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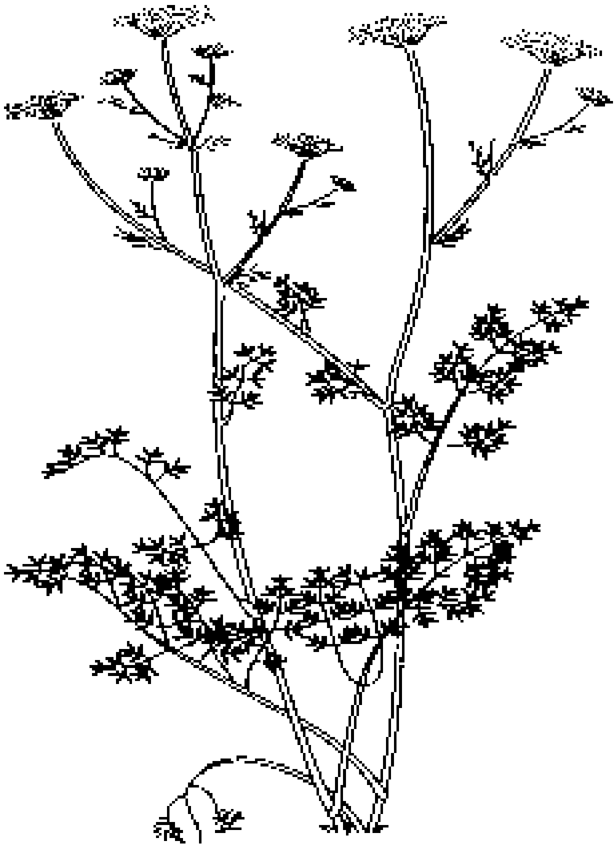

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A review of the ecology, hydrology and nutrient dynamics of floodplain meadows in England

David J.G. Gowing[1], Jerry R.B. Tallowin[2], Nancy B. Dise[1], Joanne Goodyear[2], Mike E. Dodd[1] and Rebecca J Lodge[1].

[1]Open University, Walton Hall, Milton Keynes MK7 6AA
[2]Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB

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Executive summary

This report aims to summarise existing knowledge, identify practical management guidelines and highlight deficiencies in our understanding of the ecology of *Alopecurus pratensis-Sanguisorba officinalis* (MG4) grassland. MG4 grassland, which is restricted to floodplain habitats, has undergone a severe decline during the last century. The conservation importance of this community is now recognised at a European level. Remaining stands of MG4 grassland are known to be sensitive to both site hydrology and nutrient availability and are therefore dependent on appropriate river management, both in terms of water quantity and water quality. This report is based on a review of relevant literature and the results of a questionnaire survey of conservation officers responsible for floodplain meadow sites.

Hydrology

Our questionnaire survey revealed that alteration to water management was considered a threat to the integrity of more than one in three sites and concerns related to both river management and floodplain drainage.

The literature review highlighted the vegetation’s susceptibility to waterlogging. Most MG4 species are intolerant of anoxic soils during the growing season. Excess water is a much more acute threat to the community than is soil drying. These grasslands have developed under agricultural management, an important aspect of which has been an efficient surface drainage system. Many sites further rely on sub-surface drainage provided by shallow seams of sand or gravel, which underlie them. The continued functioning of such minor aquifers is important for MG4 conservation.

River engineering is not necessarily detrimental to floodplain meadows. Indeed, maintenance of high stage levels and promotion of frequent transient floods by structures such as weirs, are probably beneficial. Flood protection by deepening, straightening or embanking rivers, however, is likely to be damaging, as silt deposition by floods and the associated input of nutrients is important in terms of compensating for nutrient losses via the harvest of hay from these meadows.

Similarly, interference with the functioning of shallow aquifers may compromise both the meadows’ drainage in winter and sub-irrigation in summer. Therefore, mineral extraction on floodplains is a significant threat to site integrity. Whilst river restoration projects may be able to rectify some of the negative impacts of past river engineering, restoration of appropriate hydrology on an extracted site is more difficult.

Nutrients

The MG4 community has high species richness (up to 38 species per m^2). Such communities typically have intermediate levels of net primary production (4 – 7 t dry matter ha^{-1} yr^{-1}) and intermediate soil fertility (eg 5-15 mg kg^{-1} Olsen extractable phosphorus, which equates to a P index of 0 or 1.) The question of whether floodplain meadow productivity is limited by the supply of nitrogen (N) or phosphorus (P) has not been satisfactorily resolved. An experimental test of this question would greatly inform conservation management. In response to our questionnaire, nutrient availability (either excess or deficiency) was identified

as a concern at a quarter of MG4 sites. The survey also revealed a general lack of documentation relating to the nutrient status of these grasslands and its management.

Whilst techniques for lowering soil nutrient status exist (eg sod cutting, chemical amendments, soil inversion, hydrological manipulation) none lend themselves readily to the floodplain meadow situation. Improved control of inputs and off-takes would be a more appropriate approach. For phosphorus, the main input to the system is in silt deposited by river floods. To estimate the magnitude of this input, the flood frequency, suspended load and silt P content of the river are needed. Concentration of soluble P may be of little relevance. Meadow conservation will be suited by moderate deposition rates, but quantitative guidelines are difficult to formulate because the internal cycling and hence availability of silt-derived P is not well understood.

The literature suggests that in general, deposition of atmospheric N and river derived P steadily increased during the last century, putting floodplain meadows at risk of eutrophication. Conversely, some sites show signs of nutrient deficiency as a result of flood protection measures excluding their nutrient supply. In this context, not only the macronutrients, but also other minerals, particularly calcium, should be considered. Cessation of flooding may lead to surface acidification, a decline in hay yield and possibly a reduction in species diversity, but the evidence is not conclusive. Further research is required to quantify nutrient budgets in order to improve the conservation management of the community.

Agronomy

The traditional management of MG4 floodplain meadows, which has maintained the species diversity of the grassland, comprises a mid summer hay cut followed by grazing the hay regrowth. Shutting the meadow up in spring is necessary to allow phenological development of tall herbs, such as greater burnet (*Sanguisorba officinalis*), though it should be noted that there is no need for long-lived perennials such as these to set seed each year. The hay cut itself helps to prevent an accumulation of nutrients in the system, and early (eg June) cuts may be more effective in this regard. Grazing the regrowth in autumn and winter is considered necessary to create gaps in the sward for seedling establishment.

Hay yields from MG4 sites generally fall in the range 2.8-4.9 t ha^{-1} yr^{-1} (compatible with Verhoeven's range for high species diversity). They are approximately half what could be expected from intensively managed grassland. The mineral content of the hay is generally adequate for livestock, though a high calcium: phosphorus ratio may increase the risk of trace element deficiency when the hay is used as the primary winter feed. Information is lacking on the feed value of the hay and its potential use as part of the feed ration for productive livestock requires further evaluation.

