coexistence in systems of competition between plants. In Chapter 1, the largely overlooked distinction between the concepts of fundamental niche and competitive ability is established and a comprehensive perspective for the meaning of the latter is offered. This enables the thesis to proceed with minimal ambiguity in the parlance of competition and coexistence. In Chapter 2, ordination of time-series percentage cover surveys (Fig. 4) revealed trends which support the suggestion that the three pastures under study represent different stages in a common progression of community development. This is further corroborated by time-series surveys of contact sampling presented in Chapter 3 (Fig. 8). Contacts between individuals are interpreted as reflecting an operational measure of species interaction. The dynamics of interspecific contacts therefore represent patterns of association and coexistence at the fine-scale level of individual experience. A trend of increasing stability of inter-specific association in older pastures was discovered and this is used as a basis for constructing a 'portrait' of pasture community evolution which attributes within-community temporal changes to the selective forces accruing from biotic interactions (Fig. 9). Armed with this information, the stage was set for addressing the central issue of this thesis: What mechanisms are responsible for this 'settling down' of community

dynamics and permitting coexistence in these systems?

It is tacitly assumed that predation (i.e. grazing) and other disturbances are important factors permitting diversity in pastures through their effects in suppressing potential dominants (e.g. Harper 1969, Watkin & Clements 1978, Grime 1979). It is also axiomatic in ecology that a phenomenon as broad as coexistence will rarely be fully explained by a single factor. The present work therefore focuses on the hypothesis that the biotic factor of neighbour interactions, especially competition is important. With different stages of community development available at the same time, an opportunity was available for studying precisely how the competitive relationship between a particular pair of species changes during community evolution.

Natural selection leading to coexistence in contexts of competition and other neighbour interactions may be defined as selection for 'combining ability'. The three experimental designs for studying competitive interactions (Chapters 4, 5 and 6) yielded corroborative data. Evidence indicates that combining ability may be of two contrasting types: 1) 'ecological' combining ability (niche differentiation), and 2) 'competitive' combining ability (balanced competitive abilities). The ramifications of these findings to contemporary coexistence theory are pursued here in relation to systems in which competition is an important force of natural selection. The arguments presented follow from recognizing a clear distinction between the concepts of 'niche' and 'competitive ability' (Chapter 1).

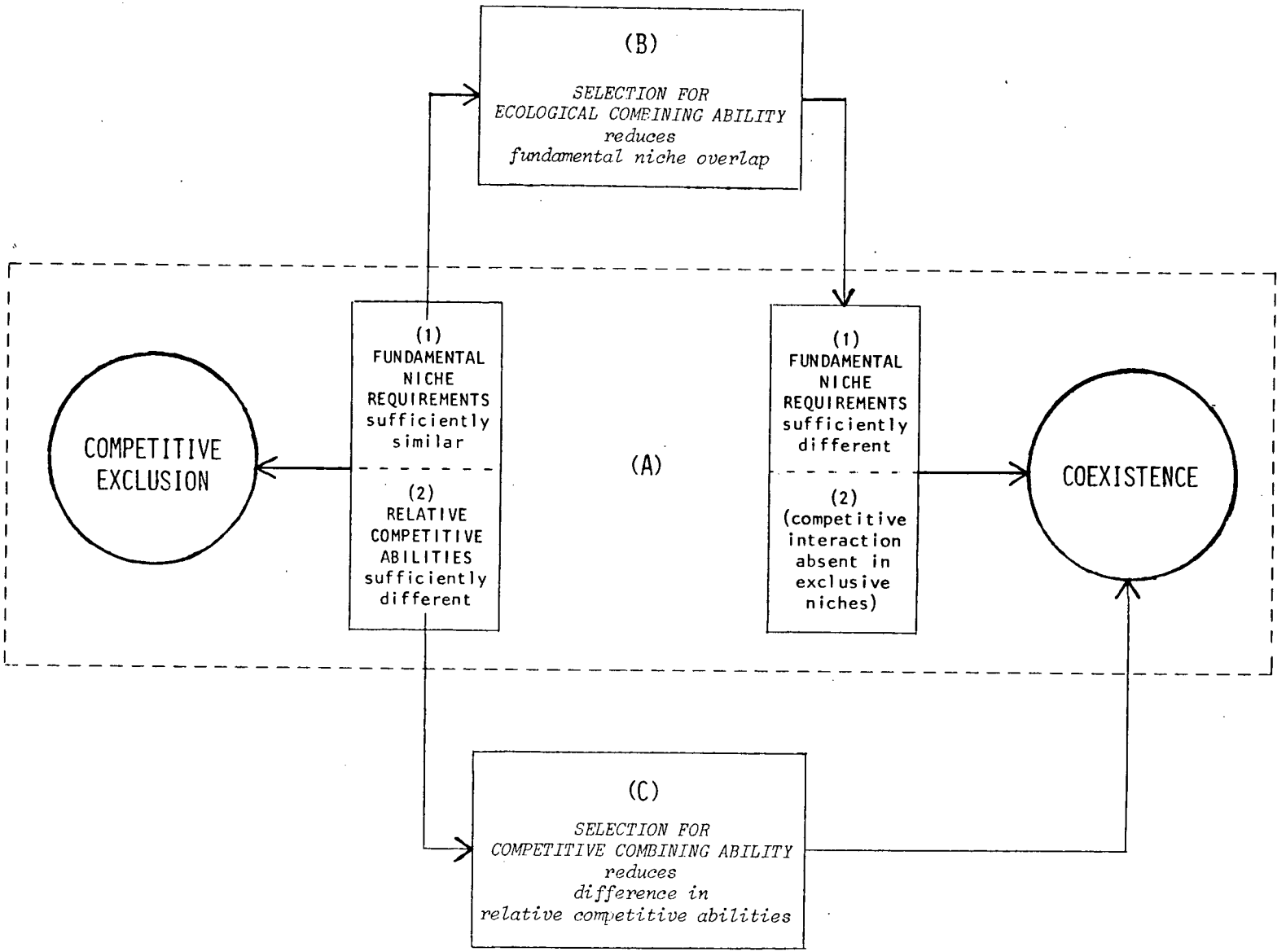
COMPONENTS OF A GENERALIZED COEXISTENCE THEORY

