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Management of European floodplain grasslands for plant biodiversity

by

Christopher Brian Joyce

A Doctoral Thesis

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for the award of**

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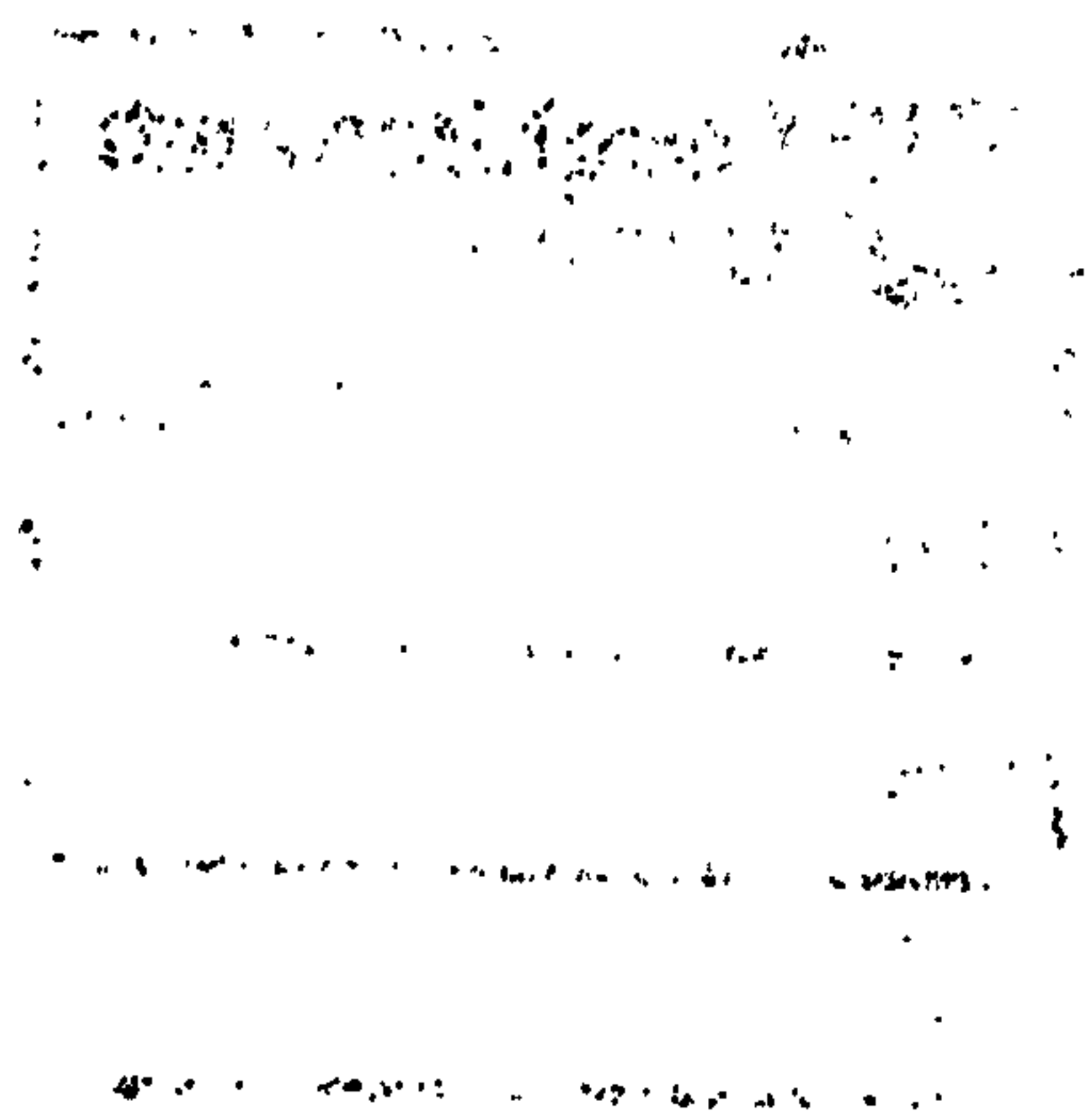
What if the gorse-flowers shrivelled, and I were gone?

What if the waters ceased, where were the marigolds then, and the gudgeon?

What is this thing that I look down upon?

White on the water wimples my shadow, strains like a dog on a string, to run on.

D.H. Lawrence, *The Wild Common*



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Abstract

European floodplain grasslands are characterized by periodic flooding and regular management, usually cutting and grazing as part of an agricultural system. Past losses and ecological degradation have been due largely to river regulation and either agricultural intensification or abandonment and have resulted in a substantial reduction in area across Europe. Nevertheless, the remaining resource supports considerable biodiversity and a high level of biological production. A better quantitative understanding of the functioning of these grasslands is required in order to establish effective conservation management within a sustainable land use system. The thesis examines the impact of key management factors on three important functional characteristics of the biodiversity of floodplain plant communities, namely plant diversity (measured by species diversity), cover (%) and primary production (above-ground biomass), on two floodplain grasslands of the River Trent, UK and a third on the the Lužnice river, the Czech Republic. Field investigations of the effects of cutting, grazing, cessation of management, the influence of floodborne litter, and the impact of fertilizer nitrogen were undertaken over periods of between one and three seasons. These demonstrated that floodplain grassland plant communities are sensitive to variations in management and that impacts on communities are mediated particularly through effects on plant competition. Productive competitive species were encouraged both by abandonment and fertilizer application whereas cutting and grazing management, and the imposition of litter, favoured stress-tolerating perennials. Species diversity decreased both with high inputs of litter and additions of fertilizer. Plant community responses and competitive strategies of key species are discussed in the context of biodiversity conservation, ecological restoration and management of European floodplain grasslands.

Keywords: Biodiversity, Europe, Floodplain grasslands, Grassland management, Nature conservation, Plant competition, Restoration

Chapter 1 Introduction

Floodplain grasslands are an integral component of the European biodiversity resource. Although they are largely dependent upon human management for their maintenance, land-use changes have reduced the extent and ecological quality of the floodplain grassland resource in Europe, with important implications for biodiversity. There is therefore a pressing need to understand the key processes that operate within the floodplain grassland system in order to direct effective conservation management and restoration.

1.1 Ecological attributes of floodplains

Floodplains are areas of low relief that are periodically inundated by the overflow of rivers and lakes (Junk *et al.*, 1989). Floodplain ecosystems represent a dynamic transitional interface between terrestrial and aquatic environments (Naiman and Décamps, 1990). They possess properties of both systems, as well as having unique properties of their own, and are therefore biodiverse (Junk *et al.*, 1989; Risser, 1990), support a high level of biological processing (Gregory *et al.*, 1991), and are sensitive to environmental change including natural and anthropogenic stress and disturbance (Prach *et al.*, 1990; Sparks *et al.*, 1990; Décamps, 1993; Nilsson and Jansson, 1995). These areas are a valuable ecological resource, possessing characteristic physical properties and distinct plant communities (Amoros *et al.*, 1987; Ellenberg, 1988) and representing key elements in the maintenance and management of local and landscape biodiversity (Naiman *et al.*, 1993). In particular, riparian areas form important routes for the dispersal of plants and animals, and provide corridors for migratory species (Gregory *et al.*, 1991; Johansson *et al.*, 1996). Similarly, they allow flows of energy, water, nutrients and materials such as dissolved and particulate matter across and through the landscape (Malanson, 1993). Such fluxes are not solely in a downstream direction; floodborne nutrients, sediments and organic matter move laterally and are deposited onto floodplains, as well as being transported off the land into the channel. Hence, floodplains are a vital source of energy for rivers, indeed terrestrial litter can constitute their main supply of organic matter (Pinay *et al.*, 1990). The water resource benefits of floodplains include floodwater retention and control, which can result in enhanced sediment storage, fewer erosion problems and improved groundwater recharge (Dister *et al.*, 1990). Floodplain vegetation can also maintain or improve water quality through retention of suspended matter and natural purification of nutrients (Brinson *et al.*, 1984; Pinay *et al.*, 1990). The dense root

system of grasses plays a key role in both filtration and reduction of erosion as it contributes substantially to soil formation (Kvet, 1996).

Floodplain zones also contain valuable fisheries and opportunities for agricultural production. Consequently, floodplain ecosystems are also among those environments with the longest history of human modification and management (Nilsson *et al.*, 1993; Petts *et al.*, 1989). For example, since the 17th century the Garonne floodplain corridor in southern France has been influenced by river navigation development, flood protection, agriculture, urbanization and industrialization, which have resulted in hydrological modification and fragmentation of natural vegetation (Décamps *et al.*, 1988). The recreational, educational/scientific and cultural value of the European floodplain landscape is widely acknowledged (Beaufoy *et al.*, 1994; Rychnovská *et al.*, 1994; Bignal and McCracken, 1996).

1.2 European floodplain grasslands

Most floodplain grasslands in Europe are located on riverine floodplains (rather than lake margins) and are primarily a lowland habitat, hence are often referred to by the generic term lowland wet grasslands (e.g. Dargie, 1993; Jefferson and Grice, 1998). Floodplain grasslands are characterized by an abundance of grasses, periodic but not perpetual flooding with fresh or brackish water, or a high water table, and regular management, usually cutting (mowing) or grazing. They may support a mosaic of associated plant communities (e.g. swamp, mire and fen) and habitats, including wetland features such as drainage channels and floodplain pools. A number of terms have been used to identify and describe different types of floodplain grasslands in Europe, including inundation grasslands, alluvial or flood meadows, washlands, polders, and grazing marshes or pastures.

1.2.1 Flooding and hydrological regulation

Rivers exert strong effects on floodplain habitat formation and stability, on vegetation structure and species composition, and on the diversity of ecological functions primarily through flooding (Naiman *et al.*, 1993). Flood events influence the vegetation both directly, by the level of the water table above or below the soil surface, and indirectly, by periodic enrichment of the soil with nutrients transported from other parts of the catchment. Flooding influences lateral fluxes of material between the river and floodplain (Pinay *et al.*, 1990) and also redistributes nutrients

and organic matter such as litter and acts as an agent of plant dispersal (Ellenberg, 1988; Nilsson *et al.*, 1991). Flood events can therefore introduce spatial and temporal heterogeneity into the floodplain environment, for example by the patchy deposition and accumulation of floodborne sediment and litter (Facelli and Pickett, 1991; Xiong and Nilsson, 1997). Floodborne litter provides the focus for chapter 4 of this study.

Human management of the river-floodplain system frequently incorporates river regulation, which in Europe has evolved over more than 200 years (Petts, 1989), including channel modification and flood protection. Regulation has dramatically altered the flooding characteristics of rivers, such as flood magnitude and timing, impaired hydrological and ecological interactions between the main fluvial channel and its floodplain, and has had a major negative impact on the biodiversity of the floodplain corridor (Décamps *et al.*, 1988; Petts *et al.*, 1989). Reduced flooding may be particularly detrimental to plant species diversity, as flooding facilitates dispersal by transporting and depositing diaspores (Nilsson and Grelsson, 1990; Johansson *et al.*, 1996).

Hydrological manipulation for nature conservation objectives is primarily concerned with the maintenance of an appropriate water regime, particularly achieving wet conditions for certain periods of the year. The specific water regime depends on the target wildlife species, groups or habitats. For example, many waterfowl and waders require shallow flooding to provide feeding opportunities and secure roost sites in winter (Thomas, 1982; Self *et al.*, 1994). For breeding waders, a high soil water table during the breeding season (approximately March-June) is probably the single most important hydrological factor (Ward, 1994). Plant communities are substantially influenced by the depth and annual variation of the water table. The composition of a plant community may be radically altered by shifts in water regime, as some species are adapted to survive in anaerobic soil conditions due to high water tables (Ernst, 1990). Newbold and Mountford (1997) document many floodplain grassland plant communities and species that require or tolerate moist and even waterlogged soil conditions, and periodic inundation, although some floodplain grasslands are characterized by drought stress in summer due to reduced water supply and free-draining top soils. In addition, many plant and animal species have exacting water quality requirements, being influenced by factors such as pH, salinity, and nutrient status (Ellenberg, 1988; Rimes, 1992; Spieksma *et al.*, 1995).

1.2.2 Vegetation management

Few floodplain grasslands in Europe are natural. Exceptions may include plant communities of spring-fed or regularly flooded sites where frequent inundation restricts vegetation succession and the ice-governed riparian meadows of northern Europe (Arnqvist and Dynesius, 1987; Rychnovská, 1993). Most floodplain grasslands have been created by human activity, usually by forest clearance or the drainage of bogs and marshes (Ellenberg, 1988), and are maintained by human intervention, usually cutting or grazing by livestock. Hence, plant species occurring in these semi-natural floodplain grasslands are likely to have originated from the ground flora and glades of floodplain forests, natural floodplain wetlands (e.g. reedbeds, swamps, mires and fens) where a high water table restricted shrub and tree growth, and regularly inundated river banks (Ellenberg, 1988; Duffey *et al.*, 1974; Jefferson, 1997).

The distinctive and ecologically valuable plant communities of European floodplain grasslands are characterized by periodic inundation (or a high water table) and regular appropriate vegetation management which is often based on traditional farming practices. The latter is usually as part of an agricultural system that utilizes the primary production to support domestic herbivores either directly through grazing (pastures) or indirectly by harvesting hay (meadows). Pastures are grasslands that are grazed usually by cattle or sheep. Meadow management comprises cutting (mowing) for a hay crop at least once annually. The regrowth (aftermath) can subsequently be used for grazing, which is common in western Europe (e.g. Baker, 1937), or, as in many parts of central Europe, cut again for further hay crops (Prach *et al.*, 1996). Exceptionally, burning of floodplain grasslands is used as a management tool, particularly to remove accumulated litter (Royal Society for the Protection of Birds, English Nature and Institute of Terrestrial Ecology, 1997).

In England, palynological evidence indicates that floodplain grasslands have existed for more than 3 000 years (Greig, 1984) and the characteristic flood-meadow plant community has probably been a feature of the Thames floodplain for 2 000 years (Lambrick and Robinson, 1988). Indeed, some English floodplain grasslands, known as Lammas lands, are still managed using a commonland system that has been documented since medieval times (Gibbons, 1990). This incorporates mowing the fields for hay in summer and excluding livestock until Lammas day (12 August) when grazing of the regrowth is allowed on a communal basis (Duffey *et al.*, 1974). This pattern of land management has tended to inhibit intensification of grassland management, such as the application of fertilizers and increased cutting frequency and

stocking density. One such Lammas floodplain grassland, North Meadow near Cricklade, Wiltshire, supports over 80% of the British population of the internationally scarce plant *Fritillaria meleagris* (Gibbons, 1990).

Floodplain grasslands have long provided an important contribution to the agricultural economy, their agricultural value has been appreciated and actively managed for since at least the sixteenth century (Sheail, 1971). In England for example, water meadows were developed on floodplains between the 16th and 19th centuries. The hydrology of these sites was intensively manipulated, being regulated by a system of weirs, artificial channels and earthworks to provide a time table of irrigation with nutrient-rich floodwater and drainage in order to stimulate grass production, especially for grazing early in the growing season (Sheail, 1971; Duffey *et al.*, 1974). As a result, such sites were commonly noted for their lush, grass-dominant vegetation (Fream, 1888). Water meadow management declined early this century with the increasing use of inorganic fertilizers and few are now operated.

In the past, grassland management was part of an extensive or low-intensity agricultural system that was characterized by low fertilizer input, minimal land drainage, cutting for hay and low grazing livestock densities (Beaufoy *et al.*, 1994). This traditional pattern of management is summarized in Table 1.1.

Table 1.1 Typical characteristics of traditional and modern floodplain grassland management in Europe

	Traditional	Modern
<u>Hydrology:</u>		
Flooding	Unregulated	Regulated
Water table	High	Low
<u>Vegetation management:</u>		
Cutting frequency	Low (but regular)	High
Livestock density	Low	High
Use of artificial fertilizers	None	High
Use of other agro-chemicals (e.g. herbicides)	None	High

Traditional grassland management created and maintained beneficial conditions for a wide range of flora and fauna (Signal and McCracken, 1996). However, widespread losses and ecological degradation of European floodplain grasslands have occurred, especially in the last 50 years (van Dijk, 1991; Large *et al.*, 1994; Grootjans *et al.*, 1996). This has been largely due to agricultural intensification, often facilitated by river regulation and land drainage (Table 1.1) in order to increase grass production or to convert permanent grassland to arable crops (Fuller, 1987; Wells and Sheail, 1988; Haury *et al.*, 1990). The general characteristics of modern intensive grassland management systems are shown in Table 1.1. They often include the use of agrochemicals, particularly artificial inorganic fertilizers, increased cutting frequencies (e.g. for silage) and increased stocking densities (International Union for Conservation of Nature and Natural Resources, 1991; van Dijk, 1991; International Union for Conservation of Nature and Natural Resources, 1993).

The main impact of land-use changes in Europe has been to reduce biodiversity through the degradation and fragmentation of semi-natural vegetation and the elimination of characteristic, often rare, species. Evidence of this conflict between nature conservation and the intensification of floodplain management is widespread. For example, approximately 12.5×10^6 ha of floodplain marsh of the River Tisza in Hungary were drained following regulation beginning in 1845 (Petts, 1989). Widespread river regulation since the 1940s in the Czech Republic was followed by ploughing of botanically diverse floodplain grasslands (Kundrata *et al.*, 1995) such that floodplain grassland plant communities are now among the most endangered in the country (Straškrabová *et al.*, 1996). Also, between 1950 and 1990 the area of wet meadows in Hungary declined from 600 000 to 200 000 ha as a result of drainage and agricultural intensification to increase production. During this period, fertilizer usage on Hungarian grasslands doubled (International Union for Conservation of Nature and Natural Resources, 1990). In the Czech Republic, the use of inorganic fertilizers has increased 30 fold since 1937, exceeding $300 \text{ kg N ha yr}^{-1}$ in many regions (Kundrata *et al.*, 1995). In 1950 the average input of nitrogen fertilizer to grasslands in the Netherlands was approximately $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, whereas in 1980 this had increased to approximately $400 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (van der Meer, 1982). Evidence indicates that inorganic fertilization may alter plant community composition and reduce species diversity in many semi-natural grasslands, favouring taller productive species (Traczyk *et al.*, 1984; Mountford *et al.*, 1993); this is examined in detail for flood-meadows in chapters 5 and 6. Furthermore, leaching of nitrogenous fertilizers has led to increased nitrates in ground and surface water, contributing to considerable eutrophication of floodplain ecosystems. Eutrophic floodwater can also induce vegetation change, for example by encouraging the development of *Glyceria maxima*

swamp (Burgess *et al.*, 1990). European floodplain grasslands have also been eliminated and degraded through pollution, water abstraction, mineral extraction and industrial and urban development (Vermeer, 1986; International Union for Conservation of Nature and Natural Resources, 1993).

Many remaining European floodplain grasslands of nature conservation value are deteriorating through a lack of management with, for example, agricultural over-production and policy reform in western Europe has led to the withdrawal of marginal areas from agriculture (Bignal and McCracken, 1992). Also, many central and eastern European countries have recently undergone change in their agricultural as well as political systems, resulting in uncertainty over land ownership and the neglect or abandonment of many areas (Baldock, 1994; Straškrabová *et al.*, 1996). For example, in Estonia cutting and grazing management of floodplain grasslands has almost completely ceased, due to uncertainties over land ownership and the use of intensively managed cultivated grasslands for fodder production (Truus, 1996). Unmanaged grasslands tend to exhibit reduced nature conservation value, becoming dominated by just a few robust competitive plant species (Bakker, 1989; Rychnovská *et al.*, 1994; Guth and Prach, 1996) at the expense of plant diversity (Regnéll, 1980; Oomes and Mooi, 1981). They eventually succeed to shrubland or forest although succession can be arrested if plant litter, which tends to accumulate in the absence of management, or competition from the herbaceous field layer, exclude woody species (Prach, 1994). The effects of abandonment on floodplain grassland plant communities are explored in chapter 3.

In recent years, heightened scientific and political concerns over the decrease in extent and deterioration of the European floodplain grassland resource, coupled with recognition of its international importance for biodiversity conservation, have led to its inclusion within a number of environmental treaties, including those fostered by the United Nations and the European Union as well as national governments. Several international initiatives, such as NATURA 2000 and the Convention on Biological Diversity (and its national Biodiversity Action Plans), have emerged recently that build upon the foundation established by existing strategies to protect key European sites, such as the Ramsar Convention (Hill *et al.*, 1996; Wascher, 1998), and encourage expansion of the resource in order to facilitate the conservation of species and communities that were formerly more widespread. Governments and environmental organisations have made the maintenance and restoration of the biodiversity of floodplain grasslands at both national and international levels a focus of their conservation efforts (e.g. Royal Society for the Protection of Birds, 1993; Ministry of Agriculture of the Czech Republic, 1994; The UK Steering Group, 1995).

These initiatives not only reinforce protective legislation but also offer opportunities for the sustainable management and restoration of the floodplain grassland resource in order to conserve biodiversity.

1.2.3 Biodiversity

Biodiversity has been defined as the variety of living organisms and the ecological complexes of which they are a part, including diversity between species and of ecosystems (Hill *et al.*, 1996). The concept therefore encompasses the presence of ecological processes as well as species. The benefits of biodiversity to humans may include the maintenance of ecosystem functions; storage and cycling of nutrients; absorbing and breaking down pollutants; recharging groundwater, protecting catchments and buffering extreme water conditions; producing soil and protecting it from excessive erosion; providing food and raw material for industry and medicine; providing the basis for new foods, chemicals and pharmaceuticals, and improvements to domesticated plants and animals; and providing aesthetic and spiritual attributes (The UK Steering Group, 1995; Hill *et al.*, 1996). The rapid global decline in biodiversity has both heightened appreciation of the importance of the resource and reinforced international concern over the effects of environmental change associated with human activities. As a result, attention is increasingly being drawn towards the conservation of areas of high biodiversity.

European floodplain grasslands support considerable biodiversity including rare and threatened plant species and vegetation types (Rodwell, 1992; Rychnovská, 1993; Straškrabová *et al.*, 1996), nationally and internationally important bird populations (BirdLife International European Agriculture Task Force, 1996; Hötker, 1991b) and a range of invertebrates, some of which are also rare (Drake, 1998). Botanical diversity can be high, particularly at the small-scale. For example, Pasternak-Kuśmierska (1984) found 24 vascular plant species m^{-2} in an alluvial meadow in Poland and Mediterranean flood-grasslands can display more than 50 species 2.5 m^{-2} (Puerto *et al.*, 1990). Prach and Straškrabová (1996) recorded almost 80 species from a transect of approximately 150 metres length from the floodplain grassland of the Lužnice River in the Czech Republic. Approximately 540 species of vascular plants have been recorded from the Morava river floodplain, Slovakia, of which 12% are nationally rare or endangered (Ružička, 1994), whilst as many as 655 vascular plant species have been found from a 500m reach of the Adour River floodplain in France (Décamps and Tabacchi, 1994).

A number of globally threatened and declining plant species are associated with floodplain grasslands in Europe, including *Apium repens*, *Selinum carvifolia* and *Scorzonera humilis* (Jefferson and Grice, 1998), as well as aesthetically attractive and emblematic species such as *Fritillaria meleagris*, which has its European stronghold in English floodplain meadows (Oswald, 1992). Some of the plant communities of floodplain grassland have become very restricted in extent. These include the *Alopecurus pratensis*-*Sanguisorba officinalis* flood meadow community which is confined largely to south and central England (Jefferson, 1997) and meadow communities of the *Cnidion venosii* alliance, which typically contain more than 30 species m⁻² and are associated with central European floodplains (Balátová-Tuláčková, 1969). Both of these grassland types are specially protected by the European Union through the Habitats Directive (Council of the European Communities, 1992).

Floodplain grasslands provide breeding or wintering habitats for a number of bird species, particularly wading birds (waders) and wildfowl. Recent estimates of the populations of waders breeding in the countries of the European Union found that more than half of all the waders in the region breed on wet grasslands and that nearly 90% of the species are declining due to habitat loss (Hötter, 1991a). In the UK, over 40 bird species of conservation concern are dependent or partly dependent on wet floodplain grasslands, including globally endangered species such as *Crex crex* (corncrake), and other internationally important species, e.g. *Limosa limosa* (black-tailed godwit), *Cygnus columbianus bewickii* (Bewick's swan), *Anser fabalis* (bean goose), and *Anas acuta* (pintail) (Royal Society for the Protection of Birds, English Nature and Institute of Terrestrial Ecology, 1997).

Floodplain grasslands can support a high diversity of invertebrates (Kirby, 1992) although relatively few rare species appear to be dependent upon the grass sward itself (Greenwood *et al.*, 1995; Drake, 1998). Invertebrate diversity and the number of rare species tends to be associated with environmental heterogeneity in the floodplain grassland landscape (Greenwood *et al.*, 1991), which is provided by habitats such as damp hollows and temporary pools (Kirby, 1992), drainage channels (Hingley, 1979; Verdonschot and Higler, 1989) and old trees (Drake, 1998). Some internationally rare invertebrates are associated with floodplain grasslands including the butterfly *Eurodryas aurinia* (marsh fritillary) which has a restricted and declining European distribution and is globally threatened (Thomas and Lewington, 1991). The invertebrate fauna of floodplain grasslands is of considerable value in providing prey items for waders (Blake and Foster, 1998).

Other wildlife of importance that utilize floodplain grasslands and their associated habitats in Europe include amphibians, fish, and mammals such as *Lutra lutra* (otter), *Arvicola terrestris* (water vole) and *Alces alces* (moose) (Kminiak, 1994; Bejček and Šťastný, 1996; Leibak and Lutsar, 1996).

The maintenance of the biodiversity of European floodplain grasslands depends upon regular human intervention in the form of appropriate vegetation management. An understanding of plant community dynamics is therefore important for effective conservation management. Inter-specific competition operating at the scale of the plant community provides a framework for elucidating plant diversity and community dynamics in relation to the management of floodplain grasslands.

1.3 Competition and the floodplain grassland plant community

Plant communities are assemblages of populations that live in an environment and interact with one another (Whittaker, 1975). A plant community may therefore be considered as a vegetation type characterized by its floristic composition. Both the community itself, and the species that constitute the community, are considered to be a very sensitive expression of biotic and environmental relationships (Grootjans *et al.*, 1996), particularly because relations between the components of the plant community vary spatially and temporally (Watt, 1947).

Most plant communities consist of several or many species which compete, at least partially, for resources such as light and nutrients. Hence, the plant species composition of floodplain grassland communities reflects the competitiveness of individual species under particular circumstances and, because competitive interactions between species are potentially intense, local competitive interactions can have a strong influence on species diversity (Huston, 1994). Thus, among plant species that potentially compete, diversity may be regulated by competition.

Models presented by Grime (1973a, 1979) propose that intensities of disturbance and stress are important determinants of the competitive abilities of plants and plant species diversity. Specifically, Grime described a unimodal species diversity response to plant productivity regulated by intensities of stress and disturbance. Thus, it was suggested that maximum species diversity in established vegetation occurs at intermediate intensities of stress and/or disturbance as this reduces the vigour of potentially dominant competitive species, limiting above-ground plant production, and thereby allowing subsidiary species to co-exist with them. In

contrast, low intensities of stress or disturbance allow increased growth rate and production and lead to competitive exclusion and so reduced species diversity, echoing the assertion of Whittaker (1965) that diversification is restricted by dominance. At the other extreme, with intense stress or disturbance species of high competitive ability are suppressed and species diversity is similarly limited but in this case by the scarcity of species tolerant of the specific conditions limiting productivity.

Competitive plant species are able to use surplus resources and maximize dry matter production, often having a tall and robust stature (Grime, 1973b, 1979). Both stress and disturbance function as modifiers of competition in established vegetation by debilitating potentially competitive dominants from attaining maximum size and vigour, allowing species of smaller stature and lower competitive ability to co-exist, as well as exerting a direct impact on species composition at high intensities. Stress may be considered as external constraints which limit production (e.g. shortages of light) (Grime, 1979). These may be an inherent characteristic of the environment, or they may be induced or intensified by the vegetation itself (Al-Mufti *et al.*, 1977). Disturbance arises from the partial or total destruction or removal of plant biomass (Grime, 1979), in floodplain grasslands by such activities as cutting and grazing and by severe flooding (see 1.2.1). In productive habitats exposed to repeated and severe disturbance plants with a ruderal strategy, able to exploit environments intermittently favourable for rapid plant growth, may prevail (Grime, 1979). Perturbations related to stress and disturbance can also influence the species composition and diversity of floodplain grassland plant communities by creating gaps and other opportunities for regeneration, as germination and establishment are two key factors in plant community organization (Grubb, 1977).

Huston (1979, 1994) concurred with Grime that species diversity may be reduced by the processes of intense competition when there is a high potential productivity, or by mortality when there is a high degree of disturbance. However, he suggested that diversity is maintained by periodic small-scale disturbances that slow plant growth and hence competitive displacement. This is the process of one population monopolizing resources at the expense of another population which decreases and ultimately becomes eliminated (Huston, 1994). Thus, anything that slows the population growth of competitors will tend to slow the rate of competitive displacement. High species diversity therefore exists when there is a dynamic equilibrium between disturbance and the rate of competitive displacement because a reduced rate of competitive displacement allows a longer period of co-existence among competitors. The dynamic equilibrium theory applies specifically to local species diversity within interacting communities, but it influences and is itself

influenced by environmental heterogeneity and species diversity at the landscape and regional scales (Huston, 1994).

Variations in resource availability may also alter competitive interactions between plant species in floodplain grasslands. Tilman (1982) hypothesized that spatial and temporal heterogeneity in resource availability (e.g. nutrients, light and water) were a major factor allowing species to co-exist and that species diversity is regulated by the proportion of resources available. Patterns of species richness in plant communities may therefore be explained by an equilibrium theory of plant competition for limiting resources. Extremely resource-poor habitats will support few species. Rather, plant community diversity will be maximal in moderately resource-poor habitats, as an increased number of species can live in more resource-rich habitats. However, in particularly resource-rich habitats, or if resource enrichment occurs, species richness will decline due to inter-specific competition, as superior competitors for resources in the particular proportion available will increase. It has been suggested that resource richness will also determine species composition and community structure, as each species is a superior competitor for only a small range of resource supply ratios (Tilman, 1982; Tilman, 1987). Disturbance in this context may be considered not as a mechanism that periodically interrupts competition within floodplain grassland communities, but as a process that influences the relative supply rates of the resources for which competition occurs.

1.3.1 Flooding and vegetation management as modifiers of competition

Floods control the spatial and temporal plant community dynamics of river-land interfaces (Décamps and Tabacchi, 1994) by altering the competitive relations between interacting species, both in the established and regenerative phases of plant life strategies. Flood events represent either a stress or disturbance on established plants depending on the severity (i.e. intensity, frequency and duration) of their impact on the floodplain vegetation (Décamps, 1993; van der Sman, 1993). Exclusion of species in floodplain vegetation may occur as result of competition for space after flood events (Décamps and Tabacchi, 1994). However, the frequent occurrence of floods may allow re-establishment during the growing season, particularly if plants possess the capacity to reproduce vegetatively, and losses in plant productivity due to flooding can be recovered by quick growth, early maturity and high reproduction rates, and rapid dispersal (Junk *et al.*, 1989). Indeed, it has been suggested that regular flooding plays a positive role in floodplain plant species diversity by disturbing dense vegetation and dispersing diaspores, to the extent that

productive sites in floodplains may have a greater species richness than comparable sites elsewhere (Prach *et al.*, 1996). The timing of flooding may also be of importance, particularly with regard to the creation of canopy gaps that facilitate plant regeneration (Grubb, 1977).

Most grassland species are perennials which maintain themselves by means of vegetative reproduction and occasional seed germination (Parr and Way, 1988). Vegetation management involving defoliation, such as cutting and grazing, helps maintain plant species diversity by limiting the ability of competitive species to attain maximum size and vigour. Management therefore limits the expression of dominance, increasing the incidence of light at ground level (Ellenberg, 1988), and its effect is usually to allow plants of smaller stature to co-exist with the potential dominants (Grime, 1979). Periodic management-related perturbations, particularly through grazing and trampling but also cutting, can create gaps in the sward allowing the establishment of new grassland plants and species in the regenerative phase (Grubb, 1977). This may be particularly important for the long-term maintenance of species richness and nature conservation value in floodplain grasslands. The actions of grazing herbivores, in particular, create spatial heterogeneity, which is likely to increase species richness (Huston, 1994). In addition, cutting and grazing management generally helps prevent the build up of litter that accumulates when uncut senescent vegetation collapses at the end of the season (Parr and Way, 1988).

1.4 Thesis aims and structure

With the rapid global decline in biodiversity and intense concern over the effects of environmental change associated with human impact, attention is being directed towards the conservation and sustainable management of the remaining biodiversity resource, particularly areas of high biodiversity. Recent studies of competition within the plant community have focused on the relationships between biodiversity and community processes, such as inter-specific competition and productivity, in response to environmental perturbation and change (Tilman, 1996; Tilman *et al.*, 1996). In particular, declining biodiversity associated with human activities has prompted concerns over whether such impacts can alter the performance and dynamics of ecosystems (Naeem *et al.*, 1994).

The considerable past reduction in the extent and ecological quality of the floodplain grassland resource in Europe means that protection and management of the remaining sites of conservation value, and expansion of the resource through restoration, is

essential. However, a detailed understanding of the small-scale processes responsible for maintenance of plant species diversity and community composition is critical if efforts to manage and restore the biodiversity of floodplain grassland ecosystems are to be effective.

This thesis focuses on the management of European floodplain grasslands for plant biodiversity. It describes fine-scaled, short-term impacts of key management factors on floodplain grassland plant community dynamics in order to inform effective conservation management. Field investigations incorporate two sites in England (Gunthorpe and Besthorpe) and one in the Czech Republic (Lužnice). The study sites are characterized by a range of plant diversity and production values that represent a broad spectrum of European floodplain grasslands. The sites and their plant communities are described in chapter 2, together with the general methodology applied. Specific aims of the following four chapters are to:

- i). elucidate the effects of cutting and grazing management, and abandonment, on plant diversity and community dynamics (chapter 3),
- ii). review and examine the impact of floodborne litter on plant species diversity and production (chapter 4),
- iii). examine the effects of fertilizer nitrogen on plant community composition of a traditionally-managed flood-meadow (chapter 5), and
- iv). determine the effects of increased nitrogen supply on a species-rich flood-meadow plant community (chapter 6).

In the final chapter (chapter 7), results are compared to other temperate managed grasslands and responses and competitive strategies of key communities and plant species are discussed in the context of biodiversity conservation and ecological management of European floodplain grasslands.

Chapter 2 General methodology

2.1 Study sites

Two of the three study sites, Gunthorpe and Besthorpe, were situated in the floodplain of the River Trent in England and were studied in 1993, 1994 and 1995. The fluvial hydrosystems and floodplain of the River Trent have provided a focus for interdisciplinary research at Loughborough University for over 10 years, including investigations of water quality (José, 1989), invertebrates (Greenwood *et al.*, 1991; Greenwood *et al.*, 1995) and hydrogeomorphological and ecological linkages (Petts *et al.*, 1992; Large *et al.*, 1994). The Gunthorpe and Besthorpe sites used in this study represent the two types of floodplain grassland that are of particular biodiversity interest, being semi-natural in character, of restricted occurrence in Britain and supporting important populations of plant species and other wildlife of conservation value (Rodwell, 1992; Jefferson and Grice, 1998).

The third study site was located in the Lužnice River floodplain in the Czech Republic and was investigated in 1994 and 1995. This floodplain has been studied by the Czech Academy of Sciences since 1986 because it is considered to be representative of small rivers in central Europe and displays a high biodiversity (Prach *et al.*, 1990; Prach *et al.*, 1996). Studies have focused on hydrological and ecological functioning and management of the river-floodplain system (e.g. Prach, 1992; Prach and Rauch, 1992; Klimešová, 1995) and they provided a context for the selection of the site used in this study, it being chosen primarily because of its high small-scale plant species diversity.

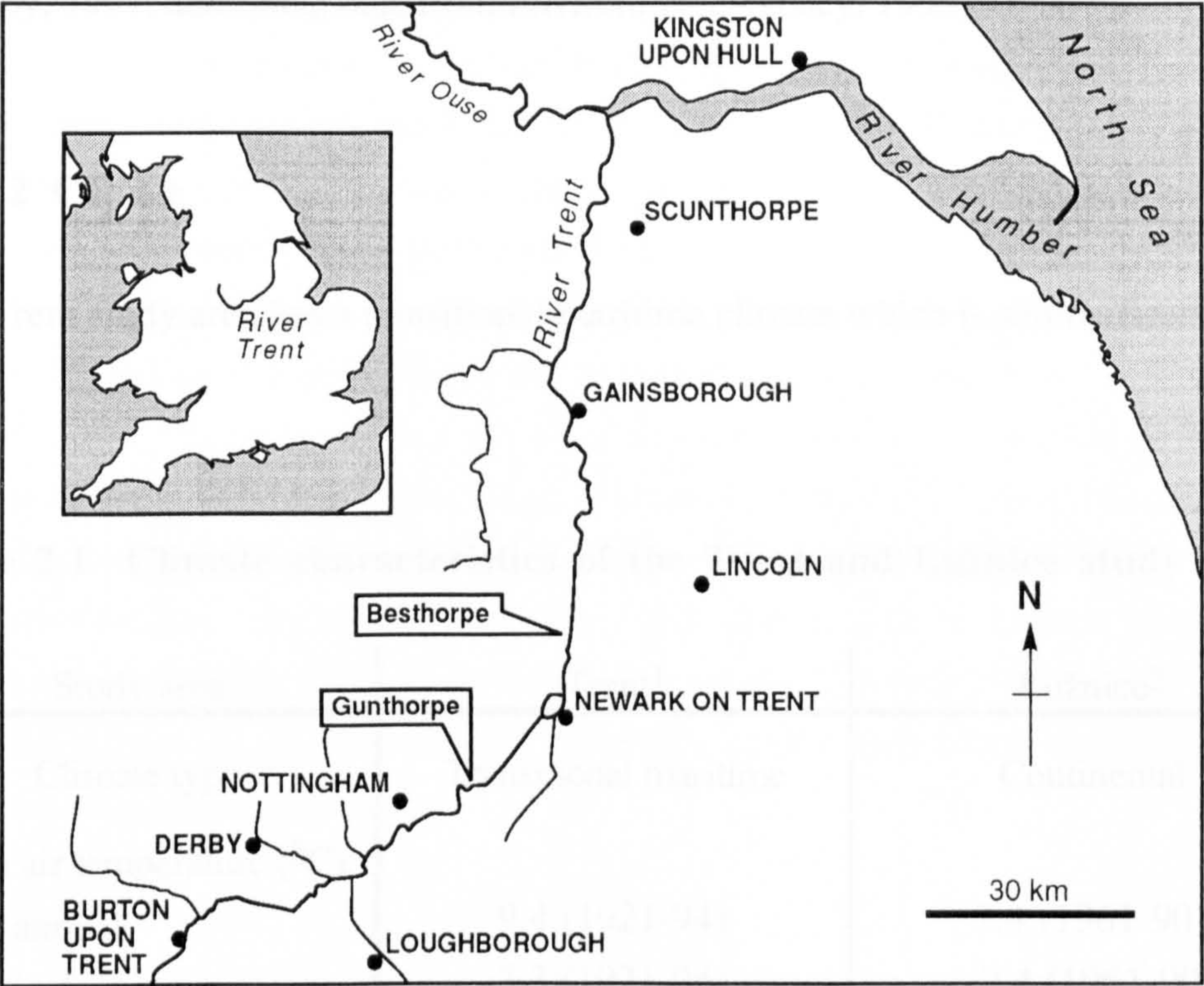
2.1.1 The River Trent and its floodplain

2.1.1.1 The River Trent

The River Trent is one of the largest regulated rivers in the UK (Petts, 1988). It is 274 km long, flowing generally from south-west to north-east through the English Midlands (Figure 2.1), and drains an area of approximately 10 435 km² containing a population of more than 5 million people. The catchment is primarily underlain by sedimentary rocks of Carboniferous, Permo-Triassic and Jurassic origin and mean catchment elevation is 30 m.

The Gunthorpe and Besthorpe study sites are located in the Trent floodplain in Nottinghamshire, east of the city of Nottingham and south of the town of

Figure 2.1 Location of the Gunthorpe and Besthorpe study sites



Gainsborough (Figure 2.1). In this section, the floodplain is up to 3 km wide. The mean daily discharge of the River Trent is approximately 81 m³ s⁻¹ (at Colwick, National Grid Reference SK 615393, during 1972-92; data supplied by the Environment Agency, 1995). In recent years, river water quality has been classified as "fair" with values for nitrate (NO₃N) usually between 1.7-4.2 mg l⁻¹, total ammoniacal nitrogen (NH₃N) 0.23-0.38 mg l⁻¹, and phosphate (PO₄) 1.3-1.6 mg l⁻¹ (Environment Agency, 1997; additional data from Environment Agency, 1995).

2.1.1.2 Climate

The Trent study area has a transitional maritime climate which is summarized in Table 2.1.

Table 2.1 Climate characteristics of the Trent and Lužnice study areas

Study area	Trent ¹	Lužnice ²
Climate type	Transitional maritime	Continental
Mean air temperature (°C):		
annual	9.4 (1921-94)	7.4 (1961-90)
in January	3.3 (1921-94)	-2.4 (1961-90)
in July	17.1 (1921-94)	16.8 (1961-90)
Mean annual ground frost (no. days)	129 (1921-94)	147 (1988-93)*
Mean annual precipitation (mm)	606 (1916-94)	656 (1961-90)
Mean evapotranspiration (mm yr ⁻¹)	526 (1969-94)	578 (1977-9)†

¹ Data collected from University of Nottingham, Sutton Bonington, SK 505621

² Data collected from Dvory nad Lužnici, two km from study site, by the Czech Hydrometeorological Institute, České Budejovicé, except *Priban (1996) and †Priban and Ondok (1985)

Figures 2.2-4 illustrate monthly variations in air temperature, precipitation and amount of sunshine for the Trent study area during the study period, 1993-5, compared to the

long-term mean values. Generally, the study period was characterized by slightly warmer, drier and sunnier weather than usual, although there is no evidence to suggest that this caused major modifications to plant phenology or production. The January to April periods were warmer than average in all three years (Figure 2.2). In 1993, this was followed by a cooler than average year, and in 1994 by an average May to October and then a relatively warm November and December, giving a warmer than average year overall. It was also warmer than usual in 1995, most months being warmer than their equivalent long-term mean values (Figure 2.2). The long-term precipitation pattern in the Trent area shows relatively little monthly variation (Figure 2.3). During the study period, after a drier than average January to March in 1993, it was wetter than usual over the rest of the year, yielding a wetter year overall. In 1994, the comparatively wet weather continued from January to May, followed by a relatively dry June to August period and then a return to wetter than normal weather. This continued until March 1995, after which a period of dry weather persisted until August (Figure 2.2), resulting in a much drier than average year overall. Peak sunshine hours generally occur in the months May to August (Figure 2.4). In 1993 and 1994, the monthly sunshine values were consistent with the long-term pattern, although the period January to July 1994 was sunnier than usual. The year 1995 was sunnier than the long term-average, including a generally sunny spring and summer (March-August), despite a cloudy June.

2.1.1.3 The Trent floodplain

The Trent floodplain is generally underlain by sand and gravel with a 1-2 m overburden of alluvial silts and clays (Salisbury *et al*, 1984). Soils tend to be relatively mature with moderately high amounts of incorporated organic matter in the surface horizons (Bridges, 1973).

The history of the Trent is characterized by human modification, particularly systematic attempts at river regulation for navigation and flood protection since the 17th century and land-use changes, often accompanied by a marked reduction in ecological diversity in the floodplain (Petts *et al.*, 1992; Large *et al.*, 1994). The floodplain has a long history of productive grassland agriculture. Indeed, pollen analysis has indicated that grassland management was well established on the Trent floodplain by 3200 BP (Lillie and Grattan, 1995). Subsequently, the valley has been highly valued as an agricultural resource with the rich alluvial soils supporting productive grazing for cattle and sheep, and rough grassland cut for hay, throughout the 18th, 19th and into the 20th centuries (Edwards, 1944). A history of episodic flooding, including periodic extensive

Figure 2.2 Mean monthly air temperature (°C) for the Trent study area

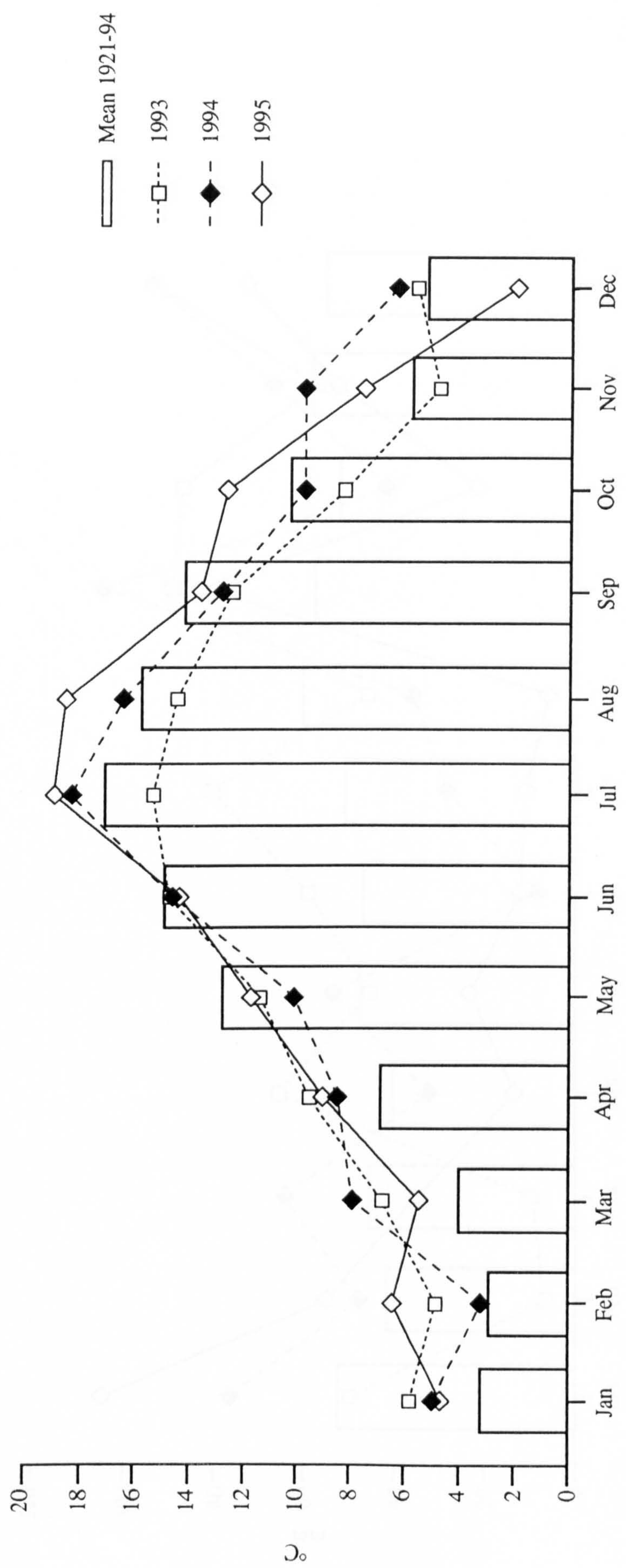


Figure 2.3 Mean monthly precipitation (mm) for the Trent study area

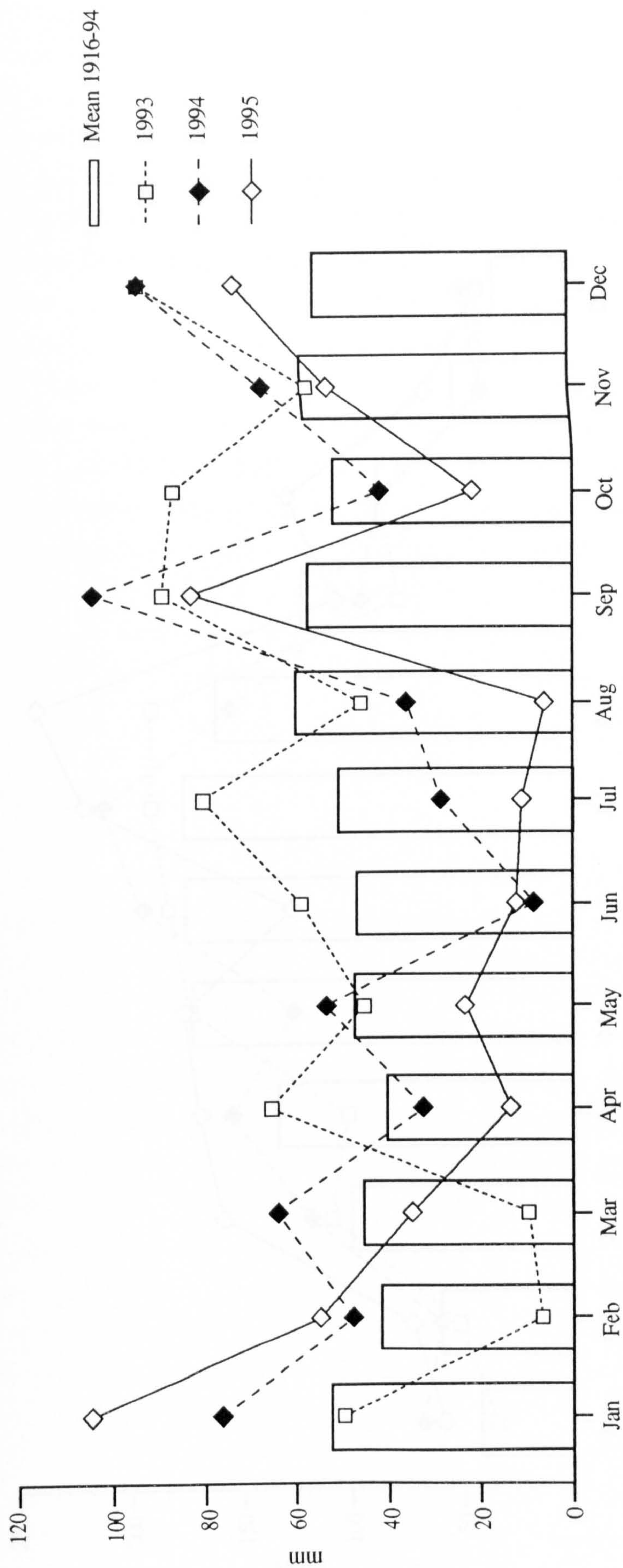
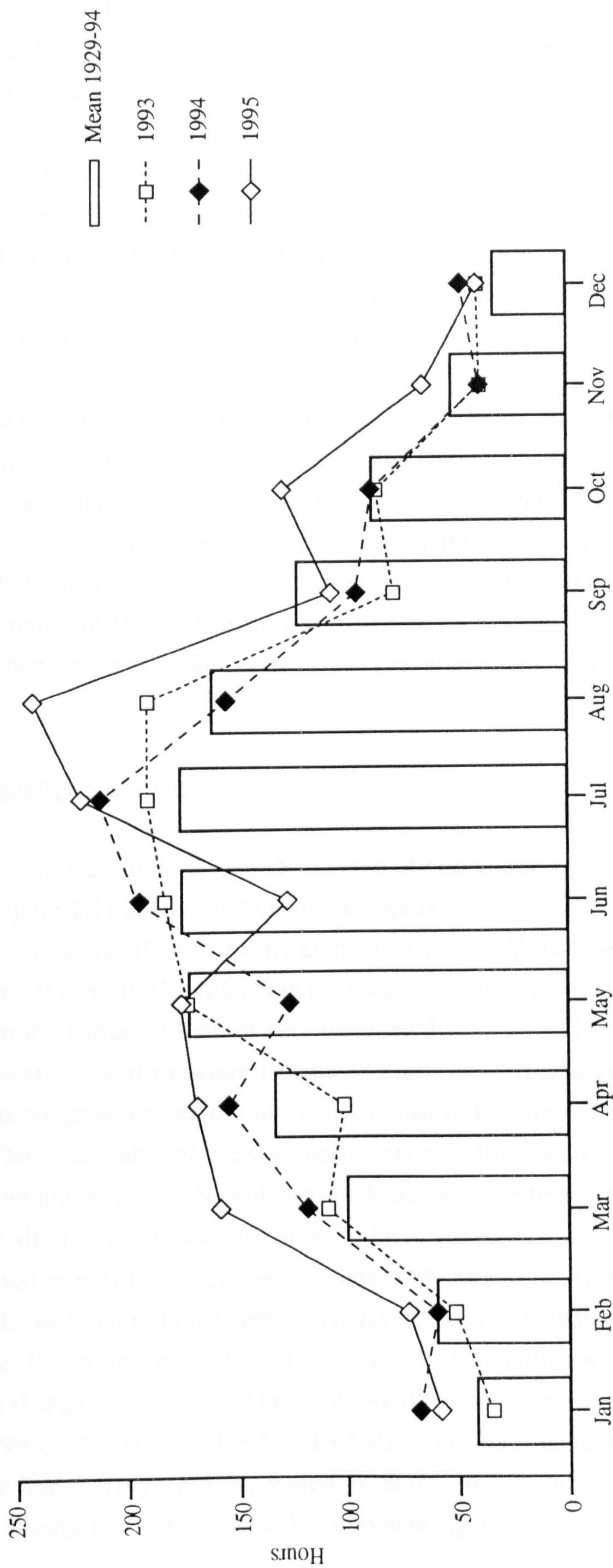


Figure 2.4 Mean monthly number of sunshine hours for the Trent study area



inundation (Marshall, 1955), has been an important influence maintaining this land-use on the floodplain, as the floods deposited nutrients that sustained grassland productivity and limited the development of arable agriculture (Edwards, 1944). Indeed, the ancient practice of fertilizing the land by the addition of silt carried by tidal waters (known as "warping") was regularly practised until the late 20th century (H. Potter, pers. comm., 1994). However, increasingly effective flood control, particularly in the 1960s-70s, facilitated improved land drainage and therefore more intensive agriculture on the floodplain, with a consequent subsequent reduction in biodiversity and in areas of natural and semi-natural vegetation (Large *et al.*, 1994).

Today, the river is regulated for most of its length, being channelized and with long reaches impounded by weirs and sluices, and flooding is largely controlled within embanked washlands. Arable agriculture and intensively exploited, floristically-impoversished grasslands predominate in the floodplain. Nevertheless, Dargie (1993) reported that much of the 2 700 ha of permanent wet grassland of potential ecological value remaining in Nottinghamshire was located on the alluvium of the River Trent, indicating that the Trent floodplain remained a notable ecological resource.

2.1.2 Gunthorpe study site

This study site was situated near the village of Gunthorpe (52° 58' N, 1° 00' W; SK 665431; Figure 2.1) at 16.5 m AOD in an approximately level field of 11.5 ha (Plate 1). The site was underlain by loamy alluvial silts of the Wharfe series (Soil Survey of England and Wales, 1983) with pH in the surface 15 cm averaging 6.7. Plant-available nitrogen in the surface 15 cm of soil averaged 26 mg l⁻¹ soil solution during 1994. During the study, soil moisture fluctuated markedly but was generally above 40% throughout the growing season; mean soil moisture for April-November 1993-5 was 44.6%. The water table of the Gunthorpe site also fluctuated considerably but was generally within 60 cm of the soil surface throughout the three years of study (Figure 2.5). The site has been, and continues to be, characterized by episodic, sometimes severe, flood events (Plate 2). For example, Marshall (1955) described a series of floods in the early part of the twentieth century in which "Gunthorpe farmers suffered" and in the 1980s and early 90s several areas of standing water persisted in the floodplain (Large *et al.*, 1994). During the study period, the site was inundated for 59 days in 1993, 110 days in 1994 and 65 days in 1995, usually during the period December-March (Figure 2.5), which is within the normal pattern of variation according to long-term information (Environment Agency, unpublished data, 1995).

Plate 1 The Gunthorpe study area was grazed by cattle and horses.
River Trent to left. June 1993



Plate 2 Extensive flooding characterized the Gunthorpe study area.
Same view as Plate 1. December 1993



Figure 2.5 Water table and flooding pattern at Gunthorpe during the study period

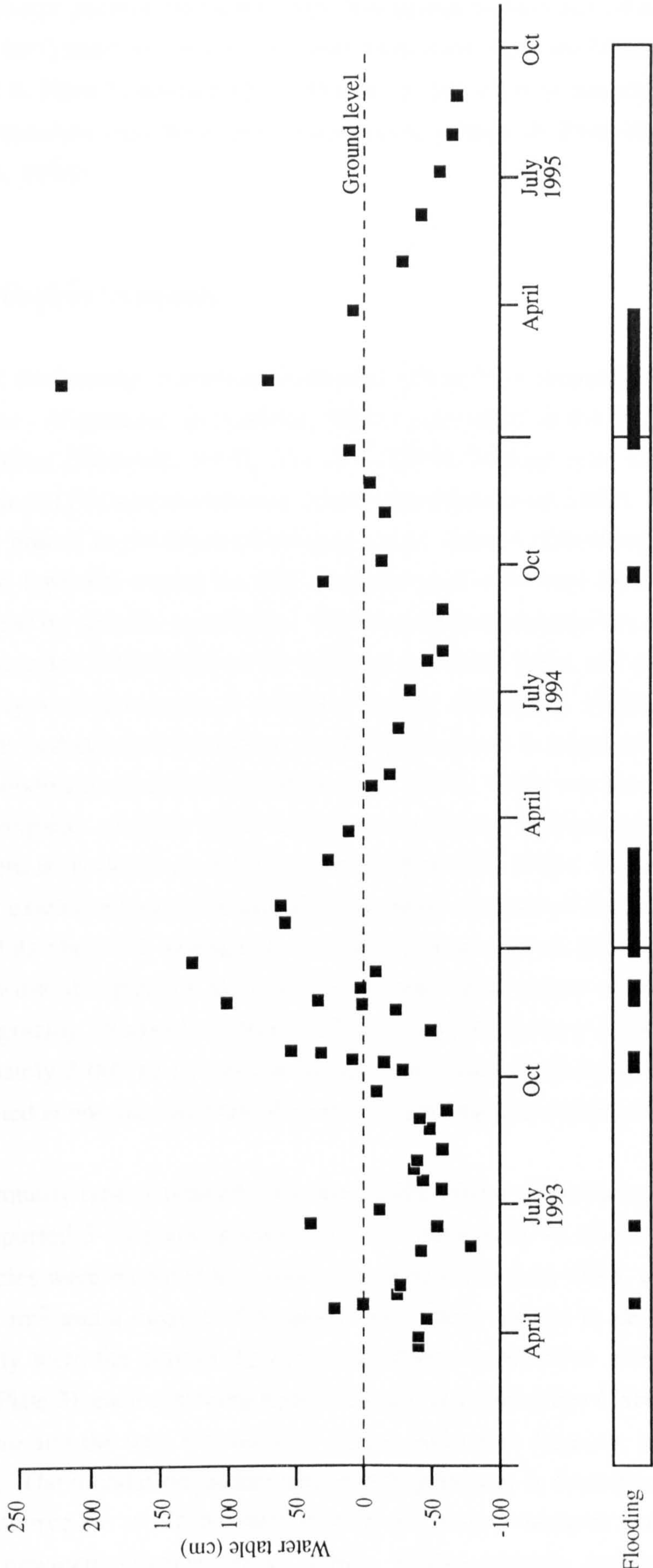
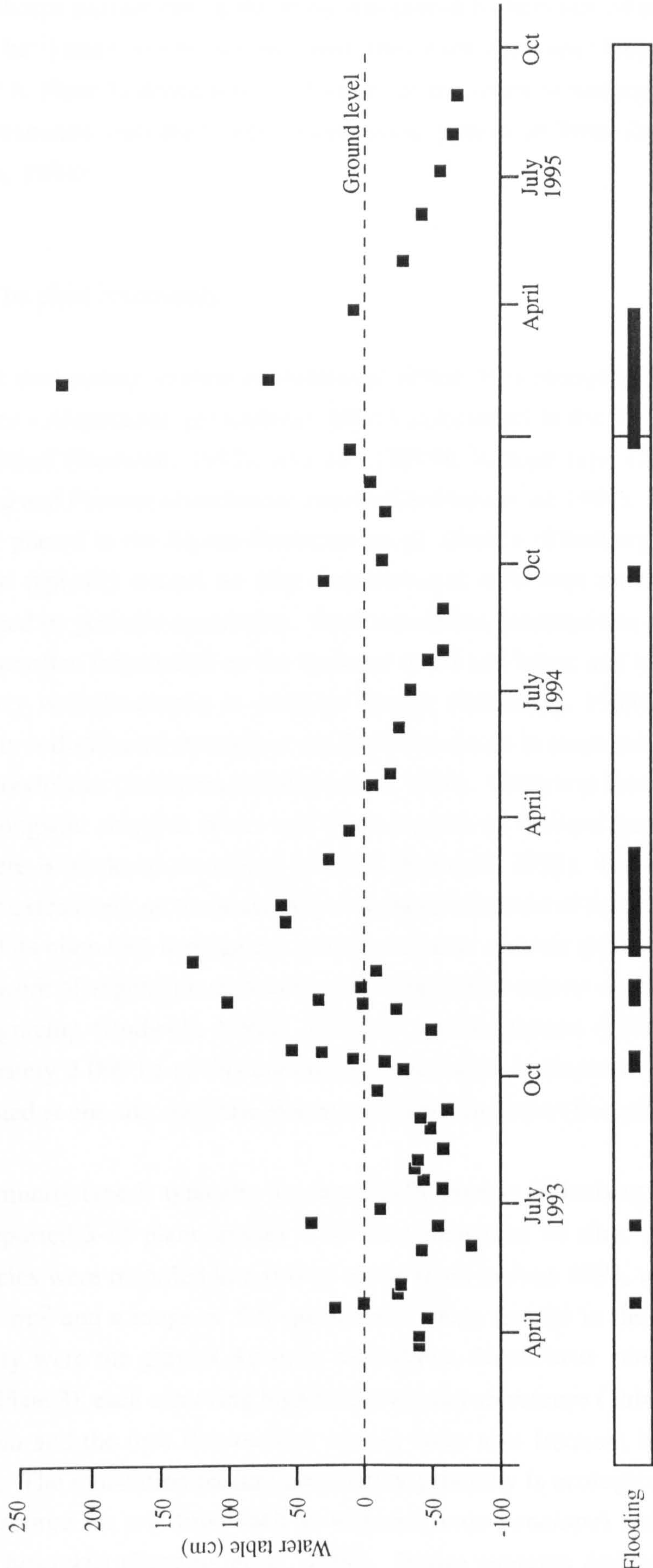


Figure 2.5 Water table and flooding pattern at Gunthorpe during the study period



The Gunthorpe pasture during the study was grazed by between 24 and 44 cattle (2.1-3.8 cattle ha⁻¹) and 6 to 8 horses each year, from early April until October or November (Figure 2.6; Plate 1) depending on flooding or the onset of waterlogged conditions. This corresponds with the typical management pattern of Trent floodplain pastures (Edwards, 1944).

2.1.2.1 The plant community

The plant community studied at Gunthorpe (Plate 3) is recognized as the *Agrostis stolonifera* - *Alopecurus geniculatus* MG13 association in the National Vegetation Classification (Rodwell, 1992), and as CORINE biotope type C37.242, *Agrostis stolonifera* and *Festuca arundinacea* swards (Devillers *et al.*, 1991). It is a community generally placed in the Elymo-Rumicion *crispi* alliance (Ellenberg, 1988; Rodwell, 1992) and typically occurs on silty circumneutral soils kept moist and sometimes waterlogged by periodic inundation. Such inundation communities are widespread in Europe but often fragmented on the banks of rivers and lakes, and a coastal variant is particularly well-developed in northern Europe (Ellenberg, 1988). In Britain, the community is distributed throughout the British lowlands in scattered localities, usually in river floodplains (Jefferson and Robertson, 1996). Often it is found as fragmentary stands alongside sluggish rivers and around pools in lowland pastures, especially where there is moderate trampling by stock (Rodwell, 1992). In eastern England, it can occur extensively on the seasonally-inundated alluvium of the floodplains of large rivers and its often lush herbage can provide valuable summer grazing, forming part of the patchwork of vegetation associated with a traditional regime of winter flooding and summer grazing (Rodwell, 1992). Jefferson and Robertson (1996) estimated that approximately 2 000 ha of this community type exists in England, including 800 ha concentrated at one site, the Ouse Washes in Cambridgeshire (Burgess *et al.*, 1990).

The community type is typically not botanically diverse (Ellenberg, 1988). Rodwell (1992) reported 3-15 plant species 4 m⁻² in a sample of 17 sites. At Gunthorpe, 16 plant species were recorded in a survey of the stand in June 1993, with a mean of 10 species 4 m⁻² and a range of 5-9 species m⁻². Key species in the Gunthorpe plant community were the grasses *Agrostis stolonifera*, *Alopecurus geniculatus* and *Poa trivialis* (Plate 3), each achieving high frequency and abundance (Table 2.2). The grass *Poa annua* and the forb *Ranunculus repens* were also frequent but generally less abundant. The inundation pasture community generally is ecologically valuable as a forage resource for wildfowl such as wigeon (*Anas penelope*) and Bewick's swan (*Cygnus bewickii*) (Burgess *et al.*, 1990). It also supports *Apium repens*, a plant

Figure 2.6 Management cycle at Gunthorpe study site.
Timings are based upon archival and anecdotal information and observations made during the study period 1993-5.

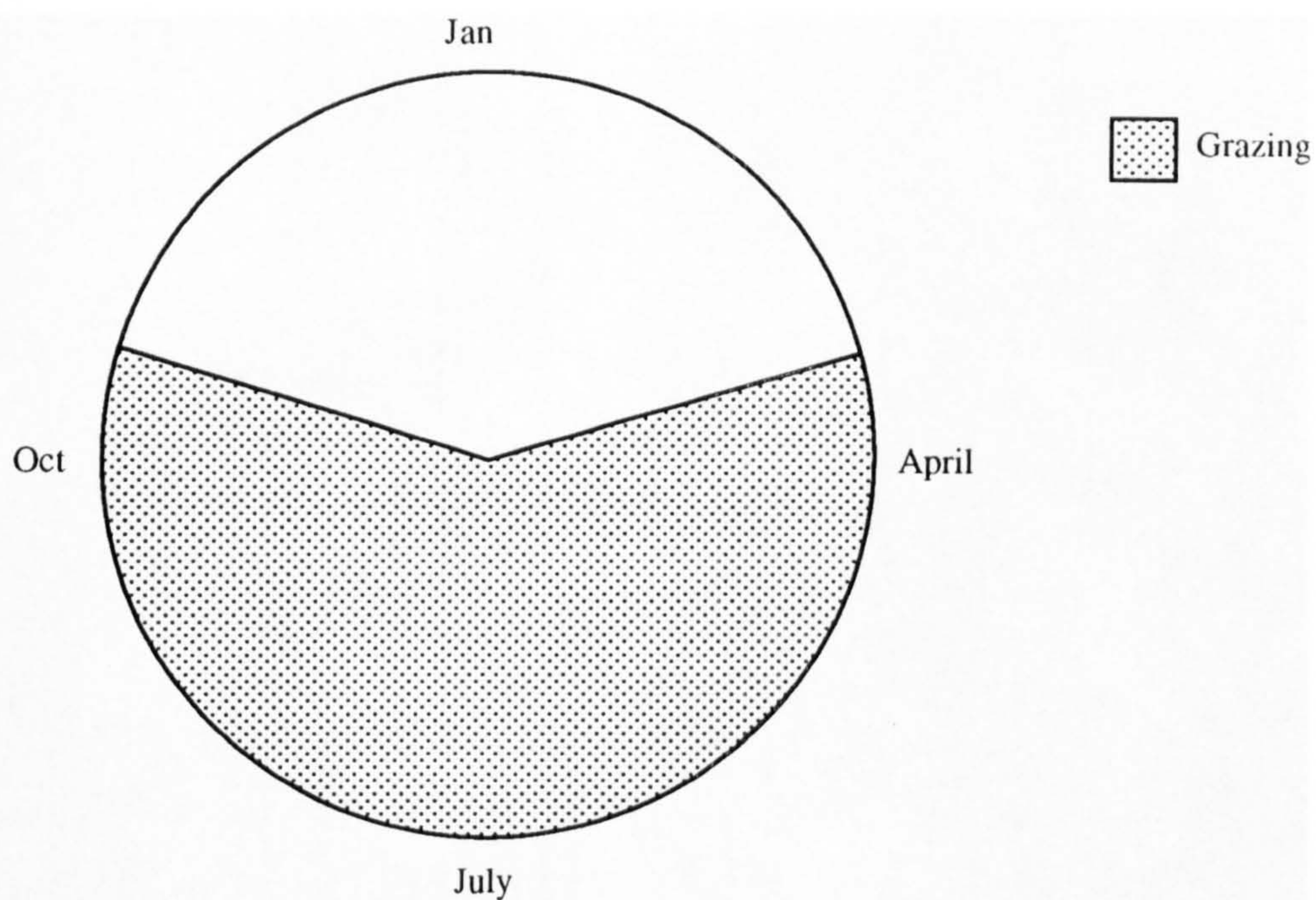


Table 2.2 Floristic table for the Gunthorpe plant community

Plant species nomenclature follows Tutin *et al.* (1964-80) *Flora Europaea* Volumes 1-3, Cambridge University Press, Cambridge. * = grasses, remaining vascular plant species are forbs.

Derived from a survey in June 1993 of 22 randomly-located 1m² samples.

Frequency refers to how often a species is found on moving from one sample to the next, irrespective of how much of that species is present in each sample: 1-20% frequency (i.e.

Plate 3 The Gunthorpe plant community. *Agrostis stolonifera*, *Alopecurus geniculatus*, *Poa trivialis* and *Poa annua* can be seen. May 1993



<i>Rumex obtusifolius</i>	Broad-leaved Dock	II (1-2)
<i>Trifolium repens</i>	White Clover	II (1-2)
<i>Rumex conglomeratus</i>	Cuscutted Dock	I (1-2)
<i>Rumex crispus</i>	Curled Dock	I (1)

Rare species (i.e. recorded in less than two samples): **Glyceria fluitans* (Floating Sweet-grass), *Plantago major* (Greater Plantain), *Rumex acetosa* (Common Sorrel), *Urtica dioica* (Common Nettle).

Table 2.2 Floristic table for the Gunthorpe plant community

Plant species nomenclature follows Tutin *et al.* (1964-80) *Flora Europaea Volumes 1-5*. Cambridge University Press, Cambridge. * = grasses; remaining vascular plant species are forbs.

Derived from a survey in June 1993 of 22 randomly-located 1m² samples.

'Frequency' refers to how often a species is found on moving from one sample to the next, irrespective of how much of that species is present in each sample: 1-20% frequency (i.e. up to one sample in five) = I; 21-40% = II; 41-60% = III; 61-80% = IV; 81-100% = V. 'Abundance' describes how much of a species is present in a sample, irrespective of how frequent or scarce it is among the samples. Abundance is shown as bracketed numbers using the Domin scale of ground cover (*sensu* Rodwell, 1992): cover of <4% with few individuals = 1; <4% with several individuals = 2; <4% with many individuals = 3; 4-10% = 4; 11-25% = 5; 26-33% = 6; 34-50% = 7; 51-75% = 8; 76-90% = 9; 91-100% = 10.

Scientific name	English name	Frequency and abundance
* <i>Agrostis stolonifera</i>	Creeping Bent	V (4-8)
* <i>Poa trivialis</i>	Rough-stalked Meadow-grass	V (4-8)
* <i>Alopecurus geniculatus</i>	Marsh Foxtail	V (3-7)
* <i>Poa annua</i>	Annual Meadow-grass	V (2-4)
<i>Ranunculus repens</i>	Creeping Buttercup	IV (1-4)
<i>Rorippa sylvestris</i>	Creeping Yellow-cress	III (1-3)
<i>Cirsium arvense</i>	Creeping Thistle	III (1-2)
* <i>Lolium perenne</i>	Perennial Rye-grass	II (1-4)
<i>Rumex obtusifolius</i>	Broad-leaved Dock	II (1-2)
<i>Trifolium repens</i>	White Clover	II (1-2)
<i>Rumex conglomeratus</i>	Clustered Dock	I (1-2)
<i>Rumex crispus</i>	Curled Dock	I (1)

Rare species (i.e. recorded in less than two samples): **Glyceria fluitans* (Floating Sweet-grass), *Plantago major* (Greater Plantain), *Rumex acetosa* (Common Sorrel), *Urtica dioica* (Common Nettle).

species that is nationally rare in Britain (Jefferson and Robertson, 1996). The community may be productive: at Gunthorpe mean above-ground biomass in 1993-4 was 7.9 tonnes dry weight ha⁻¹ yr⁻¹.

2.1.3 Besthorpe study site

This study site was situated in a 5.2 ha field near to Besthorpe village (53° 10' N, 0°46' W; SK 817641; Figure 2.1) at 6 m AOD. The field is generally level with soils belonging to the Fladbury 2 series, being clayey and of alluvial origin (Soil Survey of England and Wales, 1983). Soil pH averaged 6.3 and plant-available N approximately 8 mg l⁻¹ soil solution in the surface 15 cm during 1994-5. Mean soil moisture for March-November 1993-5 was 34.1%. The water table between March and November 1993-5 was consistently greater than 100 cm below soil surface at the Besthorpe study site and in 1993 was usually at least 180 cm below soil surface (Figure 2.7). Prior to flood control measures being completed in 1981, the area was likely to have been inundated annually (Marshall, 1955), although since then flood events have been less frequent (N. Lewis, pers. comm., 1994). During the three years of study, the site flooded once, for 10 days in January-February 1995 (Figure 2.7).

The vegetation at Besthorpe is characteristic of areas where a traditional hay-meadow management regime of cutting followed by grazing has been applied to seasonally flooded alluvial land. Indeed, there is a long history of low-intensity grassland management comprising cutting for hay, followed by grazing of the re-growth, and minimal inorganic fertilization. Archival information indicates that hay meadow management at Besthorpe has been practised since at least the 18th century, including a written agreement by villagers for sheep grazing at Besthorpe in 1721 and reference to the site as a "meadow" in plans associated with an auction of land in 1860. The typical management pattern is shown in Figure 2.8. Typically, cutting takes place in late June or early July (Plate 4) and the aftermath is grazed by sheep (Plate 5). During the study, between 180 and 250 sheep (35-48 sheep ha⁻¹) were grazed for approximately 20 days in September-October each year. There is no history of inorganic fertilizer use in the area other than minimal applications in the 1980s.