Tolerances

MG4 communities often occur as a component of a matrix of inter-related plant communities on a floodplain. Quite subtle changes in water regime and nutrient availability appear to be responsible for substantial changes in species composition, emphasising the sensitivity of this grassland type to these environmental factors. Numerous researchers have attempted to define water-regime requirements for the community. The most quantitative and comprehensive to date are expressed in terms of Sum Exceedence Values (SEVs). There is much less literature with respect to nutrient availability requirements. MG4 is cited as occurring on soils with Olsen available P in the range 5-15 mg kg^{-1}, but there has been no publication of a quantified nutrient budget for the community.

The review has highlighted a number of areas in which our understanding is deficient and therefore our ability to manage optimally for conservation objectives is impaired. Topics for future research and monitoring on MG4 grasslands are discussed. They include: establishment of long-term monitoring, modelling of nutrient budgets, investigation of mechanisms generating plant community structure, a study of genetic diversity within and gene flow between existing communities, economic appraisal of management and studies in the physiological ecology of component species.

Practical guidelines for managers

The following is a distillation of knowledge to date, which could further refined, as more data become available.

Hydrology

All MG4 meadows require adequate surface drainage, both to allow water to flow freely back to watercourses, following the cessation of a flood, and to prevent the retention of rainwater on the surface, following storms. Due to the flat topography of floodplains, surface drainage features such as grips, gutters and foot drains will become ineffective over time, due to the accumulation of silt. Therefore a regular maintenance programme is required to sustain their function.

Many meadows rely on lateral water movement at depth in shallow aquifers composed of coarse river sediments (sands and gravels). Such systems provide drainage in winter and sub-irrigation in summer. Obstruction to flow in shallow aquifers, due to mineral abstraction in neighbouring sites or heavy silt deposition within watercourses, should be discouraged as it carries a risk of disrupting the meadow's water regime.

MG4 meadows require a soil with high available water capacity. Natural floodplain soils, usually alluvial clay loams, provide this property. The water holding capacity of a soil can be reduced by compaction. Therefore it is necessary to avoid situations, which result in soil compaction, such as heavy vehicles crossing the grassland, especially when soils are wet, and prolonged poaching (puddling) of wet soil by livestock.

Many meadows receive water from adjacent watercourses via sub-irrigation and therefore are dependent on high stage levels in rivers. Structure such as weirs and locks may be important in providing this situation and should not be altered or removed without full consideration of the effect on river stage alongside the meadow.

Nutrients

The MG4 grassland is a productive, species-rich community. To maintain its productivity and help ensure continued agricultural management, it requires inputs of nutrients to replace those removed in harvested hay. Replacement nutrients have traditionally been supplied in silt deposited by floodwaters. Exclusion of floodwaters from a site should not be undertaken without a full consideration of the impact on the nutrient budget. It is possible that wellrotted farmyard manure can substitute for lost silt inputs, but this has not been fully tested. Hay yields of less than three tonnes per hectare might indicate a need for supplementary nutrients.

Excess nutrient deposition is likely to change the character of the community. Hay yields of 5 tonnes per hectare or above would indicate nutrient availability is above the usual range for a species-rich community. Increasing cover of perennial ryegrass (>20%) or a total grass cover greater than 60% would also indicate this trend. Soil tests should show Olsen extractable phosphorus to be below 15 mg kg^{-1} soil (P index of 1 or 0). If signs of nutrient enrichment persist, catchment management is needed to decrease flood frequency and/or to decrease suspended sediment load or site management is needed to allow floodwaters to leave the site more rapidly and/or limit the amount of silt entering the site.

Effects of climate variation between years on nutrient availability in spring/early summer will influence hay dry matter yields. It is therefore necessary to estimate hay yield over several seasons before drawing conclusions regarding nutrient status of the site. It would be a useful practice to ask hay-makers to provide some estimate of yield each year, even if only a count of bales removed.

Vegetation management

Many of the characteristic species of the MG4 community appear to be intolerant of grazing during the period mid-March to end June. However, in order to maintain this grassland and allow seedling recruitment to occur, it appears that grazing in late summer and winter is important. Animals should be removed once the soil is saturated to avoid excessive damage to soil structure via poaching.

Hay cutting is an essential part of meadow management. It prevents the accumulation of nutrients in the system – especially nitrogen in the current scenario of high loads of nitrogen compounds from atmospheric deposition. It also prevents the large, competitive species that may depress species diversity becoming frequent. Increased cover of species such as hogweed (*Heracleum sphondylium*), cow parsely (*Anthriscus sylvestris*) and tall oat-grass (*Arrhenatherum elatius*) may indicate the need for hay to be cut earlier in the season.

Botanical monitoring of fixed quadrat (2m x 2m) positions should be promoted wherever resources allow, with the aim of compiling a long-term data set that could be used to complement the existing condition assessment monitoring in guiding management decisions. Whilst annual surveys in June are the ideal, data from irregular surveys still have value, especially if from a fixed locations.

1. Introduction

1.1 Scope of the review

The plant community of semi-natural, floodplain meadows is a rare and threatened assemblage. It has been recognised as a discrete community within the National Vegetation Classification (Rodwell 1992) and given the label of MG4 *Alopecurus pratensis-Sanguisorba officinalis* grassland. It has also been recognised as a habitat of conservation importance on a European scale (Council of the European Communities 1992).

Typically, the community is composed of a wide range of grass species (up to 18 within a single site) with no single species achieving dominance. Furthermore there is a selection of sedge and rush species, which make a minor contribution to the sward. The most notable feature, however, is an abundance of dicotyledonous herbs which come to dominate the community in midsummer. Two species of particular prominence are the great burnet (*Sanguisorba officinalis*) and the Meadowsweet (*Filipendula ulmaria*). This assemblage of species is now restricted to old hay meadows, which have received constant treatment (midsummer hay cut and aftermath grazing) for a prolonged period, and which occur on deep, moisture retentive, alluvial soils on lowland river floodplains. For further description, refer to Rodwell (1992) or Jefferson (1997).

The community was decimated during the last century as a result of the extensive changes, which occurred on lowland floodplains during that time. These fall into three categories; agricultural intensification of the rich soils on which the community grew, urbanisation of the flat areas along rivers, and the industrial extraction of the coarse river sediments, which often underlie the meadows. Most remaining stands of the community now receive some form of statutory protection and attempts at recreation have begun. The community typifies the flower-rich meadow, which for many forms their idyllic representation of the English rural landscape.
This review arises from a concern that the processes that sustain such grasslands, especially the delivery of nutrients by alluvial silt, are not well understood (Jefferson & Robertson 1999). The aim of the review is to summarise the current state of knowledge with regard to:

- the nutrient dynamics of floodplain meadows,
- the influence of hydrology on nutrient availability, and
- the impact of nutrient availability on the meadow's ecology and agronomy.

The floodplains of England form the geographical focus of this review, as the plant community in question is almost entirely confined to that country.

1.2 Review methodology

Three basic approaches were taken in order to compile information for the review. Firstly a questionnaire was circulated to those Local teams within English Nature, which have extant stands of the community within their area. The purposes of this were:

- to determine the main concerns with respect to the conservation of the vegetation type,

- to identify the threats to its integrity as they were perceived at a local level, and
- to discover if there were any relevant unpublished information held on site files.

