CHAPTER ONE

INTRODUCTION

Traditional pasture improvement on the Northern Tablelands of New South Wales (NSW) involves replacement of native species with high producing exotic grasses and clovers from Europe (McDonald 1968). The clover is the key to the animal productivity of these pastures, while the perennial grass component provides stability (Robinson and Lazenby 1976). Native grasses are important components of about 80% of grazed pastures on the Northern Tablelands of NSW despite several decades of attempts to replace them (Robinson and Archer 1988). These grasses are adapted to local environmental conditions, including periodic drought and inherent low soil fertility (Lodge and Whalley 1989), while exotic grasses tend to disappear during droughts and have a high fertiliser requirement for survival.

Warm season, frost susceptible perennial grasses are dominant in many pastures with a substantial component of native grasses and these pastures provide little green forage during winter and early spring (Cotsell 1956, Roe *et al.* 1959, Lodge and Roberts 1979). Several year-long green and cool-season perennial grasses including *Microlaena stipoides**, *Danthonia* spp. and *Poa sieberiana* have been identified as valuable components in fertilised pastures (Robinson and Archer 1988, Lodge and Whalley 1989). Year-long green perennial grasses remain green throughout winter provided soil water is available, although their major growth period is during summer (Lodge and Whalley 1989) and therefore, provide some forage during winter and early spring (Whalley *et al.* 1978, Taylor and Hedges 1984, Robinson and Archer 1988).

Knowledge of the ecology of individual native species (Lodge and Whalley 1989), population dynamics (Wilson 1984) and patterns and processes of coexistence among pasture species is vital in the management of these pastures. Such information on native Australian grasses is scarce and few management systems have been developed for native and natural pastures (Lodge and Whalley 1989).

Plant communities, including pastures, are assemblages of coexisting species that have become adapted to local abiotic and biotic environmental conditions. These pasture communities exhibit patterns in time and space caused by variations in the physical attributes

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* Botanical nomenclature throughout this thesis is according to Harden (1990, 1991, 1992 and 1993).

of the environment which interact with the species present and by interactions among neighbouring species. Wide genetic variation within populations enables some species to adjust to changing environmental conditions resulting in ecotypes that are finely adjusted to local microenvironments.

Species diversity and stable coexistence in pasture communities is maintained through several mechanisms, including life form differences, breeding differences, phenological differences, environmental fluctuations, adaptations to gradients in physical environmental attributes and competitive interactions among species (Harper *et al*. 1961, Grubb 1977, Aarssen 1983, Giller 1984, Tilman 1984, Hill 1990). Competition between neighbouring species has been regarded as the major force of natural selection in organising community structure and microevolution of plant species (Darwin 1859, Giller 1984, Benton 1987).

Microlaena stipoides is an important component of native, natural and improved pastures. It has become dominant in some improved pastures on parts of the Northern Tablelands following drought (Wyndham 1986). It grows well in association with introduced exotic pasture grasses including *Lolium perenne* and *Dactylis glomerata*, and naturalised grasses such as *Poa pratensis* in permanent pastures. The primary aim of this thesis was to determine patterns and processes of divergence in *M. stipoides* populations that allow coexistence with neighbouring naturalised and introduced perennial grasses.

CHAPTER TWO

REVIEW OF LITERATURE

2.1 *Microlaena stipoides*

2.1.1 Botanical nomenclature and description

The genus *Microlaena* comprises about 10 species and is native to Australia, New Zealand, Indonesia, Hawaii, Papua New Guinea and some Pacific Islands (Connor and Matthews 1977, Wheeler *et al.* 1990). *Microlaena stipoides* is one of the two species of *Microlaena* found in Australia, in which it occurs everywhere except the Northern Territory.

Microlaena stipoides is a slender, tufted perennial grass which grows to a height of 15-70 cm (Wheeler *et al.* 1990) depending on environmental conditions. It roots at the nodes and can produce new tillers through rhizomes, which can be contracted (Wheeler *et al.* 1990), or stolons (Whalley *et al.* 1978). *Microlaena stipoides* has a slender culm and can be identified easily in the field through its characteristic linear-lanceolate and flat leaf blades (Fig. 2.1). Leaf blades of different ecotypes can vary in smoothness, hairiness, length and width. The species has a ligule which is a short membranous rim fringed with hairs, and a leaf sheath with small hairy auricles or silky hairs at the orifice (Wheeler *et al.* 1990).

2.1.2 Floral biology of *Microlaena stipoides*

The inflorescence of *M. stipoides* is a narrow, delicate panicle or a raceme, about 7-17 cm long, which droops at flowering with branches and pedicels to one side (Connor and Matthews 1977, Wheeler *et al.* 1990) (Fig. 2.2). The spikelets are pedicellate, solitary, laterally compressed, narrow and 8-10 mm long. The glumes of *M. stipoides* are reduced to tiny scales and the rachilla disarticulates above the glumes. Spikelets are composed of three florets located above the glumes on a rachilla which may or may not be hairy. The lower two florets are sterile and reduced to lemmas (Clifford 1962) while the uppermost floret is fertile and without an awn. The sterile lemmas are rigid and rough along the keel (Wheeler *et al.* 1990), drawn out at their tips and inrolled to form long scabrid awns (Clifford 1962) while the fertile lemma is shortly mucronate (Clifford 1962). The palea is

Fig. 2.1. *Microlaena stipoides*, showing its characteristic linear-lanceolate and flat leaf blades (Photo by RDB Whalley).

Fig. 2.2. The inflorescence of *Microlaena stipoides* (Photo by Chris Jones).

narrow lanceolate and shorter than the lemma (Wheeler *et al.* 1990). The number of anthers per floret often varies from 2, 3, 4 or 6 (Clifford 1962).

Microlaena stipoides produces inflorescences during summer with three distinct types of spikelets, i.e. chasmogamous, cleistogamous (Clifford 1962) and clandestine spikelets at the nodes (Connor and Matthews 1977). Clifford (1962) found distinct differences between chasmogamous and cleistogamous spikelets in that the sterile lemmas of chasmogamous spikelets were longer than those from cleistogamous spikelets and the lodicules were 2-3 mm long in chasmogamous spikelets and were very small or absent in cleistogamous spikelets. The chasmogamous spikelets usually have four anthers and the cleistogamous two. Anthers and stigmas are exserted at anthesis in chasmogamous spikelets but not in cleistogamous spikelets. Anthers of chasmogamous spikelets are longer (2.5-4.5 mm) than those of cleistogamous spikelets (< 1.0 mm) at maturity. The length of the palea in chasmogamous spikelets varies from 4.5 to 14.5 mm while in cleistogamous spikelets, the palea is less than 5.5 mm or may be absent.

A third kind of spikelet produced by *M. stipoides* was noted by Connor and Matthews in 1977. Clandestine spikelets are non-emergent axillary spikelets produced in the leaf axil of the upper 3-5 nodes (Huxtable 1990) and are accompanied by swelling of the node (Connor and Matthews 1977). Huxtable (1990) found single and occasionally two clandestine spikelets at each node, and Connor and Matthews (1977) noted that the awns of clandestine spikelets are much shorter than those of cleistogamous spikelets. Clandestine spikelets are characterised by a reduction of the sterile lemma into long hairs or some scabrous teeth on the keels, of the number of callus hairs and of the length of the callus (Connor and Matthews 1977). Clandestine spikelets have a marked groove where the spikelet lies against the internode and are asymmetric. They also have two small stamens which may be entangled with the feathery stigma, while aerial cleistogamous spikelets have two, three or four stamens and chasmogamous spikelets have four (Connor and Matthews 1977, Huxtable 1990). There are greater paternal and ancillary costs in chasmogamous flowers while there is greater maternal expenditure in cleistogamous flowers compared with chasmogamous flowers (Schoen 1984). The caryopses of clandestine spikelets are larger than the caryopses of chasmogamous and cleistogamous spikelets (Connor and Matthews 1977). Development of all three types of spikelets can occur at the same time in an *M. stipoides* plant (Huxtable 1990).

Both self-fertilisation and cross fertilisation may occur in chasmogamous spikelets. On the other hand, only obligate self fertilisation can occur in both cleistogamous and clandestine spikelets wherein pollen grains germinate within the anther and the pollen tubes grow out through the anther wall and onto the stigma (Clifford 1962, Connor and Matthews

1977). Greater fertilisation success, larger fruits, more successful fruit set and higher seedling survival have been observed in cleistogamous seeds compared with chasmogamous seeds (Schoen 1984). Fertilisation and seed formation precedes inflorescence emergence in both cleistogamous spikelets and clandestine spikelets (Connor and Matthews 1977).

Seeds of chasmogamous and cleistogamous spikelets are dispersed when the single seeded spikelet disarticulates above the glumes. On the other hand, seed dispersal in a clandestine spikelet involves drying and falling off from the culm through a rupture in the leaf sheath (Connor and Matthews 1977). A delay in seed dispersal from clandestine spikelets compared with aerial chasmogamous and cleistogamous seeds may result in a supply of *M. stipoides* seeds over a longer time frame (Huxtable 1990) and the three progenies may experience different growing conditions (Schoen 1984).

2.1.3 Morphological variation in *Microlaena stipoides*

Whalley and Rose (1988) collected several populations of *M. stipoides* from a wide range of ecological sites on the Northern Tablelands of New South Wales, ranging from Walcha (latitude 30° 59' S) to Tenterfield (latitude 29° 03' S). They observed wide variation in the morphology of the different *M. stipoides* populations. Upright plants were observed along roadsides, while prostrate and leafy plants were observed under heavily grazed conditions. Plants growing in less fertile and granitic areas have shorter, more rigid and rough leaves, while plants growing in more fertile and basaltic areas have longer, soft and smooth leaves. Great variation in leaf width was also observed among the different populations. Plants growing in shaded lawns had narrower leaves, prostrate growth and a rhizomatous growth habit (Whalley and Rose 1988).

2.1.4 Importance, general occurrence and habitat requirements of *Microlaena stipoides*

Microlaena stipoides is one of the few Australian native grasses that provide forage during the critical winter-early spring period on the Northern Tablelands of NSW (Taylor and Hedges 1984; Robinson and Archer 1988), and is a year-long green perennial. It remains green during winter provided it is kept short by grazing or mowing and has an indeterminate growth pattern, with rapid growth and flowering whenever soil water is available from spring through autumn.

Lodge and Whalley (1989) reported that _M. stipoides_ is more common at higher elevations on the eastern parts of the Northern Tablelands. It has become dominant in pastures on some properties on the eastern parts of the Tablelands since the 1977-1982 drought and is valuable for maintaining stock in dry times (Wyndham 1986). The frequency of _M. stipoides_ increased with a decrease in soil pH to 4 (Munnich _et al._ 1991), indicating acid tolerance. It is more abundant in minimally cleared paddocks with natural pastures compared with areas which have been cultivated and sown to improved grasses and clovers (Munnich _et al._ 1991).

When grown with _Trifolium_ sp., the productivity of the resultant pasture approaches that of an improved pasture (Lodge and Whalley 1989, Munnich _et al._ 1991) as _M. stipoides_ is responsive to nitrogen and phosphorus fertilisation (Vieira 1980). The green leaves of _M. stipoides_ have high grazing value (Lodge and Whalley 1989), and the regrowth can have up to 4.6% nitrogen expressed as a percentage of organic matter (OM), high phosphorus concentration (0.38 to 0.59% OM) and high digestibility (Vieira 1980, Archer and Robinson 1988). The highest digestibility (63-79%) of the forage occurs during winter and spring and then declines in the late summer and autumn months (from 45 to 67%) (Vieira 1980, Archer and Robinson 1988). _Microlaena stipoides_ has been regarded as a weed by some graziers because of its high competitive ability, seeds with a pointy callus and high biomass production during summer (Wyndham 1986).

Microlaena stipoides is most frequently found in the more fertile areas of natural pastures such as sheep camps (Vieira 1980), in protected areas, particularly where there is some timber cover (Whalley _et al._ 1978), around tree stumps and under shade trees frequented by resting stock (Taylor and Hedges 1984) and along margins of sheep camps. It thrives under conditions of high stocking rate (Wyndham 1986) and fertiliser application (Vieira 1980, Lodge and Whalley 1989).

2.2 Patterns within plant communities

A community has been defined in a variety of ways: a dynamic combination of patches which differ in species composition, species abundance and population structure, varying with time and space (Picket and White 1985); an assemblage of species which are able to survive in a given habitat (Gleason 1926); a repeated occurrence of particular combinations of species (Thórhallsdóttir 1990a); a set of organisms that occur together and that significantly affect each other's distribution and abundance (Connell and Slatyer 1977); a montage of evolving neighbourhoods which converge on the organism as a pivotal unit of interaction (MacMahon _et al._ 1978); a real biological unit that has a definite structure

moulded by ecological integration and coevolution among the species (Benton 1987); or an assemblage of species which have existed over periods of geological time long enough for each species to adapt to some extent to the other members of the community through natural selection (Lawlor and Maynard Smith 1976).

Fig. 2.3. *Microlaena stipoides* growing under shade trees (Photo by Chris Jones).

The species which compose a community exhibit a pattern: a non-random arrangement and distribution within an area (Greig-Smith 1957, 1959). The pattern may be small scale due to the morphology of the individual plant, or large scale resulting from either competition between two or more individuals (sociological pattern) or from variations in topography, soil depth, soil nutrient status, water availability and other environmental factors (physiographic pattern) (Kershaw 1957, 1959, Greig-Smith 1961b, Austin 1968, Pemadasa *et al.* 1974).

2.2.1 Sociological pattern

A pattern caused by interactions among species shows that neighbouring species are important components of a plant's environment (Van Valen 1973) and can be the primary factor in determining community structure (Turkington and Harper 1979a, Thórhallsdóttir 1990a). Density-dependent interactions between species were clearly indicated as a causal factor in the sociological pattern observed in sand dunes (Pemadasa *et al.* 1974). Pemadasa

et al. (1974) observed negative correlations between *Aira praecox* with *Cerastium atrovirens* and *Erophila verna* with *Saxifraga tridactylites*. An increase in density of one species was accompanied by a decrease in density of the other species. Optimum growth of *Zerna erecta* was influenced by the level of competition with other grasses (Ellenberg 1963).

Thórhallsdóttir (1990b) studied the neighbour effects of six grassland species, namely *Lolium perenne, Agrostis capillaris, Holcus lanatus, Poa trivialis, Cynosurus cristatus* and *Trifolium repens* in hexagonal patches in a simulated sward. All the other physical sources of variation were eliminated, leaving the different neighbouring species as the only source of variation. All the species developed patterns similar to their spatial and temporal patterns noted in the field (Thórhallsdóttir 1990b). She concluded that species-specific interactions between plants generated and maintained the dynamic pattern of the different species.

Aarssen and Turkington (1985c) identified temporary species associations in younger communities and permanent associations in older pastures and attributed community changes in time to biotic interactions between neighbours. The detailed distribution of clover and grasses, including *Trifolium repens, Lolium perenne, Holcus lanatus, Cynosurus cristatus, Anthoxanthum odoratum, Festuca* spp., *Poa annua, Dactylis glomerata, Alopecurus pratensis* and *Agrostis tenuis* were largely influenced by the presence of hedges and trees (Turkington and Harper 1979a).

The placement and developmental stages of neighbouring associates and competitor species determines the growth rate and reproductive activity of individual plants (Turkington and Harper 1979b). Neighbouring species within a 2 cm radius of an individual plant accounted for 70% of the variation in the reproductive output of individual sand-dune annuals (Mack and Harper 1977).

2.2.2 Ecotypic variation

Physical attributes of the environment are of prime importance in regulating species diversity (Grubb 1977, Giller 1984), with the number of species increasing with environmental stability. Plant species may have broad ecological and geographical ranges, with each ecotype uniquely adapted to a local microenvironment (Baker 1974, Turkington and Aarssen 1984). Different populations of a single species experience the total effects of the environment and their accumulated effects over a long period (Bradshaw 1984). Thus, a plant population may consist of several ecological neighbourhoods (Jain 1984) adapted to different microenvironments (Bradshaw 1984).

Examples of ecotypic differentiation include heavy metal tolerance (Bradshaw and Mortimer 1986), light intensity requirements (Rossiter 1974, Boardman 1977, Bookman and Mack 1983, Pearcy 1983), local adaptation to microenvironments (Clay and Levin 1986), seed size variation in response to varying nutrient levels (Parrish and Bazzazz 1985, Elberse and Berendse 1993), adaptation to varying soil fertility levels (Fowler 1982, Bastow-Wilson 1989, Fulkerson *et al.* 1993) and soil pH levels (Snaydon 1962, Edmeades *et al.* 1991), variation in water requirements (Briggs and Shantz 1913, Thomas 1984, Guobin and Kemp 1992), adaptation to grazing and clipping (Baker and Hunt 1961, Mather *et al.* 1982, Wallace and Macko 1993), temperature requirements (Charles *et al.* 1991, Kemp and Guobin 1992), and association with soil microbial populations (Turkington *et al.* 1988, Chanway *et al.* 1989, 1990, Thompson *et al.* 1990).

2.2.3 Genotypic variation among populations

Genetic variation within populations is a prerequisite for adaptation and evolutionary change (Ennos 1983). Community-generated environmental factors are powerful influences generating changes in basic genetic processes and therefore evolution in the community (Bradshaw and Mortimer 1986). The ability of a population to adjust to changing environmental conditions is facilitated by its genetic diversity and phenotype plasticity (Cahn and Harper 1976a, b, Turkington 1989b). Genotypic variation in response to competition has been reported for several plant species (Turkington and Harper 1979b, Martin and Harding 1981, McNeilly 1981, 1984; Mather *et al.* 1982; Aarssen 1983, 1989, Aarssen and Turkington 1985a; Evans *et al.* 1985, 1989, Clay and Levin 1986, Merhoff and Turkington 1990). Genetic variation in response to physical environmental conditions including irradiance (Björkman and Holmgren 1963, Gauhl 1976, Bookman and Mack 1983, Kuiper and Smid 1985, Thompson and Harper 1988, Thompson *et al.* 1988, Skálová and Krahulec 1992) and water stress (Mack and Finn 1970, Wilson 1971, Walton 1974, Ludlow and Muchow 1990, Guobin and Kemp 1992) has been reported among populations of several plant species.

2.2.4 The methodology for determining genotypic variation

The use of electrophoresis to study variation at the protein and enzyme levels has led to the discovery of a large amount of genetic variation in large populations (Antonovics 1976). Protein and isozyme electrophoresis have been useful genetic markers in the estimation of genetic diversity and evaluation of population differentiation (Yang and Quiros

1993, Orozco-Castilo *et al.* 1994). The major limitation of these techniques, however, was the lack of sufficient polymorphism among closely related cultivars (Yang and Quiros 1993). Because proteins are products of gene expression, the resulting polymorphisms may vary in different tissues, developmental stages and environments (Beckman and Soller 1983), and hence were not stable. Isozyme analysis was found to be inappropriate and failed to generate polymorphisms in *Coffea arabica* which is known to have six enzyme systems (Orozco-Castillo *et al.* 1994).