2.1.3.1 The plant community

The plant community present at Besthorpe is described by the National Vegetation Classification as MG4, the *Alopecurus pratensis* - *Sanguisorba officinalis* association

Figure 2.7 Water table and flooding pattern at Besthorpe during the study period

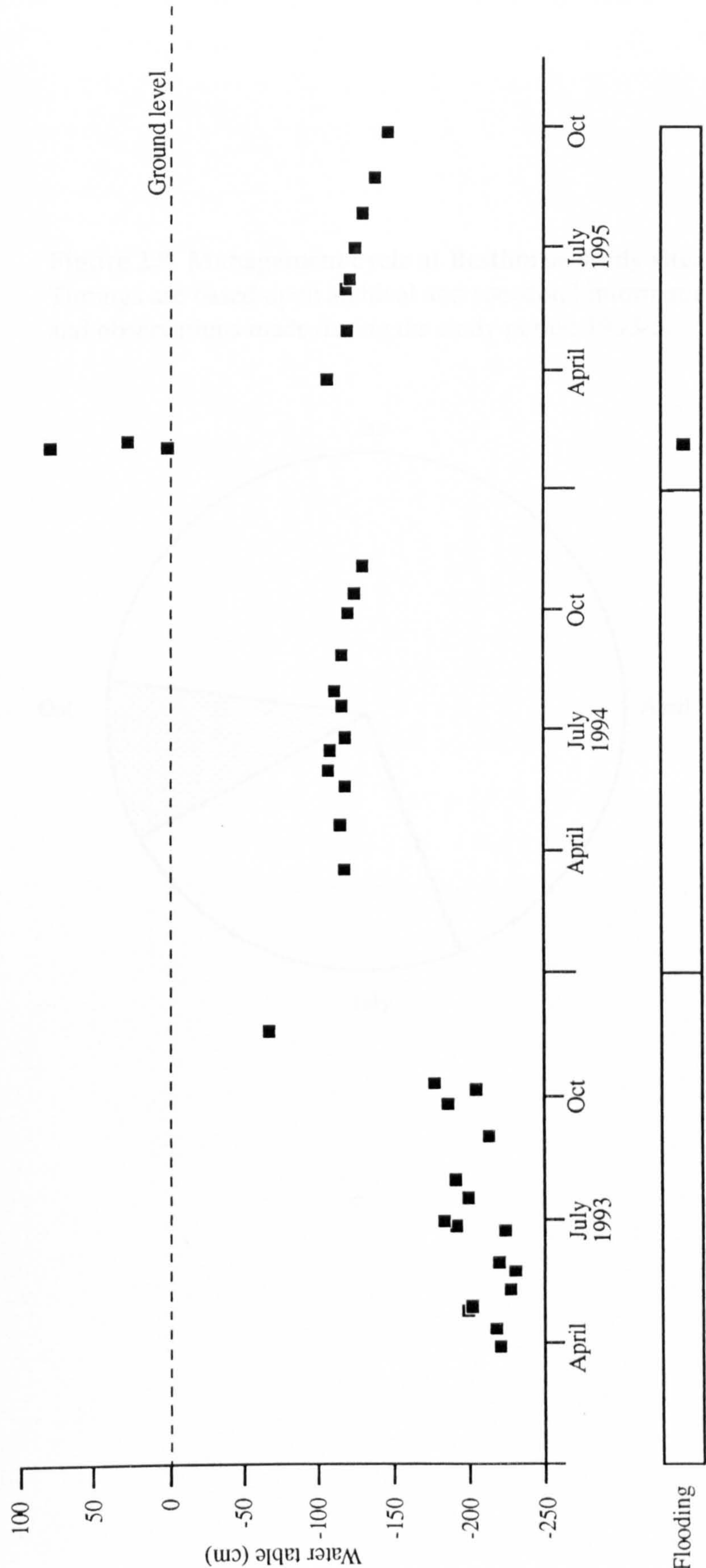


Figure 2.8 Management cycle at Besthorpe study site.
Timings are based upon archival and anecdotal information and observations made during the study period 1993-5.

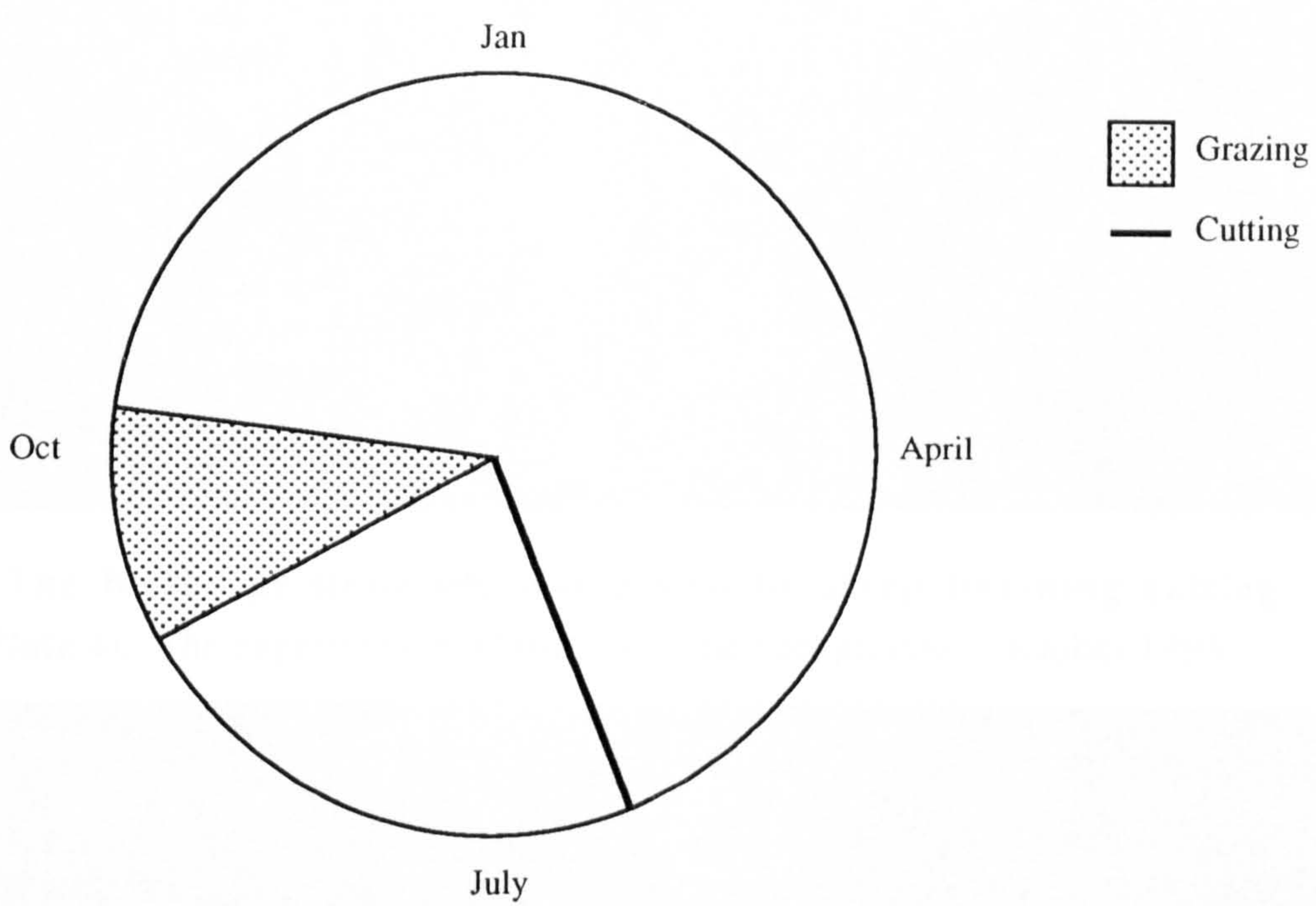


Plate 4 Traditional management at the Besthorpe study site comprised cutting for hay with grazing of the regrowth (Plate 5) The experiment enclosure is in the background. June 1995



Plate 5 The Besthorpe study site was grazed by sheep following cutting for hay (Plate 4). The experiment enclosure is in the background. October 1993



(Rodwell, 1992). This type of community lies within the *Molinio-Arrhenatheretea* of continental phytosociology, CORINE biotope type C38.2 lowland hay meadows (Devillers *et al.*, 1991), but has an extremely limited European distribution, being restricted largely to south and central England (Jefferson, 1997). It has consequently become known as the English flood-meadow community and is a lowland vegetation especially characteristic of areas where traditional hay meadow management has been applied to seasonally flooded land with circumneutral, clay-rich or silty alluvial loam soils (Rodwell, 1992; Jefferson, 1997). This type of meadow has probably existed for almost 3 000 years (Greig, 1984). For example, it is likely that the plant community has been a feature of the Thames floodplain for 2 000 years (Lambrick and Robinson, 1988). Hay meadow treatment has traditionally comprised taking an annual hay crop in late June to early July, extensive autumn or winter grazing of the regrowth and a light application of organic manures, but no herbicide or inorganic fertilizer use (Rodwell, 1992; Crofts and Jefferson, 1994). Often sites have received this form of low-intensity management for many centuries with the result that a poly-dominant species-rich community has developed. For example, some sites, such as North Meadow National Nature Reserve at Cricklade in Wiltshire, have been continuously managed as Lammas or common meadows where the land is divided into strips each mown for hay by different landowners and subsequently the whole meadow is available for communal grazing on Lammas day (12 August) (Brian, 1993).

The English flood-meadow plant community was first described by Baker (1937). Typically, it is a species-rich community, supporting approximately 28 plant species 4 m^{-2} (Rodwell, 1992) and contains a varied mixture of grasses and forbs of which the tall, robust perennial *S. officinalis* is particularly prominent. By July, this species has generally overtopped the grasses and the vegetation forms a dense sward up to 70 cm tall (Baker, 1937). Some stands support populations of nationally scarce species such as *Fritillaria meleagris* and *Oenanthe silaifolia* (Wells and King, 1975; Stewart *et al.*, 1994). Jefferson and Robertson (1996) estimated that less than 1 500 ha of the English flood-meadow community exist and the resource is fragmented, with the majority of remaining sites under 10 ha in extent (Jefferson, 1997). Due to its botanical diversity and limited European distribution, the community is recognized as having a high nature conservation value on both national and international levels (Jefferson and Grice, 1998). It is included as a key habitat within the UK Biodiversity Action Plan (The UK Steering Group, 1995) and is specially protected by the European Union being listed in Annex 1 of the Council Directive on the Conservation of Natural Habitats and Wild Flora and Fauna (The Habitats Directive) (Council of the European Communities, 1992).

Table 2.3 Floristic table for the Besthorpe plant community

Plant species nomenclature follows Tunn *et al.* (1964-80) *Flora Europaea* Volumes 1-3, Cambridge University Press, Cambridge. * = grasses; remaining vascular plant species are forbs.

Derived from a survey in June 1993 of 44 randomly located 1m² samples.

For explanation of frequency and abundance see Table 2.1.

Plate 6 The Besthorpe plant community. *Sanguisorba officinalis* is prominent.
June 1993



<i>Cardamine pratensis</i>	Cuckooflower	1(1-3)
<i>Galium verum</i>	Ladies Bedstraw	1(1-3)
<i>Rumex acetosa</i>	Common Sorrel	1(1-3)
* <i>Dactylis glomerata</i>	Cock's-foot	1(1-2)
<i>Lathyrus pratensis</i>	Meadow Vetchling	1(1-2)
<i>Taraxacum officinale</i> agg.	Dandelion	1(1-2)
<i>Tragopogon pratensis</i>	Goat's-beard	1(1)

Rare species (i.e. recorded in less than three samples): *Silene silaus* (Pepper Saxifrage), *Lotus uliginosus* (Greater Bird's-foot Trefoil), *Vicia cracca* (Tufted Vetch), *Cirsium arvense* (Creeping Thistle), **Elymus repens* (Common Couch), *Senecio jacobae* (Ragwort), *Senecio olivaceus* (Smooth Sow-thistle).

Table 2.3 Floristic table for the Besthorpe plant community

Plant species nomenclature follows Tutin *et al.* (1964-80) *Flora Europaea Volumes 1-5*. Cambridge University Press, Cambridge. * = grasses; remaining vascular plant species are forbs.

Derived from a survey in June 1993 of 44 randomly located 1m² samples.

For explanation of frequency and abundance see Table 2.1.

Scientific name	English name	Frequency and abundance
<i>Sanguisorba officinalis</i>	Great Burnet	V (2-8)
* <i>Alopecurus pratensis</i>	Meadow Foxtail	V (4-7)
* <i>Agrostis capillaris</i>	Common Bent	V (3-7)
* <i>Holcus lanatus</i>	Yorkshire Fog	V (4-6)
* <i>Festuca rubra</i>	Red Fescue	V (4-5)
* <i>Arrhenatherum elatius</i>	False Oat-grass	V (1-5)
* <i>Bromus hordeaceus</i>	Meadow Brome	V (1-5)
* <i>Anthoxanthum odoratum</i>	Sweet Vernal-grass	V (1-4)
Bryophytes (all species)	Moss	V (1-3)
<i>Cerastium fontanum</i>	Common Mouse-ear	IV (1-4)
* <i>Lolium perenne</i>	Perennial Rye-grass	IV (1-4)
<i>Anthriscus sylvestris</i>	Cow Parsley	III (1-5)
* <i>Trisetum flavescens</i>	Yellow Oat-grass	III (1-5)
* <i>Poa trivialis</i>	Rough-stalked Meadow-grass	III (2-4)
* <i>Hordeum secalinum</i>	Meadow Barley	III (1-4)
<i>Ranunculus bulbosus</i>	Bulbous Buttercup	III (1-4)
<i>Stellaria graminea</i>	Lesser Stitchwort	II (1-3)
<i>Ranunculus acris</i>	Meadow Buttercup	II (1-2)
<i>Centaurea nigra</i>	Black Knapweed	I (4)
<i>Heracleum sphondylium</i>	Hogweed	I (1-4)
<i>Cardamine pratensis</i>	Cuckooflower	I (1-3)
<i>Galium verum</i>	Ladies Bedstraw	I (1-3)
<i>Rumex acetosa</i>	Common Sorrel	I (1-3)
* <i>Dactylis glomerata</i>	Cock's-foot	I (1-2)
<i>Lathyrus pratensis</i>	Meadow Vetchling	I (1-2)
<i>Taraxacum officinale</i> agg.	Dandelion	I (1-2)
<i>Tragopogon pratensis</i>	Goat's-beard	I (1)

Rare species (i.e. recorded in less than three samples): *Silaum silaus* (Pepper Saxifrage), *Lotus uliginosus* (Greater Bird's-foot Trefoil), *Vicia cracca* (Tufted Vetch), *Cirsium arvense* (Creeping Thistle), **Elymus repens* (Common Couch), *Senecio jacobea* (Ragwort), *Sonchus oleraceus* (Smooth Sow-thistle).

The Besthorpe plant community (Plate 6) is a good example of the flood-meadow association that develops in England where a traditional management regime of cutting followed by grazing has been applied to periodically flooded alluvial land. The association is described by the species *Sanguisorba officinalis* and *Alopecurus pratensis* (Rodwell, 1992), both of which are frequent and abundant at the study site along with *Festuca rubra*, *Agrostis capillaris* and *Holcus lanatus* (Table 2.3). Characteristically, a range of subsidiary grasses and some forbs are also present. Thirty three species of vascular plants were recorded in a survey of the field in June 1993, with a mean of 22 species 4 m^{-2} and a range of 8-18 species m^{-2} . During the three-year study, mean above-ground plant production was $6.1\text{ tonnes dry weight ha}^{-1}\text{ yr}^{-1}$.

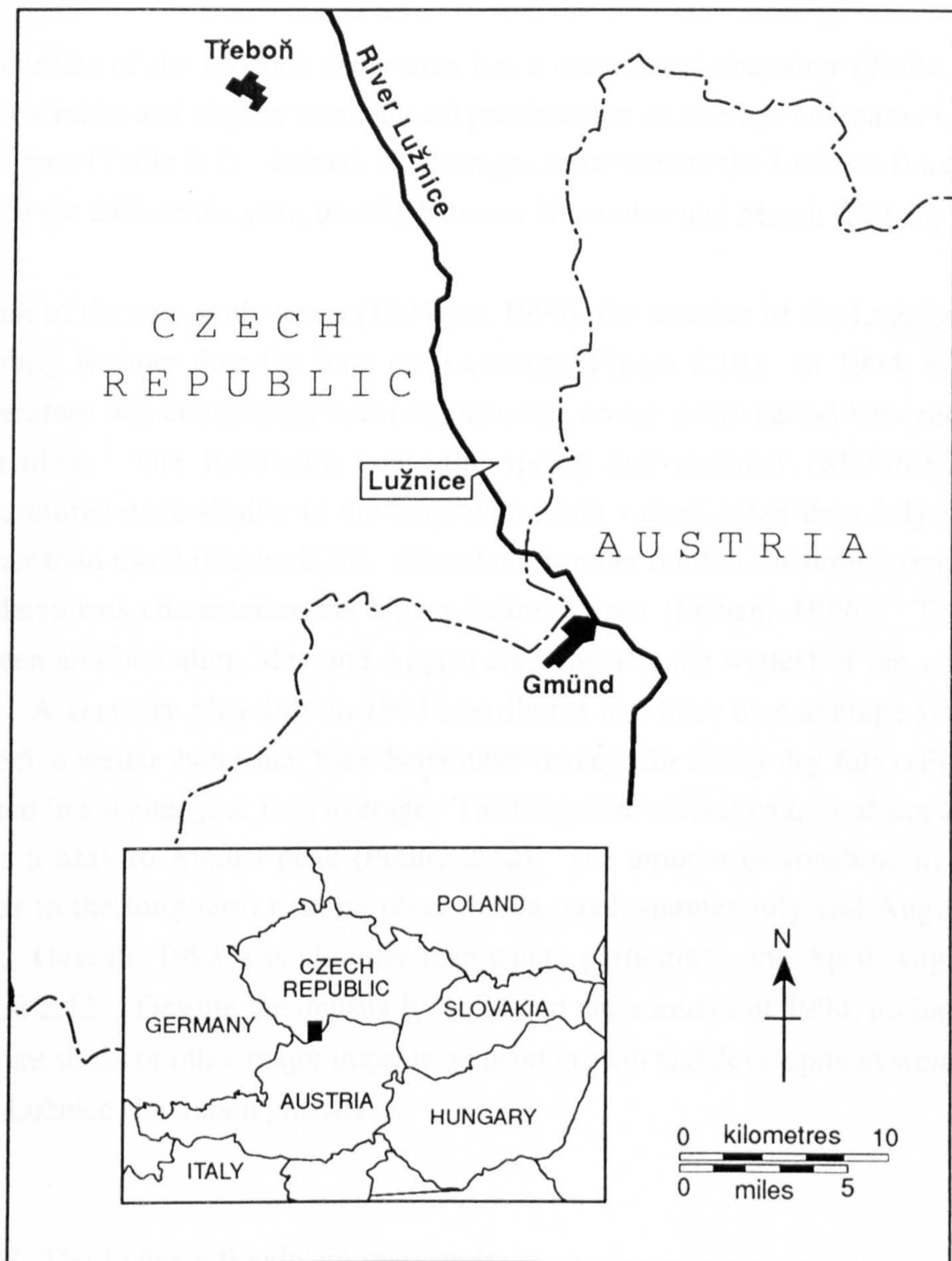
2.1.4 The Lužnice River and its floodplain

2.1.4.1 The Lužnice River

The Lužnice River originates in Austria and flows generally NNW through South Bohemia in the Czech Republic to its confluence with the Vltava approximately 200 km from its source (Figure 2.9). It drains a total of $4\,225\text{ km}^2$, including most of the Třeboň basin, a large depression infilled with sand, gravel and clay sediments of Cretaceous to Miocene age (Janda, 1994) with a mean altitude of 410 to 470 m. The flat landscape of the basin is characterized by extensive forests and wetlands, including more than 500 artificial fish ponds, mires, valley bogs, acidic fens, and floodplain grasslands (Jeník and Kvet, 1984).

The study site is located in the Třeboň basin in the Czech Republic approximately 5 km from the Austrian border (Figure 2.9). This section is generally known as the Upper Lužnice River and is relatively natural, being characterized by a lack of conventional river engineering and exhibiting many meanders, oxbows and pool and riffle sequences. The floodplain varies from 150 m to 1000 m in width and the mean discharge of the Lužnice River in this section is $5\text{ m}^3\text{ s}^{-1}$ (data for 1961-90 supplied by Czech Hydrometeorological Institute, České Budějovice). River water quality is generally good, despite past eutrophication and other pollution (Drbal and Rauch, 1996). For example, nitrate (NO_3N) content was less than 2 mg l^{-1} in 14 samples taken during this study in the summer of 1994 and phosphate (PO_4) ranged from 0.32-0.64 mg l^{-1} . Flood events occur annually, particularly in spring when snow melt occurs in the headwaters (Šmilauer *et al.*, 1996). The river and its floodplain are of considerable biodiversity value, supporting a mosaic of wetland, grassland and forest habitats, which are internationally recognized by being included within the

Figure 2.9 Location of the Lužnice study site



Třeboň Basin Biosphere Reserve and Ramsar site (Jeník and Kvet, 1984; Janda, 1994). The river and its floodplain have been described in detail by Prach *et al.* (1996).

2.1.4.2 Climate

The climate of the Lužnice study area has a continental character (Table 2.1), with colder winters and slightly more annual precipitation on average compared to the Trent study area (Table 2.1). Indeed, on average, snow covers the Lužnice floodplain soil surface for 24% of the year, usually between November and March (Priban, 1996).

In both of the two study years (1994 and 1995), the weather of the Lužnice area was generally warmer than the long term average (Figure 2.10). In 1994, monthly air temperature was consistently warmer, including a very warm period between June and September. The following year, the spring and summer (March-September) temperatures were similar to the long-term mean values, other than July which was warmer than usual (Figure 2.10). Abundant summer rainfall, including frequent local thunderstorms characterize the Upper Lužnice area (Priban, 1996). The months between and including May and August are generally the wettest of the year (Figure 2.11). A very dry May-July in 1994 contributed to a drier than average year overall. In 1995, a wetter than usual May-September (except for a very dry July) (Figure 2.11) resulted in a wetter year than average. The long-term annual pattern of sunshine hours shows a May to August peak (Figure 2.12). The amount of sunshine in 1994 was similar to the long-term pattern, other than a much sunnier July and August (Figure 2.12). Overall, 1995 was cloudier than usual, particularly the April-August period (Figure 2.12). Despite the unusually warm and dry summer of 1994, no indication of moisture stress or other major impacts on plant growth and development were observed at the Lužnice floodplain grasslands.

2.1.4.3 The Lužnice floodplain grasslands

Grasslands were first created in the Lužnice floodplain in the 12th century (Janda, 1994) and by the 19th century, grasslands that were annually cut for hay and straw dominated the floodplain landscape (Guth, 1996). Up to the 1950s, these grasslands were generally used for hay-making with some grazing and little or no addition of inorganic fertilizers (K. Prach, pers. comm., 1994) but for the next 40 years were subject to a range of agricultural practices due to communist policies, including intensive cultivation (Prach, 1992). This resulted in changes in meadow management,

Figure 2.10 Mean monthly air temperature (°C) for the Lužnice study area

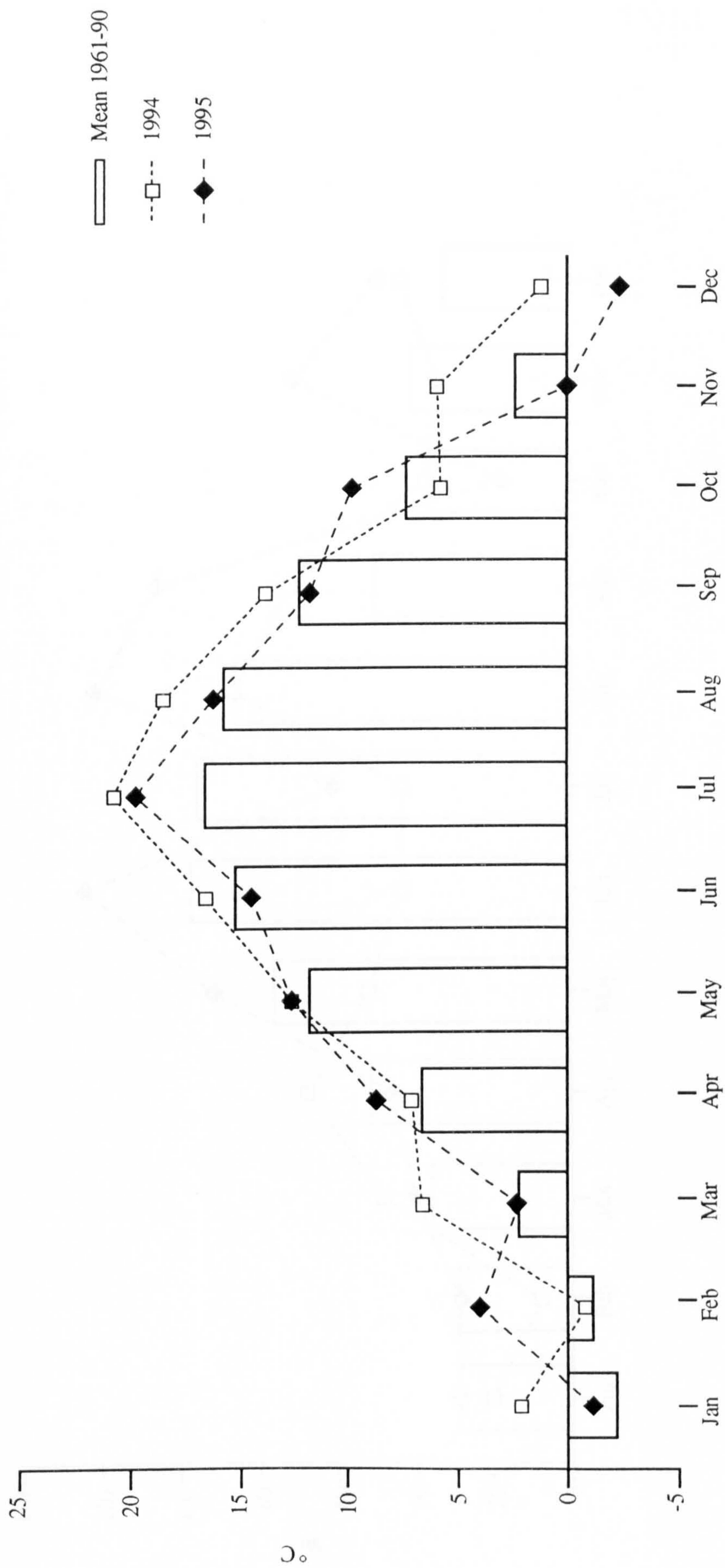


Figure 2.11 Mean monthly precipitation (mm) for the Lužnice study area

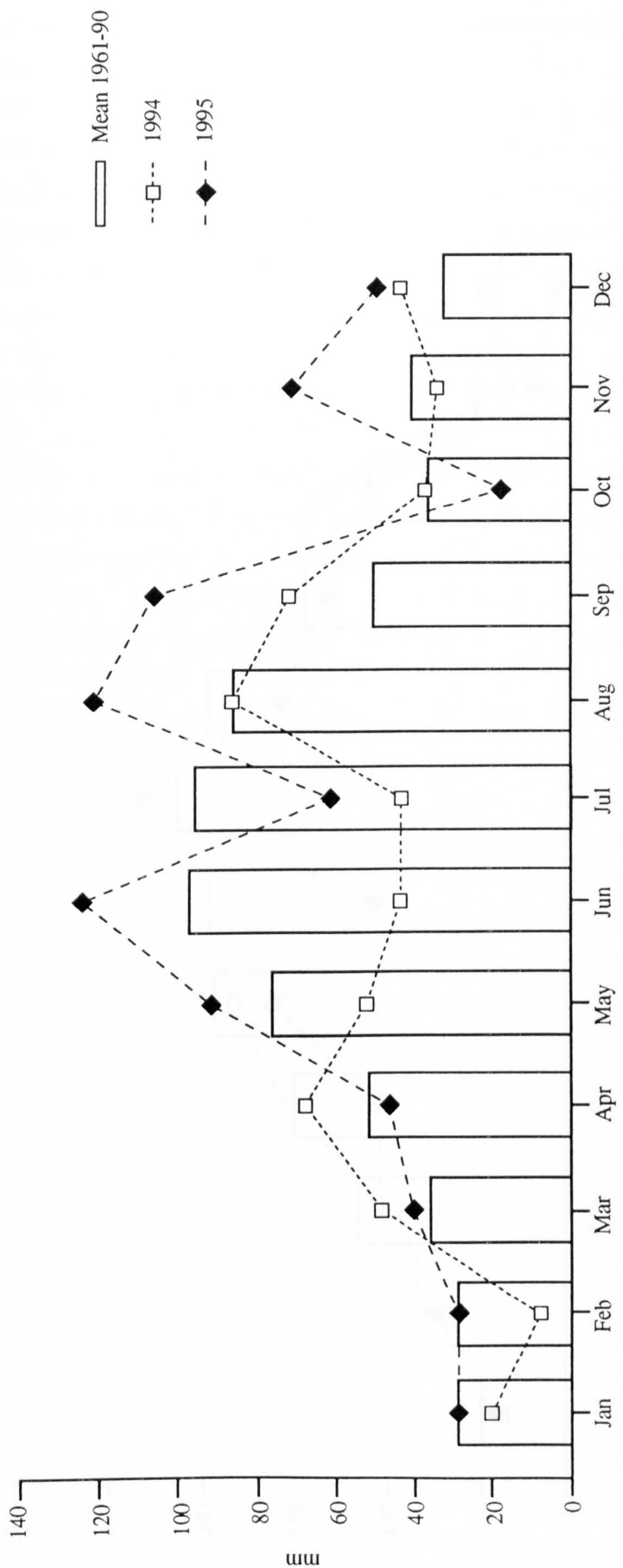
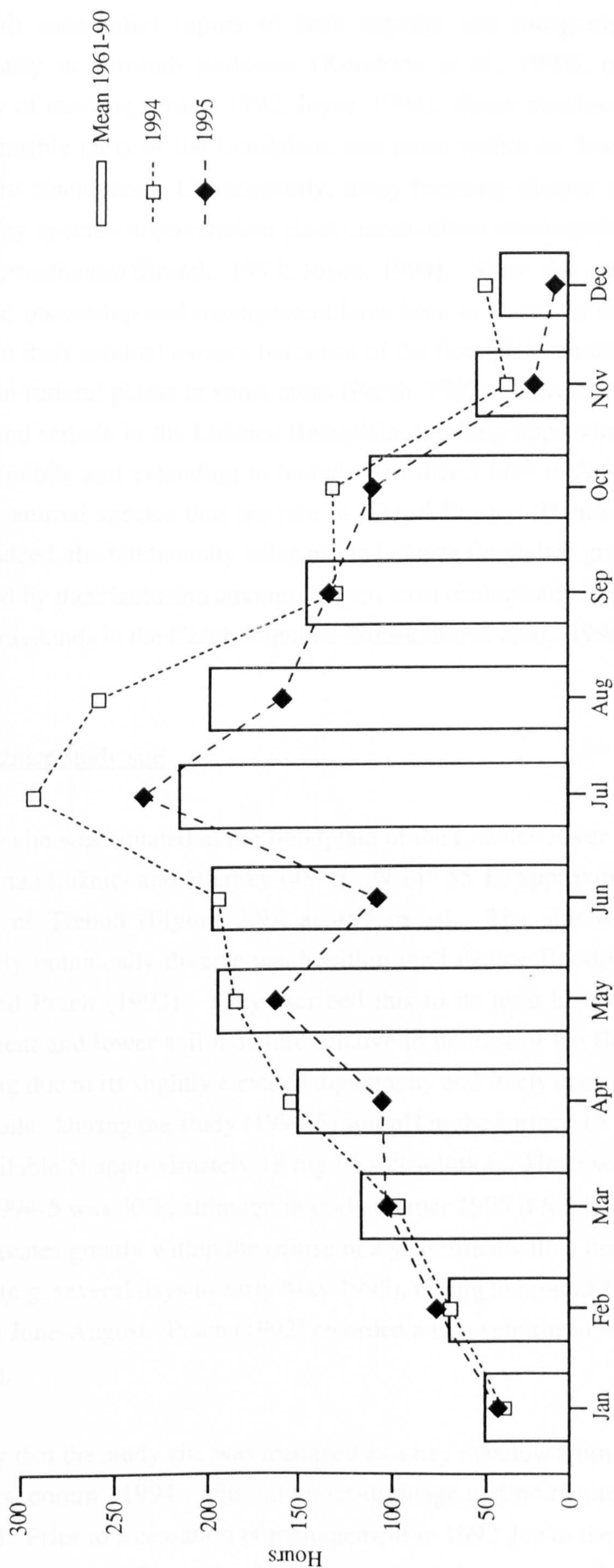


Figure 2.12 Mean monthly number of sunshine hours for the Lužnice study area



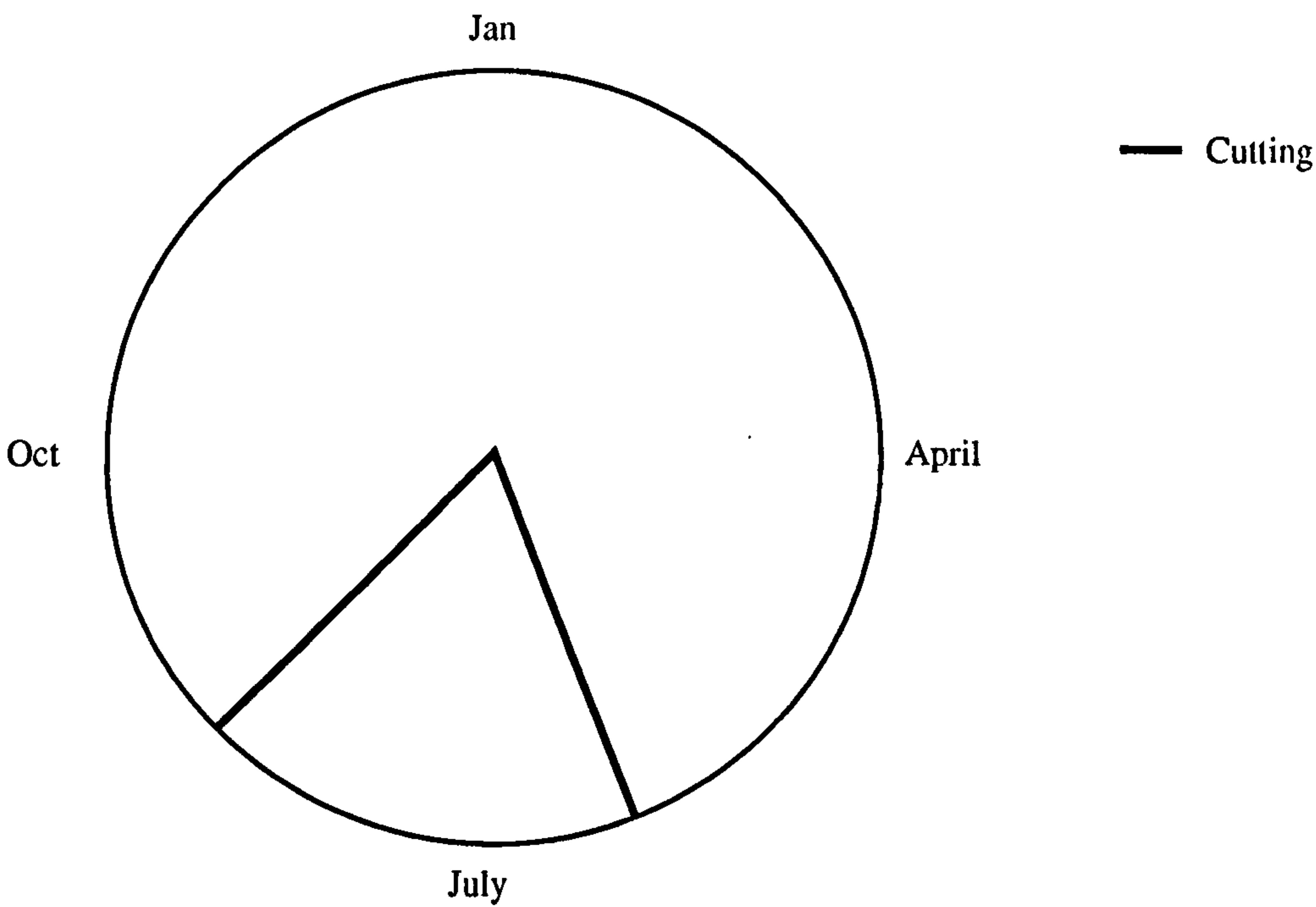
often with substantial inputs of both organic and inorganic fertilizers, either intentionally or through pollution (Kundrata *et al.*, 1995), or a decrease in the frequency of mowing (Prach, 1992; Joyce, 1994). Some meadows were also drained. Less accessible parts of the floodplain, and those within an 'Iron Curtain' exclusion zone, were abandoned. Consequently, many formerly diverse meadows have been replaced by species-impoverished plant communities dominated by *Urtica dioica* or *Phalaris arundinacea* (Šrutek, 1993; Joyce, 1994). Since the end of communism in 1989, land ownership and management have been in a state of flux, with some areas restored to their original owners but much of the floodplain unmanaged, leading to an increase in ruderal plants in some areas (Prach, 1992). Nevertheless, extensive areas of grassland remain in the Lužnice floodplain, totalling approximately 10 km² in the Czech Republic and extending to include a further 3 km² in Austria, and supporting plant and animal species that are rare in central Europe (Hanek *et al.*, 1988; Janda, 1994). Indeed, the biodiversity value of the Lužnice floodplain grasslands was recently recognized by their inclusion amongst the ten most ecologically important complexes of alluvial grasslands in the Czech Republic (Straškrabová *et al.*, 1996).

2.1.5 Lužnice study site

The study site was situated in the floodplain of the Lužnice River between the villages of Dvory nad Lužnici and Hlamky (48° 51' N 14° 55' E) approximately 20 km SSE of the town of Třeboň (Figure 2.9), at 457 m asl. The site was recognized as a particularly botanically diverse patch within the Lužnice floodplain by Prach *et al.* (1990) and Prach (1992). They ascribed this to its long history of regular cutting management and lower soil moisture relative to the rest of the floodplain locally, the latter being due to its slightly elevated topography and freely draining, somewhat sandy alluvial soils. During the study (1994-5) soil pH in the surface 15 cm averaged 6.6 and plant-available N approximately 18 mg l⁻¹ soil solution. Mean soil moisture for May-August 1994-5 was 30%, although in mid-summer 1995 it fell below 20%. The water table fluctuates greatly within the course of a year, often with a brief period of flooding in spring (e.g. several days in early May 1995), falling to around 150 cm below the soil surface in June-August. Prach (1992) recorded a two-year mean water table for the site of -68 cm.

It is likely that the study site was managed as a hay meadow from at least the 1780s (J. Guth, pers. comm., 1994), with no under-drainage and no record of fertilizer having been used. Prior to a cessation of management in 1992 due to the collapse of the State agricultural system, the study site was cut for hay at least once and usually twice

Figure 2.13 Management cycle at Lužnice study site.
Timings are based upon archival and anecdotal information and observations made during the study period 1994-5.



annually (Figure 2.13). The first cut took place in June or July, the second normally in late August or September, depending on weather and flooding conditions (K. Prach, pers. comm., 1994). The timing of the second cut was more variable, not only due to weather but also the availability of human resources and equipment. In particularly favourable years, a third, later crop would occasionally be taken

2.1.5.1 The plant community

The plant community of the Lužnice study site (Plate 7) consists of a species-rich association of grasses, some sedges and mostly perennial forbs that attain 40-80 cm height prior to cutting in mid-summer. The fine-leaved grass *Festuca rubra* is frequent and *Sanguisorba officinalis* is a prominent member of the varied and plentiful dicotyledonous component (Table 2.4), dominating in mid-season. The community lies within the *Molinio-Arrhenatheretea* alliance of continental phytosociology and shows floristic affinities with the English flood-meadow community described as MG4 by Rodwell (1992) (of which the Besthorpe study site is an example, Table 2.3), sharing many of its species and an abundance of *S. officinalis*. A survey of the Lužnice stand undertaken in May 1994 recorded 45 vascular plant species in total, with 20-31 species m⁻² and a mean of 36 species 4 m⁻². Above-ground plant production in 1994-5 averaged 4.7 tonnes dry weight ha⁻¹ yr⁻¹. The botanical diversity of the Lužnice study site (Plate 8) was recognized in 1994 when it was designated as part of a National Nature Reserve (Janda, 1994; Lexová *et al.*, 1996).

2.1.6 Comparison of the plant communities studied

The three plant communities studied are summarized in Table 2.5. Gunthorpe is an English inundation pasture dominated by grasses that has a low plant species diversity and is comparatively productive. Besthorpe is a traditionally-managed English flood-meadow supporting a characteristic plant community comprised of a mixture of grasses and forbs. Plant species diversity and production at Besthorpe are intermediate between the other two study sites. The Lužnice study site is a relatively unproductive Czech flood-meadow characterized by low-intensity management, high plant species diversity and an abundant forb component. They therefore represent a spectrum of plant communities that describe the variation in species diversity, composition and plant production in European floodplain grasslands.

Plate 7 The Lužnice plant community. *Sanguisorba officinalis* and *Succisa pratensis* are conspicuous in this patch of uncut vegetation adjacent to the study site. August 1994



Plate 8 The Lužnice plant community was distinguished by high plant species richness. The plate shows approximately 1 m² of vegetation. August 1995



Rare species (i.e. recorded in less than two samples): *Festuca pratensis* (Narrow-leaved Fescue), *Nardus stricta* (Mat-grass), *Achillea ptarmica* (Sneezewort), *Hypochaeris radicata* (Common Cat's-foot), *Lythrum hyssagifolia* (Creeping Jenny), *Campanula rotundifolia* (Harebell).

Table 2.4 Floristic table for the Lužnice plant community

Plant species nomenclature follows Tutin *et al.* (1964-80) *Flora Europaea Volumes 1-5*. Cambridge University Press, Cambridge. * = grasses; † = sedges; x = wood-rush; remaining vascular plant species are forbs.

Derived from a survey in May 1994 of 24 randomly-located 1m² samples.

For explanation of frequency and abundance see Table 2.1.

Scientific name	English name	Frequency and abundance
* <i>Festuca rubra</i>	Red Fescue	V (4-7)
<i>Sanguisorba officinalis</i>	Great Burnet	V (4-7)
* <i>Alopecurus pratensis</i>	Meadow Foxtail	V (3-5)
* <i>Luzula campestris</i>	Field Wood-rush	V (2-4)
<i>Ranunculus acris</i>	Meadow Buttercup	V (2-4)
* <i>Agrostis capillaris</i>	Common Bent	V (1-4)
<i>Hieracium umbellatum</i>	A Hawkweed	V (1-4)
<i>Plantago lanceolata</i>	Ribwort Plantain	V (1-4)
* <i>Poa pratensis</i>	Smooth-stalked Meadow-grass	V (1-4)
<i>Potentilla erecta</i>	Tormentil	V (1-4)
Bryophytes (all species)	Moss	V (2-3)
<i>Rumex acetosa</i>	Common Sorrel	V (2-3)
<i>Cardamine pratensis</i>	Cuckooflower	V (1-3)
<i>Cerastium fontanum</i>	Common Mouse-ear	V (1-3)
<i>Trifolium repens</i>	White Clover	V (1-3)
<i>Succisa pratensis</i>	Devil's-bit Scabious	IV (1-5)
* <i>Deschampsia cespitosa</i>	Tufted Hair-grass	IV (2-4)
<i>Achillea millefolium</i>	Yarrow	IV (1-4)
* <i>Anthoxanthum odoratum</i>	Sweet Vernal-grass	IV (1-4)
<i>Centaurea jacea</i>	Brown Knapweed	IV (1-4)
* <i>Holcus lanatus</i>	Yorkshire Fog	IV (1-4)
<i>Taraxacum officinale</i> agg.	Dandelion	IV (1-4)
<i>Leontodon autumnalis</i>	Autumn Hawkbit	IV (1-3)
<i>Pimpinella saxifraga</i>	Burnet Saxifrage	IV (1-3)
<i>Stellaria graminea</i>	Lesser Stitchwort	IV (1-3)
<i>Lychnis flos-cuculi</i>	Ragged-robin	III (1-3)
<i>Trifolium pratense</i>	Red Clover	III (1-3)
† <i>Carex caryophylla</i>	Spring Sedge	III (1-2)
<i>Campanula patula</i>	Spreading Bellflower	III (1-2)
<i>Polygonum bistorta</i>	Common Bistort	II (1-5)
<i>Angelica sylvestris</i>	Angelica	II (1-4)
* <i>Avenula pubescens</i>	Hairy Oat-grass	II (1-4)
† <i>Carex brizoides</i>	Quaking-grass Sedge	II (1-4)
<i>Lotus uliginosus</i>	Greater Bird's-foot Trefoil	II (1-2)
<i>Dianthus deltoides</i>	Maiden Pink	II (1)
<i>Anemone nemorosa</i>	Wood Anemone	I (1-4)
* <i>Briza media</i>	Quaking-grass	I (1-2)
† <i>Carex panicea</i>	Carnation Sedge	I (1-2)
<i>Galium uliginosum</i>	Fen Bedstraw	I (1)
<i>Leontodon hispidus</i>	Rough Hawkbit	I (1)

Rare species (i.e. recorded in less than two samples) : **Festuca pratensis* (Meadow Fescue), **Nardus stricta* (Mat-grass), *Achillea ptarmica* (Sneezewort), *Hypochoeris radicata* (Common Cat's-ear), *Lysimachia nummularia* (Creeping Jenny), *Campanula rotundifolia* (Harebell).

Table 2.5 Summary of the plant communities studied

Name	Gunthorpe	Besthorpe	Lužnice
Location	River Trent, England	River Trent, England	Lužnice River, Czech Republic
Community type	Inundation pasture	Flood-meadow	Flood-meadow
Key species	<i>Agrostis stolonifera</i> <i>Alopecurus geniculatus</i> <i>Poa trivialis</i>	<i>Agrostis capillaris</i> <i>Alopecurus pratensis</i> <i>Festuca rubra</i> <i>Holcus lanatus</i> <i>Sanguisorba officinalis</i>	<i>Festuca rubra</i> <i>Sanguisorba officinalis</i>
Species diversity (no. m ⁻²)	7	13	25
Above-ground production (t dry weight ha ⁻¹ yr ⁻¹)	7.9	6.1	4.7
Management:			
cutting	None	Once annually: end June-beginning July	1-3 times annually: June - Sept
grazing	April - Oct/Nov: 6-8 horses, 24-44 cattle (11.5 ha)	Sept - Oct: 180-250 sheep (5.2 ha)	None
Flooding	Annual: in winter	Some years: in winter	Most years: in spring

2.2 General methods

This section introduces the field sampling and data analytical methods that are common to all experiment protocols undertaken at the three study sites. Further information, and methods that relate to specific protocols, are presented in the relevant chapters (3-6).

2.2.1 Field sampling

The programme of field sampling at the three study sites is shown in Table 2.6. Gunthorpe and Besthorpe were used to investigate plant community dynamics of managed and unmanaged floodplain grasslands and the role of floodborne litter in their functioning. The effects of fertilizer N addition on flood-meadow plant communities were examined at the Besthorpe and Lužnice sites. The study in total encompassed the period March 1993 - September 1995 (Table 2.6). Within this, field sampling at Gunthorpe and Besthorpe was undertaken usually on a monthly basis through the growing season (as defined by Robson *et al.*, 1989), and at regular intervals during the main growing period at the Lužnice study site.

2.2.2.1 Permanent plots

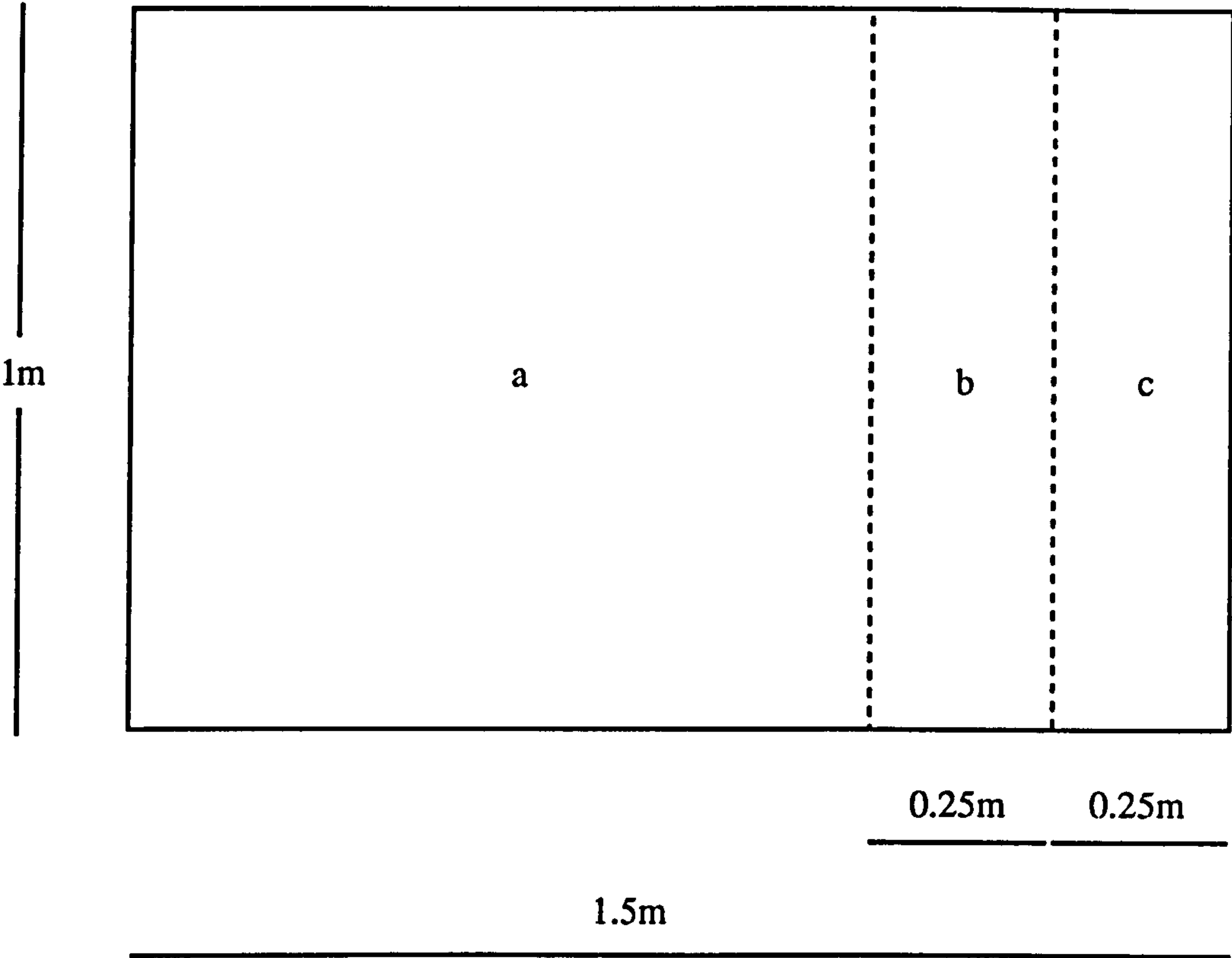
Field sampling at each of the three study sites utilized permanent plots. These are widely used for repeated sampling of grasslands because they ensure measurements collected on different dates refer to exactly the same area of vegetation and so are directly comparable (Smith *et al.*, 1985). In this study, plots were marked in all four corners by durable plastic discs 10 cm in diameter, fixed at ground level by plastic-coated wire pegs. They were set up randomly, allowing for the following two constraints. First, reconnaissance surveys prior to the establishment of permanent plots had indicated areas of relative homogeneity in vegetation composition and structure, enabling plots to be located so as to avoid obvious vegetation boundaries and unrepresentative floristic or physiognomic features, such as those often encountered at field edges or near paths. Second, plots were set up at least 3 m apart to ensure independence between the treatments applied. No plots were lost due to unforeseen circumstances during the study (e.g. vandalism or inability to relocate plots).

Botanical sampling within the plots consisted of measurements that characterize plant diversity and community composition, namely species presence, ground cover, and above-ground biomass. Each permanent plot measured 1 m x 1.5 m (Figure 2.14). On

Figure 2.14 Plan of permanent plot

Sampling strategy:

- a. Plant diversity and cover: species presence and % cover
- b. Plant production: above-ground biomass
- c. Soil variables: e.g. pH, moisture



each sampling occasion, the same 1 m² within each plot was used to record all vascular plant species and their % cover (a in Figure 2.14), the latter assessed visually as a vertical projection on to the ground of all the live, above-ground parts of the plant in the quadrat. At the same time, the cover occupied by moss, litter and bare ground was recorded. Quadrats 1 m² are recommended for botanical survey and monitoring of grasslands (Smith *et al.*, 1985). The sample unit is convenient for detailed species-searching and for assessment of cover, yet large enough to include subordinate species such as many forbs, which strongly affect species richness (Whittaker, 1965). This size of quadrat was confirmed by visual examination at the beginning of the study to be appropriate to the spatial heterogeneity of the species composition and structure of the swards. There was no evidence that sward management (cutting or grazing) eliminated temporarily all the above-ground portion of any plant species that would have made detection impossible. Indeed, no particular difficulty in vascular plant species identification was encountered. Plant species nomenclature of Tutin *et al.* (1964-80) was followed.

Plant production was determined by clipping above-ground vegetation with shears from a 0.04 m² quadrat located at random within the 0.25 m x 1 m section of each plot not used for sampling other botanical or soil variables (b in Figure 2.14). On each occasion, different sections of the plots were harvested. Each sample was sorted to species level and dried to constant weight at 105 °C.

The remaining 0.25 m x 1 m section of the permanent plot was available to sample soil variables (c in Figure 2.14), such as moisture and pH.

2.2.2 Data analysis

Data analysis generally incorporated graphical presentation with inferential (univariate) statistical testing using analysis of variance (ANOVA), Tukey's multiple comparison test and *t*-tests. The validity of the significance tests used in the study depends upon the usual assumptions of normality and constant variance for sampled populations (Sokal and Rohlf, 1981). An emphasis has been placed on obtaining equal sample sizes within experiments as analyses are much more sensitive to assumptions, and are generally more powerful, when sample sizes are equal (Day and Quinn, 1989). Data from replicate plots that were not interspersed were examined by graphical comparison and multivariate techniques.

Most plant communities consist of several or many species which compete for light, water and nutrients. Data analyses focused on the individual species that constitute the plant community, particularly key floodplain grassland species (e.g. *Sanguisorba officinalis*) and also examined aggregates or 'groups' of species which would be expected to show a similar response to experiment treatments (e.g. moss, grasses, forbs), an approach that has successfully demonstrated trends in grassland vegetation in other studies (Smith *et al.*, 1985).

Measurements from successive sampling occasions from the same experiment plots are correlated with each other and therefore not statistically independent (Hurlbert, 1984). Hence, initial statistical testing was undertaken separately for each date, although this does not invalidate the examination of treatment means for contrasts and consistencies over time. Multiple comparisons within species richness, % cover and biomass data were undertaken firstly using ANOVA, followed by Tukey's test where a significant difference in the treatment means was evident. Tukey's test is an unplanned multiple comparison test that is commonly used in ecological studies and is appropriate and effective for smaller sample sizes (Zar, 1984; Day and Quinn, 1989). Comparisons between individual treatment means used *t*-tests when the values were derived from the same sampling occasion. Specific temporal changes were examined by applying paired *t*-tests to examine whether the mean of sample differences between pairs of measurements is significantly different from a hypothetical mean, which the null hypothesis puts at zero (Sokal and Rohlf, 1981). The pairs used in this study were individual experiment plots sampled at two points in time. Results of all statistical analyses were termed significant only if $P < 0.05$.

Initial visual assessments of the experiment sites indicated considerable uniformity with regard to botanical composition. This was subsequently statistically tested by applying ANOVA to the species richness and % cover values recorded from the plots on the first sampling occasion, prior to the random allocation of the experiment treatments. For species richness and cover values for all community variables included and shown in the results, no significant differences in mean values were detected on this occasion, confirming that the null hypothesis of equality between the plots prior to the experiment should be accepted.

2.2.2.1 Plant species diversity

The concept of diversity has two main components (Magurran, 1988; Huston, 1994). These are first the number of different species and secondly the relative amount of each

species. The number of species in a sample is generally called species richness. The relative abundance of species in a sample is usually referred to as 'evenness', since the more equal the distribution of abundance, the greater the diversity as perceived intuitively or as measured by certain statistics (Pielou, 1966).

In this study, species richness and relative abundance were the two statistical properties used to quantify diversity. The index that emphasizes the richness component of diversity, with no effect of dominance, is simply the number of species in the sample. In this study, species richness was ascertained by recording all species present in each 1 m² plot and was expressed as number of species m⁻². An index that expresses the degree of dominance in the data is Simpson's index (Simpson, 1949), which is calculated from the formula:

$$D = \sum_{i=1}^s (p_i)^2$$

where p_i is the proportion (measured in this study as mean % cover) of individual species i in each set of treatment plots and s is the mean number of species in each set of plots. Simpson's index tends to be inversely related to evenness and richness, so it is often expressed as $1/D$ so that as it increases diversity (evenness) tends to increase whilst dominance decreases. It is weighted towards the most abundant species in the sample and emphasizes changes in the abundances of the commonest species while being less sensitive to species richness. Simpson's index has low sensitivity to sample size and has been widely used in other ecological studies (e.g. Magurran, 1988), partly because it can indicate the effect of important processes on diversity when species number does not change, for example in short-term comparisons.

2.2.2.2 Cover

In a given community, one or few species tend to dominate all others in their mass and biological activity and may strongly affect environmental conditions for other species (Whittaker, 1965). An assessment of the degree of plant cover provides an appropriate and well-established measure of relative abundance (Poore, 1956), with dominant species having the greatest degree of cover in the community.

The normality and equality of variance of proportional data such as percentages cannot be assumed since it is known on theoretical grounds that such populations are not normal and that variances can vary as a function of the mean (Zar, 1984). In particular,

the deviation from normality can be great for small or large percentage values (0-30%; 70-100%). However, non-normality and heteroscedasticity can be corrected by suitable transformation (i.e. replacing values with a different scale of measurement such as their log or arcsine angle), although transformation can hinder clear data presentation and interpretation. This is because confidence limits computed in the transformed scale and changed back to the original scale for presentation are asymmetrical. However, showing standard errors in their original scale for a mean value that had been derived from transformed data would also be misleading (Sokal and Rohlf, 1981). Drawing meaningful conclusions from such data can therefore be problematic (Day and Quinn, 1989).

Comparisons of mean and standard deviation values can elucidate whether transformation is appropriate (Day and Quinn, 1989), but in this study such comparisons proved inconclusive although extreme skewness, variance inequality and outliers were not detected. Hence, the results of analysis of transformed % cover data were compared with those derived from untransformed data. For the multivariate analysis only, discrimination between treatments was improved by transformation and so transformed cover values are shown. For all inferential statistics, the performance of the analyses using transformed and untransformed values was extremely similar, and did not affect any subsequent conclusions. Hence, and in order to promote interpretation, clarity in presentation and compatibility between results, these cover results are shown using untransformed mean and standard error % values.

2.2.2.3 Plant production

Plant production is a key measure of competitive success that was determined in this study by above-ground biomass. Plant biomass demonstrates the importance of a species or group of species within the community as it expresses the biological activity of a species or group and indicates the share of the community's environmental resources that it utilizes (Whittaker, 1965). Preliminary visual assessments had indicated the botanical uniformity of the study areas. This was confirmed by measures of species richness and % cover taken during the first sampling occasion (before treatment application). It was therefore considered unnecessary to examine plant biomass for significant variation prior to the application of experiment treatments, as any notable differences in biomass recorded between treatments during the study were unlikely to be caused by initial botanical variation.

2.2.3 Methodological limitations

2.2.3.1 Quadrat size and replication

In this study, permanent plots and quadrats were replicated 4-6 times within each experiment protocol, the sample number and size depending on practical constraints of time and extent of study site available. This sampling intensity was effective for sampling and analysing fine-scale floristic variation to plant group level (e.g. grass and forbs), and was sensitive to the changes of individual species that achieved a high frequency. However, the resolution was less effective for assessing the dynamics of infrequent or patchily-distributed species, although these tended to be incidental within the community rather than core components. Statistical analysis of plant species biomass, particularly, would have been improved by increasing sample size, enhancing precision by reducing the effects of random variation. Thus, gathering a larger number of data from larger sample units or more replicates would have tended to yield more decisive conclusions, as the statistical tests would have had more power to discriminate small differences among means (Day and Quinn, 1989).

2.2.3.2 Pseudoreplication

Pseudoreplication is defined as the use of inferential statistics to test for treatment effects using data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent (Hurlbert, 1984). If treatments are spatially segregated, then replicates are not independent and tests using inferential statistics are inappropriate as they can only demonstrate significant differences between location, not significant differences between treatments. In this study, plot interspersion was constrained by practical limitations in the field experiment design, namely the use of an enclosure to control management of experiment plots at two of the three study sites. This meant that quadrats located within the enclosed section of the study site were not interspersed with quadrats in the remainder of the site. Therefore, comparison between the two sets of plots was uncontrolled for the possibility that any initial dissimilarities within sections of the same study site could impinge on treatment effects. Moreover, as a result of uncontrolled extraneous influence or stochastic events, differences between locations could arise or become greater while the experiment is in progress independently of any true treatment effect (Hurlbert, 1984). Pseudoreplication could not be avoided in this study, however graphical comparison and multivariate techniques provided appropriate, effective and powerful means of summarizing and analysing data.

Chapter 3 Plant diversity and community dynamics of managed and unmanaged floodplain grasslands

3.1 Introduction

There has been a widespread loss of habitat diversity in European river floodplains over the past 300 years (Décamps *et al.*, 1988; Petts *et al.*, 1989) and a marked reduction in the extent and biodiversity of semi-natural grasslands in Europe, particularly in the last 50 years (Fuller, 1987; International Union for the Conservation of Nature and Natural Resources, 1991; van Dijk, 1991). Consequently, semi-natural floodplain grasslands have been similarly degraded and lost (Wells and Sheail, 1988; Dargie, 1993; Joyce, 1994). Such grasslands are often of high biodiversity and nature conservation value, especially as they support rare plant species and vegetation types (Rodwell, 1992; Jefferson and Robertson, 1996; Jefferson and Grice, 1998) and internationally important concentrations of wintering wildfowl and breeding wading birds (Hötter, 1991; Jefferson and Robertson, 1996).

The distinctive and ecologically valuable plant communities of European semi-natural floodplain grasslands are characterized by periodic inundation and are maintained by regular appropriate management, usually mowing and/or grazing. Indeed, past degradation and losses have been due largely to alterations in these factors through the implementation of flood defence, land drainage and agricultural intensification (Wells and Sheail, 1988).

In contrast, there are many other remaining floodplain grasslands that are threatened by a lack of management. In northern and western Europe, for example, agricultural overproduction and policy reforms are leading to a reduction in the number of livestock in lowland areas and the withdrawal of marginal areas from agriculture (Signal and McCracken, 1992). In addition, following the dissolution of the Soviet Union, many central and eastern European countries have undergone reform in their agricultural as well as political systems. This has not only led to a shortage of public funds for agricultural subsidies and the abandonment of many areas, but also a lack of finance for grassland management for nature conservation objectives (Straškrabová *et al.*, 1996). At the same time, re-privatization of land ownership is creating uncertainty in a number of these countries (Baldock, 1994), since many owners who have had land returned, or allocated, to them often have little incentive to manage it.

A number of studies have investigated the effects of management on the botanical composition of semi-natural grasslands (e.g. Baker, 1937; Hopkins, 1986; Bakker,

1989; Smith and Jones, 1991) and the changes brought about by neglect have been summarized (e.g. Ellenberg, 1988 p. 642-3; Wells, 1989). However, the rate of community change can vary considerably between different grassland types (Fossati and Pautou, 1989; Wells, 1989; Gibson and Brown, 1992). Little is known about the dynamics of semi-natural floodplain grassland plant communities in relation to management, or their sensitivity to the cessation of management. This chapter therefore seeks to explore the effects of management and abandonment on floodplain grassland plant diversity and community dynamics.

The main analytical method selected for this study is ordination. Ordination techniques provide an effective means of describing temporal or spatial variation in vegetation composition. They have often been used to summarize or expose major features of the variation in plant community composition over time and to generate hypotheses about the underlying environmental factors, particularly from large observational data sets (Austin, 1977; ter Braak, 1995). Indeed, the study of grassland plant community dynamics in relation to management and succession has provided a focus for ordination. For example, Gibson and Brown (1992) assessed vegetation change in an early successional calcicolous grassland during six years of grazing and concluded that ordination analysis clearly separated grazing and temporal effects at the community scale. Studies of succession in abandoned damp meadows also found that ordination clearly differentiated the effects of cessation of grazing (Persson, 1984), including impacts on species diversity (Regnéll, 1980).

This study aims to use ordination as a framework upon which to:

- elucidate the influence of particular management activities on floodplain grassland plant diversity and community dynamics,
- describe the short-term responses of different floodplain grassland communities to the cessation of management, and
- examine factors that influence floristic diversity and variation.

The chapter concludes by indicating how an appreciation of such information may promote effective conservation management and rehabilitation of European floodplain grasslands.

3.1.1 Study sites

The study was undertaken at two sites along the River Trent in the English Midlands (Figure 2.1). The Trent floodplain in this area is generally underlain by sand and gravel with a 1-2 m overburden of alluvial silts and clays. The history of the Trent is characterized by human modification, particularly systematic attempts at river regulation and land-use changes, often accompanied by a marked reduction in ecological diversity (Petts *et al.*, 1992; Large *et al.*, 1994). Pollen analysis has indicated that grassland utilization for agriculture was well established on the floodplain by 3 200 BP (Lillie and Grattan, 1995). Subsequently, the rich alluvial soils supported productive grazing for cattle and sheep, and rough grassland cut for hay, into the 20th century (Edwards, 1944), although the area was prone to periodic severe inundation (Marshall, 1955). However, increasingly effective flood control facilitated land drainage and more intensive agriculture on the floodplain. Today, the river is regulated for most of its length, being channelized and with long reaches impounded by weirs and sluices. Flooding is largely controlled within washlands and arable agriculture and intensively exploited grasslands predominate. Nevertheless, Dargie (1993) indicated that the Trent floodplain is a major source of the remaining wet grassland of potential nature conservation value in eastern England.

The study sites represent the two types of floodplain grassland plant communities that are of particular nature conservation interest along the Trent. One site was situated near the village of Gunthorpe (Figure 2.1) and was located in an approximately level pasture of 11.5 ha grazed by cattle and horses (Table 2.5). The grassland is regularly inundated and supports a plant community characteristic of wet circumneutral soils. This is recognized as the *Agrostis stolonifera* - *Alopecurus geniculatus* MG13 association in the National Vegetation Classification (Rodwell, 1992), and as CORINE biotope type C37.242, *Agrostis stolonifera* and *Festuca arundinacea* swards (Devillers *et al.*, 1991). This type of vegetation is typically not floristically diverse but is a valuable forage resource for wildfowl (Burgess *et al.*, 1990; Rodwell, 1992).

The second study site was situated in a 5.2 ha field near to Besthorpe village (Figure 2.1). The plant community present at Besthorpe is described by the National Vegetation Classification as MG4, the *Alopecurus pratensis* - *Sanguisorba officinalis* association (Rodwell, 1992), and by CORINE biotope type C38.2, lowland hay meadows (Devillers *et al.*, 1991). This community type is of considerable nature conservation value because of its botanical diversity and limited European distribution, being effectively confined to England (Rodwell, 1992; Council of the European Communities, 1992). The vegetation type is characteristic of areas where

traditional, less intensive, hay-meadow management has been applied to seasonally flooded land with alluvial soils. At Besthorpe, there is a long history of late hay cutting, with the regrowth grazed by sheep (Table 2.5). There is no history of fertilizer use in the area other than occasional small applications in the 1980s. Prior to flood defence works being completed in 1981, the area was likely to have been inundated annually (Marshall, 1955), although since then it has flooded less frequently (N. Lewis, pers. comm., 1994).

3.2 Methods

3.2.1 Field study

The period of field study was March 1993-September 1995. In March 1993 an enclosure was established at each of the two study sites, excluding a section of the floodplain grassland from subsequent management, but not from flooding. Within the enclosure, no management activity (including cutting and/or grazing) took place during the entire study period. Over the rest of the floodplain grassland, outside the enclosure, management continued as described in Table 2.5. There was also evidence of grazing by rabbits but only outside the enclosure. Flooding patterns at both sites are also summarized in Table 2.5.

The vegetation at both Gunthorpe and Besthorpe was monitored, usually monthly, between March and September in 1993, 1994 and 1995. The presence and percentage cover of all vascular plant species were recorded in permanently marked 1 m² quadrats at both sites, four quadrats located at random within the enclosure (unmanaged) and either four or six located randomly in the floodplain grassland outside the enclosure (managed), the latter in order to facilitate comparison with other experiments at the sites.

3.2.2 Data analysis and presentation

Comparisons using graphical plots and ordination analysis were most appropriate to investigate the effects of management regime and abandonment on plant diversity community dynamics at each of the two different sites, particularly as statistical analysis was restricted by practical limitations in the field experiment design (see Hurlbert, 1984). At both study sites, quadrats located within the enclosed unmanaged section of the floodplain grassland were segregated from quadrats in the managed

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remainder of the site. The study was therefore not controlled for the possibility that any small initial dissimilarities between the two parts of the same study site, or a chance event during the study, could have had an influence on plant community composition. Testing between such spatially segregated quadrats using inferential statistics would therefore only enable examination of the relationship between different parts of the floodplain rather than the effects of management or its cessation.

3.2.2.1 Plant species diversity

Plant diversity was examined using species richness, expressed as the number of species m^{-2} . Mean species richness for managed and unmanaged sets of experiment plots was graphed against time for each study site.

3.2.2.2 Plant community dynamics

The effects of management regime and abandonment on plant community dynamics, as expressed by species' abundance, were examined by descriptive ordination analysis. Ordination methods are used to represent visually the arrangement of units (species or samples) in two or more spatial dimensions. The position of each unit in the ordination will be uniquely determined by its particular combination of observed values. Units with similar sets of values will therefore occupy adjacent positions, or points, in the ordination diagram. The axes of the ordination diagram are either constrained, expressing measured environmental variables, or unconstrained, representing theoretical variables that explain point dispersion such that the points on each axis can subsequently be interpreted in relation to underlying environmental variables.

The unconstrained technique Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980) was used to ordinate data sets from both study sites. DCA is appropriate for normally distributed species data with a long gradient of variation (ter Braak, 1995). It is based on the observation that, within their range, species tend to be most abundant around their particular environmental optimum, i.e. they are unimodal (ter Braak and Prentice, 1988). The method estimates the optima of the species response by a process known as reciprocal averaging (Hill, 1973). This orders samples according to their species complement, and species by the samples in which they occur, by weighted averaging. With abundance data (e.g. % cover), weighted averaging applies weights proportional to species abundance. These

orderings form the basis of the DCA axes, which each consists of a set of species scores derived from weighted averages and a corresponding set of sample scores which are weighted averages of the species scores. The first axis is constructed to maximize the dispersion of the species values; a second and further axes which maximize species dispersion can also be extracted by the same process such that they are uncorrelated with previous axes to ensure that additional information is expressed.

DCA yields species and sample scores that can be plotted against each other to fix the species or samples as points on a diagram. The species points are approximately the optima of their response to the environmental variables described by the DCA axes. Hence, the abundance or probability of occurrence of a species tends to decrease with distance from the location of its point in the diagram. Species plot closest to those samples in which they attain maximum abundance and species near the centre of the diagram may be ubiquitous or they may be genuinely specific with an optimum near the centre of the sample range. Each sample score is the weighted average score of the species that occur in it. Hence, the species composition of a particular sample can be inferred from nearby species points and samples that lie close to the point of a species are likely to have a high abundance of that species. Thus, samples which are most similar plot closest together and the degree of community change is positively related to distance on the DCA diagram.

Hill and Gauch (1980) noted that the variance of the optima of the species present in a sample is an estimate of the average response curve breadth of those species. They used the standard deviation as a measure of this breadth and defined the length of the DCA axis in standard deviation units (sd). This can aid interpretation of the DCA output because a species may be expected to appear, rise to its optimum, and disappear again in approximately 4 sd; a 50% change in sample composition will occur in approximately 1 sd (Hill and Gauch, 1980).

Ordination was performed using the computer package CANOCO (ter Braak, 1988). An exploratory Correspondence Analysis (CA) on each of the Gunthorpe and Besthorpe data sets revealed an 'arch effect' distortion in the arrangement of points, indicating that the second axis of each diagram was systematically related to the first in a way that could impede interpretation (Hill and Gauch, 1980). However, CA confirmed that variation within the sample data was sufficient to allow effective ordination using DCA. Hence, DCA was performed on both data sets incorporating detrending by polynomials to remove the arch effect (ter Braak, 1995).

Plant community composition in the analysis was expressed as mean % cover for every species recorded from the managed and unmanaged sets of quadrats on each sampling date. Two other important parameters that help define community composition and vegetation change were also included, namely bare ground and litter (defined as dead plant material of small size lying on the ground). These were also treated as response variables expressed as mean % cover, giving a total data set of 32 samples x 30 'species' for Gunthorpe and 33 samples x 29 'species' for Besthorpe. Cover data were transformed using $\ln(y+1)$ so that data were approximately normally distributed. This log scale is commonly used in quantitative ecology; it is particularly effective at reducing the heteroscedasticity of high and low percentages, and avoids the problems of having zero values (Sokal and Rohlf, 1981). In this study, it also yielded a clearly interpretable set of ordination results.

Separate diagrams for Gunthorpe and Besthorpe were constructed from DCA by plotting scores for samples and species together against the first two axes of the ordination to summarize the main gradients of variation in the data.

3.3 Results

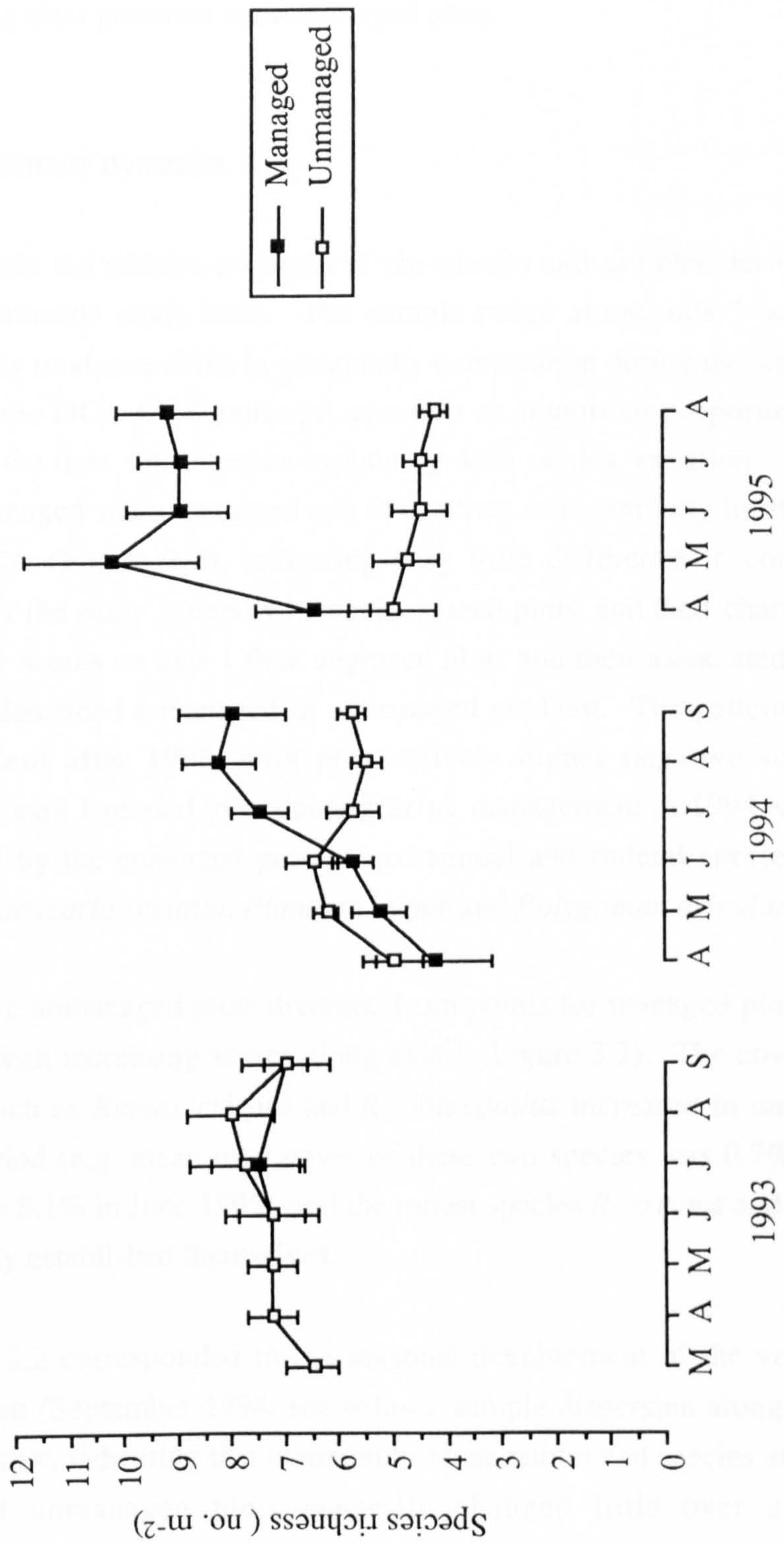
3.3.1 Gunthorpe

3.3.1.1 Plant species diversity

Plant species richness in the managed (grazed) plots at Gunthorpe during the 1993-5 study seasons averaged approximately 7 species m^{-2} . Values for the managed plots showed marked fluctuations, but generally increased slightly over the three years (Figure 3.1). In contrast, there was a gradual decline in species richness for the unmanaged plots during the study, and less within-season variation in mean values (Figure 3.1). At the end of the study in August 1995, these divergent trends in species richness resulted in on average twice as many species in the managed as unmanaged plots.