The questionnaire was followed up by telephone conversations with the appropriate member of each team to collate any further sources of information.

The second approach was an extensive search of the literature, primarily within Britain, but also drawing on evidence from European sources, where similar plant assemblages are found and, where appropriate, from further afield.

The final line of enquiry was an interpretation of any primary data, which may help to inform our understanding of the relevant processes. The review reports on the initial analysis of such data and identifies where further study may be usefully directed.

The specific areas, which this review aims to address, are as follows:

- An assessment of threats to semi-natural, floodplain meadows and the influence of previous river regulation and drainage schemes.
- The hydrology of floodplain habitats, particularly grasslands.
- The nutrient content of floodwater, sediment, soils, vegetation and nutrient cycling in lowland river floodplains and their interaction with hydrology.
- The agronomy and vegetation management of floodplain meadows.
- The vegetation ecology of floodplain grasslands, including the influence of hydrology, soils, nutrients and agricultural management.

The structure of this report reflects this sequence of issues.

1.3 Current distribution of Floodplain meadows in England

Jefferson (1997) collated data from all the regions of England to compile a list of sites holding the MG4 floodplain meadow community. The combined area of the 92 sites listed was 1543 ha, but this was recognised as an over-estimate of the community's extent, because many of the sites in question held other plant assemblages alongside MG4. Five additional sites have been added to the list since that date (Appendix 1.) Figure 1.1 shows the distribution of the community within England. Its range centers on the floodplains of the larger rivers in southern England, where deep alluvial soils have formed since the last glaciation. A more recent review of the extent of semi-natural grasslands, including MG4 (Blackstock *et al* 1999), found that just 477 ha of the floodplain meadow community had been recorded in surveys. The surveys did not represent a complete coverage of the country however, and it was suggested that the total extent may fall in the range 500-1000 ha. The most recent approximation of the extent of MG4 (Jackson & McLeod 2000) uses the value "<1500 ha" as a compromise between the earlier estimates.

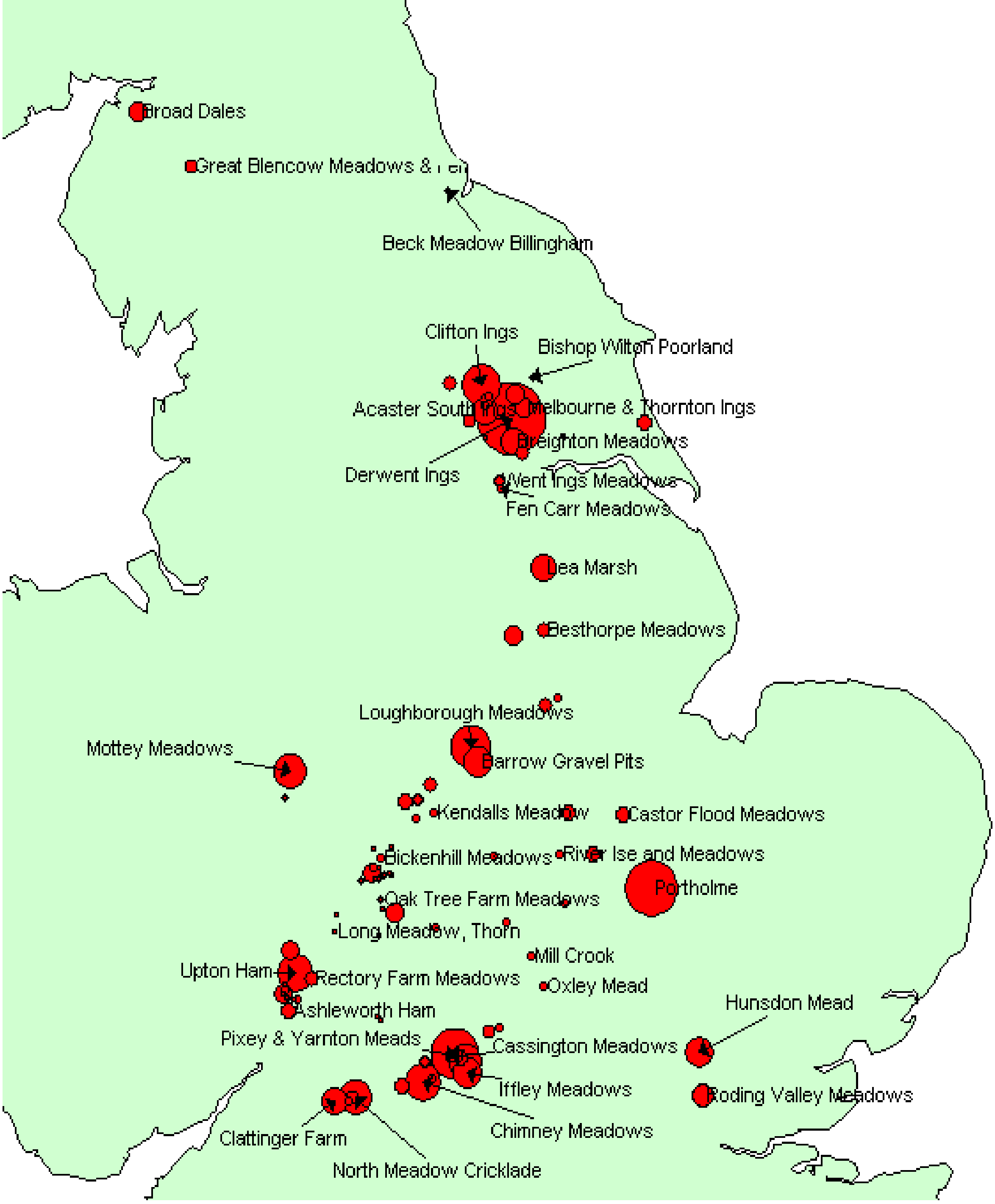


Figure 1-1 The distribution of sites containing the MG4 flood-plain meadow in England

The size of the symbol reflects the size of the site

1.4 Perceived threats to the habitat

The questionnaire circulated to the Local Teams of English Nature received a high response rate. Information on 81 of the 97 sites listed in Appendix 1 was collated. The local officers were asked to identify any perceived threats to the integrity of the site and to categorise them under the following headings:

- Altered water management.
- Increased nutrient availability.
- Decreased nutrient availability.
- Habitat fragmentation.

- Other (neglect, over-grazing or other inappropriate management).

Figure 1.2 demonstrates that water management is the single issue of greatest concern with respect to the conservation of MG4 grassland. Relatively recent alterations to site hydrology have occurred at more than one third of the sites surveyed.