2.2.4.1 Rapid amplification polymorphic DNA (RAPD)

The development of molecular biology in the last two decades has resulted in alternative DNA-based procedures for the detection of polymorphism (Welsh *et al.* 1991, Orozco-Castillo *et al.* 1994). DNA markers such as restriction fragment length polymorphism (RFLP) and randomly amplified polymorphic DNA (RAPD) provide a much higher degree of polymorphism and stability (Yang and Quiros 1993). The most widely used is RFLP, but it is time consuming, labour-intesive and costly (Orozco-Castillo *et al.* 1994). RAPD, on the other hand, is technically a simpler and faster method (Williams *et al.* 1990, Caetano-Anolles *et al.* 1991, Welsh *et al.* 1991). The technique involves using single oligonucleotides of arbitrary sequence for the polymerase chain reaction (PCR) amplification of genomic DNA (Williams *et al.* 1990, Halward *et al.* 1992, Kazan *et al.* 1993a). The amplification products, when separated in ethidium bromide-stained agarose gels, give banding patterns that can be used for assessment of genetic variation (Halward *et al.* 1992, Kazan *et al.* 1993a). RAPDs may be used to detect various levels of DNA variation that could result from single base changes to deletions and insertions (Williams *et al.* 1990).

Random amplified polymorphic DNA (RAPD) has recently been employed in studies of genetic relationships and variation within plant species, including *Stylosanthes giantesses* (Kazan *et al.* 1993a, b), *Arachis hypogea* (Halward *et al.* 1991, 1992), *Zea mays* (Welsh *et al.* 1991, Ragot and Hoisington 1993), *Fragaria vesca* (Scott *et al.* 1992), alfalfa (Yu and Pauls 1992), *Hordeum* sp. (Gonzáles and Ferrer 1993), *Juniperus* sp. (Adams *et al.* 1993), *Brassica napus* (Mailer *et al.* 1994), *Oryza sativa* (Shimada *et al.* 1993, Yu and Nguyen 1994), *Vaccinium* sp. (Rowland and Levi 1994), barley (Chalmers *et al.* 1993), *Buchloë dactyloides* (Huff *et al.* 1993), *Allium* sp. (Wilkie *et al.* 1993), *Coffea arabica* (Orozco-Castillo *et al.* 1994), *Brassica oleracea* (dos Santos *et al.* 1994), *Populus* sp. (Castiglione *et al.* 1993), chrysanthemum (Wolff *et al.* 1993) and *Apium graveolens* (Yang and Quiros 1993).

2.2.4.2 DNA-DNA hybridisation

Nucleic acid hybridisation has been widely used by molecular biologists in determining genetic relatedness among organisms (Bot *et al.* 1989, Ivanov and AbouHaidar 1992, Adnan *et al.* 1993). The technique allows comparison of large quantities of DNA sequences (Entingh 1970) regardless of their function in coding for a particular protein (Bot *et al.* 1989). DNA-DNA hybridisation of single-copy DNA sequences enables a comparison of base sequences to be made (Bendich and Mccarthy 1970a), and thus provides a sensitive and useful method of revealing the rate and pattern of genome evolution (Entingh 1970, Hunt *et al.* 1981, Britten 1986). This approach depends upon the accumulation of heritable changes in the sequential order of bases in the polynucleotide structure of the DNA (Bendich and McCarthy 1970a).

Measurement of the thermal stability of DNA hybrid strands from different species provides an estimate of evolutionary relatedness (Springer *et al.* 1992). DNA-DNA comparisons were conducted to analyse the phylogenetic relationships of *Gymnobelideus leadbeateri* (Edwards and Westerman 1992), eight bacterial strains of *Butyrivibrio fibrisolvens* (Hudman and Gregg 1989), *Drosophila* sp. (Entingh 1970, Hunt *et al.* 1981, Caccone *et al.* 1992, Powell *et al.* 1993), primates (Springer *et al.* 1992), wheat, barley, oats and rye (Bendich and McCarthy 1970a), bacterial strains of *Streptococcus* spp. (Adnan *et al.* 1993), *Atriplex* sp. (Belford and Thompson 1981a, b), *Spinacea oleracea* (Belford and Thompson 1981a, b), *Cladophora* sp. (Bot *et al.* 1989) and rodents (Brownell 1983).

2.3 Mechanisms supporting species diversity and coexistence

The species present in a plant community are a product of the interactions of physical environmental factors (Wallacian forces) and biotic processes (Darwinian forces) over evolutionary time (Giller 1984, Bradshaw and Mortimer 1986, Hill 1990). Diversity is a function of the total range of resources and the degree of specialisation of each species to occupy different parts of the niche or use a particular resource (niche diversification) (Lawlor and Maynard Smith 1976, Giller 1984). Species diversity is maintained through several possible mechanisms, including life form differences, phenological differences, differences in breeding behaviour of the species, environmental fluctuations, balance of inter- and intra-specific competition, edaphic factors and the production of toxic substances (Harper *et al.* 1961, Grubb 1977).

There are two opposing schools of thought on the environmental factors affecting natural selection and hence species diversity. The first refers to the Wallacian forces of natural selection which state that intraspecific or intrapopulation variation in plants has been largely influenced by abiotic factors of the environment including soil moisture, soil type, soil fertility, heavy metal contamination, temperature, irradiance, topography and other physico-chemical factors. The other school of thought refers to the Darwinian forces of natural selection which emphasise the importance of the local biotic components of the environment such as identity, age, size of neighbours and competitive interactions between neighbouring species or individuals in producing and maintaining plant population variation (Burdon 1980).

2.3.1 Wallacian forces

Plant species can coexist in a spatially heterogeneous environment if the species differ in their adaptations along gradients of quantitative variation in environmental factors such as light, water, soil nutrient level, elevation, slope, aspect and soil type, for example (Giller 1984, Tilman 1984, Wedin and Tilman 1993). Shmida and Ellner (1984) observed differences in demographic responses to environmental fluctuations and differences in species composition turnover between different habitat patches. Differences in site requirements for seedling establishment have been reported by Harper *et al.* (1961). The ability of a population to adjust to changing environmental conditions is facilitated by its genetic diversity and phenotypic plasticity (Turkington 1989b).

Indefinite and stable coexistence of species could result from stochastic environmental disturbance (Chesson 1986). Disturbance in the habitat has been found to be a major factor in the organisation of vascular plants in limestone pavements (Silvertown 1983). Variation in recruitment, juvenile mortality, reproductive rates and resource allocation for reproduction may be related to environmental conditions (Harper 1977, Fowler 1982, Chesson 1986). Species richness may also be enhanced by increased intervals between environmental disturbances resulting from increased time for species invasion of the disturbed area, and insufficient time for competitive exclusion to occur so that a wider range of species from all successional stages can be supported (Giller 1984).

Species richness can be enhanced by changes in weather and climate (Strong 1983) because the flowering and fruiting patterns of individual species respond in different ways to seasonal weather patterns (Giller 1984).

2.3.2 Darwinian forces

Species richness in a plant community can be maintained by several biotic mechanisms including differences in growth form and phenology (Grubb 1977, Giller 1984), differences in germination time or requirements for breaking dormancy (Harper *et al.* 1961), trade-offs between seed yield and seed survivorship (Ellner 1987), seed dispersal, arrival time and germination rate (Aarssen 1989), maternal inputs affecting seed size, seed quality, germination time and seedling growth rate (Cavers and Harper 1966), more successful establishment of seedlings in the vicinity of interspecific neighbours than intraspecific neighbours (Aarssen 1983), spatial contact (Schoener 1983), differences in susceptibility to parasites or predators (Harper *et al.* 1961, Harper 1969, Connell 1978, Grime 1979, Aarssen 1989), differences in regeneration requirements (Grubb 1977), production of toxic substances, balance of inter- and intra-specific competition and differences in competitive abilities within local neighbourhoods (Aarssen 1983, 1989).

Species diversity is more related to differences in regeneration requirements than partitioning of the habitat niche by the adult plants (Grubb 1977). Variation among species at all stages in the regeneration cycle, including flowering, pollination, seed set, seed dispersal in space and time, germination, seedling establishment and growth of the immature plants is potentially important in maintaining species richness in plant communities (Grubb 1977). Differences in growth form and regenerative strategies can also allow indefinite coexistence of plant species (Giller 1984).

2.4 Competition

Competition is a major force of natural selection (Darwin 1859), organising the structure of communities and the evolution of organisms in many communities (Connell 1983, Schoener 1983, Giller 1984, Murray 1986, Benton 1987) occurring over time spans ranging from hours to hundreds of millions of years (Van Valen 1980). Competition occurs when two or more individuals or populations of plants are dependent upon limited resources (Milne 1961) and growth, survival, fitness and population size are adversely affected (Giller 1984). Competition for limited resources has been the primary determinant of species packing and hence species diversity (Giller 1984).

Competition is important in ecological systems and Schoener (1983) found competition in 90% of 150 field experimental studies and 76% of the species involved. Underwood (1986), however, expressed doubts on the validity of applying the results of controlled competition experiments to the occurrence of competition in nature at natural

plant densities. The interactions can be direct through interference or indirect through exploitation, involving joint use of some limited resource (Giller 1984). Among terrestrial plants, consumptive competition is quite apparent (Schoener 1983) and patterns of local scale population differentiation are generated by competition (Turkington and Aarssen 1984). Supporting evidence for competition (Pianka 1981) includes change in number and change in resource use of individual plants (niche shift) which could either be morphological or evolutionary.

The local component of environmental variation is determined almost exclusively by biotic factors such as identity, age, size of neighbours and the degree to which they compete (Burdon 1980). Divergence from each other to avoid competition facilitates successful co-occurrence of closely related species in an area (Harper *et al*. 1961). Genotypic variation in response to competition has been reported for several plant species (Turkington and Harper 1979c, Martin and Harding 1981, McNeilly 1981, 1984, Mather *et al*. 1982, Aarssen and Turkington 1985a, Evans *et al*. 1985, Clay and Levin 1986, Aarssen 1989).

2.4.1 Theories on interspecific competition

Competition can occur among individuals of the same species (intraspecific) or among individuals of different species (interspecific) (Giller 1984). It is a widely accepted paradigm among ecologists that interspecific competition is the primary force in determining plant community structure and ecological diversity (Connell 1983, Schoener 1983, Giller 1984).

Both types of interaction have important effects on the community (Giller 1984). Intraspecific competition tends to increase niche width through an increase in the within-phenotype component of the niche (behavioural or physiological flexibility), or through an increase in the between-phenotype component (differences between individuals) (Giller 1984). One of the effects of intraspecifc competition is self-thinning resulting from competition for limiting nutrients, water and light, as the root systems and above ground parts increasingly overlap.

Interspecific competition results in competitive exclusion, niche shift, character displacement, changes in species composition and changes in niche size (Giller 1984). The consequences of interspecific competition are varied and include competitive exclusion (Gause 1934), character displacement (Arthur 1980), ecological diversification or niche separation (Schoener 1974, Diamond 1978), and evolution of competitive abilities (Aarssen 1983, 1985).

2.4.1.1 Gause's principle

Gause's competitive exclusion principle states that it is not possible for two species to coexist for more than a short period of time if they are competing for a homogeneously distributed, limiting resource (Gause 1934, Murray 1986). Competitive exclusion could result from intense above- and below-ground exploitation competition (Grime 1988) utilising a similar and limited resource at the same time and place (Giller 1984) and interference competition can prevent access to sufficient resources leading to exclusion of one or more competitors (Giller 1984). Coexistence of these competing species will occur if they undergo niche differentiation through natural selection (Schoener 1974, Diamond 1978, Aarssen 1985).

2.4.1.2 Character divergence

Character divergence is one possible outcome of competition (Lundberg and Stenseth 1985). Character displacement is a process by which changes in the morphological, behavioural or physiological character state of a species occurs in response to the presence of other ecologically similar species in the same environment through natural selection (Giller 1984).

Character divergence could lead to either character displacement, character convergence or character release (Arthur 1980). Character displacement is a selection for adaptations that result in sympatric species differing in their use of resources. Character convergence, on the other hand, is selection for increasing similarity in the characters of two species in sympatry, while character release is an increase in the variance of a character or characters, when a population moves into a relatively competitor-free environment.

2.4.1.3 Niche divergence

The persistence of competitors together in a community without competitive exclusion could result from selection leading to niche divergence (Schoener 1974, Grubb 1977, Diamond 1978, Aarssen 1983, Turkington and Aarssen 1984, Luescher and Jacquard 1991). Niche is defined as the total relationship of a plant with its physico-chemical and biotic environment (Grubb 1977) allowing a species to carry out its life history (James *et al.* 1984). Niche diversification is based on genetic differences within populations resulting from directional, stabilising or disruptive selection (Mather 1953, 1973). Genetic variation and differentiation within a population allows individuals to coexist in communities because

of differences in resource utilisation, i.e. niche divergence (Bradshaw and Mortimer 1986) which results from evolution through selection pressures produced by competition (Aarssen 1983).

The importance of niche diversification as an ecological interaction is that by diversity of resource utilisation, each interacting species in a mixture can succeed without having a negative effect on the others (Harper *et al.* 1961, Bradshaw and Mortimer 1986). Niche theory provides a mechanism by which competition can produce and maintain a pattern of resource partitioning among coexisting competing species (Roughgarden 1983). Niche variation may also permit greater phenotypic variation within a species population under conditions of relaxed interspecific competition where there is an increased variety of resources available for specialisation (Giller 1984).

Niches differ spatially and temporally (Hill 1990) and have four components. They are the: (i) habitat niche, which is the physico-chemical limits of the environment tolerated by a mature plant; (ii) life-form niche, which is an expression of size and annual productivity; (iii) phenological niche, which refers to the pattern of seasonal development; and (iv) the regeneration niche, which is an expression of the requirements for a high chance of success in the replacement of a mature individual by a new mature individual of the next generation (Grubb 1977).

2.4.1.4 *Competitive ability*

Competitive ability is a combined measure of the ability of an individual to reduce the availability of contested resources to another either through exploitation and interference competition, or the ability to tolerate reduction in contested resource availability produced by another individual (Arthur 1980, Aarssen 1983). Competitive ability or relative success in mixtures can be altered by evolution in natural conditions over a few generations (Bradshaw and Mortimer 1986).

Genetic variation occurs within a population both in terms of the type of niche requirements and the relative competitive ability for these niche requirements (Aarssen 1983). Relative competitive ability of a plant to avail itself of contested resources or to deny contested resources to neighbouring individuals may be a function of several attributes or attribute combinations (Aarssen 1989), including earlier germination time (Aarssen 1983), differential performance under cutting treatments (McNeilly 1981, 1984), age of the sward from which the grass population was collected (Merhoff and Turkington 1990), seed size (Wulff 1986, Goldberg and Fleetwood 1987), faster rate of seed germination (Weaver

1984), greater early growth with respect to height and leaf number (Weaver 1984), higher mean relative growth rate (Eissenstat and Caldwell 1987), adaptation to its local microenvironment (Clay and Levin 1986), higher flower production (Clay and Levin 1986), greater nutrient uptake efficiency by roots, lower shoot to root ratio and absence of thick roots (Bastow Wilson 1989), intervals between immigrations (Platt and Weis 1985), plant size or abundance (Goldberg 1987, Goldberg and Fleetwood 1987), plant weight, unit leaf rate and leaf area ratio (Roush and Radosevich 1985).

In nature, selections for ecological combining ability and competitive combining ability operate in harmony, facilitating reconciliation between convergent adaptation to a common habitat and divergent adaptation to other members of the community (Aarssen 1983). More balanced competitive abilities for contested resources are important evolutionary mechanisms of coexistence in plant communities through the forces of competition on natural selection (Aarssen and Turkington 1985a, Luescher and Jacquard 1991). It is possible that precisely-defined biotic specialisation in several neighbouring genotype pairs occurs in different localities of a single community, resulting in a more even distribution of yield in combinations of natural neighbours (Aarssen and Turkington 1985a).

In several competition experiments involving five populations of *Trifolium repens*, it was found that all five populations produced their highest yields when associated with their coexisting grass (Turkington and Harper 1979c, Evans *et al.* 1985, 1989, Aarssen and Turkington 1985a, Turkington 1989a), which shows that pasture populations of *T. repens* have diverged into a number of subpopulations based on the identity of the grass neighbour (Turkington and Harper 1979c, Evans and Turkington 1988, Turkington 1989a). This implies that natural neighbours have more balanced competitive abilities for contested resources than non-natural neighbours (Aarssen and Turkington 1985a).

2.4.2 Criticisms on competition as the sole organising force in plant community structure

The role of interspecific competition in establishing the structure of natural communities has been challenged mostly by animal ecologists in the 1970's and since then belligerent debate has flooded the literature (Jain 1984, Evans *et al.* 1985, Underwood 1986, Aarssen 1989). A number of ecologists have questioned the singular emphasis on competition in determining community structure and proposed alternative and complementary forces in the community, including environmental fluctuations (Schoener 1982), variation in weather and climate (Strong 1983), variation in food supply (Strong

1983), predation (Simberloff 1983), and chance (Harvey and Silvertown 1983), which may also be important in addition to interspecific competition in communities. Giller (1984) stated that experimental manipulations did not reveal the expected changes in niche size and patterns to demonstrate that past competition is important in establishing present day communities. There are many studies that demonstrate the importance of competition in many ecological systems as revealed by the syntheses of Connell (1983) and Schoener (1983), but evidence suggesting that competition has evolutionary consequences were weak (Connell 1983, Aarssen 1989). Underwood (1986) suggested experimental designs on competition studies which tested both intraspecific and interspecific competition in order to fully understand the importance of interspecific competition in determining community structure.

The heated debate centres on the Gaussian-based assumption that differentiation, which provides an opportunity to avoid some critical level of interaction (e.g. by making demands on different resource units), is the only evolutionary consequence of competition that permits species coexistence (Aarssen 1989). Other consequences include character divergence (Lawlor and Maynard Smith 1976, Arthur 1980, Harvey and Silvertown 1983, Lundberg and Stenseth 1985) and niche separation (Lawlor and Maynard Smith 1976, Arthur 1980, Pianka 1981, Giller 1984). Connell (1980) believes that evidence for such differentiation is not sufficient to prove the importance of competition as a selection pressure.

On the other hand, others believe that competition is an important force of natural selection (Roughgarden 1983, Turkington and Aarssen 1984). Similarity in niche requirements and of competitive abilities are two parameters that define the competitive relationship between two species (Aarssen 1985, Goldberg and Fleetwood 1987).