Species turnover occurred at Gunthorpe during the study, with a net gain of species for the managed plots and a loss overall from the unmanaged ones. Several species newly colonized the managed plots (but not the unmanaged ones), including *Stellaria media*, *Taraxacum officinale*, and *Juncus bufonius*. Only one species, *Rumex obtusifolius*, was eliminated from the grazed plots during the study. *R. crispus* and *Phalaris arundinacea* newly established themselves in the unmanaged plots (and not

Figure 3.1 Comparison of plant species richness in managed and unmanaged plots at Gunthorpe in 1993-95.
 Data are mean values $\pm 1\text{SE}$ ($n=4$)



in the managed plots) during the study period. Three species, *Lolium perenne*, *Poa annua* and *Trifolium repens*, were lost from the unmanaged plots during the study, despite maintaining their presence in the managed plots.

3.3.1.2 Plant community dynamics

Figure 3.2 illustrates the relative positions of the species and samples derived from DCA for the Gunthorpe study sites. The sample range along axis 1 was 2 sd, indicating relatively moderate shifts in community composition during the study. The first two axes of the DCA for Gunthorpe represent an important proportion of the total variation in the data set, together explaining 42% of this variation. Initially, scores for both managed and unmanaged sets of quadrats were similarly located along axis 1 of the DCA (Figure 3.2), indicating very little difference in community composition. Over the study generally however, grazed plots, and their characteristic species, had lower scores on axis 1 than ungrazed plots and their associated species. Axis 1 therefore described a managed to unmanaged gradient. The pattern became increasingly evident after 1993, with progressively higher negative scores for managed plots on axis 1 related to ongoing grazing management in 1994 and 1995. This was typified by the enhanced presence of annual and ruderal species of low stature, such as *Matricaria recutita*, *Plantago major* and *Polygonum aviculare*.

Points representing unmanaged plots diverged from points for managed plots during the study period with increasing scores along axis 1 (Figure 3.2). The cover of tall ruderal species such as *Rumex crispus* and *R. obtusifolius* increased in unmanaged plots over the period (e.g. mean total cover of these two species was 0.7% in June 1993, compared to 8.1% in June 1995), and the robust species *R. crispus* and *Phalaris arundinacea* newly established themselves.

Axis 2 in Figure 3.2 corresponded to the seasonal development of the vegetation. With one exception (September 1994; see below), sample dispersion along this axis was relatively narrow, indicating that community composition and species abundance in managed and unmanaged plots generally changed little over a season. Nevertheless, some temporal succession was evident. Species that were prominent earlier in the season, and study plots in which these species were relatively abundant, had low values along axis 2. In contrast, species that tended to achieve maximal abundance later in the season, and their corresponding plots, displayed higher axis 2 scores. Such species tended to be later successional ones, such as *R. obtusifolius* and *R. crispus*, that increased cover in a single season in the unmanaged plots (e.g. from a

Figure 3.2 Diagram showing positions of species and sample scores (standard deviation units) on the first two axes of a Detrended Correspondence Analysis (DCA) of species abundance data (mean % cover) from Gunthorpe 1993-5. (overpage)

Species are signified by a cross which represents the location of their optimal abundance in relation to the environmental variables described by the axes. Hence, species that respond similarly to the variables are positioned close to each other.

Samples are signified by filled circles for managed plots and open circles for unmanaged plots. Sample points represent weighted average abundance values of species recorded in those plots. The degree of community change is therefore indicated by distance on the diagram, i.e. the closer the sample points, the greater their similarity.

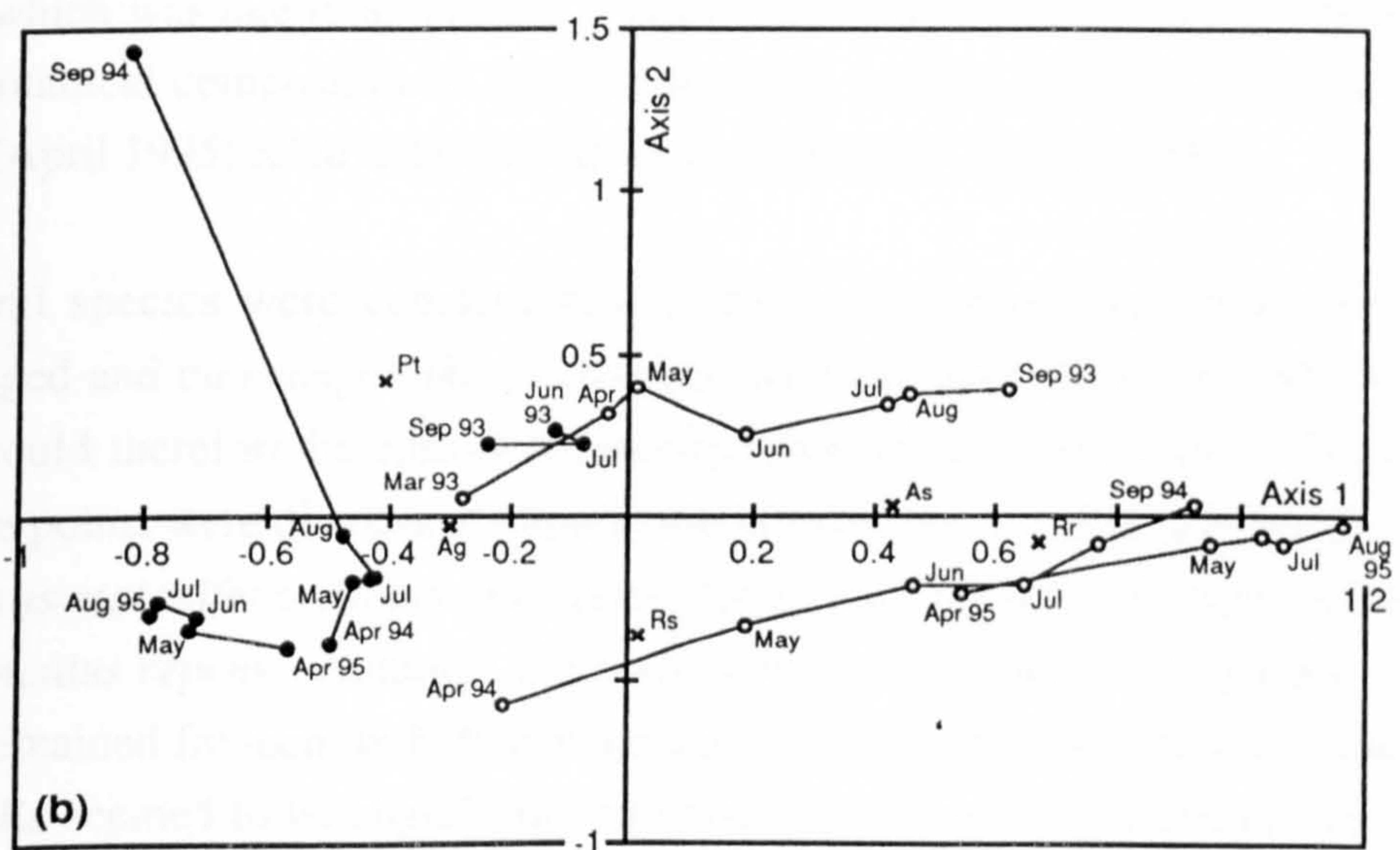
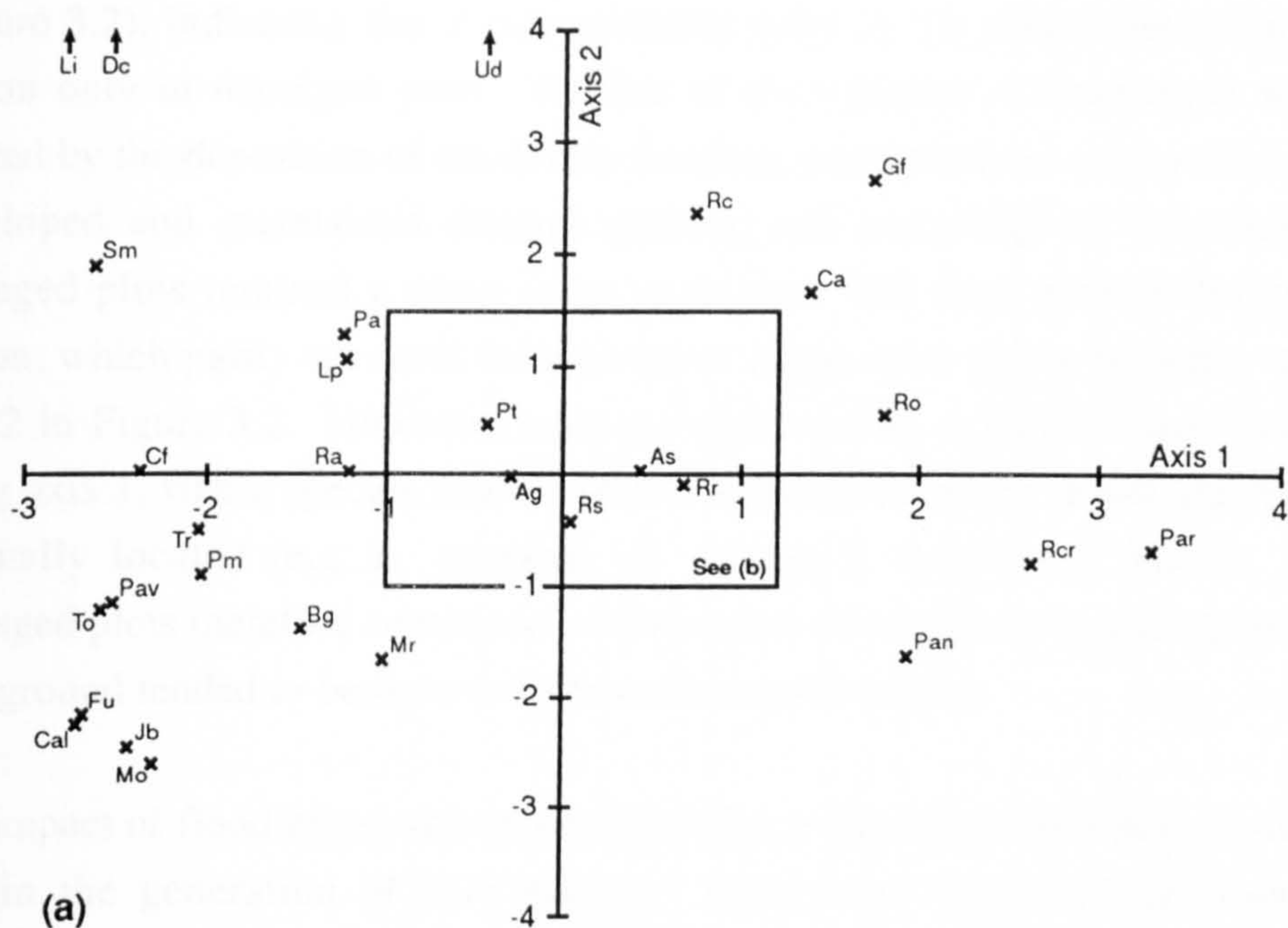
The diagram is in two parts:

a) shows the distribution of species scores (and other measured community variables). Positions of outliers are indicated by arrows.

b) shows the centre of a) enlarged to display sample scores. Lines linking samples recorded on different dates have been added to clarify temporal relationships.

Species codes: As, *Agrostis stolonifera*; Ag, *Alopecurus geniculatus*; Cf, *Cardamine flexuosa*; Cal, *Chenopodium album*; Ca, *Cirsium arvense*; Dc, *Deschampsia cespitosa*; Fu, *Filaginella uliginosum*; Gf, *Glyceria fluitans*; Jb, *Juncus bufonius*; Lp, *Lolium perenne*; Mr, *Matricaria recutita*; Mo, Moss; Par, *Phalaris arundinacea*; Pm, *Plantago major*; Pa, *Poa annua*; Pt, *Poa trivialis*; Pav, *Polygonum aviculare*; Pan, *Potentilla anserina*; Rr, *Ranunculus repens*; Rs, *Rorippa sylvestris*; Ra, *Rumex acetosa*; Rc, *Rumex conglomeratus*; Rcr, *Rumex crispus*; Ro, *Rumex obtusifolius*; Sm, *Stellaria media*; To, *Taraxacum officinale*; Tr, *Trifolium repens*; Ud, *Urtica dioica*.

Other measured variables: Bg, Bare ground; Li, Litter.



mean total cover value of 1.5% in April 1994 to 10.5% in September) and also increased cover in unmanaged plots over the three year study period as a whole.

An important factor influencing the distribution of sample points for Gunthorpe was the extent of bare ground. This parameter had relatively low scores on both axes (Figure 3.2), indicating that it was prevalent early in the season but throughout the season only in managed plots. Patches of bare ground at Gunthorpe were often created by the deposition of silt during flooding, particularly in winter, and were also developed and maintained through grazing and trampling by livestock. Thus, managed plots retained a mean value of at least 10% bare ground throughout the season, which partly accounts for the narrow range these points typically display on axis 2 in Figure 3.2. However, managed plots tended to exhibit decreasing scores along axis 1, where species that are able to withstand grazing and/or trampling were optimally located (e.g. *L. perenne*, *P. annua*, *S. media*, and *Rumex acetosa*). Managed plots therefore contrasted with the more dynamic unmanaged plots in which bare ground tended to become overgrown during the season.

The impact of flooding on vegetation dynamics at Gunthorpe was not restricted to its role in the generation of bare ground. Plant litter deposited by flooding was responsible for the outlying DCA score for managed plots in September 1994 (Figure 3.2) which was due to an unusually high mean litter cover of 18.7%. Nevertheless, the botanical composition of the affected plots had recovered by the next sampling date (April 1995) relative to records for the same plots in April 1994.

Several species were constant and relatively abundant components of both the managed and unmanaged plots at Gunthorpe throughout the three seasons of study, and could therefore be considered as describers of the community. These species, whose points were distributed close to the intersection of the axes in Figure 3.2, were *Agrostis stolonifera*, *Alopecurus geniculatus*, *Poa trivialis*, *Rorippa sylvestris* and *Ranunculus repens*. Although the species were all tolerant of temporary inundation and remained frequent in both managed and unmanaged plots, *A. geniculatus* and *P. trivialis* seemed to be slightly favoured by the grazing management, whilst a weak preference for the ungrazed treatment was shown by *A. stolonifera* and *R. repens*.

3.3.2 Besthorpe

3.3.2.1 Plant species diversity

Both managed and unmanaged plots at Besthorpe displayed a seasonal pattern of plant species richness (Figure 3.3), with maximum diversity in spring (April-May) when it attained 16 species m⁻². This was due to the presence of species that were conspicuous earlier in the season but tended to be absent later in the year, including *Bromus hordeaceus*, *Poa trivialis* and *Cerastium fontanum*. Consequently, the vernal peak in richness was followed by decline in both managed and unmanaged plots (Figure 3.3). However, in the managed plots, there was a recovery of mean species richness towards the end of the growing season, after cutting management, due to the re-appearance of perennial species such as *Ranunculus bulbosus*, *Cardamine pratensis* and *Trisetum flavescens*.

The seasonal pattern of species richness for managed and unmanaged swards was similar for each year and no evidence of either a decline or increase in mean richness for managed or unmanaged plots during the three year study was found (Figure 3.3). Indeed, no species was either eliminated from, or newly established itself in, the managed or unmanaged plots at Besthorpe during the study.

3.3.2.2 Plant community dynamics

The relative positions of the species and samples derived from DCA for the Besthorpe study site are shown in Figure 3.4. The sample range along axis 1 was 1.5 sd, indicating relatively subtle changes in community composition during the study. Twenty one % of the variation in the Besthorpe data set was contained in the first two DCA axes. This was less than for Gunthorpe, indicating that the Besthorpe community was generally not as responsive to management and seasonal factors. Nevertheless, managed and unmanaged treatments at Besthorpe were clearly separated along axis 1 of the DCA (Figure 3.4). Plots that received annual cutting and grazing management usually had higher scores along this axis than unmanaged plots. Species and other measured parameters that reflected these treatments were similarly distributed. Thus, managed plots were characterized by the presence of litter following mowing for hay (e.g. mean of 6.5% litter cover in managed plots in August 1995, compared to none in unmanaged plots at the same time), probably due to ineffective removal of the cut material. Earlier in the season, managed plots also exhibited a greater cover of *Cardamine pratensis* and moss (mean moss cover of

Figure 3.3 Comparison of plant species richness in managed and unmanaged plots at Besthorpe in 1993-95.
 Data are mean values $\pm 1\text{SE}$ (n=4, except n=6 for managed plots 1994-95). V indicates timings of cutting the managed plots

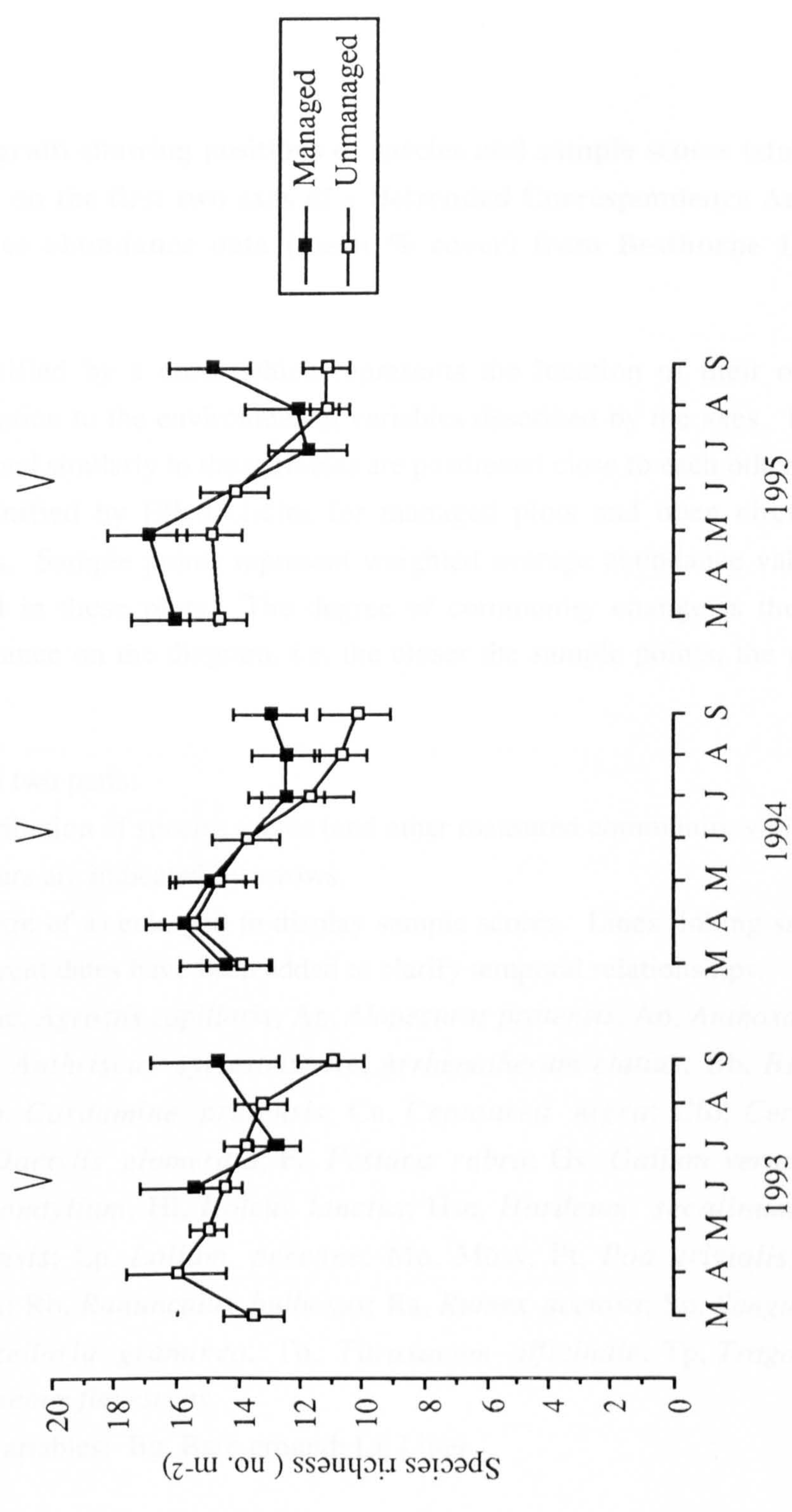


Figure 3.4 Diagram showing positions of species and sample scores (standard deviation units) on the first two axes of a Detrended Correspondence Analysis (DCA) of species abundance data (mean % cover) from Besthorpe 1993-5. (overpage)

Species are signified by a cross which represents the location of their optimal abundance in relation to the environmental variables described by the axes. Hence, species that respond similarly to the variables are positioned close to each other.

Samples are signified by filled circles for managed plots and open circles for unmanaged plots. Sample points represent weighted average abundance values of species recorded in those plots. The degree of community change is therefore indicated by distance on the diagram, i.e. the closer the sample points, the greater their similarity.

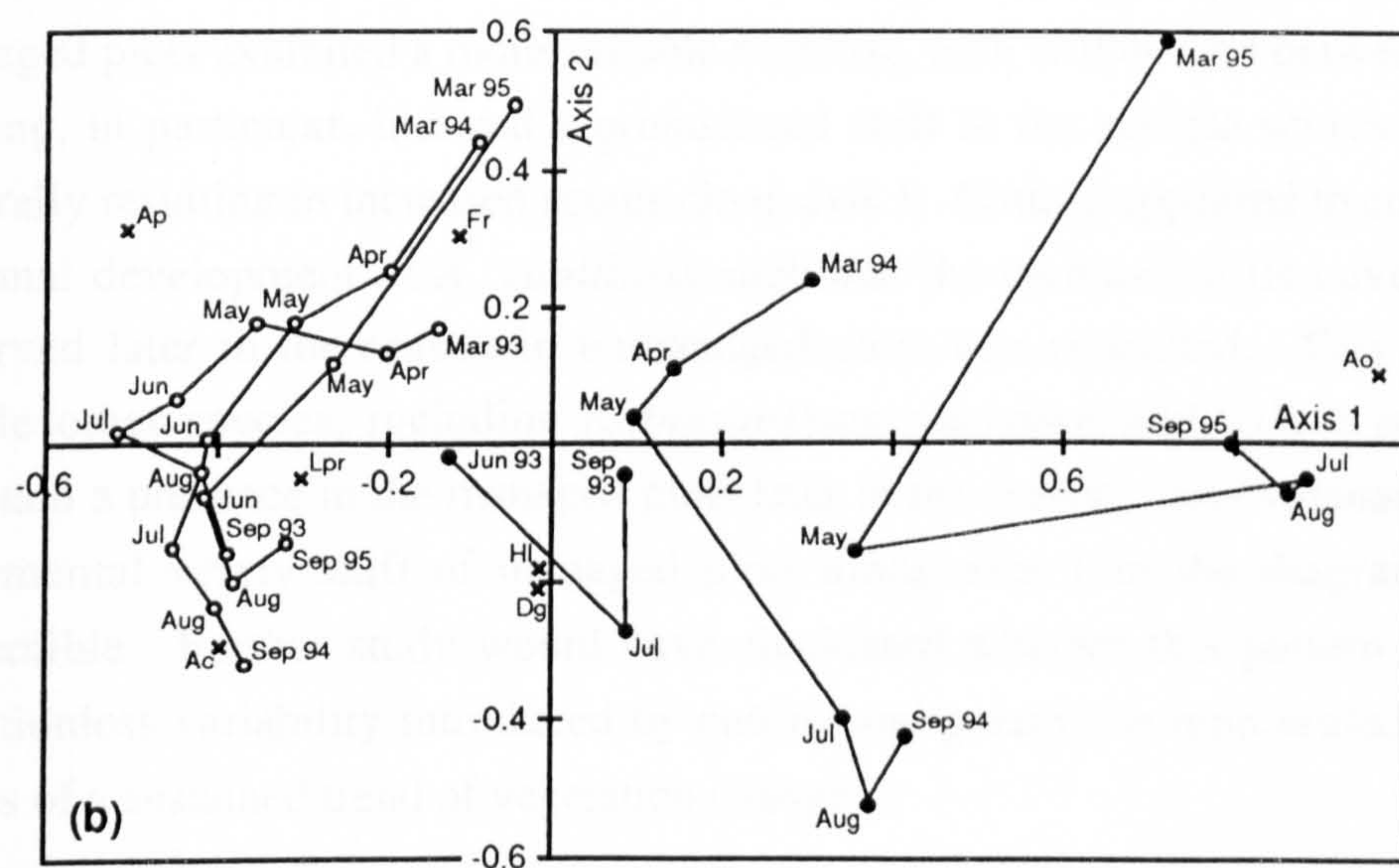
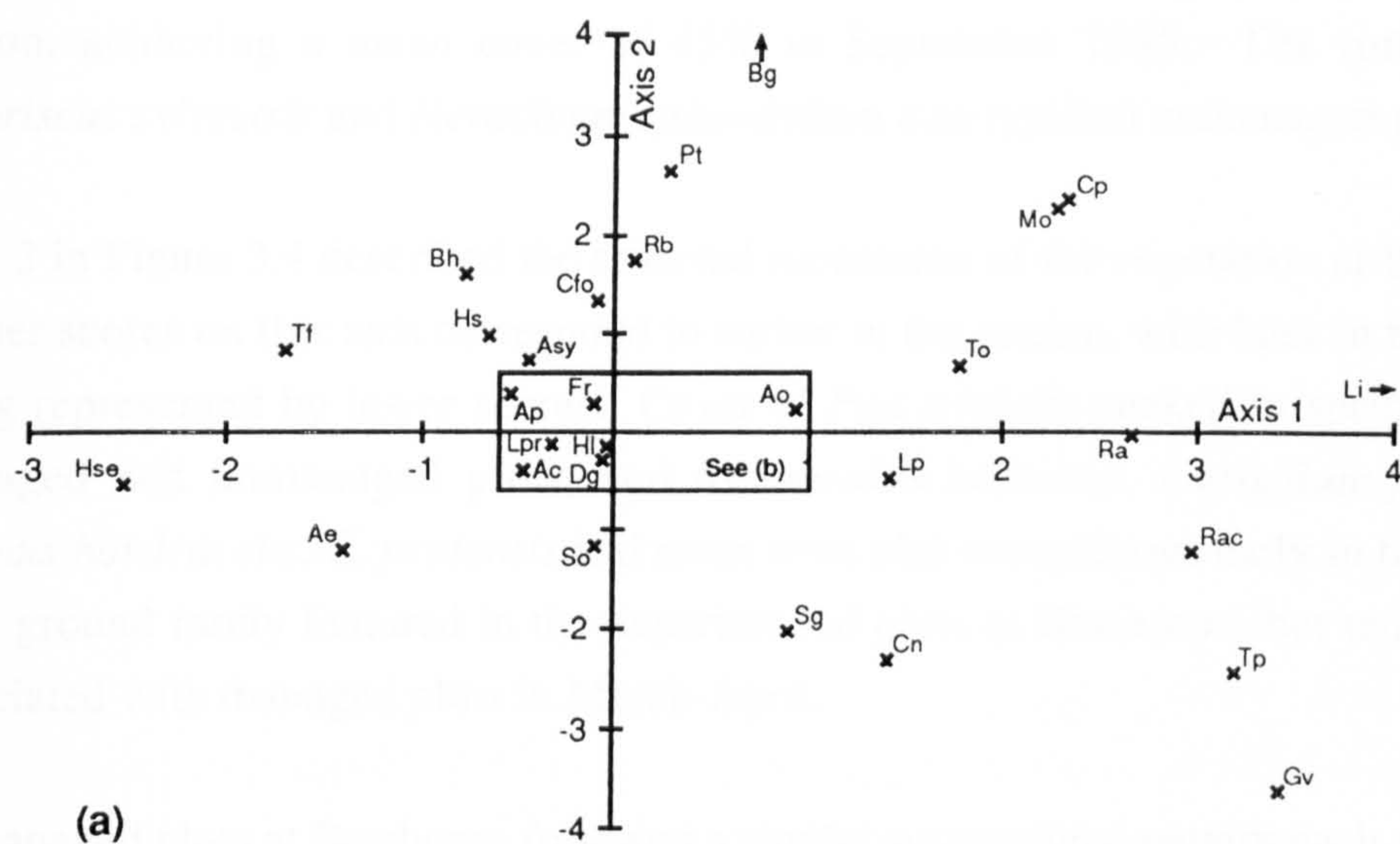
The diagram is in two parts:

a) shows the distribution of species scores (and other measured community variables). Positions of outliers are indicated by arrows.

b) shows the centre of a) enlarged to display sample scores. Lines linking samples recorded on different dates have been added to clarify temporal relationships.

Species codes: Ac, *Agrostis capillaris*; Ap, *Alopecurus pratensis*; Ao, *Anthoxanthum odoratum*; Asy, *Anthriscus sylvestris*; Ae, *Arrhenatherum elatius*; Bh, *Bromus hordeaceus*; Cp, *Cardamine pratensis*; Cn, *Centaurea nigra*; Cfo, *Cerastium fontanum*; Dg, *Dactylis glomerata*; Fr, *Festuca rubra*; Gv, *Galium verum*; Hs, *Heracleum sphondylium*; Hl, *Holcus lanatus*; Hse, *Hordeum secalinum*; Lpr, *Lathyrus pratensis*; Lp, *Lolium perenne*; Mo, Moss; Pt, *Poa trivialis*; Rac, *Ranunculus acris*; Rb, *Ranunculus bulbosus*; Ra, *Rumex acetosa*; So, *Sanguisorba officinalis*; Sg, *Stellaria graminea*; To, *Taraxacum officinale*; Tp, *Tragopogon pratensis*; Tf, *Trisetum flavescens*.

Other measured variables: Bg, Bare ground; Li, Litter.



9.5% in managed plots in March 1995 compared to 2.5% in unmanaged plots). In contrast, unmanaged plots were described by the enhanced presence of grasses that flower later in the season, most notably *Hordeum secalinum*, and a greater cover of *Arrhenatherum elatius* and *Agrostis capillaris* than cut and grazed plots. *A. capillaris*, in particular, was present in abundance in unmanaged plots late in the season, achieving a mean cover of 45% in September 1995. The robust forbs *Anthriscus sylvestris* and *Heracleum sphondylium* also typified unmanaged plots.

Axis 2 in Figure 3.4 described the seasonal succession of the vegetation at Besthorpe. Higher scores on this axis correspond to earlier in the season, with later in the season being represented by lower scores. Cover of *Poa trivialis* peaked in spring in both managed and unmanaged plots, and *Ranunculus bulbosus*, *Cerastium fontanum*, *Bromus hordeaceus*, *C. pratensis* and moss were also conspicuous early in the season. Bare ground rarely featured in the experimental plots at Besthorpe, but tended to be associated with managed plots in March-April.

Unmanaged plots at Besthorpe followed a similar successional pattern each year, with very little between-year variation, as shown by the clustering of points in Figure 3.4. Managed plots exhibited a more variable response, both within- and between-seasons. Cutting, in particular, induced a pronounced shift in the sample scores each year, generally resulting in increased scores along axis 1. Cutting appeared to constrain the seasonal development of *A. capillaris* such that the increase in its cover that was observed later in the season in unmanaged plots was restricted. This seemed to enable other species, including *Anthoxanthum odoratum* and *Lolium perenne*, to maintain a presence in the managed plots later in the season. An explanation for the incremental yearly shift of managed plots along axis 1 in the diagram was not discernible. Further study would have elucidated whether this pattern was either directionless variability introduced by cutting and grazing or represented the initial stages of a sustained trend of vegetation change.

It could be expected that managed and unmanaged plots at Besthorpe sampled in June 1993 would be similar in plant community composition, and hence DCA scores, since management during the study did not commence until hay cutting in July. However, DCA differentiated slightly between the two treatments (Figure 3.4) even at this early period of the experiment. These initial differences may have been due to the effects of rabbits grazing the managed plots outside the enclosure, as access to the unmanaged plots by rabbits was prevented following erection of the enclosure in March 1993. Alternatively, or in addition, they could have been caused by environmental heterogeneity within the study site, e.g. soil variability.

A number of plant species were relatively constant constituents of the community at Besthorpe during the study, irrespective of the implementation or absence of management. These included *A. capillaris*, *Alopecurus pratensis*, *Festuca rubra*, *Holcus lanatus*, *Sanguisorba officinalis* and, at low cover, *Dactylis glomerata* and *Lathyrus pratensis*. Typically, points for these species are distributed around the axes intersection on the DCA diagram (Figure 3.4).

3.4 Discussion

Graphical comparisons and ordination analyses described impacts of management and its cessation on floodplain grassland plant communities. Species composition and abundance appeared to follow a similar pattern to competition models presented by Grime (1979), which indicate that disturbance intensity and resource availability are important determinants of species diversity and the competitive abilities of plants.

3.4.1 Management

The Gunthorpe environment was variable, being disturbed by grazing, trampling, and episodic inundation. In such productive habitats exposed to repeated and severe disturbance, species diversity tends to be low and highly competitive plant species are suppressed and plants with a more ruderal strategy prevail (Grime 1979), often featuring short life-cycles able to exploit environments only intermittently favourable for rapid plant growth. At Gunthorpe, recurrent flooding, and grazing and trampling facilitated the availability of moist bare mud and silt which provided colonization and regeneration niches that encouraged species richness and were rich in available mineral nutrients, and therefore able to support rapid growth. However, the period available for growth was often relatively short, favouring annuals that germinated early and had a high potential growth rate, such as *Poa annua*, *Polygonum aviculare* and *Stellaria media*. Annual ruderal species were also prominent in particularly heavily grazed patches and trampled ground. Species such as *P. annua*, *Matricaria recutita*, *Plantago major*, and *Trifolium repens* could withstand intensive grazing and trampling because of their small size, prostrate habit, tough and elastic tissues and rapid regeneration.

In contrast to Gunthorpe, the Besthorpe plant community was characterized by higher species richness (Figure 3.3) and competitive stress-tolerant species. These were

adapted to the relatively unproductive habitat and greater stability facilitated by the long history of extensive management comprising annual cutting for hay and grazing of the regrowth. Grime (1979) asserted that such low intensities of disturbance function as a modifier of competition by debilitating potential dominants, thereby maintaining or promoting species diversity, and favouring those species which tend to maintain their competitive ability either by avoidance of damage or by rapid recovery from its effects. At Besthorpe, the former were represented by rosette species (e.g. *Taraxacum officinale*) and species able to exploit the period of the year prior to hay cutting (e.g. *Poa trivialis* and *Cardamine pratensis*). Species able to recover from cutting included *Sanguisorba officinalis*, *Festuca rubra* and *Agrostis capillaris*.

Management, notably hay-cutting in mid-summer, limited the expression of dominance in the Besthorpe vegetation, allowing species of smaller stature (such as *Ranunculus bulbosus* and *C. pratensis*) to co-exist which enhanced species diversity at the end of the season (Figure 3.3). Regular cutting and grazing are likely to have a major impact on shorter-lived species unless they can recover vegetatively or have a persistent seed bank. Indeed, very few species at Besthorpe were short-lived with transient seed banks (a notable exception being *Bromus hordeaceus*) suggesting that hay making generally took place before many annuals shed seed. However, although most species at Besthorpe were perennials able to tolerate regular defoliation and reproduce vegetatively, they could also reproduce by seed production. In this context, the sheep that grazed Besthorpe were likely to be an important factor influencing species diversity and composition, for example by dispersing seeds in dung and wool (Bakker, 1989; Fischer *et al.*, 1996).

Floristic diversity and variation at Gunthorpe was not only related to grazing management, but was also associated with flooding. Regular inundation contributed to the preponderance of moisture-loving plants in the community and also created regeneration gaps through sediment movement and deposition. Grubb (1977) asserted that for many grassland species, including *Agrostis* and *Poa* which were key grass genera in this study, the creation of relatively large gaps (e.g. 5 cm or more) may be necessary for regeneration by seed. As well as generating gaps of this size, flooding can also provide a supply of nutrients so that damaged plants can regenerate strongly and seedlings develop, and it can aid dispersal by transporting diaspores (Ellenberg, 1988). Many species of flooded swards can disperse by means of water-transported seeds or shoots, for example *Alopecurus geniculatus*, *Rumex crispus* and *Ranunculus repens*, which were all prominent species at Gunthorpe. Regular flooding at Gunthorpe also helped maintain the wet conditions which many

characteristic species of the site require for germination, e.g. *Plantago major* and *Polygonum aviculare*.

3.4.2 Cessation of management

Three years without management at the Gunthorpe and Besthorpe study sites induced changes in their plant communities that are largely consistent with the successional patterns widely described for neglected grasslands in Europe (Ellenberg, 1988; Bakker, 1989; Wells, 1989; Rychnovská *et al.*, 1994). It is generally accepted that following abandonment, grasses increase in leaf area and above-ground biomass accumulates as standing dead material and litter. Productive, robust herbaceous species with a strong competitive ability prevail, excluding lower-growing, less competitive plants. Hence, plant species diversity is reduced and just one or two species, often grasses, become dominant. In relation to Grime's (1979) models of competition, this initial sequence suggests that more competitive plant species displace ruderal and stress-tolerant strategists with decreasing disturbance. Eventually shrubs invade and the grassland succeeds to scrub and woodland, although this can be slowed by the presence of accumulated litter and the dense competitive plant cover (Facelli and Pickett, 1991; Prach, 1994).

In most studies of grassland succession a loss of floristic diversity in the absence of management has been reported (e.g. Regnéll, 1980; Oomes and Mooi, 1981; Persson, 1984; Parr and Way, 1988), particularly when assessed at a small scale, e.g. 5 m² or less (Regnéll, 1980; Facelli *et al.*, 1989; Chaneton and Facelli, 1991). However, the rate at which the decline proceeds varies considerably in different grassland types (Bakker, 1989; Wells, 1989) and depends upon the spatial scale considered (Chaneton and Facelli, 1991). Species decline in unmanaged grasslands has generally been attributed to the development of dominance by one or a few tall, coarse species. This reduces the incidence of light at ground level, thereby eliminating low-growing and prostrate subordinate species which were formerly indirectly encouraged by regular cutting and/or grazing management. Thus, unmanaged grassland vegetation tends to proceed from a fine-grained intimate mixture of species to a patchy mosaic of tall herbs and grasses.

At Gunthorpe, an absence of grazing management led to reduced species richness within the three years of study (Figure 3.1). Many authors have demonstrated the importance of grazing for the maintenance or enhancement of plant species diversity in grasslands and found that grazing exclusion decreases diversity (e.g. Persson,

1984; Facelli *et al.*, 1989; Smith and Rushton, 1994; Green and Kaufman, 1995). Grazing at Gunthorpe contributed to spatial and temporal heterogeneity by promoting a variable but generally low, open sward structure and providing niches for subsidiary species to co-exist alongside the community dominants. In such situations, reduced species richness is due to declines in disturbance created by livestock that facilitated the establishment of species, particularly the creation of gaps that provide micro-habitats for the colonization of species (Smith and Rushton, 1994). The results from Gunthorpe concur with those of Facelli *et al.* (1989) and Chaneton and Facelli (1991) who studied the Argentine Pampa, an area of grasslands for which grazing and hydrological dynamics are considered the main factors affecting the diversity and structure of the vegetation. There, the joint action of livestock grazing and episodic flooding favoured small-scale diverse plant assemblages because of inter-specific differences in the response to these alternative environmental constraints (Chaneton and Facelli, 1991). In contrast, prolonged cattle exclusion allowed tall grasses to form a dense canopy that excluded prostrate species from the lower layers and a coarse-grained vegetation pattern developed (Facelli *et al.*, 1989).

Thus, the cessation of grazing management at Gunthorpe removed some of the regeneration opportunities that the smaller ruderal plants had been able to exploit, leading to lower species diversity, although disturbance through inundation continued. A group of competitive ruderal strategists of taller stature were therefore favoured, particularly *Rumex obtusifolius* and *R. crispus* (Figure 3.2). In the absence of management, these species are able to complete their life-cycle and maximize seed production to produce large reserves, and they are also able to tolerate flooding (van der Sman *et al.*, 1993). Bakker (1989) found that *R. obtusifolius* increased its cover from 0 to 15% over 8 years in an abandoned wet grassland in the Netherlands, and Rychnovská *et al.* (1994) observed that *R. obtusifolius* and *R. crispus* were characteristic invaders of flooded meadows in central Europe. Although the subsequent course of succession at Gunthorpe cannot be predicted accurately, continued neglect would probably enable further expansion of the Rumices and the establishment and increase of other tall competitive ruderal species. At the Ouse Washes in eastern England, absence of management and reduced grazing intensity over 16 years contributed to reduced plant species diversity in inundation grasslands and the loss of *Alopecurus geniculatus* (a key Gunthorpe species) from some sites, coupled with a substantial increase in stands of *Glyceria maxima* (Burgess *et al.*, 1990).

Species richness at Besthorpe did not decline nor increase in the absence of cutting and grazing management over the three years of study (Figure 3.3). Whilst

comparison with other species-rich European grasslands indicates that abandonment can induce decreased species richness within this time frame, generally such changes are first observed after more than three years of neglect (Bakker, 1989). In particular, the presence at Besthorpe of many plant species with strategies enabling them to persist in vegetation characterized by a dense canopy prior to hay cutting suggests that successional changes in species diversity and composition due to neglect may be relatively slow.

At Besthorpe, species of later phenological development that were previously suppressed by the cutting and grazing regime, notably *Arrhenatherum elatius* and *Agrostis capillaris*, increased in the unmanaged sward (Figure 3.4). Thus, removal of management favoured particularly competitive species able to tap any surplus resources and rapidly maximize production. Both of the above species are relatively coarse grasses. *A. elatius* quickly develops a tall, tussocky physiognomy that facilitates lateral expansion (Grime, 1979; Rodwell, 1992). *A. capillaris* is also capable of rapid growth and is moderately competitive when conditions are favourable (Grime *et al.*, 1988). At Besthorpe, both species achieved a dense canopy of leaves from mid-summer when conditions for high productivity were suitable. Prach (1992) reported a similar succession in neglected floodplain grasslands in central Europe, where competitive and robust grasses such as *A. elatius*, *Alopecurus pratensis* and *Phalaris arundinacea* first increased and then dominated. At Besthorpe, further neglect would probably encourage the continued expansion of coarse grasses and the possible formation of an *Arrhenatheretum elatioris* community (Rodwell, 1992).

A difference between the typical scheme of grassland succession and those described by this three year study was the lack of litter accumulation in neglected grassland at both study sites. Litter may be an important influence on species diversity and composition in riparian grasslands (Xiong and Nilsson, 1997; chapter 4). It is likely that flooding removed litter at Gunthorpe, although its potential importance was highlighted by the deposition of floodborne litter in September 1994, which had a temporary effect on species abundance. However, litter may begin to accumulate in these floodplain grasslands after longer than three years of abandonment, particularly in the absence of flooding.

3.4.3 Community dynamics

Changes in management generally induced a greater community response at Gunthorpe than Besthorpe. This suggests that variation is more likely to be expressed through the shorter-lived plant species in the short-term, and that impact on the longer-lived perennials is delayed. The community at Gunthorpe, containing a large proportion of annual and biennial species able to tolerate unpredictable disturbance, was dynamic and sensitive to environmental influences. Yearly species turnover was observed, particularly in the managed vegetation where grazing and trampling removed plant biomass and also maintained gaps suitable for plant colonization, and species diversity trends emerged. In contrast, the Besthorpe plant community was composed almost entirely of perennial species able to regenerate vegetatively and was comparatively resistant to the cessation of management with respect to species diversity and composition. This may have been a function of the long history of consistent hay meadow management at the site, as the community contained many competitive strategists adapted to a taller dense canopy, which is a feature of hay meadows in the period before cutting as well as a characteristic of abandoned grasslands.

The results in this study have clearly illustrated changes in floodplain grassland plant communities in response to management activities and abandonment. However, there is a limit on the extrapolation of the results, partly because some floristic variation was not explained by ordination, some of which could have been due to spatial heterogeneity (e.g. within-site soil differences), but particularly as the study period of three years was insufficient to allow the grassland plant communities to respond fully to the cessation of management. In some unmanaged grasslands, reductions in species richness have been observed within three years (Oomes and Mooi, 1981; Persson, 1984; Bakker, 1989), but in others reliable changes have not been demonstrated after more than ten years of neglect (Bakker, 1989). Species richness in a range of European grasslands reviewed by Bakker (1989) tended to decrease after between five and ten years of abandonment, but considerable temporal fluctuations in diversity occurred. Although Rychnovská *et al.* (1994) reported that derelict flooded meadows in Europe deteriorate relatively rapidly and that visible quantitative and incipient qualitative changes in the vegetation can occur after two years of neglect, abandoned wet grasslands in the Netherlands are characterized by the occurrence of *Rumex obtusifolius* after five years and *Heracleum sphondylium* after eight years (Bakker, 1989). Also, Fossati and Pautou (1989) observed that it was nine years before *Sanguisorba officinalis*, a key component of the community at Besthorpe, was eliminated from a French wet grassland following the cessation of mowing.

Furthermore, variations in management tend to have a more immediate effect on the structure and dominance of grassland vegetation than on species composition (Parr and Way, 1988; Rychnovská *et al.*, 1994). Indeed, many grassland plant species, including *Festuca rubra*, *Agrostis capillaris* and *Ranunculus repens*, which were all prominent in this study, exhibit large population fluctuations, even in successive years (Bakker, 1989).

3.5 Conclusions: implications for conservation

For biodiversity and nature conservation reasons, it is important that the dynamic effects of management and neglect of floodplain grasslands are better understood. This study has illustrated the role of regular management in the form of grazing and cutting in maintaining floristic variation and characteristic species. Impacts on communities were mediated particularly through their effects on plant competition and regeneration. Thus, disturbance from grazing and trampling, and periodic inundation, created variable conditions suitable for a dynamic community characterized by short-lived ruderal species that responded rapidly to perturbations. A more stable environment featuring a long history of low-intensity management was expressed in a relatively diverse community that was composed mostly of perennial competitive stress-tolerant species and exhibited some inertia to management cessation. However, an absence of management in both types of grassland encouraged the expansion of robust competitive species, although the rate of successional change was greater in the community of short-lived plants from the unpredictable floodplain environment.

In Europe there are substantial areas of neglected floodplain grasslands that were dependent on appropriate management to maintain their biodiversity and nature conservation value. Reinstatement of regular management at an appropriate intensity could restore recently abandoned floodplain grasslands to their former community type as cutting and grazing alters the competitive relationships in floodplain grassland vegetation by reducing the vigour of the taller growing coarse species that tend to dominate derelict sites. Straškrabová and Prach (1998) reintroduced regular cutting to a floodplain meadow in the Czech Republic abandoned for 20 years. After five years species diversity and composition were restored to a quality comparable with local floodplain meadows that had received uninterrupted management. However, this relatively rapid rehabilitation was supported by the seed bank of the neglected meadow, in which species typical of cut grasslands persisted, and by flooding which transported diaspores from nearby sources (K. Prach, pers. comm., 1996).

Rehabilitation of floodplain grasslands abandoned for longer than this example may be more problematic, particularly where a viable seed source and flooding are lacking. Cutting may lead to gaps appearing between the tall tussocks that characterize derelict grasslands, enabling undesirable herbaceous and woody species to colonize (Rychnovská *et al.*, 1994). Time will therefore be needed for the desired grassland species, with their specialized ecological niches, to establish themselves naturally. As this study has indicated, however, although the superficial response of different floodplain grasslands to management change is similar, impact at the community level can vary greatly and individual communities will respond differently to the resumption of management. Proposals for rehabilitation and conservation of floodplain grasslands should not overlook their inherent heterogeneity and should therefore focus on developing management prescriptions for specific floodplain grassland ecosystems.

One particularly dynamic element of floodplain grasslands is plant litter, particularly when its deposition and accumulation are influenced by flooding. The following chapter reviews the role of litter in plant communities and examines the impact of floodborne litter on floodplain grassland plant diversity and production in order to provide a reference for conservation management.

Chapter 4 The role of floodborne litter in the functioning and management of floodplain grasslands

4.1 Introduction

Floodplain ecosystems represent a dynamic interface between terrestrial and aquatic environments. They possess properties of both systems and are therefore biodiverse (Risser, 1990), support a high level of biological processing (Gregory *et al.*, 1991) and are sensitive to natural and anthropogenic stress and disturbance (Prach *et al.*, 1990; Sparks *et al.*, 1990; Décamps, 1993). They are key elements in the maintenance and management of local and landscape biodiversity (Naiman *et al.*, 1993), particularly because riparian areas form important corridors for the flows of species and organisms, as well as water, energy, dissolved and particulate matter, through the landscape (Malanson, 1993). These areas are a valuable ecological resource, possessing characteristic physical properties and distinct plant communities (Amoros *et al.*, 1987; Ellenberg, 1988).

Floodplain grasslands in the UK and throughout the rest of Europe have with few exceptions been created by human activity, often deforestation, and are maintained by regular management, usually cutting or grazing (Rychnovská, 1993). They are often characterized by periodic inundation which brings regular inputs of floodborne nutrients that promote biological production. Indeed, the agricultural value of floodplain grasslands has been appreciated and actively managed for since at least the sixteenth century (Sheail, 1971). The nature conservation value of appropriately maintained grasslands is also recognized, in terms of the characteristic plant communities, rare species and the considerable biodiversity which they support (Baker, 1937; Rodwell, 1992; Jefferson and Grice, 1998). In particular, traditional relatively low-intensity management incorporating regular cutting or grazing can maintain and encourage plant species diversity (Oomes and Mooi, 1981; Bakker, 1989; Smith and Rushton, 1994).

However, such semi-natural floodplain grasslands have undergone a dramatic reduction in extent and ecological quality and a consequent decrease in biodiversity, especially over the last 50 years. This is largely due to human management of the riverine environment, including river regulation, drainage and conversion to more intensive agriculture (Wells and Sheail, 1988; Mountford, 1994). River regulation has often included channel modification and flood protection, which has dramatically altered the flooding characteristics of rivers, such as flood magnitude and timing, and impaired hydrological and ecological interactions between the channel and its

floodplain (Hellowell, 1988; Petts *et al.*, 1989). Moreover, channelization, bank construction for flood prevention and land drainage have reduced the ability of impacted riverine systems to retain dissolved and particulate inputs. For example, a constrained section of river in Oregon, USA was found to transport leaves three times further than an unconstrained reach, reflecting the more retentive nature of rivers connected with their natural floodplain (Gregory *et al.*, 1991). In order to establish effective conservation management of the remaining valuable resource and to implement sustainable restoration of floodplain grasslands, a better quantitative understanding of their ecological dynamics needs to be obtained and key environmental parameters and biological processes sensitive to environmental change identified.

An important component affecting the composition and dynamics of plant communities is litter, which has been defined as dead plant material of small size lying loose on the ground (Facelli and Pickett, 1991). Knapp and Seastedt (1986) assert that plant litter can affect virtually every ecosystem process. For plant communities this can be through direct and indirect alteration of the physical, chemical and biological environments. The physical environment may be modified by litter creating a barrier, for example to incoming seeds, precipitation and light (Weaver and Rowland, 1952; Knapp and Seastedt, 1986; Facelli and Pickett, 1991) and also inhibiting plant recruitment from a seed bank and preventing seedling emergence (van der Valk, 1986; Langlade and Décamps, 1994). Moreover, accumulated litter can alter the microclimatic conditions of the soil surface layers, particularly their thermal and moisture regimes, while litter decomposition releases nutrients and phytotoxins that can change the chemical conditions of the local environment (Facelli and Pickett, 1991). Litter may enhance nutrient availability to plants by intercepting and retaining suspended substances in flood water (Xiong and Nilsson, 1997). Litter deposition influences the biological composition of communities by creating patches or niches for colonization and regeneration, and by aiding diaspore transport (Nilsson *et al.*, 1993). A dense litter mat can also affect microbial processes and invertebrate activities (Knapp and Seastedt, 1986), the latter being an important process governing litter decomposition in riparian areas (Malanson, 1993). The effects of litter deposition and persistence on the competitive relations between plants has also been identified as a key factor controlling the species diversity and composition of herbaceous vegetation (Al-Mufti *et al.*, 1977; Grime, 1979).

Grassland vegetation management affects both the rate and degree of litter deposition and accumulation. Regular management such as grazing or cutting (with removal of

the crop) reduces above-ground biomass, preventing the build-up of senescent vegetation and litter (Parr and Way, 1988; ter Heerdt *et al.*, 1991). This is documented for prairie grasslands, which are characterized by substantial detritus accumulation and for these ecosystems grazing or mowing represents an essential integral process maintaining productivity by the removal of standing and fallen litter (Weaver and Rowland, 1952; Knapp and Seastedt, 1986). In contrast, nutrient enrichment, such as the use of artificial fertilizers to increase plant production within intensive agricultural management, may encourage litter accumulation in grassland ecosystems when the productivity of dead plant material exceeds the rate of decomposition and removal (Bakker, 1989; Tilman, 1993). In the absence of vegetation management, grassland succession is also characterized by large and persistent surface accumulations of litter (Regnéll, 1980; Dickinson, 1983).

Investigations of the effects of surface litter on grassland plant communities have indicated that the impacts of litter deposition and accumulation on plant diversity and production can be both positive and negative. The uncertainties associated with the role of litter in structuring floodplain vegetation were highlighted by Xiong and Nilsson (1997), who recognized the high potential for influences on riparian plant communities but also the inherent highly dynamic properties of litter in the riparian zone and the particular paucity of information on the impact of litter on floodplain grasslands. Carson and Peterson (1990) found that deposited litter promoted plant species diversity in productive old-field communities in New Jersey, USA, where litter accumulation may be substantial. In contrast, Tilman (1993), also working on successional grasslands in the USA (in Minnesota), suggested that the lower plant species diversity found in productive grasslands was due to high rates of species loss, probably via competitive displacement and accumulated litter limiting the establishment of new species. Knapp and Seastedt (1986) reported a loss of plant production in a tall grass prairie in response to detritus accumulation.

These studies have focused on grassland ecosystems where herbaceous litter is produced and accumulates mostly *in situ*. By comparison, litter deposition on floodplain grasslands is more dynamic and complex, as flood events not only transport and deposit allochthonous herbaceous and woody plant debris, but also redistribute autochthonous litter (Tesařová, 1976; Nilsson *et al.*, 1993). Gregory *et al.* (1991) noted that the contribution of herbaceous plants to the food resource within rivers is influenced largely by the spatial distribution of herbs and by temporal patterns of flooding, as herbaceous material primarily enters the river during floods. Moreover, Day *et al.* (1988) found that the removal of litter by spring flooding was one of the main factors controlling vegetation composition in a riverine wetland.

Evidently, during flood periods much plant litter is redistributed locally and between regions, following erosion, transport and deposition of litter (Xiong and Nilsson, 1997). Although Nilsson and Grelsson (1990) reported that the species diversity of riparian vegetation along the Vindel River in Sweden decreased with increasing deposition of riverborne litter, the role of waterborne litter on floodplain grassland plant communities in the UK has not been characterized. This chapter examines the impact of floodborne litter on two important functional characteristics of floodplain communities, biodiversity (measured by plant species richness) and primary production (above-ground biomass), on floodplain grasslands of the River Trent, UK.

The chapter has four specific objectives:

- i). to determine whether there is a short-term impact of litter on plant species diversity and production,
- ii). to establish whether there are thresholds above or below which plant species diversity and production are affected,
- iii). to elucidate the potential mechanisms for impacts on plant species diversity and production, and
- iv). to evaluate the role of litter deposition in the wider context of implementing effective conservation management and restoration of ecologically valuable floodplain grasslands.

4.2 Study sites

The two study sites at Besthorpe and Gunthorpe, situated along the River Trent in Nottinghamshire (Figure 2.1), have a long history of productive grassland agriculture (section 2.1). The Trent floodplain has supported grazing for cattle and sheep, and rough grassland cut for hay, throughout the 18th, 19th and into the 20th centuries (Edwards, 1944). A history of periodic severe inundation (Marshall, 1955) has been an important influence maintaining this land-use on the floodplain, since floods deposited nutrients that sustained grassland productivity and restricted the development of arable agriculture (Edwards, 1944). However, increasingly effective flood control has facilitated improved land drainage and therefore more intensive agriculture on the floodplain, with a consequent reduction in biodiversity and areas of natural and semi-natural plant communities (Large *et al.*, 1994). Today, flooding is largely controlled within "washlands", and arable agriculture and drained, intensively exploited, species-poor grasslands dominate the Trent floodplain, although some grasslands of ecological value remain (Dargie, 1993).

The Besthorpe study site has a long history of low-intensity grassland management comprising cutting for hay, followed by grazing of the re-growth, and minimal use of artificial fertilizers (Figure 2.8; Table 2.5). The site is level with clayey, circumneutral soils of an alluvial origin, supporting a plant community recognized as the *Alopecurus pratensis-Sanguisorba officinalis* MG4 association in the National Vegetation Classification (Rodwell, 1992). This community type is botanically diverse and nationally scarce (Crofts and Jefferson, 1994), being characteristic of areas where less intensive hay-meadow management has been applied to seasonally flooded alluvial land.

The Gunthorpe study site is a level, grazed pasture (Figure 2.6; Table 2.5) underlain by loamy alluvial silts. This floodplain is a designated washland which supports a grassland community described by NVC MG13, the *Agrostis stolonifera-Alopecurus geniculatus* association (Rodwell, 1992). This community type is typically not diverse, but is valuable as a forage resource for wildfowl (Burgess *et al.*, 1990).

4.3 Methods

4.3.1 Experiment plots

The same experiment protocol was followed at both study sites between mid March and late September during 1993 and 1994. In March 1993, a fenced enclosure of approximately 600 m² was erected at each study site, which permitted management within the areas to be controlled. Within each enclosure, plots measuring 1 m x 1.5 m were established and used for the litter treatments. These were set up at least 3 m apart to assure their independence with regard to the treatments. In October 1993, standing dead vegetation in the enclosure was cut and removed to simulate the usual management regimes outside the enclosure.

4.3.2 Litter treatments

Local plant litter from the Trent floodplain was collected in February 1993 and 1994 and dried at room temperature. The litter consisted mostly of small woody matter, tree and shrub leaves, and herbaceous (including graminaceous) material. Prior to the addition of litter, the negligible amount of naturally deposited floodborne litter in the plots was removed. Control plots were also set up where litter was neither removed nor added. Observations of the amount of floodborne litter deposited on the

experiment plots (i.e. additional to this experiment) were maintained throughout the period March 1993 - September 1994 and found to be minimal, although relatively large deposits were noted locally elsewhere on the floodplain.

In late March 1993 and 1994, following an initial survey of species composition and diversity of each plot, dried litter was applied to the treatment plots. Litter treatments were randomly assigned to each plot, with four replicates of each treatment. The litter was evenly applied over each plot and, to prevent the wind from blowing litter from the plots, each plot was fenced using a 10 cm high, galvanized metal net and pegs. In order to reduce edge effects, litter was also applied in a 10 cm wide strip against the outside of the fence. Immediately after litter application, ten litres of river water were sprinkled onto each plot in order to mimic flooding.

In 1993, five litter treatments were used: control (i.e. no litter), 150 g m⁻² (dry litter weight at room temperature), 300 g m⁻², 600 g m⁻² and 1200 g m⁻² (Table 4.1). Following initial analysis of the results, the treatments were modified for 1994, and consisted of a second year of 1200 g m⁻² on the same plots used for this treatment in 1993, and new plots were used for a higher level of litter addition of 2400 g m⁻² (Table 4.1) The gradient of treatments over the two years is within the range of litter deposition that occurs naturally in European rivers (e.g. see Nilsson and Grelsson, 1990; Langlade and Décamps, 1994; Xiong and Nilsson, 1997).

Table 4.1 Litter treatments applied at the Gunthorpe and Besthorpe study sites.
Four replicates of each treatment were used.

	Litter treatment (g m ⁻²)					
	Control	150	300	600	1200	2400
1993	√	√	√	√	√	
1994	√				√	√

4.3.3 Species diversity

Species richness, a measure of plant species diversity, was ascertained by recording all species present in 1 m² of each plot once a month during the main growing periods of 1993 and 1994.

4.3.4 Production

Annual primary production was determined by harvesting above ground vegetation in August in both years, when biomass had reached its maximum. A 0.04 m² quadrat was located by random means within the 0.5 m x 1 m section of each plot not used for monitoring species richness. Where treatments were continued for a second year (i.e. control and 1200 g m⁻²) different sections of the plots were clipped. Each biomass sample was sorted to species level and dried to constant weight at 105°C.

4.3.5 Data analysis

Data from 1993 and 1994 were analysed separately. Multiple comparisons of species richness and biomass data from 1993 were undertaken using analysis of variance (ANOVA), followed by Tukey's test if a significant difference in the treatment means was evident. Analysis of treatment effects on species richness and biomass in 1994 used *t*-tests. The effects of the treatments on species richness were compared on a month by month basis in both 1993 and 1994. Results were termed significant only if $P < 0.05$.

4.4 Results and discussion

The effects of the litter treatment on plant species diversity and production at the Besthorpe study site in 1993 are shown in Figure 4.1. Besthorpe displayed a mean maximum value of approximately 15 species m⁻² in the control plots in April-June, with a slight decrease observed later in the season (Figure 4.1a). The seasonal pattern in species richness is evident irrespective of the amount of litter applied (Figure 4.1a). Generally, there were no significant differences between any of the treatments in any month in relation to species diversity. Only one significant difference between the means of the 150 g m⁻² and 300 g m⁻² treatments in July was recorded which resulted from the ephemeral appearance of a higher proportion of vernal species (e.g. *Bromus hordeaceus* and *Cerastium fontanum*) in the plots receiving the lower litter treatment. The litter treatments had no significant effect on annual production (Figure 4.1b), which had a mean value of 726 g dry weight m⁻² in the control plots in 1993. Plots experiencing a second year application of 1200 g litter m⁻² in 1994 also showed no significant effect on the seasonal pattern of species diversity (Figure 4.2a), nor on annual production (Figure 4.2b), which had a mean of 691 g dry weight m⁻² in the control plots.

Figure 4.1 Effect of litter application on plant species diversity and above-ground production at Besthorpe in 1993. * denotes significant difference at $P<0.05$ (ANOVA, Tukey's test). a) Diversity. Data are mean values ± 1 SE (n=4). The arrow indicates the timing of litter application. b) Production. Data are mean values ± 1 SE (n=4). Sampling date : 30 August.

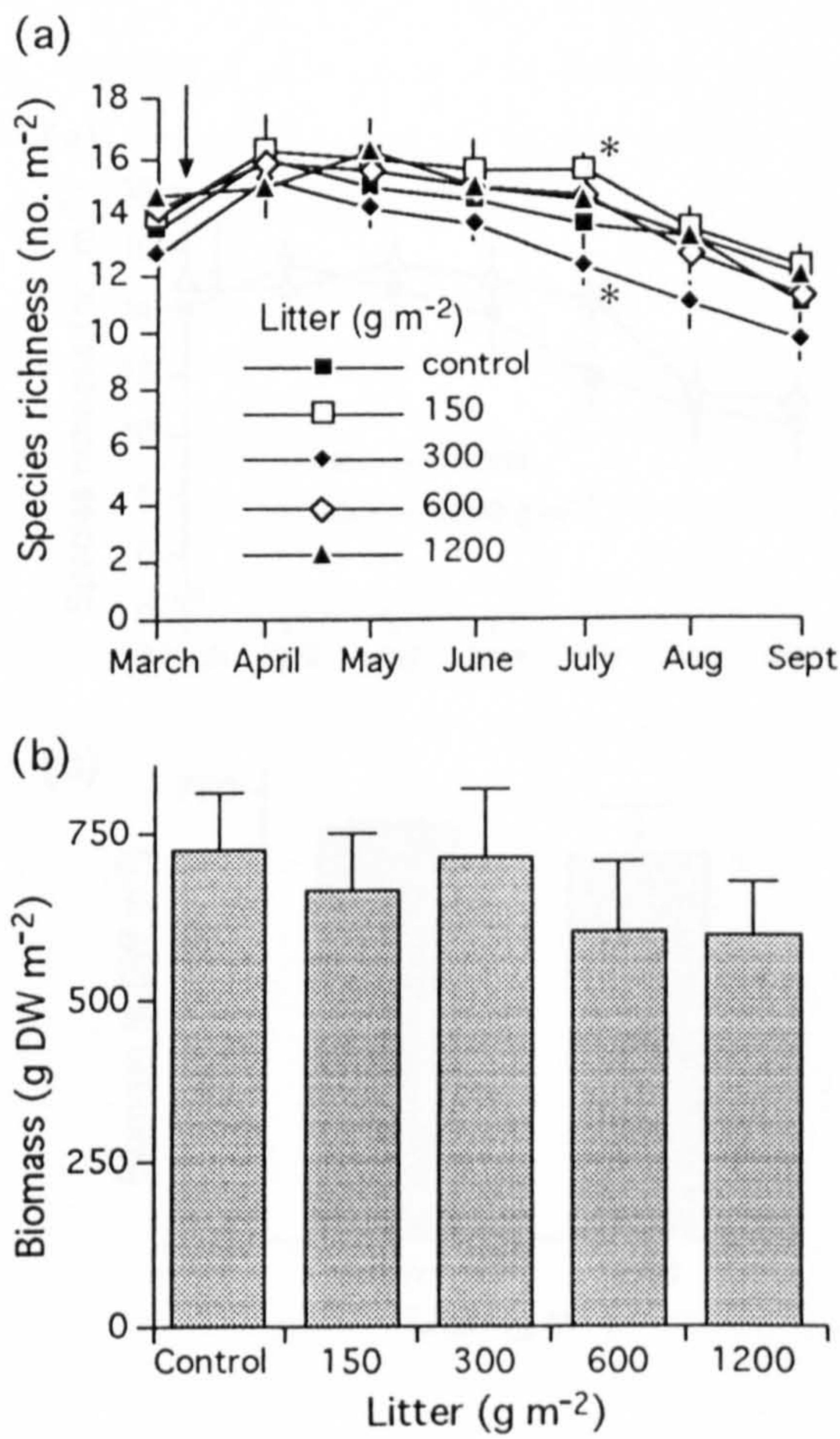
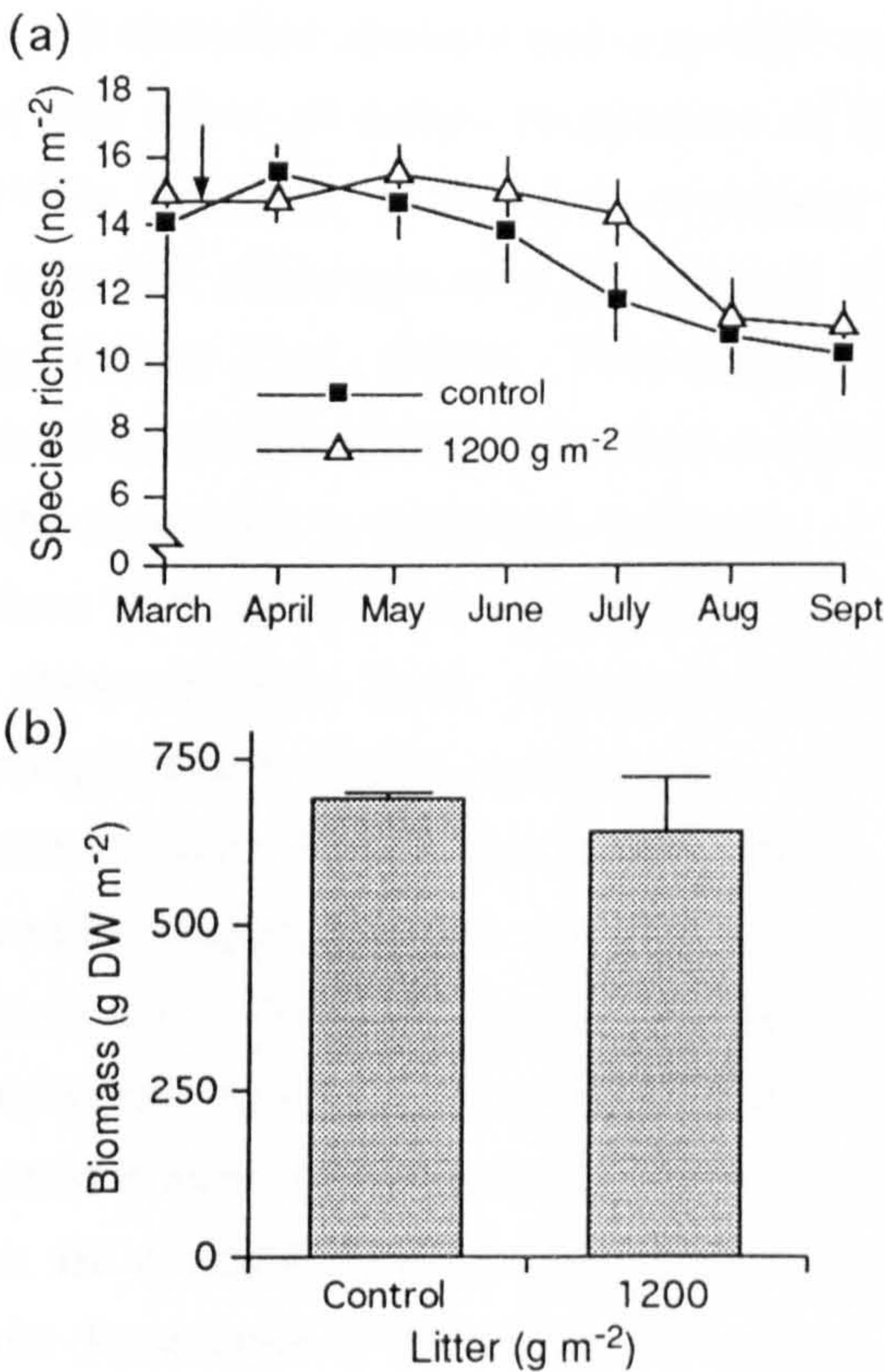


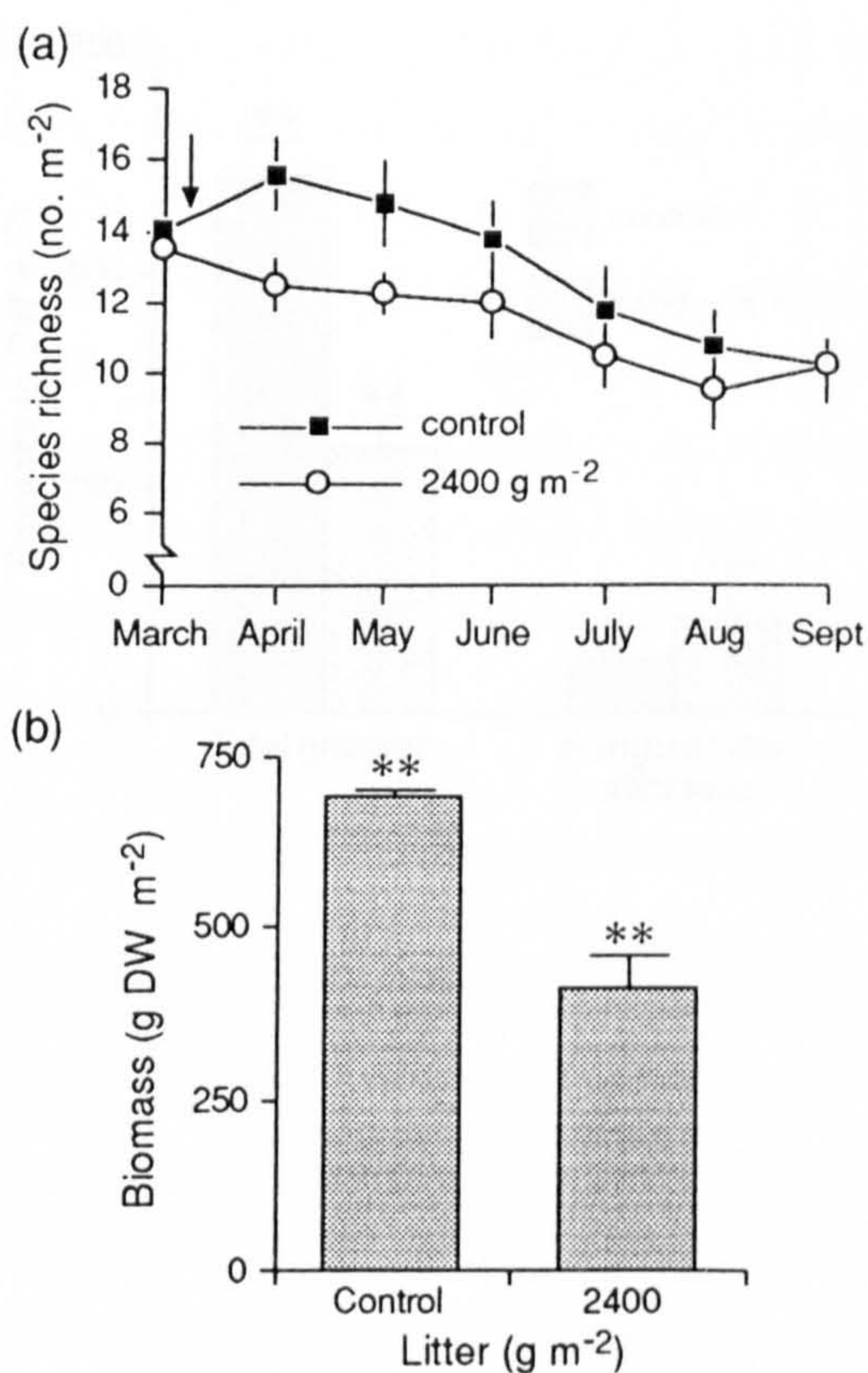
Figure 4.2. Effect of a second year application of 1200 g litter m⁻² on plant species diversity and above-ground production at Besthorpe in 1994. a) Diversity. Data are mean values ± 1 SE (n=4). The arrow indicates the timing of litter application. b) Production. Data are mean values ± 1 SE (n=4). Sampling date : 26 August.



A single litter treatment of 2400 g m⁻² applied in 1994, representing an increase over any of the range of treatments used in 1993, appeared to suppress species diversity in the initial months following addition (Figure 4.3a). However, these trends were not significant, and there was a recovery later in the season. Production, however, was significantly affected, with mean annual biomass of the litter treated plots reduced by more than 40% as compared with control plots (Figure 4.3b). Figure 4.4 shows that there was a significant effect on the grasses, of which four species, *Agrostis capillaris*, *Alopecurus pratensis*, *Holcus lanatus* and *Festuca rubra*, constituted most of the biomass at Besthorpe. Whilst grass production was significantly constrained by this heaviest loading of litter, the other major contributor to biomass, the forb *Sanguisorba officinalis*, showed a stimulation in annual production, although the effect was not significant. It therefore appears that a species such as *S. officinalis*, which is a characteristic and often abundant component of European floodplain grasslands (Ulehlová, 1973; Rodwell, 1992), can overcome the stress of litter imposition and secure a selective advantage over the grasses, which tend towards a more competitive strategy (Grime *et al.*, 1988). This differential response to litter treatment could be explained by differences both in the position of the meristems in relation to the litter and the capacities to mobilize resources. *S. officinalis* is better able to utilize resources from its extensive root system and carry its meristematic and photosynthesizing tissue above the litter layer, which may partially explain why *S. officinalis* can tolerate spring-grazing (Smith and Rushton, 1994) and persist in the early stages of wetland abandonment (Fossati and Pautou, 1989). Studies by Weaver and Rowland (1952) provide support for this, as litter accumulation suppressed flowering and plant height in native North American grasslands because plants were unable to build up a carbohydrate reserve before the period of flower initiation. In contrast to *S. officinalis*, most grasses have hemicryptophyte life-forms (Duffey *et al.*, 1974) in which meristems are maintained at or near ground level, so may be more vulnerable to stress from the dense layer of litter imposed early in the growing season.

Similar effects of the litter treatments on species diversity and annual production were also observed at the Gunthorpe study site. Species diversity values at Gunthorpe in 1993 and 1994 (means of 7.3 and 5.7 species m⁻² in the control plots in the two years, respectively) were characterized by a lack of significant effects of all treatments.