A theory for the coexistence of plant competitors is set out below which integrates traditional theory with a broader interpretation of the operation of natural selection than previously recognized. Its evolutionary premise incorporates the dynamics and variability of two primary components; 1) fundamental niche requirements, and 2) relative competitive ability. A qualitative model is portrayed in Figure 24 and is described by three underlying concepts.

A) Gaussian coexistence

The theoretical framework of Gause's principle is denoted by the contents of the dashed box in Figure 21 which is in reference to a hypothetical two-species system. In regard to the first theoretical component, if fundamental niche requirements are sufficiently similar (in the sense of 'limiting similarity' (MacArthur & Levins 1967)), Gause's principle pronounces a relentless proceeding toward competitive exclusion of one of the species. Given this condition for the first component, (although never part of any formal statement) the principle implicitly invokes an assumption for the second component - i.e. relative competitive abilities will be sufficiently different. This difference in competitive abilities is assumed to be invariably present between any two interacting species until exclusion of one species is complete. Gaussian coexistence (a corollary of the competitive exclusion principle) is possible only if fundamental niche requirements

FIGURE 21. The schematic structure of a general theory of species coexistence in contexts where competition is an important force of natural selection. The general theory recognizes two basic and distinct components: (1) Fundamental niche requirements, and (2) Relative competitive abilities. Three concepts are represented and discussed in the text: (A) traditional theory for 'Gaussian' coexistence (dashed box); and two evolutionary mechanisms which permit coexistence - i) selection for ecological combining ability (niche differentiation) (B), and ii) selection for competitive combining ability (coevolution) (C).


(B)
SELECTION FOR ECOLOGICAL COMBINING ABILITY reduces fundamental niche overlap
(1) FUNDAMENTAL NICHE REQUIREMENTS sufficiently similar
(2) RELATIVE COMPETITIVE ABILITIES sufficiently different
COMPETITIVE EXCLUSION
(A)
(1) FUNDAMENTAL NICHE REQUIREMENTS sufficiently different
(2) (competitive interaction absent in exclusive niches)
COEXISTENCE
(C)
SELECTION FOR COMPETITIVE COMBINING ABILITY reduces difference in relative competitive abilities

are different 'enough' (i.e. a 'limited' amount of overlap is permitted), the crucial consequence being that the two species do not always have to compete because each has some exclusive niche space, either spatially or temporally. According to the Gaussian view, where competition occurs between two species in respect to a broadly overlapping niche, the competitive exclusion of one is impending.

That the Gaussian philosophy is still pervasive in current ecological thinking is evident by a recent quote from Newman (1982): "It is generally accepted that in order to coexist more than transiently species must differ - they must show niche separation. If species are too similar all but one will be eliminated in competition". It is not difficult to imagine how such profound statements associated with Gause's principle could have been a product of the early evolutionists' central focus on such ideas as 'struggle for existence' and 'survival of the fittest'. Such were strong outward themes of Darwin and Wallace conceived from their awareness of the inherent capacity of populations to increase in size. This was further reinforced by early experimental studies demonstrating competitive exclusion in laboratory populations (Gause 1934, Park 1948, 1954). What is surprising is that this same theme persists largely unaltered today. As Sheppard (1975) has pointed out, the use of the word 'struggle' which suggests physical combat, has obscured the "all-embracing nature of selection" and the importance of (and potential for) the immense variation within species that Darwin was really driving at.

B) Coexistence by selection for ecological combining ability (niche differentiation)

Upon recognizing that a population will usually have genetic variation pertaining to fundamental niche requirements, ecologists turned their attention from investigations of what enables one species to win in a competitive interaction (competitive exclusion) (e.g. Sakai & Gotoh 1955, Lerner & Ho 1961, Mather & Cooke 1962, Gale 1964), to investigating the role of natural selection in the evolution of niche differentiation and hence permitting coexistence (Fig. 21-B). In plant interactions this has been termed selection for ecological combining ability (Harper 1964, 1967, 1977b). Under this theory, species coexist because evolution, by the selection pressures of competition, results in avoidance of a competitive interaction through niche differentiation.

Notice that this evolutionary approach to explaining coexistence is still entrenched within a 'Gaussian' framework (dashed box in Fig. 21). It still assumes that: 1) coexistence is only achieved if niche requirements become sufficiently different and hence interspecific competition is relaxed (or eliminated) and 2) where niche overlap remains, competitive exclusion will ensue. In essence then, selection for ecological combining ability is an extension or corollary of Gause's principle (c.f. Grubb 1977, p.107) and presupposes that under high inter-specific density, natural selection may result in niche differentiation and hence coexistence - else, competitive exclusion is forthcoming.