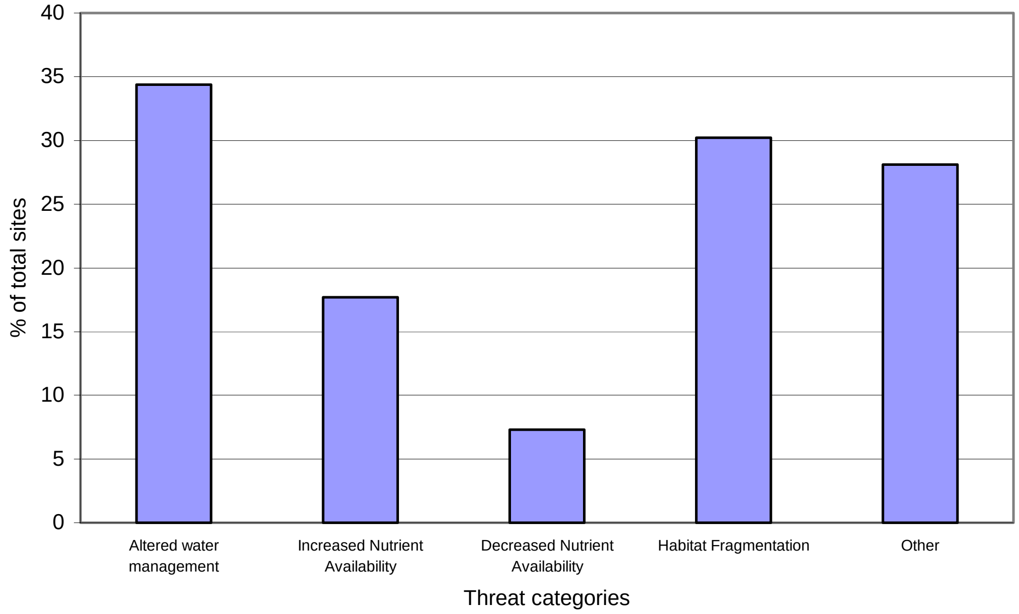


Figure 1-2 Threats to the integrity of MG4 grassland sites, as perceived by local conservation officers

To gain an impression of the stability of floodplain management at the sites, the survey also asked about any hydrological alterations in the past 30 years. The time limit reflected an assumption that the floodplain vegetation would have adjusted to any earlier alterations and its current composition would reflect the new circumstances. The main purpose of the question was to prioritise the review of hydrological management, by determining which practices were of relevance to MG4 sites.

The responses to this question were limited by the information readily available to local teams. Most of the sites have been notified as of conservation importance within the last 30 years and therefore their files do not necessarily extend back for that far. It would be possible to collate a more complete data set by approaching other organisations, but time constraints precluded this. The summary of responses in Figure 1.3 reveals that such sites have been impacted by a wide spectrum of management operations even within the time frame for which data were readily available.

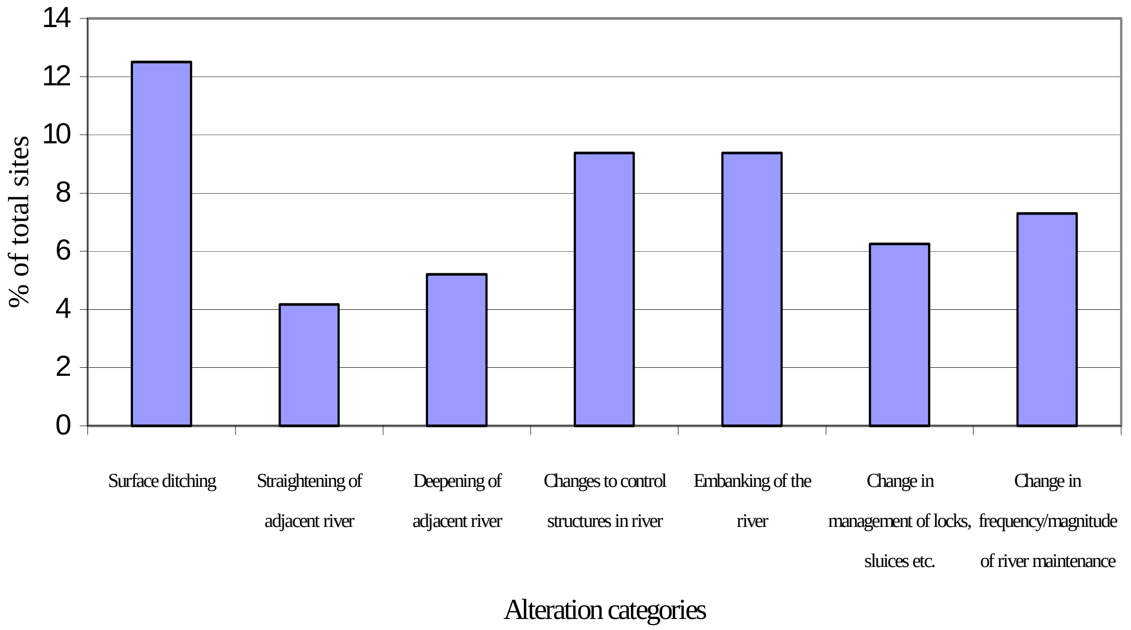


Figure 1-3 The proportion of sites which have undergone an alteration to their hydrological system in the past 30 years

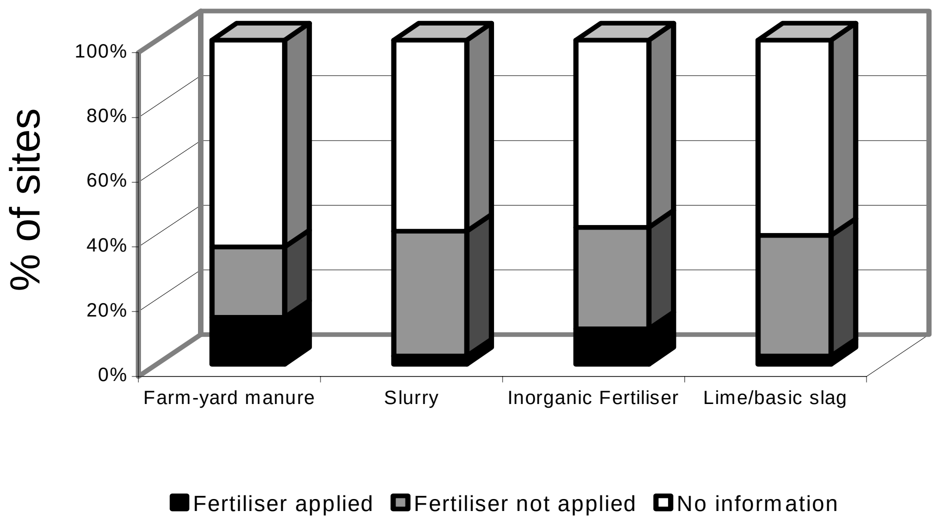


Figure 1-4 The percentage of sites known to have received fertilizer applications during the past 30 years

Whilst surface ditching is the operation cited most frequently (12% of sites surveyed), the one of potentially greatest concern is embankment of the river, which has occurred at 9% of sites. The reasons why embankment is considered a cause for concern are discussed later in the report.

A question was asked about the management of the site's nutrient inputs. Officers were asked to specify if manure, slurry, lime or inorganic fertilisers were applied to the meadows and if not currently, when was the date of last recorded application. Only a small minority of sites had any documented evidence to respond to this question especially with regard to timing or amounts of applications. The responses are summarised in Figure 1.4.