Figure 4.3 Effect of application of 2400 g litter m⁻² on plant species diversity and above-ground production at Besthorpe in 1994. ** denotes significant difference at $P < 0.01$ (t-test). a) Diversity. Data are mean values ± 1 SE (n=4). The arrow indicates the timing of litter application. b) Production. Data are mean values ± 1 SE (n=4). Sampling date : 26 August.



Impacts on annual production (mean values of 601 and 962 g dry weight m⁻² in the control plots in 1993 and 1994, respectively) were similar to those exhibited at the Besthorpe site with the heaviest application of litter (2400 g m⁻² in 1994) significantly constraining production (Figure 4.5). This was due to a substantial (> 70%) and significant reduction in the production of *Agrostis stolonifera*, whereas the only other major constituent of the biomass at this site, *Alopecurus geniculatus*, sustained its production under this litter treatment (Figure 4.6). According to Grime *et al.* (1988) these species have very similar autecologies, but *A. geniculatus* is able to exploit cool, humid situations and as a consequence may respond more quickly to changes in environmental conditions imposed by the litter treatment. Unlike *A. stolonifera*, this species may not be disadvantaged by the addition of a relatively large mass of litter that forms a dense layer early in the growing season. Vegetation monitoring of the Ouse Washes in eastern England showed that *A. geniculatus* was characteristic of areas that flooded in winter, tolerating inundation at the start of the growing season, but that the species had been eliminated from grasslands that had shown an increased incidence of summer flooding in recent years (Burgess *et al.*, 1990). This contrasted with *A. stolonifera*, which had increased in summer-flooded fields. Bakker (1989) found that the abundances of both species showed no consistent trend in response to grassland management treatments that led to litter accumulation (e.g. hay-making every two years and abandonment).

4.5 Conclusions: implications for conservation management

This short term study has indicated that relatively high deposits (e.g. >1200 g m⁻²) of plant litter have a negative impact on the plant species diversity and biomass production of floodplain grasslands along the River Trent (Figures 4.3 and 4.5). Moderate to high deposits may suppress species diversity early in the season, while annual production may be reduced by a single high deposit. Xiong and Nilsson (1997) reviewed the effects of litter on various plant communities, including temperate grasslands, wetlands and woodlands, and found that species richness and biomass production are generally inhibited by litter accumulation. Reductions in plant diversity and/or biomass through litter accumulation have been reported from a variety of wetland and grassland communities in the UK, including fens (Wheeler and Giller, 1982), chalk grassland (Watt, 1974) and amenity grassland (Dickinson and Polwart, 1982), and from Europe, e.g. Sweden (Regnéll, 1980) and the Netherlands (Oomes and Mooi, 1981). Carson and Peterson (1990) also noted a similar short term response to this study following the addition of litter to an old-field community in the

Figure 4.5 Effect of application of 2400 g litter m⁻² on above-ground production at Gunthorpe in 1994. Data are mean values +1 SE (n=4). * denotes significant difference at $P<0.05$ (t-test). Sampling date: 23 August.

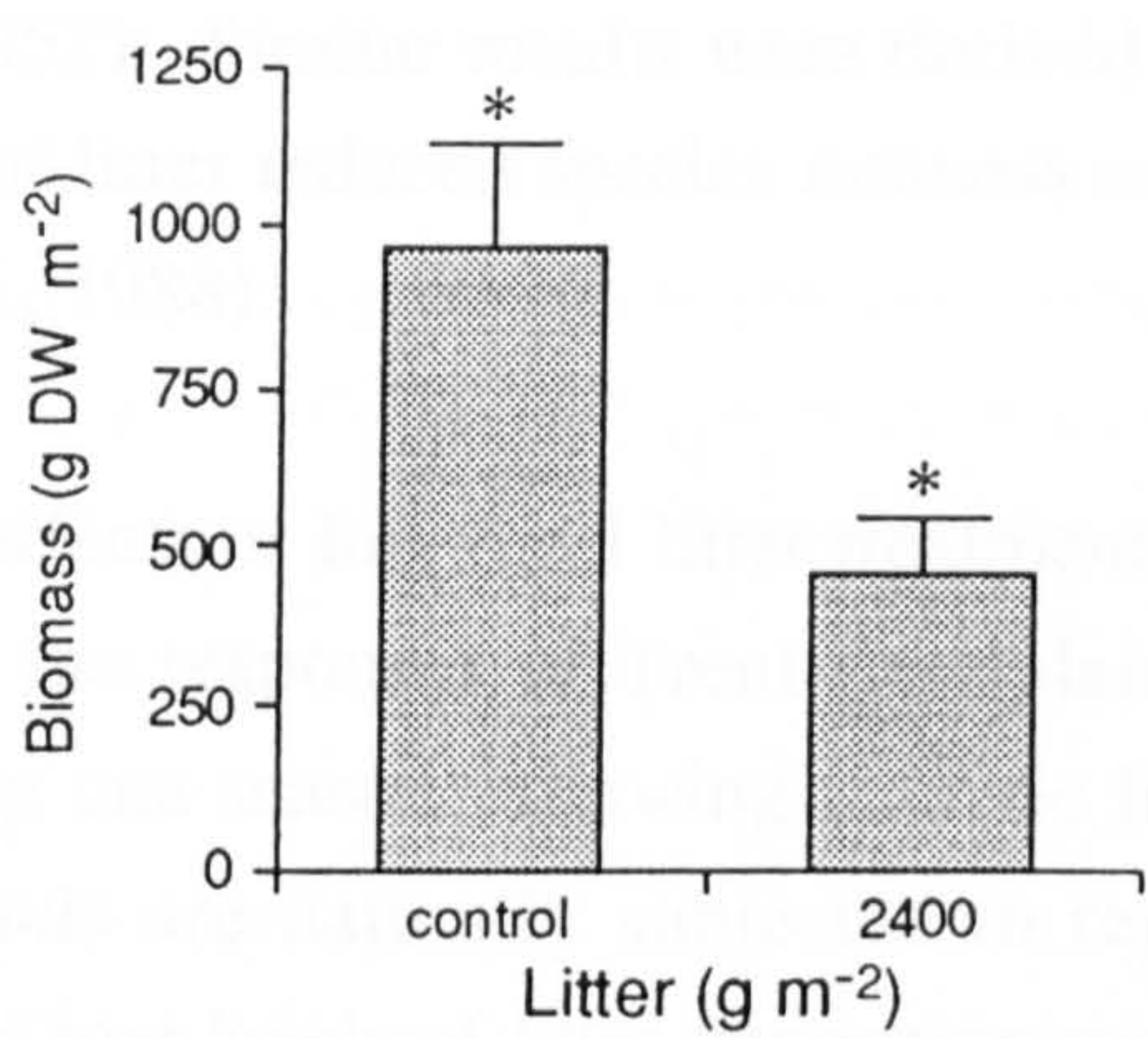
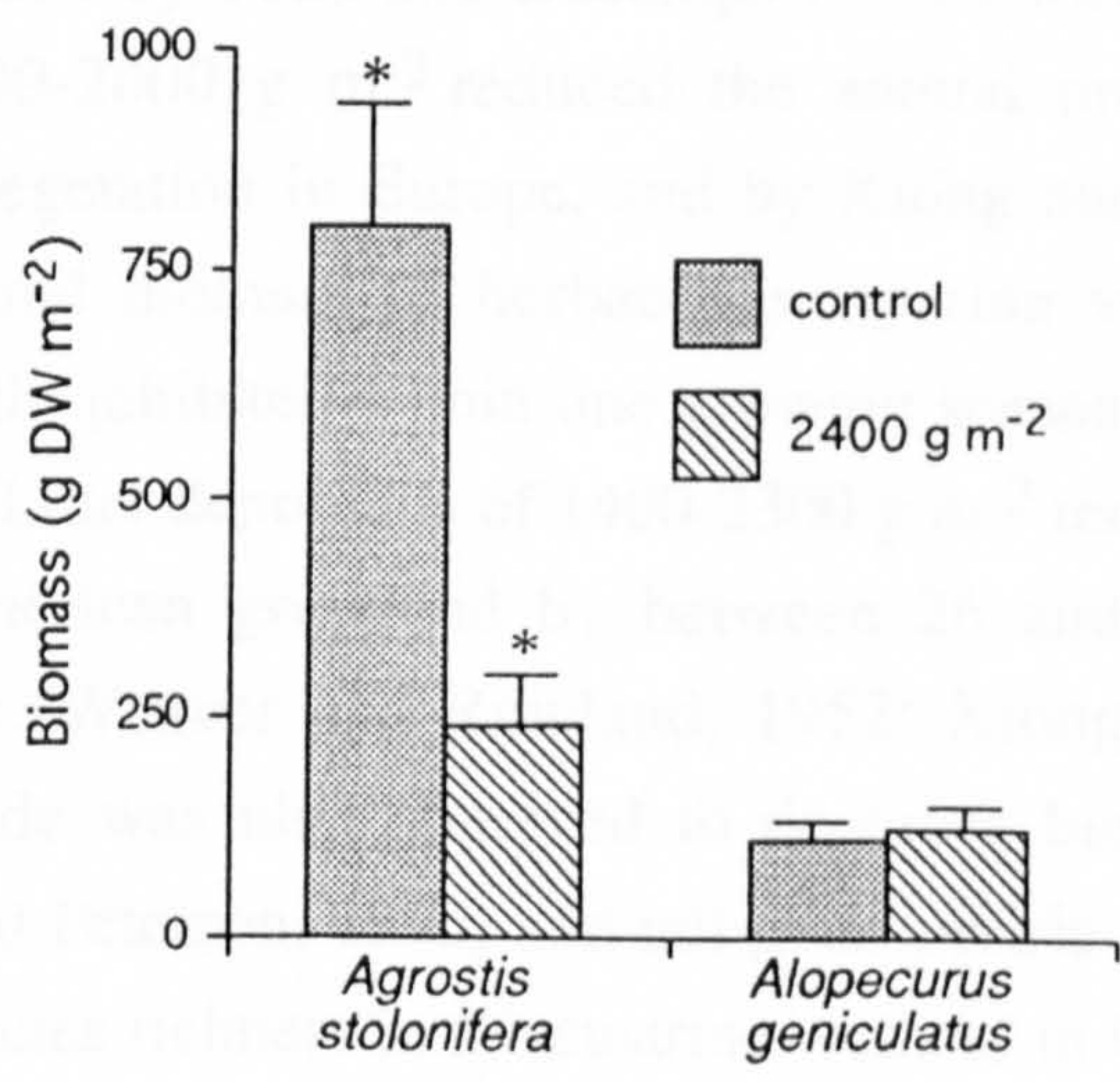


Figure 4.6 Effect of application of 2400 g litter m⁻² on above-ground production of *Agrostis stolonifera* and *Alopecurus geniculatus* at Gunthorpe in 1994. Data are mean values +1 SE (n=4). * denotes significant difference at $P<0.05$ (t-test). Sampling date: 23 August.



USA, with plant species diversity reduced at the beginning of the growing season and recovery observed towards the end of the season. Litter accumulation reduced plant production in a North American tallgrass prairie (Weaver and Rowland, 1952; Knapp and Seastedt, 1986). It restricted the quantity of light available at the soil surface by up to 95% and suppressed soil temperature, which delays the growth and emergence of shoots in spring and shortens the growing season. Vegetative reproduction is also reduced beneath dead plant material, leading to lower shoot densities (Hulbert, 1969; Weaver and Rowland, 1952). Similar results were derived from Canadian wetlands, in which a high amount of litter reduced species richness and seedling densities (van der Valk, 1986; Day *et al.*, 1988).

In the current study, no effects of low level litter treatments were observed (Figures 4.1 and 4.2). However, the responses of Trent floodplain grassland communities were monitored over only one season following a single litter application, whereas many floodplain grasslands are naturally subjected to repeated litter depositions. Thus a potential impact of low levels of litter deposition sustained over several years cannot be excluded. Alternatively, the lack of effect may indicate that the communities have developed in response to regular litter inputs, and that sensitive species have been excluded. Clearly further work is required to test these hypotheses.

Nevertheless, the threshold figure of $>1200 \text{ g m}^{-2}$ proposed here is consistent with those indicated for other types of herbaceous communities. Carson and Peterson (1990) summarized the effects of litter quantity on species diversity and productivity for a range of grassland communities and concluded that in general only litter deposits greater than 900 g m^{-2} decreased productivity and plant diversity. Further elucidation was provided by Petts and Decamps (1995) who suggested that litter deposition above $1600\text{-}2000 \text{ g m}^{-2}$ reduced the annual production and species diversity of riparian vegetation in Europe, and by Xiong and Nilsson (1997) who found that above-ground biomass of herbaceous riparian vegetation in northern Europe was significantly inhibited within one growing season after riverborne litter exceeded 2400 g m^{-2} . Litter deposition of $1400\text{-}2300 \text{ g m}^{-2}$ reduced plant production in a native North American grassland by between 26 and 57%, depending on community dominants (Weaver and Rowland, 1952; Xiong and Nilsson, 1997). Litter of this magnitude was also observed to decrease biomass in an old-field community (Carson and Peterson, 1990) and tall grass prairie (Hulbert, 1969) in the USA, and inhibited species richness in a lacustrine wetland in Canada (van der Valk, 1986).

The impact of litter deposition on floodplain grassland communities is mediated through its effects on its constituent species. Deposition seems to favour species able to tolerate the stress of litter imposition (e.g. *Sanguisorba officinalis*) and inhibits more competitive species (e.g. many floodplain grassland grasses) (Figure 4.4). Litter-tolerant plants may therefore possess underground energy reserves and shoots that can penetrate the litter mat, and tend to have robust, erect, leafy stems that can place their leaves above the litter layer (Nilsson and Grelsson, 1990). They may also respond to the stress of litter by exploiting a faster growth rate (Grime, 1979), a strategy apparently adopted by *Alopecurus geniculatus* plants in this study. Studies of other plant communities have reported similar results. Robust plants over 50 cm tall developed on river gravel bars following high litter accumulations (Langlade and Décamps, 1994) and Nilsson and Grelsson (1990) noted that erect riparian plant species were more resistant to the impacts of water scouring and litter accumulation than species with the most of their photosynthesizing tissues close to the ground. Day *et al.* (1988) found that Canadian riverine marsh vegetation was dominated by tall, leafy species where litter accumulated and suggested that low litter levels may be essential for the persistence of small, low-growing species and hence high species richness. Furthermore, accumulation of plant debris reduced the number of species and the abundance of lower-growing grasses and forbs in North American grassland, inducing plant community change (Weaver and Rowland, 1952). Facelli and Pickett (1991) suggested that the persistence of some dicotyledonous plants in grass-dominated communities in the Argentine Pampa was likely to be due to the ability of these species to place their leaves above the litter layer, while Dickinson and Polwart (1982) observed that large accumulations of litter had a limiting effect on grass species but favoured the proliferation of forbs. Similarly, accumulated litter in a prairie grassland substantially reduced grass productivity and reproduction (vegetative and sexual) whereas the biomass and reproductive effort of most forbs and woody species increased (Knapp and Seastedt, 1986). Indeed, it has been suggested that by limiting productivity, the persistence of accumulated litter may mark the decline of community dominance by grasses in temperate grasslands where cutting or grazing management has been discontinued (Dickinson and Polwart, 1982). For example, a vegetation of robust sedges and tall forbs developed when a dense litter layer accumulated following the cessation of grazing a damp meadow in Sweden (Regnéll, 1980). In contrast to these studies, forbs were more affected by litter than grasses in the oldfield vegetation in the USA examined by Monk and Gabrielson (1985). In addition, litter eliminated or reduced subsidiary species, particularly forbs, in a North American prairie grassland, leaving an almost monospecific stand of the dominant grass and only a few of the taller forbs remaining (Weaver and Rowland, 1952). Furthermore, experiments involving litter removal from herbaceous roadside

vegetation in England led to an increase in species richness, mainly due to an increase in forbs (Parr and Way, 1988).

The timing of litter deposition may also be an important factor, since this may have differential effects on individual species depending on their life history strategy and the stage of development attained at the time of deposition. Establishment is another key factor in plant community functioning (Grubb, 1977) which seems to be sensitive to the presence of litter. The establishment of many species is negatively affected by litter as a result of the impact of shading, physical impedance, and reduced thermal amplitude in the soil (Facelli and Pickett, 1991). In this study, *Agrostis stolonifera* may be an example of a species impacted in this manner, since the investment of time and energy necessary to penetrate the litter mat may place these plants at a competitive disadvantage later in the season. Alternatively, litter may enhance the establishment of some species by improving water conditions or by reducing competition. For example, *Alopecurus geniculatus* in this study appeared to have a competitive advantage over *Agrostis stolonifera* following the deposition of litter early in the growing season (Figure 4.6). This study therefore suggests that litter deposition affects the emergence and growth of floodplain grassland species. This observation is substantiated by a study of fen vegetation in Norfolk by Wheeler and Giller (1982), who reported that species diversity halved as the amount of litter recorded in April increased by 1630 g m^{-2} . It is also supported by results from experimental additions of litter to a lacustrine wetland, which reduced seedling recruitment almost completely (van der Valk, 1986), and to a river gravel bar, where germination decreased with litter deposition greater than 600 g m^{-2} (Langlade and Décamps, 1994). Lower shoot densities and delayed plant development have been observed in undisturbed prairies with litter layers compared to those where litter has been removed either experimentally or by fire (Weaver and Rowland, 1952; Hulbert, 1969).

Thus, floodborne litter deposition and accumulation may be an important factor in introducing and maintaining biodiversity, and in the longer term, inducing changes in plant communities in floodplain grasslands. This is of particular relevance since the deposition and accumulation of floodborne litter is not uniform over a floodplain (as observed at Besthorpe and Gunthorpe during this study). Although much litter is deposited on the ground along the maximum floodwater level, there is a dynamic interplay between litter import, redistribution and export on both temporal and spatial scales, depending on flood intensity and regime, management practices, floodplain topography and the presence of barriers and obstacles, such as hedges and trees (Nilsson *et al.*, 1993). In managed floodplain meadow communities subject to

relatively natural patterns of inundation, Tesařová (1976) found that there was an equilibrium between litter production and disappearance (i.e. transport by floods, herbivory, decomposition etc.). However, in situations where flood or grassland management regimes are intensively manipulated by humans, this balance may be upset. In any case, the redistribution of litter is known to vary greatly between years and between patches (Nilsson and Grelsson, 1990). Cuffney (1988) reported that between 0 and 98% of locally produced litter was removed by a flood event, being redistributed not only in an upstream-downstream direction but also from lower to upper parts of the floodplain. Thus, differential floodborne litter deposition and accumulation, and episodic removal and redistribution by flooding, may introduce large variability in the quantity of litter within a floodplain grassland. On the basis of the effects on species diversity and production observed in this study, this would promote spatial and temporal heterogeneity within the grassland communities. For example, patches which tend to accumulate litter may develop a community comprising species able to tolerate this stress, whilst species which are inhibited by litter and competitive species may be favoured in areas of low litter deposition.

An appreciation of these factors is of importance when conservation management objectives for floodplain grasslands are set, as many wet grassland species of conservation value can be categorized as stress tolerators (Grime *et al.*, 1988). Examples of stress-tolerant species include *Caltha palustris*, an aesthetically attractive plant often recommended for habitat creation and restoration schemes (e.g. Emery, 1986), and *Succisa pratensis*, which supports the declining and protected Marsh Fritillary (*Euphydryas aurinia*) Lepidoptera (butterfly) (Thomas and Lewington, 1991), for which a specific biodiversity action plan has recently been developed in order to achieve favourable management of the remaining UK colonies (The UK Steering Group, 1995).

This study suggests that floodborne litter may play an important and overlooked role in the community dynamics of floodplain grasslands. Litter deposition and accumulation may limit production and help maintain biodiversity and, in the longer term, induce changes in floodplain grassland plant communities. This highlights the importance of vegetation and hydrological management at an appropriate intensity to maintain a target floodplain grassland community, as cutting, grazing and fertilization, and flooding, may not only directly impact community structure, they also affect species composition and community dynamics through their influence on litter deposition and accumulation. These interactions serve to illustrate the complexity and dynamic nature of floodplain grasslands, and exemplify the

difficulties of developing and implementing effective conservation management and restoration.

The effect of increasing the intensity of grassland management on floodplain grasslands is explored in the following chapter, which examines the response of a flood-meadow plant community to fertilizer nitrogen application.

Chapter 5 The impact of fertilizer nitrogen on the plant community composition of a traditionally-managed English flood-meadow

5.1 Introduction

It is established that inorganic fertilizers, particularly nitrogen (N), can cause considerable botanical change when applied to mixed-species grassland, usually increasing the dominance of a limited number of species, especially some grasses, with a coincident decrease in floristic diversity (Rabotnov, 1977; Wells, 1989). The celebrated "Park Grass" trials of a meadow at Rothamsted demonstrated this, showing that there is a negative correlation between increased plant production due to fertilization and species diversity (Williams, 1978; Silvertown, 1980; Digby and Kempton, 1987). This relationship has been found for a range of grassland plant communities, including dry mesotrophic meadows, chalk grassland, and wetland hay meadows on peat soil (Table 5.1) and at a range of fertilizer application rates from 50 to approximately 900 kg N ha⁻¹ yr⁻¹ over periods of three to 21 years (Table 5.1). Comparable data for flood-meadows developed on alluvial soils are not available, and results from other studies cannot be reliably extrapolated to flood-meadow vegetation, particularly because it has been shown that the species that benefit from fertilization depend upon the original composition of the plant community (Table 5.1). Moreover, most studies have monitored botanical change in relation to fertilization on an annual basis over a period of several years, whereas the detailed response of the community in the first months of fertilization has not been specifically investigated. The study reported in this chapter provides that information, examining the fine-scaled impact of fertilization during two successive growing seasons on a traditionally-managed English flood-meadow community.

European flood-meadows have been created by human activity, usually by forest clearance or drainage of marshes (Ellenberg, 1988), and are maintained by human intervention, typically cutting and grazing by livestock (section 1.2.2). In the past, management was part of a low-intensity agricultural system characterized by low fertilizer input, cutting for hay and low stocking densities (Beaufoy *et al.*, 1994), and periodic flooding which brought regular inputs of nutrients that promoted biological production. Indeed, the agricultural value of flood-meadows has been appreciated and actively managed for since at least the 16th century (Sheail, 1971; Duffey *et al.*, 1974; Rychnovská *et al.*, 1994).

Table 5.1 Response to fertilization by a range of grassland plant communities
+ = increase; - = decrease; 0 = no change. t = tonnes; DW = dry weight

Plant community type	Location	Author(s)	Rate and duration of fertilization (kg N ha ⁻¹ yr ⁻¹)	Response to fertilization		
				Species diversity	Community production (above ground)	Most favoured species
cut chalk grassland	Netherlands	Willems <i>et al.</i> (1993)	100 for 5 yrs	- 50% reduction in richness	+ doubled	Generally grasses e.g. <i>Brachypodium pinnatum</i>
chalk grassland	England	Smith <i>et al.</i> (1971)	106 for 10 yrs	- 28 → 12 in 320 m ²	+ 0.7 → 2 t DW ha ⁻¹ yr ⁻¹	<i>Festuca rubra</i>
mesotrophic meadow	Poland	Traczyk <i>et al.</i> (1984)	680 for 7 yrs	- 35 → 16 in 1250 m ²	+ 3.2 → 12.2 t DW ha ⁻¹ yr ⁻¹	<i>Dactylis glomerata</i>
mesotrophic hay meadow	England	Smith <i>et al.</i> (1996)	80 for 4 yrs	- 22 → 19 m ²	no data	<i>Alopecurus pratensis</i> , <i>Holcus lanatus</i>
wet meadow on peat	England	Mountford <i>et al.</i> (1993); Kirkham and Wilkins (1994)	50 for 3 yrs	- significant reduction in richness and Simpson's index	+ 4.7 → 10.5 t DW ha ⁻¹ yr ⁻¹	<i>Holcus lanatus</i> , <i>Lolium perenne</i> , <i>Rumex acetosa</i>
wet grassland on clay	Netherlands	Oomes and Mooi (1981)	50 for 8 yrs	0 52 → 52 in 100 m ²	+ 6 → 7.8 t DW ha ⁻¹ yr ⁻¹	<i>Agrostis stolonifera</i> , <i>Glechoma hederacea</i>
wet meadow	Czech Republic	Halva and Lesak (1979)	200 for 4 yrs	no data	+ 5 → 11.8 t DW ha ⁻¹ yr ⁻¹	<i>Festuca rubra</i> , <i>Deschampsia cespitosa</i>
sown, frequently cut grassland	Belgium	van Hecke <i>et al.</i> (1981)	300 for 16 yrs	- especially forbs	no data	<i>Agrostis capillaris</i>
acidic meadow	Czech Republic	Fryček <i>et al.</i> (1992)	320 for 21 yrs	- forbs	+ 3.5 → 7.8 t DW ha ⁻¹ yr ⁻¹	<i>Holcus mollis</i>
unimproved native pasture	New Zealand	Grant <i>et al.</i> (1981); Luscombe <i>et al.</i> (1981)	896 for 3 yrs	no data	+ significant increase	<i>Agrostis capillaris</i> , <i>Lolium perenne</i>
old field	Minnesota, USA	Tilman (1987)	272 for 4 yrs	- 60% reduction in richness	+ significant increase	<i>Elymus repens</i>

Traditional flood-meadow management created and sustained beneficial conditions for a range of flora and fauna, and developed distinctive plant communities including rare and threatened plant species (Rodwell, 1992; Rychnovská, 1993; Straškrabová *et al.*, 1996). However, widespread losses and ecological degradation of the European flood-meadow resource have taken place, particularly over the last 50 years, largely due to river regulation and agricultural intensification including the increased use of inorganic fertilizers (Fuller, 1987; Wells and Sheail, 1988; van Dijk, 1991). The continued existence of remaining flood-meadows of nature conservation value is therefore dependent upon regular appropriate management.

In England, the flood-meadow plant community is particularly distinctive and, given the complement of characteristic species, forms an important component in the European biodiversity resource. It is a lowland community especially characteristic of areas where traditional hay meadow management has been applied to seasonally flooded land with circum-neutral, clay-rich or silty alluvial loam soils (Rodwell, 1992; Jefferson, 1997). This type of meadow has probably existed for almost 3 000 years (Greig, 1984) and it is likely that the plant community has been a feature of the Thames floodplain for 2 000 years (Lambrick and Robinson, 1988). Hay meadow treatment has traditionally comprised taking an annual hay crop in late June to early July, extensive autumn or winter grazing of the regrowth and a light application of organic manures, but no herbicide or inorganic fertilizer use (Rodwell, 1992; Crofts and Jefferson, 1994). Many sites have received this form of low-intensity management for many centuries with the result that a poly-dominant species-rich community has developed.

The English flood-meadow plant community was first described by Baker (1937) and lies within the *Molinio-Arrhenatheretea* of continental phytosociology, CORINE biotope type C38.2 (Devillers *et al.*, 1991). It has an extremely limited European distribution, being restricted largely to south and central England, and is classified as MG4, the *Alopecurus pratensis*-*Sanguisorba officinalis* community, in the British National Vegetation Classification (Rodwell, 1992). Typically, it is a species-rich community, supporting approximately 28 plant species in a sample area of 4 m² (Rodwell, 1992) and contains a varied mixture of grasses and forbs of which the tall, robust perennial *S. officinalis* is particularly prominent. By July, this species has generally overtopped the grasses and the vegetation forms a dense sward up to 70 cm tall (Baker, 1937). Some stands support populations of nationally scarce species such as *Fritillaria meleagris* and *Oenanthe silaifolia* (Stewart *et al.*, 1994). Jefferson and Robertson (1996) estimated that less than 1 500 ha of the English flood-meadow community exist and, with the majority of remaining sites under 10 ha in extent, the

resource is fragmented (Jefferson, 1997). For the above reasons, the community is recognized as having a high nature conservation value at both national and international levels (Jefferson and Grice, 1998). It is included as a key habitat within the UK Biodiversity Action Plan (The UK Steering Group, 1995) and is specially protected by the European Union through the Habitats and Species Directive (Council of the European Communities, 1992).

An understanding of the processes responsible for the maintenance of the traditionally-managed English flood-meadow plant community is important in order to conserve this important grassland system. In particular, a better quantitative understanding of the impact of fertilization, including an appreciation of the changes in the relationships between community components, is necessary. This is because variations in the response of species to nitrogen and the competitive conditions existing within diverse grassland communities may lead to large changes in botanical composition, including plant diversity (Bradshaw *et al.*, 1964; Ellenberg, 1988). Species response to fertilization may be governed by three key factors: a) initial plant community composition, b) quantitative participation of species in the community, and c) management regime (Rabotnov, 1977; Morrison, 1987; Snaydon, 1987). Consequently, the response of grassland species and communities to fertilization is difficult to predict and the data on reactions by meadow species to fertilization are often contradictory (Rabotnov, 1977; Titlyanova *et al.*, 1990). At present, the information necessary to guide vegetation management with respect to the use of fertilizers is not available for the English flood-meadow community.

This chapter aims to extend knowledge of the characteristic English flood-meadow by examining the fine-scaled impact of fertilizer N on plant community composition under a traditional cutting and grazing management regime. It focuses on the immediate effects of fertilization within a two-year time scale. Specific objectives are:

1. to quantify the impact of fertilizer N application on plant diversity, cover and production,
2. to describe the effects of cutting and grazing management on plant diversity, cover and production, and
3. to elucidate interactions between fertilizer N application and cutting and grazing management.

Such information will be invaluable in establishing the conservation management of the remaining valuable flood-meadow resource, particularly in relation to the integration of agricultural practices with biodiversity conservation objectives.

5.2 Methods

5.2.1 Study site

The study was undertaken along the River Trent, at Besthorpe in Nottinghamshire, central England (Figure 2.1). The Trent floodplain in this area is described in detail in section 2.1.1. It is underlain by sand and gravel with an overburden of up to 2 m of alluvial silts and clays. Soils tend to be relatively mature with moderately high amounts of incorporated organic matter in the surface horizons (Bridges, 1973).

Grassland management for agriculture was probably well established on the Trent floodplain by 3 200 BP (Lillie and Grattan, 1995) and the floodplain supported predominantly semi-natural grasslands used for hay and cattle and sheep grazing into the 20th century (Edwards, 1944). Episodic flooding was an important influence maintaining this land-use as it limited the development of arable agriculture and also deposited nutrients that, along with the use of animal excreta, sustained grassland productivity (Edwards, 1944; Marshall, 1955). However, increasingly efficient flood control, particularly in the 1960s-70s, facilitated more intensive agriculture on the floodplain with a consequent substantial reduction in floristic diversity (Large *et al.*, 1994). A key feature of agricultural intensification was the increasing use of inorganic fertilizers to improve yields. In England, the application of inorganic fertilizers to lowland grasslands effectively began in the 1940s and rose sharply in the 1960s until by 1985 93% of all lowland meadows received fertilizer nitrogen (Fuller, 1987). Along the Trent in Nottinghamshire currently, arable farming and intensively exploited, species-impoverished grasslands predominate in which inorganic fertilizer application has largely replaced fluvial and animal sources of nutrients. Only fragments of the characteristic semi-natural flood-meadows remain.

The study site at Besthorpe (section 2.1.3) consisted of a 5.2 ha level field underlain by soils belonging to the Fladbury 2 series, which are clayey and of alluvial origin (Soil Survey of England and Wales, 1983). Soil moisture averaged 34% during March-November. Soil pH averaged 6.3 and plant-available N in the surface 15 cm was low (approximately 8 mg l⁻¹ soil solution). The Besthorpe plant community is a good example of the flood-meadow association that develops in England where traditional low-intensity hay meadow management has been applied to periodically flooded alluvial land (Rodwell, 1992). The association is described by the species *Sanguisorba officinalis* and *Alopecurus pratensis*, both of which are abundant at the study site along with *Festuca rubra*, *Agrostis capillaris* and *Holcus lanatus*. Characteristically, a range

of subsidiary grasses and forbs are also present (Table 2.3). Archival information indicates that hay meadow management at Besthorpe has been practised since at least the 1720s, comprising cutting for hay with grazing of the regrowth and minimal inorganic fertilizer use. Typically, cutting takes place in late June or early July and the aftermath is grazed by sheep for 2-3 weeks in September-October. The area was likely to have been inundated annually in the past (Marshall, 1955), but control measures completed in 1981 have reduced the frequency of flood events (N. Lewis, pers. comm., 1994).

5.2.2 Core experiment

The field study was conducted between March and September in 1994 and 1995, these months describing the approximate length of the growing season over much of lowland England (Robson *et al.*, 1989). Following an initial survey of species composition of the field that indicated its homogeneity, 12 plots measuring 1 m x 1.5 m were permanently marked within the area in April 1994. These were set up at random, apart from being least 25 m away from the field periphery to eliminate any edge effects. Each plot was assigned one of two fertilizer N treatments, giving six replicates of each treatment in two interspersed sets of plots. The treatments consisted of fertilizer application equivalent to a total of 0 (i.e. control plots) and 600 kg N ha⁻¹ yr⁻¹ (fertilized plots). The latter treatment represents the rate of fertilizer N addition recommended for maximal grass production in agriculture (Jackson and Williams, 1979; Robson *et al.*, 1989). Nitrogen was applied as granular ammonium sulphate fertilizer (21% N), an inorganic fertilizer widely used in agriculture, by hand in two equal instalments each year, one early in the growing season and one soon after hay cutting and removal. These timings are typical of many agricultural grassland fertilization regimes (Morrison, 1987). Actual dates of application were 4 May and 18 July in 1994 and 24 March and 3 July in 1995. With each application, fertilizer N was also applied to a 25 cm wide strip surrounding each plot at a rate appropriate to the treatment within that plot in order to reduce edge effects. Five litres m⁻² of water were applied to all plots at each instalment to dissolve the ammonium sulphate as required. Due to the remote location of the site, river water was used. However, the N content of the water was maximally 14 mg l⁻¹, representing a total input to each plot equivalent to less than 1.5 kg N ha⁻¹ yr⁻¹, a negligible amount in relation to the fertilizer treatment (i.e. 600 kg N ha⁻¹ yr⁻¹).

Vegetation management of the field during the experiment continued the traditional cutting, hay harvesting and grazing regime (with no applications of fertilizers), and was

implemented by a local farmer. This meant that the experiment plots were incorporated into the conventional farming management of the field as a whole. The field was cut once annually using a tractor-mounted disc mower on 26 June in 1994 and 29 June 1995. Following each cut, the hay crop was baled and removed within five days. Grazing of the regrowth by 220 sheep took place between 3 and 21 October 1994 after the first sampling season had ended. In the second year, the experiment concluded before grazing by 180 sheep began on 30 September 1995. Flooding of the study site occurred for approximately 10 days in January-February 1995, between the two sampling seasons.

5.2.2.1 Field sampling

Botanical sampling of the plant community comprised measurements of species diversity, cover and above-ground production. The first two variables were measured throughout the two growing seasons usually on a monthly basis. On each sampling occasion, the same 1m² in each plot (a in Figure 2.14) was used to record all vascular plant species and their % cover, the latter estimated visually. At the same time, the cover occupied by moss (species not determined), litter and bare ground was recorded. Plant detection after the hay cut was possible because cutting did not eliminate, even temporarily, all of the above-ground portion of any species. The third variable, plant production, was determined by harvesting above-ground biomass twice in each season, the first timed to examine hay production in mid-June and the second in late August to measure regrowth biomass. Biomass was not assessed prior to treatment application, as measures of species diversity and cover taken at that time had affirmed the botanical homogeneity of the experiment plots. Vegetation was clipped from a 0.04 m² quadrat located at random within the 0.25 m x 1 m section of each plot not used for monitoring other botanical or soil variables (b in Figure 2.14). On each occasion, different areas of the plot were harvested. Each biomass sample was sorted to species level and dried to constant weight at 105 °C.

Soil variables were measured using the 0.25 m x 1 m area of each plot not used for botanical sampling (c in Figure 2.14). Soil pH in the experiment plots was monitored during the study because it is known that the application of ammonium sulphate fertilizer can lead to acidification of the soil environment (Haynes and Goh, 1978; Johnston *et al.*, 1986). Soil samples from the surface 15 cm were analysed for pH (in deionized water) using the electrometric method (McLean, 1982). Soil pH varied little within treatments throughout the experiment and there were no significant differences between the fertilized and unfertilized plots, possibly because clay soils have a

buffering capacity reducing the acidifying impact of ammonium sulphate (Johnston *et al.*, 1986).

The performance, including productivity, of plants in fertilized meadows can be limited by insufficient soil moisture (Rabotnov, 1977; Titlyanova *et al.*, 1990). In this study soil moisture was monitored in both study seasons by sampling monthly from the plots to a depth of 15 cm and determining weight loss of each sample after drying to constant weight at 105 °C (Gardner, 1965). No significant differences were found between the two fertilizer treatments on any sampling occasion during the two years of study, indicating that any enhanced plant growth due to fertilizer application did not reduce soil moisture to an extent where plant response to fertilizer N was constrained.

5.2.2 2. Data analysis

The methodology followed for the data analysis is detailed in section 2.2.2. Plant species diversity was quantified using species richness, a count of the number of species in the sample, and Simpson's index (Simpson, 1949). Statistical comparisons of mean values for the control and fertilized treatments within species richness, % cover and biomass data were undertaken for each sampling occasion because botanical measurements made on any one sampling occasion were correlated with subsequent measurements from the same plot. These comparisons used *t*-tests. Paired *t*-tests were applied to examine temporal changes within the same treatment. All results were termed significant only if $P < 0.05$.

Analysis of the effects of meadow management (i.e. the cutting and grazing of the regrowth) focused on the impact of cutting, as this took place twice during the experiment, both times during the two experiment sampling seasons. It was not possible to provide this comparison for grazing, however, as this was undertaken just once during the experiment, between the two sampling seasons.

5.2.3 Supplementary experiment

In order to gain further insight into the role of management and any interactions with fertilization, a supplementary experiment was run concurrently with the core experiment utilizing an enclosure to exclude cutting and grazing management (but not flooding). The enclosure was located near the centre of the field used for the core study. At the outset of the experiments, the physiognomy and botanical composition of the vegetation

outside and within the enclosure exhibited considerable similarity with each other. The protocol for the supplementary experiment was essentially as described above for the core study except that, due to limited space within the enclosure, each of the two fertilizer treatments was replicated by four rather than six plots.

Statistical comparisons between the core and supplementary experiments were not possible because there was no interspersion of plots between the two experiments (section 2.2.3.2; Hurlbert, 1984). Instead, changes in the composition of the uncut and ungrazed plant community that formed the supplementary experiment were illustrated graphically to enable specific comparison with results from the cut and grazed vegetation from the core study.

The treatments applied to the core and supplementary experiments are summarized in Table 5.2.

Table 5.2 Summary of the core and supplementary experiments at Besthorpe

	Core plots	Supplementary plots
Managed (cut and grazed)	√	
Unmanaged (not cut and not grazed)		√
Experimental application of fertilizer N	√	√

5.3 Results

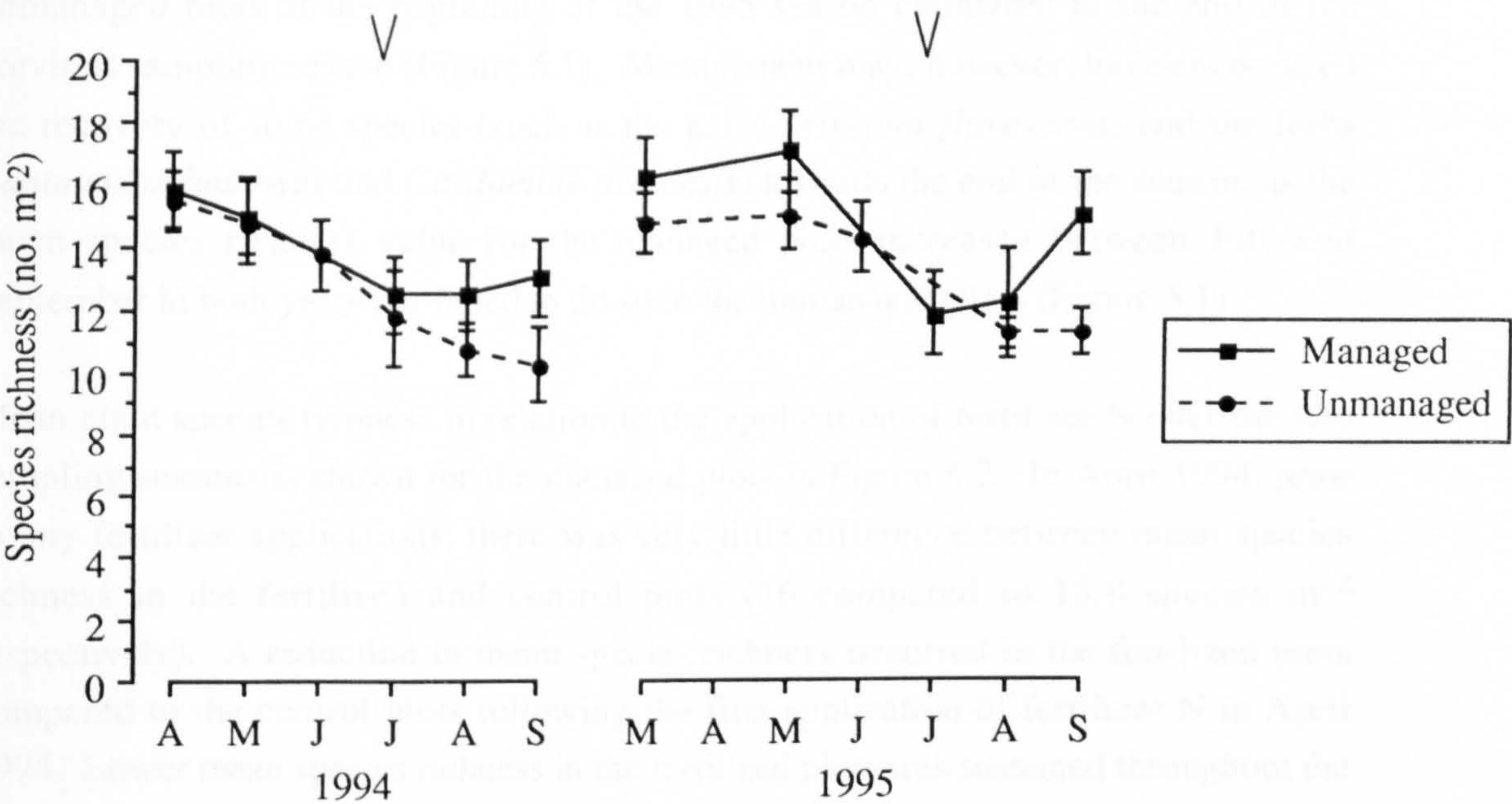
Results refer to the core experiment unless otherwise stated.

5.3.1 Plant species diversity

5.3.1.1 Species richness

The effect of cutting and grazing management in relation to the seasonal pattern of plant species richness (number of species m^{-2}) was examined by comparing values for unfertilized managed (core) and unmanaged (supplementary) plots in 1994 and 1995 (Figure 5.1). This figure shows that mean species richness at Besthorpe peaked at

Figure 5.1 Comparison of plant species richness in managed (core) and unmanaged (supplementary) unfertilized plots at Besthorpe in 1994-95. Data are mean values (n=6 for managed plots; n=4 for unmanaged plots) ± 1 SE. V indicates timings of cutting the managed plots.



approximately 16 species m⁻² early in both years and that there were seasonal variations in richness in both sampling periods, including a reduction in mid-season. Indeed, the decrease in richness observed between May and July samples was significant in both years for managed plots ($P < 0.002$) and for unmanaged plots ($P < 0.05$) in 1994. (It was not tested for 1995 because the unmanaged plots were not sampled in July). This shows that some species at Besthorpe (e.g. the grasses *Bromus hordeaceus* and *Poa trivialis*, and the forb *Cerastium fontanum*) tended to be conspicuous in spring but were generally not recorded for the rest of the season, irrespective of management such as cutting in June, and could explain the higher species richness for both managed and unmanaged plots at the beginning of the 1995 season compared to the end of the previous sampling season (Figure 5.1). Management may, however, have encouraged the recovery of some species (such as the grass *Trisetum flavescens*, and the forbs *Ranunculus bulbosus* and *Cardamine pratensis*) towards the end of the season, as the mean species richness value for the managed plots increased between July and September in both years but failed to do so in the unmanaged plots (Figure 5.1).

Mean plant species richness in relation to the application of fertilizer N over the two sampling seasons is shown for the managed plots in Figure 5.2. In April 1994, prior to any fertilizer applications, there was very little difference between mean species richness in the fertilized and control plots (16 compared to 15.8 species m⁻² respectively). A reduction in mean species richness occurred in the fertilized plots compared to the control plots following the first application of fertilizer N in April 1994. Lower mean species richness in the fertilized plots was sustained throughout the 1994 sampling season and, despite some recovery in the fertilized plots relative to the control plots between the two sampling seasons, it was again reduced in fertilized plots following treatment application in March 1995 (Figure 5.2). Consistently lower mean species richness in the fertilized plots compared to the control plots was shown throughout the second sampling season, culminating in a significant difference between the treatments ($P = 0.03$) in September 1995.

The temporal pattern described by total plant species richness was also observed for the grasses (Figure 5.3), with significant ($P < 0.004$) mid-season reductions in mean richness in both years in the control treatments. The application of fertilizer N generally had a small negative effect on grass species richness, with a slightly greater effect in the second year (Figure 5.3).

Figure 5.2 Effects of fertilizer N application on plant species richness at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

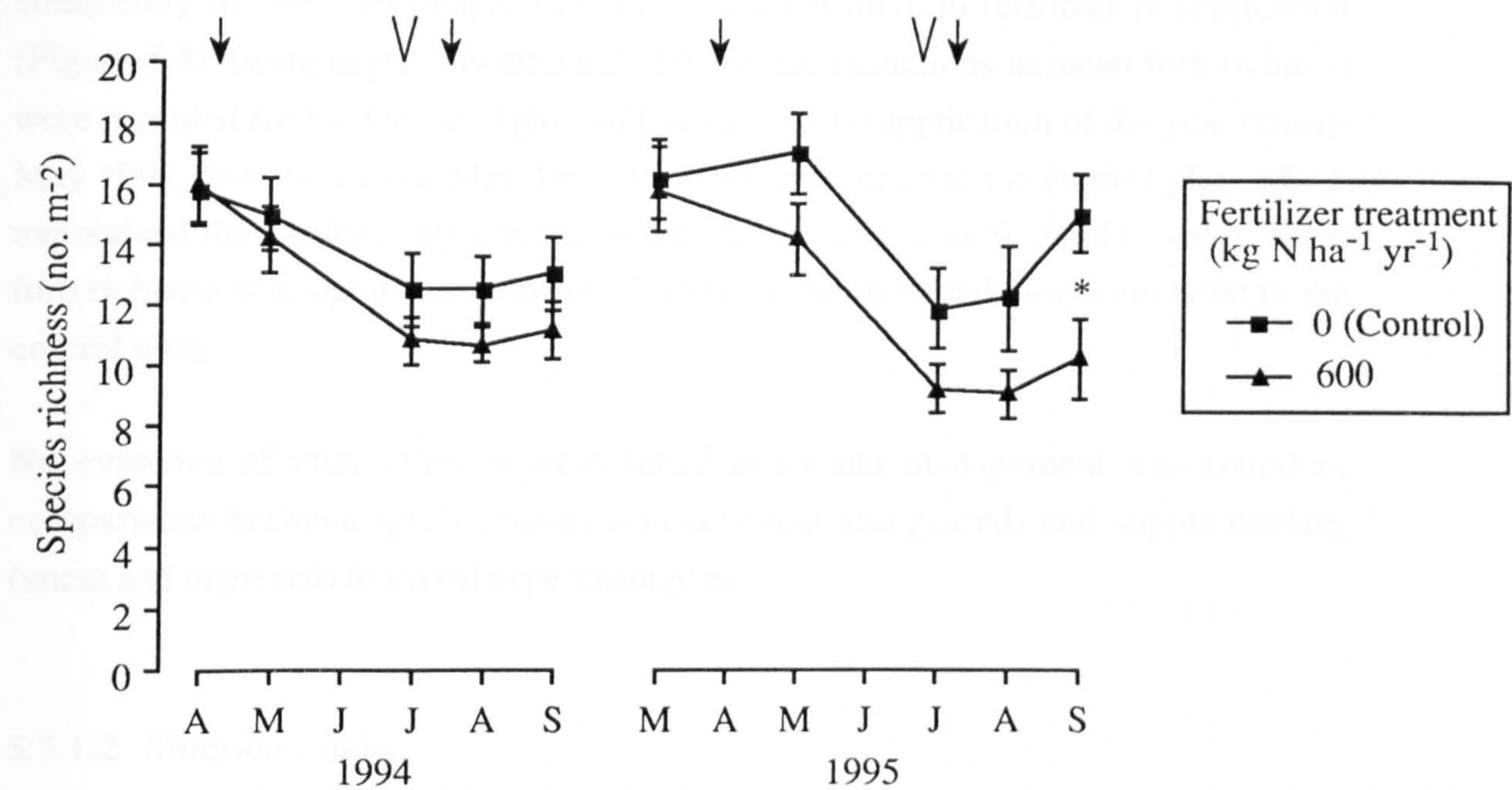


Figure 5.3 Effects of fertilizer N application on grass species richness at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values did not differ significantly (t -test). Arrows indicate timings of fertilizer application; V indicates timings of cutting.

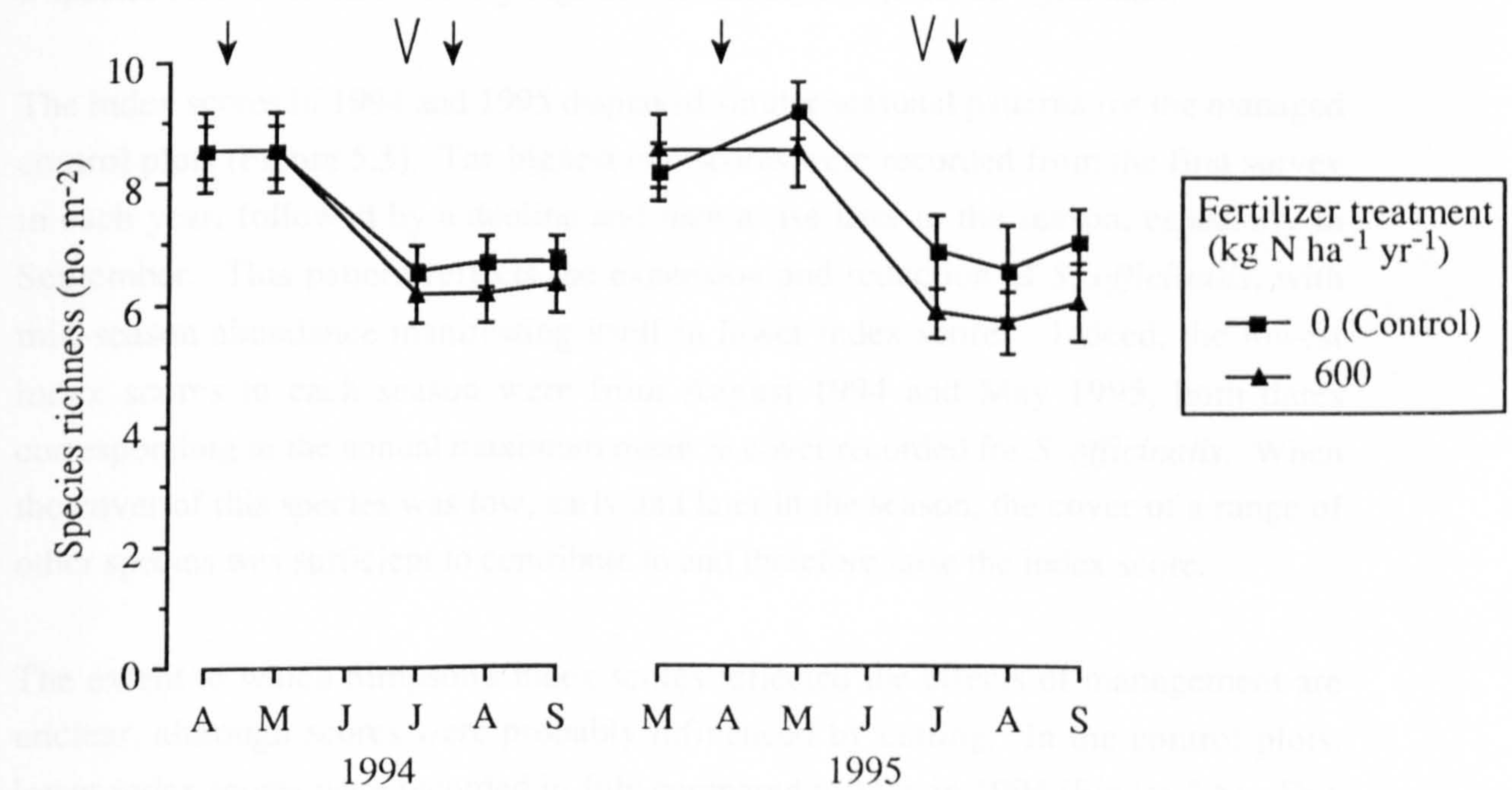


Figure 5.4 shows a marked seasonal variation in forb richness for the control plots. The pattern closely resembles that shown by total species richness and includes a significant decrease in mean forb richness between May and July ($P < 0.05$). However, mean forb values in the control plots recovered partially later in the 1994 season, and completely in 1995. Forb species richness was sensitive to fertilizer N application (Figure 5.4), being negatively affected. Significant reductions in mean forb richness were recorded for the fertilized plots following the first application of the year (April-May 1994, $P = 0.04$; March-May 1995, $P = 0.04$), in contrast to the control plots which maintained their values. By the end of the second season, in September 1995, mean forb richness was significantly lower ($P = 0.04$) in the fertilized plots compared to the control plots.

No evidence of interaction between fertilization and management was found in comparisons between species richness in core (cut and grazed) and supplementary (uncut and ungrazed) fertilized experiment plots.

5.3.1.2 Simpson's index

Simpson's index scores for control and fertilized core experiment plots are presented in Figure 5.5. Scores derived from Simpson's index reflect the number of species present in a sample and their proportional abundance. Simpson's index scores for Besthorpe derived from species richness and % cover values reflected the seasonal development of a species that achieved relatively high cover, namely *Sanguisorba officinalis*.

The index scores in 1994 and 1995 displayed similar seasonal patterns for the managed control plots (Figure 5.5). The highest two scores were recorded from the first survey in each year, followed by a decline and then a rise later in the season, especially in September. This pattern reflects the expansion and reduction of *S. officinalis*, with mid-season abundance manifesting itself in lower index scores. Indeed, the lowest index scores in each season were from August 1994 and May 1995, both dates corresponding to the annual maximum mean % cover recorded for *S. officinalis*. When the cover of this species was low, early and later in the season, the cover of a range of other species was sufficient to contribute to and therefore raise the index score.

The extent to which Simpson's index scores reflected the effects of management are unclear, although scores were probably influenced by cutting. In the control plots, lower index scores were recorded in July compared to May in 1994 (Figure 5.5). This was partly due to a decrease in species richness (Figure 5.1) but also because of lower

Figure 5.4 Effects of fertilizer N application on forb species richness at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

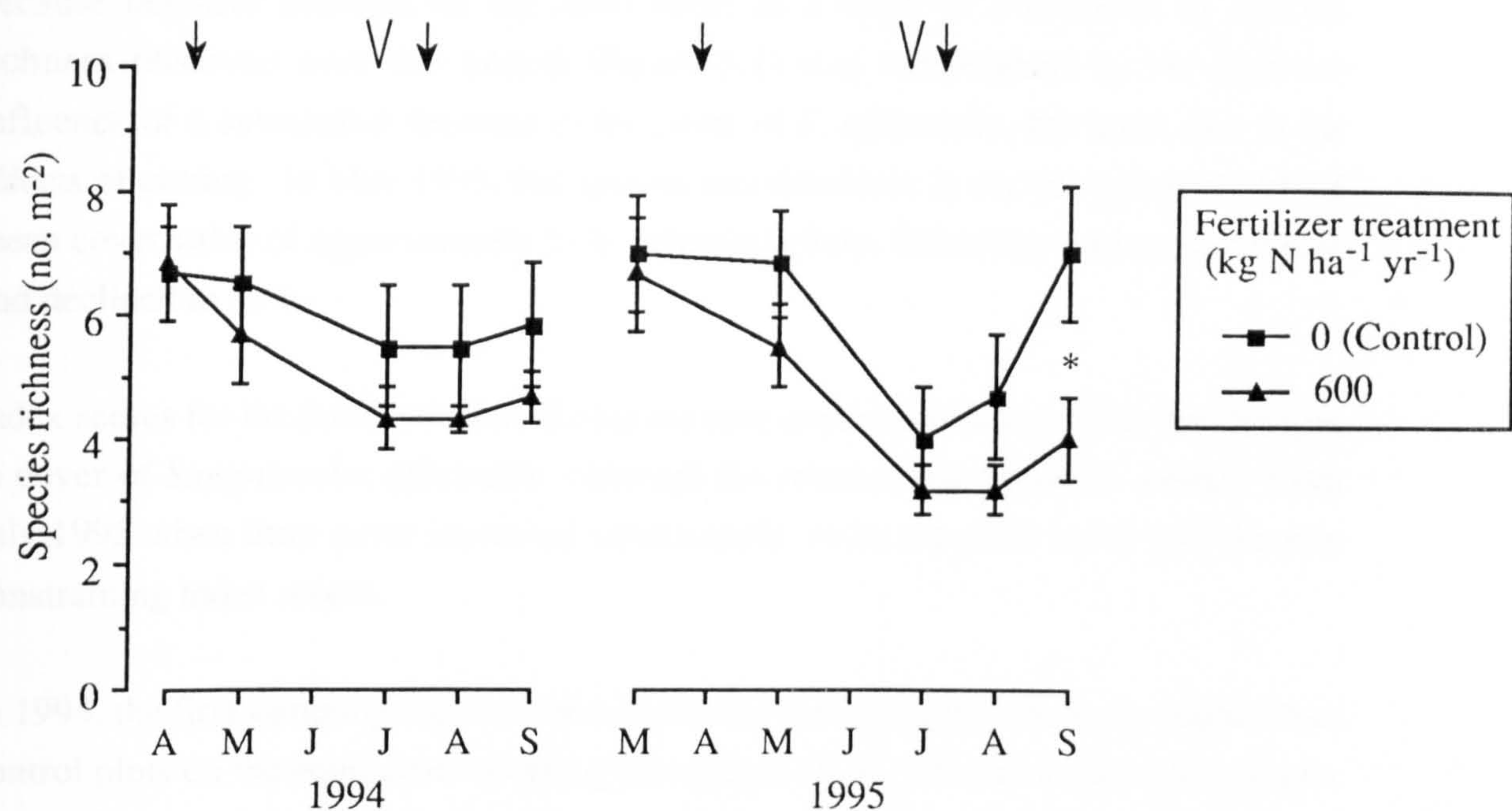
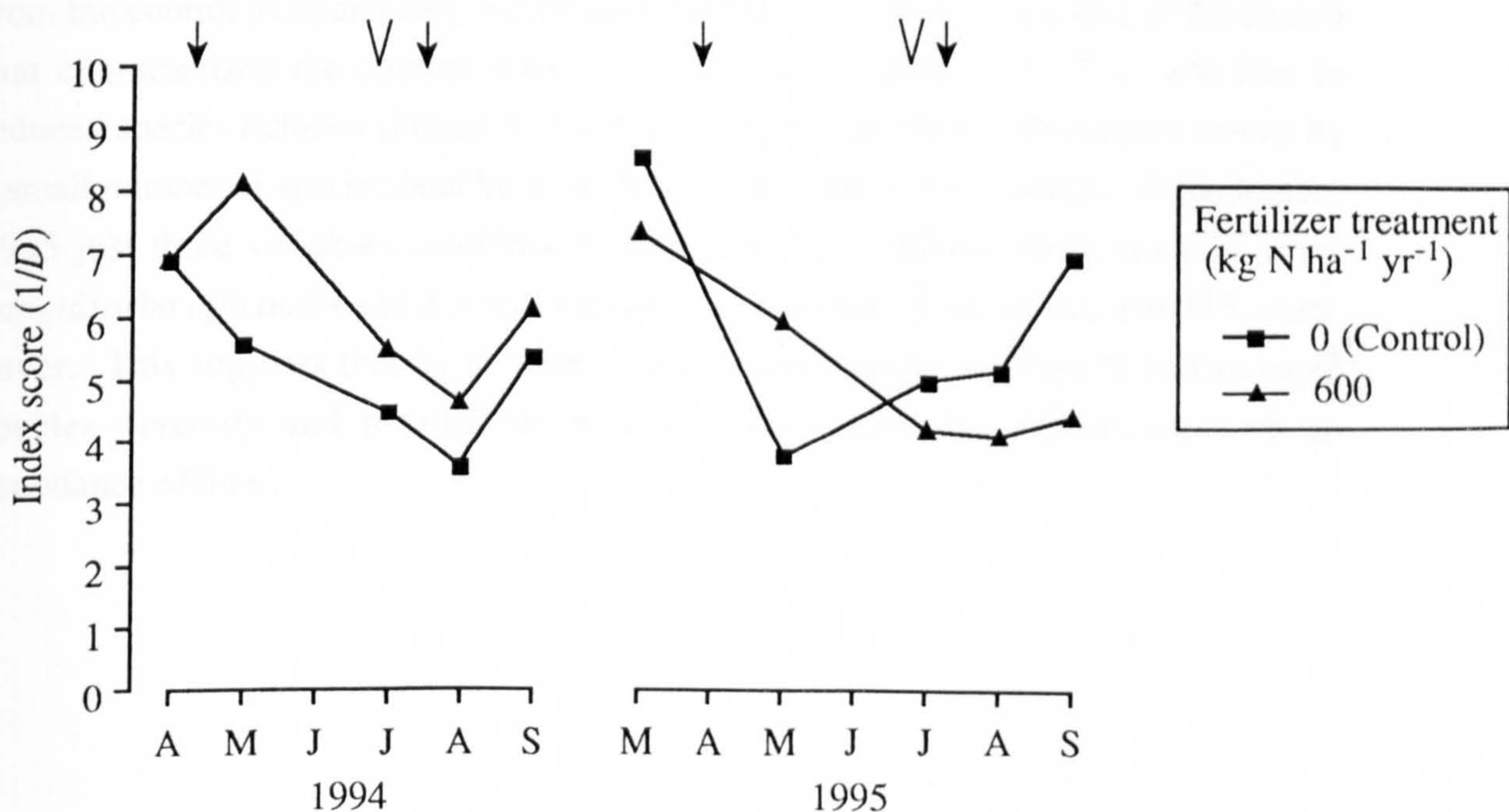


Figure 5.5 Effects of fertilizer N application on Simpson's index ($1/D$) scores at Besthorpe in 1994-95. Scores are derived from mean species richness and cover values for six experiment plots for each treatment. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



community evenness as the mean cover of some species (e.g. *Anthoxanthum odoratum* and *Arrhenatherum elatius*) was reduced to negligible levels following cutting in June. A similar pattern was not evident in the control plots in 1995, when the post-cutting index score for July was higher than the pre-cut value for May. This may have been because negative pressure on the index score as a result of a decrease in species richness observed over this period (Figure 5.1) was outweighed by the positive influence of a substantial decrease in the cover of *S. officinalis*, the latter due to the effects of cutting. In May 1995, this species was dominant in the control plots with a mean cover value of approximately 51%, whereas in July, following cutting, this figure had declined to 31%.

Index scores for the fertilized plots during the core experiment also reflect the changes in cover of *Sanguisorba officinalis*, although the relationship becomes weaker from July 1995 when litter cover increased substantially, reducing plant cover and thereby constraining index scores.

In 1994, the first sampling season, index scores for the fertilized plots were higher than control plots on the equivalent sampling date (Figure 5.5). This was due to the greater cover of many grasses, including *Agrostis capillaris*, *Alopecurus pratensis*, *Holcus lanatus* and *Lolium perenne*, which limited the cover of *S. officinalis* and promoted evenness in the fertilized plots relative to the control plots. This was particularly evident in May, following the first application of fertilizer N (Figure 5.5).

Index scores for the fertilized plots in 1995 were generally lower than scores derived from the control plots and they lacked the pronounced recovery at the end of the season that characterized the control scores in both years (Figure 5.5). This was due to reduced species richness (Figure 5.1) and to the high proportional abundance shown by a small number of species (and litter) in the fertilized plots. For example, in September 1995 just three variables combined to dominate the fertilized plots, namely litter, *Sanguisorba officinalis* and *Agrostis capillaris* which totalled approximately 75% mean cover. This suggests that by the end of the second season fertilizer N had reduced species diversity and resulted in relatively few species co-dominating with an abundance of litter.

5.3.2 Cover

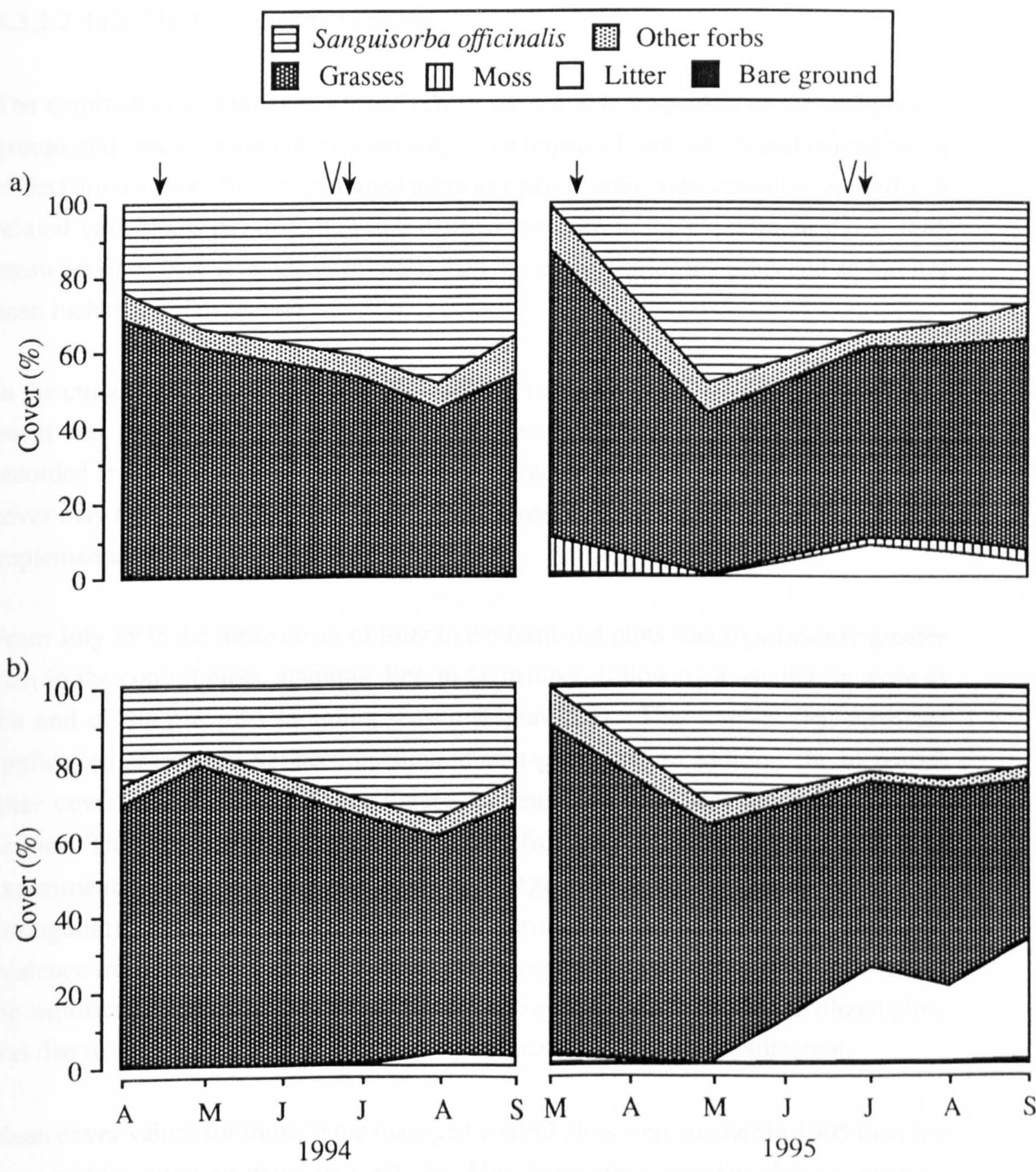
5.3.2.1 Community dynamics

The dynamics of the Besthorpe plant community as represented by % cover and the associated variables of litter and bare ground during the two sampling seasons of the core experiment are illustrated in Figure 5.6 (a and b). *Sanguisorba officinalis* and grass form the main components of the community in terms of cover. The relationship between these two components largely defined the dynamics of the community during the course of the experiment, with a cover response by one component usually proportional to an inverse change in the other. Hence, in the control plots in both years as *S. officinalis* cover increased early in the season grass cover decreased, and later as the cover of *S. officinalis* decreased grass cover increased.

Seasonal plant community dynamics in the control plots differed between the two sampling seasons of 1994 and 1995 (Figure 5.6a). In 1994, the mean cover of *S. officinalis* continued to increase following cutting management in June, whereas in 1995 the cover of this species contracted after cutting. Also, litter was found in the control plots only in 1995, attaining a maximum mean cover of approximately 9% in July, after cutting. Such differences may have been due to annual variations in plant populations, particularly *S. officinalis*, or related to minor variations in the management practised each year. Ineffective removal of the hay cut in June 1995, for example, may have led to the elevated litter cover recorded from July of that year. The effects of a brief period of flooding in 1995, or an interaction between management and other factors, such as climate, may also have contributed to between-year variations in community dynamics of the managed vegetation.

Comparison of Figure 5.6a with b illustrates the effects of fertilizer N on the managed plant community at Besthorpe. Compared to the control plots, the fertilized plots exhibited a lower mean cover of *S. officinalis*. Seasonal maxima for this species exceeded 50% in both years in the control plots, compared to less than 40% in the fertilized plots. In particular, the mean cover of *S. officinalis* decreased in the fertilized plots between April and May 1994, following the first application of fertilizer N, while grass cover increased (Figure 5.6b). This was in contrast to the unfertilized control plots over the same period, where the opposite trend was observed (Figure 5.6a), indicating that fertilization may have reduced the cover of *S. officinalis* allowing grasses to expand, or stimulated grass growth which increased its cover at the expense of *S. officinalis*. Indeed, grass cover was generally greater in the fertilized plots until litter increased in the fertilized plots later in 1995, reaching a mean value of 32% in

Figure 5.6 Time series of the effect of fertilizer N treatments on plant community dynamics at Besthorpe in 1994-5. Data are mean % cover values (n=6). Arrows indicate timings of fertilizer application; V indicates timings of cutting the managed plots. a) 0 kg N ha⁻¹ yr⁻¹ (control) b) 600 kg N ha⁻¹ yr⁻¹.



September. Forb cover was reduced in the fertilized plots, attaining little more than a third of the cover of the control plots by the end of the experiment period despite similar initial cover values. Moss in the control plots peaked at almost 10% mean cover in March 1995, in contrast to the fertilized plots, where it was negligible throughout the two sampling seasons.

5.3.2.2 Individual community variables

The community dynamics described reflect the variable responses of the component groups and species within that community. The impact of fertilizer N and management effects are therefore further examined using key plant community variables, as well as a related variable, litter, that showed a marked presence in the experiment plots. The mean cover of bare ground never constituted more than 1% of the plots and so has not been included in this section.

In the cut and grazed control plots, no litter was recorded in the 1994 sampling season but it was present in 1995, with the highest mean values of 4 to approximately 9% recorded from July after cutting management (Figure 5.7). Annual differences in litter cover may therefore have been related to management, particularly differences in cutting implementation.

From July 1995 the mean cover of litter in the fertilized plots was significantly greater than in the control plots, attaining 30% in September, following a smaller increase at the end of the previous sampling season (Figure 5.7). This implies that fertilizer application promoted litter accumulation in managed plots. In addition, the increased litter cover evident after cutting (Figure 5.7) suggests litter was generated by this action. This hypothesis is supported by data from the supplementary, unmanaged experiment plots, in which litter cover was negligible in the fertilized plots (<3% throughout) and absent from the control plots during both sampling seasons. Thus, the evidence from both the core and supplementary experiments at Besthorpe suggests that the significantly enhanced litter accumulation observed in the managed fertilized plots was due to a combination of management, particularly cutting, and fertilization.