If each species is affected more by the presence of the

other than by the presence of intraspecific individuals, then competition is of the 'interference' type (Harper 1977b). One species may be more aggressive than the other, but directional selection may be strong in both species and differences in relative fitness amongst individuals (in each species) occupying different regions of niche space may result in niche divergence. In the more common 'exploitation' type of competition in plants however, if competitive abilities are unequal, the weaker competitor is generally affected more by the presence of interspecific individuals and the stronger competitor by the presence of intraspecific individuals (Harper 1977b). The greatest selection pressure here will be exerted on a weak competitor when faced with a much stronger competitor. If the difference in the species' relative competitive abilities is large, directional selection will be strong and niche shift (displacement) may result in the weaker competitor, but there would be no reason to expect niche displacement in the stronger competitor. Significant competitive pressure for the stronger competitor comes primarily from individuals of its own species. From the standpoint of preventing competitive exclusion, the most important requisite is that the weaker competitor secure an exclusive niche space.

The central feature of this mechanism is that coexistence is permitted as long as competitive interaction is reduced or virtually eliminated and this is accomplished by selection for niche differentiation when competitors encounter one another resulting in each having an exclusive niche space. If competition is avoided, more efficient exploitation of the

environment results and two species will have a higher total yield in combination after selection than before selection. Evidence for this mechanism may be interpreted for some species pairs in the mixture diallel study (Fig. 11) and in the replacement series analysis for Holcus lanatus and Trifolium repens (Fig. 16). Selection operating in this manner will be limited by the species' potential to generate new genetic variants capable of pre-empting novel niches. This theme has become nearly axiomatic in recent ecological studies far too numerous to list (see for example Cody 1974, Grubb 1977, Diamond 1978, van den Bergh & Braakhekke 1978). Most evidence however is circumstantial; some have recently argued that in fact there is little empirical basis to support the commonly held view that coexistence in multi-species guilds is a result of niche divergence (Wiens 1977, Connell 1980).

C) Coexistence by selection for competitive combining ability (coevolution)

Genetic variation will be present in a population pertaining not only to particular types of fundamental niche requirements, but also pertaining to relative competitive ability for any common niche requirements. The same selectional force of competition will operate on both of these components of genetic variation. The exhaustive literature on plant genetics suggests that the number of genes controlling plant characters, is very large (Solbrig 1980). Indeed, a vast number of alleles will be present in a population which determine the various states of all the characters in Table 1 (Chapter 1) which govern

competitive ability. Possibilities are even further multiplied in considering that one genotype may for example have a greater uptake efficiency for one nutrient while a second genotype may have a greater uptake efficiency for a second nutrient; which will have the selective advantage will depend on the nature of the prevailing competitive pressures. The opportunities for natural selection to improve relative competitive ability in a plant population seem innumerable. Sakai (1961) has proposed that competitive ability in plants can be treated itself as a 'character' under at least partial genetic control.

Under this mechanism for coexistence, any genotype that is a superior competitor acts as a selective agent on its own competitors. The crucial point is that such selection pressure will operate reciprocally and sequentially in two competing populations so any 'superior' genotype ultimately loses its competitive advantage. 'Superiority' in competition therefore alternates between (and amongst) members of the two populations as various characters which confer competitive ability are generated, combined, recombined, selected for, selected against, and selected for once again. Local neighbourhoods are constantly engaged in a fine-tuning process that alters the way members respond to one another. A species population therefore need not avoid competition in order to avoid competitive exclusion; it may instead maintain the potential to generate (or acquire, through mutation, gene flow or recombination) and propagate new genetic variants with increased competitive power under the prevailing competitive pressures. In each such event of natural selection, once again the strongest selection

pressure will be exerted by the more powerful competitor on the weaker competitor. Competitive exclusion is avoided if natural selection favours those genetic variants in the weaker competitor that have an overall competitive ability at least comparable to that of the stronger competitor. If some form of beneficence also occurs between competitors, selection may concurrently favour those genetic variants in the stronger competitor that have an overall competitive ability more comparable to that of the weaker competitor (Chapter 6).

Coexistence under this mechanism is achieved by reciprocal natural selection operating sequentially within both species, each time to reduce the difference in relative competitive abilities which might otherwise lead to competitive exclusion of the weaker competitor (Fig. 21-C). Following convention, this mechanism may be termed, 'selection for competitive combining ability' (c.f. ecological (=niche) combining ability). Total yield in combination need not increase after selection for competitive combining ability. This is consistent with the results for 5 species combinations in the diallel analysis (Table 14) and in the combining ability of natural neighbouring genets of Trifolium repens and Lolium perenne compared to genet combinations of these two species from alien neighbourhoods discussed in Chapter 6 (Fig. 19).

It is important not to be mislead in the above discussion by the terms 'stronger' and 'weaker' competitor. 'Reciprocal selection' under this mechanism is not an 'arms race' in a perpetual 'fight' implying an increasingly costly enterprise as one might imagine in the context of aggressive interference in

animals. In contrast, it is possible that any one of several more subtle characterstics in plants (e.g. Table 1, Chapter 1) may afford an individual a competitive edge. Moreover, at different times, at different ages and under different types of competitive pressures, different charactersitics or suites of characteristics may be important in providing competitive 'staying power'. Selection is therefore not unidirectional but multidirectional and one need not think of a population 'running out' of genes or characteristics for competitive ability. Development of more balanced competitive abilities is seen in the replacement series analysis of Holcus lanatus and Lolium perenne from the different aged pastures (Fig. 16c, Chapter 5). Any measure of superiority acquired by one species affecting the fitness of a second species will in turn be tracked by genetic changes in the second species. The result is ongoing coevolution.