To date, much work has been done on the role of competition in the distribution and abundance of *Trifolium repens,* the *Drosophila* of plant ecology. Evidence shows that natural selection, in the context of competition, resulted in the adaptation of *T. repens* to site effects (Turkington and Harper 1979a, Merhoff and Turkington 1990), interspecific competitors (Turkington and Harper 1979a, c, Martin and Harding 1981, Turkington and Aarssen 1984, Aarssen and Turkington 1985a, b, Evans *et al.* 1985, 1989, Evans and Turkington 1988, Turkington 1989a, Merhoff and Turkington 1990) and to soil microorganisms (Turkington *et al.* 1988, Chanway *et al.* 1989, 1990, Thompson *et al.* 1990). The results seem to support both niche differentiation and more balanced competitive ability theories (Luescher and Jacquard 1991).

2.5 Conclusion

The species which comprise a community exhibit patterns resulting from relationships between the physical environmental factors and biotic processes. Sociological patterns arise from biotic interactions between neighbouring species, while ecotypic patterns result from adaptations of species to variations in the physical components of the environment. Genetic variation within populations is vital to the adaptation and microevolution of these populations. Selection forces generated by species-interactions greatly influence divergence in population performance and competitive ability. Competition experiments conducted to date have produced much evidence on the primary importance of competition as an evolutionary force in natural selection and hence, species diversity and community patterns.

2.6 Aims and objectives

The hypothesis to be tested in this thesis is that competition is the driving force in the divergence of *M. stipoides* populations. The specific aims include: to determine the distribution and abundance of *M. stipoides* on the Northern Tablelands of NSW in relation to variations in environmental and pasture management correlates; to investigate small scale spatio-temporal distribution and association of *M. stipoides* with other grasses in a small paddock of permanent pasture; to assess ecotypic and genotypic differences among *M. stipoides* populations; to test if competition is the driving force in the divergence of *M. stipoides* populations; and to determine if divergence among *M. stipoides* populations allows coexistence with neighbouring perennial grass species.

CHAPTER THREE

DISTRIBUTION AND ABUNDANCE OF
Microlaena stipoides ON THE NORTHERN TABLELANDS
OF NEW SOUTH WALES

3.1   INTRODUCTION

The distribution pattern of pasture species depends upon climatic (Kemp and Dowling 1991), edaphic and management factors (Harper 1977), as well as biotic interactions among species (Turkington and Harper 1979a, Kemp and Dowling 1991). Kemp and Dowling (1991) found that distribution patterns of annual and perennial herbaceous species in improved pastures in central New South Wales varied with rainfall and altitude.

Wide variations in edaphic factors may occur over very short distances and micro-distribution of plant species may be related to these small-scale variations. Raupach (1951) found large variations in soil pH and in contents of exchangeable cations Ca^{2+}, Mg^{2+}, K^+ and Na^+ and of clay and organic matter in Australian soils. Downes and Beckwith (1951) reported that differences as great as 1 pH unit occurred over a distance of 1 ft and observed that the distribution of several annual species in the area was apparently determined by soil pH. The microtopographical control of species distribution may be determined by the interaction of several environmental factors which could be related to variations in soil level. It is likely that drainage, moisture regime, leaching, nutrient regime, pH, and microclimate could well be related to variations in the soil level (Pemadasa *et al.* 1974).

Native grasses are more inclined to occur on the tablelands of New South Wales than the slopes and on lower fertility soils (Kemp and Dowling 1991). *Microlaena stipoides*, a native year-long green perennial appears to be more common at higher elevations in the eastern parts of the Northern Tablelands (Lodge and Whalley 1989). If *M. stipoides* is present in a paddock, then it almost invariably occurs under trees, or if there are no trees in the paddock, on the margins of sheep camps (Whalley *et al.* 1978, Taylor and Hedges 1984). It was observed to invade pastures on some properties on the Northern Tablelands following the 1979-82 drought. However, most of these data are anecdotal and fragmentary with respect to the Northern Tablelands.

Results of a survey on the Southern Tablelands of New South Wales indicated that the abundance of *M. stipoides* was strongly influenced by management and soil factors (Munnich *et al.* 1991). *Microlaena stipoides* was highly correlated with the type of pasture sown, soil pH and clearing history. Frequency of *M. stipoides* was greater in pastures sown with *Lolium rigidum* than in pastures sown with either *Phalaris aquatica* or *Dactylis glomerata*. Percentage frequency of *M. stipoides* increased with a decrease in soil pH down to 4.0, and greater frequency was observed in minimally cleared paddocks (Munnich *et al.* 1991).

The aim of this study was to determine the distribution and abundance of *M. stipoides* on the Northern Tablelands of NSW in relation to environmental and pasture management correlates.

3.2 METHODS

3.2.1 Selection of survey sites

Thirty-three properties were selected throughout the Northern Tablelands of NSW so that they were distributed within fifteen zones, five latitudinal 0° 29' wide and three longitudinal zones, 0° 30' wide, which were distributed on the three major types of parent material, viz. basaltic, granitic and sedimentary rocks.

3.2.2 Survey methods

In each property, at least three paddocks with different degrees of management intensity were surveyed giving a total of 101 paddocks. Rainfall data were obtained from the nearest meteorological station for each property. Annual total rainfall (mm) was categorised into 7 classes as: (1) 601-700, (2) 701-800, (3) 801-900, (4) 901-1000, (5) 1001-1100, (6) 1101-1200, (7) 1200+.

Abundance of *M. stipoides* was estimated visually according to five abundance classes, chosen because of the way *M. stipoides*, if present, will occur under trees and/or on the margins of sheep camps:

(1) No *M. stipoides*;

(2) *M. stipoides* scattered under trees and/or on sheep camp margins. Only very scattered *M. stipoides* in open areas;

(3)   Dense *M. stipoides* under trees and/or on sheep camp margins. Scattered plants in open areas;

(4)   Dense *M. stipoides* under trees and/or on sheep camp margins. Scattered dense patches in open areas;

(5)   Dense *M. stipoides* under trees and/or on sheep camp margins. Dense in open areas.

The following information was collected on each paddock and classified into the following groups:

Tree density:

(1)   no trees;

(2)   projected tree canopy cover less than 30%;

(3)   projected tree canopy cover 30% or greater.

Pasture improvement:

The classification of pastures was similar to that proposed by Southwood (1972):

(1)   native pasture - consisting mainly of native species;

(2)   natural pasture - native pasture containing some exotic,naturalised pasture species or a reverted improved pasture consisting principally of native and/or naturalised pasture species;

(3)   improved pasture - containing mainly sown species and some other species.

Period since last cultivation:

(1)   1-5 yr;

(2)   6-20 yr;

(3)   never cultivated.

Degree of cultivation:

(1)   regular cropping;

(2)   intermittent cropping;

(3)   cultivation for pasture establishment;

(4)   never cultivated.

Length of spell period if not set stocked:

(1)   none;

(2)   1 month;

(3)   2-3 months.

Stock:

   (1)   sheep;

   (2)   cattle;

   (3)   sheep + cattle.

Grazing method:

   (1)   set stocked;

   (2)   rotation;

   (3)   opportunistic.

Pasture species sown:

   (1)   legume;

   (2)   perennial grass + legume;

   (3)   annual grass + legume;

   (4)   crop;

   (5)   none.

Total amount of superphosphate (kg/ha) applied over the years:

   (1)   1-1000;

   (2)   1001-3000;

   (3)   3000+.

Lime application:

   (1)   yes;

   (2)   no.

Soil pH

Surface soil samples (0-10 cm) collected from each paddock were air-dried and sieved to pass through a 2.8 mm sieve. Ten grams of each soil sample were weighed and placed in a plastic vial, then 10 ml of distilled water was added and shaken for one hour. After shaking, the soil particles were allowed to settle for ten minutes and soil pH was read using a glass electrode (672 digital pH/mV/temp meter, Jenco, Taiwan) standardised against buffer solutions at pH 4.0 and 7.0.

All other grasses and graminoids found in the paddock were collected and identified (see Appendix 3.2).

3.2.3 Data analysis

Prior to analysis, data were examined through various SYSTAT programs for accuracy of data entry, missing values, outliers, fit between their distribution and the assumptions of multivariate analysis.

The dependence between abundance of *M. stipoides* and each of the environmental and management correlates was assessed with χ^2 tests using BMDP4F two-way frequency tables for measures of association. Univariate regressions were executed, using simple linear regression between abundance of *M. stipoides* (dependent variable) and each of the other independent variables except for pH and altitude when exponential regression, for rainfall, polynomial regression, and for degree of cultivation, logarithmic regression showed the best fit. Standard multiple and stepwise multiple regressions were done between *M. stipoides* and all the other independent variables. Bivariate correlations among all the independent variables were determined using SYSTAT Listwise Pearson correlation analysis. Cluster analysis using SYSTAT-join (Pearson distance) was done to group all the variables and BMDP K-means clustering to classify paddocks based on grass species composition. Category levels for altitude, rainfall and total superphosphate applied were used only in the χ^2 tests, while actual integer data were used in the correlation, regression and cluster analyses.

3.3 RESULTS

3.3.1 Distribution and abundance of *Microlaena stipoides* on the Northern Tablelands of NSW in relation to environmental correlates

The distribution and abundance of *M. stipoides* on the Northern Tablelands (NT) was highly dependent on location (Table 3.1). More *M. stipoides* was observed in the eastern side of the Tablelands which had higher elevation than on the western side as well as more in the southern half than in the northern part (Fig. 3.1). Dense *M. stipoides* was observed in 19 of the 78 paddocks having an elevation greater than 800 m above sea level. There was a highly significant association ($\chi^2 = 59.5$, P < 0.001) between *M. stipoides* and altitude (Table 3.1). A positive exponential relationship between *M. stipoides* and altitude is shown in the results of regression analysis (Fig. 3.2).
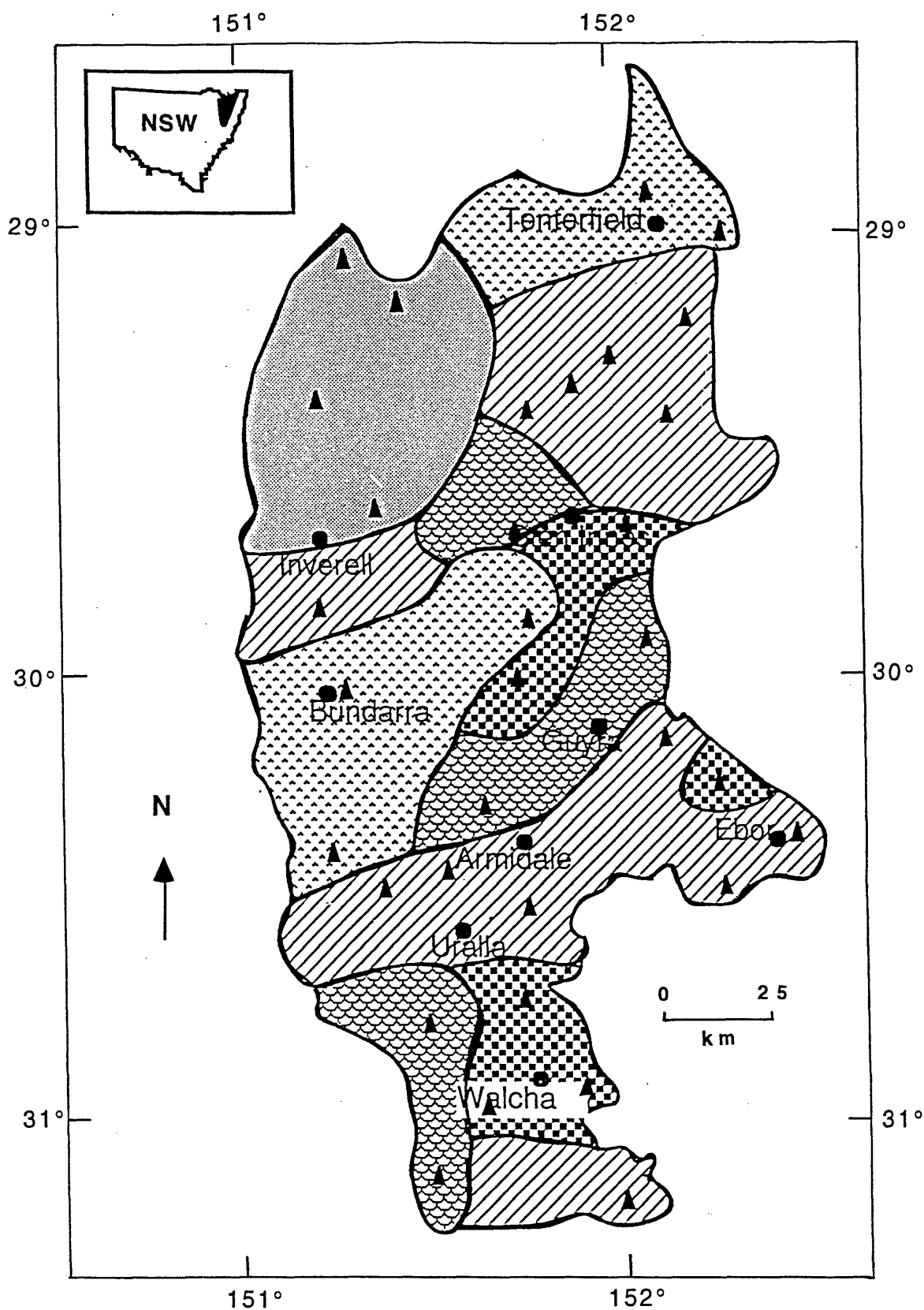
Fig. 3.1. Map showing the mean distribution and abundance of *Microlaena stipoides* in the paddocks surveyed in different parts of the Northern Tablelands. Locations of the properties on which these paddocks occurred are shown by ▲. Abundance classes: ▦ no *Microlaena*; ▨ *Microlaena* scattered under trees and/or sheep camp margins;

▨ dense *Microlaena* under trees and/or sheep camp margins and a few scattered patches in the open; ▨ dense *Microlaena* under trees and/or sheep camp margins and scattered dense patches in the open; ▣ dense *Microlaena* patches all over the paddock.

Table 3.1. Pearson χ^2 values for the test of independence between abundance of *M. stipoides* and the different paddock characteristics.