Mean cover values for moss in the managed control plots were greater in 1995 than for comparable sampling dates in 1994, i.e. May-September, perhaps due to intrinsic population fluctuations, abiotic environmental variation or management effects. A pronounced peak in moss cover was observed at the very beginning of the season in the control plots in 1995 (Figure 5.8). Although this was considerably greater than the

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Figure 5.7 Effects of fertilizer N application on litter cover at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$; $\ast\ast=P<0.01$; $\ast\ast\ast=P<0.001$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

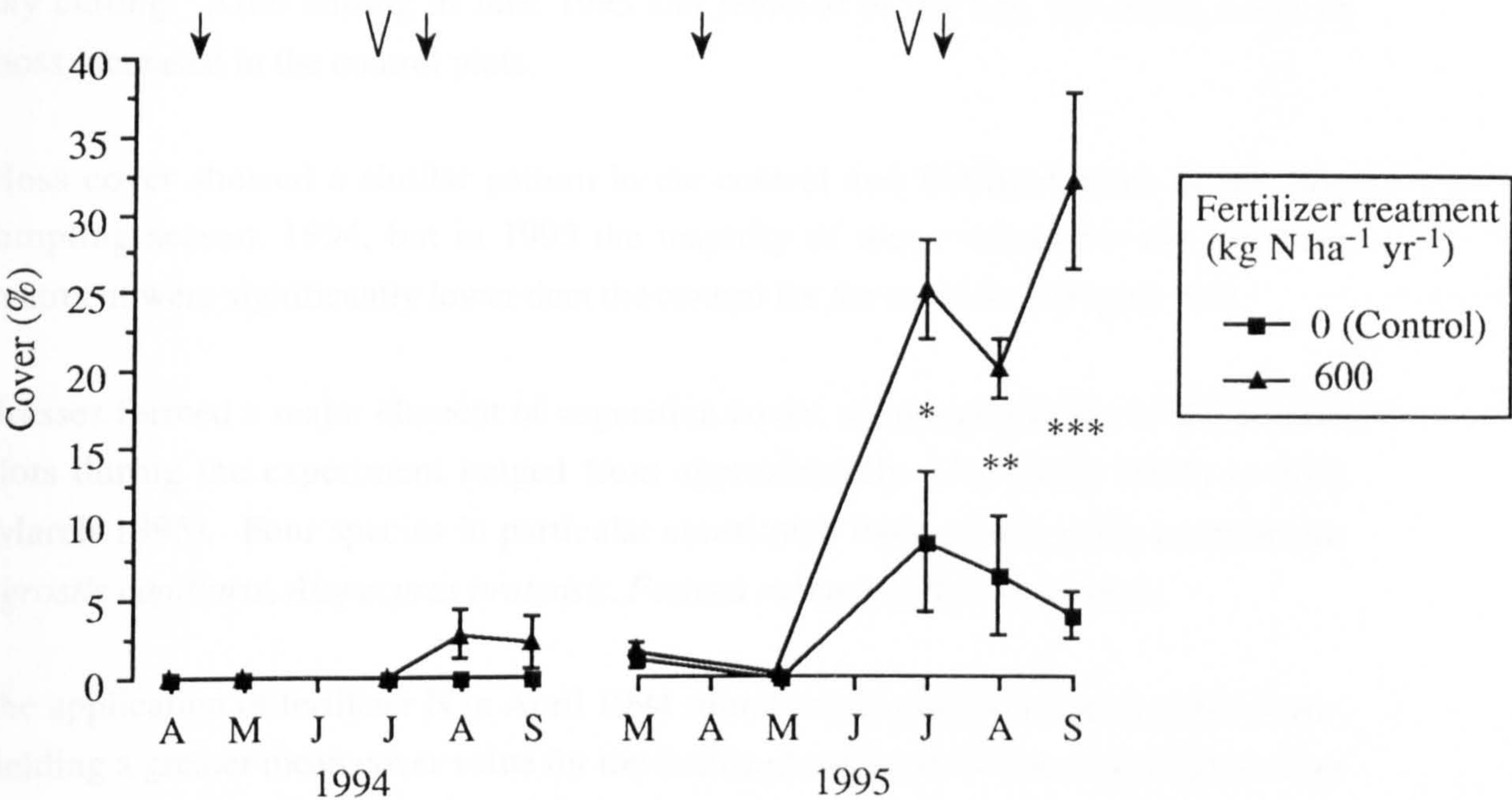
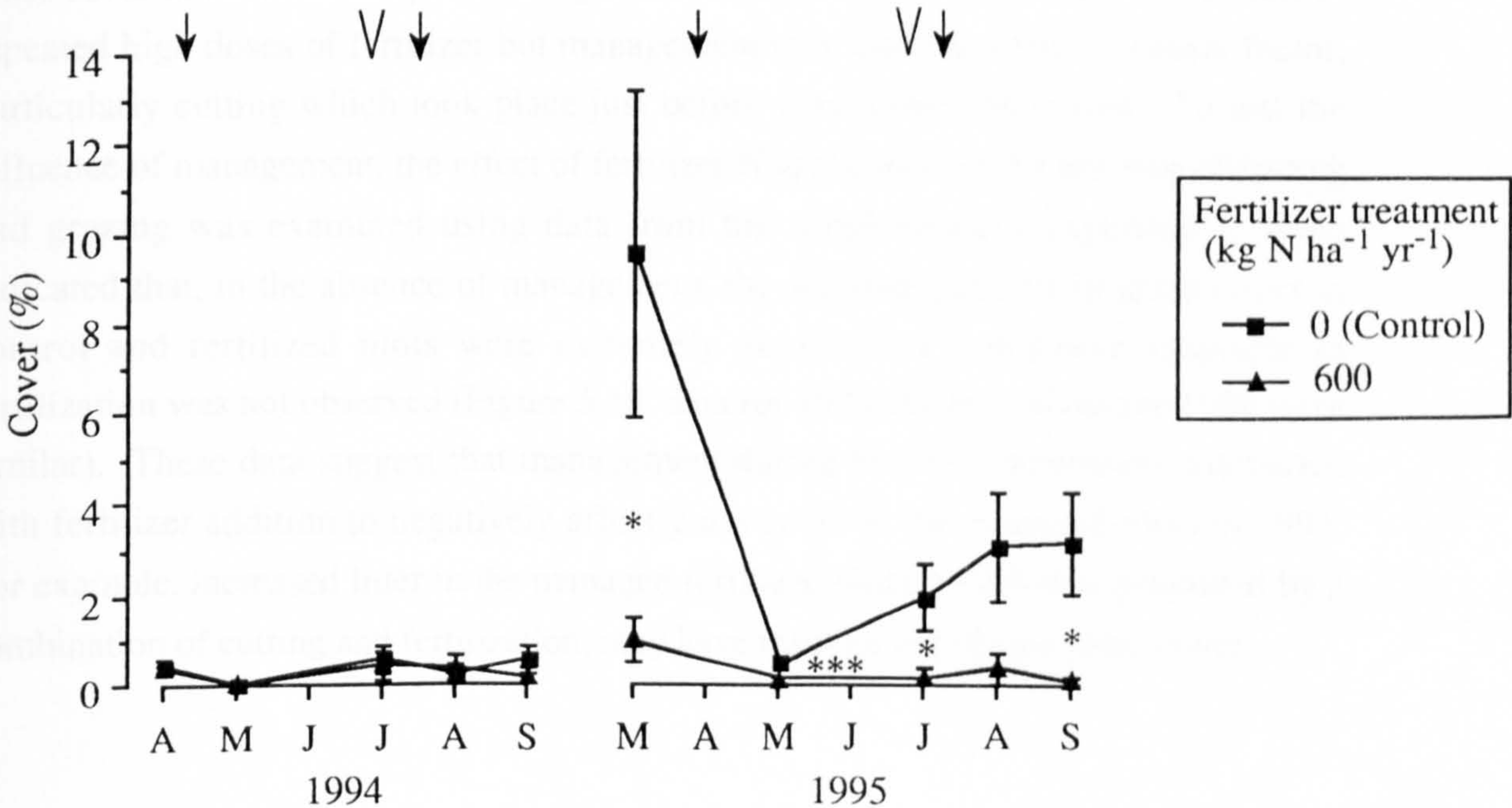


Figure 5.8 Effects of fertilizer N application on moss cover at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$; $\ast\ast\ast=P<0.001$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



mean cover recorded at the start of the previous season (April 1994), this reflected the early-season growth that was a feature of these plants as the sample in 1995 took place one month earlier, in March. Moss cover decreased substantially as 1995 progressed while the cover of some vascular plants, most notably *S. officinalis*, developed prior to hay cutting. After cutting in June 1995 and removal of the hay, the mean cover of moss increased in the control plots.

Moss cover showed a similar pattern in the control and fertilized plots in the first sampling season, 1994, but in 1995 the majority of mean values for the fertilizer treatment were significantly lower than the control for the same date (Figure 5.8).

Grasses formed a major element of vegetation cover; mean grass cover in the control plots during the experiment ranged from approximately 43% (May 1995) to 76% (March 1995). Four species in particular constituted most of this grass component: *Agrostis capillaris*, *Alopecurus pratensis*, *Festuca rubra* and *Holcus lanatus*.

The application of fertilizer N in April 1994 stimulated a rapid increase in grass cover, yielding a greater mean cover value for the fertilized compared to the control plots after only one month (Figure 5.9). Enhanced grass cover in the fertilized plots was observed throughout the 1994 sampling season and in March and May in 1995. In July 1995, following cutting management, mean grass cover had decreased in the fertilized plots but increased in the control plots such that both treatments showed similar values. Later, in September 1995, mean % cover of grass for the fertilized treatment had declined further and was significantly lower than the control values. This reduction in grass cover in the fertilized plots during 1995 may have been due the negative effects of repeated high doses of fertilizer but management may also have been a causal factor, particularly cutting which took place just before grass cover decreased. To test the influence of management, the effect of fertilizer N application in the absence of cutting and grazing was examined using data from the supplementary experiment. This indicated that, in the absence of management, the seasonal patterns of grass cover in control and fertilized plots were extremely similar and a negative response to fertilization was not observed (Figure 5.10, data for 1995 shown; values for 1994 were similar). These data suggest that management during the core experiment interacted with fertilizer addition to negatively affect grass cover in the managed plots in 1995. For example, increased litter in the managed fertilized plots, which was generated by a combination of cutting and fertilization, may have resulted in reduced grass cover.

Figure 5.9 Effects of fertilizer N application on grass cover at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

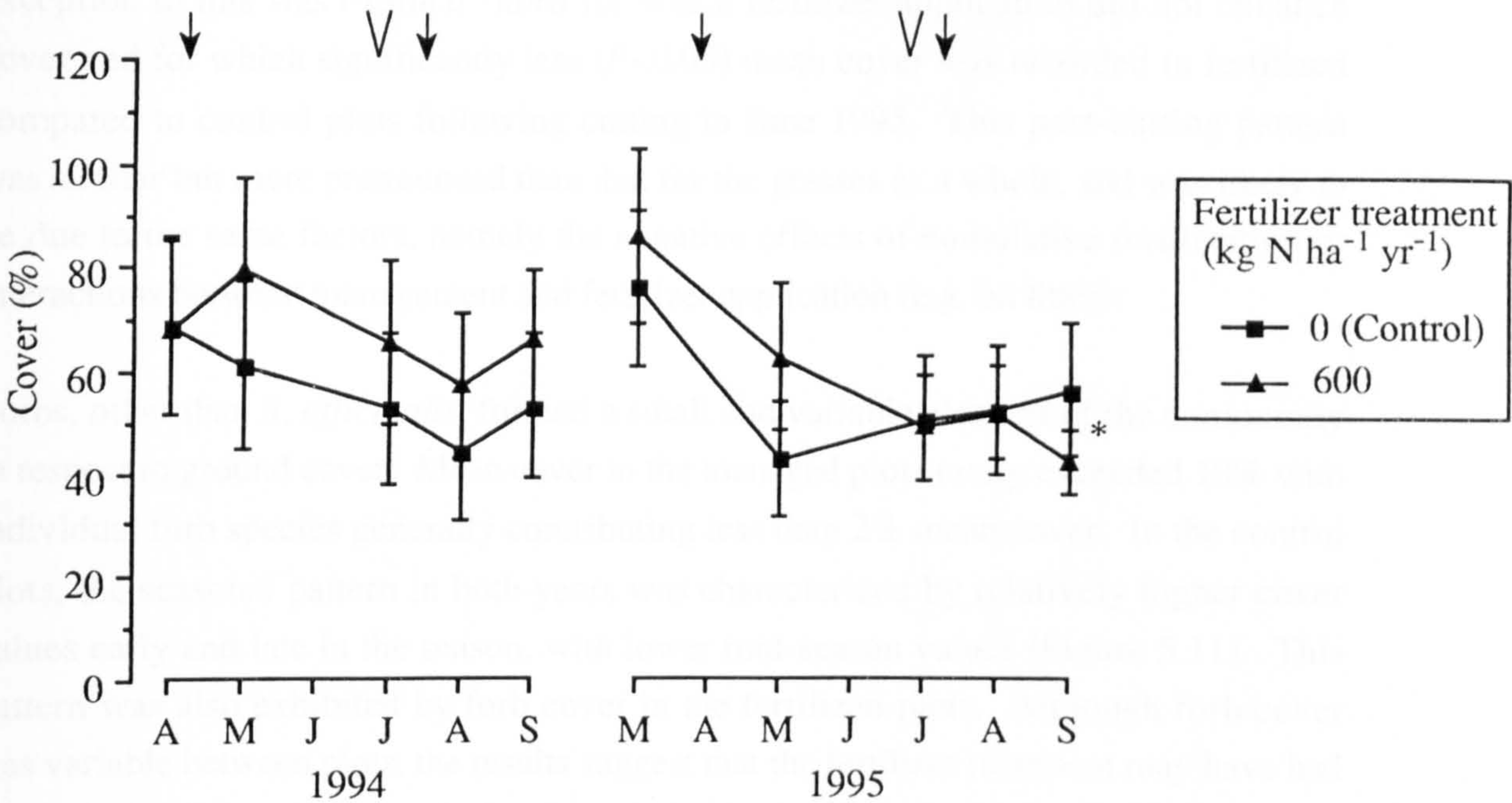
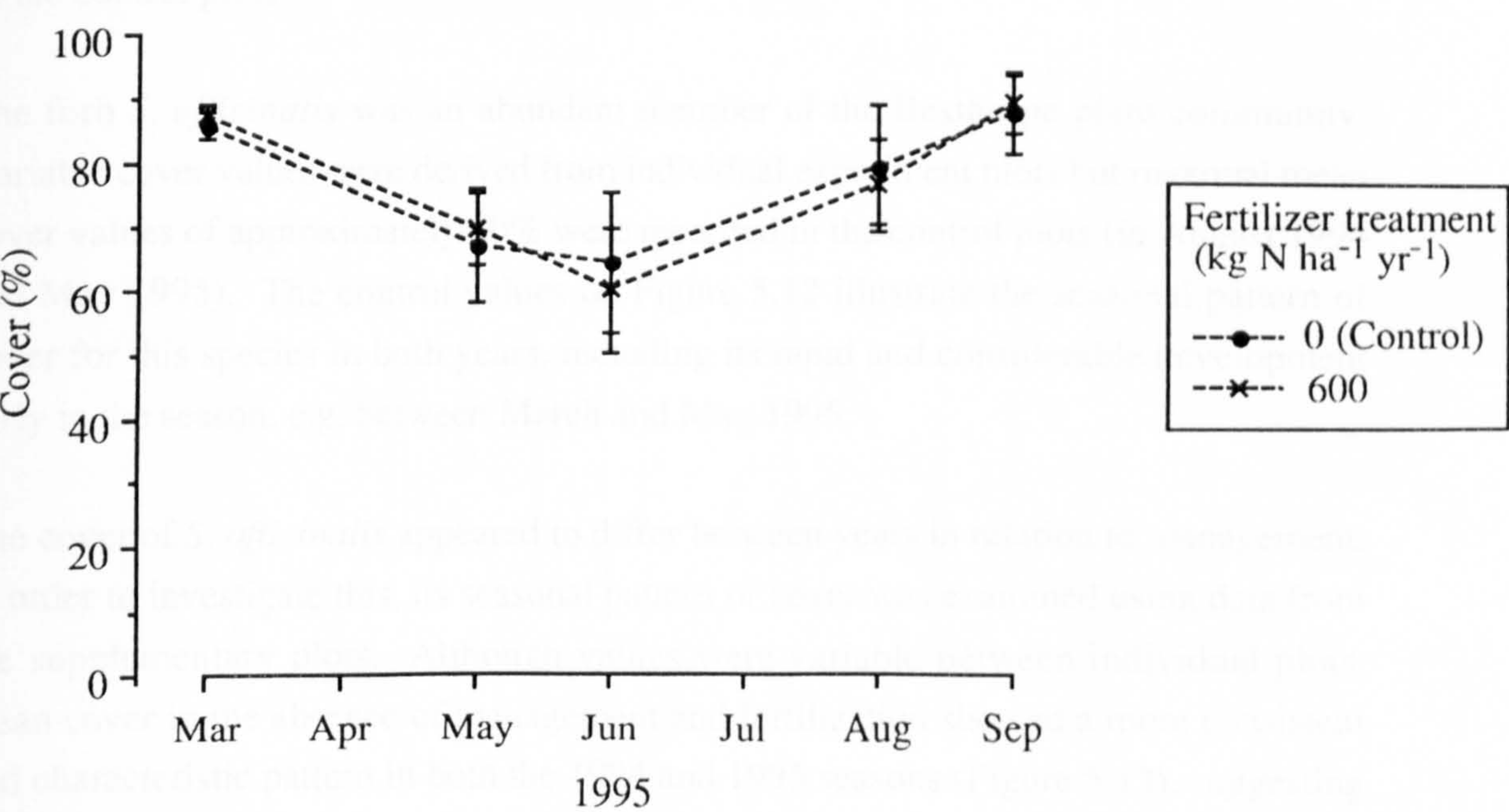


Figure 5.10 Comparison of grass cover in unmanaged (supplementary) fertilized and unfertilized plots at Besthorpe in 1995. Data are mean values ($n=4$) ± 1 SE.



When the cover of individual grass species was examined, several species showed a similar response to fertilization of the managed plots as the grass group as a whole. These included *Alopecurus pratensis*, *Agrostis capillaris* and *Holcus lanatus* which all exhibited increased mean cover following fertilization that was sustained into 1995. An exception to this was *Festuca rubra* for which fertilizer application did not enhance cover and for which significantly less ($P < 0.03$) mean cover was recorded in fertilized compared to control plots following cutting in June 1995. This post-cutting pattern was similar but more pronounced than that for the grasses as a whole, and was likely to be due to the same factors, namely the negative effects of cumulative fertilization or interactions between management and fertilizer application (e.g. on litter).

Forbs, other than *S. officinalis*, formed a small and variable element of the community in respect to ground cover. Mean cover in the managed plots rarely exceeded 10% with individual forb species generally contributing less than 2% mean cover. In the control plots, the seasonal pattern in both years was characterized by relatively higher cover values early and late in the season, with lower mid-season values (Figure 5.11). This pattern was also exhibited by forb cover in the fertilized plots. Although forb cover was variable between plots, the results suggest that the fertilizer treatment may have had a negative effect on forbs, with significantly less mean cover in the fertilized plots at the end of the second sampling season, in September 1995, compared to the control plots (Figure 5.11). One forb that exemplified this deleterious impact was *Ranunculus acris* which, despite similar mean values at the beginning of sampling in April 1994, displayed in the fertilized plots at the end of the experiment less than 1/10th of the cover of the control plots.

The forb *S. officinalis* was an abundant member of the Besthorpe plant community. Variable cover values were derived from individual experiment plots but maximal mean cover values of approximately 50% were recorded in the control plots (in August 1994 and May 1995). The control values on Figure 5.12 illustrate the seasonal pattern of cover for this species in both years, including its rapid and considerable development early in the season, e.g. between March and May 1995.

The cover of *S. officinalis* appeared to differ between years in relation to management. In order to investigate this, its seasonal pattern of cover was examined using data from the supplementary plots. Although values were variable between individual plots, mean cover in the absence of management and fertilization showed a more consistent and characteristic pattern in both the 1994 and 1995 seasons (Figure 5.13), suggesting that between-year environmental variations did not influence plant development substantially. In the unmanaged supplementary plots, a rapid increase from March to

Figure 5.11 Effects of fertilizer N application on forb cover (not including *Sanguisorba officinalis*) at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

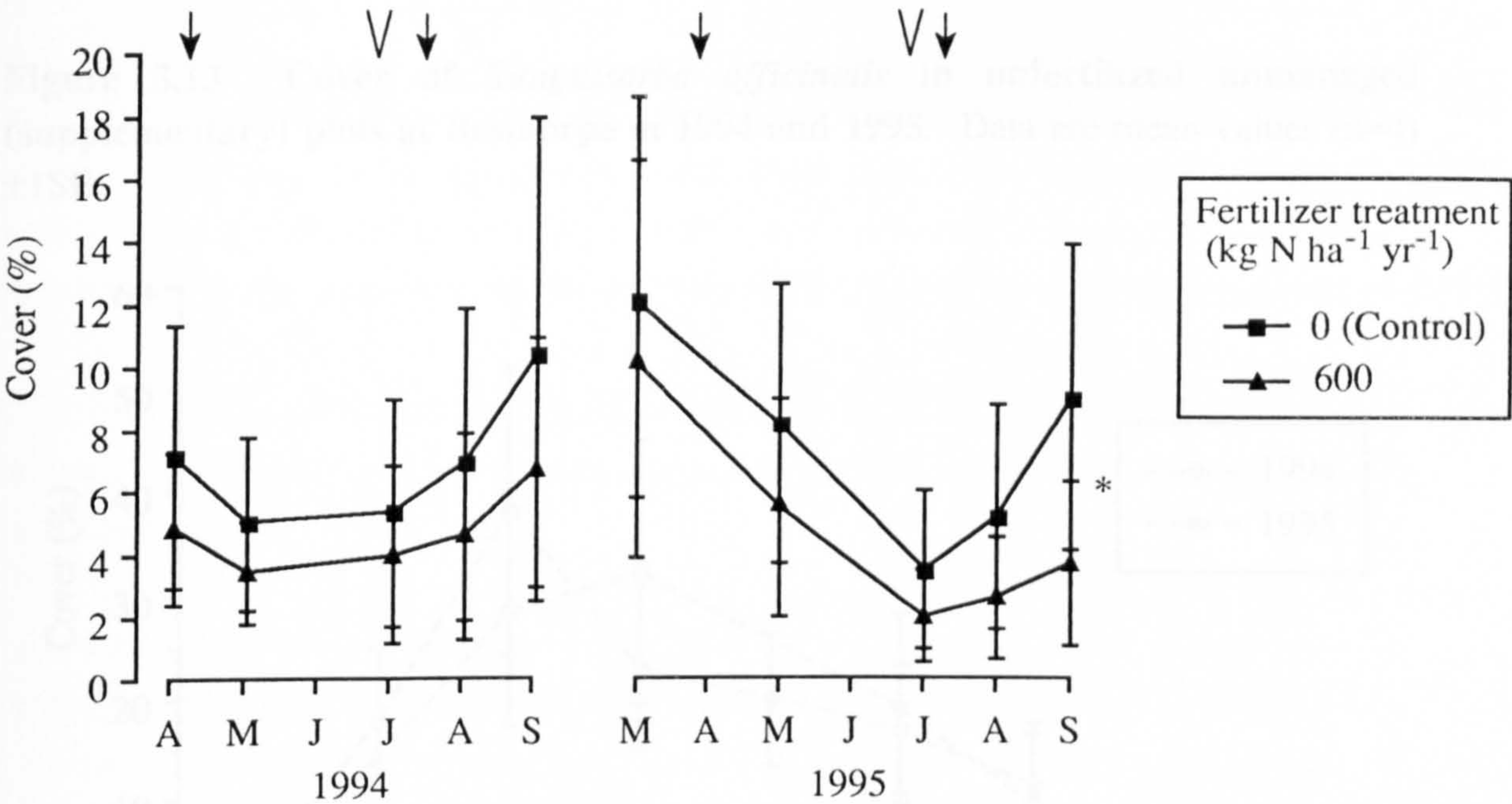


Figure 5.12 Effects of fertilizer N application on cover of *Sanguisorba officinalis* at Besthorpe in 1994-95. Data are mean values ($n=6$) ± 1 SE. For each date, values that differ significantly (t -test) are denoted by: $\ast=P<0.05$. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

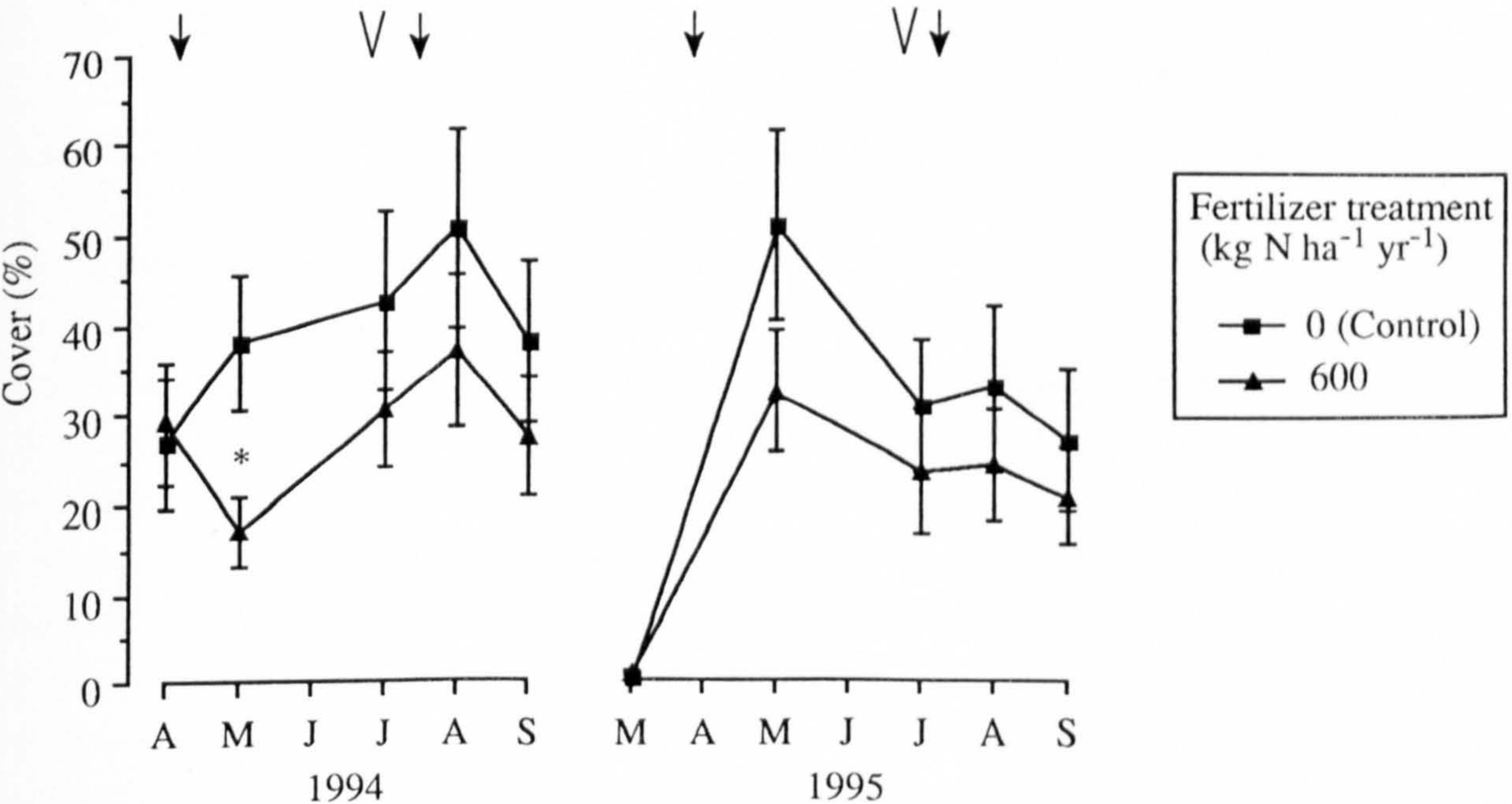
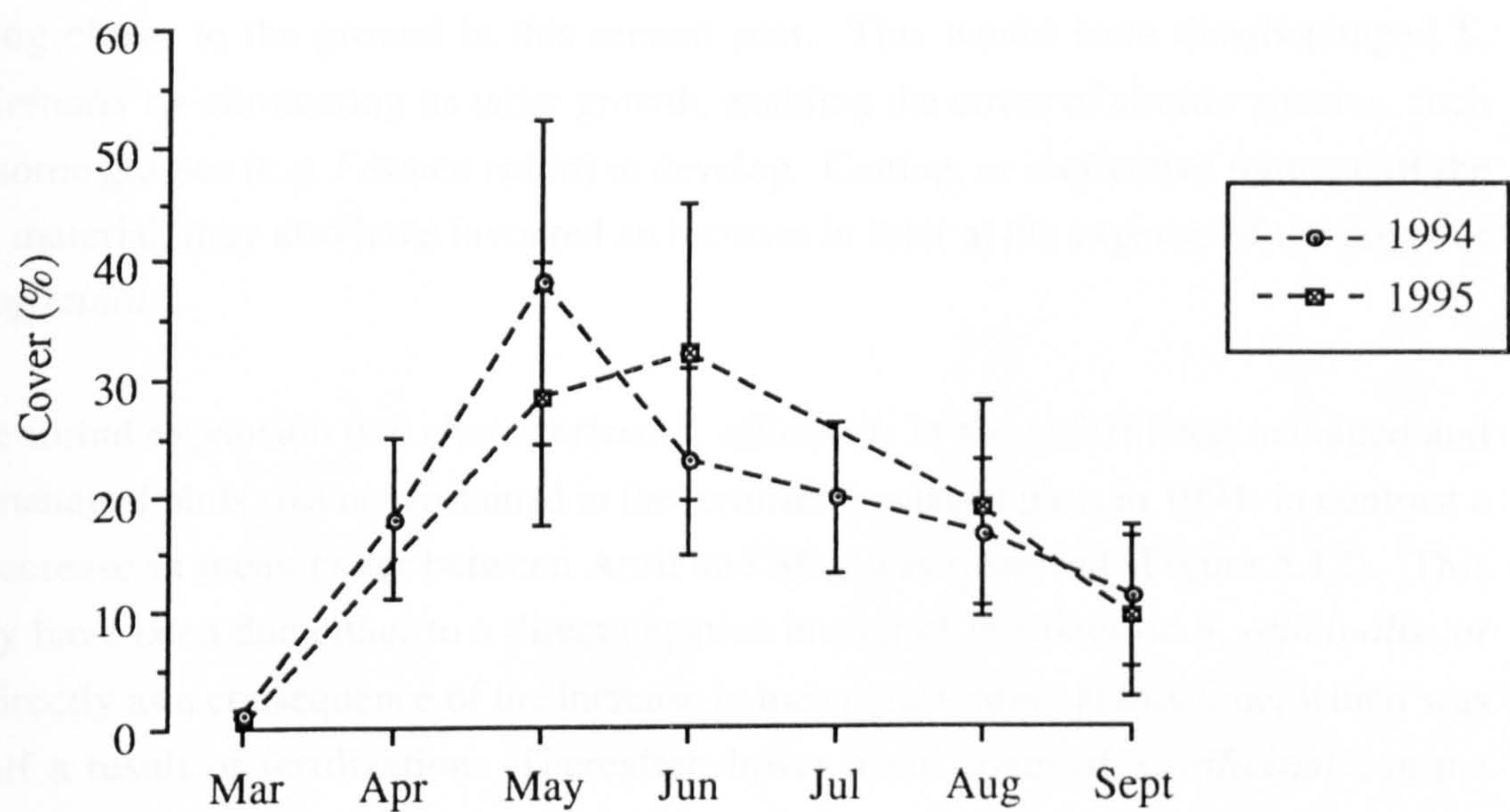


Figure 5.13 Cover of *Sanguisorba officinalis* in unfertilized unmanaged (supplementary) plots at Besthorpe in 1994 and 1995. Data are mean values (n=4) \pm 1SE.



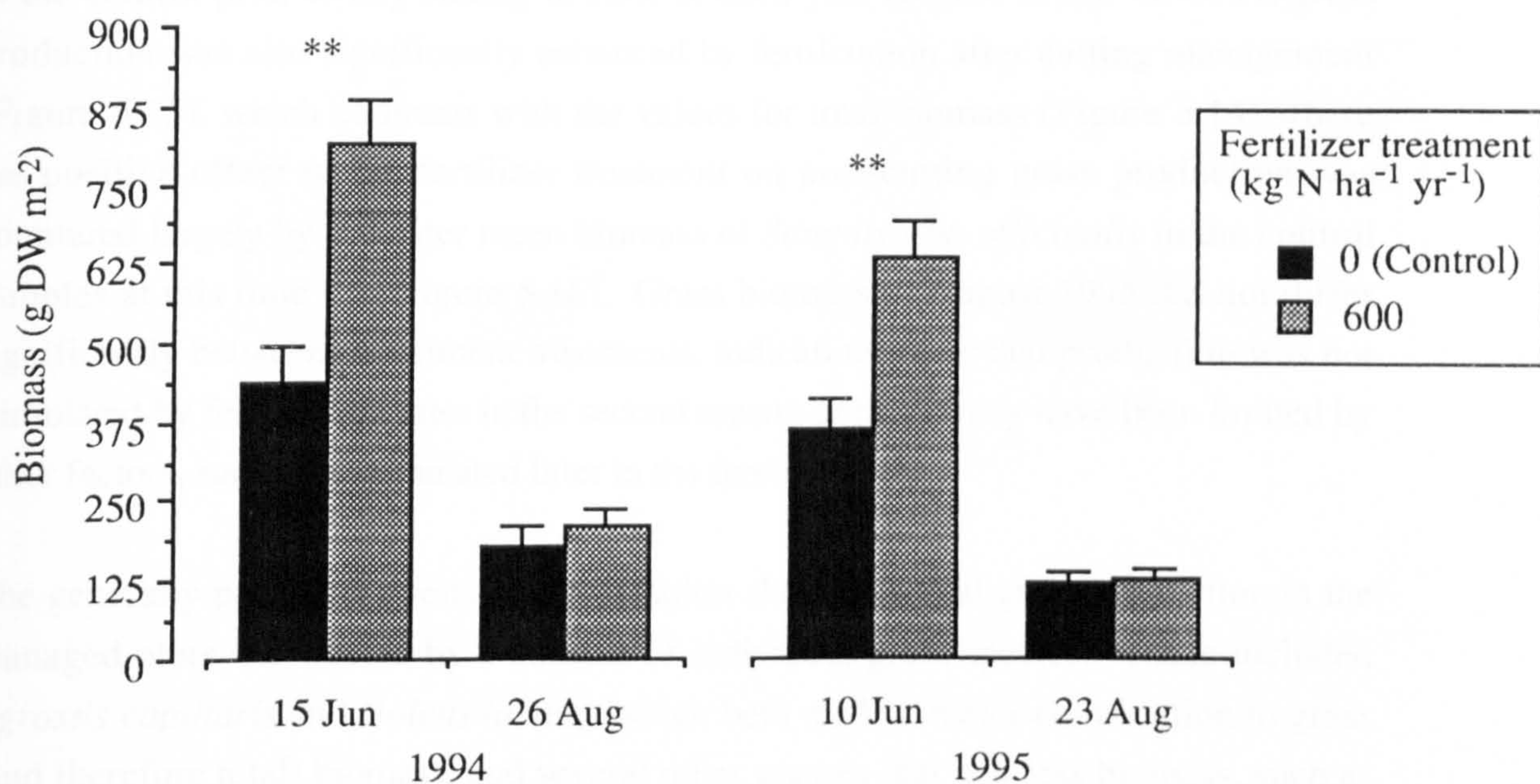
May led to maximum cover in May/June followed by a more gradual decline between June and September. In the core experiment, control plots receiving cutting and grazing management followed this pattern in 1995 but this was not the case in 1994, as mean % cover continued to increase until August, after the hay cut (Figure 5.12). Whilst this may have been an expression of the intrinsic growth variability of *S. officinalis*, it may have reflected differences in the implementation of cutting management in the two years. Although empirical evidence in this case is not available, cutting in 1994 may have stimulated regrowth of this species whereas the contrasting marked decrease between May and July in 1995 may have been due to the cutting action being closer to the ground in this second year. This would have disadvantaged *S. officinalis* by eliminating its taller growth, enabling the cover of shorter species, such as some grasses (e.g. *Festuca rubra*) to develop. Cutting, or ineffective removal of the cut material, may also have favoured an increase in litter at the expense of the cover of *S. officinalis*.

The initial expansion that characterized *S. officinalis* in the unfertilized managed and unmanaged plots was not sustained in the fertilized managed plots in 1994; in contrast a decrease in mean cover between April and May was observed (Figure 5.12). This may have been due either to a direct negative impact of fertilizer on *S. officinalis*, or indirectly as a consequence of the increase in mean grass cover at this time, which was itself a result of fertilization. Thereafter, lower mean cover of *S. officinalis* in the fertilized plots compared to the control plots characterized the two sampling seasons. This may have been due to the negative effects of fertilizer N on *S. officinalis* and/or as a result of the increased cover of other components in the fertilized plots, namely grass in 1994 and May 1995, and litter from July 1995.

5.3.3 Production

Figure 5.14 shows the total above-ground biomass production for control and fertilizer N treatments in the two sampling seasons of 1994 and 1995. In both treatments in both years biomass was greater in the early part of the season, prior to cutting in June, than in the later part of the season between the cut and the end of August. Mean biomass values for the fertilizer treatment in June, prior to cutting, in both years were significantly greater than the respective control samples, indicating that fertilizer application rapidly stimulated plant production in 1994 and similarly enhanced early-season production in 1995. Total plant production was not greatly stimulated by fertilization later in the season, after cutting, as biomass measured in August in both years was not significantly different between treatments. Production under the fertilizer

Figure 5.14 Effects of fertilizer N treatments on above-ground plant production at Besthorpe in 1994-5. Data are mean values (n=6) +1SE. For each date, values that differ significantly (*t*-test) are denoted by: **=*P*<0.01.



treatment may have been limited by the presence of litter later in the second season, however, as the fertilized experimental plots had accumulated a mean litter cover of 20% in August 1995 compared to just 6% in the control plots.

The various plant groups and individual species that contributed to total above-ground biomass showed different production responses to fertilization under managed conditions at Besthorpe. Grass formed the largest component of the biomass. It displayed a similar pattern of production to total plant biomass during 1994 and 1995, including significantly greater mean biomass values for the fertilizer treatment compared to the control prior to hay cutting in June of each year (Figure 5.15). In 1994, grass production was also significantly enhanced by fertilization after cutting management (Figure 5.15), which contrasts with the values for total biomass (Figure 5.14) where the positive effect of the fertilizer treatment on post-cutting grass production was countered largely by a greater mean biomass of *Sanguisorba officinalis* in the control samples at this time (see Figure 5.16). Grass biomass in August 1995 did not differ significantly between experiment treatments, indicating either that production was not stimulated by fertilization later in the second season or that it may have been limited by other factors, such as accumulated litter in the fertilized plots.

The generally positive response to fertilization shown by total grass production in the managed plots was shared by a number of individual grass species. These included *Agrostis capillaris* and *Holcus lanatus* which both made a major contribution to grass (and therefore total) biomass, and several other grasses that had less biomass, such as *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Lolium perenne* and *Poa trivialis*. One grass species that also made a notable contribution to biomass but displayed a different pattern in relation to fertilization and management was *Festuca rubra*. Production by this species was significantly enhanced by fertilization only in June 1995, whereas in August of that year the mean value of *F. rubra* biomass for the fertilizer treatment was significantly less than the control value. The negative effects of fertilization in this case may have been mediated through the deleterious incremental effects of repeated applications of fertilizer N on *F. rubra* or the competitive advantage conferred by fertilization on other species, e.g. *Agrostis capillaris*, which displayed significantly enhanced production in the fertilized samples compared to the controls ($P=0.03$) in August 1995. An interaction between the effects of fertilization and cutting at the end of June (e.g. the constraining effects of enhanced litter cover in the fertilized plots at this time) may also have occurred.

In addition to the grasses, the other key constituent of the biomass at Besthorpe was *Sanguisorba officinalis*. This species displayed no clear trend in production with

Figure 5.15 Effects of fertilizer N application on above-ground grass production at Besthorpe in 1994-5. Data are mean values (n=6) +1SE. For each date, values that differ significantly (*t*-test) are denoted by: *=*P*<0.05; **=*P*<0.01.

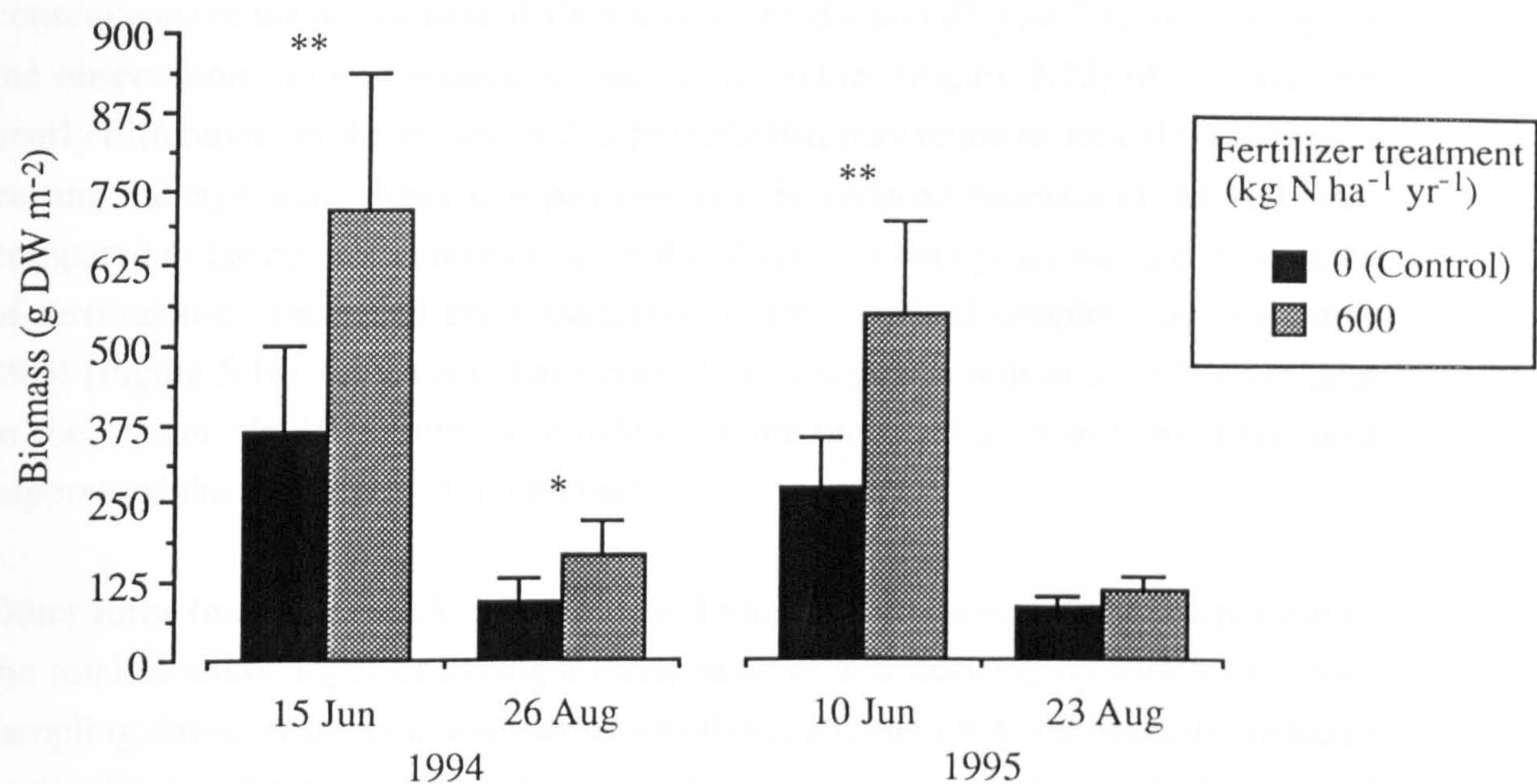
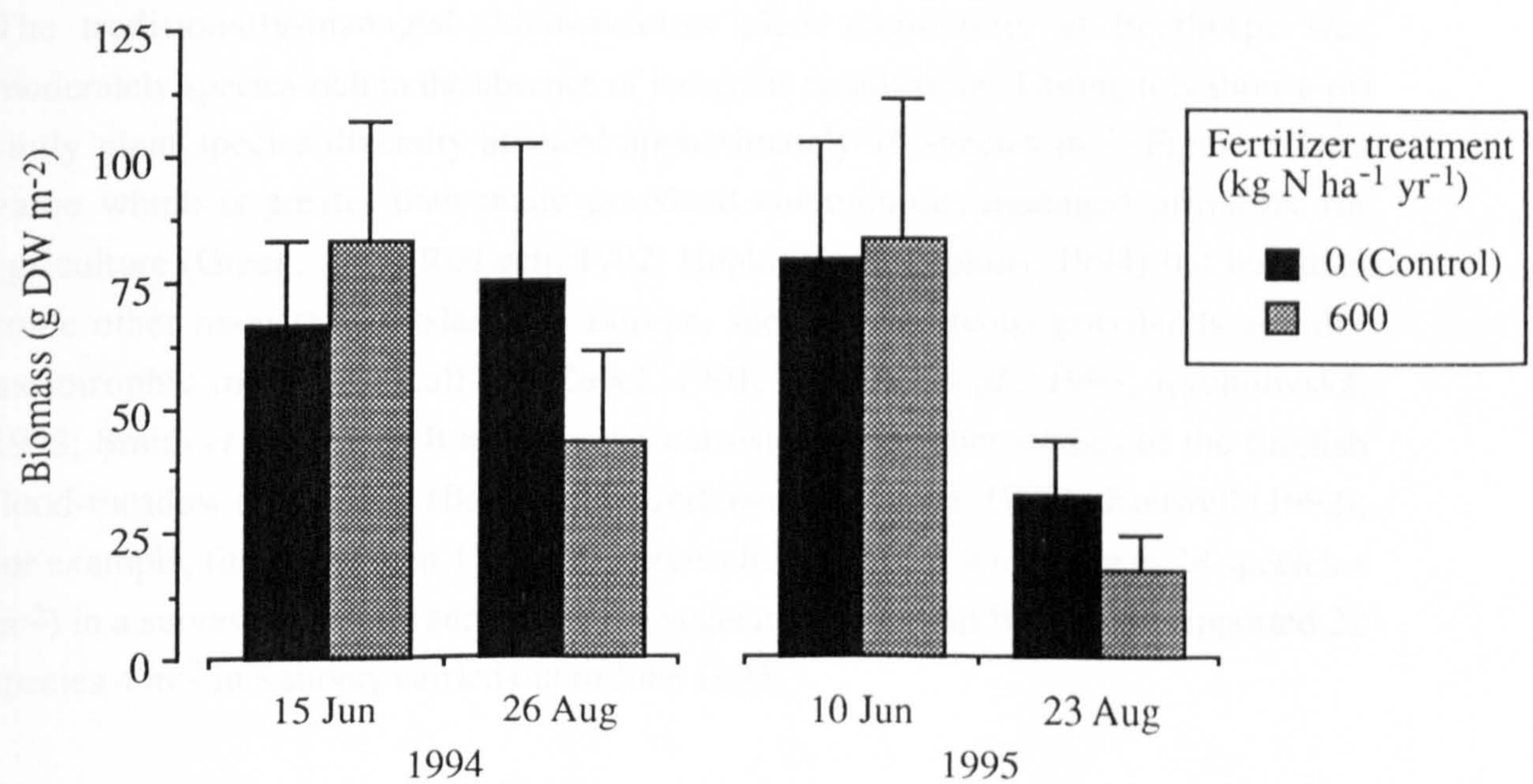


Figure 5.16 Effects of fertilizer N treatments on above-ground production of *Sanguisorba officinalis* at Besthorpe in 1994-5. Data are mean values (n=6) +1SE. For each date, values did not differ significantly (*P*<0.05, *t*-test).



variable biomass values both between treatments, where no significant differences were recorded, and between years (Figure 5.16). However, mean biomass values for *S. officinalis* for the control samples were significantly greater in August 1994 than for the same treatment in August the following year ($P=0.04$). This may have been a consequence of the dry climate of 1995 limiting production (Figure 2.3), but it supports the observation made in relation to mean cover values (Figure 5.12) of considerable yearly differences in the growth of *S. officinalis* that may relate to annual variations in cutting management. Also, it is possible that the reduced biomass of the fertilized compared to the control samples measured in August in both years was a consequence of fertilization. Enhanced grass production in the fertilized samples was evident in 1994 (Figure 5.16), which may have constrained the production of *S. officinalis* later in the season. In 1995, litter accumulated in the fertilized plots and this may have suppressed the production of *S. officinalis*.

Other forbs (not including *S. officinalis*) and moss both constituted a small portion of the total biomass, together having a mean value of less than 5% on each of the four sampling dates. Moss biomass was substantially, although not significantly, reduced by fertilizer application. Although forb production was generally less in the fertilizer N samples than the controls, suggesting a negative impact of fertilization, no significant differences between the treatments were found.

5.4 Discussion

The traditionally-managed flood-meadow plant community at Besthorpe was moderately species-rich in the absence of inorganic fertilization. During this short-term study plant species diversity attained approximately 16 species m^{-2} (Figure 5.1), a value which is greater than many grassland communities managed primarily for agriculture (Green, 1989; Rodwell, 1992; Hopkins and Hopkins, 1994) but less than some other managed grasslands in Europe, such as calcareous grasslands and dry mesotrophic meadows (Kull and Zobel, 1991; Willems *et al.*, 1993; Rychnovská, 1993; Smith *et al.*, 1996). It is, however, consistent with other studies of the English flood-meadow community (Baker, 1937; Jefferson and Grice, 1998). Rodwell (1992), for example, found between 17 and 38 species in samples of 4 m^{-2} (mean 28 species 4 m^{-2}) in a survey of 22 sites supporting the vegetation type, and Besthorpe supported 22 species 4 m^{-2} in a survey carried out in June 1993.

Above-ground plant biomass at Besthorpe during the two years of study averaged 5.5 t dry weight $ha^{-1} yr^{-1}$ without fertilizer addition. Table 5.1 indicates that this is

comparable with similar unfertilized grassland communities in Europe (e.g. Halva and Lesak, 1979; Oomes and Mooi, 1981) and with traditionally-managed wet meadows in England developed on peat (Kirkham and Wilkins, 1994). In addition, Traczyk (1971) reported very similar production values of 5.6 and 5.8 t dry weight ha⁻¹ yr⁻¹ for two wet meadows in Poland, and a flood-meadow in the Czech Republic dominated by *Alopecurus pratensis* produced an average above-ground biomass of 7.5 t dry weight ha⁻¹ yr⁻¹ (Jakrlová, 1975). Above-ground plant production at Besthorpe is therefore intermediate between unfertilized acidic and chalk grasslands, where available nutrients may be particularly limiting (Milton, 1940; Fryček *et al.*, 1992; Willems *et al.*, 1993), and intensively managed agricultural grasslands in England and Wales where artificial fertilization can achieve an average of 12, and up to 15 t dry weight ha⁻¹ yr⁻¹ (Morrison *et al.*, 1980).

This study successfully elucidated fine-scaled changes in community composition, including identification of relatively small differences in numbers of species, in relation to fertilizer N application and cutting and grazing management.

5.4.1. Impact of fertilizer N on community composition

Table 5.3 summarizes the response of the components of the Besthorpe flood-meadow community to fertilizer N application over the two years of the experiment.

Table 5.3 Summary of changes in plant community composition in response to application of fertilizer N to the traditionally-managed Besthorpe flood-meadow

++ = strong increase; 0 = no overall change; - = weak decrease; -- = strong decrease; N/A = not applicable

Community component	Species diversity	Cover	Above-ground production
Total plant	--	N/A	++
Moss	no data	--	--
Grass	-	0	++
Forb	--	-	-
<i>Sanguisorba officinalis</i>	N/A	-	0
Litter	N/A	++	no data

Plant species diversity (i.e. species richness and Simpson's index) declined with fertilization (Figures 5.2 and 5.5) and total above-ground production was enhanced by 60% (Figure 5.14), attaining 8.9 t dry weight ha⁻¹ yr⁻¹ averaged over the two study seasons. Much of this was due to increased grass biomass, which is a common response to fertilization in managed semi-natural grasslands (e.g. Williams, 1978; Oomes and Mooi, 1981; Traczyk *et al.*, 1984). The trend of increased above-ground biomass coincident with reduced plant species diversity observed in this study (Table 5.3) concurs with comparable experimental evidence (Table 5.1) and with predictions presented by Grime (1979) and Huston (1979) that maximum species diversity occurs at low-to-intermediate levels of production. At such levels, conditions are not too severe to exclude most species nor too fertile to allow competitive exclusion of most others by superior competitors. With reference to Besthorpe, therefore, fertilization may have intensified competition within the plant community for resources such as light and space, leading to competitive displacement, increased mortality rates and lower species diversity.

Fertilization induced rapid changes in floristic composition during this study and the structure of the managed Besthorpe plant community was transformed. Initially, grasses were favoured by fertilization at the expense of other community constituents, including its other major component, the forb *Sanguisorba officinalis* (Figure 5.6b). Later, some of the other forbs, moss and the cover of many grasses declined. This culminated at the end of two seasons of fertilizer application in a simplified community structure co-dominated by *Agrostis capillaris*, *S. officinalis* and accumulated plant litter. The species disadvantaged tended to be of small stature (e.g. moss and some forbs) whilst the limited number that were favoured (e.g. some grasses) were productive species able to exploit fertilization by rapidly assuming a larger growth form thereby monopolizing space and light (Grime, 1979). Although the change described by the Besthorpe flood-meadow community appeared to be directional, leading to reduced species diversity and structural homogeneity, an extension of the two years of study would have been necessary to confirm whether these trends would continue until a new equilibrium was attained.

As well as altering and intensifying competitive relations, fertilizer N can exert selective pressures on plant communities through its toxic effects, including the elimination of susceptible species (Maynard and Barker, 1969). In particular, ammonium sulphate can restrict photosynthetic activity and suppress the uptake of cations and nitrate at rates applied in this study (Haynes and Goh, 1978; Lewis, 1986), which results in small, weak plants or death of the entire plant (Maynard and Barker, 1969; Haynes and Goh,

1978). However, some species, such as *Holcus lanatus* which responded positively to ammonium sulphate application in this study, are more tolerant of ammonium addition than others (McGrath, 1983).

In this short term study, the species that responded most positively to fertilizer N application in terms of cover and biomass were the grasses *Alopecurus pratensis*, *Agrostis capillaris* and *Holcus lanatus*. Other studies of indigenous grasslands have also shown that these species, and particularly *H. lanatus*, are encouraged by artificial fertilization, e.g. Titlyanova *et al.* (1990) and Smith *et al.* (1996) for *A. pratensis*; Thurston (1969) and van Hecke *et al.* (1981) for *A. capillaris*; and Thurston (1969), Mountford *et al.* (1993) and Smith *et al.* (1996) for *H. lanatus*. At Besthorpe, these three grasses had a competitive advantage over many species as they are relatively tall and robust, and/or possess the capacity to respond vigorously to fertilization through vegetative expansion (Grime *et al.*, 1988; van Hecke *et al.*, 1981; Kirkham and Tallowin, 1995).

In contrast, the grass *Festuca rubra*, most forb species and moss responded negatively to fertilizer N application in the cut and grazed Besthorpe flood-meadow (Table 5.3). *F. rubra* may tolerate low nutrient levels but not high rates of fertilization (Traczyk *et al.*, 1976) and has generally been found to be negatively affected by fertilizer N in managed grasslands (Fryček *et al.*, 1992; Mountford *et al.*, 1993; Kirkham and Tallowin, 1995). Grassland forbs, also, are typically negatively impacted by fertilization, particularly those species that are of small stature and consequently unable to compete effectively with taller productive plants for light and other resources (Rabotnov, 1977; Traczyk *et al.*, 1984; Mountford *et al.*, 1993). It is widely appreciated that mosses are generally very sensitive to nitrogen availability and can find increased nitrogen supply toxic (Rabotnov, 1977; Bell, 1994). In grasslands such as Besthorpe, they may also be unable to tolerate increased shading from the dense biomass of productive species that develops following inorganic fertilization (Mountford *et al.*, 1994) and litter accumulation can limit their occurrence (Bakker, 1989).

Plant litter accumulated on the soil surface under managed fertilized conditions in this study (Figure 5.7), reducing plant cover and possibly also production and species diversity. Other studies on a range of different grassland types have also found that fertilization leads to litter accumulation, probably due to enhanced plant production, and that a dense litter layer generally inhibits above-ground biomass and species diversity, thereby inducing floristic change (Knapp and Seastadt, 1986; Bakker, 1989; Facelli and Pickett, 1991; Xiong and Nilsson, 1997).

In this study the cover of *Sanguisorba officinalis*, a characteristic member of the English flood-meadow community that was co-dominant at Besthorpe, was somewhat suppressed with fertilizer N application (Figure 5.12). This may have been due to the toxic effects of fertilizer N or the constraints imposed by competition from grasses and litter accumulation, but the nature of these relationships is difficult to determine, particularly as little published information is available on the effects of artificial fertilization on *S. officinalis*. Baker (1937) and Fisher *et al.* (1996) observed that it competed effectively with grasses for light and other resources, possibly because (as this study has shown) it tends to attain maximum ground cover in mid-summer when conditions are favourable for high rates of photosynthesis, but it has been stated that high rates of inorganic fertilizer may suppress this species (Royal Society for the Protection of Birds, English Nature and Institute of Terrestrial Ecology, 1997).

Although overall fertilizer N application reduced total plant species richness (particularly forbs) in this study, there was some recovery in the five months between the two sampling seasons (Figure 5.2). This may have been due to the vegetative regeneration of the above-ground parts, or the establishment of new plants in the gaps created by the death of plants (Grubb, 1977) that had been eliminated through the toxic or competitive effects of fertilizer N. Halva and Lesak (1979) reported that grassland plant species suppressed by fertilization can persist for years either as seeds or underground organs and then re-establish themselves in the above-ground vegetation when conditions permit.

5.4.2 Effects of cutting and grazing management on community composition

It is widely recognized that regular cutting or grazing management maintains plant species diversity in semi-natural grasslands (Oomes and Mooi, 1981; Bakker, 1989; Smith and Rushton, 1994). Cutting and grazing can constrain species of high competitive ability in mixed-species vegetation, preventing them from attaining maximum size and vigour and allowing a variety of species of lower competitive ability to co-exist (Grime, 1973b). At Besthorpe, the effects of cutting and grazing management were elucidated and it was found that species diversity (species richness and Simpson's index) was characterized by a peak in spring followed by decline and then a recovery after cutting for hay. Whilst several vernal species tended to be conspicuous only in spring, other species (e.g. *Ranunculus bulbosus*, *Cardamine pratensis*, *Trisetum flavescens*) re-appeared later in the season, apparently benefiting from vegetation management. Cutting in mid-summer, for example, limited potential

community dominance by relatively productive species such as some grasses by removing their dense biomass, probably increasing the incidence of light at ground level and allowing subsidiary species to co-exist. Grazing can also create and maintain small-scale structural heterogeneity and species diversity by limiting more competitive plants, often grasses that achieve a high biomass later in the summer, through defoliation and other disturbance, e.g. trampling (Harper, 1971; Grime, 1979; Smith and Rushton, 1994; Crofts and Jefferson, 1994). Oomes and Mooi (1981) demonstrated the importance of a combined hay cutting and autumn grazing regime such as the one practised at Besthorpe for producing an open meadow sward in autumn and spring that contributed to plant species diversity. The same traditional management prescription also provided niches for many subsidiary species alongside the normal sward dominants in a floristically-rich English hay meadow (Smith *et al.*, 1996). Furthermore, substantial botanical change occurred in a diverse wetland hay meadow as a result of the cessation of autumn grazing, despite the continuation of hay cutting (Kirkham *et al.*, 1996). Published information therefore concurs with results from this study, suggesting that the continuation of a low-intensity management regime of cutting with grazing is necessary for sustaining the floristic diversity of the Besthorpe grassland.

Temporal and spatial community dynamics at Besthorpe were greatly influenced by the morphology and phenology of *Sanguisorba officinalis*, and its response to management. *S. officinalis* is a characteristic component of English and continental European flood-meadow vegetation (Baker, 1937; Ulehlová, 1973; Rodwell, 1992; Rychnovská, 1993), occurring in abundance at Besthorpe. It is a perennial forb that over-winters as an underground rhizome and develops rapidly in spring into a tall, robust forb with dense foliage before dying back later in the year. Its ability to maintain a considerable presence in the Besthorpe vegetation after annual hay cutting may have been associated with a capacity to tolerate low intensities of disturbance by utilizing resources from its underground carbohydrate reserves. Although *S. officinalis* was favoured by spring grazing in a mesotrophic dry meadow (Smith and Rushton, 1994), Baker (1937) suggests that frequent or prolonged grazing results in its elimination. Thus, the traditional management pattern of hay cutting with a period of grazing in autumn appears an important factor for the continued prominence of *S. officinalis* in the Besthorpe plant community.

Evidence from this study at Besthorpe suggests that minor variations in management can generate changes in plant community composition. For example, between-year variations in the implementation of cutting for hay and subsequent crop removal may have led to differences in the performance of *S. officinalis*, moss and grasses as a

group, and in the creation of plant litter, and therefore influenced botanical diversity. In particular, *S. officinalis* may have been disadvantaged by cutting close to ground level in 1995. Whilst there is no information in the literature on the sensitivity of *S. officinalis* to cutting height, particularly intense defoliation is known to generally reduce plant growth (Korte and Harris, 1987) and a low hay cut at Besthorpe would have removed a greater proportion of the photosynthetic tissue of this tall species, thereby reducing light interception, compared to lower-growing competing grasses. Several studies of species-rich hay meadows have shown that variations in cutting practice (particularly timing) can affect botanical composition, including plant diversity (Bakker, 1989; Smith and Jones, 1991; Kirkham and Tallowin, 1995; Smith *et al.*, 1996). Variations in grazing management may also have a major influence on the plant species composition and diversity of grassland (Puerto *et al.*, 1990; Smith and Rushton, 1994). Although there was no strong evidence from this study that an abiotic factor (such as soil, water table or climate) acting on its own was a major cause of differences between the yearly development of plant species (e.g. cover and production of *S. officinalis*) or community dynamics, it is possible that interactions between management and such factors may have influenced the managed plant community (Smith and Jones, 1991; Fisher *et al.*, 1996). Furthermore, a period of flooding that lasted approximately 10 days in January-February 1995 may have contributed to between-year variation in community composition, particularly as some grassland plants are more sensitive to inundation than others (Newbold and Mountford, 1997).

5.4.3 Interactions between application of fertilizer N and cutting and grazing management

In this study, the key effect of an interaction between fertilizer N application and management on the Besthorpe flood-meadow plant community was to reduce the cover and production of grasses in the second year, most dramatically for *Festuca rubra* but also for other grass species (Figures 5.9 and 5.15). This interaction effect may have been mediated through two routes. Firstly, it may have been as a direct consequence of cutting (and grazing) management damaging plants already weakened by heightened competition or toxicity due to inorganic fertilization. In particular, *F. rubra* is a perennial grass of small stature and relatively slow growth so may not have been able to respond sufficiently rapidly to cutting and grazing disturbance in order to maximize the capture of resources following fertilization (Grime, 1979; Grime *et al.*, 1988). This is in contrast with grasses such as *Alopecurus pratensis*, *Holcus lanatus* and *Agrostis capillaris* which are favoured by a combination of fertilization and defoliation in grasslands by responding vigorously to fertilization and being able to recover from

cutting or grazing (van Hecke *et al.*, 1981; Mountford *et al.*, 1993; Smith *et al.*, 1996). Support for these observations can be derived from a study by Frame (1991) who found that the production of some meadow grasses, including *F. rubra* and *H. lanatus*, was greater than an agricultural variety of *Lolium perenne* at low rates of fertilizer N (up to 120 kg N ha⁻¹ yr⁻¹) and a frequent disturbance intensity of six cuts per annum, but was lower at higher rates of N application under the same cutting regime. In contrast, applications of fertilizer N to a flood-meadow co-dominated by *F. rubra* and *Agrostis* spp. and subjected to frequent defoliation by intensive grazing produced only minor changes in community composition after six years, although *Agrostis* spp. declined and *Poa trivialis* increased (Elliot *et al.*, 1974). Furthermore, *F. rubra* continued to dominate a chalk grassland following fertilizer N application in both cut and uncut plots (Smith *et al.*, 1971).

Secondly, impaired grass performance could have been brought about indirectly through the deposition of copious amounts of litter as a result of cutting fertilized vegetation, as in this study the combination of cutting and fertilizer application generated substantially more litter than management or fertilization alone. Some support for this may be drawn from a study by Tesařová (1976), who observed that plant litter production was positively correlated with above-ground biomass in regularly cut flood-meadow communities. In common with Besthorpe, Bakker (1989) found that fertilization of a meadow cut for hay resulted in litter accumulation and that this decreased the cover of some grass species, including *F. rubra*, and reduced plant species diversity significantly. Large deposits of floodborne litter suppressed plant species diversity and production of floodplain grasslands in England (chapter 4).

Clearly in this study, the composition of the Besthorpe flood-meadow community was altered by the application of fertilizer N irrespective of cutting and grazing, and fertilization effects were to some extent exacerbated by the traditional farming management. This suggests that a key challenge facing the future conservation of the flood-meadow resource will be reconciling land management for the encouragement of plant biodiversity with the current widespread agricultural use of inorganic fertilizers.

5.5 Conclusion: integrating biodiversity conservation with agricultural practice

This short-term study effectively discriminated fine-scaled impacts of the application of fertilizer N to a traditionally-managed English flood-meadow. Fertilization rapidly and fundamentally altered plant community composition. In particular:

- fertilizer N reduced plant species diversity, notably forb species richness,
- most grasses were favoured by fertilizer N, and plant litter increased, but the grass *Festuca rubra*, moss and forbs were discouraged, and
- increased plant production under fertilizer N, due to stimulation of grasses, was not sustained, being limited by accumulated litter.

In addition, the forb *Sanguisorba officinalis*, which is typically an abundant component of the English flood-meadow community (Rodwell, 1992), exhibited an important influence on community dynamics in this study, particularly in relation to hay cutting management.

The characteristic English flood-meadow plant community has been generated by the development of a low-intensity farming system over hundreds or even thousands of years. The community is both distinctive and rare, representing an important element of European biodiversity, and maintenance of its nature conservation importance is closely related to management intensity (Jefferson, 1997). The application of inorganic fertilization to grasslands is a key indicator of agricultural management intensification (Beaufoy *et al.*, 1994) and this study has demonstrated that the conservation value of the flood-meadow community is negatively impacted by the application of inorganic fertilizer, resulting in an almost immediate reduction in species diversity. This is consistent with other, longer-term studies of hay-meadow communities characterized by traditional low-intensity management regimes. For example, Mountford *et al.* (1993) found that even modest applications of inorganic fertilizer reduced species diversity and elicited botanical change in a wetland meadow on peat soils within three years, and any deviations from the traditional management combination of cutting and grazing without inorganic fertilization resulted in loss of conservation value in mesotrophic upland hay meadows after four years (Smith *et al.*, 1996).

Most contemporary agricultural grassland management aims at maximizing production through fertilization at the expense of plant diversity (Hopkins and Hopkins, 1994), therefore making the reconciliation of modern agricultural objectives and biodiversity conservation difficult. Whilst there is insufficient information from this short-term

study to suggest that particular flood-meadow plant species will be eliminated by fertilizer application, nor when this might occur, the study has demonstrated that many characteristic flood-meadow species are deleteriously impacted from the onset of fertilizer N application. The conservation of the English flood-meadow community clearly depends upon a low intensity of agricultural management, particularly inorganic fertilizer use. It is therefore vital to ensure that initiatives to promote agricultural management systems that are sympathetic to the conservation requirements of flood-meadows include the continuation of the traditional low-intensity land-use practices on which they depend and incorporate severe restrictions on the use of inorganic fertilizers.

The following chapter examines whether a particularly species-rich flood-meadow community is sensitive to nitrogen fertilization or whether high plant diversity confers a degree of resistance to such systems in relation to land-use intensification and environmental change.

Chapter 6 The impact of increased nitrogen supply on a species-rich flood-meadow plant community

6.1 Introduction

With the rapid global decline in biodiversity and intense concern over the effects of environmental change attention is being directed towards the conservation and sustainable management of areas of high biodiversity, not least because it raises the issue of whether the functioning and sustainability of ecosystems will be impaired by the loss of species. The relationships between biodiversity and ecosystem functioning remain unclear, however, and until recently few experiments had been conducted to elucidate and test these relations (Schulze and Mooney, 1993). Researchers have proposed that higher diversity leads to enhanced functioning and increased ecological stability and, in contrast, that community dynamics are increasingly less stable as the number of competing species increases (Walker, 1989; Naeem *et al.*, 1994; Tilman, 1996; Tilman *et al.*, 1996). Nilsson and Grelsson (1995) suggest that the sensitivity and stability of an ecosystem relate to the degree of change in species abundance and composition following perturbation. High rates of change characterize fragile or sensitive ecosystems, and *vice versa*. The identification of species and communities likely to be eliminated or negatively impacted by human activities forms an essential part of conservation management.

At the small scale (under 10 m²), temperate grasslands are among the most species-rich plant communities in the world (Rychnovská, 1993; Willems *et al.*, 1993). For example, Kull and Zobel (1991) found 63 plant species m⁻² in an Estonian meadow that was cut regularly for hay and areas of 2.5 m² in managed Mediterranean grasslands can support more than 50 species (Puerto *et al.*, 1990). A characteristic of semi-natural grasslands supporting high plant diversity is regular appropriate vegetation management, such as cutting for a hay crop. It has been demonstrated that cutting, for example, reduces the vigour of tall competitive species, allowing smaller species to co-exist (Bakker, 1989). In the past, such management was part of a low-intensity agricultural system characterized by low fertilizer input, minimal land drainage, cutting for hay and low grazing livestock densities (Beaufoy *et al.*, 1994) which created and sustained beneficial conditions for a considerable biodiversity resource (Bignal and McCracken, 1996). However, in recent decades a widespread decrease in grassland biodiversity has taken place, due largely to land-use change, particularly intensified agricultural exploitation through increased fertilizer utilization (van Dijk, 1991).

Most diverse grassland communities are associated with low soil nutrient availability (Rychnovská *et al.*, 1994) and in many mixed-species grasslands nutrient enrichment, particularly with nitrogen, alters community composition by favouring taller productive species capable of rapid growth, especially some grasses, with a coincident reduction in plant species diversity (Rabotnov, 1977; Traczyk *et al.*, 1984; Tilman, 1987; Mountford *et al.*, 1993; Willems *et al.*, 1993). Nitrogen is a major ecological factor determining the distribution and abundance of plant species. Indeed, because of variations in the response of species to nitrogen and the competitive conditions existing within multi-species grassland communities, variations in nitrogen supply may lead to large differences in botanical composition (Bradshaw *et al.*, 1964). The direct application of inorganic fertilizers for agriculture has been the major source of nitrogen causing plant diversity losses and botanical change in semi-natural grasslands (Hopkins, 1986; van Dijk, 1991), although they are also threatened by eutrophication of ground and surface waters and from increased deposition of nitrogenous atmospheric pollutants (Burgess *et al.*, 1990; Bobbink, 1991; Bell, 1994).

Floodplain grasslands are ecotonal, representing a dynamic interface between terrestrial and aquatic environments (Naiman and Décamps, 1990). They possess properties of both systems and are biodiverse (Risser, 1990; Naiman *et al.*, 1993). However, they are also anthropogenic ecosystems that need regular perturbation of a specific kind (e.g. cutting management) to remain stable; such ecosystems tend to be fragile (Nilsson and Grelsson, 1995). Thus, of all grassland types, flood-meadows (which are floodplain grasslands cut usually for hay) may be particularly intrinsically sensitive to environmental change such as increased nitrogen input.

It can therefore be hypothesized that a managed flood-meadow possessing a diverse plant community will be unusually responsive to environmental change. Alternatively, species-rich grasslands may be resistant to change, partly because interspecific competition may allow more diverse communities to utilize limiting resources more fully so that any decreases in species susceptible to change are compensated for by other species (Schulze and Mooney, 1993; Tilman *et al.*, 1996). For example, Tilman (1996) found that biodiversity stabilized grassland community processes in relation to drought perturbation. This chapter aims to determine the sensitivity of a biodiverse managed flood-meadow to environmental change by quantifying the impact of increasing nitrogen supply on the plant community. It investigates the stability of community structure, particularly in the context of its persistence in relation to selective nitrogen addition, and examines the temporal and spatial degree of community change.

Specifically, the study examines the short-term and small-scale:

- impact of nitrogen (N) addition,
- role of cutting management, and
- interactions between N addition and cutting management

in relation to three critical determinants of plant community structure and dynamics, namely species diversity, cover and primary production. The study was carried out on the Lužnice floodplain in the Czech Republic.

6.2 Methods

6.2.1 Study area

The study site was situated in the floodplain of the Lužnice river between the villages of Dvory nad Lužnici and Hlamky approximately 20 km SSE of the town of Třeboň in the Czech Republic (Figure 2.9). The reach within which the study site is located is relatively natural, being characterized by a lack of conventional river engineering and exhibiting many meanders, oxbows and pool and riffle sequences. Flood events occur annually, particularly in spring when snow melt occurs in the headwaters (Smilauer *et al.*, 1996). The floodplain is of considerable biodiversity value, supporting a mosaic of wetland, grassland and forest habitats, and is included within the Třeboň Basin Biosphere Reserve (Janda, 1994). The river and its floodplain are described in detail in section 2.1.4.

Grasslands were first created in the Lužnice floodplain in the 12th century (Janda, 1994) and by the 19th century they dominated the floodplain landscape (Guth, 1996). The grasslands have generally been used for hay-making with some grazing (K. Prach, pers. comm., 1994). It is probable that the study site was managed as a hay meadow from at least the 1780's until 1992 (J. Guth, pers. comm., 1994), with no under-drainage and no record of fertilizer having been used before the establishment of the experiment. Typically, the study site was cut at least once and usually twice annually for hay (Figure 2.13). The first cut took place in June or July, the second normally in late August or September, depending on weather and flooding conditions (K. Prach, pers. comm., 1994). The site was recognized as a particularly botanically diverse patch within the Lužnice floodplain by Prach *et al.* (1990) and Prach (1992) who ascribed this to its long history of regular cutting management and a lower soil moisture status than the surrounding floodplain, the latter due to its slightly elevated topography and permeable alluvial soils. Soil moisture during the study (1994-5) averaged 30% in May-August and soil pH in the surface 15 cm was 6.6. Plant-available nitrogen

averaged 18 mg l⁻¹ soil solution. This is relatively high compared to other floristically diverse grasslands but explained by the Lužnice fluvisols being characterized by nitrogen inputs from both flooding and lateral groundwater movement from the arable terraces (Rauch *et al.*, 1996). The water table fluctuates greatly, with a brief period of flooding usual in spring, falling to around 150 cm below the soil surface in June-August. Prach (1992) recorded a two-year mean of -68 cm.

The plant community of the study site is presented in Table 2.4. It consists of grasses, some sedges and mostly perennial forbs that attain a height of 40-80 cm prior to cutting in mid-summer. *Sanguisorba officinalis* is a prominent member of the varied and plentiful dicotyledonous component of the vegetation, dominating in mid-season. The community lies within the *Molinio-Arrhenatheretea* alliance of continental phytosociology and shows floristic affinities to the English flood-meadow community described by Rodwell (1992), sharing many of its constant species, most notably an abundance of *S. officinalis*.

6.2.2 Field study

The field study was conducted between May and August in 1994 and 1995. Prior to the beginning of the study, the site had been unmanaged (i.e. not cut) for one year in 1993. Evidence from the literature suggested that such a short period of neglect was unlikely to have had a major effect on plant community composition (Bakker, 1989; Rychnovská *et al.*, 1994). This was subsequently supported by results from this study. Table 6.1 gives details of site management during the experiment and the sampling programme. No flooding of the study site occurred during the two sampling periods.

6.2.2.1 Experiment design

Experiment plots were sited within a visually homogeneous area of floodplain grassland approximately 25 m x 50 m (0.125 ha) in extent. In May 1994, 18 plots measuring 1 m x 1.5 m were laid out within this area, set up at least 3 m apart to ensure their independence from treatment interaction. Each plot was randomly assigned one of three nitrogen treatments (including control), allowing six replicates of each treatment. The treatments consisted of N addition equivalent to a total of 0 (i.e. control), 300 (N₃₀₀) and 600 (N₆₀₀) kg N ha⁻¹ yr⁻¹. The N₆₀₀ treatment represents the rate of N

Table 6.1 Fieldwork programme for the Lužnice study

Year	Application of fertilizer N	Cutting	Botanical sampling		Soil sampling		
			Species presence and cover	Biomass	pH	Moisture	Nitrogen
1994	15 May 11 July	6 July	10-13 May	—	10 May	14 May	14 May
			2-4 July	5 July	—	5 July	5 July
			8-10 August	11 August	—	12 August	12 August
1995	22 May 15 July	13 July	17-20 May	—	17 May	21 May	21 May
			7-11 July	12 July	—	12 July	12 July
			27-30 August	31 August	27 August	31 August	31 August

addition recommended for maximal production response by agricultural grasses (Jackson and Williams, 1979; Robson *et al.*, 1989), whilst rates in the order of 300 kg N ha⁻¹ yr⁻¹ (i.e. the N₃₀₀ treatment) are commonly applied as fertilizer to managed grasslands in the Czech Republic and Europe generally (van der Meer, 1982; Hopkins and Hopkins, 1994; International Union for the Conservation of Nature and Natural Resources, 1995). Nitrogen was supplied as granular ammonium sulphate fertilizer (21% N) of a type widely used in European agriculture (Wild, 1988). This was applied by hand in two equal instalments each year, one in May early in the growing season and one soon after hay cutting and removal in July (Table 6.1). These timings are comparable with agricultural grassland management regimes in the Czech Republic and elsewhere in Europe (Morrison, 1987). With each instalment, fertilizer N was also applied to a 25 cm wide strip surrounding each plot at a rate appropriate to the treatment within that plot in order to reduce edge effects. Water (5 litres m⁻²) was applied to all plots at each instalment to dissolve the ammonium sulphate as required. River water was used due to the remote location of the site but the N content of the water was less than 2 mg l⁻¹, representing a negligible total input to each plot equivalent to approximately 0.2 kg N ha⁻¹ yr⁻¹.

Vegetation management of the study site during the experiment mimicked the normal traditional cutting and hay harvesting regime of the area. Experiment plots were cut once annually, in July, using hand-held shears and the cut material was removed (Table 6.1). Each experiment plot was surrounded by an area 0.5 m-wide which was also cut and harvested at the same time in order to reduce edge effects.

Traditionally, the Lužnice grasslands have been cut twice annually, except when adverse weather conditions would restrict this (K. Prach, pers. comm., 1994). Such circumstances occurred during this study in 1994, when a hot and particularly dry July (Figures 2.10 and 2.11) did not favour a second later cut for hay. Sampling in 1995 ended before the second annual cut would typically have taken place.

6.2.2.2 Botanical sampling

Botanical sampling enabled fine-scaled community changes to be discriminated. Sampling comprised measurements of species richness, cover and above-ground production taken at regular intervals throughout the two seasons (Table 6.1). On each sampling occasion, the same 1 m² in each plot (a in Figure 2.14) was used to record all vascular plant species present together with their % ground cover, estimated visually. At the same time, the cover occupied by moss (species not determined), plant litter and

bare ground was also recorded. Production was determined by harvesting above-ground vegetation twice in each season (Table 6.1). Biomass was not assessed prior to the addition of N, as measures of species richness and cover taken during the first sampling occasion (before treatment application) affirmed the botanical homogeneity of the study area. Thus, the first biomass sample was collected approximately seven weeks after the first application of fertilizer N of the year, immediately before the annual cut in July. The second, aimed to assess the regrowth, was collected towards the end of the growing season in August, approximately 5-6 weeks after the second annual application of N. Vegetation was clipped from a 0.04 m² quadrat which was located randomly within the 0.25 m x 1 m section of each plot not used for monitoring other botanical or soil variables (b in Figure 2.14). On each occasion, different sections of the plots were harvested. Each biomass sample was sorted to species level and dried to constant weight at 105°C.