Competitive pressure will of course come from members of the same species as well as from different species and selection for competitive combining ability will operate both intra- and inter-specifically. In fact, intra-specific coexistence can be largely interpreted by this process. Selection for inter-specific competitive combining ability operating in two species in effect means that they coexist because they continue to behave competitively as essentially a 'single species' in which the average difference in competitive ability between individuals is comparatively small regardless of species. Under high density and resource limitation, such a collection of individuals would be expected to experience a process analagous

to 'self-thinning'. From the perspective of the 'individual' in the community there is no reason to differentiate between inter-specific and intra-specific competitive combining ability for species with broadly overlapping niches. The only matter of any consequence to the individual faced with competition with another individual is the difference in their relative competitive abilities regardless of species identity.

As pointed out earlier, selection for ecological combining ability implies an increase in total yield of a mixture. Measuring the total yield of a species mixture is analagous to measuring the yield of a heterozygote resulting from a cross between two homozygotes for assessing their 'genetic combining ability' (Harper 1964). However, in the product of a species mixture,in contrast with the product of a genetic cross, the two components which are being assessed for combining ability remain distinct and the contribution of each to the total yield can be measured separately. Competitive combining ability is a special type of combining ability which takes account of the variability which may occur in the relative contribution of the two components and is a reflection of their potential to contribute equally to the total yield. In selection for competitive combining ability, an increase in yield also occurs (as with ecological combining ability), but only in the inferior component.

Based on the above considerations, interpretations of the competitive relations between species from the experimental investigations reported in this thesis are summarized in Table 21.

TABLE 21. A summary of interpretations of competitive relations between species reported from the experimental investigations.

SPECIES PAIR	EXPERIMENTAL DESIGN USED FOR INVESTIGATING COMPETITIVE RELATION	CHAPTER IN THIS THESIS	INTERPRETATION OF THE TYPE OF COMBINING ABILITY RESULTING FROM SELECTION
DACTYLIS GLOMERATA / HOLCUS LANATUS	Diallel	4	Ecological
DACTYLIS GLOMERATA / LOLIUM PERENNE	Diallel	4	none (Competitive Exclusion)
DACTYLIS GLOMERATA / POA COMPRESSA	Diallel	4	Competitive
DACTYLIS GLOMERATA / TRIFOLIUM REPENS	Diallel	4	none (Competitive Exclusion)
HOLCUS LANATUS / LOLIUM PERENNE	Diallel	4	Competitive
	Replacement Series	5	Competitive
HOLCUS LANATUS / POA COMPRESSA	Diallel	4	Ecological & Competitive
HOLCUS LANATUS / TRIFOLIUM REPENS	Diallel	4	Ecological & Competitive
	Replacement Series	5	Ecological & Competitive
LOLIUM PERENNE / POA COMPRESSA	Diallel	4	Competitive
LOLIUM PERENNE / TRIFOLIUM REPENS	Diallel	4	Competitive
	Replacement Series	5	Competitive
	Reciprocal Transplanting	6	Competitive
POA COMPRESSA / TRIFOLIUM REPENS	Diallel	4	Competitive

OTHER MECHANISMS FOR COMPETITIVE BALANCE

The mechanism of selection for competitive combining ability implies a tenuous 'balance' between competitors for the same resources and that this balance is maintained by natural selection. Other mechanisms of coexistence also based on a 'balance' between competitors have been proposed and it is necessary to point out how they differ from selection for competitive combining ability.

1) Non-evolutionary mechanisms

As relative competitive ability is mediated by environmental conditions, temporal variation in the environment may allow coexistence by continually altering (e.g. seasonally) the prevailing relative competitive abilities of populations inhabiting it, where first one species, then another then the first again (etc.) has the competitive advantage (Hutchinson 1948, Gulmon 1979, Fowler 1982). 'Non-equilibrium coexistence' may result when factors such as disturbance, disease or predation serve to suppress superior competitors which would otherwise competitively exclude other species (Caswell 1978, Huston 1979, Pickett 1980). Coexistence may also be possible if relative competitive abilities vary with age so that each species has an advantage in different phases of the life cycle (Watt 1955, Grubb 1977, Fagerstrom & Agren 1979). In a multispecies system coexistence may be possible by a circular network of relative competitive abilities . Species A for example may be a superior competitor to species B while species

B in turn excludes species C which wins in competition with species A (Pianka 1979). These mechanisms may be important to some extent in the pasture system in the present study. Such explanations however are nonevolutionary; they are not concerned with the genetically dynamic and variable potential of relative competitive ability in populations or the role of natural selection in continually adjusting it in a process of ongoing coevolution. It is this factor which sets apart the mechanism of selection for competitive combining ability.

2) Frequency dependent selection

Models for frequency dependent balancing of competitors have also been considered as possible mechanisms of stable coexistence of competitors (e.g. Pimentel et al . 1965, Ayala 1966, 1970, 1971, 1972, Levin 1969, 1971, Leon 1974, Levin & Udovic 1977). Pimentel (1968) argues that the rarer of two competing species will be involved more often in interspecific encounters and the commoner in intraspecific encounters. Hence, the rarer species will experience stronger selection for improvement in interspecific competition and likewise the commoner species for improvement in intraspecific competition. This would theoretically lead by a process of genetic feedback to ecological stability. A genetic basis for such reversals in species dominance may exist when at least at one of the loci controlling competitive performance (in each species), one of the homozygotes has maximum interspecific competitive ability but minimum intraspecific fitness, and vice versa for the other homozygote (Ayala 1970).