Few conclusions can be drawn from the data, given the large number of sites where responses were received but information was unavailable. It is interesting that, of the sites for which data were obtained, approximately one third are receiving farm-yard manure (FYM). The impact of FYM on species-rich grassland has recently been reviewed by Simpson and Jefferson (1996) for meadows and by Chalmers *et al* (2000) for pastures.

Finally, a question was asked about the existence of data in any of the following categories, which were held for the site:

- Hydrological regime
- Hay yields
- Grazing pressure
- Nutrient content of hay
- Nutrient status of soil
- Nutrient status of floodwaters or sediments
- Vegetation composition (quadrat surveys undertaken)
- Vegetation change (2 or more quadrat surveys undertaken in separate years)

Figure 1.5 reveals the paucity of baseline data for these sites. The very small percentage with results of laboratory nutrient analysis is probably a reflection of its expense. It may be unrealistic to monitor nutrient content regularly at a large number of sites, even given their threatened status.

The low number of sites with any repeat botanical survey is of more concern. Without this basic information, it is not possible to ascertain how resilient the community is to environmental variables and hence the degree of risk associated with external influences. The condition assessment monitoring programme for lowland grasslands recently instigated by English Nature (Robertson & Jefferson 2000) will generate a broad data set of those MG4 sites, designated as SSSI (site of special scientific interest,) and should help to redress this deficiency.

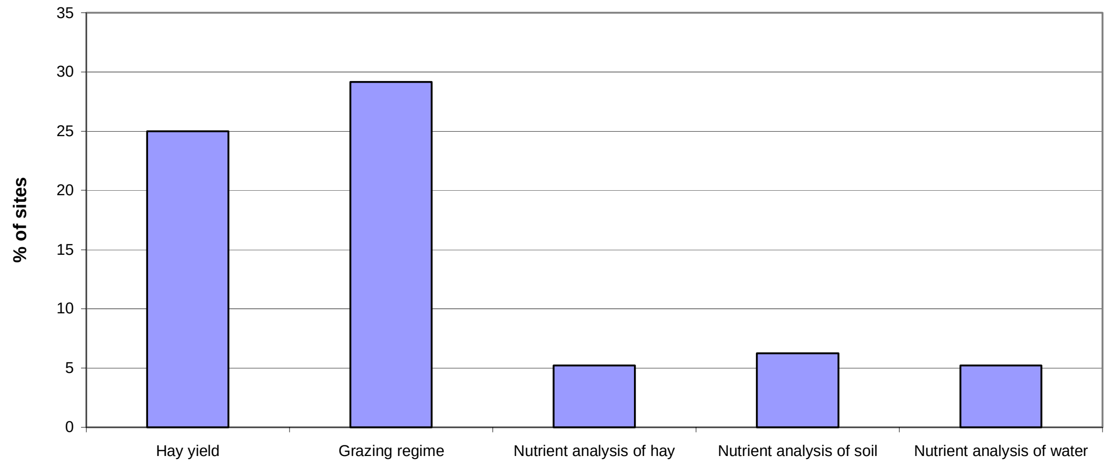


Figure 1-5 Availability of data from sites holding the MG4 community

Quantitative botanical data from more than one year were available at only 1 in 6 sites. Where such repeat surveys had been conducted, the methodology rarely followed that of the original, so any conclusions about vegetation change based on comparisons of records from different years will be limited. It was not possible within the preparation of this review to analyse such botanical data in terms of compositional change over time. The analysis may need to be carried out in liaison with the field surveyors to establish the spatial arrangement of samples. Many sites are spatially heterogenous and where random sampling is used, a reliable description of the vegetation may not be given unless a large number of samples were taken.

2. Hydrology of floodplain meadows

2.1 Introduction

Water is one of the basic requirements for plant growth and its ease of acquisition is a major determinant of plant species distribution. Therefore the hydrological system, which determines the availability of water to plants, is of central importance in the conservation of a vegetation type. In considering floodplains, however, hydrology has a second and equally important dimension; the control of soil aeration status. This is because floodplain soils may be at or close to saturation for significant periods during the year, with a consequent restriction on the volume of air present, which has profound effects both on their ability to recycle nutrients and to support plant growth (Crawford 1982).

This section will initially consider the variety of hydrological systems operating within floodplains, then address the effect of soil water regime on the vegetation. Firstly the issue of limited soil aeration will be reviewed, secondly the supply of moisture to plants and thirdly the effect of water regime on soil temperature. The final part will consider hydrological management of floodplains and its impact on the soils and vegetation.

2.2 Water balance on floodplains

The consideration of floodplain hydrology is often focussed on the role of floodwater from the river, which shaped the landscape. This however is rarely the most important factor in the water balance of the floodplain soil. In most cases the dominant input and output of the system will be rainfall (R) and evapotranspiration (E) respectively. These factors are climatically determined and vary quite markedly across England. In the North-west, rainfall may be more than twice the potential evapotranspirational demand leading to a large excess of water on an annual basis, whilst in the South-east the two factors' yearly totals may be approximately equal, leading to a potentially substantial soil moisture deficit in summer (Table 2.1) MG4 communities exist in a broad range of climatic environments and this should be taken into consideration when considering any aspect of their hydrology.

Table 2-1 Contrasting patterns in long-term averages for rainfall and potential evapo-transpiration in different parts of the geographical range of MG4 (after Smith & Trafford 1976.)

Annual means/ mm yr^{-1}	Rainfall/ mm yr^{-1}	Potential ET/ mm yr^{-1}	Excess rainfall/ mm yr^{-1}	Expected maximum soil moisture deficit/mm
Cumbria	1663	375	1288	10
Cambridgeshire	574	523	51	92

Surface water inputs are often not of prime importance to the moisture status of floodplain soils, because floods tend to occur in the winter or spring months, when the soil is already at or close to saturation due to excess rainfall. The amount of floodwater that actually infiltrates into the soil may be quite limited. Floods occurring during the summer and autumn would have more impact on soil moisture status, but for most English floodplains that support the MG4 community, such floods are the exception rather than the rule (Table 2.2)

Table 2-2 The number of weeks, by season, over the period 1986-1996, during which river water flooded onto Cricklade North Meadow (data supplied by the Environment Agency).

Season	Weeks in which flooding occurred
Winter (Dec-Feb)	27
Spring (Mar-May)	2
Summer (June-Aug)	0
Autumn (Sep-Nov)	3

In terms of water-balance, the situation when surface water floods are important to the water balance is when they are retained on the surface of the floodplain by microtopographic depressions. It should be emphasised that flood waters do not emanate solely from the main river, but may also spill from minor water courses draining the local catchment behind the floodplain or come from rain falling directly on the site, creating areas of standing surface water. On some floodplains water drains to the river via valves that are designed to prevent water from an embanked river flowing into the floodplain. In these cases, prolonged high water levels in the river result in "back-up flooding" on the floodplain, because local drainage water cannot escape.