6.2.2.3 Soil sampling

Soil nitrogen was monitored by sampling regularly from the same subset of plots on each occasion (Table 6.1). One sample per plot was taken, yielding three replicates per treatment. Soil was collected to a depth of 15 cm using a corer of 25 mm diameter from within the 0.25 m x 1 m section of the plot not used for any botanical sampling (c in Figure 2.14). Each sample was air-dried and analysed for both available nitrate and ammonium by the Palintest colorimetric procedure (Palintest Ltd., Kingsway, Gateshead, England, NE11 0NS. E-mail: palintest@palintest.com).

Soil moisture can be a factor limiting the performance of plants capable of responding to enhanced N supply (Rabotnov, 1977). In this study soil moisture was monitored by sampling regularly from the same subset of plots on each occasion (Table 6.1), taking one sample per plot to give three replicates per treatment. Soil was collected to a depth of 15 cm using a 25 mm diameter core from within the 0.25 m x 1 m section of the plot not used for any botanical sampling (c in Figure 2.14). Each wet sample was weighed, oven-dried to constant weight at 105°C and reweighed to determine the amount of moisture removed (Gardner, 1965).

Soil pH was examined on three occasions during the study because it is known that the application of ammonium sulphate can lead to acidification of the soil environment (Haynes and Goh, 1978; Johnston *et al.*, 1986). Prior to the start of the experiment in May 1994, ten soil samples from a depth of 0-15 cm were taken at random from the study area but outside the newly established experiment plots, using a trowel. This was

repeated twice in 1995 (Table 6.1), on these occasions sampling from within the 0.25 m x 1 m area of each plot not used for botanical survey (c in Figure 2.14). All samples were analysed for pH (in deionized water) using the electrometric method described by McLean (1982).

6.2.3 Data analysis

Plant species diversity was quantified using species richness (the number of species in the sample) and Simpson's index (Simpson, 1949; section 2.2.2.1). Data analytical methods are described in detail in section 2.2.2.

Generally, statistical comparisons were carried out for each sampling occasion because measurements made on any one sampling occasion were correlated with subsequent measurements from the same plot. Multiple comparisons used ANOVA and, if a significant difference in the treatment means was detected, was followed by Tukey's test to identify where these differences lay (Zar, 1984). Specific comparisons between two mean values used *t*-tests. Paired *t*-tests were used to examine specific temporal changes within the same treatment. All results were termed significant only if $P < 0.05$.

6.3 Results

6.3.1 Plant species diversity

6.3.1.1 Species richness

Figure 6.1 illustrates total plant species richness over the experiment period of two seasons, in relation to additions of N and cutting management. It indicates that the plant community tolerated annual cutting, since management did not significantly affect mean species richness in the control plots. It also suggests that cutting did not eliminate or prevent the identification of species. However, the application of fertilizer N had a significant effect in both treatments, i.e. 300 and 600 kg N ha⁻¹ yr⁻¹ (N₃₀₀ and N₆₀₀ treatments respectively). Both application rates resulted in significant reductions in mean species richness compared to the control. This was observed in the case of N₆₀₀ at the first sampling occasion after a period of approximately 7 weeks (i.e. 11 May - 3 July) and after 13 weeks for N₃₀₀ (11 May - 9 August) (Figure 6.1). At the end of the experiment in August 1995, mean species richness in the N₃₀₀ and N₆₀₀ plots was 61.8% and 42.7% of the value of the control plots, respectively. The decline in species

Figure 6.1 Effects of fertilizer N treatments on plant species richness at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter (a, b or c) in common. The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

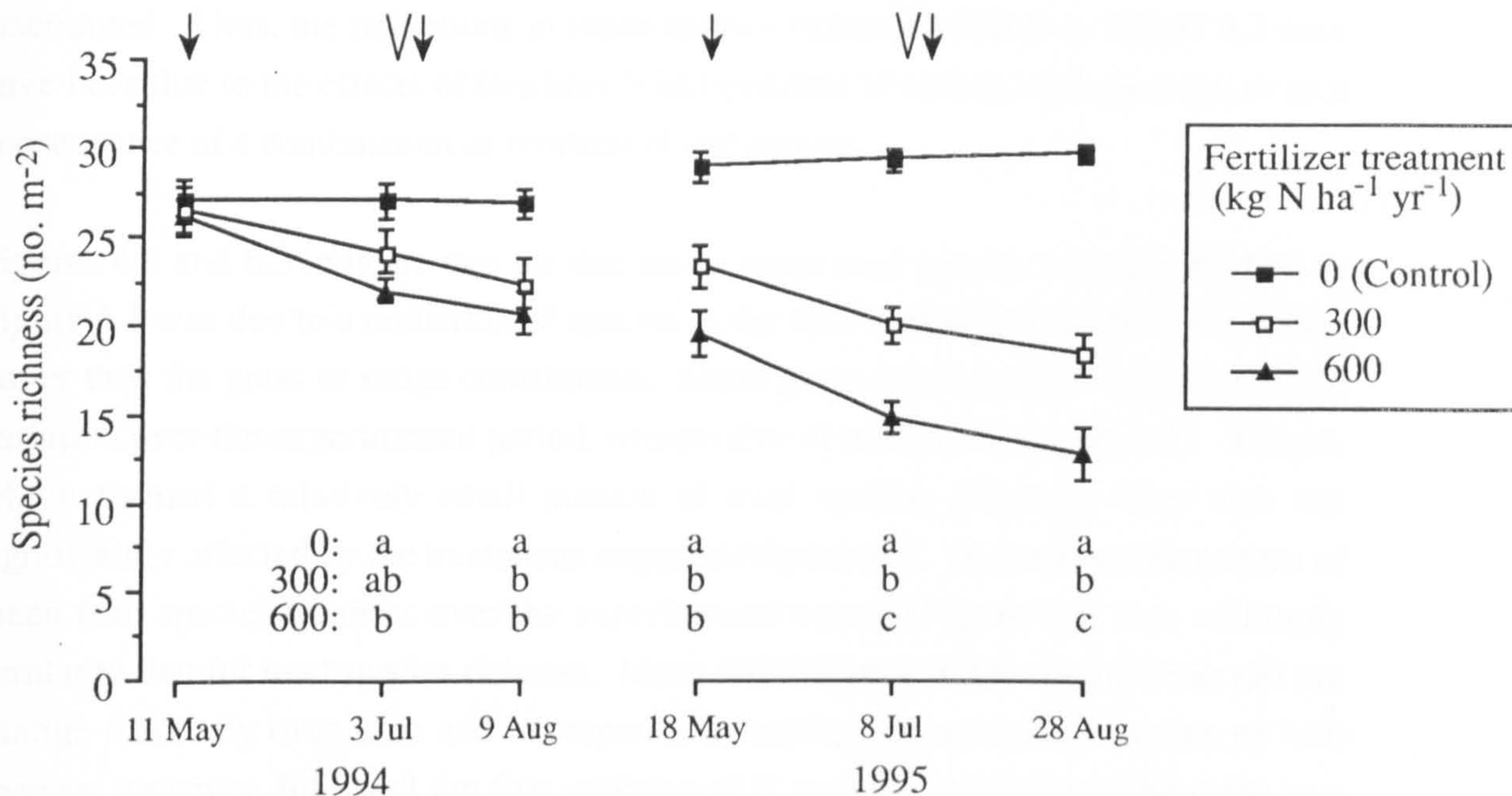
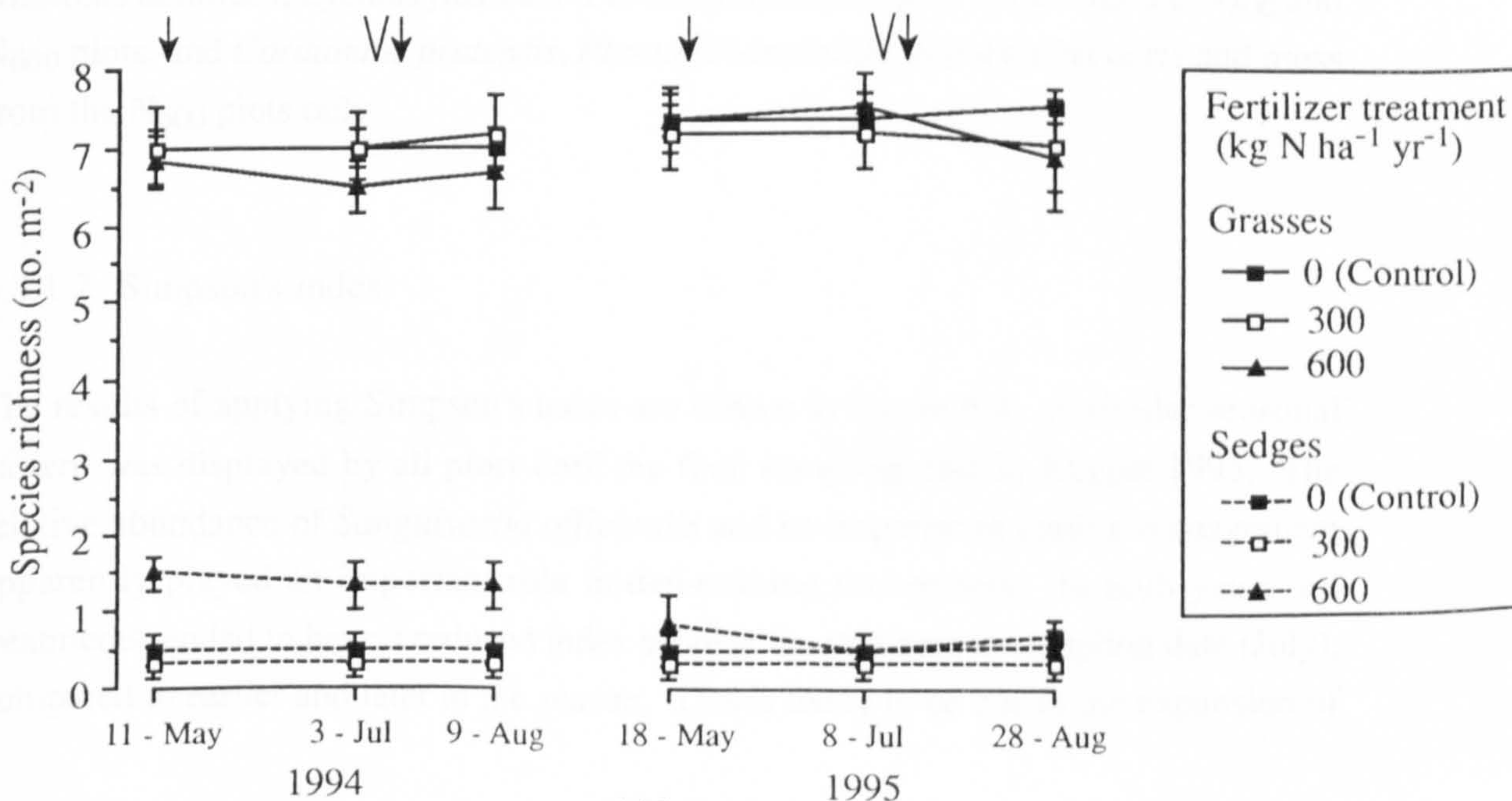


Figure 6.2 Effects of fertilizer N treatments on grass and sedge species richness at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.



richness in the N treated plots was sustained over the experimental period, although there was a slight, but not significant ($P=0.25$), increase in mean richness between the August 1994 and May 1995 sampling dates in the N300 plots, a period when no application of fertilizer N took place. Although cutting by itself appears not to have had a deleterious effect on species richness, and addition of N negatively affected richness, the possibility that cutting and fertilizer N interacted to influence richness cannot be discounted. Thus, the reductions in mean species richness evident in Figure 6.1 may have been due to the effects of fertilizer N independent of cutting management, or as a consequence of a combination of fertilizer N and cutting.

Figures 6.2 and 6.3 indicate that the decline in mean total species richness evident in Figure 6.1 was due to a reduction of species in the forb component of the community, rather than the grass or sedge constituents. Mean grass species richness showed little variation over the experimental period, irrespective of treatment (Figure 6.2). Sedges, which formed a relatively small portion of total species richness, were also not significantly affected by the treatments imposed (Figure 6.2). In contrast, the pattern of mean forb species richness over the experimental period (Figure 6.3) was strikingly similar to that for total species richness. Mean forb richness in the control plots did not change markedly over time and in response to cutting management. Losses of forb species, however, followed the first addition of N and continued throughout the two seasons of the experiment, with a greater reduction in mean forb richness in the N600 plots than the N300. Also, there was a partial but significant ($P=0.007$) recovery in mean forb species richness between the last sample of 1994 (August) and the first of 1995 (May) in the N300 plots, which was not evident in the N600 plots.

Species lost from the fertilized plots during the experiment included *Campanula patula*, *Dianthus deltoides*, *Lychnis flos-cuculi* and *Trifolium pratense* from both the N300 and N600 plots, and *Cardamine pratensis*, *Plantago lanceolata*, *Ranunculus acris* and moss from the N600 plots only.

6.3.1.2 Simpson's index

The results of applying Simpson's index are shown in Figure 6.4. A similar seasonal pattern was displayed by all plots until the final sampling date in August 1995. The relative abundance of *Sanguisorba officinalis* and its response to cutting management apparently played an important role in determining this pattern. In both years, all treatments tended to have a reduced index score at the mid-season sampling date (July), compared to earlier and later in the season. This is likely to be due to the expansion of

Figure 6.3 Effects of fertilizer N treatments on forb species richness at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter (a, b or c) in common. The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

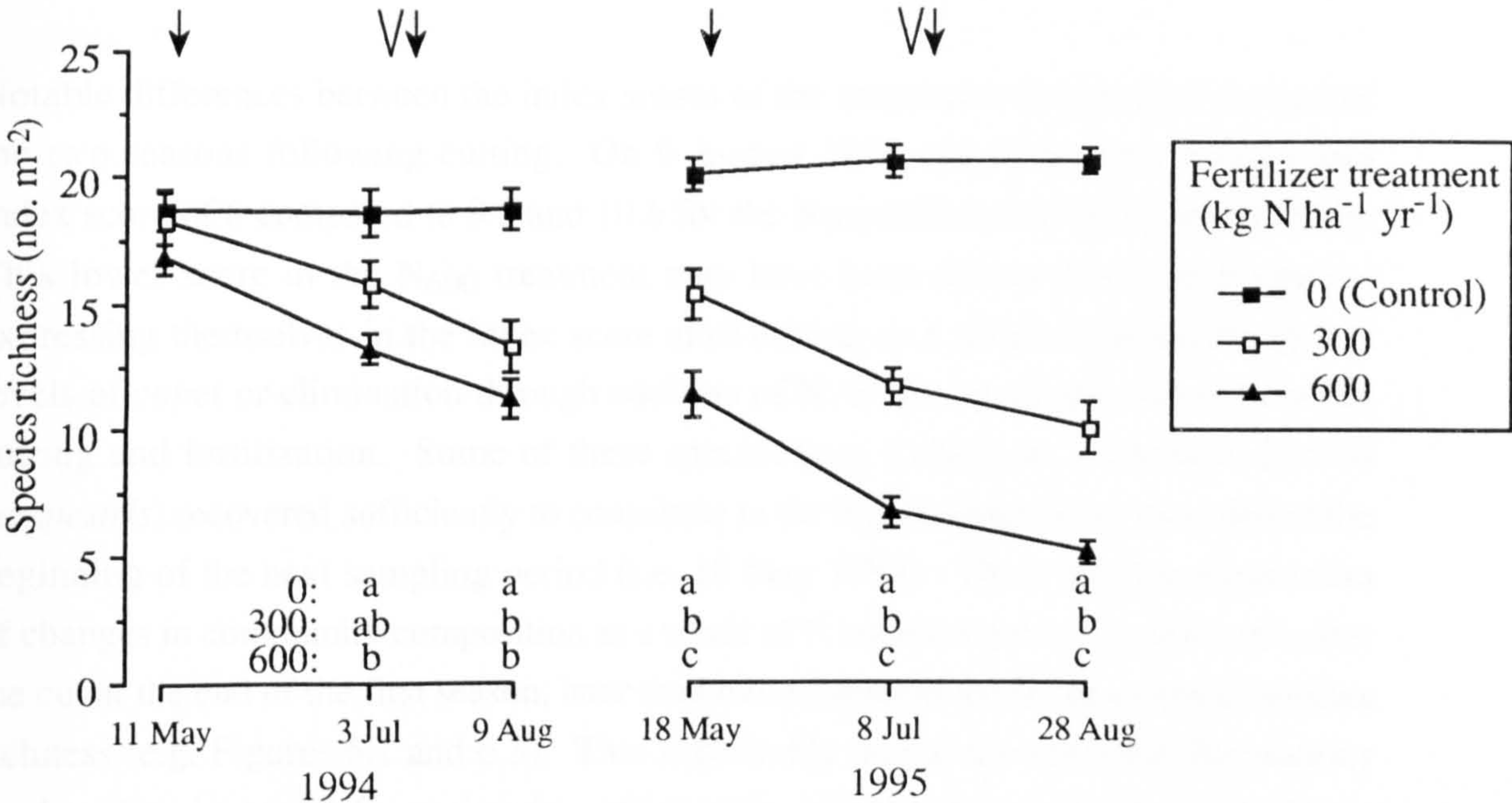
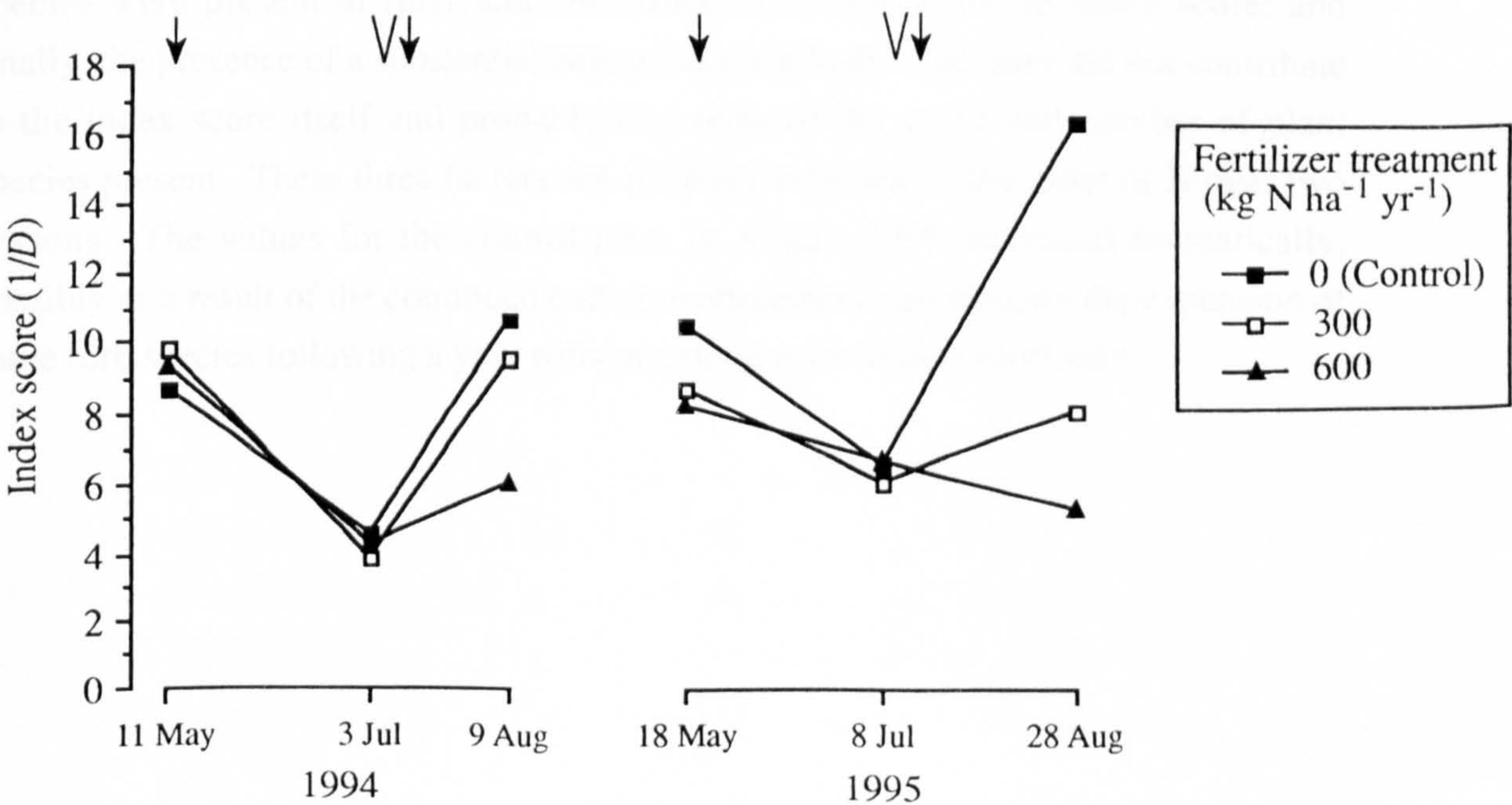


Figure 6.4 Effects of fertilizer N treatments on Simpson's Index ($1/D$) scores at Lužnice in 1994-5. Scores are derived from mean species richness and cover values for six experiment plots for each treatment. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



Sanguisorba officinalis prior to cutting, and also to the relative abundance of several grass species (e.g. *Agrostis capillaris*, *Deschampsia cespitosa*, *Festuca rubra*) in the case of the N₆₀₀ plots in 1995. Cutting reduced the relative abundance of *Sanguisorba officinalis*, allowing a range of smaller forbs to subsequently increase their cover in the control plots in both years, and in the N₃₀₀ plots in August 1994, giving a higher index score.

Notable differences between the index scores of the treatments occurred at the end of the two seasons following cutting. On 9 August 1994, the N₆₀₀ plots had a mean index score of 6 compared to 9.5 and 10.6 for the N₃₀₀ and control plots respectively. This lower score in the N₆₀₀ treatment may have been due to fewer forb species expressing themselves in the index score after cutting as a result of reduction to low levels of cover or elimination through addition of N, or due to an interaction between cutting and fertilization. Some of these species (e.g. *Cerastium fontanum*, *Luzula campestris*) recovered sufficiently to contribute to the higher index score recorded at the beginning of the next sampling period (i.e. 18 May 1995). Thus, the first expression of changes in community composition as a result of N addition did not appear until after the cut at the end of the first season, later than those apparent in the measures of species richness (e.g. Figures 6.1 and 6.3). This is probably due to the seasonal fluctuations in the abundance of *Sanguisorba officinalis*, which obscured any underlying community changes that were a consequence of the addition of N.

Index values for the final sampling date, 28 August 1995, showed the greatest differences between treatments. Plots receiving the two N treatments had values of less than half the control plots, probably due to the combination of the following three factors. Firstly, fewer species were present in the N treated plots; second, fewer forb species were present in sufficient abundance to contribute to the index score; and finally, the presence of a substantial amount of plant litter. The litter did not contribute to the index score itself and probably also reduced the cover and number of plant species present. These three factors are all likely to be due to the input of N over two seasons. The values for the control plots in August 1995 increased dramatically, possibly as a result of the continued cutting management encouraging the expansion of some forb species following a year without cutting prior to the experiment.

6.3.2 Cover

The dynamics of the plant community, and the related variables of litter and bare ground, over the two seasons of the experiment are presented as mean % cover values in Figure 6.5 (a-c). Grasses and forbs (including *Sanguisorba officinalis*) form the main components of the plant community in terms of cover, while the cover of sedges, moss and bare ground tended to be lower.

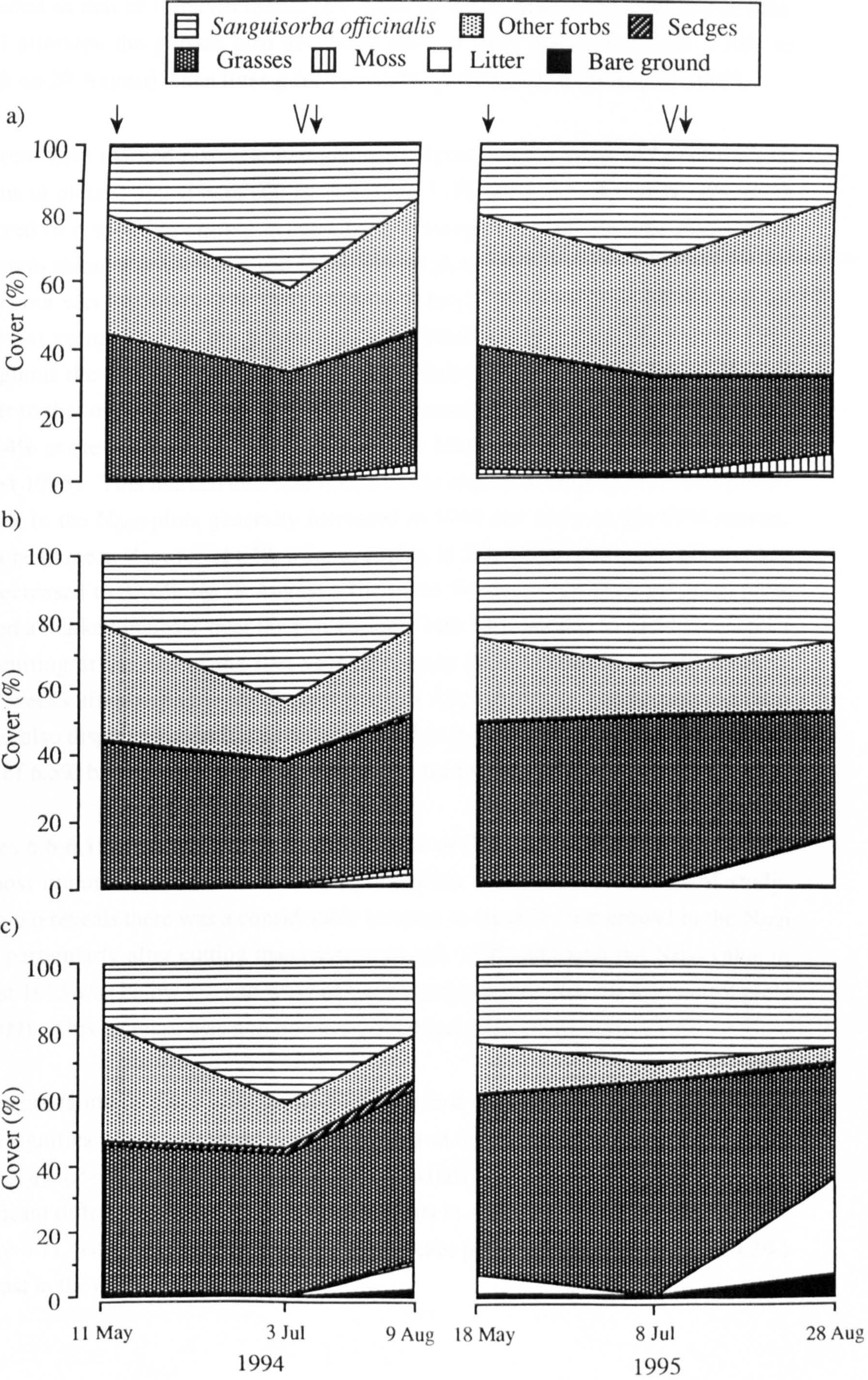
In the control plots, the pattern of community composition and change was similar in 1994 and 1995 (Figure 6.5a). The total forb community (ie. all forbs including *S. officinalis*) increased slightly in mean % cover early in both seasons, followed by a decrease after cutting and phytomass removal in 1994. Little change followed this management in 1995. One forb species, *S. officinalis*, exhibited major temporal changes in cover, however. In both years, its cover markedly expanded early in the season (from an average for the two years of 21.7% in May to 39.6% in July) until cut, when there was a pronounced decrease in cover (two-year mean 17.9% for August).

The grass community in the control plots in both years largely exhibited the inverse of the above pattern (Figure 6.5a). Grass % cover decreased prior to cutting (two-year mean values of 40.9% in May and 31.3% in July) and then increased later in 1994 to 39.5% following cutting management. However, this recovery was not observed in 1995, when the seasonal decrease in cover continued after the cut to a mean level of 24% in August 1995.

Cutting in mid-season therefore appeared to play an important role in influencing community composition in the control plots, representing a point in time either side of which marked differences in % cover occurred. The impact of cutting was perhaps most markedly exhibited by *S. officinalis*, which attained a pronounced maximum % cover immediately before cutting. Reduction of the cover of this species following cutting may have encouraged the expansion of the rest of the plant community, especially forbs and moss. Alternatively, cutting itself may have stimulated the expansion of the other plants. Other forbs, under control conditions, showed a marked increase in % cover following cutting management in July 1995.

Plots receiving 300 kg N ha⁻¹ yr⁻¹ exhibited different responses in the seasonal dynamics of community composition from those observed in the control plots (Figure 6.5b). *S. officinalis* in the N₃₀₀ plots again showed a mid-season maximum cover (43.3% on 3 July 1994 and 35.8% on 8 July 1995) and maintained its proportion relative to the control plots throughout the two seasons, never falling below 22%. The

Figure 6.5 Time series of the effect of fertilizer N treatments on plant community dynamics at Lužnice in 1994-5. Data are mean % cover values (n=6). Arrows indicate timings of fertilizer application; V indicates timings of cutting. a) 0 kg N ha⁻¹ yr⁻¹ (control) b) 300 kg N ha⁻¹ yr⁻¹ c) 600 kg N ha⁻¹ yr⁻¹.



cover of other forbs, however, although exhibiting a seasonal pattern similar to the control plots, generally declined over the two-year period. Grass cover generally expanded as that of forbs decreased (e.g. from 42.3% in May 1994 to 47.3% in May 1995) although the grasses also decreased later in 1995 (from 50.1% on 8 July to 36.1% on 28 August) when litter gained a notable presence (14% in August 1995).

An even more marked response in community dynamics was observed over the two seasons in plots supplied with 600 kg N ha⁻¹ yr⁻¹ (Figure 6.5c). Again, *S. officinalis* appeared to respond to cutting management, although the characteristic mid-season maximum mean % cover displayed in the control plots was present in 1994 (44.2% on 3 July) but was less marked in 1995 (30% on 8 July). However, this species was an important component of the community, maintaining a mean cover of over 19% throughout the two sampling seasons. Other forbs, however, displayed a decline similar to that of the N₃₀₀ plots, only more pronounced, with a reduction from a mean of 35.4% at the beginning of the experiment (11 May 1994) to 4.9% at the close (28 August 1995). This marked decrease obscured the impact of cutting on forb % cover. Grasses in the N₆₀₀ plots generally increased in 1994 and early in the 1995 season, with a peak mean % cover of 64% prior to cutting in July 1995. However, grass cover had decreased to 33.6% by 28 August. The mean % cover of litter in the N₆₀₀ plots showed a marked increase over the two seasons, with 7.8% measured some five weeks after cutting at the end of the first year (9 August 1994) and 29.2% approximately seven weeks after cutting in the second year (28 August 1995). The % cover of bare ground also displayed a similar pattern, although it increased to a lesser extent, with a mean of 6.5% bare ground recorded at the end of the experiment on 28 August 1995.

Figures 6.6-6.11 show the effects of the addition of 0, 300 and 600 kg N ha⁻¹ yr⁻¹ on the most important measured community variables over the two seasons of study. Figure 6.6 reveals there was a considerable increase in mean % bare ground in the N₆₀₀ plots, particularly after cutting management in July 1995, although the N₆₀₀ value in August 1995 was below 7% and was not significantly greater than for the control plots ($P=0.09$). This increase was not, however, observed in the N₃₀₀ plots.

An accumulation of plant litter in the plots supplied with N is evident in Figure 6.7, with a significantly greater mean % cover of litter in the N₆₀₀ plots observed compared to the N₃₀₀ ($P=0.02$) and control treatments ($P=0.01$) at the end of the 1994 season. Significant differences between all three treatments in August 1995 were also measured (Figure 6.7), with the greatest mean % cover of litter present in the N₆₀₀ plots (29.2%) and least in the control plots (1%).

Figure 6.6 Effects of fertilizer N treatments on cover of bare ground at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.

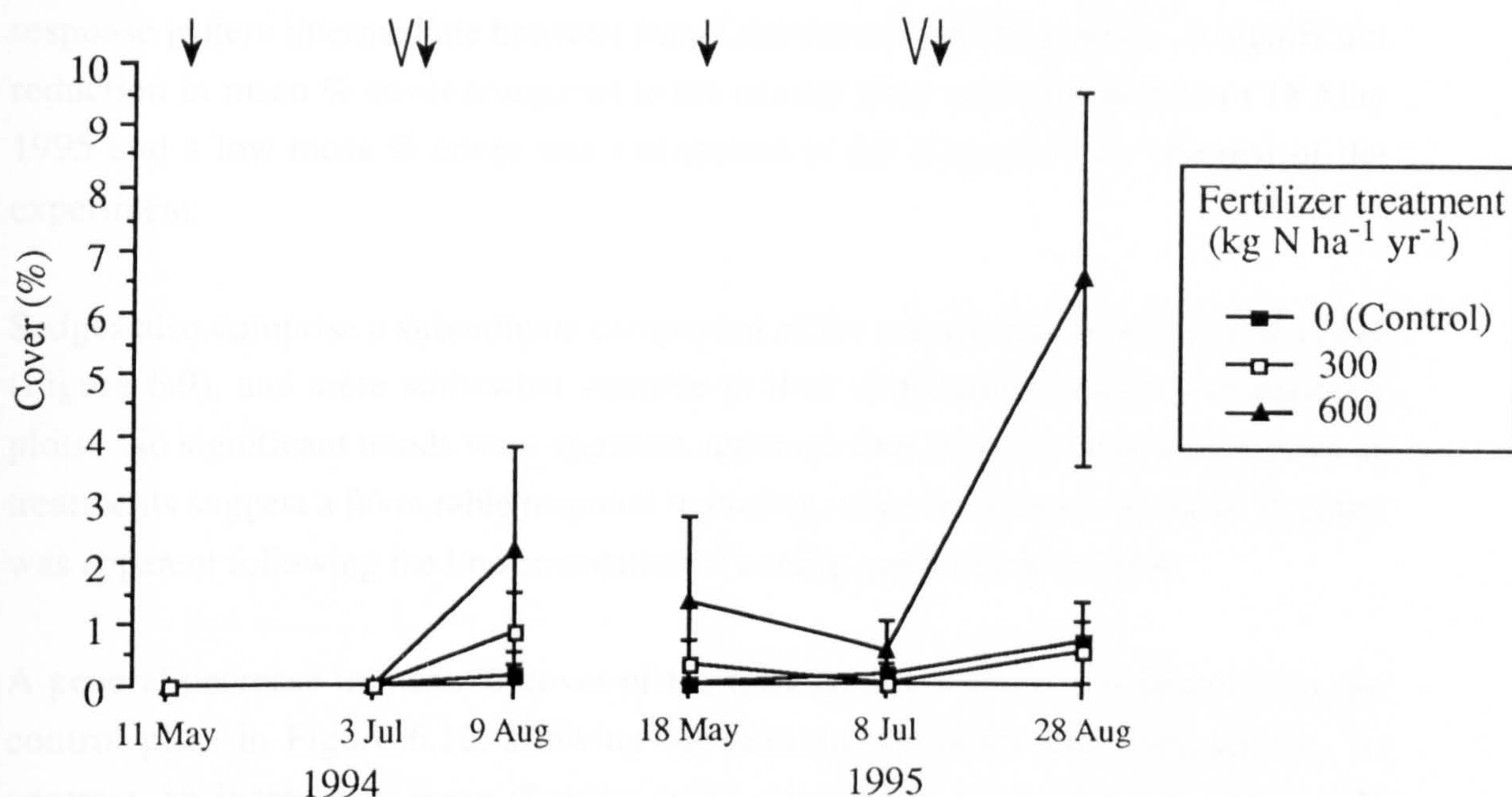
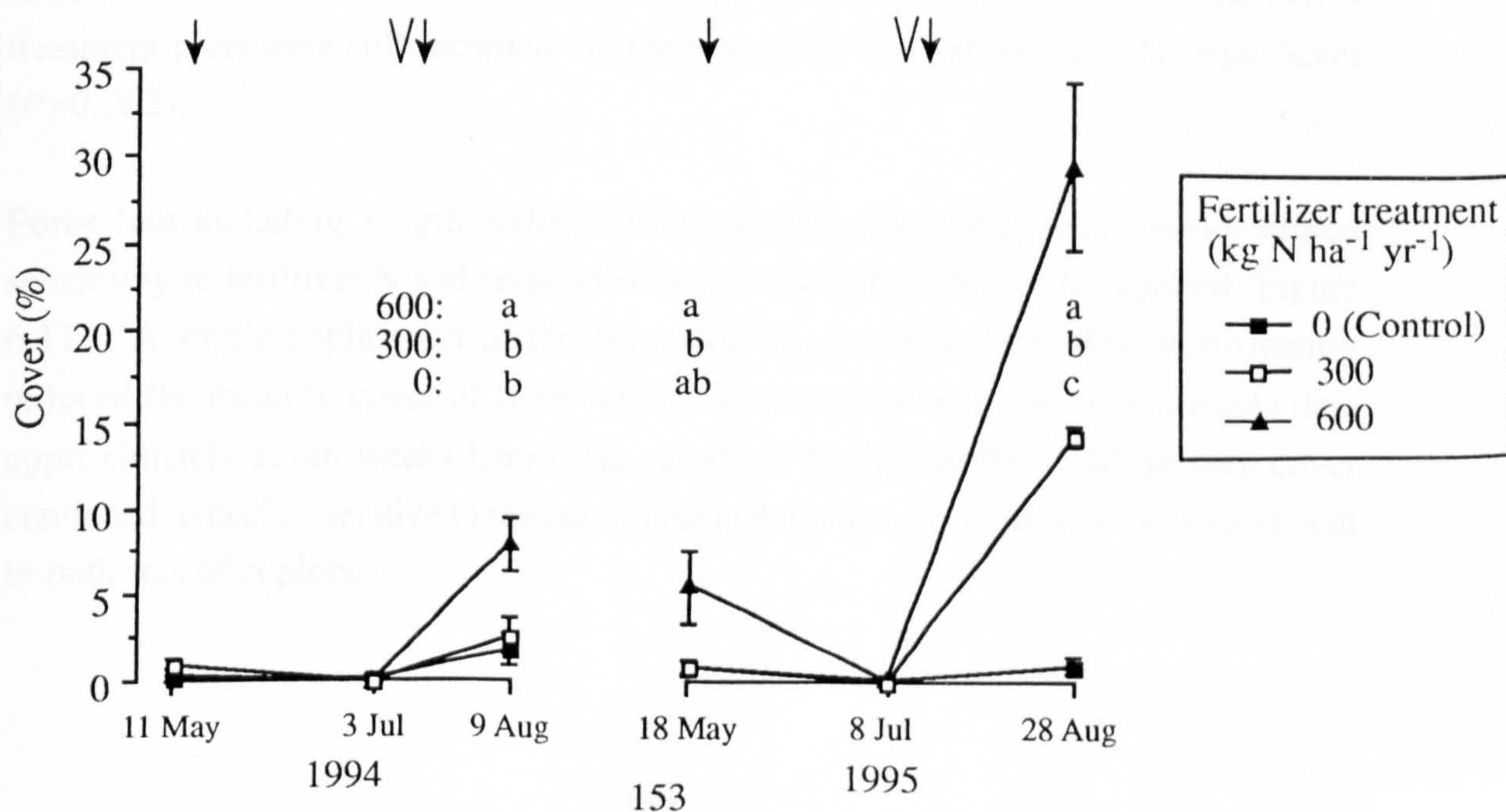


Figure 6.7 Effects of fertilizer N treatments on litter cover at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



Mean cover of moss within the studied plant community was generally lower than 2.5%, although it achieved 5.3% in the control plots in August 1995, following cutting management (Figure 6.8). Moss cover also showed a negative response to the addition of N, with % cover in the N₆₀₀ plots significantly reduced relative to the control plots on 9 August 1994 ($P=0.03$) and throughout the 1995 study period. Indeed, moss was eliminated from all of the N₆₀₀ plots by mid-season 1995. The N₃₀₀ plots showed a response pattern intermediate between that of the control and N₆₀₀ plots. A significant reduction in mean % cover compared to the control plots was recorded from 18 May 1995 and a low moss % cover was maintained in the N₃₀₀ plots for the rest of the experiment.

Sedges also comprise a subordinate component of the community in terms of % cover (Figure 6.9), and were somewhat variable in their distribution within and between plots. No significant trends were apparent, although data from all plots irrespective of treatments suggest a favourable response to cutting, since an increase in mean % cover was apparent following the implementation of cutting, particularly in 1994.

A general decrease in mean % cover of the total grass community is apparent in the control plots in Figure 6.10, allowing for seasonal variation and fluctuations. In contrast, an increase in mean % grass cover emerged in plots receiving the two N treatments, with N₆₀₀ plots showing the highest mean % cover and N₃₀₀ intermediate values. Relative to the control plots, these differences were mostly significant from 9 August 1994 for the N₆₀₀ treatment and from 8 July 1995 for the N₃₀₀ treatment (Figure 6.10). The temporal divergence between the control and N treatment plots ended at the final sampling date (28 August 1995), when a marked decline in grass cover was apparent in the fertilized plots. However, notable differences between the lower mean % cover of grasses in the control plots and the higher values of the two N treatment plots were still recorded. In the case of the N₃₀₀ plots, this was significant ($P=0.002$).

Forbs (not including *S. officinalis*, but including *Luzula campestris*) demonstrated sensitivity to fertilizer N and responded negatively to the rates of N supplied (Figure 6.11). A single application of the N₃₀₀ and N₆₀₀ treatment in May significantly reduced the mean % cover of forbs relative to control plots by the next sample date approximately seven weeks later (N₃₀₀, $P=0.03$; N₆₀₀, $P=0.001$). Mean forb cover continued to decline relative to the control throughout the two seasons of the experiment in both sets of N plots.

Figure 6.8 Effects of fertilizer N treatments on moss cover at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

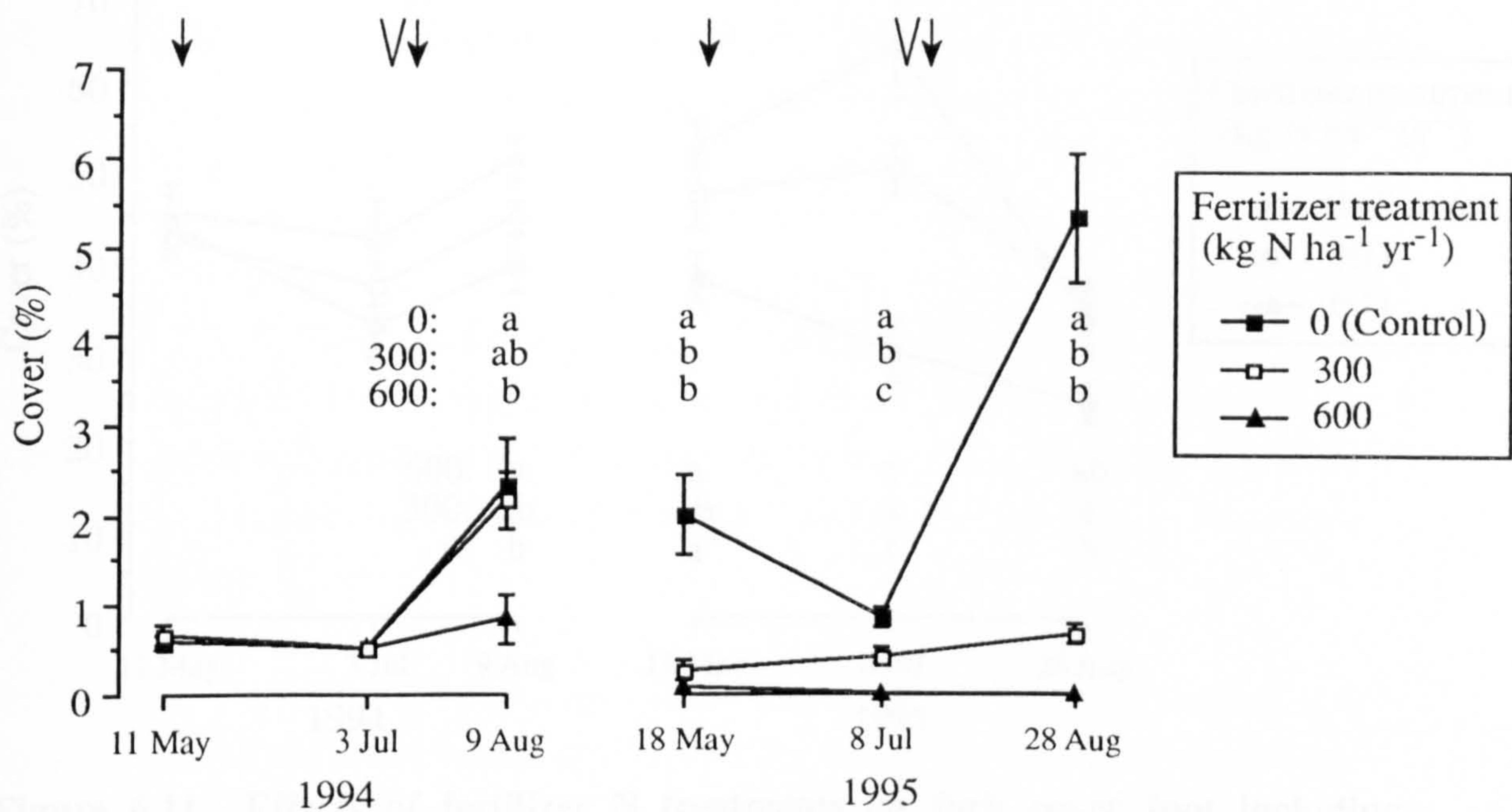


Figure 6.9 Effects of fertilizer N treatments on sedge cover at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.

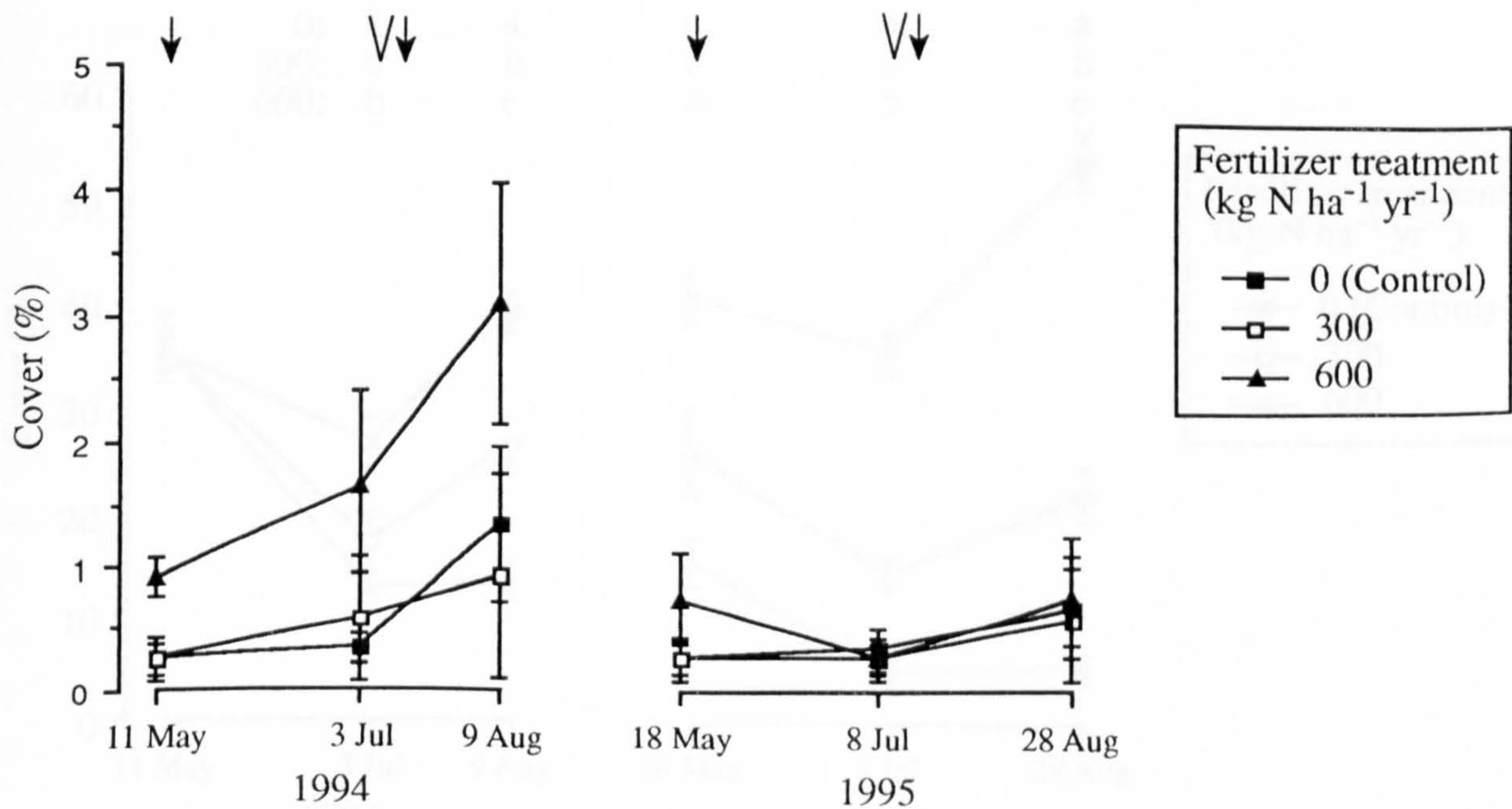


Figure 6.10 Effects of fertilizer N treatments on grass cover at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

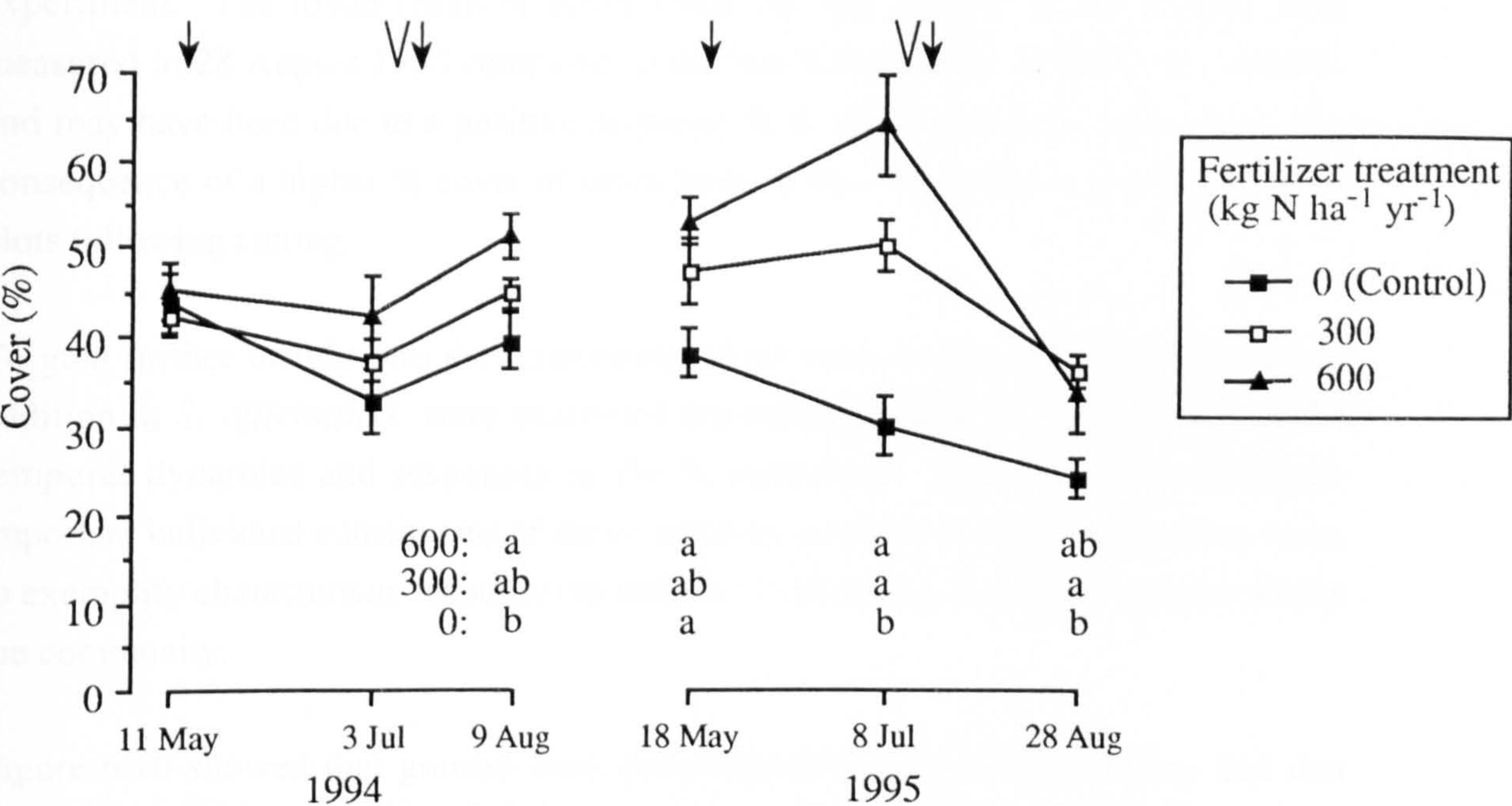


Figure 6.11 Effects of fertilizer N treatments on forb cover (not including *Sanguisorba officinalis*) at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

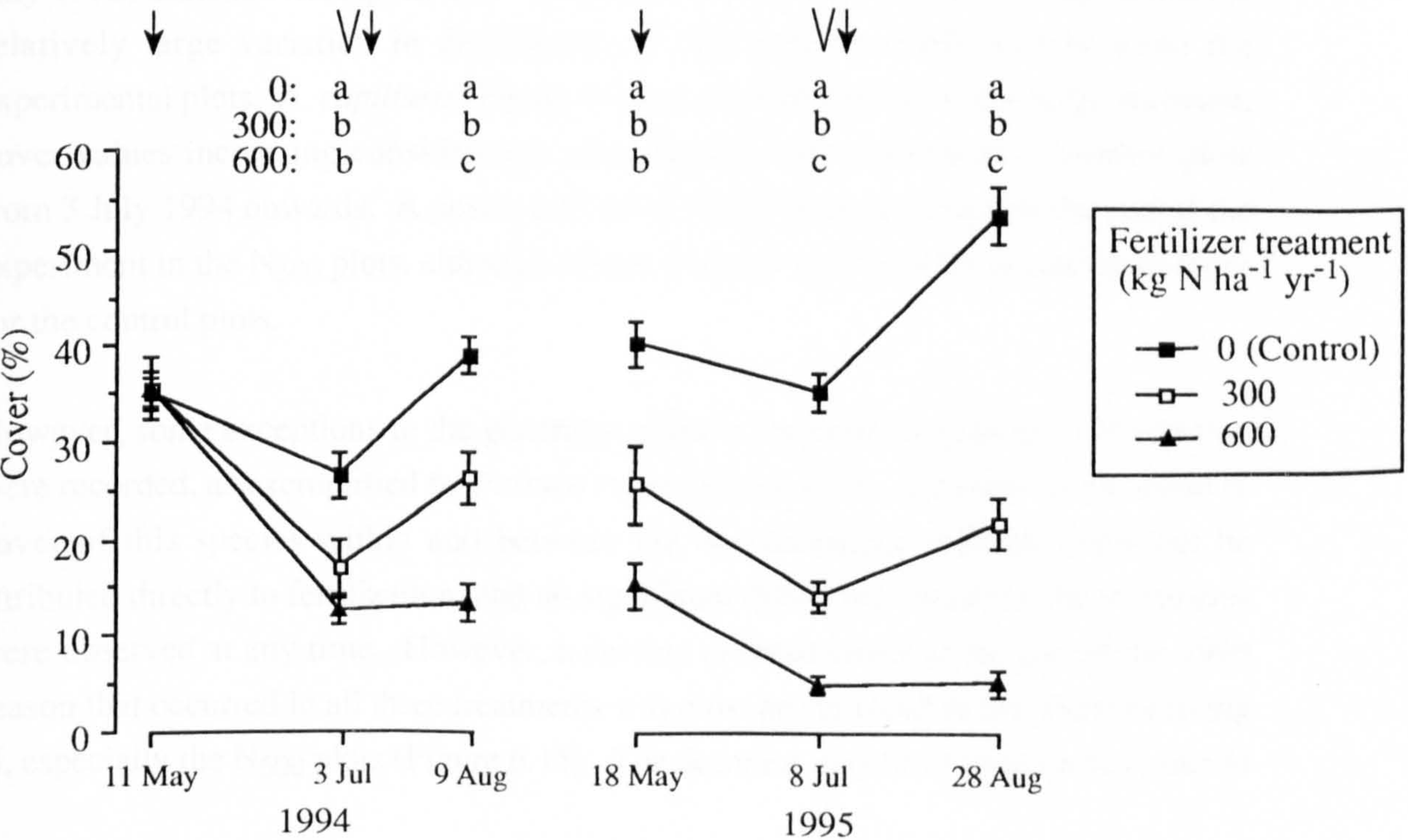


Figure 6.12 shows the marked seasonal and inter-year variation in mean % cover of a key component of the vegetation, *Sanguisorba officinalis*, particularly in relation to cutting management, and apparently irrespective of N treatment. Indeed, no significant differences in mean % cover were found between any treatment at any time during the experiment. The lower mean % cover value for this species in the control plots measured in 28 August 1995 compared to the two N treatments is, however, notable, and may have been due to a positive response by *S. officinalis* to N addition, or as a consequence of a higher % cover of other forbs in the control plots relative to the N plots following cutting.

To gain further insight into the functioning of the community, other key species (in addition to *S. officinalis*) were examined separately in relation to their fine-scaled temporal dynamics and responses to the N treatments. The species selected are important individual constituents of the community in terms of cover, and/or they serve to exemplify characteristic responses to fertilizer N shown by a range of species within the community.

Figure 6.10 showed that grasses were generally stimulated by N addition, and that N₃₀₀ plots displayed intermediate increases in % cover relative to control and N₆₀₀ plots. Two individual species that responded in this manner were *Deschampsia cespitosa* and *Agrostis capillaris*. *D. cespitosa* (Figure 6.13) responded positively to the addition of N, with N₃₀₀ plots showing intermediate mean cover values between those recorded for N₆₀₀ and control plots. The differences were relatively substantial (e.g. plants in N₆₀₀ plots exhibited more than four times the cover of control plots in July 1995) although not significant. The absence of a significant result may reflect the relatively large variation in distribution of this species within and between the experimental plots. *A. capillaris* (Figure 6.14) responded rapidly to the N₆₀₀ treatment, cover values increasing considerably, often significantly, compared to control plots from 3 July 1994 onwards. A positive effect of N also emerged towards the end of the experiment in the N₃₀₀ plots, although values were not significantly greater than those for the control plots.

However, some exceptions to the generally positive response by grasses to N addition were recorded, as exemplified by *Festuca rubra* (Figure 6.15). Changes in the mean % cover of this species within and between the two recording seasons could not be attributed directly to fertilization, and no significant differences between the treatments were observed at any time. However, a decline in mean cover at the end of the 1995 season that occurred in all three treatments was most pronounced in the plots receiving N, especially the N₆₀₀ plots (Figure 6.15). The decrease may have been directly due to

Figure 6.12 Effects of fertilizer N treatments on cover of *Sanguisorba officinalis* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.

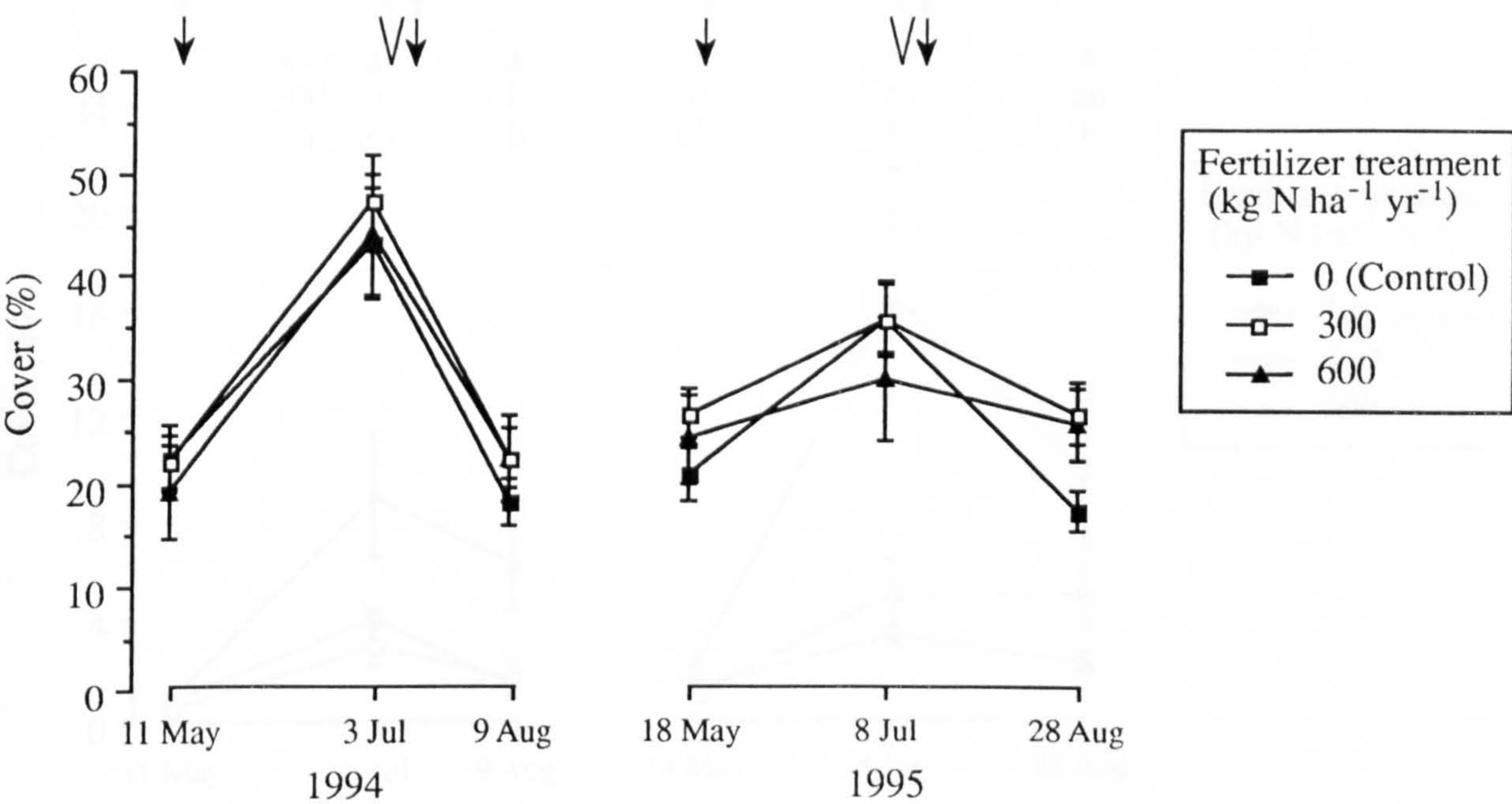


Figure 6.13 Effects of fertilizer N treatments on cover of *Deschampsia cespitosa* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.

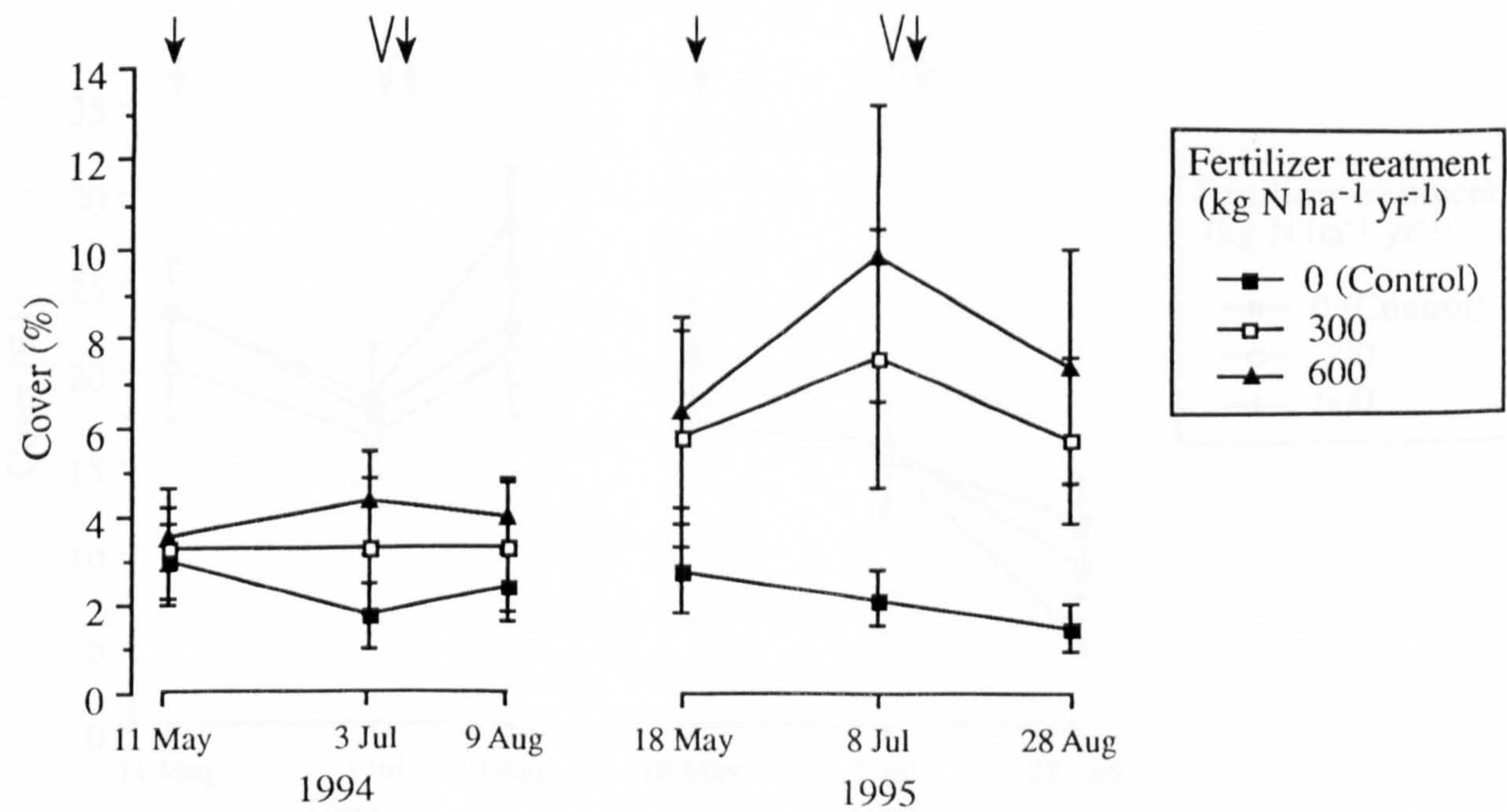


Figure 6.14 Effects of fertilizer N treatments on cover of *Agrostis capillaris* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

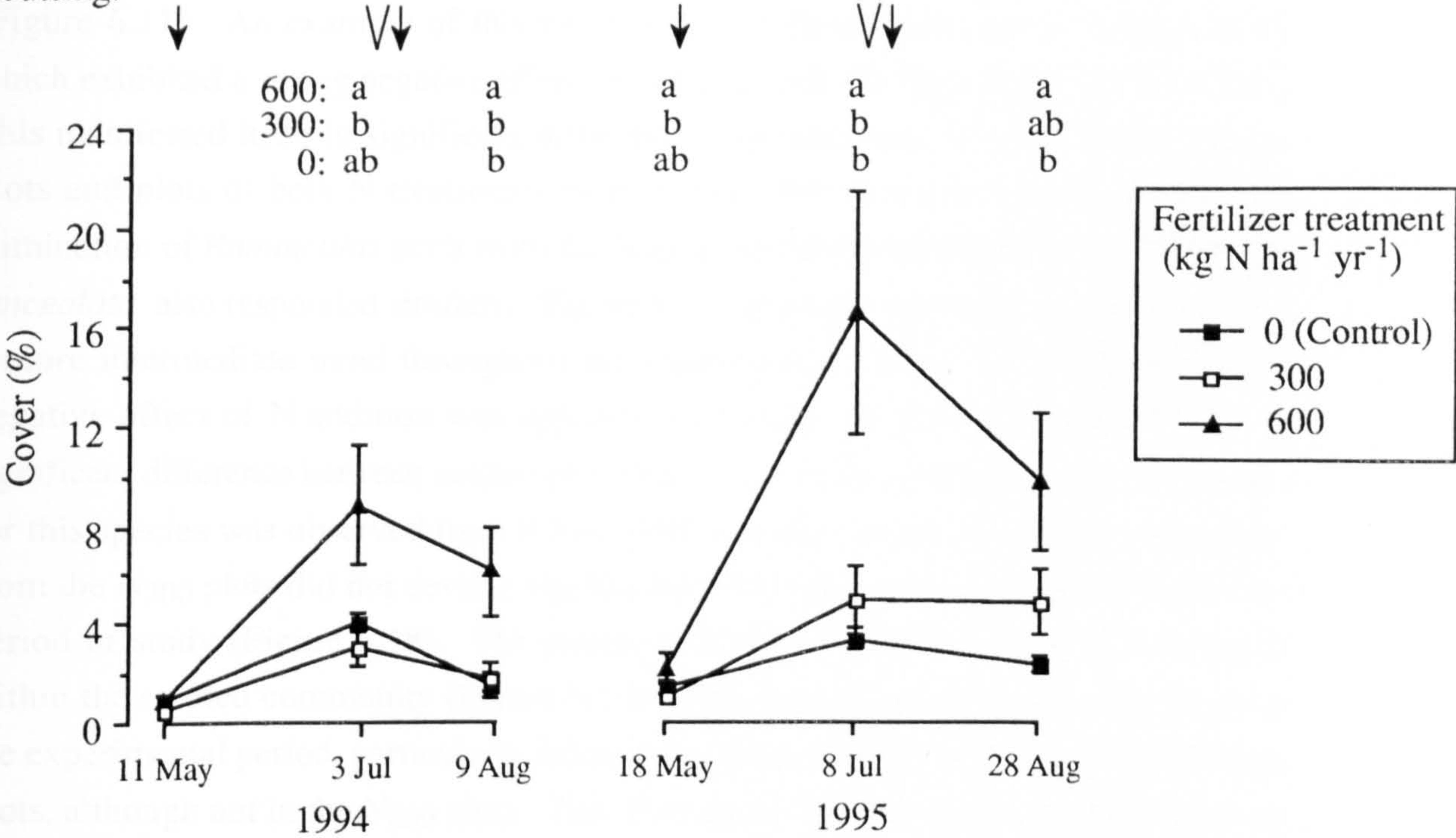
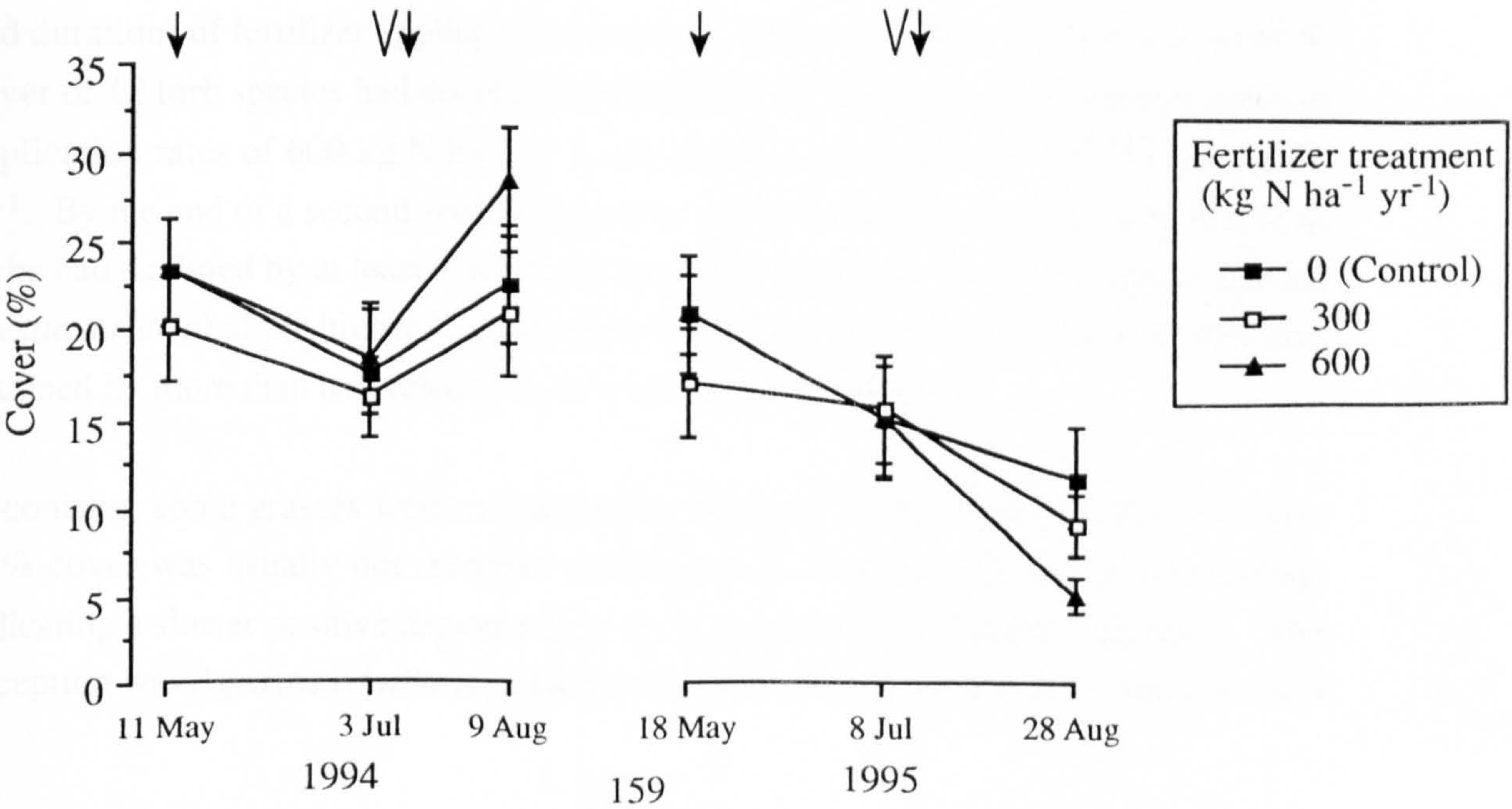


Figure 6.15 Effects of fertilizer N treatments on cover of *Festuca rubra* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, no significant treatment difference was observed ($P<0.05$, ANOVA). Arrows indicate timings of fertilizer application; V indicates timings of cutting.



N addition or a consequence of litter accumulation, or an interaction between these factors.

Although *Sanguisorba officinalis* showed no significant response to experimental fertilization (Figure 6.12), most of the forbs were discouraged by the addition of N (Figure 6.11). An example of this trend is that of *Ranunculus acris* (Figure 6.16) which exhibited a strong negative effect on cover at both the N₆₀₀ and N₃₀₀ treatments. This manifested itself in significant differences between mean % cover in the control plots and plots of both N treatments from 3 July 1994 onwards, and resulted in the elimination of *Ranunculus acris* from the N₆₀₀ plots from mid-season 1995. *Plantago lanceolata* also responded similarly (Figure 6.17), although the N₃₀₀ treatment showed a more intermediate trend throughout the experimental period. A less pronounced negative effect of N addition was apparent on *Luzula campestris* (Figure 6.18). A significant difference between control plot mean cover values and N₆₀₀ treatment values for this species was observed from 8 July 1995 onwards, although mean cover values from the N₃₀₀ plots did not deviate significantly from the control plot values over the period of study (Figure 6.18). The pattern exhibited by *Rumex acetosa* is unusual within the studied community (Figure 6.19). This species increased its cover later in the experimental period, particularly following cutting in 1995, in the control and N₃₀₀ plots, although not in the N₆₀₀ plots. This divergence led to a significant difference in mean % cover between the N₃₀₀ and the N₆₀₀ plots from July 1995 onwards, and between the control and N₆₀₀ plots in August 1995.