There are important assumptions built into this frequency-dependent model that are not found in the mechanism of selection for competitive combining ability. In the former, two populations are purportedly maintained due to a dampening of wide oscillations of species dominance. The only evidence for such oscillations have come from laboratory populations of animals; in nature such oscillations have never been observed in sessile higher plants (Antonovics 1978). Moreover, as this mechanism makes no stipulation regarding the degree of niche overlap, it implies that selection for intraspecific competitive ability may be in opposition to selection for interspecific competitive ability in respect to the same contested resources. It implies that attributes which make an individual a good interspecific competitor are different from those attributes that make it a good intraspecific competitor and that their effects are in fact conflicting. To suggest that this is common in plants is unfounded. In a plant species which is a good intra -specific competitor but experiences high inter -specific density, selection in the population may indeed result in improved inter -specific competitive ability, but there is no apparent reason that it should necessarily also result in reduced intra -specific competitive ability. If an individual has a rapid uptake rate for nutrients which are in limited supply for example, this will confer a superior competitive ability over individuals with a slower uptake rate, regardless of species. Lawlor and Maynard Smith (1976) argue that such models are more directly applicable to cases in which competition is mediated by behavioural interference (as in many

animals) rather than merely relative exploitation of resources as is more common in plants. Selection for competitive ability here involves 'α-selection' discussed by Gill (1974) which "... refers explicitly to the acquisition of interference phenomena, mechanisms which prevent a competitor from gaining access to the resources ...". It is therefore especially difficult with plants to imagine an instance where Pimentel's genetic feedback mechanism for competitors should be important in nature with the possible exception of auto-toxicity by allelopathy (e.g. Webb et al . 1967). That such a mechanism should be important at all in nature is viewed unlikely by some (Levin 1971).

In stark contrast to the above perspective focussing on animals, frequency dependent competitive phenomena in plants is usually considered a consequence of the fact that two species escape some measure of competition with each other (i.e. they have niche differences) (Harper 1977b). (See Figure 12 and theory presented in Chapter 5). This is evident, for example, from frequency dependent behaviour in replacement series analysis, e.g. between Holcus lanatus and Trifolium repens (Fig. 16c, Chapter 5). It is important to understand how this differs from the frequency dependent competition discussed above. With niche differentiation, intraspecific competitive pressure is not the same as interspecific competitive pressure but this is because each species always suffers more from competitive interaction with an individual of the same species than with an individual of the other species. In this situation there are no forces which should produce oscillations in dominance and there is no reason to invoke an explanation

involving any genetic alterations of intra- versus inter-specific competitive ability. Competition is frequency dependent here because intraspecific competition is more intense than interspecific competition in both species (because of more niche overlap between intraspecific individuals). Competition is frequency dependent in Pimentel's genetic feedback model because intraspecific competition is of a different nature than interspecific competition (because behavioural interference effects are different between intraspecific individuals than between interspecific individuals).

In Pimentel's genetic feedback mechanism, the same selection that favours characters important in intraspecific competition, operates against characters important in interspecific competition, and vice versa. In selection for competitive combining ability, competitive ability is improved according to the prevailing competitive pressures, intra- or inter-specific, and no assumption is imposed that characters important in intra-specific competition need conflict with , or even be any different from, characters important in interspecific competition.

3) Different limiting factors

Another mechanism that has been proposed for the 'balance' of more than one similar species in close proximity occurs when the density of each species is limited by a different independent factor, or by the same factor at different times (Harper et al . 1961). Braakhekke (1980) reviews relevant recent literature. This idea was referred to earlier with

regard to such limiting factors as drought tolerance, pathogen or predator resistence, etc. Such factors may suppress otherwise superior competitors or keep population densities of all competitors low enough so that resources are not usually limiting and hence competition rarely ever occurs (Grime 1979). It is necessary however to draw attention to instances where resources are the differential limiting factors operating as is often purported to be the case under this mechanism. Grubb (1977) gives the following examples: "...on some soils nitrogen is the primary limiting mineral for grasses, but phosphorous and potassium limit the growth of legumes (Thurston 1969); on other soils phosphorus may be the primary limiting mineral for grasses and nitrogen for sedges (Willis 1963). Similarly the root growth of one species may be best in soil pores of a certain size and that of another species may be best in adjacent pores of a different size (Sheikh & Rutter 1969)". Tilman (1977) found in experiments with two species of freshwater algae that when both species were limited by phosphate, one species was competitively dominant over the other, whereas when both species were limited by silicate, the second species was competitively dominant. At intermedite levels of phosphate and silicate, each species was limited by a different resource and stable coexistence occurred.

It is apparent that this mechanism is at least partially interpreted in terms of niche differences. Clearly, if one species is limited much more by one factor than is another species then the niche space within which each species is capable of success, even in the absence of competitors, will be

different. For example, grasses may be limited by nitrogen in a community while legumes may not because the latter have symbiotic nitrogen fixing bacteria. Here, the legumes have a different source (or niche) for nitrogen.

In overlapping niche space however, where competition occurs for the same resource units, coexistence requires another explanation. The prevailing environment in a particular habitat will determine the degree of richness or limitation of particular resources for a particular species. If the population size of each of two species is limited by two different limiting resources in a given habitat, this is not in itself a sufficient condition for coexistence. Coexistence hinges on the condition of balanced competitive abilities. For example, each species might be a better competitor for one of the two resources (but not the same one) required by both species. In this sense the two species would have competitive combining ability. If one of the species is a better competitor for both resources, coexistence will not be possible in spite of the fact that the particular habitat features a different limiting resource for each species.