Paddock characteristics	χ^2 values
latitude	23.2 **
longitude	20.5 **
altitude	59.5 ***
parent material	14.4 NS
rainfall	47.3 **
tree density	21.6 **
pasture improvement	30.4 **
period since last cultivation	19.4 *
degree of cultivation	24.6 *
stock type	17.2 NS
grazing method	9.5 NS
spell period	18.2 *
species sown	14.7 NS
total superphosphate applied	7.2 NS
lime application	8.2 NS
soil pH	28.5 ***

```
***   P < 0.001
**    0.001 < P < 0.01
*     0.01 < P < 0.05
NS    not significant
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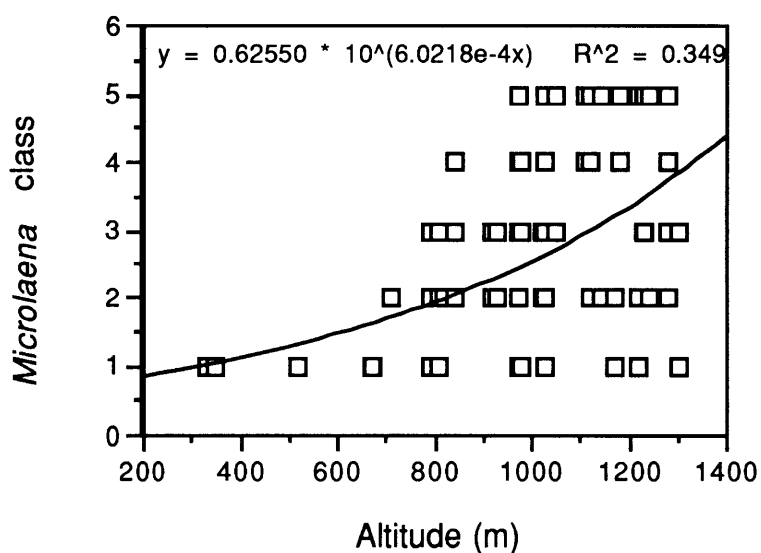

Fig. 3.2. Regression between altitude and abundance classes of *M. stipoides*.

Total annual rainfall was positively associated with *M. stipoides* abundance (Table 3.1). *Microlaena stipoides* was abundant in paddocks with mean annual rainfall greater than 750 mm. Results of cluster analysis using Pearson distance show that *M. stipoides* is grouped closely with altitude, rainfall, longitude, degree of cultivation and period since last cultivation (Fig. 3.3).
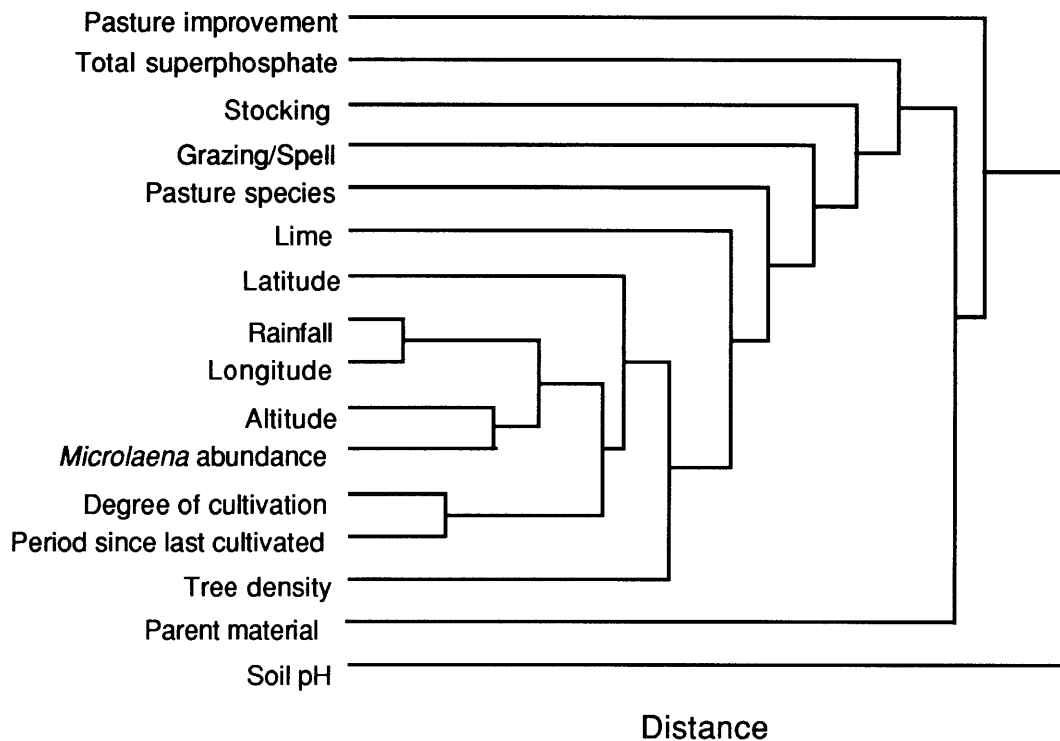
Fig. 3.3. Dendrogram showing the groupings of all paddock characteristics.

Soil pH had a highly significant association with abundance of *M. stipoides* (χ^2 = 28.5, P < 0.001) (Table 3.1). Paddocks with more acid soil (pH 4-5) had dense *M. stipoides* and the density of *M. stipoides* decreased with a decrease in soil acidity. When the *M. stipoides* score of each of the paddocks was plotted against soil pH, the negative exponential relationship between abundance and soil pH was clear (Fig. 3.4).

Results of tests for linearity showed that there were linear relationships between *M. stipoides* and all the other variables except soil pH, altitude, degree of cultivation and rainfall. Squared correlation values resulting from univariate regression analyses between *M. stipoides* (dependent variable) and all the other variables show the unique relationship of the independent variables with *M. stipoides* (Table 3.2, left-hand column). Soil pH, altitude and degree of cultivation have higher R^2 values. The squared multiple correlation resulting from standard multiple regression between *M. stipoides* and all the variables was 0.575 and the semipartial correlation (sr^2) values for each independent variable shows that deletion of
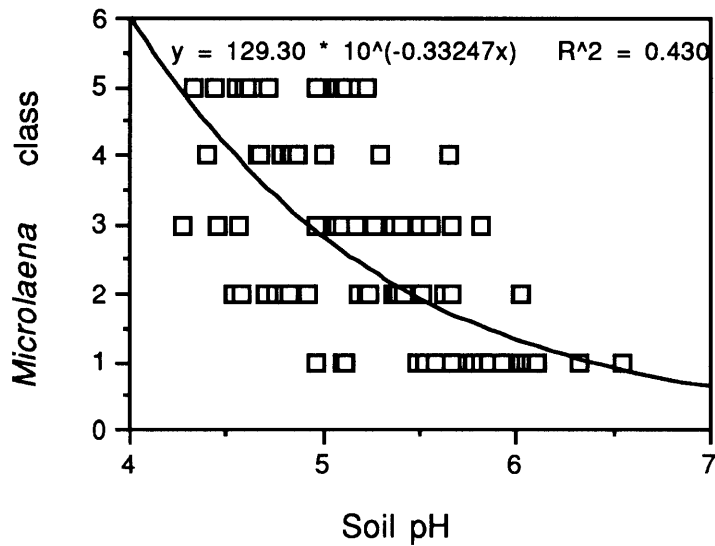
Fig. 3.4. Regression between soil pH level and the abundance classes of *M. stipoides*.

Table 3.2. Squared correlation and semipartial correlation values of all paddock characteristics on abundance of *M. stipoides*.

Paddock characteristic	Bivariate regression R^2	Standard multiple regression sr^2
latitude	0.118	0.000293
longitude	0.049	0.006901
altitude	0.349	0.024343
parent material	0.008	0.033207
rainfall	0.033	0.013044
tree density	0.042	0.004100
pasture improvement	0.027	0.000545
period since last cultivation	0.085	0.028995
degree of cultivation	0.200	0.001891
stock	0.004	0.004901
grazing	0.000	0.010919
spell period	0.013	0.008892
species sown	0.002	0.001395
total superphosphate	0.033	0.007620
lime	0.008	0.000036
soil pH	0.430	0.066960
		$R^2 = 0.575$
		Adjusted $R^2 = 0.474$

soil pH from the regression equation would result in greatest reduction (0.06696) in the multiple R^2 (Table 3.2, right-hand column). Likewise, deletion of parent material and period since last cultivation would cause a great reduction (Table 3.2). When a stepwise multiple regression was performed, the subset model included soil pH, altitude, parent material and period since last cultivation as predictors of the abundance of *M. stipoides*.

M. stipoides abundance = 4.378 - 1.039 soil pH + 0.002 altitude + 0.395 parent material + 0.417 period since last cultivated

$$R^2 = 0.536$$
$$\text{Adjusted } R^2 = 0.513$$

Listwise Pearson correlation results showed that high correlations exist among some of the independent variables. Altitude had high correlations with latitude, longitude, rainfall and soil pH. Period since last cultivation had high correlations with degree of cultivation and pasture improvement.

All abundance classes of *M. stipoides* were found on soils derived from basalt, granite or sedimentary parent material and the χ^2 (14.4) value was not significant (Table 3.1).

3.3.2 Distribution and abundance of *M. stipoides* on the Northern Tablelands of NSW in relation to pasture management correlates

Pasture management factors that had highly significant associations with abundance of *M. stipoides* were tree density and pasture improvement (Table 3.1). A higher proportion of paddocks with no trees had no *M. stipoides* compared with paddocks with 30% projected canopy cover (Fig. 3.5).

Pasture improvement had a significantly negative association with abundance of *M. stipoides*. About 35% of the native and natural pastures surveyed had dense *M. stipoides* all over the paddock, 52% had *M. stipoides* in the shady areas in the paddock and only 13% of these pastures had no *M. stipoides*. On the other hand, only 23% of the improved pastures surveyed had dense *M. stipoides* all over the paddock, 41% had dense *M. stipoides* in shady and open areas and 35% of these pastures had no *M. stipoides*.

Soil disturbance had a significant negative association with abundance of *M. stipoides*. Paddocks that had been cultivated in the last five years had the highest percentage (47%)

with no *M. stipoides*, while paddocks that had not been cultivated for 20 years or more had the lowest percentage (11%) with no *M. stipoides*. On the other hand, 26% of paddocks that had not been cultivated for a long time (20 years or more) had dense *M. stipoides* compared with 5% in those cultivated in the past five years (Fig. 3.6). Frequent cultivation (regular and intermittent) of the paddock was associated with absence or very low abundance of *M. stipoides*. Minimal cultivation and no cultivation were associated with abundant *M. stipoides* both in the shady and open areas of the paddock.
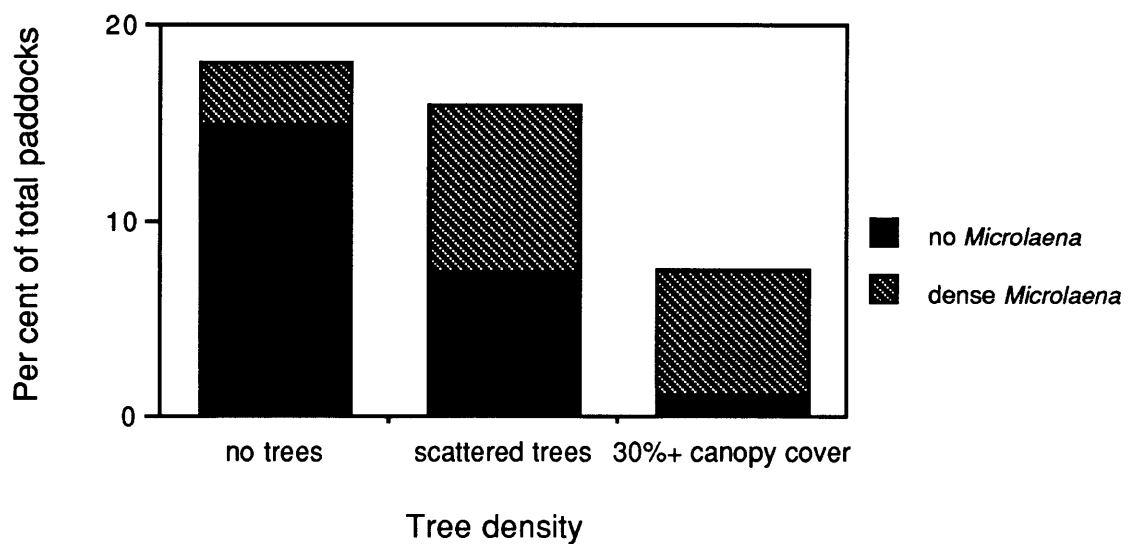
Fig. 3.5. Relationship between tree density and abundance of *M. stipoides*.

There was an association between the length of spelling from grazing and abundance of *M. stipoides* (Table 3.1). Spell periods of two to three months were associated with less, while no spell period was associated with more *M. stipoides*.

Abundance of *M. stipoides* was not associated with type of livestock, grazing method (apart from the spell period), total amount of phosphate applied over the years or lime application (Table 3.1).

3.3.3 Species cluster analysis

A total of one hundred species of grasses was identified from the survey sites.
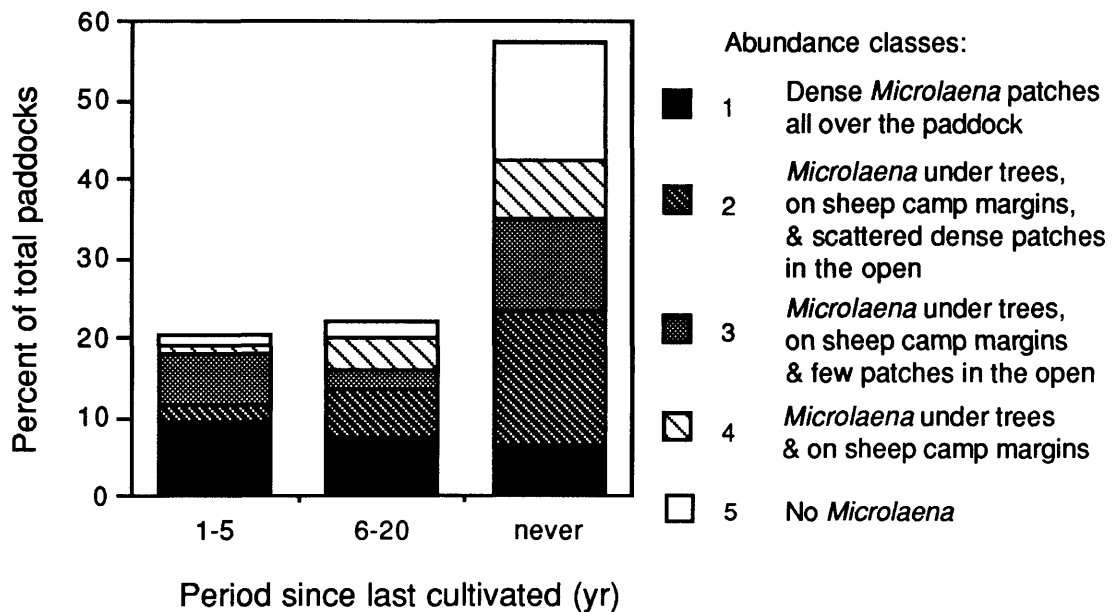
Fig. 3.6. Relationship between period since last cultivated and abundance of *M. stipoides*.

Presence (1) or absence (0) of the species was recorded in each paddock and the paddocks were grouped into 5 clusters based on species composition (Table 3.3). Only species having a frequency of 0.20 and above in at least one of the five clusters were included in the table.

Cluster 1 included eight properties in the northernmost part of the Northern Tablelands, i.e., the Tenterfield and Bonshaw areas (Fig. 3.7). It was composed mainly of warm season perennials and *Sporobolus creber* was present in almost all paddocks (.96) (Table 3.3). A few year-long green perennials were recorded, including *M. stipoides*, *Dichelachne rara* (.25), *Danthonia pilosa* (.21), *Poa pratensis* (.21) and *Stipa verticillata* (.21). The average rating of *M. stipoides* (2.16) in this cluster was the lowest of the five clusters.

Cluster 2 was composed of eight properties in the Inverell, Glen Innes and Aberfoyle areas (Fig. 3.7). Apart from the warm season perennials and annuals (Table 3.3), this cluster was also characterised by the presence of exotic year-long green perennials including *Phalaris aquatica* (.36), *Festuca elatior* (.23) and *Lolium perenne* (.23).

Cluster 3 included properties in the Bundarra, Guyra and Ebor areas (Fig. 3.7). This cluster was composed of a mixture of warm season perennials, year-long green perennials,
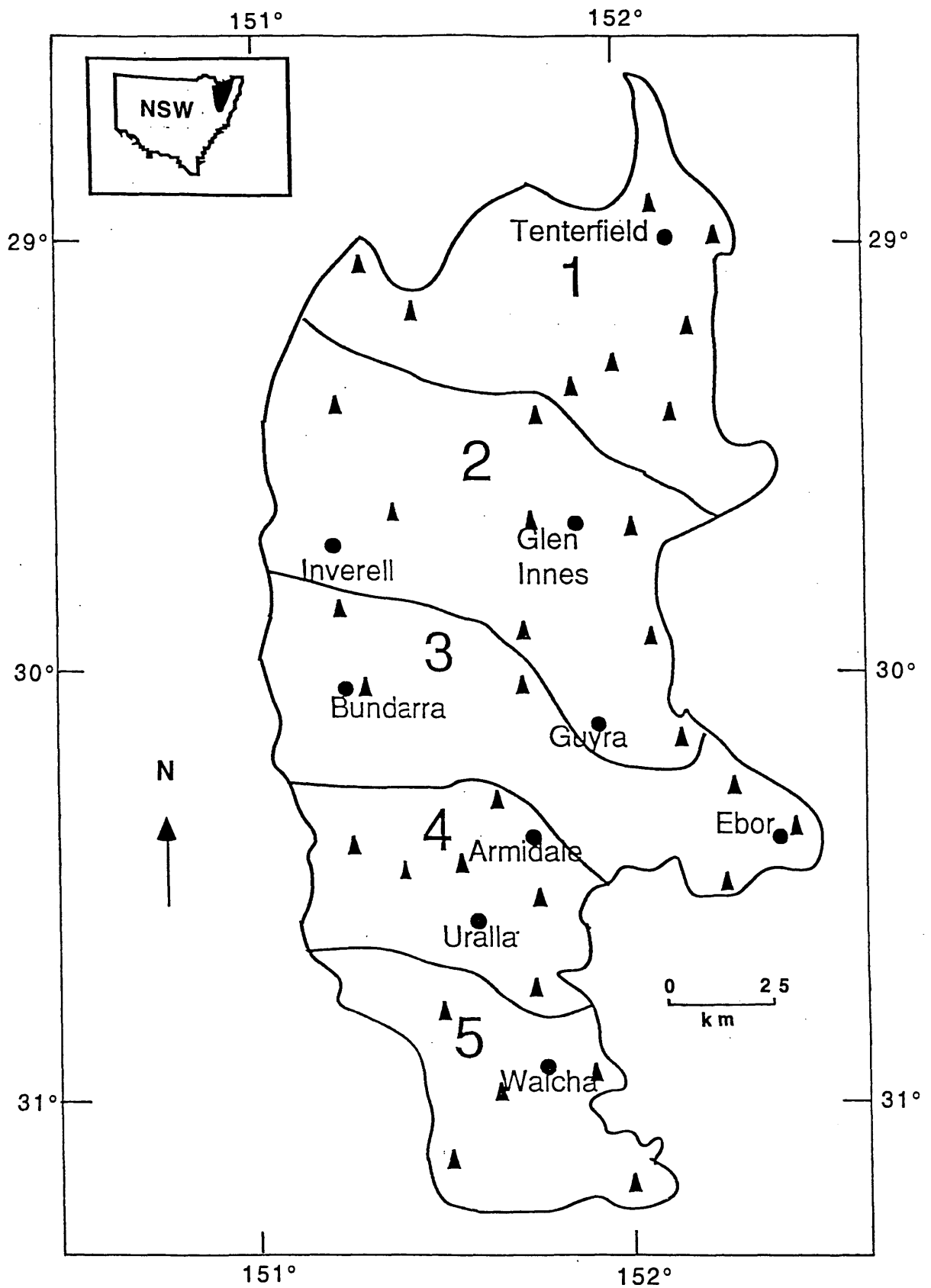
Fig. 3.7. Map showing the five clusters of paddocks based on grass species composition. The location of the properties on which paddocks were sampled are shown by ▲.

Table 3.3. Native and naturalised (*) species composition of the five clusters of paddocks, species frequency, average *M. stipoides* abundance rating (1-5) and growth (wsp-warm season perennial; wsa-warm season annual; csp-cool season perennial; csa-cool season annual; ygp-year-long green perennial). Only species having a frequency of 0.20 and above were included in this table.

Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Microlaena stipoides rating 2.16	*Microlaena stipoides* rating 2.45	*Microlaena stipoides* rating 3.10	*Microlaena stipoides* rating 3.00	*Microlaena stipoides* rating 3.29
Sporobolus creber wsp .96	*Eragrostis* spp. wsp/wsa .82	*Eragrostis* spp. wsp/wsa .55	*Sporobolus creber* wsp .83	*Bothriochloa macra* wsp .76
Eragrostis spp. wsp/wsa .79	*Sporobolus creber* wsp .68	*Sporobolus creber* wsp .50	*Eragrostis* spp. wsp/wsa .83	*Agrostis avenacea* csa .65
Bothriochloa macra wsp .54	*Eleusine tristachya* wsp (short lived)* .55	*Eleusine tristachya* wsp (short lived)* .35	*Panicum effusum* wsp .72	*Cynodon dactylon* wsp .59
Aristida ramosa wsp .42	*Bothriochloa macra* wsp .50	*Juncus* sp. .35	*Bothriochloa macra* wsp .61	*Eragrostis* spp. wsp/wsa .59
Cymbopogon refractus wsp .38	*Chloris truncata* wsp .50	*Bothriochloa macra* wsp .30	*Chloris truncata* wsp .61	*Lolium perenne* ygp* .47
Panicum effusum wsp .38	*Danthonia pilosa* ygp .45	*Dactylis glomerata* ygp* .30	*Eleusine tristachya* wsp (short lived)* .50	*Bromus cartharthicus* csp (short lived)* .41
Echinopogon ovatus wsp .33	*Paspalum dilatatum* wsp* .45	*Danthonia pilosa* ygp .30	*Cynodon dactylon* wsp .39	*Holcus lanatus* ygp* .41
Paspalum dilatatum wsp* .33	*Bromus cartharthicus* csp (short lived)* .36	*Panicum effusum* wsp .30	*Setaria gracilis* wsp* .33	*Pennisetum alopecuroides* wsp .41
Cynodon dactylon wsp .29	*Phalaris aquatica* ygp .36	*Aristida ramosa* wsp .25	*Danthonia linkii* ygp .28	*Sporobolus creber* wsp .35
Eleusine tristachya wsp (short lived)* .29	*Bromus brevis* csa* .27	*Chloris truncata* wsp .25	*Pennisetum alopecuroides* wsp .28	*Carex inversa* wsp .35