Individual species responses to the experimental addition of the two different rates of N are summarized in Table 6.2. Overall far more species were discouraged by fertilizer N application than were favoured. This indicates that many forb species were disadvantaged by N addition, and that they were sensitive to the rate (i.e. the amount and duration) of fertilizer applied. For example, by the end of the first season mean % cover of 12 forb species had decreased by at least half, relative to their control plots, at application rates of 600 kg N ha⁻¹ yr⁻¹, compared to seven species for 300 kg N ha⁻¹ yr⁻¹. By the end of a second season, the cover of four additional species categorized as forbs had declined by at least half at both application rates, as well as one grass species (*Festuca rubra*) at the higher N application rate. Moss cover in the fertilized plots also declined by more than half relative to the control plots (Table 6.2).

In contrast, some grasses were stimulated by inputs of N, although a notable increase in % cover was usually not recorded until the end of the second year of monitoring, indicating a slower positive response than those species that responded negatively. The exception was *Agrostis capillaris*, which more than doubled its % cover within the first

Figure 6.16 Effects of fertilizer N treatments on cover of *Ranunculus acris* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

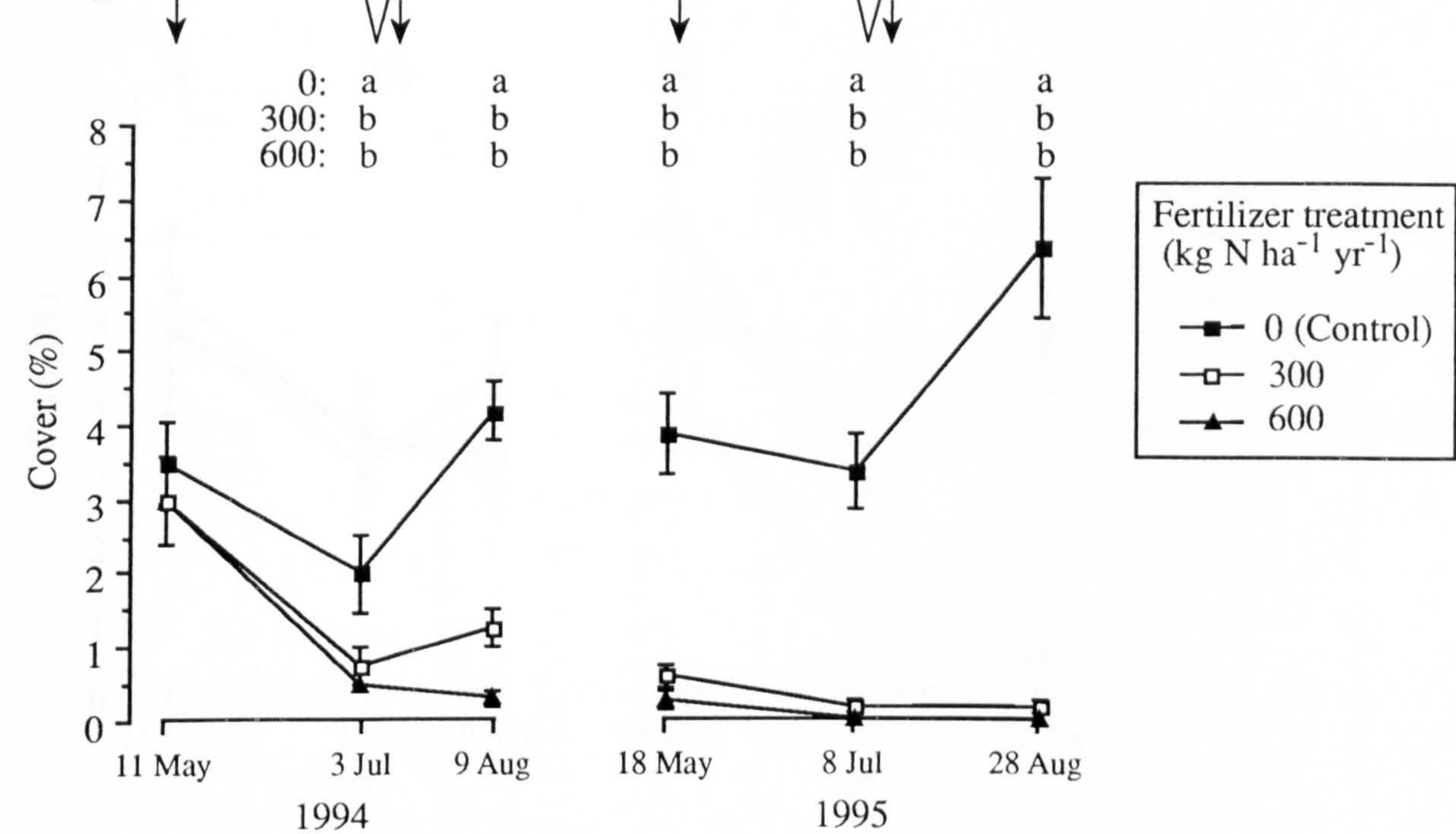


Figure 6.17 Effects of fertilizer N treatments on cover of *Plantago lanceolata* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

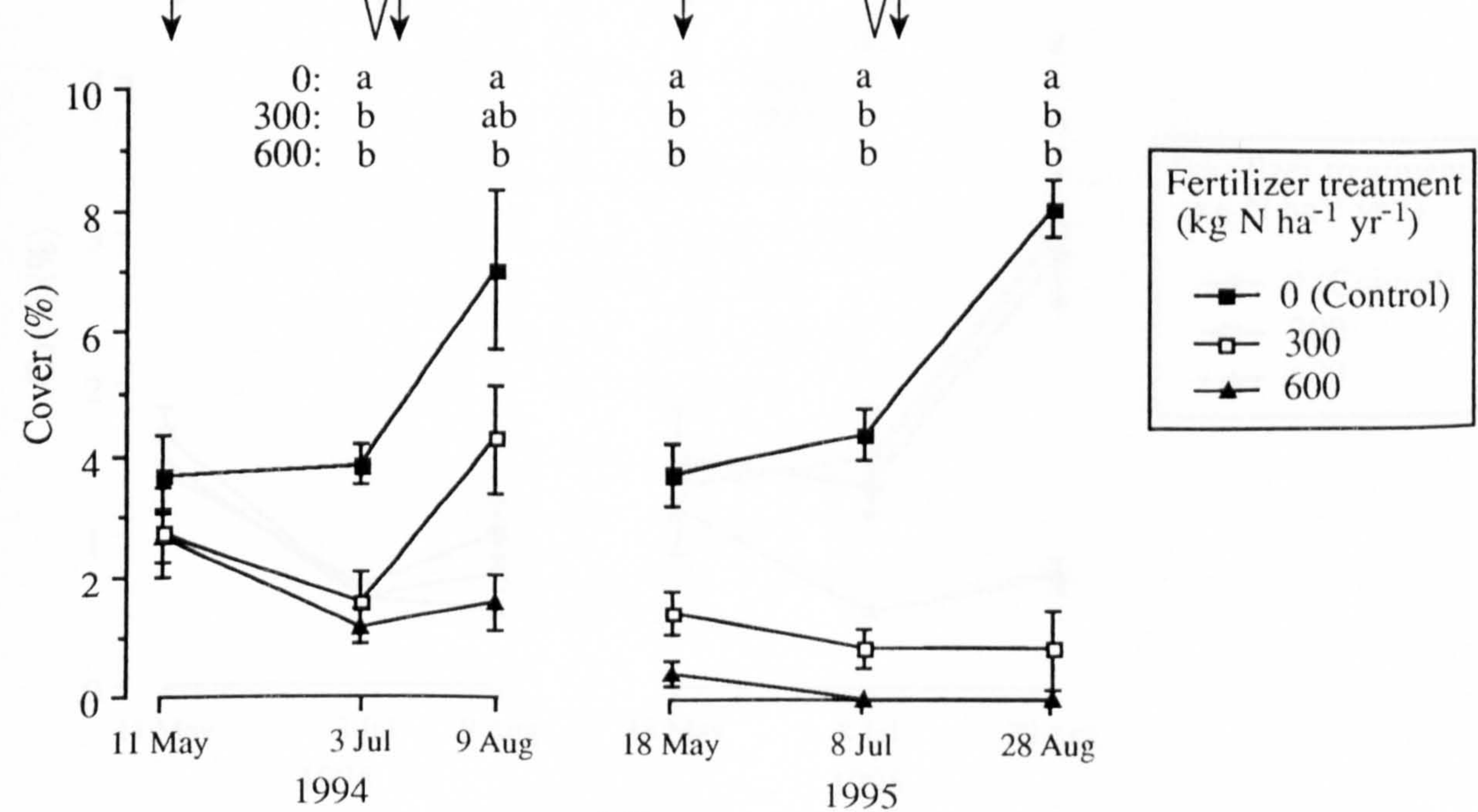


Figure 6.18 Effects of fertilizer N treatments on cover of *Luzula campestris* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

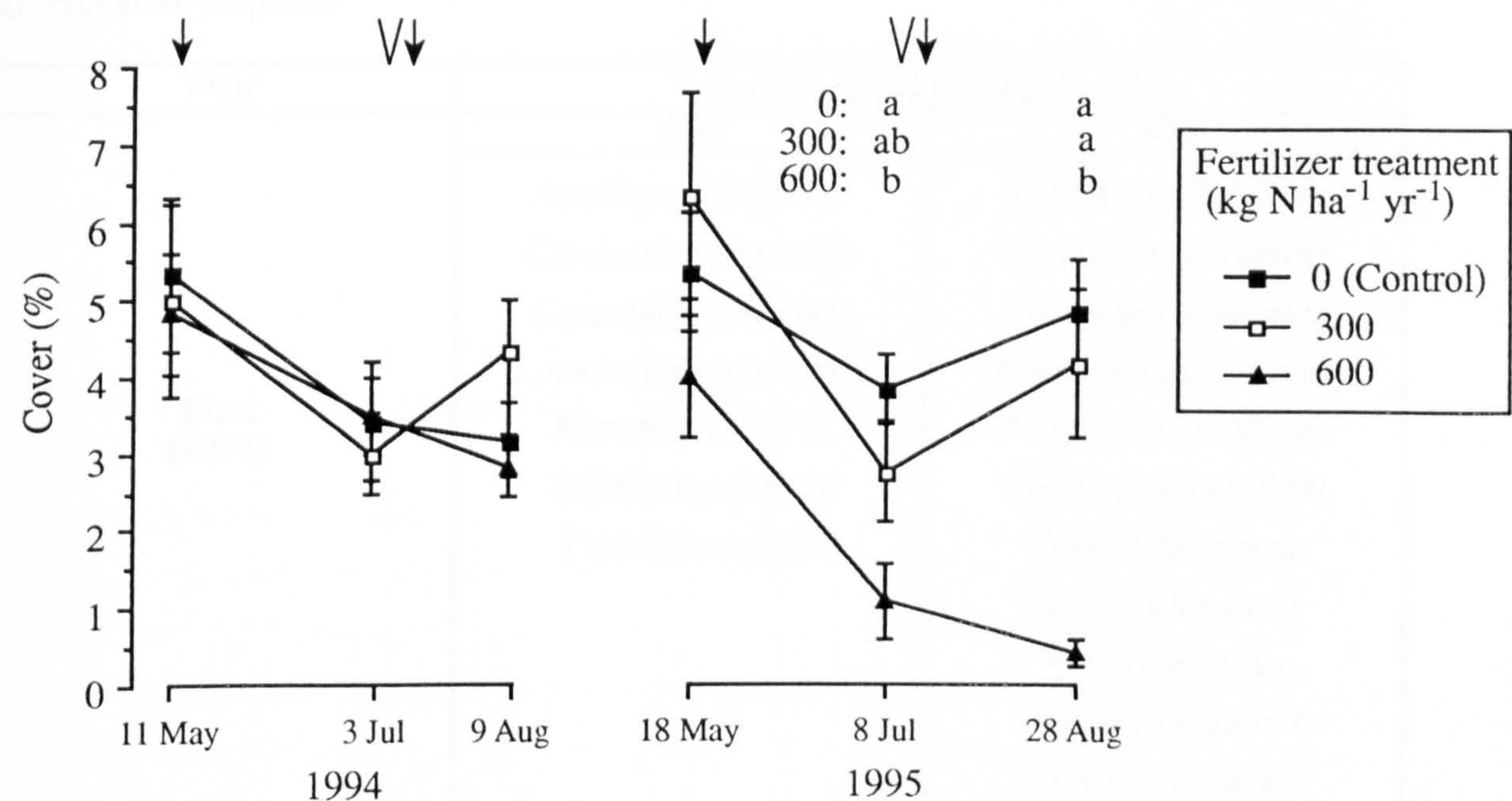


Figure 6.19 Effects of fertilizer N treatments on cover of *Rumex acetosa* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

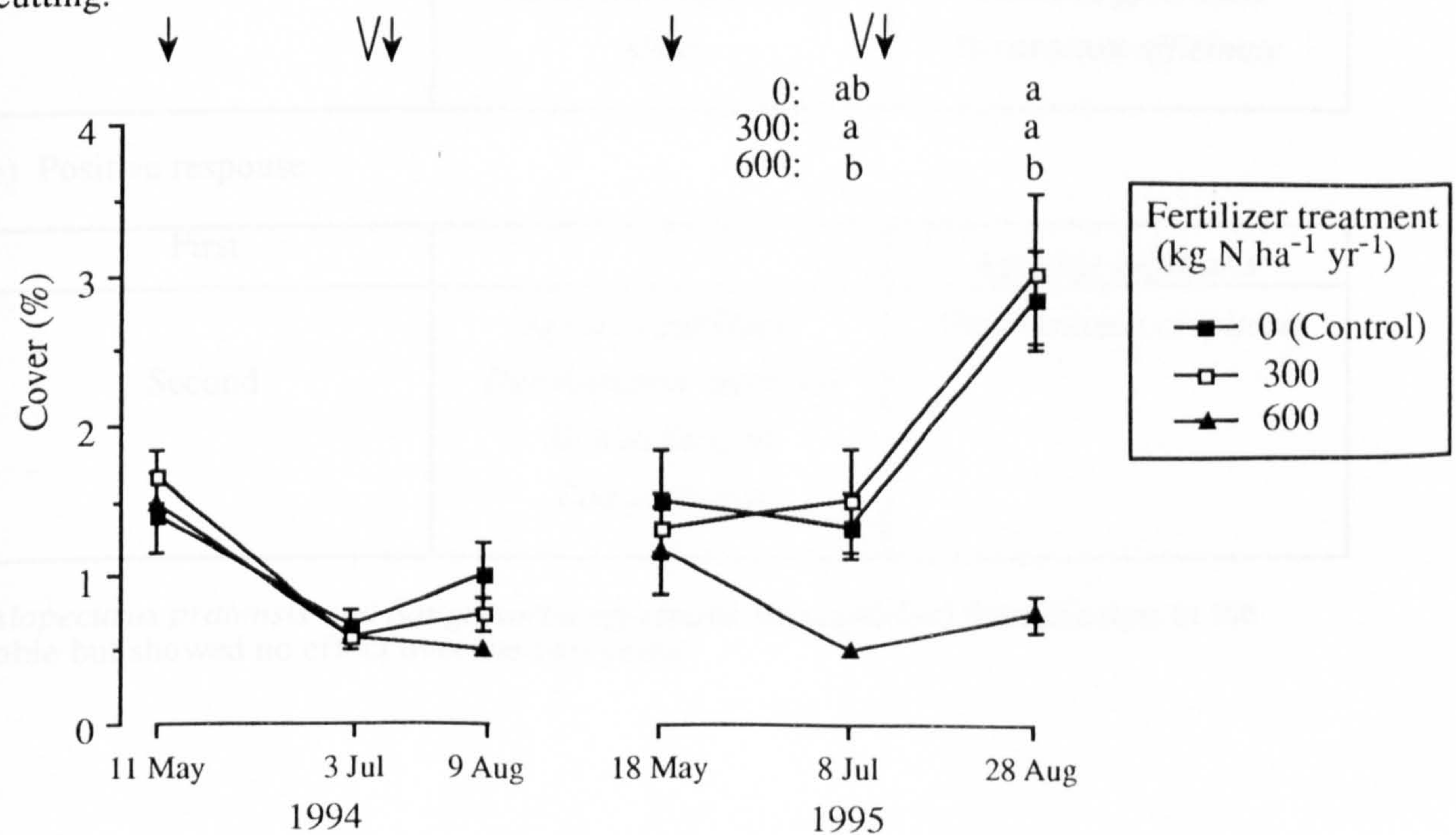


Table 6.2. Response of plant species to fertilizer N application at the Lužnice flood-meadow. Species shown are those with mean % cover values for all treatments within ± 0.5 of each other at the first (pre-treatment) survey (i.e. 11 May 1994). (a) species cover decreased by more than half, compared to the control plots, at the last survey of the year (i.e. 9 August 1994, 28 August 1995). (b) species cover increased by more than half, as (a). Species listed in the second year are additional to those listed in the first year.

a) Negative response

Year	Treatment (kg N ha ⁻¹ yr ⁻¹)	
	300	600
First (1994)	<i>Achillea millefolium</i> <i>Cardamine pratensis</i> <i>Cerastium fontanum</i> <i>Leontodon autumnalis</i> <i>Ranunculus acris</i> <i>Trifolium pratense</i> <i>Trifolium repens</i>	<i>Achillea millefolium</i> <i>Cardamine pratensis</i> <i>Cerastium fontanum</i> <i>Hieracium umbellatum</i> <i>Pimpinella saxifraga</i> <i>Plantago lanceolata</i> <i>Potentilla erecta</i> <i>Ranunculus acris</i> <i>Rumex acetosa</i> <i>Succisa pratensis</i> <i>Trifolium pratense</i> <i>Trifolium repens</i> Moss
Second (1995)	<i>Hieracium umbellatum</i> <i>Plantago lanceolata</i> <i>Stellaria graminea</i> <i>Taraxacum officinale</i> Moss	<i>Festuca rubra</i> <i>Leontodon autumnalis</i> <i>Luzula campestris</i> <i>Stellaria graminea</i> <i>Taraxacum officinale</i>

b) Positive response

First	—	<i>Agrostis capillaris</i>
Second	<i>Agrostis capillaris</i> <i>Deschampsia cespitosa</i> <i>Holcus lanatus</i> <i>Poa pratensis</i>	<i>Deschampsia cespitosa</i>

Alopecurus pratensis and *Sanguisorba officinalis* also qualified for inclusion in the table but showed no effect over the two years.

season at 600 kg N ha⁻¹ yr⁻¹. By the end of the second season of recording, one further grass species (*Deschampsia cespitosa*; Table 6.2) had increased its cover two fold at the highest rate of N input and four grass species (*A. capillaris*, *D. cespitosa*, *Holcus lanatus* and *Poa pratensis*; Table 6.2) showed similarly increased mean % cover at rates of 300 kg N ha⁻¹ yr⁻¹.

Table 6.2 suggests that the concept of a threshold of N supply rate may be applicable to the plant community studied. For example, more species decreased their % cover by half compared to control plots in the first season under the N₆₀₀ than N₃₀₀ treatments as well as over the two seasons in total. Also, four species (*Pimpinella saxifraga*, *Potentilla erecta*, *Rumex acetosa* and *Succisa pratensis*) declined by at least half within one season under the N₆₀₀ treatment, but maintained more than half their cover, compared to control plots, throughout the experiment at the N₃₀₀ treatment.

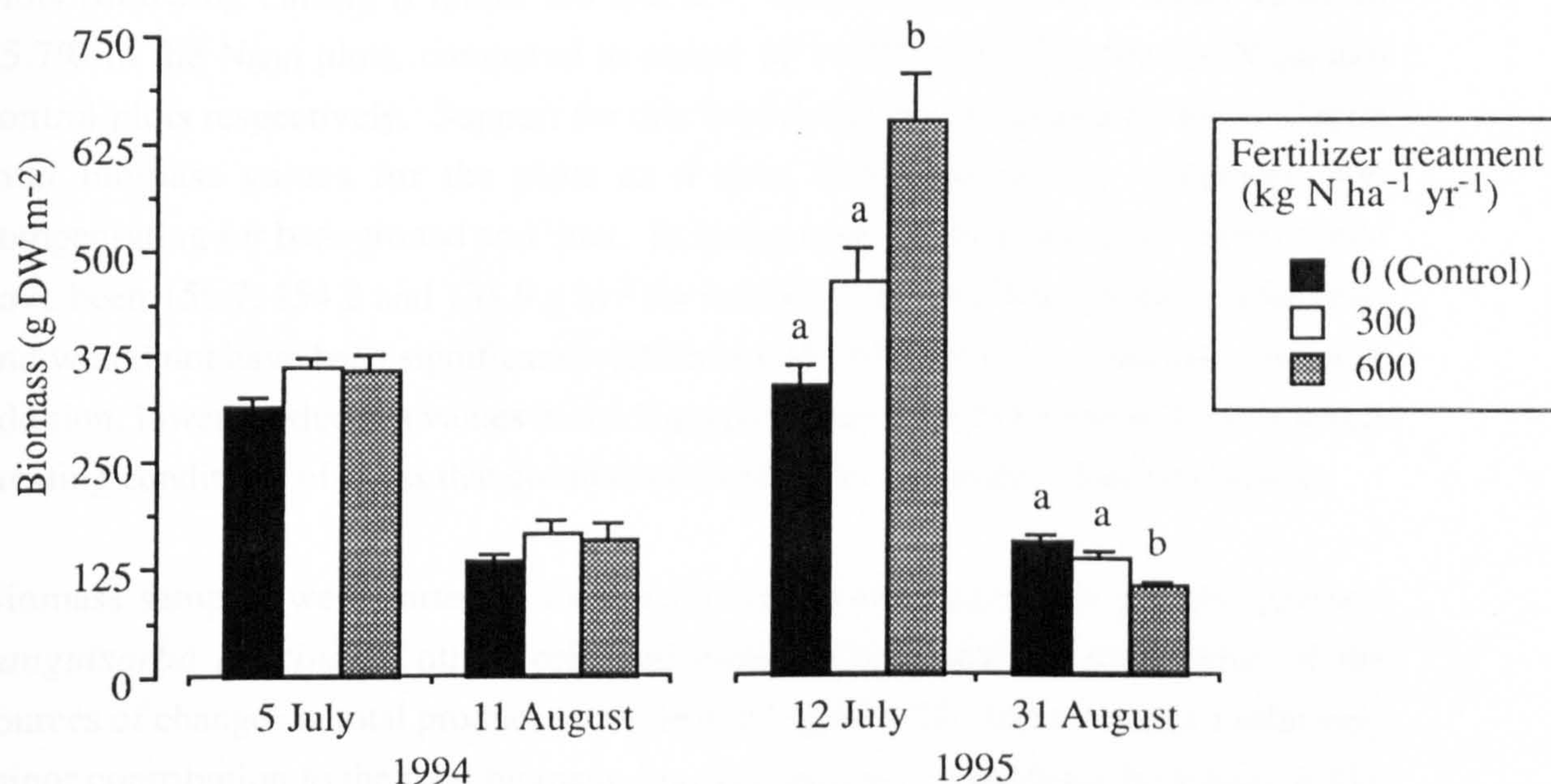
The species most sensitive to increased N tended to be of a small stature (e.g. *Cerastium fontanum*), indicative of nutrient-poor conditions (e.g. *Hieracium umbellatum* and *Potentilla erecta*) or leguminous (e.g. *Trifolium pratense* and *T. repens*). Legumes are able to fix their own nitrogen and were therefore probably placed at a competitive disadvantage with more robust species with the increased nitrogen availability following the experimental application of fertilizer N.

Two species, *Sanguisorba officinalis* and *Alopecurus pratensis*, showed neither a positive nor negative trend in association with N inputs. A number of forb, grass and sedge species were not included in Table 6.2 because of the variability of their frequency and % cover (often very low) within the experiment plots.

6.3.3 Production

Mean total biomass production for 1994 and 1995 is shown in Figure 6.20. Production measured in July (before cutting management) and August (the regrowth following cutting) in 1994 was slightly, although not significantly, higher in the N treated plots than the control plots. Mean values in July 1995, however, showed significant differences between treatments. Mean biomass in the N₆₀₀ plots was significantly higher than the control and N₃₀₀ plots, with N₃₀₀ values intermediate between the two. This was likely to be as a result of the sustained addition of N, as production in the control plots had not changed significantly between July 1994 and July 1995 ($P=0.41$). In both years, post-cutting production sampled in August was

Figure 6.20 Effects of fertilizer N treatments on above-ground plant production at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.



lower compared to measurements taken prior to the cut in July, irrespective of N treatment.

The proportional relationship between the rate of N supply and biomass production recorded in July 1995 was not evident in the final sample of the experiment on 31 August 1995, which measured regrowth following cutting management. Significantly less biomass was recorded in the N₆₀₀ plots than either the N₃₀₀ or control plots, which were not significantly different from each other (Figure 6.20). This may have been related to the higher proportion of bare ground and, particularly, litter in the N₆₀₀ plots following cutting (Figures 6.6 and 6.7) which together had a mean value of 35.7% in the N₆₀₀ plots, compared to means of 14.5% and 1.7% for the N₃₀₀ and control plots respectively. Support for this hypothesis can be gained by recalculating total biomass values for the plots as if they had been wholly vegetated, i.e. compensating for bare ground and litter. In such a case, mean production values would have been 156.7, 154.2 and 135.9 g m⁻² for control, N₃₀₀ and N₆₀₀ plots respectively, and would not have been significantly different (ANOVA, $P=0.1$). Alternatively, or in addition, lower production values in the N₆₀₀ plots may have been due to high N levels creating conditions of stress that constrained rather than stimulated plant production.

Biomass samples were sorted to their main component vegetation groups (grasses, *Sanguisorba officinalis*, other forbs and moss), which enabled elucidation of the sources of changes in total production evident in Figure 6.20. Moss formed a relatively minor contribution to the total biomass, but was sensitive to fertilizer N (Figure 6.21). Mean moss biomass was significantly lower in both sets of N treatment plots compared to control plots in July and August 1995. Also N₆₀₀ treatment values were consistently lower than either N₃₀₀ or control measurements throughout the two seasons of the experiment. Cutting may have stimulated or encouraged moss growth, as mean production in the control plots increased following cutting in 1994 and was significantly greater in a comparison of pre- and post-cutting values for 1995 ($P=0.007$).

Grass production was a major constituent of total biomass (Figure 6.22), and reflected the patterns of change observed in the total biomass values (Figure 6.20). Indeed, it appears that the grasses largely accounted for the marked differences in total production measured in July 1995, described above. Mean grass biomass at this time was more than three times greater in the N₆₀₀ plots than the control plots, a significant difference, with N₃₀₀ values also significantly different from, but intermediate between the two (Figure 6.22). *Agrostis capillaris* made an important contribution to total grass biomass, and showed a markedly higher production under the N₆₀₀ treatment

Figure 6.21 Effects of fertilizer N treatments on above-ground moss production at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.

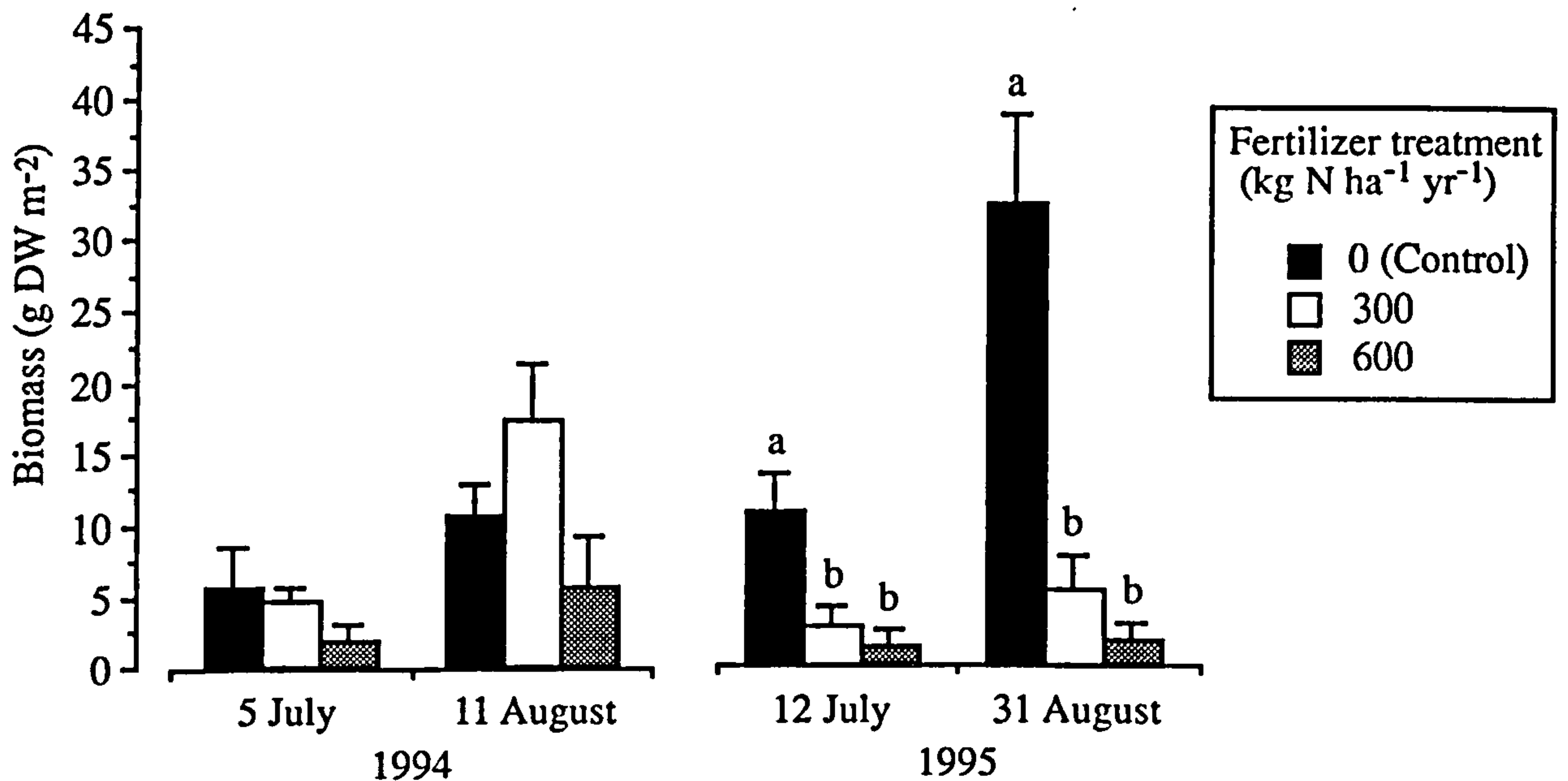
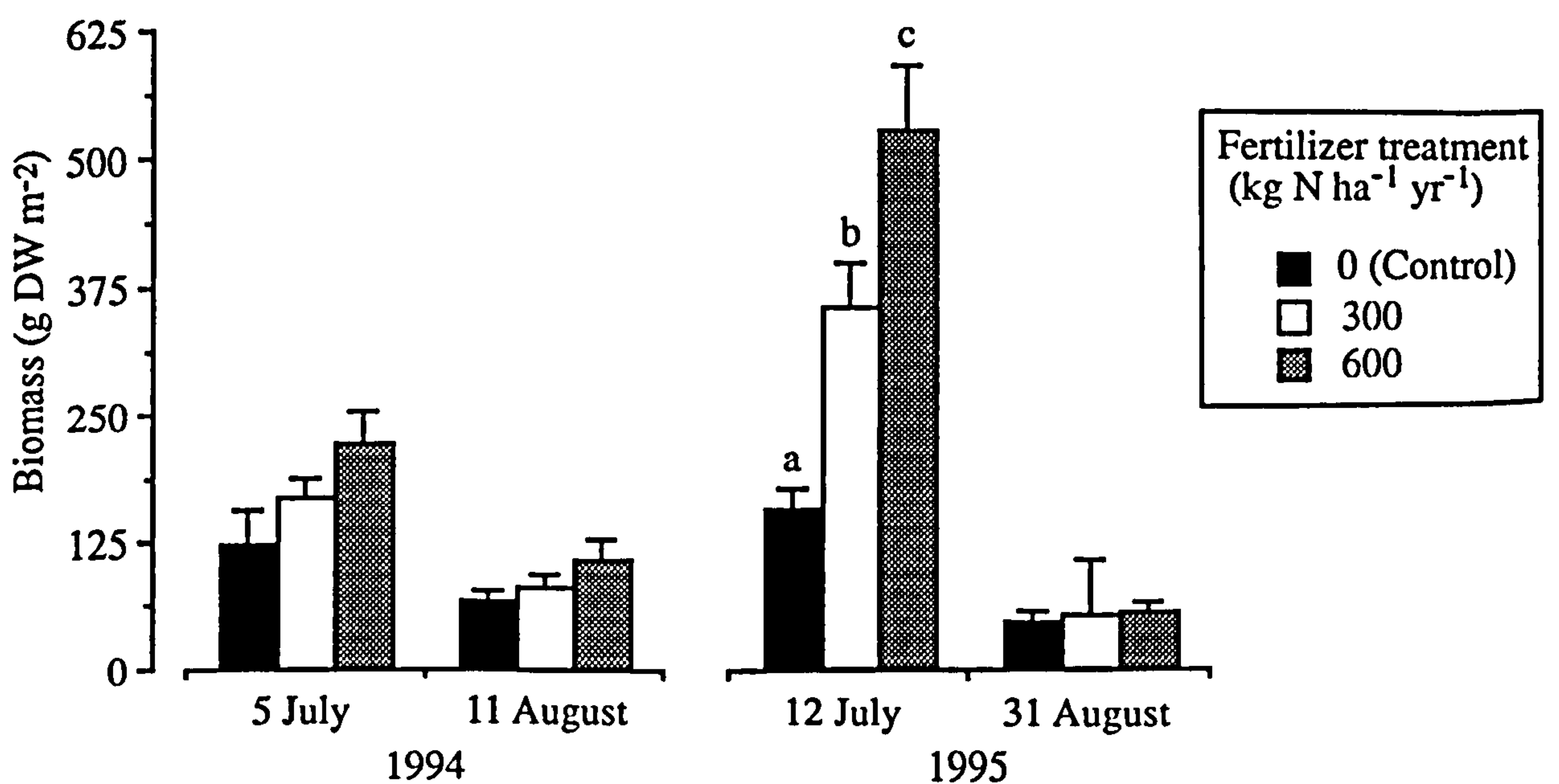


Figure 6.22 Effects of fertilizer N treatments on above-ground grass production at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.



throughout the two seasons (Figure 6.23). It also exhibited a significantly greater biomass in the N₆₀₀ plots in July 1995, with mean production over 800% greater than the control plots. N₃₀₀ plots exhibited an intermediate mean value. Mean total grass biomass measured in August 1995 was very similar across all treatments, although *Agrostis capillaris* displayed significantly enhanced production in the N₆₀₀ plots compared to control and N₃₀₀ values (Figure 6.23).

Figure 6.24 shows that mean forb production, not including *Sanguisorba officinalis*, was significantly reduced by the highest application of fertilizer N (600 kg N ha⁻¹ yr⁻¹) throughout the experiment, relative to the control. Indeed, by the end of the experiment (August 1995) forb biomass in the N₆₀₀ plots was little more than 10% of the value recorded for the control plots, thereby accounting for most of the significant difference in total biomass evident in Figure 6.20. Production of the grass *Festuca rubra* was also disadvantaged by fertilization later in the 1995 season (Figure 6.25). Mean biomass values for this species in August 1995 were significantly lower in the N₆₀₀ and N₃₀₀ plots than the control plots. All previous samples, taken in 1994 and July 1995, did not demonstrate any significant differences between the treatments (Figure 6.25).

Production values for *Sanguisorba officinalis* were somewhat variable (Figure 6.26), reflecting the patchy nature of the local distribution and growth habit of this species. No significant differences between values from the control or either of the two N treatment plots were observed over the two seasons.

6.3.4 Soil variables

6.3.4.1 Nitrogen

Soil nitrate values remained low during the two sampling seasons and there was no overall trend in soil nitrate concentration in relation to applications of ammonium sulphate fertilizer (Figure 6.27). This suggests that little of the nitrogen supplied by this type of fertilizer was in the form of nitrate and/or that any nitrate that was supplied did not persist in the surface horizons of the soil. In contrast, concentrations of ammonium in the soil reflected the pattern of fertilizer application (Figure 6.28). High values were recorded for the N₆₀₀ plots in August 1994 and July and August 1995 following additions of fertilizer, while soil ammonium concentrations in the N₃₀₀ plots showed levels intermediate between the N₆₀₀ and unfertilized control plots (Figure 6.28).

Figure 6.23 Effects of fertilizer N treatments on above-ground production of *Agrostis capillaris* at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.

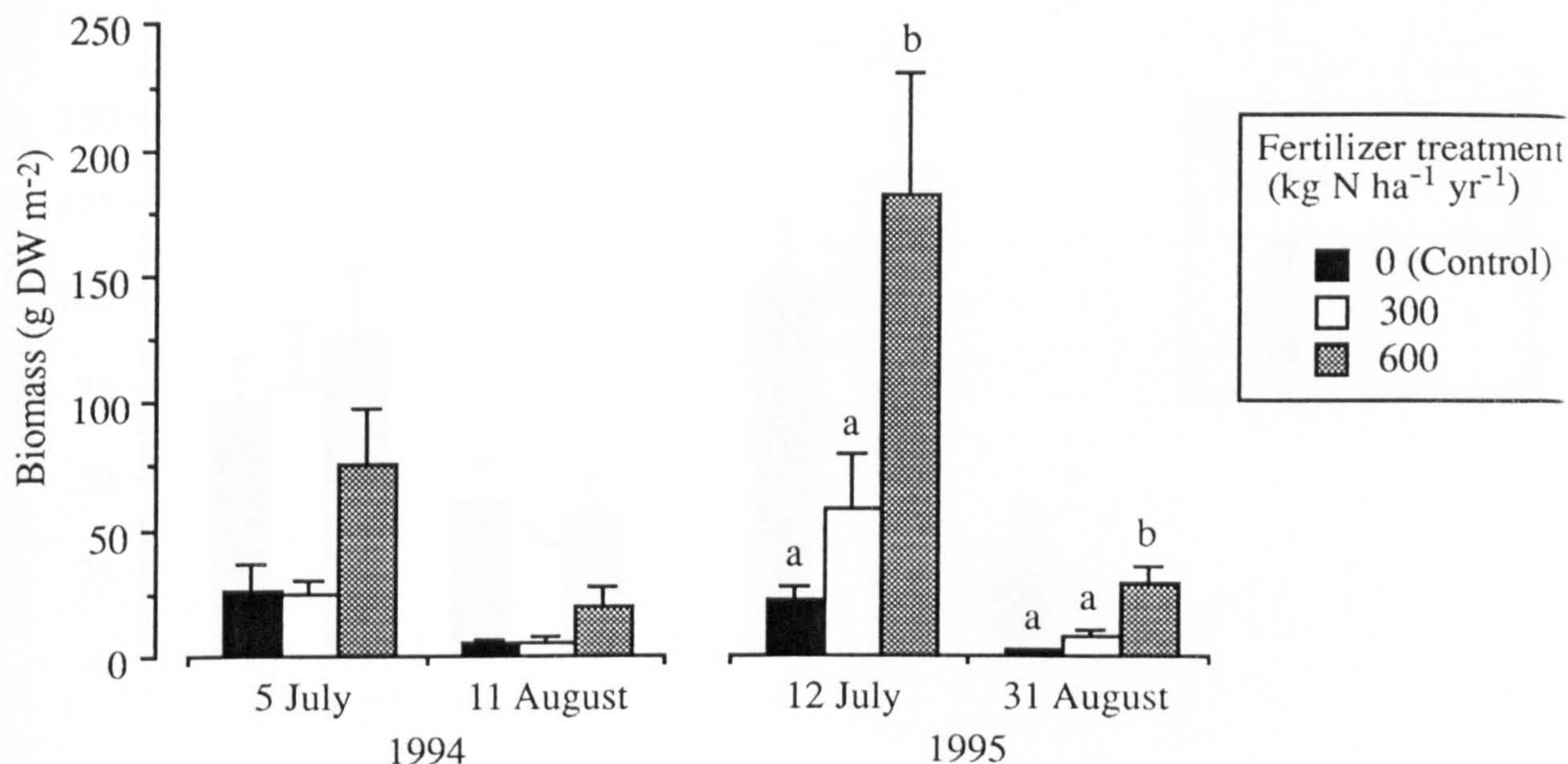


Figure 6.24 Effects of fertilizer N treatments on above-ground forb production (not including *Sanguisorba officinalis*) at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.

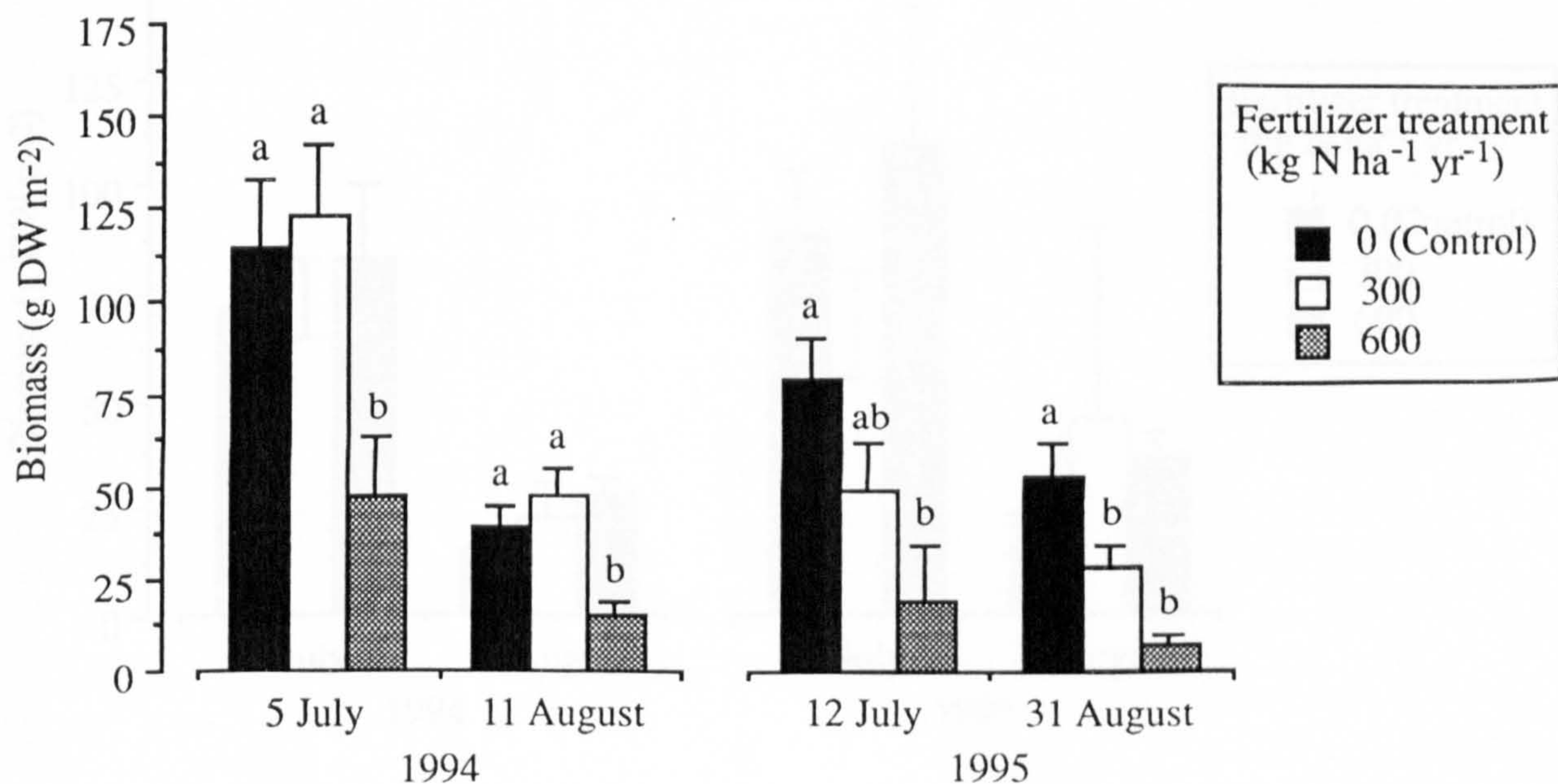


Figure 6.25 Effects of fertilizer N treatments on above-ground production of *Festuca rubra* at Lužnice in 1994-5. Data are mean values (n=6) +1SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed.

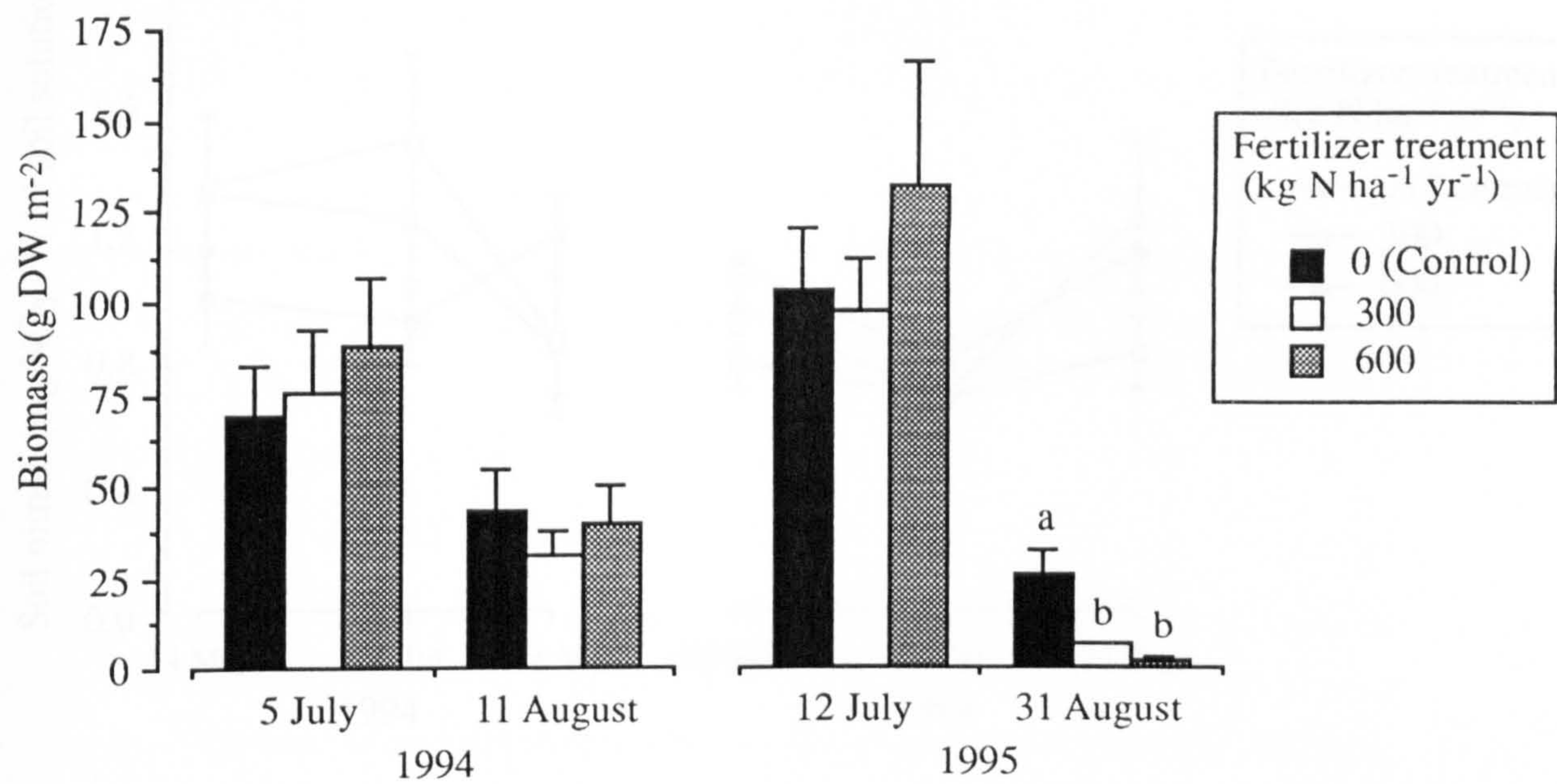


Figure 6.26 Effects of fertilizer N treatments on above-ground production of *Sanguisorba officinalis* at Lužnice in 1994-5. Data are mean values (n=6) +1SE. For each date no significant treatment difference was observed ($P<0.05$, ANOVA).

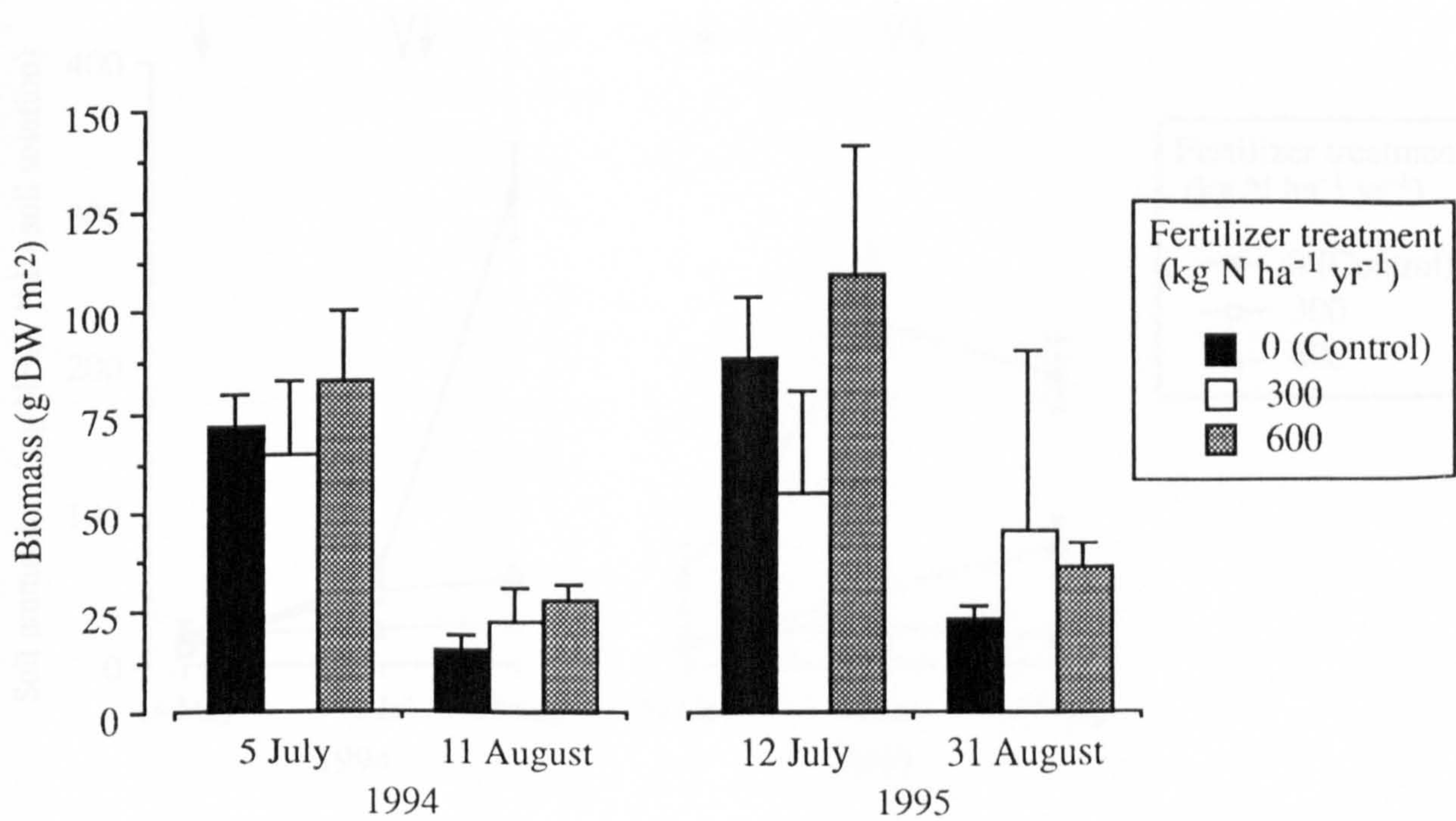


Figure 6.27 Effects of fertilizer N treatments on soil nitrate-nitrogen at Lužnice in 1994-5. Data are mean values ($n=3$) ± 1 SE. Arrows indicate timings of fertilizer application; V indicates timings of cutting.

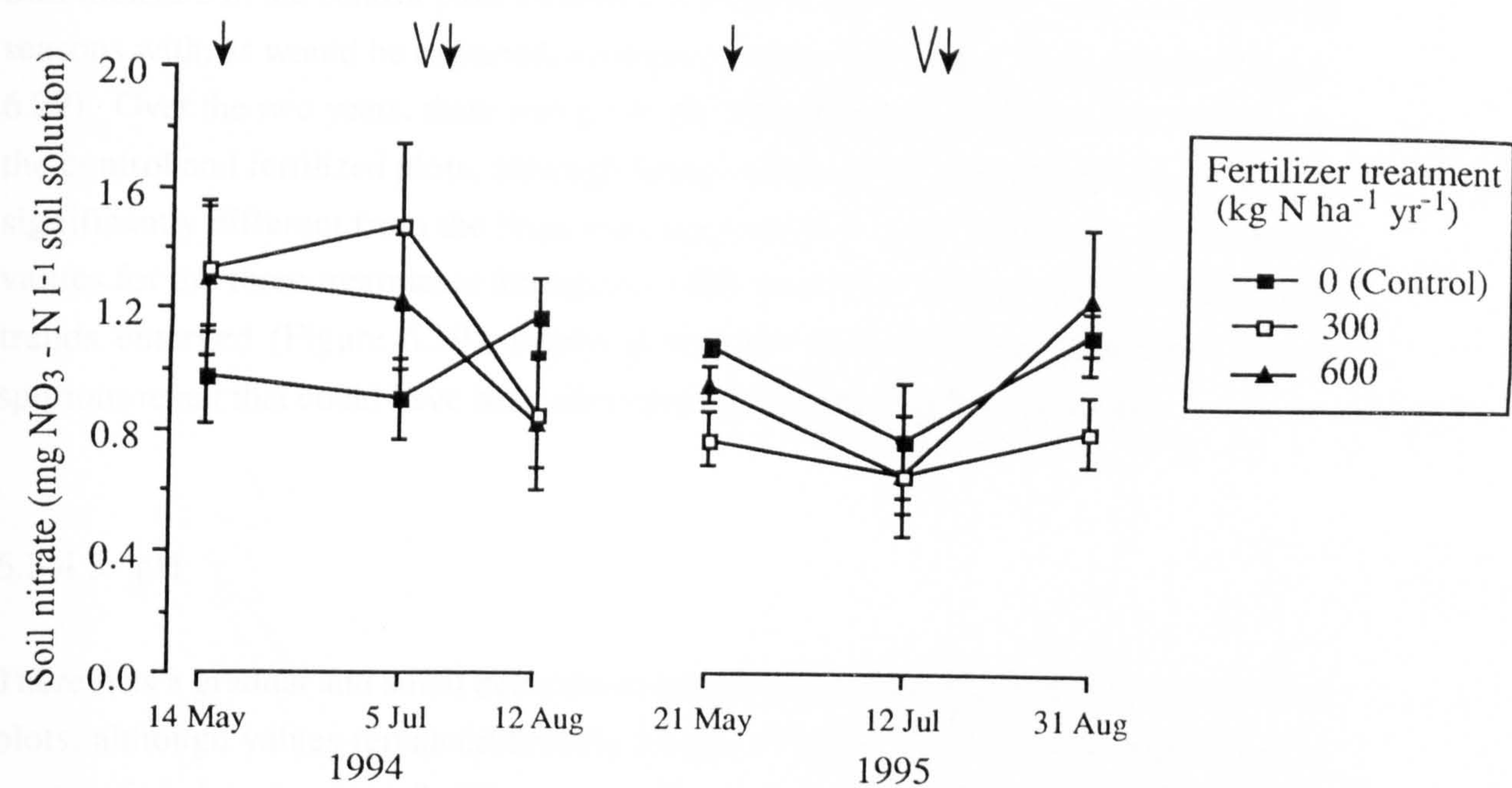
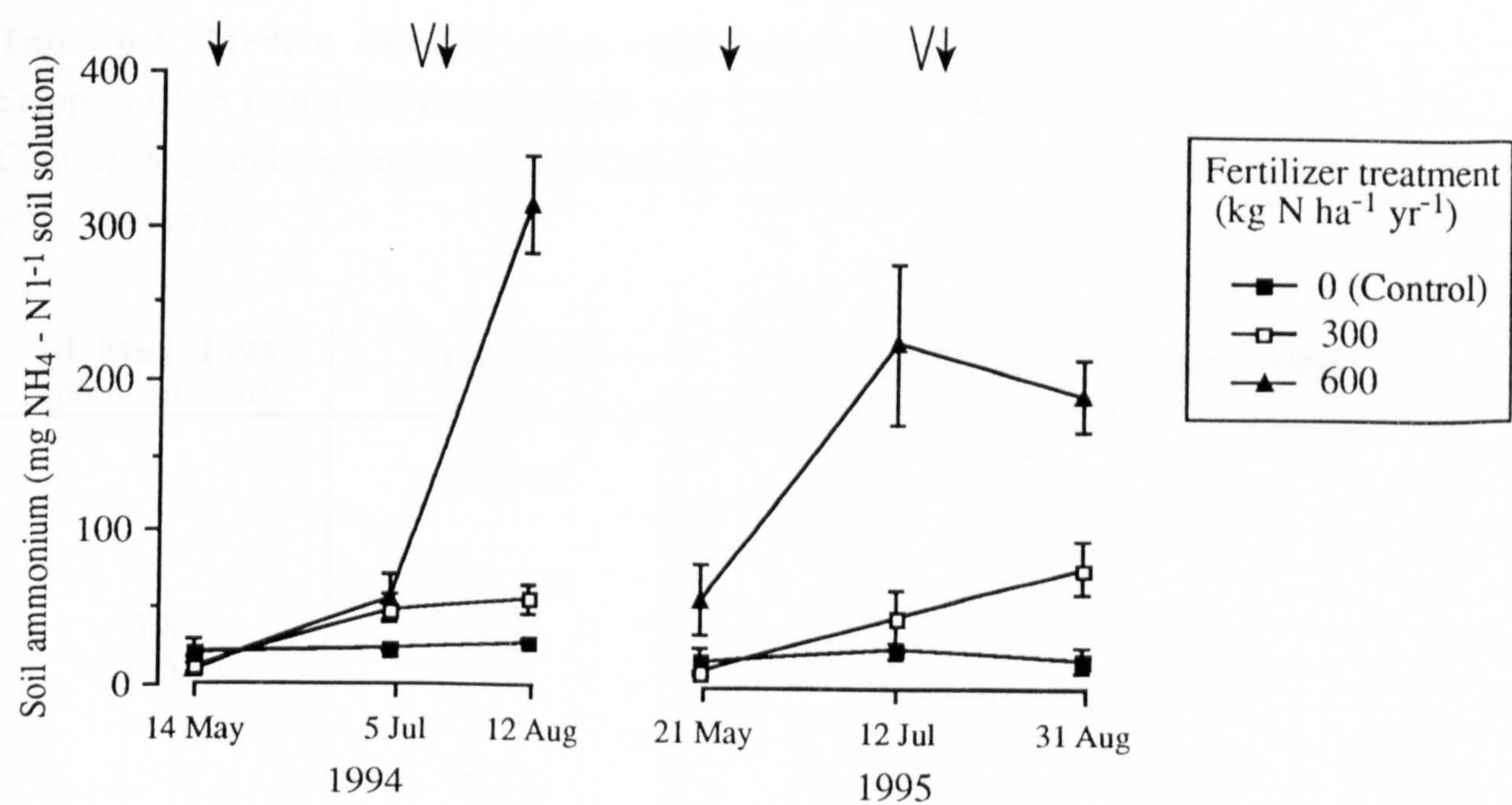


Figure 6.28 Effects of fertilizer N treatments on soil ammonium-nitrogen at Lužnice in 1994-5. Data are mean values ($n=3$) ± 1 SE. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



6.3.4.2 Moisture

Soil moisture in the control plots showed a consistent pattern between the two sampling seasons with, as would be expected, minimum values exhibited in mid-summer (Figure 6.29). Over the two years, there was generally little difference between soil moisture in the control and fertilized plots, although lower values in the control plots in 1994 were significantly different from the N₃₀₀ and N₆₀₀ values in July. However, soil moisture values for the three treatments throughout 1995 were very similar and no longer term trends emerged (Figure 6.29), implying that the one significant difference was a spurious result that could have been eliminated by greater sample replication.

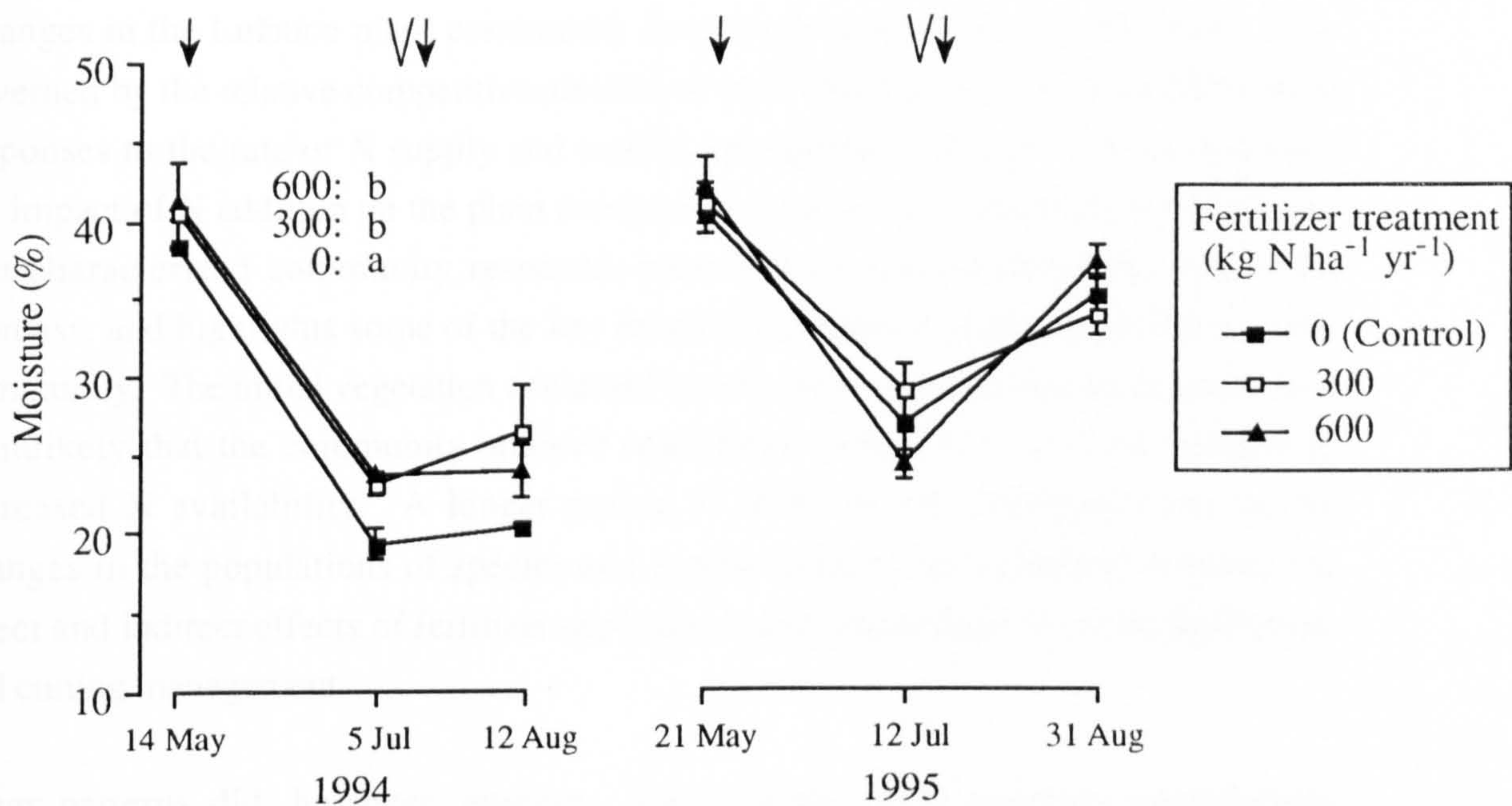
6.3.4.3 pH

There was a gradual and small decrease in soil pH during the experiment in the control plots, although values remained broadly neutral (Table 6.3). In the fertilized plots, a progressive decrease in soil pH was recorded, proportional to the rate of N addition. Thus acidification was most rapid and greatest for the N₆₀₀ treatment and less in the N₃₀₀ plots (Table 6.3). By the end of the two years of the experiment, soil in the fertilized plots had become mildly acidic.

Table 6.3 Median soil pH values (and range) at the Lužnice study site. Samples taken from 0-15 cm soil depth. $n = 6$, except 10 May 1994 when $n = 10$. Control, N₃₀₀ and N₆₀₀ refer to fertilizer application rates of 0, 300 and 600 kg N ha⁻¹ yr⁻¹ respectively.

10 May 1994 (pre-treatment)	Treatment	17 May 1995	27 August 1995
	Control	6.6 (6.4-6.7)	6.4 (6.3-6.5)
6.8 (6.6-6.9)	N ₃₀₀	6.2 (6.0-6.5)	5.5 (5.4-5.8)
	N ₆₀₀	5.9 (5.3-6.3)	5.4 (5.1-5.6)

Figure 6.29 Effects of fertilizer N treatments on soil moisture at Lužnice in 1994-5. Data are mean values ($n=6$) ± 1 SE. For each date, values that do not differ significantly ($P<0.05$, ANOVA, Tukey's test) have a letter in common (a, b or c). The outcome of the test is shown only if significant treatment difference was observed. Arrows indicate timings of fertilizer application; V indicates timings of cutting.



6.4 Discussion

This study elucidated in detail the short-term impact of N addition and the effects of cutting management on the Lužnice flood-meadow plant community, including identifying fine-level responses of individual species.

6.4.1 Impact of N addition

Changes in the Lužnice plant community described during this two-year study were governed by the relative competitive abilities of individual species and their differential responses to the rate of N supply and cutting management. Figure 6.30 summarizes the impact of N addition on the plant community. It illustrates the sequence of phases that characterized community response, measured by species diversity, cover and biomass, and highlights some of the key relationships between the components of the community. The initial vegetation contained mostly slow-growing perennial plants so it is unlikely that the community attained equilibrium within two years in relation to increased N availability. A longer period of study would distinguish any cyclic changes in the populations of species and enable further discrimination between the direct and indirect effects of fertilizer application, and interactions between fertilization and cutting management.

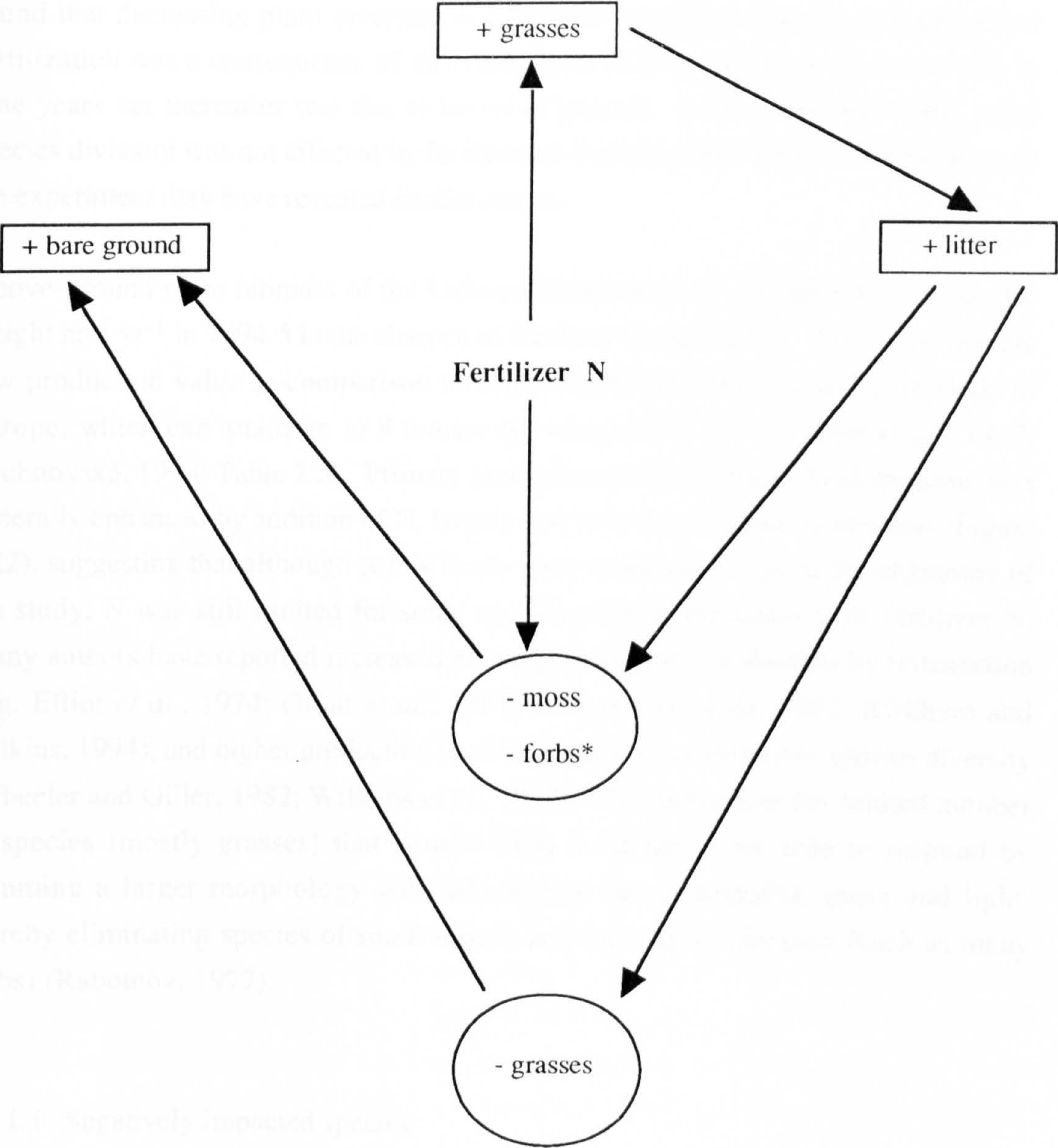
Clear patterns did, however, emerge. Two seasons of N addition considerably impacted community structure, including reductions in diversity and altered abundance hierarchies. Fertilization initially stimulated grasses, which increased cover and biomass and may have displaced forbs and moss, and subsequently contributed to enhanced litter cover (Figure 6.30). Transient grass dominance was curtailed, however, by litter accumulation which restricted grass cover and production. Fertilization directly negatively impacted forb species richness, cover and biomass, and moss cover and biomass. Elimination and suppression of plants promoted bare ground. Increased litter cover may also have constrained moss and forb cover and production, and negatively affected forb species diversity. The cover and production of *Sanguisorba officinalis*, another major constituent of the community, did not show any trends in relation to fertilization over the period of study.

A survey of the Lužnice flood-meadow community carried out in May 1994 as part of this study identified up to 31 vascular plant species m^{-2} (and a mean of 25 species m^{-2}), affirming it as being of considerable floristic diversity in relation to other

Figure 6.30 Scheme indicating main responses of the Luznice flood-meadow plant community to the addition of fertilizer N

⊕ = positive response; ⊖ = negative response. For clarity, the diagram does not include possible changes mediated through competitive relations e.g. a positive response by grasses impacting negatively on forbs and moss.

* the forbs group does not include *Sanguisorba officinalis*, for which no clear trends were discernible.



temperate semi-natural grasslands (Grime, 1973b; Persson, 1984; Willems *et al.*, 1993; Table 7.1). The reduction in plant species diversity through the addition of N recorded during this experiment (Figure 6.1) conforms with the majority of similar studies of species-rich grasslands in Europe and elsewhere (e.g. Williams, 1978; Tilman, 1987; Willems *et al.*, 1993). In particular, the significant decrease in forb diversity in this study (Figure 6.3) concurs with a range of published information. For example, Traczyk *et al.* (1976) reported a reduction in forb species from 22 to nine after two years of adding 680 kg N ha⁻¹ yr⁻¹ to a Polish meadow. Species diversity in a wet grassland in England declined significantly within three years at 50 kg N ha⁻¹ yr⁻¹, mostly due to a reduction in forbs (Mountford *et al.*, 1993). Van Hecke *et al.* (1981) found that decreasing plant diversity in a Belgian grassland subject to experimental fertilization was a consequence of the elimination of forb species in the initial five to nine years but thereafter was due to losses of grasses. In this two year study, grass species diversity was not affected by fertilization but it is possible that a continuation of the experiment may have revealed similar results.

Above-ground plant biomass of the Lužnice flood-meadow averaged 4.7 tonnes dry weight ha⁻¹ yr⁻¹ in 1994-5 in the absence of fertilizer N application. This is a relatively low production value in comparison to other unfertilized semi-natural grasslands in Europe, which can attain up to 9 tonnes dry weight ha⁻¹ yr⁻¹ (Elberse *et al.*, 1993; Rychnovská, 1993; Table 7.2). Primary production of the Lužnice flood-meadow was generally enhanced by addition of N, largely due to increased grass production (Figure 6.22), suggesting that although soil N levels were moderately high at the beginning of the study, N was still limited for some species prior to the addition of fertilizer N. Many authors have reported increased above-ground grass production by fertilization (e.g. Elliot *et al.*, 1974; Grant *et al.*, 1981; Oomes and Mooi, 1981; Kirkham and Wilkins, 1994), and higher production is often negatively correlated to species diversity (Wheeler and Giller, 1982; Willems *et al.*, 1993). This is because the limited number of species (mostly grasses) that benefit from fertilization are able to respond by assuming a larger morphology with which they can monopolize space and light, thereby eliminating species of small stature and low shade tolerance (such as many forbs) (Rabotnov, 1977).

6.4.1.1 Negatively impacted species

The species that were negatively impacted by fertilization in this study are characterized by being of small stature, adapted to conditions of reasonably low nutrient status, leguminous, or a combination of these. Small leguminous plants, for example

Trifolium pratense and *T. repens*, are able to bacterially fix atmospheric N which gives them a competitive advantage over other plants in relatively low nutrient environments, such as many species-rich grasslands (Robson *et al.*, 1989). However, the ability of bacteria to fix atmospheric N declines with increasing supply of mineral N (Rabotnov, 1977). Consequently, legumes are extremely sensitive to nitrogenous fertilizer, competing poorly against other species, particularly grasses, when N levels are high (Mountford *et al.*, 1993). For example, the dense cover of grasses that developed following applications of ammonium sulphate fertilizer eliminated all leguminous species from a diverse grassland in England (Thurston, 1969). In New Zealand, increased grass biomass in response to N addition depressed legume growth in a cut grassland (Grant *et al.*, 1981). Furthermore, all leguminous species were lost from a series of meadows in Poland within seven years at rates of 280 kg N ha⁻¹ yr⁻¹ (Traczyk *et al.*, 1984). In this Czech study, both *T. pratense* and *T. repens* declined rapidly with elevated N supply, the former ultimately being eliminated from the fertilized plots. This accords with Elliot *et al.* (1974), Rabotnov (1977), Oomes and Mooi (1981) and Kirkham *et al.* (1996) who all measured reductions in cover or biomass of these *Trifolium* species in managed grasslands as a consequence of fertilization.

Other forbs eliminated or substantially suppressed by fertilization during this study of the Lužnice grassland and generally acknowledged to be negatively affected by fertilizer N include *Ranunculus acris*, *Plantago lanceolata*, *Leontodon autumnalis* and *Taraxacum officinale* agg. (Traczyk *et al.*, 1976; Williams, 1978; Oomes and Mooi, 1981; Fryček *et al.*, 1992; Mountford *et al.*, 1993).