Shallow ponded water from whichever source can have a profound effect on the spring and summer soil moisture status. If it is assumed that drainage through the profile is entirely impeded, then it would typically take 3-4 months for a depth of just 5 cm of standing water, retained after a single flood in February to be evaporated, even in the relatively dry climatic region of South-east England. This illustrates the central importance of microtopography in determining the soil water regime on floodplains (Grevilliot *et al* 1998).

The assumption of zero drainage through the profile, which was made above, is a gross one. In almost all floodplain situations there would be some sub-surface drainage of floodwaters back to the river during spring. The actual magnitude of this flux can vary widely, depending on the depth of the river below its floodplain once it has returned to its channel, sometimes referred to as its freeboard (H), and the hydraulic conductivity (K) of the soil profile. According to Darcy's Law, the rate of drainage (Q) is directly proportional to the product of these variables.

$$Q \propto H * K$$

Whilst freeboard values (H) are only likely to vary by a single order of magnitude between floodplain situations (typically they would range from 0.2 m to 2.0 m), values of conductivity (K) may vary by many orders of magnitude; from less than 0.01 m day^{-1} in compacted clay layers to more than 10 m day^{-1} in gravel seams. The physical composition of the soil profile is therefore an important factor in determining the water regime of floodplain soils. Many of the large floodplains of Southern England are underlain by gravel terraces, which were deposited by the river in the post-glacial environment. These can have a marked impact on the floodplains's hydrology, due to their high hydraulic conductivity. They can effectively act as a drain, allowing floodwater trapped on the surface to return to the river. Many of the remaining stands of MG4 meadow and presumably much of its former range were on such gravel terraces. The valleys of the Thames, Great Ouse, Nene, Trent and Severn and those of their tributaries contain extensive deposits of sand and gravel. The commercial value of which is one reason for the widespread destruction of floodplain meadows during the last century (Brian 1993).

The importance of sand and gravel terraces does not end with their drainage function. They have the potential to act as shallow aquifers, which may serve to sub-irrigate the floodplain by either allowing river water to move laterally within its floodplain (eg North Meadow NNR and Portholme SSSI) or by providing a sub-surface route for drainage water from the higher catchment bordering the floodplain (eg Stanford End SSSI[1] and Mottey Meadows SSSI) or through contact with a major aquifer (eg Clattinger Farm SSSI, K.Rushton, pers.comm.) It is important to note that groundwater can sometimes be the dominant driver of the floodplain water balance. There are numerous examples of such situations from studies in the Netherlands where the superficial geology is dominated by highly permeable layers (Grootjans *et al* 1998) and from the East Anglian chalk (eg Wheeler & Shaw 2001). Those floodplains that support MG4 communities, however, tend to be in the clay vales of England, where the influence of deep aquifers is rarely significant.

In summary, the water regime of floodplain soils is controlled by a combination of the climatic water balance, surface flooding, particularly the entrapment of surface water, soil conductivity, water-storage capacity and groundwater movements. The relative importance of these factors will vary from site to site and it is hard to generalize with respect to sites containing flood meadows. Some are in climatically wet regions, others dry, some have regular flooding, others very rarely flood, some are influenced by groundwater, others not. One can say however, that sites supporting good stands of MG4 grassland generally do not retain pools of surface water, due to the operation of a surface drainage system. These systems are often composed of very shallow features which allow water to flow back to the rivers following a flood. Good examples of the community also tend to be associated with deep, well-structured soils which have not been significantly compacted by agricultural operations, and which have a large storage capacity for water. In regions with large soil moisture deficits in summer, the community is usually found on sites which receive water from a river and/or the local catchment via sub-irrigation (Gowing *et al* 1998.)

2.3 Soil aeration

Before discussing the aeration requirements of the floodplain meadow community, the aeration status of soil and the implications for plant growth will be briefly reviewed.

A moist soil, from which excess water has drained by gravity, is termed by soil scientists as being at field capacity. In this state, most soils include between 5 and 25% air by volume. The presence of this air is important for living organisms in the soil (bacteria, fungi, detritivores and plant roots), because it provides both a reservoir and a diffusion route for oxygen. Soil organisms consume oxygen in their respiration, which is replaced from the atmosphere by the process of diffusion. If the supply of oxygen is cut-off, then the reservoir within the soil may become exhausted within a few days (dependent on soil temperature.) The depletion of soil oxygen, or soil anoxia as it is termed, has major ramifications for the vegetation growing on it (Vartapetian 1978; Jones & Etherington 1971). Without an adequate supply of oxygen, plant roots become limited in their ability to take up water and nutrients from the soil, both of which require energy derived from respiration. Likewise, the decomposition of organic matter by microbes is limited, which may restrict the amount of soluble nutrients, especially nitrogen, available for plant uptake (Stanford & Epstein 1974).

[1] Stanford End SSSI, Berkshire does not appear on the list of MG4 sites in Appendix 1, because it has not been formally recognized as that community type. It lacks *Sanguisorba officinalis,* but its species composition is otherwise close to that of MG4.

The continued supply of oxygen to the soil depends on there being a sufficient volume of air within the soil to allow oxygen diffusion to proceed at a rate that matches oxygen consumption. As oxygen diffuses through water at only 1/10 000 of the rate it does so in air, a water-saturated soil is at much higher risk of becoming anoxic (Armstrong 1979). It has been determined by experiment that the air-filled fraction of the soil volume necessary for free diffusion is in excess of 10% (Taylor 1952). Drainage engineers have worked with this assumption to improve crop productivity on potentially waterlogged soils (Wesseling & van Wijk 1957). Soils with air contents below 10% are liable to anoxia, especially when soil temperatures are above 5^oC. The lack of soil air may either be the result of low porosity, which is related to compaction, or the result of air being displaced by water in wet soils.

Anoxia has many implications in terms of soil chemistry. The chemical state of the soil with respect to oxygen availability is measured as its redox state. The redox potential (E_h), which takes millivolts (mV) as units, is used to quantify the soils redox status. It is a measure of a system's ability to oxidise substances relative to the standard hydrogen electrode. For a given redox half-equation such as the reduction of manganese oxide in the soil,

$$MnO_2 + 4H^+ + 2e^- = Mn^{2+} + 2H_2O \qquad E^o=+1.23V$$

E_h is defined by the Nernst equation,

$$E_h = E^o - 2.303\ RT/nF(\log([\text{reduced state}]/[\text{oxidised state}]) + m(\text{pH}))$$

Where *n* is the number of electrons transferred (in this case 2) and *m* is the number of hydrogen ions involved (in this case 4). Therefore if the E_h were measured by a soil electrode as +300 mV at pH 7 and it were assumed that chemical equilibrium had been attained, one could calculate the ratio of divalent manganese ions to manganese oxide molecules in soil solution as 1000. In many soils, the divalent manganese ion is a potential toxin to plants. The lower the value of E_h and the lower the pH, the more abundant it becomes. The equation highlights the dependence of E_h values on soil pH.