Dichelachne micrantha ygp .25	*Panicum effusum* wsp .27	*Cymbopogon refractus* wsp .25	*Carex inversa* wsp .28	*Bromus brevis* csa* .29
Themeda australis wsp .25	*Aristida ramosa* wsp .23	*Danthonia laevis* ygp .25	*Juncus* sp. .28	*Eleusine tristachya* csp (short lived)* .29
Danthonia pilosa ygp .21	*Danthonia caespitosa* ygp .23	*Elymus scabrus* csp .25	*Aristida ramosa* wsp .28	*Festuca elatior* ygp* .29

Imperata cylindrica	wsp .21	*Festuca elatior*	ygp* .23	*Lolium perenne*	ygp* .25	*Danthonia laevis*	ygp .22	*Paspalum dilatatum* wsp* .29
Poa pratensis	ygp* .21	*Lolium perenne*	ygp* .23	*Stipa scabra*	ygp .25	*Dichelachne micrantha* ygp	.22	*Bromus racemosa* csa* .24
Stipa verticillata	ygp .21	*Poa pratensis*	ygp* .23	*Vulpia bromoides*	csa* .25			*Danthonia pilosa* ygp .24
Juncus sp.	.21			*Bromus brevis*	csa* .20			*Panicum effusum* wsp .24
				Paspalum dilatatum	wsp* .20			*Phalaris aquatica* ygp* .24
				Pennisetum alopecuroides wsp	.20			*Poa pratensis* ygp* .24
				Poa sieberiana	csp* .20			

cool season annuals and two exotic species, *Dactylis glomerata* (.30) and *Lolium perenne* (.25) (Table 3.3).

Six properties in the Armidale and Uralla areas comprised cluster 4 (Fig. 3.7). Warm season perennials including *Sporobolus creber* (.83), *Eragrostis* sp. (.83), *Panicum effusum* (.72), *Bothriochloa macra* (.61) and *Chloris truncata* (.61) dominated this cluster (Table 3.3). A few year-long green perennials were recorded: *M. stipoides, Danthonia caespitosa* (.28), *D. laevis* (.22) and *Dichelachne rara* (.22).

Properties in the Walcha area comprised cluster 5 (Fig. 3.7), which was characterised by high frequency of cool season annuals, including *Agrostis avenacea* (.65) and *Bromus cartharthicus* (.41). This cluster had the highest average *M. stipoides* rating (3.29). Other dominant warm season perennials recorded were *Bothriochloa macra* (.76), *Cynodon dactylon* (.59) and *Eragrostis* spp. (.59). This cluster had a high frequency of *Lolium perenne* (.47). Other exotic year-long green perennials observed were *Festuca elatior* (.29) and *Phalaris aquatica* (.24).

3.4 DISCUSSION

Microlaena stipoides occurs widely on the Northern Tablelands of NSW and its abundance and distribution is strongly associated with environmental and pasture management correlates. Paddock characteristics including soil pH, altitude, period since last cultivated, degree of cultivation, latitude, longitude, rainfall, pasture improvement, tree density and soil type could be used as predictors of the abundance of *M. stipoides*. Cluster analysis has shown that *M. stipoides* is grouped closely with altitude, rainfall, longitude, degree of cultivation and period since last cultivated.

Microlaena stipoides is more common at higher elevations on the eastern side of the Northern Tablelands, which confirms the earlier observations of Lodge and Whalley (1989). Similar to *Danthonia pilosa*, it would seem to be better adapted to cooler temperatures and higher rainfall in elevated areas (Scott and Whalley 1982). It is distributed over a wide range of soils derived from the three major types of parent material on the Tablelands. This parallels the findings of Munnich *et al.* (1991) who found *M. stipoides* on a wide range of soil types in the Goulburn District, on the Southern Tablelands of NSW.

Pasture management correlates that were significantly associated with abundant *M. stipoides* were high tree density, minimum soil disturbance and long period since last cultivation. It has been well documented that *M. stipoides* is more commonly found around

tree stumps and under tree canopies (Taylor and Hedges 1984, Rose 1986, Magcale-Macandog and Whalley 1991) and in the more protected timbered areas (Whalley *et al.* 1978). Hence this was built into the classification system. The method for rating abundance of *M. stipoides* confounded the ratings and the tree abundance. The only abundance classes that could be used to indicate the effect of trees on *M. stipoides* abundance are classes (1) (no *M. stipoides*) and (5) (*M. stipoides* in dense patches all over the paddock). Clearly, the proportion of paddocks with no *M. stipoides* decreased with increasing tree abundance and the proportion of paddocks with scattered dense patches of *M. stipoides* increased with increasing tree density (Fig. 3.5). Rose (1986) and Huxtable (1990) reported increased vegetative growth of *M. stipoides* in the shade. The negative association between soil disturbance and abundance of *M. stipoides* was exhibited by the decrease in the abundance of *M. stipoides* with both more frequent and recent cultivation. Cultivation either for cropping or for sowing improved pastures results in the destruction of *M. stipoides*.

Scott and Whalley (1982) reported that of the 13 species of *Danthonia* spp., (native year-long green perennials) found on the Northern Tablelands, *Danthonia racemosa* has an ecologically wide distribution. They found a strong association between frequency of *D. racemosa* and high level of tree cover and a long period since the last cultivation, which was similar to the present results with *M. stipoides*. Both *M. stipoides* and *D. racemosa* are sensitive to site disturbance. However, *M. stipoides* was less sensitive to cultivation with a tendency to re-invade pastures, and thus was more common in improved pastures compared with *Danthonia* spp. (Munnich *et al.* 1991).

The increased frequency of *M. stipoides* with increase in soil acidity indicated the ability of *M. stipoides* to tolerate and survive on strongly acid soils (Munnich *et al.* 1991). This attribute is of great importance in view of the increasing occurrence of acid soil problems in subterranean clover pastures particularly on the Southern Tablelands (Bromfield *et al.* 1983).

The abundance of *M. stipoides* was unrelated to the type of grazing animal or whether set stocked or rotationally grazed. However, *M. stipoides* was more abundant in pastures which were continually grazed than those spelled for 2-3 months, indicating that it is tolerant of continuous grazing. Perhaps this feature is related to its ability to withstand heavy grazing (Wyndham 1986). The total amount of phosphate fertiliser applied had no significant association with the abundance of *M. stipoides* and it can be found in both phosphate-fertilised and phosphate-poor soils. The wide adaptability of *M. stipoides* on a wide range of soil fertility levels is very significant in view of the high cost of phosphate fertilisation. However, it is very responsive to added nitrogen (Vieira 1980) which may be the reason why it is more common along the margins of sheep camps and grows well in

association with *Trifolium repens* (Magcale-Macandog and Whalley 1991). Munnich *et al.* (1991) also found no significant associations between the abundance of either *Danthonia* sp. or *M. stipoides* and fertiliser application or grazing history on the Southern Tablelands.

The presence of the associated pasture grasses was related in different ways to the same environmental and management correlates which were associated with the distribution and abundance of *M. stipoides*. Abundance of *M. stipoides* was therefore associated with the presence of particular species in the paddocks (Munnich *et al.*1991). *Microlaena stipoides* was more abundant in paddocks containing other year-long green perennials, cool season annuals and exotic sown species in addition to warm season perennials and annuals compared with pastures composed mainly of warm season perennials and annuals. In terms of the sown exotic species, more *M. stipoides* was observed in the cluster of paddocks having a higher frequency of *Lolium perenne* than in clusters of paddocks having higher frequencies of either *Phalaris aquatica* or *Dactylis glomerata*. Munnich *et al.* (1991) reported a decrease in the proportion of *M. stipoides* in paddocks sown to either *P. aquatica* or *D. glomerata* in comparison with paddocks sown only with *Lolium rigidum*. This could be explained by the fact that both *M. stipoides* and *L. perenne* are more abundant in the wetter areas of the tablelands while *P. aquatica* is more abundant in the drier areas. *Dactylis glomerata*, on the other hand, is often not persistent in sown paddocks on the Northern Tablelands and could have disappeared by the time *M. stipoides* reinvades after cultivation.

The results of this survey clearly indicated that environmental and pasture management attributes are important correlates of the distribution and abundance of *M. stipoides* on the Northern Tablelands of New South Wales. Biotic interactions between *M. stipoides* and neighbouring pasture species may also be important in determining the dynamic pattern of distribution of *M. stipoides* in a permanent pasture and this will be dealt with in the next chapter.

CHAPTER FOUR

DISTRIBUTION OF *Microlaena stipoides* AND ITS ASSOCIATION WITH INTRODUCED PERENNIAL GRASSES IN A PERMANENT PASTURE ON THE NORTHERN TABLELANDS OF NSW

4.1 INTRODUCTION

Physical neighbours are important components of the microenvironment in plant communities (Van Valen 1973, Mack and Harper 1977). Thórhallsdóttir (1990a) studied the dynamics of a permanent grassland community in North Wales and found strong evidence that patterns were generated and maintained by plants themselves through species-specific interactions. Thórhallsdóttir (1990b) reported that *Trifolium repens* was highly mobile and had a dynamic pattern of occurrence. Tufted grasses such as *Cynosurus cristatus, Festuca rubra, Anthoxanthum odoratum* and *Lolium perenne* had a high probability of occupying the same space after one or two years. Tufted grasses like *Lolium perenne* and *Cynosurus cristatus* had long-lived plants and tillers while the stoloniferous grasses *Agrostis capillaris* and *Poa trivialis* produced many small and short-lived ramets with short-lived tillers. She concluded that each species imposes its own rate and scale of change and that patterns in plant communities cannot be viewed on a single spatial or temporal scale.