Amongst the grasses, *Festuca rubra* was unusual in being negatively impacted by fertilization at both rates (300 and 600 kg N ha⁻¹ yr⁻¹) in this two-year study. However, this accords with published information which indicates that this species is sensitive to N, being disadvantaged not only by high rates of N addition but also low rates supplied over a longer period. Fryček *et al.* (1992) found that the cover of *F. rubra* in a Czech grassland was inversely proportional to the amount of fertilizer N applied during the previous 12 years: a cover value of 29% for this species was recorded where no fertilizer had been applied, compared to 7% at 160 kg N ha⁻¹ yr⁻¹ and 1% at 320 kg N ha⁻¹ yr⁻¹. Traczyk *et al.* (1976) also observed that *F. rubra* did not tolerate high rates of fertilization (i.e. 640 kg N ha⁻¹ yr⁻¹) but was able to withstand lower rates of 280 kg ha⁻¹ yr⁻¹ for up to two years. However, after seven years at this lower rate the species had declined (Traczyk *et al.*, 1984), suggesting, as in this study, a tolerance threshold was reached. The autecology of this species is described in section 7.3.5.

Moss cover and biomass were significantly depressed by increased N availability in this study (Figures 6.8 and 6.21). Mosses are small, low-growing plants whose expansion coincides with the moist conditions of spring and autumn (Al-Mufti *et al.*, 1977). They may therefore have been deleteriously affected by fertilization stimulating the rapid growth of grasses in spring and early summer. Although there is no indication in this study that depleted soil moisture caused by enhanced vascular plant growth limited moss development (as moisture values remained similar in fertilized and unfertilized swards, Figure 6.29), it is known that they are unable to compete with increased shading by grasses in fertilized grasslands (Mountford *et al.*, 1994). In addition, Rabotnov (1977) noted that fertilizers have a herbicidal effect on mosses.

6.4.1.2 Positively impacted species

The limited number of plant species that substantially benefitted from increased N supply to the Lužnice floodplain were all grasses (Table 6.2). Other comparable studies also report a positive response by many indigenous grasses to fertilization (particularly up to approximately 300 kg N ha⁻¹ yr⁻¹) in relation to the maintenance of grass species diversity (Traczyk *et al.*, 1976), enhanced cover (Titlyanova *et al.*, 1990; Mountford *et al.*, 1993) and especially increased biomass (Grant *et al.*, 1981; Traczyk *et al.*, 1984; Willems *et al.*, 1993).

In this study, the most consistently positive response to fertilization was shown by the grass *Agrostis capillaris*, particularly at the higher rate of 600 kg N ha⁻¹ yr⁻¹ (Figures 6.14 and 6.23). Evidence from the literature in relation to this is somewhat contradictory but indicates that this species can benefit from increased nutrient availability in communities characterized by low soil fertility and/or low plant production when superior competitors are absent. For example, Mahmoud and Grime (1976) found that *A. capillaris* can outcompete species restricted to unproductive grasslands for N, but not grasses that are dominant in productive sites. However, *A. capillaris* did not perform well in competition with other grasses in an experimental nutrient gradient (Austin and Austin, 1980) although Fisher *et al.* (1996) showed that it can compete effectively with a range of forb species. Mountford *et al.* (1993) recorded a negative trend in cover for this species in relation to fertilization of a moderately productive wet meadow in England. However, *A. capillaris* biomass increased when agriculturally unproductive managed grasslands in New Zealand (Luscombe *et al.*, 1981) and Serbia (Rabotnov, 1977) were fertilized. The species was also favoured in a fertilized Belgian grassland, apparently benefitting from the reduction of other species by being able to rapidly vegetatively expand into the gaps (van Hecke *et al.*, 1981).

Thurston (1969) observed that *A. capillaris* was dominant on experimental grassland plots that had received ammonium sulphate as fertilizer and had consequently acidified, and the plant is known to be able to tolerate phosphorus and potassium deficiency (Grant *et al.*, 1981). It is therefore likely that *A. capillaris* was favoured by fertilizer N application in this study, despite the moderately high background levels of soil N at the Lužnice site, because its short-term ability to compete for N was superior to other members of the plant community (see section 7.3.4). The species may have been further advantaged by its tolerance of the slightly acidic soil conditions that developed due to ammonium sulphate application and also any shortage of nutrients other than N that may have arisen as a result of increased production.

6.4.1.3 *Sanguisorba officinalis*

Sanguisorba officinalis, a tall and robust forb (section 7.3.6) that formed a prominent component of the Lužnice vegetation, was not demonstrably affected by fertilization in this study. In conditions of increased N availability, this species seemed able to compete with grasses for resources such as light and space. Baker (1937) observed that *S. officinalis* was often abundant in flood-meadows as it shaded the grasses with its dense foliage and overtopped all other species even when the vegetation formed a closed sward prior to cutting. An experimental assessment of the production of grassland plant species also found that *S. officinalis* competed effectively with grasses (Fisher *et al.*, 1996) and the species was found to persist in the early stages of grassland abandonment, despite competition from tall sedges and woody species (Fossati and Pautou, 1989).

6.4.1.4 Differential impact of N addition

The impact of fertilization on the plant community is governed by the differential spatial and temporal response to N of individual plant species. In this research, species diversity (e.g. forb richness, Figure 6.3) exhibited an intermediate value at the lower rate of N supply compared with the higher rate and where N was not added, a pattern which concurs with similar studies (e.g. Traczyk *et al.*, 1984; Mountford *et al.*, 1993; Tilman, 1993). The degree of impact of N on cover (e.g. litter, moss, grass and forbs) and production (moss, grass and forbs), whether positive or negative, also tended to be proportional to the amount and duration of fertilization, a trend which is reinforced by other comparable research (Frame, 1991; Fryčěk *et al.*, 1992; Mountford *et al.*, 1993; Tilman, 1993).

The form of the relationship between increasing N availability and grassland production usually follows an inverse quadratic model, with a linear response at low N supply, reaching a maximum and subsequently declining at high rates of addition (Morrison, 1987). For example, a botanically diverse wet meadow in England exhibited enhanced production up to $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, but responded negatively to increased N above this (Kirkham and Wilkins, 1994). Steenbergen (1977) also found a substantial increase in production in a Dutch grassland up to a rate of $300 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, but that above this the increase was much less pronounced. The reduced biomass recorded in the fertilized plots at the end of this study may therefore indicate that the Lužnice grassland behaved in a similar way, and that the optimum rate of N supply for sustained enhanced production was below those used in the experiment. Values recorded for soil N support this hypothesis, as they show that considerable concentrations of ammonium accumulated in the soil during the experiment (Figure 6.28).

In this study, a number of species showed a response proportional to the rates of fertilizer N applied over two seasons, whether they were encouraged (e.g. *Deschampsia cespitosa*, Figure 6.13) or negatively impacted (e.g. *Plantago lanceolata*, Figure 6.17) by increased N. Some species apparently had their optimum at intermediate levels, e.g. *Poa pratensis* which increased at the lower rate of N addition but was not promoted by the higher one (Table 6.2). *Rumex acetosa* was suppressed at $600 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for two years but was not disadvantaged by $300 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Figure 6.19), suggesting that for this species a threshold exists between these rates above which the impact of increased nitrogen supply is detrimental. Experiments undertaken on species-rich wetland hay meadows in England show that this species may be stimulated by ammonium at lower levels (i.e. $50\text{--}200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) especially when sufficient phosphorous is available (Mountford *et al.*, 1993; Kirkham *et al.*, 1996). Austin and Austin (1980) assessed the production response to nutrient availability of a range of grasses and concluded that most species, including *Holcus lanatus* which increased at the intermediate N rate in this study (Table 6.2), exhibited maximum production at intermediate rather than high levels of nutrient supply. Temporal patterns of species response to N were explored by Tilman (1987) who found that the relative abundances of plant species in a developing grassland changed significantly within one year along an experimental nutrient gradient, and differentiated in their distributions in relation to nutrient supply within four years. Species that reached peak relative abundance in high N treatments in the first year tended to be rare in all but the low N treatments three years later. This resonates with the results from this study, where the peak abundance of grasses in the fertilized plots was superceded

by their decline and an increase in litter, particularly in the plots receiving higher rates of N.

6.4.2 Mechanisms of fertilizer N impact

Changes in the Lužnice plant community structure due to fertilization, mediated through species elimination and variations in competitive abilities, are likely to be as a result of intensified competition for resources and litter accumulation. The toxic and acidifying effects of fertilization using ammonium sulphate are also implicated.

6.4.2.1 Resource competition

There is strong evidence from many grassland studies that the increased above-ground plant production that usually follows fertilization intensifies competition for light and other resources, leading to increased mortality and botanical change through competitive exclusion (e.g. Rabotnov, 1977; Bobbink and Willems, 1987; Mountford *et al.*, 1994). In this study of the Lužnice flood-meadow, mosses and low-growing forbs (e.g. *Potentilla erecta* and *Cerastium fontanum*) were suppressed by fertilization, apparently unable to compete for light or space with the increased grass biomass and dense, tall canopy. Although many grassland species are able to regenerate vegetatively (Grime *et al.*, 1988), some, e.g. *Plantago lanceolata* (Kirkham and Tallowin, 1995), more commonly do so by seed. They therefore depend on light for germination and establishment suggesting that the decline of species in the Lužnice grassland through fertilization may be related to the enhanced spring grass growth reducing light penetration and inhibiting the survival of other plants. Such strong competition for light inherently favoured the taller, erect species, such as *Sanguisorba officinalis* and some grasses. Species of later phenological development (e.g. *Ranunculus acris*) may also have been disadvantaged by the rapid early season growth of grasses and *S. officinalis*.

Another consequence of increased above-ground production can be the promotion of bare ground. Pasternak-Kuśmierska (1984) noted that the expansion of the grass *Dactylis glomerata* in fertilized grassland resulted in the formation of unvegetated patches, probably due to shading by the abundant biomass. In this study the extent of bare ground also increased following significantly increased biomass production in the sward receiving higher levels of N.

It is also possible that increased production by plants receiving fertilizer N in this study led to deficiencies in plants that were unable to compete effectively by enhancing their uptake of other essential elements, such as phosphorus (P) and potassium (K). The effects of nutrient deficiencies on fertilized species-rich grasslands have been demonstrated by Kirkham *et al.* (1996). They found that increases in the percentage composition and biomass production of several species, including *Holcus lanatus* and *Rumex acetosa*, were more closely associated with the application of P and K than N, indicating that deficiencies in these nutrients can restrict the presence of species.

The greater competitiveness of mesotrophic species under additional N and the increased evapotranspiration of the more productive vegetation has also been implicated in the botanical change of meadows (Rabotnov, 1977). Although under these conditions soil moisture may be limiting, enhanced productivity in this study did not deplete soil moisture (Figure 6.29), possibly because plants utilized deeper water reserves or those that responded positively to added N were able to use water more efficiently (Rabotnov, 1977; Ellenberg, 1988).

6.4.2.2 Litter accumulation

In unfertilized conditions, floodplain meadows in the Czech Republic showed an equilibrium between litter production and decomposition and removal (Tesařová, 1976). Bakker (1989) also found that two managed grasslands, characterized by *Holcus lanatus* and *Leontodon autumnalis*, exhibited no net accumulation of litter unless fertilizers were applied. Clearly, fertilization can upset the equilibrium of litter cycling when the production rate of dead plant material exceeds the decomposition rate. A number of studies, in common with this one, have found that increased plant biomass as a result of nutrient enrichment is associated with subsequent litter accumulation and further that litter mass is positively correlated with the rate of N addition (Knapp and Seastadt, 1986; Tilman, 1987; Tilman, 1993). Moreover, ammonium sulphate, which was applied in this study, can affect production and decomposition processes. Ter Heerdt *et al.* (1991) found that ammonium sulphate stimulated grass production and that grass litter (including from *Agrostis capillaris* and *Holcus lanatus* which both increased due to fertilization in this study) may decay more slowly than forb material. Ammonium nutrition also promotes earlier maturation and senescence (Haynes and Goh, 1978) which may also have generated litter development and accumulation in this study.

Accumulated plant litter has generally been found to have a negative impact on species diversity and biomass production in a range of non-forested ecosystems, including chalk grasslands, wetlands, old fields and prairie grasslands (Xiong and Nilsson, 1997). It can induce floristic change by impacting on the thermal and moisture regimes of the soil surface layers and creating a physical barrier to incoming seeds, emerging shoots and light (Facelli and Pickett, 1991). Litter can also bury and suppress established vegetation (Nilsson *et al.*, 1993), delaying growth in spring and excluding small plants, especially forbs (Weaver and Rowland, 1952; Facelli and Pickett, 1991). Bakker (1989) reported a decrease in the cover of many grassland species by litter accumulation, including mosses, *Festuca rubra*, *Trifolium repens* and *Cardamine pratensis*, all of which also declined in the Lužnice flood-meadow where litter accumulated. It is probable that the dense layer of litter that developed in the fertilized grassland by the end of the study contributed to its lower plant species diversity and limited biomass, also affecting community composition by reducing the cover of forbs and most grass species.

6.4.2.3 Toxic effects

Ammonium sulphate fertilizer, which was applied in this study, is widely used to increase grassland production in agriculture because ammonia is a rapidly available form of nitrogen for plant growth (Lewis, 1986; Wild, 1988). However, ammonia can be toxic to plants at the concentrations that accumulated during the study in the experimentally fertilized soils (Lewis, 1986) because it can restrict photosynthetic activity and suppress the uptake of cations and nitrate (Haynes and Goh, 1978). Ammonium toxicity is characterized by an immediate reduction in growth rate and leaf necrosis, resulting in small, weak plants or death of the entire plant (Maynard and Barker, 1969). However, species vary greatly in their susceptibility to ammonium toxicity, suggesting that any toxic effects of ammonium sulphate on the Lužnice plant community may have been selective. For example, *Holcus lanatus* can tolerate a proportion of its nitrogen supply as ammonium (McGrath, 1983), and this was one of the few species that was favoured by fertilization in this study. Haynes and Goh (1978) also noted that plants supplied with ammonium are more susceptible to water stress during periods of high transpiration, so by applying ammonium sulphate in mid-summer in this experiment any other detrimental effects may have been exacerbated.

6.4.2.4 Soil acidification

The application of ammonium sulphate as fertilizer can cause acidification of the soil which can retard plant production and induce botanical change. Johnston *et al.* (1986) reported that annual applications of ammonium sulphate fertilizer to a mixed species, circum-neutral grassland led to a rapid initial decrease in soil pH which then slowed to approach an equilibrium of approximately 3.6. This eliminated all except the most acid-tolerant grasses and remaining vegetation was co-dominated by *Agrostis capillaris* and *Holcus lanatus* (Thurston, 1969). Such a profound effect may have been due to the leaching of heavy metals in the soil that occurs below pH 5 which are toxic to all but a restricted range of calcifuge species (Gigon and Rorison, 1972). Although acidification occurred during this experiment, soil pH remained above 5 (Table 6.3), a tolerable level for many plants (Grime *et al.*, 1988), so it is unlikely to have had a profound effect on botanical composition during the two years of study.

6.4.2.5 Interactions between mechanisms

Interactions between the factors involved in the botanical changes measured in the Lužnice grassland may have compounded and perpetuated their impact. For example, acidification of the soil surface layers can restrict litter decomposition (Facelli and Pickett, 1991) encouraging the accumulation of litter. It has been suggested, also, that the toxic effects of ammonium are more adverse at low compared to high pH and that in acidic conditions nitrification is slowed such that ammonium accumulates and inhibits growth (Gigon and Rorison, 1972; Lewis, 1986). Given the limited acidification of fertilized plots during this short-term study (section 6.4.2.4; Table 6.3), this interaction is unlikely to have been an important process influencing plant community composition.

6.4.3 Effects of cutting management

It is widely recognized that cutting management tends to maintain plant species diversity in European grasslands (Oomes and Mooi, 1981; Parr and Way, 1988; Bakker, 1989), especially when the first annual cut takes place in mid to late summer for a hay crop (Smith *et al.*, 1996). This cutting favours less competitive plants and provides niches for many subsidiary species, such as mosses and many forbs, to co-exist with the community dominants, which are often grasses that achieve a high biomass in the summer (Bakker, 1989). The plant species that comprise the Lužnice grassland

community are adapted to defoliation by annual cutting management, all species except *Campanula patula* (Table 2.4) having a perennial capacity and able to reproduce vegetatively. Consequently, plant species richness during the two study seasons should not have been significantly impacted by cutting, and results supported this (Figure 6.1). This accords with Kirkham and Tallowin (1995) who found that species in a hay meadow that regenerate vegetatively, including *Festuca rubra* and *Rumex acetosa* which were both prominent in this study, were not affected by variations in cutting date and that altering the date caused no significant change in species diversity.

In contrast, cessation of cutting management generally leads to tall competitive species (often grasses) dominating and decreased plant species diversity, probably due to reduced light penetration (Regnéll, 1980; Oomes and Mooi, 1981; Bakker, 1989; chapter 3). The Lužnice study site was not managed for a year prior to the start of this experiment. However, it is unlikely that this period without management would have been sufficient to provoke decreased species richness or significant botanical change through competitive exclusion (Rychnovská *et al.*, 1994). Bakker (1989) ascertained that in Europe the earliest reported decrease in plant species diversity following abandonment was after three years and for most grasslands diversity did not decrease until the fourth year or later. However, reinstatement of cutting management to the site during the experiment may have reduced the accumulated biomass of coarse competitive species and encouraged a range of finer and low-growing plants. This would account for the increases in species diversity measured by Simpson's index, in forb cover and moss cover and biomass observed in the unfertilized plots during the study, particularly after cutting in the second year. This suggestion is supported by the work of Oomes and Mooi (1981) who reported that cutting a wet grassland in mid to late summer decreased dominance of grasses and the density of the vegetation, producing an open sward in autumn and spring, and therefore providing regeneration niches that are important for maintaining species diversity. Moreover, Straškrabová and Prach (1998) reinstated a regular cutting regime to an abandoned Lužnice floodplain grassland located within a kilometre of this study site. They observed that many forbs newly established in the restored grassland, including a number that also increased in the unfertilized plots in this study, e.g. *Rumex acetosa*, *Plantago lanceolata*, *Achillea millefolium*, *Leontodon autumnalis* and *Trifolium pratense*.

The dynamics of the Lužnice plant community gravitated around the phenology and morphology of *Sanguisorba officinalis*, particularly the impact of, and its response to, cutting. The species is tolerant of hay cutting but not grazing (Baker, 1937) and is a characteristic constituent of European hay meadow communities (Ellenberg, 1988). In the Lužnice floodplain, *S. officinalis* plants developed rapidly in spring, overtopping

most other species by mid-summer, prior to the cut. Although cutting removed this erect biomass, allowing smaller forbs and moss to expand in the unfertilized plots, *S. officinalis* was able to sustain a notable presence, probably by utilizing its underground carbohydrate reserves. Cutting therefore acted as a periodic disturbance that gave a selective advantage to *S. officinalis* by slowing competitive displacement by grasses. Indeed, Fisher *et al.* (1996) found that *S. officinalis* competed effectively with a variety of grass species in an experimental sward that was cut three times per year.

6.4.4 Interactions between fertilizer N addition and cutting management

In this study, the effects of fertilizer application and management by cutting for hay may have interacted to intensify some of their individual impacts on the vegetation. This has also been noted by Rabotnov (1977) who reported that fertilization compounded the shading effects of the dense canopy prior to cutting. The combination of fertilization and cutting could also have promoted litter deposition and accumulation if the increased biomass caused by added N was not effectively removed as hay. An 11-year experiment in a botanically diverse grassland that involved retention rather than removal of the material cut for hay showed a significant decline in species diversity and a decrease in the cover of *Festuca rubra* (Bakker, 1989). Also, in this study cutting may have imposed an additional negative impact on plants already weakened by ammonium sulphate toxicity and heightened competition for limited resources.

6.5 Conclusion

Grime (1979), Huston (1979) and Tilman (1982) have argued that an increase in above-ground plant production increases the intensity of competition for resources, thereby leading to a decline in diversity through competitive exclusion. In the Lužnice flood-meadow community the absence of tall, productive grasses, such as *Dactylis glomerata* and *Lolium perenne* which are superior competitors for nitrogen (Austin and Austin, 1980; Traczyk *et al.*, 1984; Kirkham *et al.*, 1996), allowed other species to benefit, notably *Agrostis capillaris*. However, community stability in relation to increased nitrogen supply was unlikely to have been reached in this two year study. Tilman (1987) suggests that some species, because of rapid rates of vegetative growth, may attain a period of transient dominance on nutrient-rich soils before being displaced by more slowly growing species that are superior competitors for those soils. The accumulations of litter that characterized this research (Figure 6.7), for example, limited plant production and cover at the end of the study, perhaps signalling the end of

community co-dominance by the grasses and encouraging the expansion of bare ground. In the future, this may have been followed by the colonization of new species, perhaps with more ruderal strategies.

The study effectively elucidated at a fine scale the dynamics of the Lužnice flood-meadow plant community in response to fertilizer N addition. Increased nitrogen supply rapidly destabilized community structure, depleting diversity, altering community composition and eventually constraining production as litter accumulated and bare ground appeared (Figure 6.30). Fertilization promoted morphological and community simplification as competitive relations between plants shifted, leading to the dominance of relatively few components, such as some grasses, *Sanguisorba officinalis* and litter, and elimination of subsidiary species, mostly forbs and moss. It therefore provoked a shift from a community in which stress-tolerating narrow-leaved grasses (e.g. *Festuca rubra*) and many low-growing forbs predominated, and more competitive species were constrained (e.g. by regular cutting), to one that was dominated by a limited number of taller competitive species. These species (e.g. *S. officinalis* and *A. capillaris*) are capable of rapid expansion and dense leaf canopies that can displace or constrain smaller or slower-growing species, and generate copious amounts of litter that can also selectively suppress or exclude species. As all ecosystems are affected by energy input, it is therefore probable that increased light interception by the dense canopy and litter layer was a key process impairing ecosystem functioning.

Cutting also changes the competitive relationships in flood-meadow vegetation. It reduces the vigour of the taller-growing species, such as *S. officinalis*, and increases the incidence of light at ground level. Cutting for hay promoted plant diversity in the unfertilized Lužnice community by limiting the expression of dominance, removing biomass from the taller and potentially dominant species (e.g. *S. officinalis* and some grasses), allowing many species to co-exist. The biodiversity value of the meadow was therefore determined by cutting, demonstrating that regular intentional human perturbation of a specific kind is essential for the stability and sustainable management of such ecosystems. This suggests that abandonment, as well as eutrophication and other management practices that degrade biodiversity, would threaten the stability and functioning of flood-meadow ecosystems.

This study has shown that biodiverse flood-meadow plant communities are fragile systems in which regular appropriate human intervention in the form of cutting management can maintain high plant species diversity but that they are extremely sensitive to the rates of nitrogen input that characterizes modern land-use. The rapidity

and extent of community change following nitrogen addition suggests that these systems may provide an early warning of some of the ecological effects of human activities that promote enhanced nitrogen levels, such as eutrophication of groundwater and atmospheric nitrogen pollution.

Chapter 7 Discussion

Floodplain grasslands are an integral component of European biodiversity, supporting distinctive and rare plant communities and species, and high species diversity (Ellenberg, 1988; Joyce and Wade, 1998). They also contribute to the maintenance of river-floodplain ecosystem functions and are of agricultural value (Duffey *et al.*, 1974; Rychnovská, 1993; Straškrabová *et al.*, 1996). Concerns over the rapid decline in floodplain biodiversity associated with human impact, particularly changes in land management, are driving measures for the conservation management and restoration of European floodplain grasslands (Wade and Joyce, 1997). However, factors that control plant community dynamics in floodplain grasslands are poorly understood (Décamps and Tabacchi, 1994). In order to focus conservation efforts and promote sustainable use of the floodplain grassland resource, it is essential that knowledge of the processes controlling biodiversity in floodplain grasslands is improved.

This study elucidated a number of core concepts and key dynamics regulating plant biodiversity in floodplain grasslands by examining responses to the management of a range of floodplain grassland plant communities in Europe (Table 2.5). It featured a field sampling strategy applied meticulously to allow detailed analysis of fine-scaled differences and short-term responses of functional plant groups and key species. Results demonstrated that an understanding of the sensitivity and dynamic properties of plant community processes is critical for the effective implementation of strategies to manage European floodplain grasslands for biodiversity.

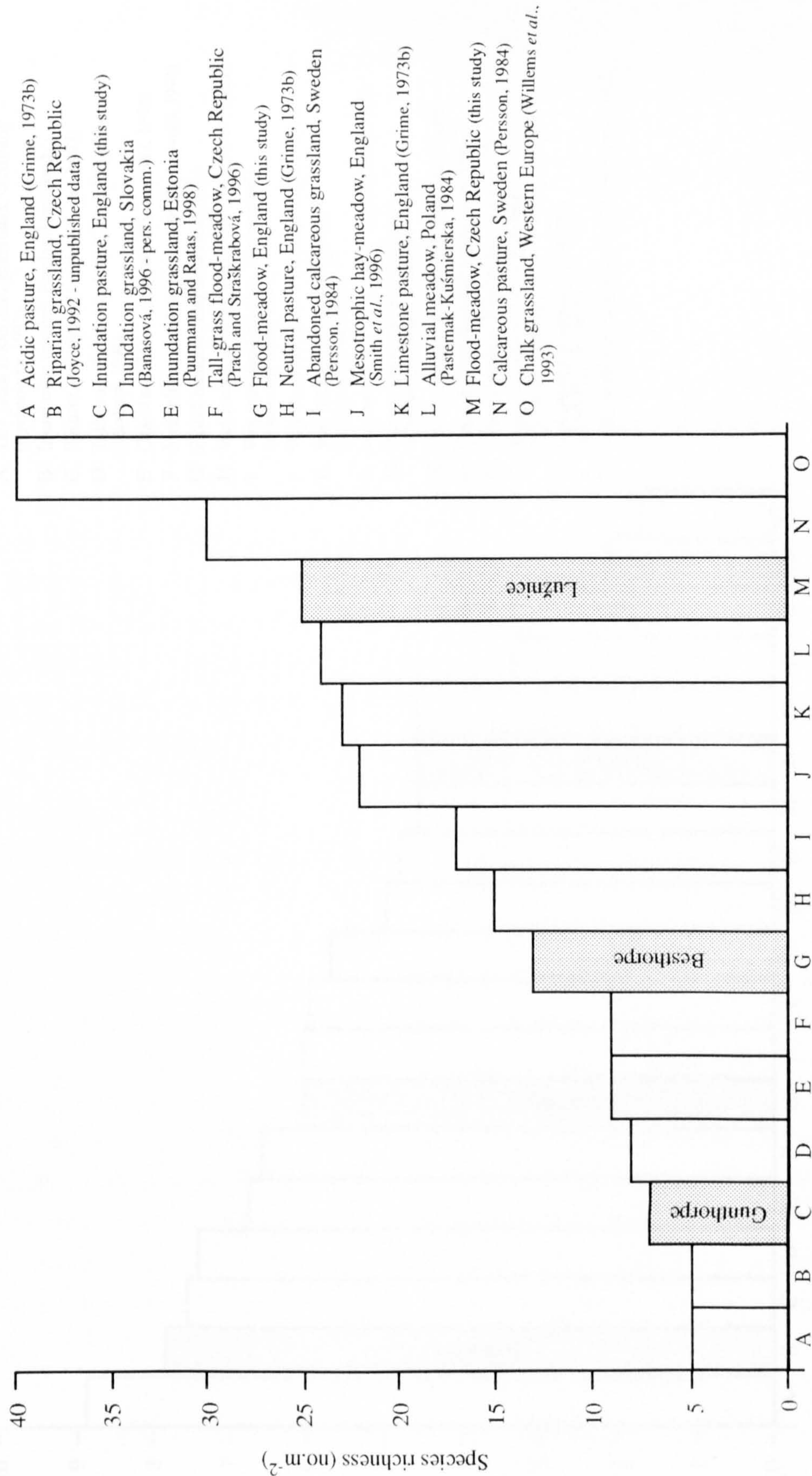
Models of plant competition presented by Grime (1973a, 1979) and developed by Huston (1979) and Tilman (1982), which predict maximal species diversity at intermediate levels of disturbance, stress and/or resource availability (section 1.3), provide a basis from which to elucidate the impacts of management factors on plant community dynamics. A unifying theme of these models is the proposal that high species diversity in plant communities occurs at relatively low levels of plant production. This prediction is examined in relation to floodplain grasslands in the following section (7.1). The management factors that determine plant community diversity and production are discussed in section 7.2, and in section 7.3 the responses of key floodplain grassland plant species to management variations are described. These sections provide the information necessary to develop ecologically sound conservation management and restoration of floodplain grasslands (section 7.4). The thesis is concluded in section 7.5.

7.1 Floodplain grassland plant species diversity and production

Figure 7.1 illustrates the plant species diversity of a range of semi-natural grasslands in Europe. In order to establish an effective context for comparison, floodplain and non-floodplain communities are included. Grime *et al.* (1988) asserted that temperate herbaceous communities supporting less than 10 species m^{-2} may be considered species-poor and that communities with more than 20 species m^{-2} demonstrate high diversity. On this basis, grasslands in Europe with acidic soils or subject to frequent or prolonged inundation tend to display low species diversity (Figure 7.1). The Gunthorpe inundation pasture used in this study represents an example of this frequently flooded type. Species diversity tends to increase in grasslands characterized by mesotrophic, moderately moist and/or circumneutral soil conditions, for example the Besthorpe study site (Figure 7.1). The most species-rich floodplain grassland communities in Europe, such as the Lužnice site in this study, tend to be located where floods are not severe and soils are relatively dry. At the highest levels of grassland plant diversity in Europe, dry calcareous soils are prevalent, as in the chalk grasslands of western Europe (Figure 7.1).

Figure 7.2 indicates that for temperate unfertilized grasslands, including floodplain meadows and pastures, average above-ground primary production is 4 - 6 t dry weight $\text{ha}^{-1} \text{yr}^{-1}$. This concurs with surveys by Rychnovská (1993) who found that unfertilized temperate grasslands produce 3 - 7 t dry weight $\text{ha}^{-1} \text{yr}^{-1}$, and Titlyanova *et al.* (1990), who reported that productivity in European meadows ranges from 3.6 - 7.2 t dry weight $\text{ha}^{-1} \text{yr}^{-1}$. However, there is considerable variation in the productivity of floodplain grassland communities in Europe (Figure 7.2), probably as a result of differences in species composition, flooding characteristics and duration of growing season (Reece *et al.*, 1994). European floodplain grasslands, particularly regularly inundated grasslands dominated by relatively few productive species such as the Gunthorpe study site, can be among the most productive of unfertilized semi-natural grasslands in the temperate zone (Figure 7.2), although they do not attain levels of production comparable with artificially fertilized agricultural grasslands (e.g. 12 t dry weight $\text{ha}^{-1} \text{yr}^{-1}$; Morrison *et al.*, 1980). Wet or moist grasslands supporting a range of plant species, including Besthorpe, tend to exhibit intermediate levels of production whilst lower productivity characterizes diverse floodplain grasslands with drier soils, such as the Lužnice study site. The lowest levels of primary production in temperate semi-natural grasslands are shown by acidic and calcareous grasslands where plant-available nutrients may be particularly limiting (Fryček *et al.*, 1992; Willems *et al.*, 1993). In addition, pasture production, as exemplified by values for Gunthorpe in this study, tends to be higher than for meadows (e.g.

Figure 7.1 Plant species diversity in unfertilized semi-natural grasslands of temperate Europe



Besthorpe and Lužnice), due to the recycling of minerals which are largely returned to the pastures in livestock excreta (Elberse *et al.*, 1983).

Thus, the three communities examined in this study span species diversity and production gradients established for temperate semi-natural grasslands and are clearly representative of the range of floodplain grasslands in Europe. Gunthorpe, an inundation pasture community, was highly productive and species-poor. Besthorpe was a flood-meadow community that showed intermediate levels of species diversity and plant production. The Lužnice site was a floristically diverse flood-meadow that was relatively unproductive. Species richness and biomass values from the three study sites (Figures 7.1 and 7.2) conform with models presented by Grime (1979) and Huston (1979) which predict that high species richness in established vegetation occurs at low-to-intermediate levels of above-ground production. Rychnovská *et al.* (1994) substantiated these models with regard to European grasslands by observing that the highest species diversity occurs with average dry mass production less than 6 t ha⁻¹ yr⁻¹. This figure was supported by Oomes *et al.* (1996) who asserted that the restoration of neutral grassland for high species diversity requires dry matter production to be returned to 4 - 6 t ha⁻¹ yr⁻¹.

7.2 Floodplain grassland plant community responses to management

Plant diversity and production are regulated by plant competition, which is itself controlled by stress, disturbance and resource availability (Grime, 1979; Huston, 1979; Tilman, 1982; section 1.3). The impact of stress and disturbance on vegetation varies according to their intensity. Intensive disturbance or stress can cause conditions inhospitable to many species and unsuitable for supporting high production. In contrast, particularly low intensities of stress and disturbance allow high productivity which may lead to competitive exclusion and so reduced species diversity. Increased resource availability may also promote competitive displacement and lower species diversity as it tends to intensify competition between plants, favouring species that are superior competitors for enhanced resource levels. Thus, maximal species diversity may occur when disturbance and stress reduce the rate of competitive displacement by slowing the growth of potential dominants, thereby allowing subsidiary species to co-exist.

Human management of the floodplain environment determines the degree of stress, disturbance and resource supply impacting on the floodplain grassland community. In this study, stress was primarily represented by the imposition and accumulation of

litter, and also flooding; disturbance by cutting and grazing, and severe flood events; and changes in resource availability by nutrient enrichment through additions of nitrogenous fertilizer.

Intensities of management and flooding regulated floodplain grassland community composition and dynamics during this study, with several similar responses shown by different communities. It was likely that regular cutting and grazing, and periodic flooding, contributed positively to species diversity by constraining potential community dominants allowing less competitive subsidiary species to co-exist, and creating spatial and temporal variability in resource availability. However, major changes in management imposed during the study induced shifts in community structure. For example, both abandonment and fertilization of floodplain grasslands encouraged competitive species and tended to reduce small-scale species diversity, suggesting that competitive displacement was operating under conditions of reduced disturbance and resource enrichment. Large deposits and accumulation of litter also reduced species diversity, as well as constraining production, probably due to the effects of stress. However, community responses to management also exhibited spatial and temporal variation depending on the characteristics of the floodplain environment and management history that had generated each community, and on the life-history strategies of component species.

7.2.1 Gunthorpe inundation pasture

The inundation pasture at Gunthorpe was a productive but variable habitat subject to repeated and severe disturbance caused by flooding, grazing and trampling (chapter 3). Flooding may have had contrary effects on plant productivity, not only enhancing growth by creating canopy gaps, maintaining moist conditions and supplying nutrients but also constraining production through stress and disturbance. Intense disturbance, as represented by the combination of flooding pattern and grazing management at Gunthorpe, limited species richness (Figure 7.1), probably as a result of the failure of populations to recover from mortality (Huston, 1979). Thus, competitive species were suppressed and opportunist species with a more ruderal strategy favoured. The latter tended to possess short life cycles and a high potential growth rate, enabling them to rapidly exploit the intermittent temporal and spatial availability of resources that characterizes such dynamic floodplain environments (Junk *et al.*, 1989; Gregory *et al.*, 1991; Décamps, 1993).

The rapidity of community response to changes in disturbance regime observed at Gunthorpe during this study highlights the sensitivity and dynamic nature of the inundation pasture community. When grazing management ceased and the level of disturbance was reduced at Gunthorpe (although some disturbance through flooding continued), small-scale species richness declined within three years (chapter 3), apparently due to competitive displacement as species able to exploit the altered resource availability and maximize reproduction increased. This indicates that although flooding may have had a positive impact on species diversity (e.g. by creating regeneration niches), inundation alone was insufficient to limit competitive species and livestock activity was a major source of disturbance contributing to species diversity. Other studies on inundation pastures also found that grazing and flooding interact to determine patterns of species diversity and community organization in these habitats. Chaneton and Facelli (1991) observed that a combination of flooding and grazing yielded the highest small-scale species diversity in the Argentine Pampa, whilst an increased incidence and duration of flooding coupled with reduced grazing have resulted in a reduction of plant species diversity in the Ouse Washes in England (Burgess *et al.*, 1990).

7.2.2 Besthorpe flood-meadow

The Besthorpe flood-meadow was characterized by an intermediate level of disturbance primarily derived from a cutting and grazing management regime that had been applied over many years. Such conditions could limit above-ground biomass and favour high species richness (Grime, 1979; Smith and Rushton, 1994; Smith *et al.*, 1996), but the intermediate disturbance pattern at Besthorpe was associated not only with moderate levels of plant production (Figure 7.2) but also species diversity (Figure 7.1). Species richness may have been suppressed by competitive exclusion, as the rate of disturbance may have been insufficient to limit the production of more competitive species (Huston, 1979). This may have been exacerbated by river regulation and flood control in recent decades, which reduced the incidence of flooding at Besthorpe considerably. Plant diversity at the site may also have been adversely affected by past high pollution levels in flood water (José, 1989). Besthorpe may support fewer species than other comparable English flood-meadows because of its northern location outside the core range for such communities (Rodwell, 1992; Jefferson, 1997).

Evidence from this study suggests that the Besthorpe plant community was resistant to minor management variations in the short-term (chapter 3) but that major changes

rapidly destabilized community organization and reduced species diversity (chapter 5). The relatively constant management history at Besthorpe manifested itself in a plant community resistant to short-term minor management variations, being composed mostly of stress-tolerant competitive perennial species that tend to exhibit a slow response to perturbations (Grime *et al.*, 1988; Smith and Rushton, 1994). Indeed, temporary minor variations in management may be beneficial to plant biodiversity in established grasslands, for example occasional delays in cutting allowing late-flowering species such as *Sanguisorba officinalis* (see 7.3.6) to set seed (Smith and Jones, 1991; Kirkham and Tallowin, 1995). In this study, a reduction in management intensity at Besthorpe, exemplified by the absence of cutting and grazing, favoured particularly competitive species able to access any surplus resources, but species richness was maintained during the three years without management (chapter 3). Also, increased stress levels imposed by moderate deposits of litter inhibited competitive species and favoured stress-tolerating strategists but species diversity and plant production were not significantly affected (chapter 4).

However, considerable community change was provoked by substantially altered resource availability. Nitrogen fertilization stimulated production and intensified competition (e.g. for light), leading to competitive displacement and reduced species diversity (chapter 5). Species that increased were grasses characterized by being relatively tall and productive with dense leaf canopies and copious production of litter, able to respond vigorously to fertilization through vegetative expansion. Moreover, severe litter deposition and accumulation negatively impacted plant species diversity and biomass at Besthorpe (chapters 4 and 5), probably because plant regeneration and establishment were affected (Grubb, 1977).

7.2.3 Lužnice flood-meadow

At the Lužnice flood meadow, intermediate disturbance levels were a result of a history of cutting management and occasional but regular flooding. This restricted productive competitive species and encouraged high species diversity (Figure 7.1). Production may also have been limited by conditions of drought-stress in summer (see 2.1.4), or other resource constraints such as soil nutrients (e.g. phosphorus), favouring a diverse small-scale assemblage of stress-tolerating perennial species (Grime *et al.*, 1988), including many small forbs. The location of the study site within a floristically diverse floodplain landscape may also have encouraged high species richness compared to similar but isolated grasslands. Furthermore, the central European locality of the Lužnice may also have enhanced richness, as the pool of

species available to contribute to the community is greater than in more peripheral regions of Europe (Prach *et al.*, 1996).

The Lužnice flood-meadow community (like Besthorpe) was very sensitive to nutrient enrichment (chapter 6). Fertilization enhanced the availability of nitrogen and probably intensified competition for other limiting resources such as space and light. This led to competitive displacement, increased rates of mortality and lower species diversity. Enrichment therefore rapidly destabilized and simplified the flood-meadow vegetation morphology and plant community structure, changing it from a diverse mixture of stress-tolerating grasses and low-growing forbs and moss to a limited number of taller, more competitive species with dense leaf canopies above a ground layer dominated by accumulated litter.

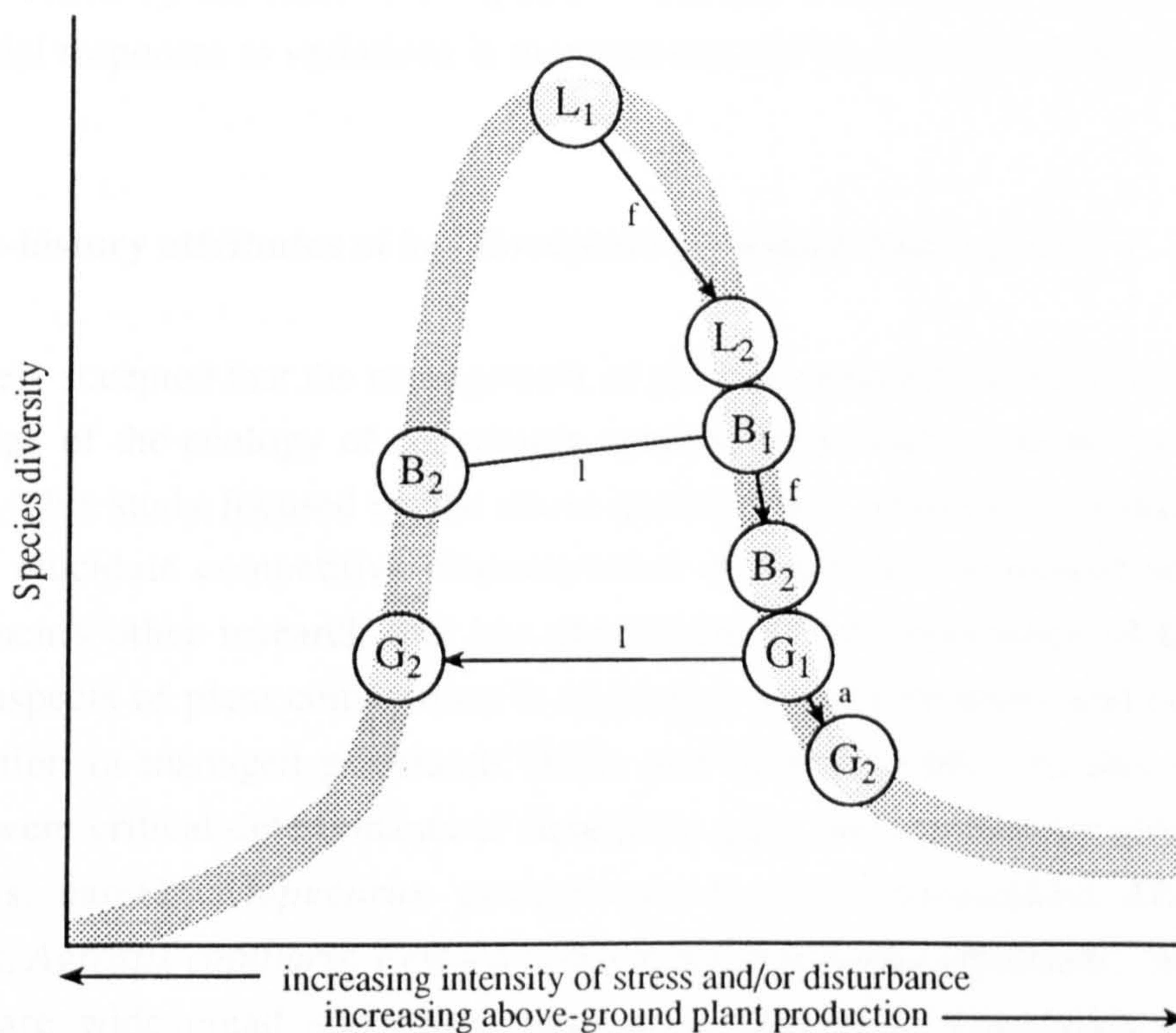
7.2.4 Synthesis

It is evident that the original species composition of the floodplain grassland plant communities studied were maintained in a dynamic equilibrium by their management regimes, and that changes in management intensity affected species composition, production and diversity. These relationships are summarized in Figure 7.3. Both fertilization (f on Figure 7.3) and the cessation of management (a on Figure 7.3) had similar impacts on community organization, reducing species diversity as resource competition apparently intensified and a limited number of productive species were encouraged. These responses to nutrient enrichment and abandonment are essentially the same as those described for other semi-natural grassland communities in Europe (Traczyk *et al.*, 1984; Ellenberg, 1988; Mountford *et al.*, 1993; Rychnovská *et al.*, 1994; Table 5.1). The deposition and accumulation of large amounts of plant litter, either floodborne or as a result of enhanced production, increased levels of stress until plant production was constrained and species diversity declined (l on Figure 7.3). Reviews of the impact of litter on riparian plant communities (Xiong and Nilsson, 1997), and on prairies and old-field grasslands (Carson and Peterson, 1990; Facelli and Pickett, 1991), also reported that large litter deposits tend to reduce productivity and species diversity.

Thus, it appears that changes from the management regime under which a particular floodplain grassland community has developed, including those that promote either intensive stress or disturbance, or intensify competition within the plant community, induce shifts in community composition and reduce species diversity. This may be particularly rapid in an inundation pasture community from a dynamic floodplain

Figure 7.3 Summary of the relationship between plant species diversity, plant production and intensity of stress/disturbance at the Gunthorpe, Besthorpe and Lužnice study sites.

Changes in vegetation at Gunthorpe ($G_1 \rightarrow G_2$), Besthorpe ($B_1 \rightarrow B_2$) and Lužnice ($L_1 \rightarrow L_2$) brought about by abandonment (a), litter (l) and fertilization (f) are shown. Diagram based on the model presented by Grime (1979)



environment in which short-lived species are present, but flood-meadows characterized by long histories of more stable management and a diversity of slow-growing perennial species are also sensitive to major change (e.g. nutrient enrichment, chapters 5 and 6), primarily because management changes alter inter-specific competitive relations.

Clearly, community responses to management changes are mediated through the reactions of component species. Variations in the diversity and composition of floodplain grassland plant communities described during these short-term studies were governed by the relative competitive abilities of individual species and their differential responses to variations in management and resource availability.

7.3 Life-history attributes of key floodplain grassland plant species

It is widely accepted that the management of plant communities should be based on a knowledge of the ecology of constituent species, particularly constant or indicator species. This study focused on the above-ground plant response to management in order to elucidate competitive characteristics of floodplain grassland species. It complements other research that has demonstrated the importance of the underground aspects of plant competition in regulating species diversity and community composition in managed grasslands (Fiala and Zelená, 1994). In this study, six species were critical determinants of floodplain grassland community structure and dynamics, namely *Alopecurus geniculatus*, *Agrostis stolonifera*, *Alopecurus pratensis*, *Agrostis capillaris*, *Festuca rubra* and *Sanguisorba officinalis*. All of these species are widespread and often frequent in floodplain grasslands in Europe (Ellenberg, 1988; Grime *et al.*, 1988; Rodwell, 1992), were abundant in at least one of the study sites, and in this study were sensitive to management manipulation, showing strong responses that could be separated from normal population fluctuations (Watt, 1947; Bakker, 1989). It is therefore important to consider the autecological characteristics of these key species when developing conservation management of floodplain grasslands. Some other species also widespread in floodplain grasslands and present at the study sites (e.g. *Holcus lanatus* and *Poa trivialis*) were omitted from this review because they are not strongly associated with floodplain grassland communities and did not show such strong responses or clear trends.

7.3.1 *Alopecurus geniculatus*

This grass is characteristic of moist, sometimes waterlogged, fertile floodplain habitats (Grime *et al.*, 1988), exemplified by the regularly flooded, productive Gunthorpe grassland of this study. It is tolerant of temporary inundation, particularly outside the growing season (Burgess *et al.*, 1990), and its seeds and shoots can be dispersed by water (Ellenberg, 1988). The species displays both ruderal and moderately competitive traits. In this study, for example, its rapid growth rate allowed it to exploit the cool, wet conditions in spring exacerbated by floodborne litter deposition at Gunthorpe (chapter 4). Furthermore, it was slightly favoured by grazing at Gunthorpe (chapter 3), suggesting that it is able to compete effectively when the growth of potential dominants, such as *Agrostis stolonifera* (see 7.3.2), was restricted by grazing and inundation. Indeed, reduced grazing and an absence of management resulted in the loss of this species from grasslands in the Ouse Washes in England (Burgess *et al.*, 1990).

7.3.2 *Agrostis stolonifera*

This grass species is of particular nature conservation value, being an important food plant for herbivorous wintering wildfowl (Burgess *et al.*, 1990). It occurs in a wide range of fertile sites (Grime *et al.*, 1988), including moist to waterlogged productive floodplain grasslands typified by the Gunthorpe study site. Its success in floodplain habitats seems to be a result of both its competitive and ruderal abilities. For example, at Gunthorpe it was tolerant of periodic inundation (chapter 3) where its ruderal nature apparently provided a selective advantage enabling it to respond rapidly to enhanced resource availability following flooding. This may have been facilitated by its fast-growing stolons and shoots which are able to exploit pockets of nutrient enrichment and canopy gaps (Grime *et al.*, 1988). *A. stolonifera* is also capable of exerting local dominance in some floodplain grasslands, such as at Gunthorpe when tall dominants were restricted by grazing and flooding. Its competitive abilities were also demonstrated by its continued abundance following the cessation of grazing management at Gunthorpe (chapter 3), and it has been known to respond positively to increased nutrient availability (Bradshaw *et al.*, 1964; Oomes and Mooi, 1981). The species is, however, sensitive to severe stress caused by litter deposition (chapter 4). Dense litter layers have been found to reduce both the frequency (Parr and Way, 1988) and biomass (this study) of *A. stolonifera*, supporting the observation by Grime *et al.* (1988) that moderate rather than intense levels of stress or disturbance are optimal for the species.

7.3.3 *Alopecurus pratensis*

A moderately productive grass, this species is therefore of agricultural importance and is particularly associated with regularly cut, productive flood-meadows in Europe, where it can be dominant (Prach *et al.*, 1996). It is a relatively competitive robust plant that can attain a height of one metre; consequently, diversity tends to decline where *A. pratensis* is particularly abundant (Grime *et al.*, 1988). The species is highly adapted to the flood-meadow habitat, such as Besthorpe and Lužnice in this study. It can tolerate moderate intensities of disturbance, including management such as some grazing (Smith and Rushton, 1994) and cutting (Smith *et al.*, 1996) providing the cutting frequency is not great (Parr and Way, 1988). It achieves maximum above-ground biomass prior to the traditional timing of hay-cutting, e.g. in June in central Europe (Šmilauer *et al.*, 1996), and is capable of rapid regrowth after defoliation. Furthermore, it can penetrate a litter mat with its robust shoots (Grime, 1979), helping it to function as a competitive dominant in productive meadows such as Besthorpe.

The competitive capacity of *A. pratensis* is demonstrated by its ability to persist in neglected floodplain grasslands in central Europe for 12 years (Prach *et al.*, 1996) and, in this study, it remained a constant member of the Besthorpe plant community during three years without cutting or grazing management (chapter 3). A key to its competitive success in flood-meadows may be its ability to develop relatively rapidly early in the season (Oomes and Mooi, 1981; Šmilauer *et al.*, 1996), enabling it to secure a selective advantage over other floodplain grassland species, including the tall forb *Sanguisorba officinalis* which matures later (see 7.3.6). *A. pratensis* also tends to be favoured by increased nutrient supply, Rabotnov (1977) describing it as one of the most positively responsive grasses to fertilizer nitrogen in western Europe. However, Ellenberg (1988) noted that the species only became dominant under fertilization on moist soils, indicating that water resource shortages constrain its competitive ability. In this study, for example, the grass exhibited a strong positive response to fertilization at Besthorpe (chapter 5), where soils were comparatively moist, but on the drier soils at Lužnice no clear trend in relation to increased nitrogen supply was observed (chapter 6).

7.3.4 *Agrostis capillaris*

Grasses were generally encouraged by increased nitrogen availability during this study. *A. capillaris* exemplified this most clearly, showing a consistent positive response to fertilization at the Besthorpe and Lužnice study sites (chapters 5 and 6).

A. capillaris has a wide ecological amplitude but is characteristic of vegetation on dry to moist sites of intermediate to low productivity (Grime *et al.*, 1988). It is moderately competitive, responding positively to fertilization at Besthorpe and Lužnice where superior competitors (such as *Dactylis glomerata* and *Lolium perenne*) were either absent or at sufficiently low amounts as to be unable to assume dominance during the two years of fertilization. Integral to the competitive success of *A. capillaris* seems to be a diversity of regeneration strategies, including dispersal by seeds, stolons and rhizomes (Williams, 1984; Grime *et al.*, 1988), and a capacity for rapid lateral spread. Of particular importance in this respect may be its ability to rapidly expand vegetatively into gaps created by the death or suppression of other plants through fertilization (van Hecke *et al.*, 1981). In addition, *A. capillaris* has been observed to tolerate acid soils and nutrient deficiencies exacerbated by fertilization, for example competing strongly for phosphorus (Thurston, 1969; Grant *et al.*, 1981). The cessation of cutting and grazing management at Besthorpe also led to an increase in the cover of *A. capillaris* (chapter 3), further highlighting its potential to compete effectively in floodplain vegetation where resource competition is intensive.

The competitive success of *A. capillaris* in the Besthorpe and Lužnice flood-meadows was probably enhanced by its resilience to cutting. The grass is capable of establishing a dense, low leaf canopy of vegetative shoots, many of which escape serious damage through defoliation, which is rapidly renewed during summer after cutting management (Grime *et al.*, 1988). Indeed, Fisher *et al.* (1996) found that *A. capillaris* suppressed grassland forb production under a defoliation regime of three annual cuts. The species may also be able to co-exist with other competitive species in flood-meadows, such as *A. pratensis* which attains maximum biomass in early to mid summer (see 7.3.3), because it develops phenologically later in the season.

7.3.5 *Festuca rubra*

In this study, *F. rubra* typified the responses to management of many other species of small stature that occur in floodplain grassland communities (Rodwell, 1992), including many of the forbs that characterize high species richness.

F. rubra is a fine-leaved stress-tolerant perennial grass most common in grasslands where competition is reduced to moderate intensities by disturbance or low productivity (Grime *et al.*, 1988). In such circumstances, it is associated with high species richness (Hopkins, 1986). It was co-dominant at the Besthorpe and Lužnice study sites, where it was able to recover from cutting and grazing (chapters 5 and 6) by regenerating vegetatively, probably using rhizomes. Indeed, it is able to tolerate a cutting frequency of up to five cuts per year (Parr and Way, 1988) and can maintain a large presence in relatively unproductive grasslands of modest nutrient status by rapid rates of leaf growth in spring, despite generally being rather slow-growing (Grime *et al.*, 1988). This suggests that temporal niche differentiation plays a critical role in co-existence with competitive species in moderately productive flood-meadows. For example, *A. capillaris*, which was also frequent at the Besthorpe and Lužnice study sites, has a much latter pattern of shoot development (see 7.3.4). Nevertheless, the limited competitive abilities of *F. rubra* were also demonstrated during this study. The species was extremely sensitive to resource enrichment in the flood-meadow habitat, decreasing with increasing nitrogen availability at Besthorpe and Lužnice (chapters 5 and 6).

7.3.6 *Sanguisorba officinalis*

Relatively little has been published on the autecology of *S. officinalis* (but see Baker, 1937; Smith and Jones, 1991), despite it being a conspicuous and sometimes dominant member of European floodplain grassland communities (Prach *et al.*, 1996). The species is a perennial forb that passes winter as underground rhizomes and develops rapidly in spring into a tall, erect, robust plant with dense foliage that attains maximum ground cover in mid-summer, after which it dies back. In England, *S. officinalis* flowers in July and the fruit is ripe in August-September (Smith and Jones, 1991).

In this study, the species displayed variable annual growth patterns but the morphology and phenology of *S. officinalis* exerted an important influence on community dynamics at the Besthorpe and Lužnice flood-meadow sites (chapters 5

and 6). The species displays a number of features that indicate a strong adaptation to the flood-meadow habitat. Its rapid development early in the season may secure a competitive advantage over species that expand later (e.g. *A. capillaris*, see 7.3.4) and this, combined with its tall stature and dense canopy, allows it to compete strongly with grasses for light and other resources (Baker, 1937; Fisher *et al.*, 1996). Indeed, in many floodplain grasslands, including Besthorpe and Lužnice in this study, this forb competes with grasses for dominance of the plant community.

In this study, *S. officinalis* was able to maintain itself at the Besthorpe and Lužnice flood-meadows during considerable variations in management, indicating that it possesses a stress-tolerating competitive strategy that confers flexibility and resilience upon it in relation to perturbations. Indeed, the species can tolerate flooding and prolonged drought (Royal Society for the Protection of Birds, English Nature and Institute of Terrestrial Ecology, 1997) and in this study was able to recover from cutting to maintain its competitive ability (chapter 3), overcome the stress of litter deposition (chapter 4) and compete effectively when resource competition was intensified by fertilization (chapters 5 and 6). The possession of underground energy reserves may be a key factor enabling effective competition in response to altered stress intensities and resource availabilities imposed by management changes. Such resources allow the plant to establish itself through the dense litter mat and carry its photosynthetic tissues above the litter layer, and may facilitate its recovery following cutting management. Support for this observation may be derived from other studies of meadows which have shown that *S. officinalis* can tolerate spring-grazing (Smith and Rushton, 1994) and cutting for hay but was absent from a floodplain grassland subject to prolonged grazing (Baker, 1937). This suggests that intensive grazing may reduce and ultimately exhaust the underground reserves of the plant. Further evidence of the competitive capacity of *S. officinalis* can be found in this study, as the species competed effectively in the absence of management over three years at Besthorpe (chapter 3), and from a study of an abandoned wetland in France in which the species persisted for nine years (Fossati and Pautou, 1989). However, over a longer period of neglect *S. officinalis* was eliminated from this French wetland, implying that cutting may give a selective advantage to *S. officinalis* by slowing competitive displacement by grasses or woody species.

7.3.7 Synthesis

It can be concluded that the dynamic floodplain grassland environment results in a variety of plant life-history strategies adapted to the various disturbance intensities

imposed by management and flooding, although in general competitive conditions predominate within floodplain grasslands. Species are able to co-exist within communities because they possess complementary phenological patterns and life-history strategies. For example, *Festuca rubra* is capable of persisting beneath the canopy of community dominants such as *Sanguisorba officinalis* in flood-meadows because it is a stress-tolerating grass of small stature. Furthermore, two of the dominant species in flood-meadows, *Alopecurus pratensis* and *Agrostis capillaris*, co-exist by exhibiting temporal niche differentiation, with the former developing in spring and the latter maturing in summer.

Plant species that successfully adapt to abrupt alterations in floodplain grassland management are characterized by morphological or life-history attributes that allow rapid response to achieve selective advantage. Regeneration abilities, such as the capacity to utilize rhizomes, stolons or underground energy stores, and/or a rapid growth rate may be particularly important mechanisms facilitating ecological resilience and the attainment of competitive dominance in floodplain grasslands.

An appreciation of the life-history and functional characteristics of key species is important because they regulate community dynamics. Such knowledge is therefore a valuable requisite for the planning and implementation of effective conservation management of European floodplain grasslands.

7.4 Ecological management of European floodplain grasslands for plant biodiversity

The European floodplain grassland resource and its associated species are continuing to decline (BirdLife International European Agriculture Task Force, 1996), particularly through agricultural intensification or an absence of management. This degradation can be arrested by adopting complementary strategies, for example those that protect priority European sites and other which conserve the habitat in the wider landscape, ensuring that the remaining resource is managed appropriately in order to prevent further habitat loss and fragmentation.

Traditionally, European floodplain grasslands have been managed within low-intensity agricultural land management systems. These incorporate extensive grazing, cutting for hay and little if any artificial fertilization, and are associated with minimal drainage and relatively natural flooding patterns (Beaufoy *et al.*, 1994; Bignal and McCracken, 1996; Royal Society for the Protection of Birds, English Nature and

Institute of Terrestrial Ecology, 1997). Such traditional land-use regimes are characterized by intermediate intensities of disturbance and stress which moderate plant productivity and limit competitive displacement by potentially dominant species, thereby creating and maintaining conditions suitable for high plant biodiversity.

Conflict exists between contemporary land-use and conservation for biodiversity. Management for nature conservation aims at maintaining high species diversity including rare and endangered species (Bakker, 1989), whereas the objective of agricultural management is to maximize production, usually at the expense of plant species diversity (Figure 7.3). This study has indicated that floodplain grasslands are vulnerable to contemporary trends in land-use change, such as agricultural intensification, hydrological regulation and abandonment. Deviations from low-intensity vegetation management tend to result in a loss of conservation value in floodplain grasslands. Indeed, both inorganic fertilization (chapters 5 and 6), which is an integral element of management intensification for agricultural exploitation, and at the other extreme, the cessation of all vegetation management (chapter 3), provoke similar community responses that are detrimental to plant biodiversity. The net effect of both of these processes is to reduce species diversity through competitive displacement, as just a few competitive dominants are favoured. Hydrological regulation of river-floodplain systems, such as flood prevention, may also induce community change including elimination of characteristic floodplain species adapted to the periodic stress and disturbance imposed by flood events (chapters 3 and 4).

Thus, in order to integrate nature conservation objectives and agriculture, the effective management of European floodplain grassland habitats of biodiversity value should focus on the continuation or re-instatement of low-intensity management that imposes intermediate levels of disturbance and stress. Ideally, this should be founded on a relatively natural hydrological regime and traditional farming practices (Bignal and McCracken, 1996), as these may facilitate sustainable management at both the site and regional scales, and are likely to prove key factors in long-term restoration of the European floodplain grassland resource.

7.4.1 Low-intensity management at the local-scale

Nature reserves and similar designations have been widely implemented to protect floodplain grassland sites and species in Europe (Wascher, 1998). Protected sites may be relatively small and, given their primary nature conservation function,

difficulties may arise in maintaining the management practices (e.g. cutting and grazing) necessary to sustain their biodiversity value. Several international initiatives, such as NATURA 2000 and the Convention on Biological Diversity (and its national Biodiversity Action Plans), have emerged recently that build upon the foundation established by existing strategies to protect key European sites, such as the Ramsar Convention (Hill *et al.*, 1996; Wascher, 1998). These not only reinforce protective legislation but also offer opportunities for the sustainable management and restoration of the floodplain grassland resource.

As this study has demonstrated, management impact at the community level is complex, varying in terms of extent and rapidity according to species composition. For example, fertilization may favour competitive grasses such as *Agrostis capillaris* (chapters 5 and 6) and, particularly where soils are moist, *Alopecurus pratensis* (chapter 5). Increased incidence or variation of flooding may promote more ruderal species adapted to wet environments, e.g. *Agrostis stolonifera* and *Alopecurus geniculatus* (chapter 3), and litter deposition is a dynamic factor that may variously reduce local species diversity and benefit tall stress-tolerating floodplain species (e.g. *Sanguisorba officinalis*) (chapter 4). Many of the most characteristic or highly valued plant species from a conservation perspective possess stress-tolerating abilities but are not particularly competitive and are sensitive to altered competitive relations. These include the grass *Festuca rubra*, which is associated with a high floristic diversity when it is abundant (Grime *et al.*, 1988), and a variety of slow-growing forbs that contribute greatly to both the aesthetic quality and biodiversity of floodplain grasslands.

Specific management prescriptions are therefore required to conserve sites supporting high species diversity, or rare or specialized species or communities. Regular vegetation management (i.e. cutting and grazing), an appropriate hydrological regime (including flooding), and careful consideration of nutrient availability (particularly inorganic fertilization) provide a framework for the development of specific management prescriptions for particular floodplain grassland communities or populations of species. Furthermore, an understanding of plant competitive relations will allow fine-scaled manipulation using vegetation and hydrological management, and can be used to maintain a range of different plant communities generated by particular disturbance:stress:nutrient availability ratios, not all of which may be floristically diverse but each contributing to the overall biodiversity resource of the river-floodplain system at the landscape or regional scale.

7.4.2 Low-intensity management at the landscape-scale

Signal and McCracken (1996) assert that traditional, low-intensity farming practices represent the only socially acceptable and sustainable management for European landscapes of high nature conservation value. The results of this study reinforce this, indicating that extensive vegetation management provides a framework for conservation management of plant biodiversity at the floodplain level. Land-use characterized by low-intensity management will enable a mosaic of communities to co-exist over the floodplain landscape, not all these individual patches may be species-rich, but which aggregate to produce high plant diversity at the landscape scale. This is because regular cutting and grazing allow environmental heterogeneity such as variations in substrate (Nilsson *et al.*, 1989) and hydrology (Décamps and Tabacchi, 1994) to be expressed in plant community composition and diversity, as well as directly contributing to small-scale structural heterogeneity in the vegetation (Oomes and Mooi, 1981; Bakker, 1989). In contrast, intensification of land-use such as for modern agricultural exploitation obscures environmental heterogeneity by promoting just a few productive species (chapters 5 and 6), and abandonment tends to lead to homogeneity of vegetation at the small-scale (Regnéll, 1980; Persson, 1984; Facelli *et al.*, 1989; chapter 3). Periodic flooding also plays a positive role in maintaining diversity at the landscape level, imposing further spatial and temporal variety, maintaining connectivity between different patches and enhancing flows of energy, materials and species (Naiman and Décamps, 1990; Gregory *et al.*, 1991; Malanson, 1993).

Reforms and reviews of international and national environmental and agricultural policies (e.g. the Common Agricultural Policy) are providing opportunities for supporting low-intensity management practices within the floodplain landscape. Schemes that integrate agricultural and conservation management by offering financial incentives to farmers to undertake management for conservation benefit have been implemented by many European countries, particularly through the European Union Agri-environment Regulation 2078/92 (BirdLife International European Agriculture Task Force, 1996). In the case of floodplain grasslands, such environmentally sensitive management prescriptions include limiting the use of agri-chemicals such as fertilizers, establishing cutting dates to benefit meadow plants, and raising water levels to encourage wintering or breeding birds (Glaves, 1998). Agri-environment schemes may adopt a whole farm, river catchment or regional perspective and are therefore capable of delivering appropriate management and initiating restoration measures over an extensive area of floodplain landscape.

7.4.3 Restoration

Management of remaining European floodplain grasslands may be complemented by expansion of the resource in order to facilitate the conservation of species and communities that were formerly more widespread. Restoration of the floodplain grassland resource can be achieved through the rehabilitation of ecologically degraded sites to a condition similar to their former state and creation of new sites of wildlife interest.

In recent years, attempts at floodplain grassland restoration through rehabilitation and creation have increased in Europe, including projects in England (McDonald, 1992; Royal Society for the Protection of Birds, English Nature and Institute of Terrestrial Ecology, 1997), the Czech Republic (Straškrabová *et al.*, 1996), Sweden (Hertzman and Larsson, 1991) and the Netherlands (Bakker, 1989; Oomes *et al.*, 1996). The objectives of rehabilitation or creation largely determine the subsequent hydrological and vegetation management of the restored site. For example, floodplain grassland sites being established for birds require appropriate hydrological conditions, such as a high water table, and may benefit from grazing by cattle. In contrast, cutting for hay (perhaps with grazing of the regrowth) may be the optimal aftercare management for a diverse flora, particularly when there is a need to reduce the soil nutrient status to limit plant productivity and promote less competitive species and so encourage botanical diversity (Olf and Bakker, 1991; Berendse *et al.*, 1992; Oomes *et al.*, 1996).

In order to maximize the effectiveness of restoration initiatives floodplains that supported grasslands in the recent past and can continue to sustain them in the future, such as in river valleys with a sufficient supply of unpolluted water, should be targeted. Straškrabová and Prach (1998) reinstated regular cutting management to a flood-meadow abandoned for approximately 20 years located within a diverse floodplain landscape. After five years species diversity and composition were restored to a quality comparable with adjacent grasslands that had received uninterrupted management, due largely to the persistence of species in the seed bank and flooding which transported diaspores from nearby sources. Restoration schemes that link remaining floodplain grassland habitats or are adjacent to existing sites of wildlife interest, such as botanically diverse grasslands that can provide a seed source, are more likely to succeed and be of strategic and lasting benefit. Flooding fulfils a key role in restoring interaction between patches by acting as an agent of dispersal

and creating plant regeneration opportunities (Ellenberg, 1988; Nilsson *et al.*, 1991; Prach *et al.*, 1996).

The restoration of floodplain grasslands that have been abandoned for many years, or have been degraded by intensive agricultural exploitation, may be more problematic than the example above. Manchester *et al.* (1998) tested the effectiveness of restoring arable land to floristically diverse floodplain grassland by natural regeneration and by seed introduction. They found that on ex-arable sites sowing seed mixtures resulted in significantly greater numbers of species in the subsequent sward but that it would take many years to restore a characteristic vegetation type by natural regeneration. This highlights the problems of attempting to restore floodplain grasslands on areas that have been managed intensively, which are characterized by impoverished seed banks, altered hydrological regimes and high nutrient availability. For example, Bekker *et al.* (1997) found that the soil seed banks of a range of grasslands in western Europe were negatively affected by intensive agricultural management such as drainage and fertilization.

7.4.4 Monitoring

Monitoring the plant community composition of floodplain grasslands may also provide an early indication of detrimental human activities because, as this study has indicated, they are sensitive to environmental change. Monitoring may include evaluating the environmental performance of strategic initiatives such as international legislation and agri-environmental schemes, not only to assess their effectiveness, but also to provide a measure of the status of the European floodplain grassland resource. This may provide valuable information in relation to several emerging or predicted threats to the floodplain ecosystem, such as the possibilities of distribution changes and local extinctions of species due to global climate change and the ecological impact of the over-exploitation of water resources, eutrophication and habitat fragmentation (Décamps, 1993; van Diggelen *et al.*, 1994; Bennett, 1996; Campbell *et al.*, 1997).

7.5 Conclusion

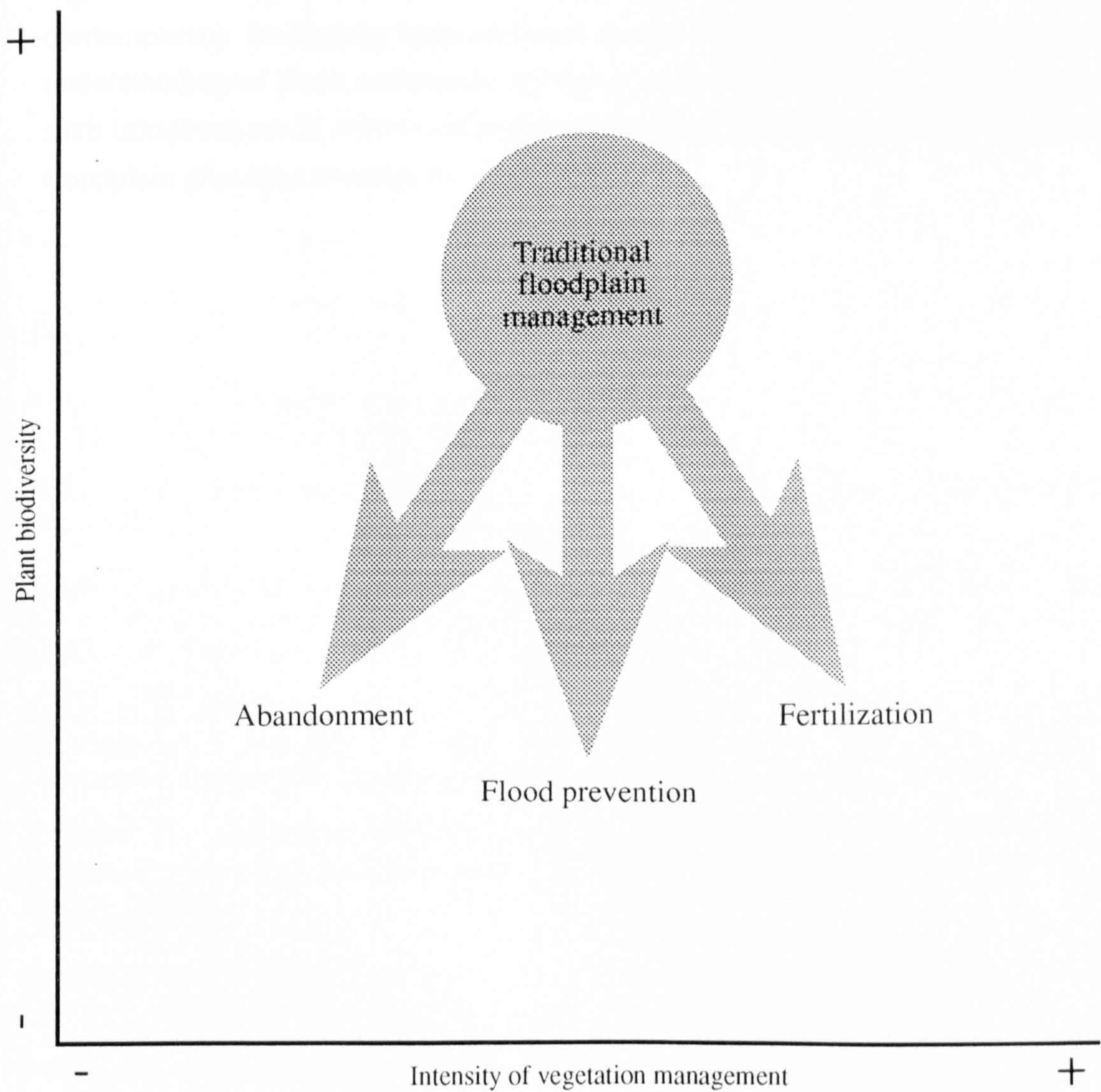
Traditional management characterized by cutting for hay, extensive grazing and no inorganic fertilization, supported by an unregulated flooding pattern, represents an intermediate disturbance regime that encourages plant biodiversity in European

floodplain grasslands. Figure 7.4 summarizes this concept and also illustrates the main outcomes of changes in this management regime, as demonstrated by this study. The study has shown that major changes in the intensity of the traditional management pattern, for example cessation of vegetation management, flood prevention, and fertilization, lead to altered community composition and reduced plant species diversity (Figure 7.4). In particular, the following key community dynamics were elucidated at small spatial scales.

- Cutting and grazing encouraged floristic diversity; an absence of vegetation management favoured the expansion of robust competitive species and, in a dynamic community from a variable floodplain environment, relatively rapidly reduced species richness (chapter 3).
- Floodborne litter deposition and accumulation may be an important factor in introducing and maintaining plant diversity and influencing community composition, particularly by favouring certain stress-tolerating species (chapter 4). However, relatively high deposits of plant litter have a negative short-term impact on plant species diversity and biomass production of floodplain grasslands (chapters 4, 5 and 6).
- The application of fertilizer nitrogen to two types of flood-meadow vegetation fundamentally altered community structure, reducing species diversity, particularly forb species richness, and favouring most grass species but discouraging moss and most forbs (chapters 5 and 6). Fertilization initially stimulated plant production, especially grasses, but grass cover and production were subsequently limited by litter accumulation.

The results demonstrate that European floodplain grasslands are vulnerable to contemporary land-use trends, notably abandonment, hydrological regulation (e.g. reducing floodborne litter deposition) and agricultural intensification (e.g. fertilization) (Figure 7.4). Specific responses are governed by plant community composition, which is controlled by site history, habitat conditions and disturbance regime. In this study, the forb *Sanguisorba officinalis*, which is characteristic of traditionally-managed floodplain grasslands in Europe, governed community dynamics in flood-meadows where management imposed a low-to-intermediate disturbance regime. Other plant species compete effectively at different intensities of flooding and vegetation management (section 7.3). Communities from variable but productive floodplain environments are likely to be particularly sensitive and exhibit rapid responses to management changes (section 7.2.1). Less productive grasslands

Figure 7.4 Generalized relationship between management and plant biodiversity in European floodplain grasslands



characterized by long, stable management histories tend to be more diverse and resistant to temporary, minor deviations in management but are destabilized by substantial impacts (sections 7.2.2 and 7.2.3). Further work would be of value to clarify the persistence and applicability to other floodplain systems of the trends shown in the study. However, it is clear from the results of this study that strategies that promote a continuation or adoption of relatively low-intensity management regimes, often based on traditional farming practices, provide a means of reconciling contemporary floodplain land-use with nature conservation. Coupled with an understanding of plant community dynamics and small-scale ecological processes, such initiatives could achieve effective conservation and restoration of the European floodplain grassland resource for plant biodiversity.

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