At pH 7, soils with a high redox potential ($E_h > 400$ mV) represent an oxidising environment and can be assumed to be adequately supplied with oxygen (Pezeshki 2001). When a soil becomes waterlogged, E_h may fall below 350 mV within a few days as the reservoir of oxygen in the soil is exhausted, it may then be considered anoxic. Soil bacteria continue to respire in the absence of oxygen, because they are able to use alternative chemical species as the final electron acceptor in their respiratory pathway. Some use the nutrient ion, nitrate (NO_3^-). The process by which bacteria consume NO_3^- is termed denitrification and results in the nitrate being lost from the soil either as nitrogen gas or nitrogen oxide, thus depleting nitrogen availability for higher plant uptake. Soils with E_h <350 mV will tend to be depleted in nitrate. This may occur after just 4 or 5 days of waterlogging, dependent on the soil temperature and the size of the original nitrate pool (eg Ross 1995).

Another electron acceptor is the Iron (III) ion (Ferric ion, Fe^{3+}) which gives soil its red colouration. Bacteria convert it to the Iron (II) form (Ferrous ion, Fe^{2+}) when E_h falls to about 20 mV and the soils tend to turn blue-grey. A third electron acceptor is the sulfate ion (SO_4^{2-}) which is converted to the sulphide ion (S^{2-}) when E_h becomes negative. It is the sulfide ion, which gives soils subjected to long-term waterlogging their distinctive smell (Ponnamperuma 1972).

The relevance of these alternative bacterial pathways to plants is that several of the products, eg Iron (II) ions and sulfide ions are phytotoxic and may kill species un-adapted to waterlogged soils (Snowden & Wheeler 1993). Soils without an adequate oxygen supply are therefore potentially very hostile environments for plant growth, the hostility increasing with soil temperature (Trought & Drew 1980). Unadapted plants rapidly show signs of nutrient deficiency in anoxic soils as their uptake mechanisms are disrupted and this leads to a decline in shoot growth (Atwell & Steer 1990). Species not regularly exposed to anoxic soils, can survive a few days (or weeks at low soil temperatures) without soil oxygen by relying on fermentation for their energy and chemical protectants to neutralize toxins (Crawford 1993.) Species of swamp communities are more highly adapted to anoxic soils. They have evolved anatomical adaptations, providing internal pathways for oxygen transport (aerenchyma) that keep their roots and rhizospheres well supplied with oxygen (Armstrong 1979). MG4 species are not so highly adapted. Some such as *Filipendula ulmaria* do tolerate waterlogged soils (Smirnoff & Crawford 1983), but many of the fine grasses such as *Cynosurus cristatus* do not (Grime, Hodgson & Hunt 1988).

No published field data on the redox status of soils supporting MG4 grassland were available. It is possible, however, to infer the likelihood of anoxia occurring in such soils from an analysis of water-table depths and the soil moisture release curve (Gowing *et al* 1998.) When the air-filled porosity of the soil is predicted to fall below 10% during the growing season, anoxia can be expected to occur within a few days. Measurement of denitrification rates on floodplain soils demonstrates the frequency of anoxic episodes (eg Machefert *et al* 2001.) It should be noted that denitrification may be induced by anoxia of the lower profile alone, whilst the upper layers are still sufficiently aerated for unrestricted plant growth.

2.4 Soil moisture

Plants are very sensitive to soil moisture status and can rapidly alter their growth rates in response to the onset of soil drying, even if only the upper part of the profile is affected (Davies & Zhang 1991). In experimental work, plants have been shown to reduce growth rates when soil moisture contents have only fallen slightly below field capacity (Henson *et al* 1989). It is possible that the often moderate soil drying which floodplain soils experience, although mild in comparison to that of other habitats is nevertheless a factor determining community composition. The results would suggest that plants can alter their physiology when water tables have dropped just 0.5 m below the surface (Davies & Gowing 2000), which occurs in most the MG4 sites studies by mid May (Gowing *et al* 1998). Such mild stress may permit continued growth of even the most sensitive species, but may nevertheless have an effect on interspecific competition as species differ in their sensitivity to soil drying (Milnes *et al* 1998).

Significant drying of the surface soil will occur when the rate of water movement by capillary action from the saturated zone beneath cannot match the rate of evapotranspiration at the surface. This condition occurs when the saturated zone falls below a critical depth. For typical floodplain soils, under high evaporative demand, the depth at which the saturated zone can no longer supply demand is about 0.5m. Once the water table has fallen to 0.8-0.9 m below the surface, then the saturated zone is contributing little to the evaporative loss and the surface layers dry more rapidly (Walker 1995). Plants may then experience more severe water stress and growth may cease. There are a number of strategies that plants employ to evade this situation. Deep-rooting gives access to the readily available water from those layers still close to saturation. A number of MG4 species show this adaptation; *Rumex acetosa* and *Silaum silaus* for example. Rodwell (1992) stated in his description of the community, that “deep-rooted species probably always have access to soil water and, except in the driest summers, water availability is probably not limiting to plant growth.” There is no experimental evidence for this assumption however.

For shallower-rooted species, an alternative adaptation is to tolerate drought by minimising water loss through structural features such as a dense coverage of leaf hairs. *Leontodon hispidus* could be cited as an example of this. It is regularly found within MG4 swards (Rodwell 1992), which suggests soil drying may be a significant environmental factor. Another alternative strategy is to avoid soil drying by growing only during those seasons when the soil is moist. *Fritillaria meleagris, Bromus racemosus* and *Ranunculus bulbosus* could be cited as examples of this amongst the species found in MG4 communities, though there are confounding factors in this argument. It could be said that the selective pressure for this trait within meadows may have more to do with completion of seed set before the midsummer hay-cut than with drought avoidance.

Several species of MG4 grassland were studied with respect to their tolerance of soil drying by Buckley (1988) at Yarnton Mead, physiological responses were discernable even during a wet summer, but the data set was insufficient to draw firm conclusions with respect to the differential tolerances of individual species.

Notwithstanding the discussion above, the floodplain soils supporting MG4 vegetation are amongst the least droughty in England. They tend to be deep alluvial soils typically of the Fladbury association (Avery 1973), which are clay loams with well-developed structure. A comparison of the soil water retention properties at several grassland sites suggested typical stands of MG4 grew on profiles with high water-holding capacities (Gowing 1996.) A useful concept for defining a soil’s ability to supply water to vegetation is that of “Readily available water,” which is defined as the amount of water a soil can hold at field capacity that can be released at suctions less that 200 kPa. It represents the amount of water a plant can extract from the soil before the onset of significant stress. On floodplain alluvial soils, such as at sites holding MG4 communities, a typical value for the readily available water in the top 0.5 m of the profile is 70 mm, which equals the expected soil moisture deficit for many parts of the country. Additional water will be supplied from the water table via capillary rise or deep roots. Therefore, plant growth is rarely halted by soil drying in this community, but it may be an important factor determining species composition nevertheless.

Soil moisture status is also important in determining nutrient availability. The rate of nitrogen mineralisation (Stanford & Epstein 1957), the solubility of phosphates, the diffusion rates of ions through the soil and the ability of plants to take up nutrients are all functions of water regime. These issues will be addressed in later sections.