Thórhallsdóttir (1990a) stated that an environmentally induced pattern is static while patterns caused by biotic interactions are dynamic. Biotic interactions may largely influence the behaviour of pasture species in a sward (Turkington and Harper 1979b). Turkington and Harper (1979b) found that niche diversification of pasture species was highly correlated with trees and hedges and that seasonal growth form differences influenced habitat mosaic. Legumes and grasses in improved pastures occupy different niches and do not compete for exactly the same limiting resource spatially and temporally (Kemp and Dowling 1991) so that competitive exclusion does not occur.

The overall composition of a community is a reflection of spatial and seasonal fluxes of the constituent species. Spatial flux includes clonal migration and seedling recruitment while seasonal flux refers to variations in seasonal growth pattern of the different species in the community (Turkintgon and Harper 1979b). Different parts of the field may display different stages of a cycle at any one particular time (Kershaw 1959).

Permanent pastures usually consist of a mosaic of different perennial and annual species associations (Turkington and Harper 1979a) and there is little reason to suspect that a permanent pasture containing *M. stipoides* would be any different. The aim of this study was to determine the spatio-temporal distribution of *M. stipoides* and its association with other grasses in a small paddock of permanent pasture which included the grasses *Lolium perenne*, *Poa pratensis* and *Dactylis glomerata* and the legume, *Trifolium repens*.

4.2 MATERIALS AND METHODS

4.2.1 Survey site

The survey site was a permanent pasture sloping towards the southeast (470 x 240 m, about 11.3 ha) grazed by cattle and sheep at 'Karuah', about 50 km north-east of Armidale. A gravel road ran through the paddock (Fig. 4.1a) and the area below the road had a lower slope than the area above it. A creek ran from the northwest across the road towards the southern end of the paddock while a small dam was located at the lower northern part. At the upper southern corner, a small area was fenced for an opportunity feedlot. Several tree species including *Eucalyptus stellulata*, *E. viminalis*, *E. nova-anglica*, *Angophora floribunda* were scattered throughout the paddock and several trees of *Salix babylonica* were beside the creek. The locations of these trees are shown in Fig. 4.1a (cross-hatched areas).

The pasture was a mixture of perennial and annual grasses, sedges, and herbaceous dicots including *T. repens*. In July 1961, 0.34 kg/ha of *T. repens* (white clover cv. 'NZ') was seeded in the paddock, while in the autumn of 1972, 0.84 kg/ha each of *L. perenne* (hybrid rye and perennial rye) and *D. glomerata* (Danish cocksfoot and Curry cocksfoot) were aerially seeded. Superphosphate has been applied annually at a rate of 125 kg/ha from 1961 until 1990. For the purpose of this study, only perennial herbaceous species were considered.

4.2.2 Vegetation survey methods

The paddock was surveyed in January 1990 and January 1993. One hundred and five systematically arranged locations were sampled in the paddock (Fig.4.1a). In 1990, the sampling locations in each line were 35 m apart with the lines 30 m apart, while in 1993, the sampling locations were every 30 m, and the lines were 35 m apart. In some instances this spacing was varied where barriers such as the creek, dam and road were encountered.

At each sampling location, a 2-m long board, 10-cm wide with ten 30-cm wires 20 cm apart was positioned and the perennial herbaceous species whose base was touched by each point was recorded. Where a point rested on bare ground or litter, the species of the nearest plant was recorded. The procedure was repeated nine times at distances of 20 cm, to make a total of 100 points at each sampling location. Percentage composition by basal cover of all the perennial herbaceous species encountered was computed for each location and then averaged for the whole paddock.

4.2.3 Data analysis

Using the percentage composition by basal cover data, isonome maps of the dominant perennial grass species *M. stipoides, L. perenne, D. glomerata, P. pratensis, P. dilatatum, C. dactylon* and the legume *T. repens* were constructed. The isonomes join points of equal percentage composition by basal cover. Bray-Curtis hierarchical classification and Incremental Sum of Squares techniques were used to classify and fuse the quadrats to produce a dendrogram. Hierarchical discriminant function analysis was done to assess membership of the sampling locations in the 20 groups formed using Bray-Curtis classification. Species ordination was also conducted following Bray-Curtis and Reciprocal Averaging techniques.

4.3   RESULTS

4.3.1 Species percentage basal cover

In the initial survey, *M. stipoides, L. perenne* and *T. repens* were the most abundant perennial grass species in the paddock (Fig. 4.2a). The area also had a high proportion of *D. glomerata* and *P. pratensis*. Three years later, *M. stipoides* and *L. perenne* were still the most abundant perennial species and their percentage basal cover remained almost the same. The percentage basal cover of *T. repens* was reduced to about half (from 24% to 12%). *Dactylis glomerata* and *P. pratensis* were also abundant and had almost the same percentage basal cover. There was a significant increase in the percentage basal cover of *Paspalum dilatatum*, from 0.65% to 11%. Other species that had increased abundance were *Cynodon dactylon* (from 0.8% to 4%), *Eleusine tristachya* (from 0% to 3%) and *Bothriochloa macra* (from 0.87% to 2%). Other perennial grasses and herbs found in the field during the 1990 survey were *Carex inversa, Sporobolus creber, Poa sieberiana* and *Elymus scaber*. Additional species identified during the 1993 survey were *Pennisetum alopecuroides,*

Festuca elatior, Holcus lanatus, Danthonia sp., *Juncus* sp., *Lomandra filiformis, Hemarthria uncinata, Pteridium esculentum* and *Eragrostis molybdea.*

4.3.2 Spatio-temporal distribution of dominant species in the paddock

In the 1990 survey, *M. stipoides* was abundant in all of the paddock except in swampy areas beside the creek and dam, and in the upper western corner area near the opportunity feedlot (Fig. 4.1b). Three years later, *M. stipoides* was more abundant in the northern part of the paddock near the fence. Increased abundance was also observed in the southeastern part of the paddock, while the abundance on the northeastern side of the creek on both eastern and western sides of the road had decreased (Fig. 4.1b).

During the 1990 survey, the cover of *L. perenne* (Fig. 4.1c) in the upper western corner area near the opportunity feedlot was high and patches of *L. perenne* were scattered all over the paddock with a higher proportion in open areas. Higher proportions of *M. stipoides*, on the other hand, were observed under tree canopies. In the 1993 survey, there was higher ground cover of *L. perenne* in the open areas in the lower eastern part of the paddock. Notable also was the decrease in abundance in the northern part of the paddock above the gravel road and in areas beside the creek in the southeastern corner of the paddock (Fig. 4.1c).

Trifolium repens was recorded at every location except one in the 1990 survey with higher proportions observed in the lower eastern part of the paddock and in the wetter areas near the creek and dam (Fig. 4.1d). Three years later, abundance of *T. repens* decreased from 22% to 11% and a marked reduction in overall ground cover of *T. repens* in the paddock was observed (Fig. 4.1d). Decrease in ground cover of *T. repens* was particularly observed in the upper western part of the paddock near the feedlot and in the lower eastern part of the paddock. However, the abundance of *T. repens* on the northwestern part of the paddock beside the fence increased (Fig. 4.1d).

Generally, abundance of *D. glomerata* was higher in areas on the upper slopes of the paddock in both surveys. In the 1990 survey, *D. glomerata* (Fig. 4.1e) dominated the area near the fence and under tree canopies in the upper northern part of the paddock above the gravel road. Three years later, ground cover of *D. glomerata* on the northern part of the paddock above the gravel road increased, replacing *L. perenne*, and decreased in the northern part of the paddock beside the fence (Fig. 4.1e). It had also invaded scattered shaded patches in the eastern part of the paddock below the gravel road.
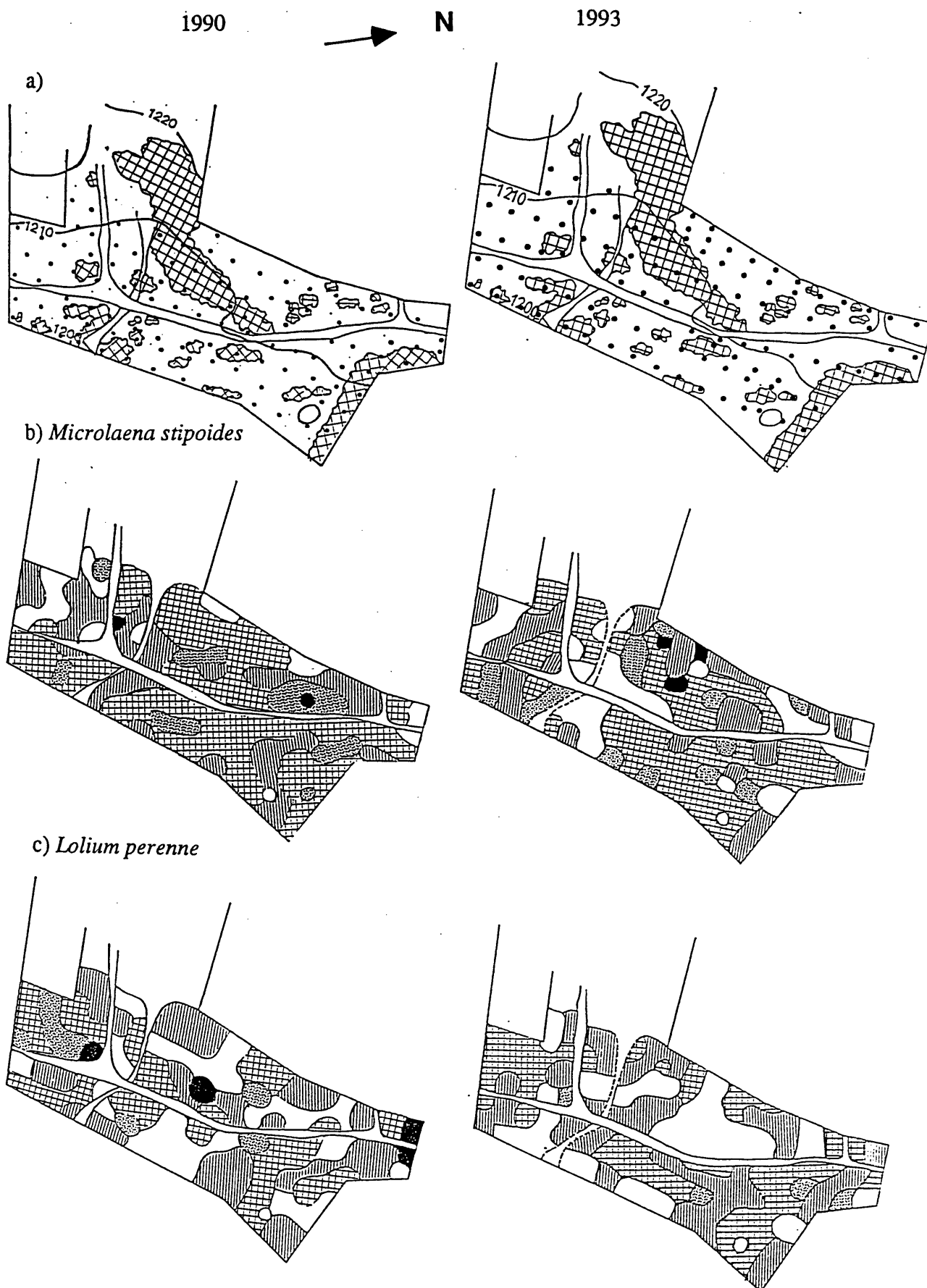
1990   **N**   1993

a)

b) *Microlaena stipoides*

c) *Lolium perenne*

Fig. 4.1. Isonome maps showing a) the location of tree canopies (cross-hatched areas), sampling locations and contour lines in the field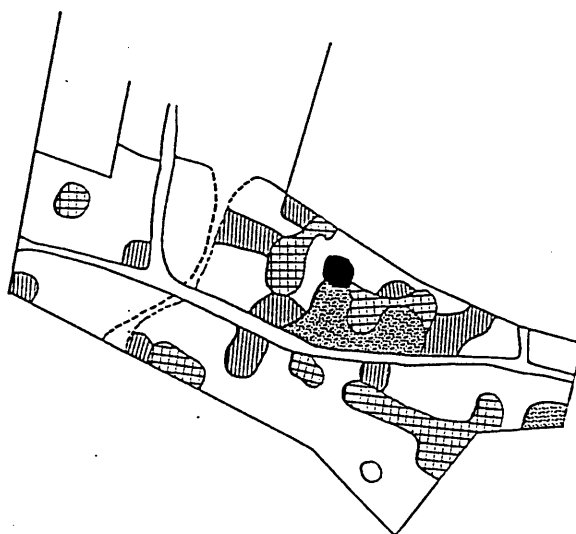, and the distribution of b) *Microlaena stipoides*, c) *Lolium perenne*, d) *Trifolium repens*, e) *Dactylis glomerata*, f) *Poa pratensis*, g) *Paspalum dilatatum* for the 1990 and 1993 surveys and h) *Cynodon dactylon* and i) *Eleusine tristachya* for the 1993 survey. Abundance classes: ■ +70%, ▦ 50-69%, ▦ 25-49%, ▦ 10-24%, □ <10%.
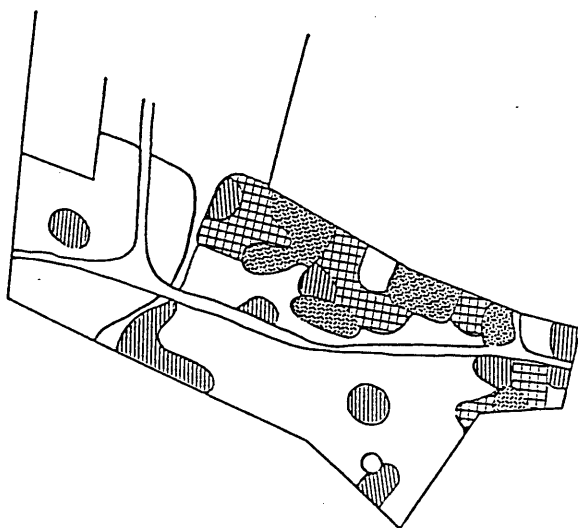
1990   1993

d) *Trifolium repens*   **N**
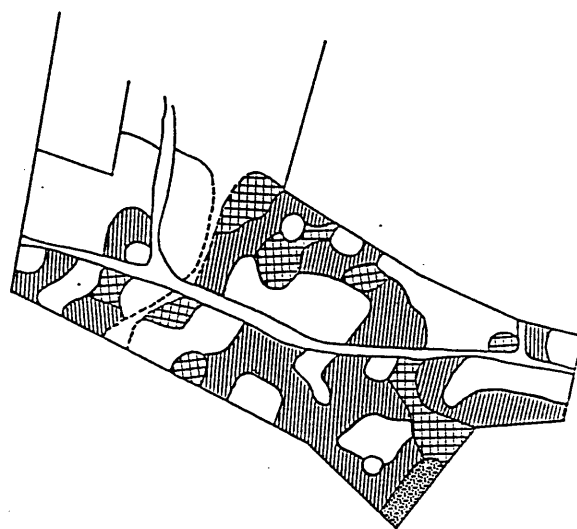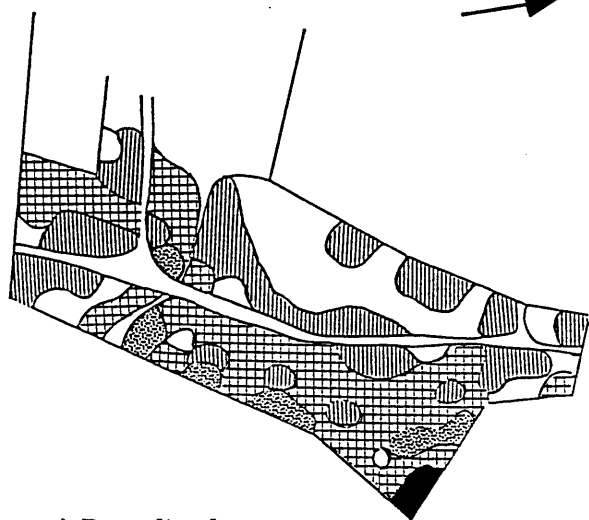
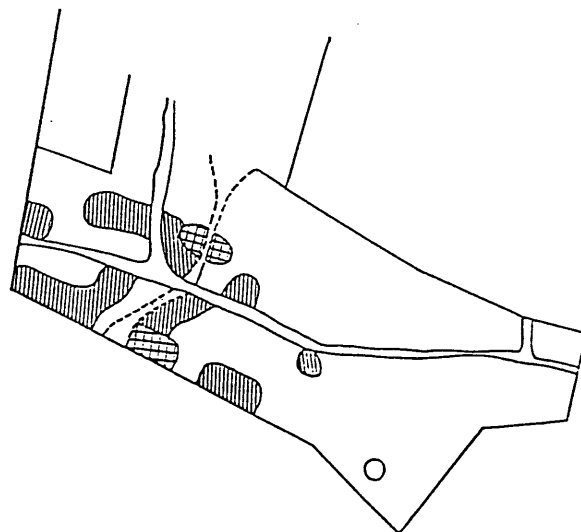e) *Dactylis glomerata*
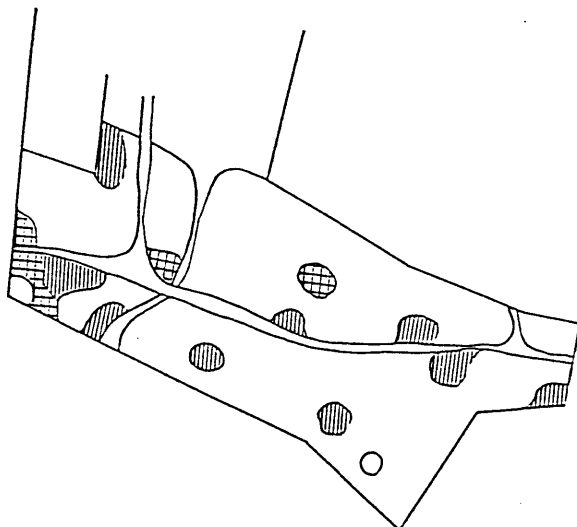
f) *Poa pratensis*

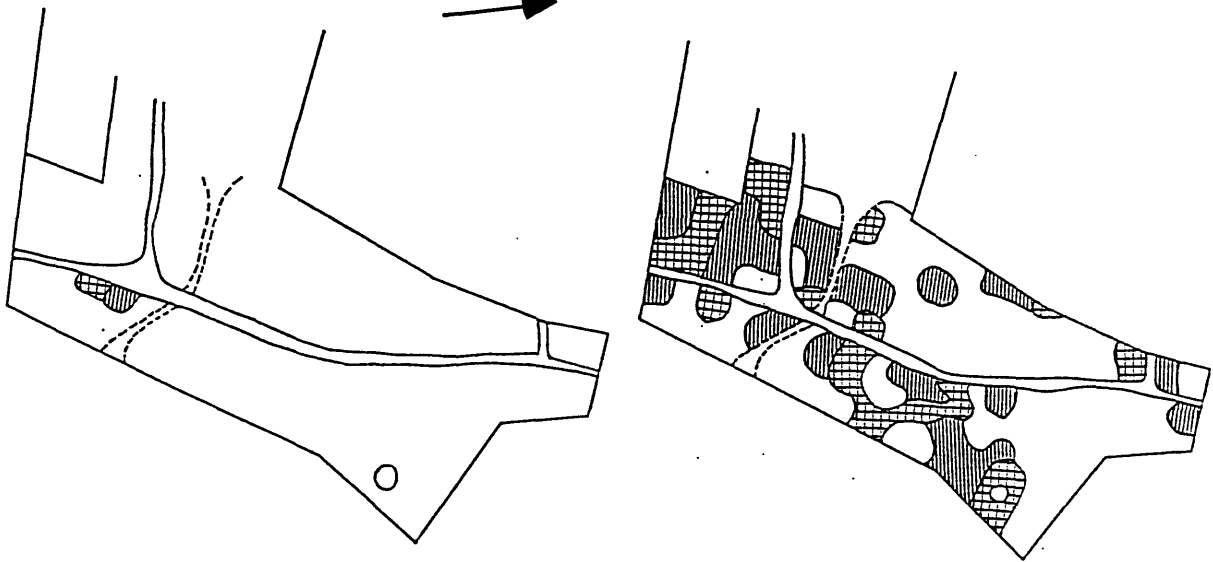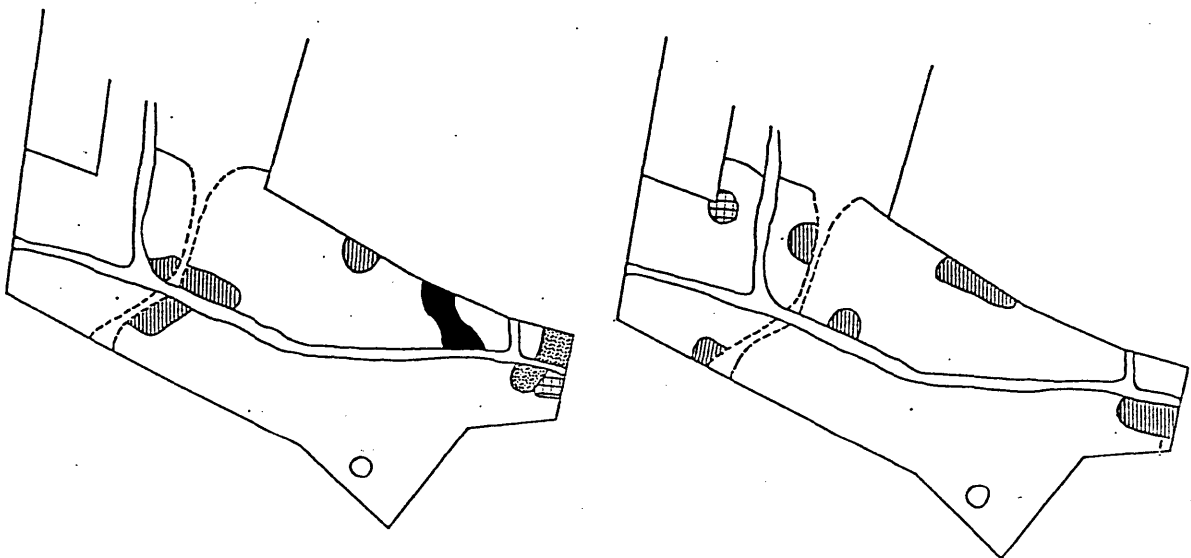1990   1993

g) *Paspalum dilatatum*   **N**

1993

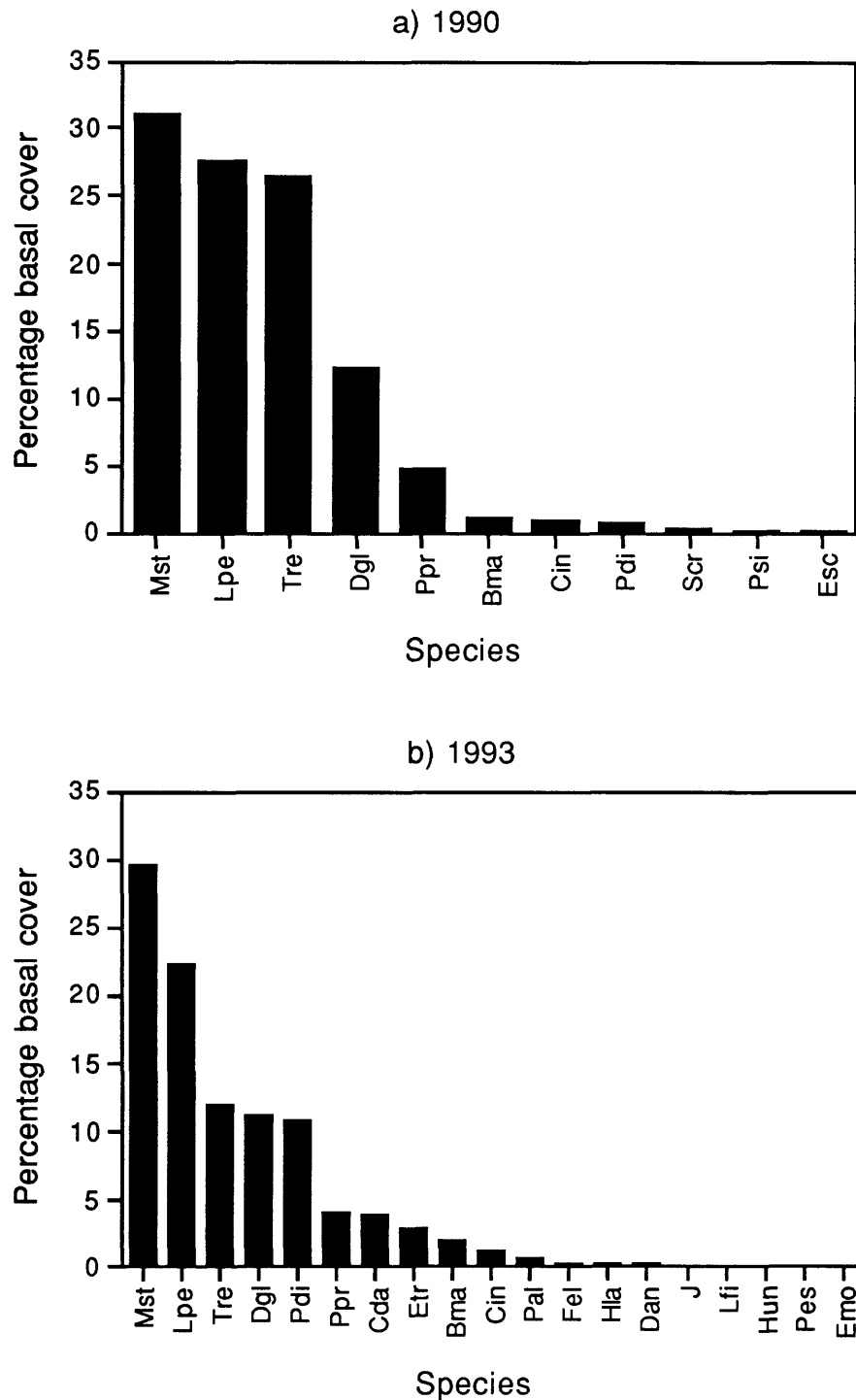h) *Cynodon dactylon*   i) *Eleusine tristachya*

Fig. 4.2. Percentage composition by basal cover of the species studied in the area. Mst, *Microlaena stipoides*; Lpe, *Lolium perenne*; Tre, *Trifolium repens*; Dgl, *Dactylis glomerata*; Ppr, *Poa pratensis*; Bma, *Bothriochloa macra*; Cin, *Carex inversa*; Pdi, *Paspalum dilatatum*; Scr, *Sporobolus creber*; Psi, *Poa sieberiana*; Esc, *Elymus scaber*; Cda, *Cynodon dactylon*; Etr, *Eleusine tristachya*; Pal, *Pennisetum alopecuroides*; Fel, *Festuca elatior*; Hla, *Holcus lanatus*; Dan, *Danthonia* sp.; J, *Juncus* sp.; Lfi, *Lomandra filiformis*; Hun, *Hemathria uncinata*; Pes, *Pteridium esculentum*; Emo, *Eragrostis molybdea*.

Poa pratensis, in the 1990 survey, was sparsely distributed in the area and was found to have higher proportions both under tree canopies and in some of the cleared spots (Fig. 4.1f). In the 1993 survey, most of *P. pratensis* was concentrated in the flat areas of the lower slopes on the southern part of the paddock. Its abundance was particularly high in areas beside the creek replacing *L. perenne* (Fig. 4.1f).