'Different limiting factors' for two species is interpreted by van den Bergh & Braakhekke (1978) as a form of 'functional' niche differentiation in the sense of Elton (1927). In the above example, this is taken to mean that each species has a different saturation level for both resources, i.e. it is capable of using different amounts of each resource (e.g. see extensive review by Andrew and Johansen 1978). This combined with the available supply dictates that one resource is limiting

for one species and the other resource is limiting for the other species. If however they are exploiting the same units of resource, any potential for coexistence must be measured against any differential capacity to reduce the availability of these resource units to the other, not simply the occurrence of different limiting factors. Coexistence here is not explained by any (e.g. functional) niche differentiation, but by balanced competitive abilities in the same niche. Furthermore, balanced overall competitive ability can also be maintained just as well by selection for competitive combining ability when both species are limited by the same resource; each species maintains a certain, but not invariable, suite of attributes (e.g. Table 1, Chapter 1) (perhaps different from the other) that permit it to reduce, to the same extent in each species, the availability of that resource to the other.

NICHE DIFFERENTIATION VERSUS COEVOLUTION OF COMPETITORS: ALTERNATIVE EVOLUTIONARY SOLUTIONS FOR SPECIES COEXISTENCE

Selection for competitive combining ability represents a mechanism by which competitors can be considered to co-evolve. Unlike the mechanism of niche differentiation where natural selection (operating largely on the weaker competitor) results in an escape from - or elimination of - the interaction between the species and thus allows coexistence, a process of coevolution must satisfy two criteria: a) The interaction is preserved by natural selection (and coexistence is therefore implied). This follows tradition in all classic contexts of coevolution, e.g. as in predator/prey, host/parasite, pollinator/host plant, etc.. b) The genetic constitution of both interacting populations must be adjusted in response to reciprocal selection pressure on each other (Janzen 1980). Leon (1974) and Levin & Udovic (1977) use coevolution in this context with reference to frequency-dependent models of competitive balance based on Pimentel's (1968) model of genetic feedback. Contrary to this context, others have regarded the coevolution of competitors as niche (or character) displacement (e.g. Lawlor & Maynard Smith 1976, Roughgarden 1976, Case 1979, Connell 1980).

According to Slobodkin (1961, p.122), "if two species persist in a particular region it can be taken as axiomatic that some ecological distinction must exist between them". The differences between species has become a universal touchstone for studies of species coexistence. Investigations repeatedly

and almost automatically entail a search for, or an interpretation involving, some 'important' difference in niche between coexisting competitors as though it were some how remarkable to have found that one entire population has not competitively excluded the other (e.g. as in the classic "paradox of the plankton" (Hutchinson 1961)). This is reflective of the inadequate typological view of the species in which ecologic ideology is embedded. Traditional thinking treats the species as more of a taxonomically distinctive unit than as a wide ranging collection of ecologically different individuals and there is much current interest by some to change this view (Antonovics 1976a, Raven 1976, Harper 1982). Although taxonomically distinct, two species with competitive combining ability represent a dynamic continuum of genetic variation in respect to their competitive relationship. The crucial contest in selection for competitive combining ability is not 'species pitted against species', but rather 'genotype against genotype', and any genotype may be confronted at different times with both inferior and superior genotypes from either taxonomic type. The present data showing reciprocal interactions between different natural genotype pairs of Lolium perenne and Trifolium repens (Figs. 18 and 19, Chapter 6) is the first demonstration of this phenomenon of 'genotype versus genotype' specialization. The relative competitive abilities of individuals for contested resources (regardless of species) appears to converge by selection into a common pool of alternative strategies defined by dynamic 'attribute complexes' which cannot be categorized on a taxonomic basis. To the taxonomist or biogeographer concerned

with community composition, the species is the relevant unit of diversity here. To the evolutionary ecologist however concerned with community processes and dynamics, the operational unit becomes the genotype and the population and community are welded into a single evolutionary arena (i.e. Fig. 9, Chapter 3).

The question of coexistence between competitors is certainly valid, but the insistence that some difference in niche or otherwise is the cause is not only *a priori*, but it contradicts the fact that their coexistence requires that they have features in *common* that render them both adapted to the same habitat (c.f. Harper 1982). In selection for competitive combining ability, the presence of (or the potential to continuously generate) relevant genetic variants with challenging relative competitive ability in each species permits a stable coexistence in a preserved interaction that is maintained by persistent reciprocal selection (coevolution). This process of competitors 'tracking each other' involving mutual shifts in gene frequencies, is not unlike that in theories for the evolution of coexistence in predator/prey (e.g. Pimentel 1961, Rosenzweig 1973), plant/herbivor or pollinator (Ehrlich & Raven 1964, Gilbert & Raven 1975), host/parasite (Pimentel *et al*. 1963), and model/mimic (Sheppard 1975) systems. Because a competitive interaction is preserved, any overlap in niche requirements may also be preserved; there is no need to assume any ambiguous conjecture that some difference in niche requirements between species (however subtle) must explain their coexistence. The 'paradox' of coincident species with little apparent niche differentiation need not be a paradox at

all. Moreover, selection for competitive combining ability provides reconciliation of the apparent paradox between "convergent adapatation" to a common environment and "divergent adaptation" to other members of the community. If selection for competitive combining ability were important in a community of plants, one might expect there to be fewer temporary significant deviations from random association of species with time, i.e. in older communities (step 3A in the model of Figure 9). This is substantiated by the present data from contact sampling (Table 12, Chapter 3).