Paspalum dilatatum, which was very sparse in the 1990 survey, had increased abundance in the 1993 survey and invaded the upper western corner near the opportunity feedlot (Fig. 4.1g). It had replaced *T. repens* in the northwestern area between the road and creek. It was also abundant in the eastern part of the paddock below the gravel road. Scattered patches were also found in the northern part of the paddock above the gravel road, beside the creek and along the upper fence.

In the 1993 survey, *C. dactylon* dominated the northern corner of the paddock and was also found in areas beside the creek (Fig. 4.1h). *Eleusine tristachya,* on the other hand, began to invade a spot in the upper western part of the paddock near the corner of the opportunity feedlot and a few patches were scattered throughout the paddock (Fig. 4.1i).

4.3.3 Hierarchical classification of the sampling sites

Bray-Curtis hierarchical classification initially fused the 105 sampling locations into 20 groups for both surveys (Table 4.1). For the 1990 survey results, these 20 groups of sampling locations were further aggregated into five main groups as shown (Fig. 4.3a): the sampling locations dominated by *L. perenne* (groups 1-5), *D. glomerata* (groups 18-20), mixed *M. stipoides, L. perenne* and *T. repens* (groups 12-17), mixed *M. stipoides, L. perenne, T. repens* and *P. pratensis* (groups 6-11) and mixed *M. stipoides* and *T. repens* (groups 16 & 17) (Table 4.1a).

The groups of sampling locations dominated by *L. perenne* (groups 1-5) were located in the upper western corner near the opportunity feedlot, in areas beside the creek and in scattered patches in open areas (Fig. 4.3b). The groups of sampling locations dominated by a mixture of *M. stipoides, L. perenne, P. pratensis* and *T. repens* (groups 6-11) were located in the lower southern part of the paddock and northern part above the gravel road (Fig. 4.3b). The groups of sampling locations dominated by a mixture of *M. stipoides, L. perenne* and *T. repens* (groups 12-15) and of *M. stipoides* and *T. repens* (groups 16 & 17) were located in the lower eastern part of the paddock below the gravel road, while groups of sampling locations dominated by *D. glomerata* were located in the upper northern part of the paddock above the gravel road (Fig. 4.3b).

Table 4.1. Average percentage composition by basal cover of different species in the 20 location groups and classification results using Fisher's linear discriminant function analysis for the 1990 and 1993 surveys.

a) 1990

Group No.	No. of loca- tions	Classi- fication (% correct)	Mst	Lpe	Tre	Ppr	Cin	Dgl	Pdi
1	8	100	42	42	8	2	0	3	1
2	4	75	23	48	12	1	10	2	1
3	1	100	0	58	0	42	0	0	0
4	5	100	11	64	11	0	0	13	0
5	12	100	14	47	33	3	0	1	1
6	5	100	38	24	12	17	0	1	0
7	2	100	44	4	6	32	1	12	0
8	1	100	12	14	21	15	0	0	38
9	7	85.7	37	20	15	1	0	25	1
10	7	100	66	4	19	8	0	2	0
11	7	85.7	54	19	19	2	1	4	0
12	7	85.7	33	17	34	12	0	1	0
13	5	100	40	12	37	1	1	5	0
14	7	100	30	32	33	1	1	2	0
15	3	100	15	28	30	0	0	26	0
16	6	100	17	9	59	5	0	10	0
17	6	100	41	3	53	0	0	2	0
18	6	100	15	16	10	0	0	58	1
19	3	100	31	1	6	1	0	61	0
20	3	100	50	3	7	0	0	40	0

b) 1993

| Group No.	No. of loca- tions	Classi- fication (% correct)	Mst	Lpe	Tre	Ppr	Cin	Dgl	Pdi	Bma	Etr	Cda	Dan
1	3	100	34	8	6	26	2	18	1	0	0	0	0
2	3	100	19	4	8	28	9	1	13	4	0	0	0
3	7	100	41	10	19	9	3	1	12	0	3	0	0
4	4	100	14	18	46	3	4	5	4	0	2	3	0
5	10	100	39	28	16	2	0	4	8	0	2	0	0
6	7	100	29	47	12	0	0	7	3	0	1	0	0
7	7	100	70	5	5	9	1	2	3	2	2	0	0
8	7	100	58	19	7	2	0	3	7	0	2	0	0
9	6	100	52	5	14	1	1	23	0	0	2	2	0
10	10	90	15	9	21	0	1	53	0	0	0	0	0
11	4	100	26	16	8	2	0	40	4	0	2	0	0
12	14	93	18	32	4	4	0	5	30	1	3	2	0
13	4	100	10	29	26	0	3	2	27	1	0	1	0
14	4	100	8	45	4	0	1	2	15	0	8	9	0
15	1	100	30	26	4	0	2	7	29	0	2	0	0
16	3	100	2	17	7	9	2	5	24	2	7	16	0
17	1	100	2	6	0	0	0	18	2	44	0	0	26
18	2	100	26	17	8	0	0	2	13	2	27	5	0
19	4	100	27	16	1	0	1	0	18	27	4	2	0
20	4	100	4	14	1	0	1	2	4	0	8	67	0

a) dendrogram
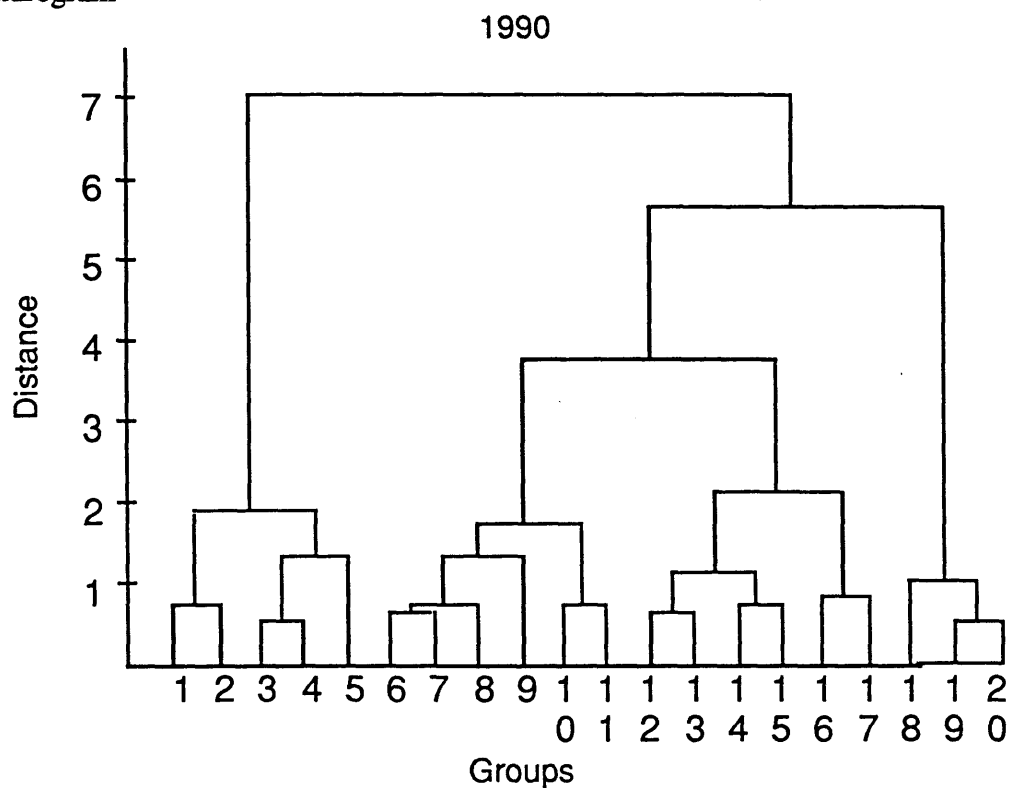
b) isonome map
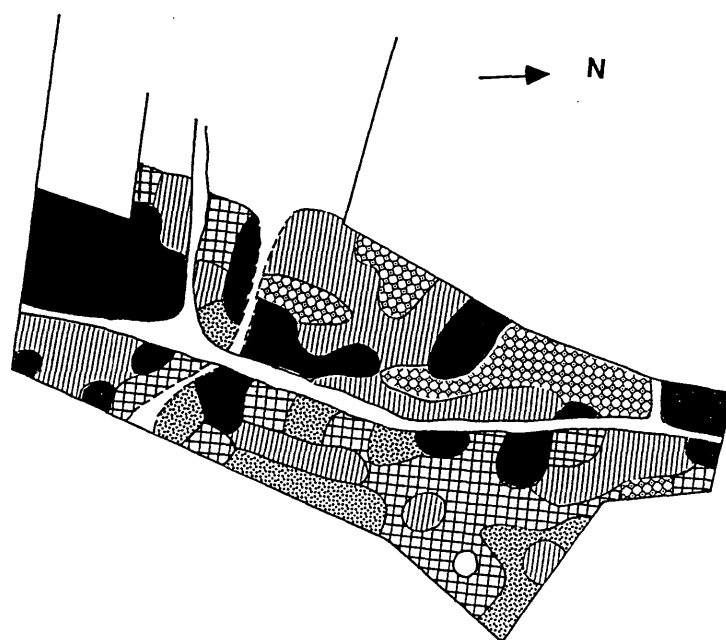
Fig. 4.3. a) Dendrogram showing the fusion of the 20 location groups into five groups; and b) location of the five groups in the paddock for the 1990 survey using Bray-Curtis hierarchical classification. Species or species associations dominating each group:■ *L. perenne,* ⊞ *M. stipoides + L.perenne + T. repens + P. pratensis,* ⊞ *M. stipoides + L.perenne + T. repens,* ▨ *M. stipoides + T. repens,* ▨ *D. glomerata.*

The 20 groups of sampling locations classified in the 1993 survey were further aggregated into seven groups (Fig. 4.4a): the sampling locations dominated by *M. stipoides*, *L. perenne*, *T. repens* and *P. pratensis* (groups 1-4); *M. stipoides*, *L. perenne* and *T. repens* (groups 5 & 6); *M. stipoides* (groups 7-9); *M. stipoides*, *L. perenne*, *T. repens* and *D. glomerata* (groups 10 & 11); *M. stipoides*, *L. perenne*, *T. repens* and *P. dilatatum* (groups 12-16); *M. stipoides*, *L. perenne*, *P. dilatatum* and *B. macra* (groups 17-19); and *C. dactylon* (group 20) (Table 4.1b).

The groups of sampling locations dominated by *M. stipoides*, *L. perenne* and *T. repens* were located in the lower eastern part of the paddock, similar to their location in the 1990 survey (Fig. 4.4b). The groups of sampling locations dominated by a mixture of *M. stipoides*, *L. perenne*, *P. pratensis* and *T. repens* were more concentrated in the lower slopes on the southern part of the paddock, in areas beside the creek and a few scattered patches in the lower eastern and upper northern parts of the paddock (Fig. 4.4b). Areas formerly dominated by *L. perenne* in the 1990 survey were occupied by a mixture of *M. stipoides*, *L. perenne*, *T. repens* and *P. dilatatum*, while areas formerly dominated by *D. glomerata* were dominated by mixture of *M. stipoides*, *L. perenne*, *T. repens* and *D. glomerata* three years later (Fig. 4.4b). A few scattered sites in the upper western and northern part of the paddock were dominated by *M. stipoides*, *L. perenne*, *P. dilatatum* and *B. macra* (Fig. 4.4b). *Cynodon dactylon* was concentrated in the northern corner of the paddock (Fig. 4.4b).

4.3.4 Discriminant function analysis

Hierarchical discriminant function analyses were performed using species percentage basal composition as predictors of membership in the 20 groups formed from the Bray-Curtis classification. For the 1990 survey results, a territorial map (Fig. 4.5a) showed that the first canonical discriminant function separated locations dominated by *L. perenne* (groups 1-5) from the locations dominated by mixed *M. stipoides*, *L. perenne* and *T. repens*, and mixed *M. stipoides*, *T. repens*, *L. perenne* and *P. pratensis*. The second canonical discriminant function separated locations dominated by *D. glomerata* from the rest.

The loading matrix of correlations between the 11 predictor variables (species) and the two discriminant functions (Table 4.2a) showed that the primary predictor (loading above +0.50 or below -0.50) for the first discriminant function (separation of locations dominated by *L. perenne*) was the percentage basal composition of *L. perenne*. Groups 1 to 5 have high percentage composition of *L. perenne* (means range from 42 to 58%; Table 4.1a).
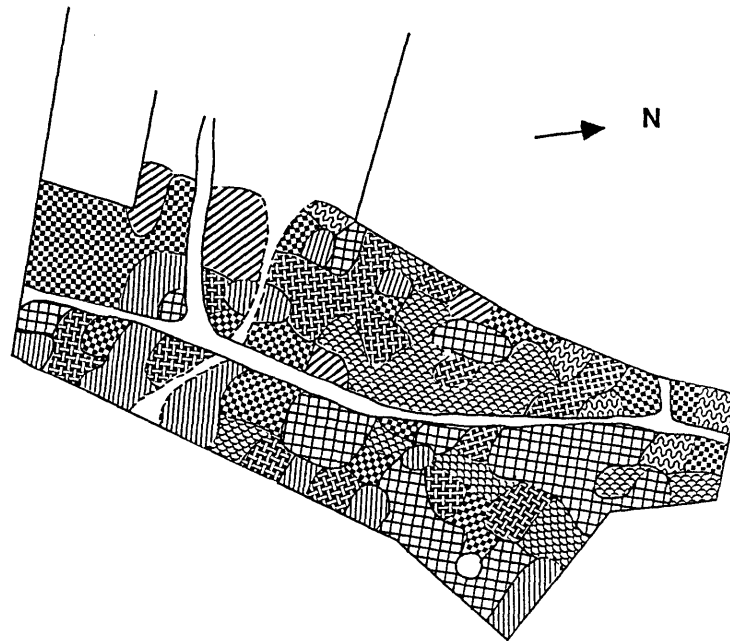
a) dendrogram
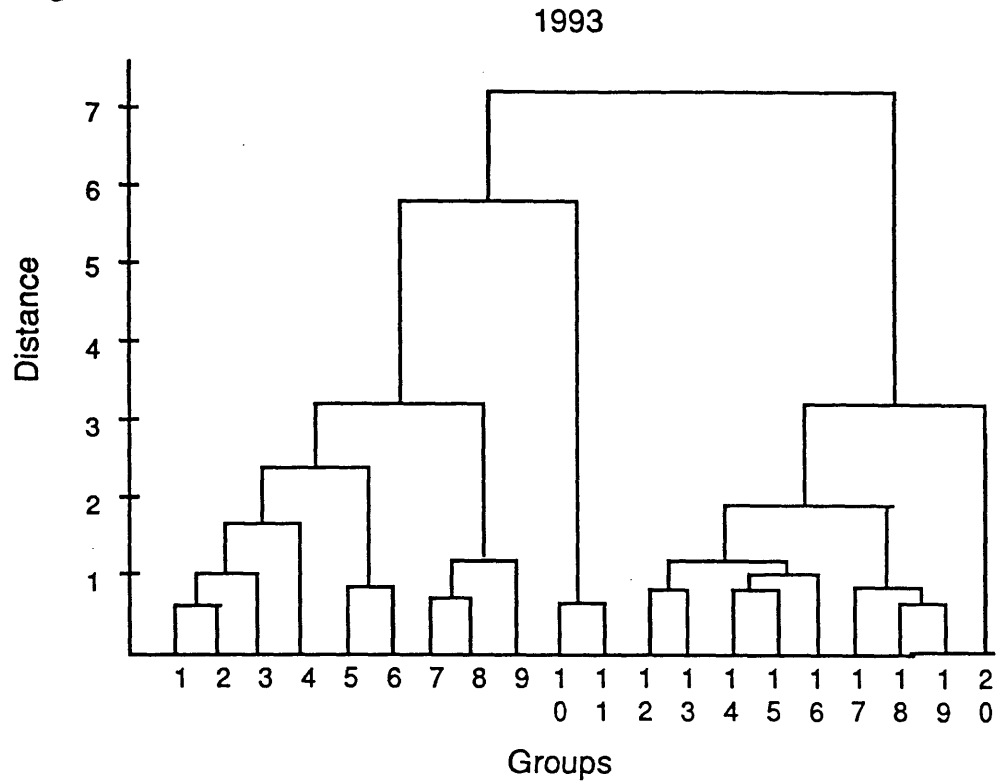
b) isonome map

Fig. 4.4. Dendrogram showing the fusion of the 20 location groups into seven groups; and b) location of the seven groups in the paddock for the 1993 survey using Bray-Curtis hierarchical classification. Species or species associations dominating each group: ▥*M. stipoides* + *L. perenne* + *T. repens* + *P. pratensis,* ⊞ *M. stipoides* + *L. perenne* + *T. repens,*▨ *M. stipoides,* ▨ *M. stipoides* + *L. perenne* + *T. repens* + *D. glomerata,* ▨ *M . stipoides* + *L. perenne* + *T. repens* + *P. dilatatum,* ▨ *M. stipoides* + *L. perenne* + *P. dilatatum* + B. macra, ▨ *C. dactylon.*
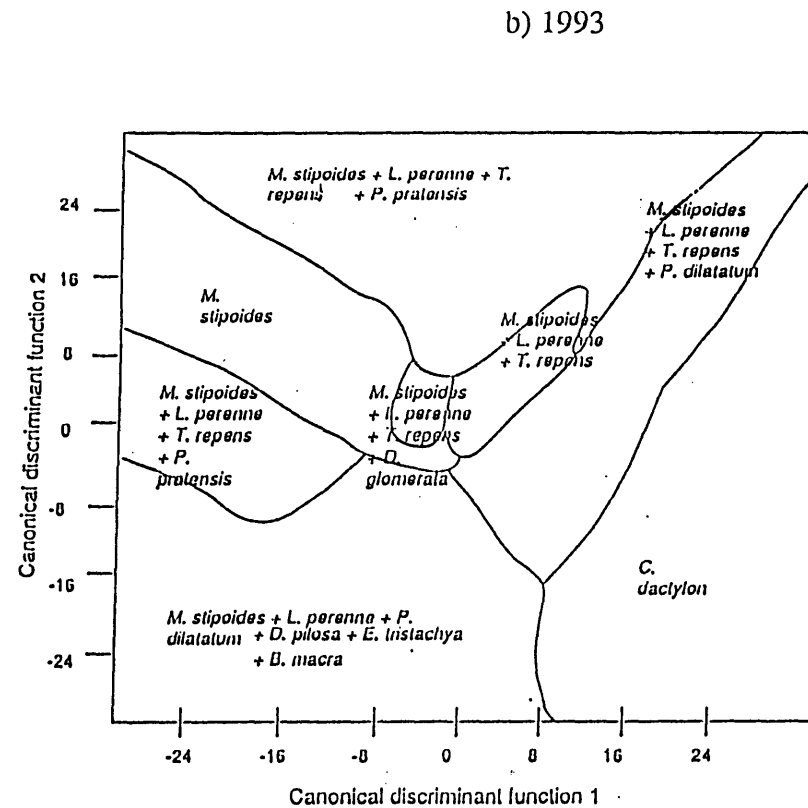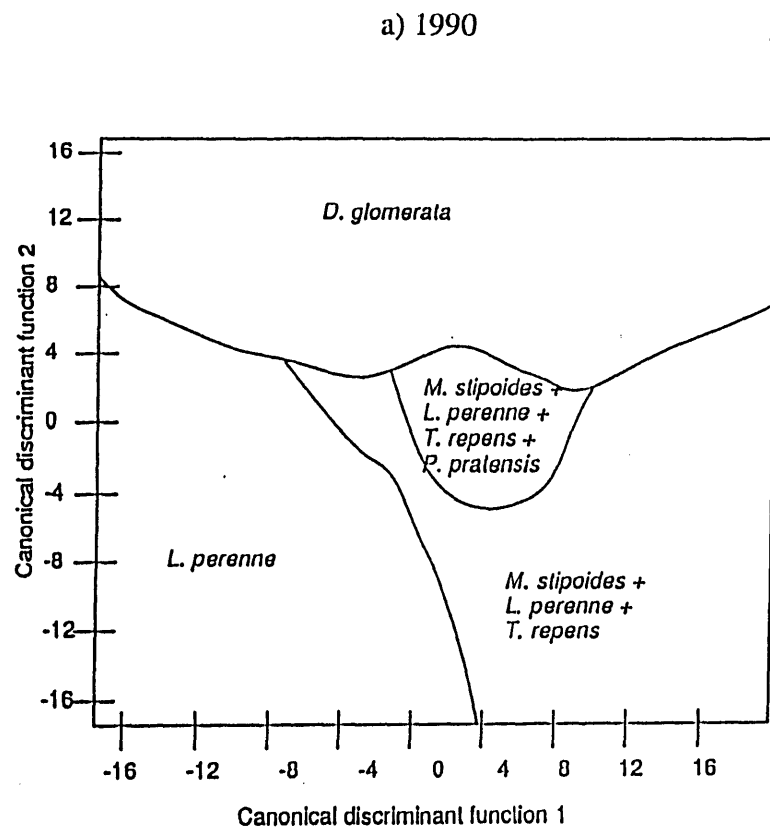
Fig. 4.5. Territorial maps of the main sampling location groups of dominated by the different species or combinations of different species using discriminant function analysis for the 1990 and 1993 surveys.

The primary predictor on the second discriminant function (separation of locations dominated by *D. glomerata*) was the percentage basal composition of *D. glomerata* (Table 4.2a). Mean basal composition of groups 18, 19 and 20 range from 40 to 61% *D. glomerata* (Table 4.1a).

In the 1993 survey results, the first canonical discriminant function separated locations dominated by *C. dactylon* from the locations dominated by mixed *M. stipoides, L. perenne, T. repens, P. pratensis, D. glomerata* and *P. dilatatum* (Fig. 4.5b). The second canonical discriminant function separated the locations of mixed *M. stipoides, L. perenne, P. dilatatum, B. macra, D. pilosa* and *E. tristachya* and the locations dominated by *C. dactylon* from the rest of combinations of mixed species.

The primary predictor for the first canonical discriminant function (separation of locations dominated by *C. dactylon*) was the percentage basal composition of *C. dactylon* (Table 4.2b). Group 20 (composed of 4 sites) had 67% basal composition of *C. dactylon*. The primary predictors on the second canonical discriminant function were the percentage basal composition of *D. pilosa* and *C. dactylon*. Percentage basal composition of *Danthonia* in group 17 was 26% and it was the only group which contained *D. pilosa*.

4.3.5 Species ordination

Species ordinations were plotted on two axes. For the 1990 results, axis 1 separated *D. glomerata* (4) from the other species (Fig. 4.6a). Along axis 2, *L. perenne* (3) was at the bottom, while *M. stipoides* (1) was located in close proximity to most of the other species studied near the middle of the axis. With the increased number of species identified in the 1993 survey, results of species ordination showed the close proximity of *M. stipoides* (1), *L. perenne* (3), *T. repens* (2) and *D. glomerata* (4) along axis 1 (Fig. 4.6b).

4.4 DISCUSSION

Patterns of distribution and fluctuations in the abundance of some of the species studied illustrate the dynamic nature of the species associations in this permanent pasture. All of the species studied showed variations in their pattern of distribution after three years.

Microlaena stipoides and *L. perenne* were the dominant perennial grasses in the paddock in both surveys. Although they were both abundant throughout the paddock, *M. stipoides* preferred shaded areas as reported by Taylor and Hedges (1984) and Rose (1986),
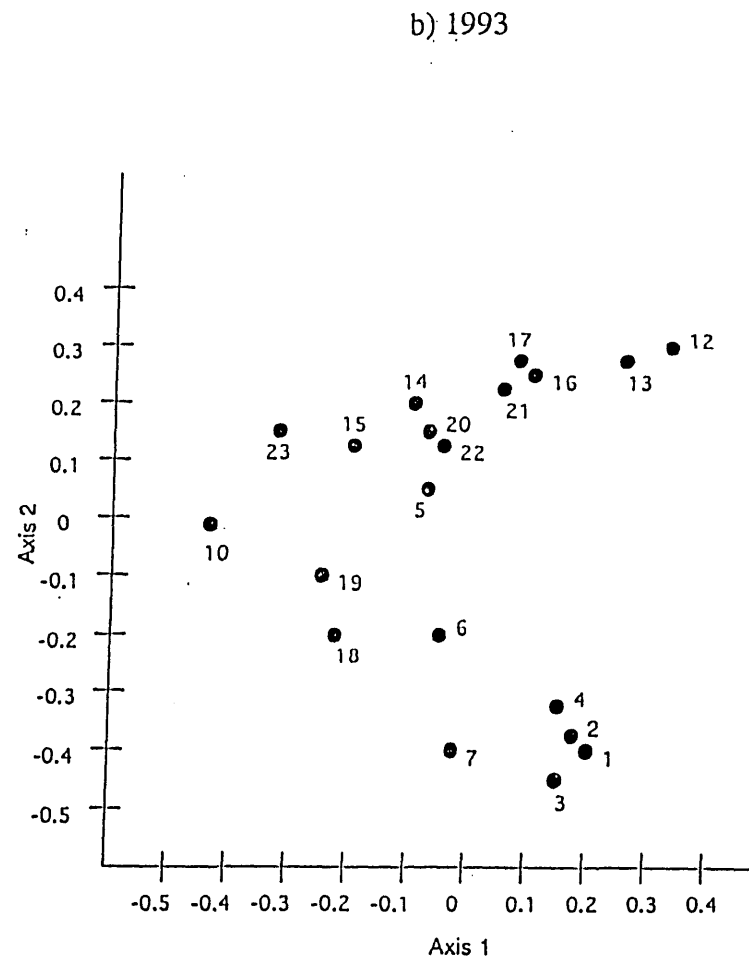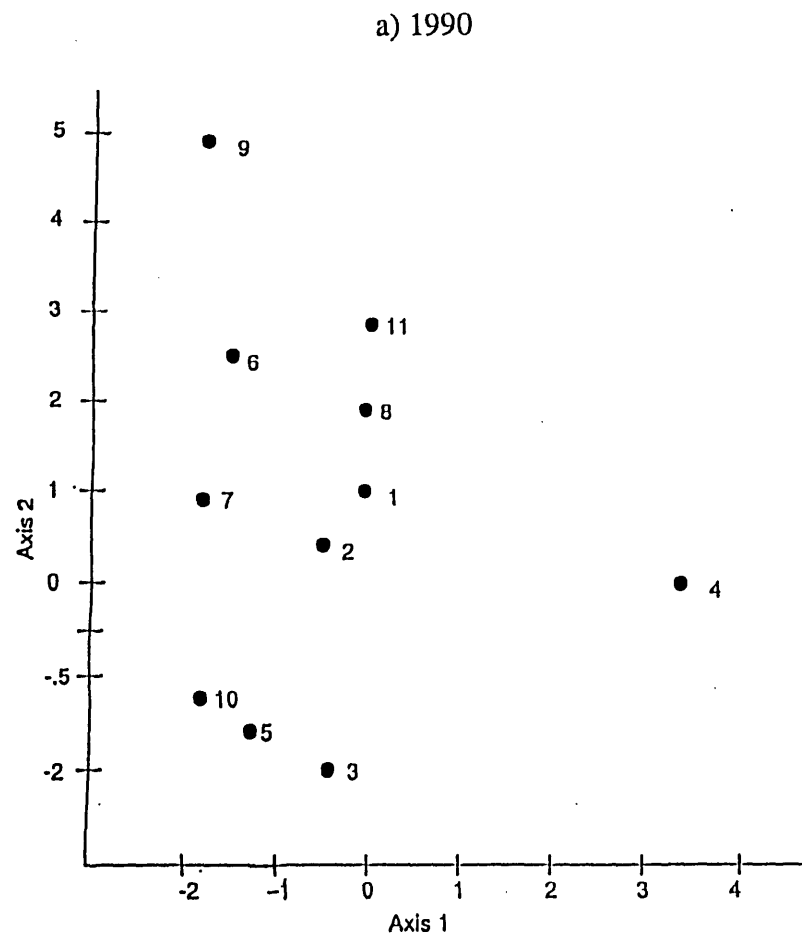
a) 1990

b) 1993

Fig. 4.6. Species ordination based on percentage composition by basal cover using the reciprocal averaging technique.

1. *Microlaena stipoides*
2. *Trifolium repens*
3. *Lolium perenne*
4. *Dactylis glomerata*
5. *Carex inversa*
6. *Poa pratensis*
7. *Paspalum dilatatum*
8. *Elymus scaber*

9. *Sporobolus creber*
10. *Bothriochloa macra*
11. *Poa sieberiana*
12. *Eragrostis molybdea*
13. *Hemarthria uncinata*
14. *Juncus* sp.
15. *Pennisetum alopecuroides*
16. *Lomandra filiformis*

17. *Pteridium esculentum*
18. *Eleusine tristachya*
19. *Cynodon dactylon*
20. *Danthonia pilosa*
21. *Holcus lanatus*
22. *Festuca elatior*
23. *Danthonia* sp.

Table 4.2. Results of discriminant function analysis for the 1990 and 1993 surveys.

a) 1990 survey

Predictor variable	Correlation of predictor variables with discriminant functions	
	1	2
M. stipoides	0.47	-0.03
T. repens	0.30	-0.23
L. perenne	-0.81	-0.42
D. glomerata	-0.14	0.95
C. inversa	-0.12	-0.06
P. pratensis	0.05	-0.12
P. dilatatum	0.04	-0.10
E. scaber	0.02	-0.01
S. creber	0.02	-0.01
B. macra	-0.01	-0.04
P. sieberiana	0.02	0.08
Canonical *R*	0.97	0.96
Eigenvalue	14.44	13.48

b) 1993 survey

Predictor variable	Correlation of predictor variables with discriminant functions	
	1	2
M. stipoides	-0.21	0.28
L. perenne	0.15	0.02
P. pratensis	-0.11	0.03
D. glomerata	-0.07	0.12
P. dilatatum	0.04	-0.08
E. tristachya	0.10	-0.05
C. dactylon	0.61	-0.42
F. elatior	0.03	-0.01
T. repens	-0.01	0.13
C. inversa	-0.04	-0.01
H. lanatus	-0.14	-0.08
E. molybdea	-0.04	-0.04
H. uncinata	-0.04	-0.04
Juncus sp.	-0.01	-0.04
P. alopecuroides	-0.03	-0.04
L. filiformis	-0.02	0.02
P. esculentum	-0.02	0.02
B. macra	0.02	-0.01
D. pilosa	-0.25	-0.55
Danthonia sp.	-0.03	-0.17
Canonical *R*	0.98	0.97
Eigenvalue	27.02	17.00

and *L. perenne* was more abundant in open areas, as found by Turkington and Harper (1979a). Rose (1986) and Huxtable (1990) found in laboratory studies that vegetative growth of *M. stipoides* increased in the shade. The absence of *M. stipoides* in both surveys at the upper western corner of the paddock near the opportunity feedlot was probably due to a spill over of molasses in July 1987 that ran down the area and killed most of the species, *L. perenne* being the first species to recover and recolonise the area.

During the first survey, locations with a high cover of either *M. stipoides* or *L. perenne* in many cases had lower cover of the other species (Table 4.1a). The complementary nature of these two species is further illustrated by the separation of the sites dominated by each species in the discriminant analysis territorial map (Fig. 4.5a) and the separation of them on axis two of Fig. 4.5a. Three years later, close associations between *M. stipoides*, *L. perenne*, *T. repens*, *D. glomerata* and *P. pratensis* were clearly shown by the discriminant analysis territorial map and species ordination (Figs. 4.5b and 4.6b).

Abundance of *D. glomerata* under tree canopies was consistent with the findings of Turkington and Harper (1979a), who also reported a highly significant positive relationship between *D. glomerata* and nitrate-N, which is highest near trees. In the 1990 survey, locations with high cover of *D. glomerata* (groups 18, 19 and 20; Table 4.1a) also tended to have high cover of *M. stipoides*, except for group 18. Although *D. glomerata* is well separated from all other species in the species ordination (Fig. 4.6a), it was obvious that at least some genotypes of *M. stipoides* can co-exist with *D. glomerata*. This association was supported by the results of the 1993 survey where groups 10 and 11 (Table 4.1b) had high abundance of *D. glomerata* and *M. stipoides*.

In both surveys, it was generally observed that the presence of *L. perenne* was greatly reduced in sampling locations where *D. glomerata* comprised more than 40% of total basal cover. These sampling locations were confined to the upper slopes on the upper north-eastern part of the paddock above the gravel road. Likewise, *D. glomerata* was rarely observed in sampling locations dominated by *L. perenne,* which was more common on the lower parts of slopes. *Lolium perenne* and *D. glomerata* have the same growth forms, both are tufted perennials with erect or spreading culms so that they form patches in the field. Kershaw (1959) reported that when the two species are established in the same area, they spread by vegetative growth until they come into contact with each other. Then, in areas unfavourable to *L. perenne*, *D. glomerata* spreads at the expense of *L. perenne*, while the reverse occurs in areas unfavourable to *D. glomerata*. Both the hierarchical fusion and discriminant function analysis using the 20 groups formed by the fusion for the 1990 survey, clearly separated locations dominated by *L. perenne* and by *D. glomerata* from the

rest. Isonome maps in the 1990 survey show that each of these species occupies distinct areas in the paddock.

Poa pratensis had an interesting species association. It was well separated from all the other major species in the species ordination (Fig. 4.6a), but was closely associated with *L. perenne* at one location (group 3, Table 4.1a) and with *M. stipoides* at two others (group 7, Table 4.1a) in the 1990 survey. Three years later, territorial maps and the dendrogram show that *P. pratensis* had improved associations with *M. stipoides*, *L. perenne* and *T. repens*. In both surveys, *P. pratensis* was confined to flat areas on the lower slopes of the paddock where soil moisture was possibly higher. Again, perhaps the genotypes of *M. stipoides* associated with *P. pratensis* are different from those associated with other species in this paddock.

The increase in abundance of *P. dilatatum* in the paddock after three years is an indication that some factors had been favourable for the seed emergence or vegetative growth of the species. Presence of *P. dilatatum* in the northwestern area between the road and creek and in the lower eastern part of the paddock below the gravel road supports the observation of Lodge and Whalley (1989) that it is widespread in damp areas and along creeks where it makes prolific growth during summer. *Paspalum dilatatum* was associated with *M. stipoides*, *L. perenne* and *T. repens* in several patches scattered all over the paddock.

The increase in species diversity in the 1993 survey could be attributed to several environmental and biotic factors. The decline in soil phosphorus level due to cessation of annual superphosphate application since 1990 may have enabled other minor species to be able to compete and become dominant in scattered patches in the paddock. The lack of rain during the period 1990 to 1993 may have favoured drought tolerant species. The decline in abundance of *T. repens* may have favoured other species that do not particularly benefit from the nitrogen fixed by the *T. repens - Rhizobium* sp. association.

The high percentage basal cover of *M. stipoides* in sampling locations in association with the other dominating perennial grasses such as *L. perenne*, *D. glomerata* and *P. pratensis* may indicate that *M. stipoides* can become adapted to grow in close association with the other species in the area. Results of the species ordination for the 1993 survey showing *M. stipoides* in close proximity with most of the other dominant grasses may imply permanency of these species associations (Fig. 4.6b). The aggregation of sampling locations dominated by mixed *M. stipoides*, *T. repens* and *L. perenne* in the discriminant function analysis using the 20 groups determined by Bray-Curtis hierarchical classification also suggests stability in this species combination (Turkington and Harper 1979a).

In both surveys, the abundance of *T. repens*, growing in association with *M. stipoides*, *L. perenne* and *P. pratensis*, in the lower eastern and southern portions of the paddock below the gravel road may have been influenced by the wetter conditions there. The reduction in the abundance of *T. repens* all over the paddock after three years may be attributed to the occurrence of drought during this period.

All the four most abundant perennial grasses were found cohabiting at least in some locations with *T. repens*. This may possibly be due to the beneficial effects of nitrogen provided by *T. repens* to its companion grass (Spedding and Diekmahns 1972), but may also be due to the marked dissimilarities in their growth cycles, which prevent competitive exclusion (Turkington and Harper 1979a). The growth forms of *T. repens* and the other four perennial grasses studied differ. *Lolium perenne* and *D. glomerata* are tufted perennials with erect or spreading culms, while the other two species, *M. stipoides* and *P. pratensis*, are more prostrate and somewhat stoloniferous. *Trifolium repens* 'wanders' (Leith 1960) by extensive stoloniferous growth.

There are general similarities between the distribution of *M. stipoides* and *T. repens* in the paddock (Figs. 4.1b and 4.1f) and these two species are quite close together in the species ordination. Snaydon (1962) reported that *T. repens* was present in scattered areas of more base-rich, fertile soils and was quite sensitive to acidic soil pH and susceptible to high concentrations of Al and Mn. The growth and infectivity of the nitrogen-fixing bacterium *Rhizobium* was sharply reduced below approximately pH 5 (Vincent 1958, Mulder and van Veen 1960). *Microlaena stipoides*, on the other hand, is more abundant in acidic soils (Munnich *et al.* 1991, Magcale-Macandog and Whalley 1994). Both were widespread throughout the paddock and are associated with different species at different locations (Table 4.1a). Turkington and Harper (1979b) found substantial differences among genotypes of *T. repens* in the field which were growing in association with different perennial grasses. Perhaps similar differences occur among genotypes of *M. stipoides* growing in association with the different perennial grasses.