It is commonly believed that, "...it is always advantageous for either party in a competitive interaction to avoid the other whenever possible" (Pianka 1976). Traditional theory assumes that niche divergence is to be expected between interspecific competitors whenever there is relevant genetic and environmental variation permitting them to do so. This seems intuitively reasonable in contexts of competition involving interspecific interference since it is possible for interference effects to be felt by interspecific competitors and not intraspecific competitors. It is also reasonable to expect that an inferior competitor, when faced with a highly superior competitor (of any type) would evolve a niche shift if 'another' niche is available and if the consequence is a reduced interaction. There are two important qualifications however to consider, especially with plants: 1) 'another' niche may not be as readily available as with animals, since resources for plants do not appear as readily partitionable; and 2) competition is often predominantly of the 'exploitation' type and, in contrast to interference

effects, exploitation effects will always be felt by both inter- and intra-specific competitors. The consequence of 1) is that, if competitive exclusion is threatening, selection may favour competitive combining ability instead of niche differentiation. The consequence of 2) is that if exploitation competitive abilities are very similar (either coincidentally or after selection), there is no reason that subsequent selection should unequivocally lead to niche divergence between the two populations, even if such opportunities for divergence were (or became) abundant. The reason for this follows from consideration of the selective forces operating on individuals in such instances. If niche divergence were to take place, both plant populations would still have to contend with intraspecific exploitation competition which in this case is no different in its effect on individual fitness than interspecific competition. Individuals of one species, say A which happen to 'find' a niche that is not exploited by species B would not be expected to leave any more descendents than those individuals of A exploiting the same niche as B. The consequence would be niche expansion for A, not divergence from B, and does not even necessarily require the presence of B. Any advantage for species A here then has nothing to do with avoidance of species B.

A question which presents itself from the above considerations is the following: How do intraspecific competitors coexist? The answer is almost trivial and it is precisely this fact that presents far-reaching implications. Intraspecific competitors coexist by and large because relative

competitive abilities are maintained roughly balanced amongst the members of the population through natural selection. The members of a population do not 'decide' to diverge from another population, and in contrast, maintain a 'balance' within their own. An individual will leave more descendents, if those descendents are better at ' avoiding competitive interaction' or are ' more successful in competitive interaction' regardless of the taxonomy of their potential contestants. The former mechanism however is restrictive as it is only relevant in explanations of the coexistence of different taxonomic units; an individual can rarely avoid competition with members of its own species in a resource limited environment. Selection for competitive combining ability however has broader application as it explains the coexistence of individuals , irrespective of taxonomy. Accordingly, if we suppose that two species have broadly overlapping niches and compete largely by 'exploitation' mechanisms, we should not expect strong selection for niche divergence if these species have competitive combining ability. Niche divergence affords little advantage because the two populations behave competitively as a 'single species' to begin with. Since, in both populations, overall inter- and intra-specific competitive abilities are virtually equivalent in their effects, niche divergence would do nothing to change the severity of competitive pressures on individuals in either population. One would no more expect divergence between two such populations in response to interspecific competition than one would expect divergence within either population in response to intraspecific competition.

Theoretical considerations using the substitutive replacement series model of competition (de Wit 1960, 1961, 1970 van den Berghe & Braakhekke 1978) have shown that a stable equilibrium of two species is possible only under frequency dependent regulation, usually thought to reflect niche differences. In contrast, there need be no difference between the overall hardships experienced from intra- or inter- specific competitors in coexisting species with competitive combining ability. It is a commonly held notion that in species with little niche differentiation and roughly balanced competitive abilities, the frequencies of the two populations will exhibit large unpredictable fluctuations in a stochastic environment, which strongly increases the risk of extinction of one of the two species (Berendse 1981b). A qualifying point however must be noted. Extinction from competition occurs when an inferior competitor is faced with a much superior competitor. Extinction due to competitive exclusion may occur if changes in the environment produces changes in the relative competitive abilities of the species, but not if the weaker competitor can respond by selection for competitive combining ability. Pigott (1982) discusses examples of competitive exclusion in vegetation in response to environmental changes, but most involve artificial treatments of fertilizer application and do not reflect all of the ways that species respond to their biotic environment against the variable background of stochastic events in nature.

A fully adequate understanding of species coexistence requires a greater emphasis on the variability within species

with respect to both fundamental niche requirements and relative competitive abilities, concurrent with an awareness of the differences between species. Selection for ecological combining ability and competitive combining ability are likely to operate in concert in nature and together describe the contribution of natural selection in the model for community evolution proposed in Chapter 3 (Fig. 9). Efforts are needed to reveal how and under what circumstances natural selection affects each of these two components and when it is likely to affect one more than the other. Whether selection for ecological combining ability (Fig. 21-B) or selection for competitive combining ability (Fig. 21-C) or both depicts the evolutionary route leading to coexistence of two species (or whether competitive exclusion is the outcome as per Gause's principle - Fig. 21-A) will depend on at least four factors:

1) The initial magnitude of difference (or extent of similarity) in both fundamental niche requirements and competitive ability upon first encounter . For example, if the niches of two species overlap extensively and one is a far superior competitor than the other, then it is reasonable to expect that competitive exclusion will be virtually immediate. Selection for competitive combining ability is unlikely in cases in which differences in competitive abilities are large.

2) The availability of (or potential to generate) different 'relevant' genetic variants pertaining to fundamental niche requirements versus relative competitive ability. Some species may have more genetic variation related to relative competitive ability than to fundamental niche requirements, and vice versa. This will be largely determined by the nature and magnitude of the available gene pool and the means of propagation in the two species (i.e. autogamy, allogamy, apomixis, clonal spread). Outcrossing species will generally have greater potential for generating adaptive genetic variants and tracking changes in the biotic environment than will incrossing or asexual species (Solbrig 1976, Glesener & Tilman 1978).

3) The range of resource space available in the prevailing environment for niche expansion or displacement . Novel niche space may be unavailable in a certain habitat or species may be constrained by a matrix of nearby potential competitors so that the option of "evolving-to-avoid-competition" is not feasible (Krebs 1979). Selection may instead favour competitive combining ability in such circumstances. This applies particularly to plants which, being mostly sessile, require a sufficiency of resources virtually in their immediate vicinity, resources which are not largely packaged in discrete partitionable units (Harper 1965, 1968), and the same resources that neighbours are also forced to make demands on.

4) The presence (or absence) of positive relationships occurring concomitantly with competition between two species . It is not difficult to imagine (but often overlooked) that individuals may compete in one sense and yet interact beneficially in another sense (e.g. Agnew & Haines 1960, Mather 1961, Harper 1964, Story 1967, Putwain & Harper 1970, Walker et al . 1972). A superior competitor may stand to 'loose out' in the long run if it eliminates a species which has something positive to offer. Commensalistic or mutualistic associations in which competitive abilities are roughly balanced may therefore be favoured (and maintained) by natural selection and stable coexistence may result. Moreover niche convergence may occur if beneficence is a strong enough selective force. This is relevant to the explanation of competitive interactions between Lolium perenne and Trifolium repens demonstrated in the present study (Fig. 16, Chapter 5; Chapter 6).

Cooperation within a single outbreeding population will be necessary for successful mating. For example, in dioecious species, or heterostylic species (e.g. primrose) the 'male' and 'female' (or 'pin' and 'thrum' in primrose) will compete with each other for resources. But in regards to reproduction they will require a cooperative relation in order to leave any descendents at all. Mather (1961) points out that in such instances selection will favour more equivalent competitive power and this may involve not only an improvement in competitive ability of the inferior form, but also a relative reduction in the aggressiveness of the superior form. This is selection for competitive combining ability and could occur not

only within a single species as above but also between two different species which interact in some other beneficial manner and yet also compete for resources (e.g. Chapter 6).

A plant species may exert a positive (enhancing) effect on another plant species in a number of possible ways. Furthermore, in a mutualism, the benefit gained by one species may not be the same kind of benefit gained by its associate. Possible beneficial interactions in plants include:

a) Providing materials in limited supply (e.g. a legume may provide nitrogen to a non-legume).

b) Providing physical protection from climate (Marshall 1967), predators (Harper & Sagar 1953), pests and diseases (Atsatt & O'Dowd 1976).

c) Providing physical support for growth (e.g. epiphytes) or against lodging (Trenbath 1976).

d) Providing special environmental conditions (e.g. shade or high humidity) favourable for germination and establishment (Harper 1964).

e) Encouragement of favourable rhizosphere components or discouragement of detrimental ones (Christie et al . 1974).

f) Liberation of stimulating chemicals (Roy 1960, Tukey 1970).

g) Dispersal with commercial seeds and protection from destruction by man by mimicing the crop plant (Wickler 1968).

CONCLUSIONS

Difference in niche requirements will certainly explain why some species are able to coexist. Much evidence, mostly from studies on animals (e.g. see Cody 1974, Schoener 1974, Diamond 1978), tend to "... support a derivative hypothesis of Darwinism that, in a population of a species, mechanisms which reduce competition between it and populations of other species tend to persist" (Gilbert et al . 1952, p. 310). To insist that this is some sort of law or axiom however is 'Gaussian' in origin and tradition and patently contradicts the enormous amount of species diversity found especially in many types of plant communities. Plants, in contrast to animals, have virtually nothing comparable to the 'food niche'. Plant ecologists are therefore largely unable to adopt most of the models and theories which are apparently adequate in explaining animal coexistence. In spite of this, some plant ecologists have attempted to account for plant species coexistence in nature largely on the basis of niche differentiation (e.g. Grubb 1977, van den Bergh & Braakhekke 1978, Newman 1982).

Coevolution by selection for competitive combining ability provides an evolutionary mechanism for coexistence which does not unequivocally require that every species occupy a different niche in a community, nor does it depend on frequency-dependent selection mediated by behavioural interference phenomena. It is a coevolutionary theory of competitive coexistence in which the consequence of reciprocal selection means that different species are persistently making demands for the same limiting resources.

Moreover, given sufficient genetic variation, there is good reason to suspect that opportunities for natural selection to improve the relative competitive ability in a population of inferior plant competitors (e.g. Table 1, Chapter 1) may be far more numerous than the opportunities for niche differentiation in vegetation. This idea has been overlooked (or dismissed) as a viable theory for species coexistence because the meaning and distinction of 'competitive ability' have been misrepresented and the role of natural selection in adjusting it has been underestimated á priori .

Slobodkin (1968) reasoned that if two species which appear to have the same ecology persist together in a uniform experimental environment, this finding does not disprove Gause's hypothesis; rather it proves that the organisms do not have the same ecology or that the environment was not uniform. This finding in fact does not even prove Slobodkin's claim; rather it suggests that the two species may exert relatively equal competitive pressures against each other and that this is maintained by reciprocal selection, i.e. they have competitive combining ability. Furthermore, even if two species have niches which do not completely overlap, the ability to coexist may be as much a consequence of selection for competitive combining ability in the region of niche overlap as it is a consequence of selection for ecological combining ability where competition can be avoided. 'Winning it/losing it' or 'avoiding it' do not completely describe the only alternatives for competitive outcome; evolution by natural selection may also proceed in such a way as to permit a 'continuation of the match'.

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