2.5 Soil temperature

Soil temperature is an important ecological variable for several reasons. Firstly, it determines the start of the growing season. Most grasses and herbs in English grasslands start growth when soil temperatures rise above 5.5^{o}C (Broad & Hough 1982), referred to as the growth temperature threshold. The timing of this event will determine:

1. the susceptibility of plants to inundation by floodwaters

2. the rate of oxygen consumption by soil organisms and therefore the onset of anoxia and
3. the rate at which soil organic matter is mineralised, this is because the metabolic rates of decomposers are highly temperature dependent.

With respect to anoxic soils, the soil temperature is an especially important consideration, since the hostility of the waterlogged soil environment for plant growth increases with increasing soil temperature, because bacteria render it a more reducing environment. MG4 stands in the south of England may therefore be susceptible to damage from standing flood waters earlier in the spring than equivalent stands in the north of England, due to an earlier warming of the soil (Broad & Hough 1982). This is a compound effect of the plants' earlier requirement for a high rate of oxygen supply and the greater competition for oxygen from microbes.

In order to quantify the combined effect of soil temperature and low oxygen status, Castelli *et al* (2000) suggested using a concept of "day degrees anaerobiosis" to estimate the cumulative amount of stress experienced by plants as a result of oxygen deficit in the root zone. No published data are available for English meadows on this scale, but Castelli at al. (2000) showed that such integrated "peak-over threshold" measures had more explanatory power with respect to species distributions in Nevada sedge meadows than did simple measures of soil temperature or mean water-table depth alone.

Soil temperature is not purely a function of climate, but is also influenced by water content. Water has a very high specific heat content and so wet soils take much longer to warm up in spring than similar soils that have drained. This can lead to phenological variations within a site, where plants in dry parts of the field start into growth and flower earlier than their conspecific counterparts in the wetter areas (Grevilliot *et al* 1997.) With respect to floodplain management, this would suggest that grasslands most susceptible to damage by flooding are ones that have commenced spring growth whilst well-drained and subsequently become saturated.

2.6 Hydrological management

Hydrological management may occur either within the river itself or upon the floodplain. The purpose of the management tends to fall into one of the following five areas, each of which will be considered in turn:

- Manipulation of flows and water depths in channels
- Flood defense
- Surface drainage
- Sub-surface drainage
- Mineral extraction

2.6.1 Channel management

Not one of the floodplains supporting the MG4 community (listed in Appendix 1) can be regarded as functioning naturally. In all cases, the river has had its flow regime altered by anthropogenic influence and has lost the freedom to move within its floodplain as a result of bank protection. The rivers are all managed to a greater or lesser degree through a combination of water abstraction, waste discharge, use of retention structures, erosion control on banks and channel straightening.

Control of river flow by the use of engineering structures in the river itself was begun in earnest in the seventeenth century (Baker 1937), mainly for reasons relating to navigation rather than land drainage and intervention for this purpose increased significantly during the eighteenth century (Large & Petts 1996.) These operations would have altered the water-regimes of many floodplain meadows. Baker believes they would have led to more frequent small floods compared to the pre-engineered situation. They would have reduced the erosive power of the rivers and together with the use of bank protection measures such as wooden piling, would have kept the river within a defined channel.

River engineering and hydrological management are therefore not modern phenomena and MG4 may have extended its range as a result of some of the management operations in the past, which promoted frequent transient floods. However, the degree of management has steadily increased during the last century and the flow regime of many rivers is to a large extent governed by relative locations of abstraction intakes and the outfalls of sewage treatment works. This has obvious implications for water chemistry, but may also alter river stage heights. High levels of water use may even occasionally increase river flows along stretches where the outfalls are some distance upstream of the intakes (Dempsey & Codling 2001). The net effect of such intervention on the quantitative hydrology of floodplain meadows cannot be generalised and will tend to be site-specific.

2.6.2 Flood defence

There are two issues with respect to flood defence which impact on floodplain meadows:

a. attempts to keep rivers in their channels by increasing their conveyance and
b. the use of floodplain areas for flood storage.

Flood embankments are designed to reduce the frequency with which the floodplain is inundated from the river. Many lowland rivers have flood embankments to protect properties built in their floodplains. The construction of these engineering structures caused the loss of some floodplain meadows. The impact on the remaining meadows, which were often behind the embankments and so isolated from the river, may not necessarily be from the perspective of a reduced water supply, but may be primarily with respect to reduced sediment deposition (see section 3). The straightening of rivers to increase their gradients also reduces flood frequency, and therefore may have similar impacts on meadows.

The designation of washlands for storage of floodwater, to protect urban areas downstream, has become a policy of the Environment Agency (EA, 2000). Whilst these areas have potential wildlife benefits, particularly for fauna, they may not be conducive to the soil water regime which favours MG4 swards. Retention of surface water on grassland leads to soil anoxia, which is potentially damaging to this community type, if water is stored on the surface for more than a few days (section 2.3).

2.6.3 Surface drainage

This report considers drainage as two entities, surface drainage and sub-surface drainage because their impacts on MG4 communities are thought to be quite different.

It is likely that the surface drainage of floodplains has been managed to some extent since MG4 first appeared in Roman Britain, or earlier, as a result of pastoral management of floodplains (Grieg 1988). Networks of anthropogenic surface-drainage systems are clearly visible either on the ground or from aerial photographs of many extant MG4 sites (eg North Meadow NNR, Yarton Mead SSSI, Upton Ham SSSI), though their antiquity is uncertain. Although the sites are inundated by natural floods, it is likely that farmers have always recognised the advantage of assisting water to drain rapidly back to the channel once river levels fell. The hydrological management of these grasslands was not as active as that of the water meadows, which were deliberately inundated or floated, then rapidly drained down (Fream 1888), but the same knowledge base was probably shared.

In recent years, with the change in emphasis from commercial agricultural management to nature-conservation management on the remaining MG4 sites, the active management of surface drainage systems has decreased. By their very nature, alluvial floodplain meadows accrete sediments and these will tend to accumulate particularly in depressions within the plain (Walling & He 1998). It can be concluded that the drainage channels will fill with silt faster than the surrounding area and that generally they do not clear themselves, as their gradients are too shallow to allow scouring during recession of the flood. Regular maintenance was probably required to keep the surface system functioning.

2.6.4 Sub-surface drainage

Sub-surface drainage, sometimes referred to as land drainage, involves the use of buried pipes or mole drains to assist water movement within the soil. As a result of the intensification of agriculture over the past 50 years, many floodplains have been subjected to sub-surface drainage schemes to improve the potential of the land for intensive grass or even arable production. A frequent component of such schemes was the lowering of the riverbed, in order to increase the freeboard and hence give better drainage efficiency. Such deepening of rivers may not have a large impact on flood frequency, but it would reduce the potential of the river to sub-irrigate its floodplain in summer.

It is rarely the case that existing species-rich meadows have pipe-drainage systems. If a landowner has gone to the expense of draining a parcel of floodplain, they would then normally intensify its use through application of fertiliser, which would eliminate species-rich stands. Where a meadow is on less well-drained land or its natural drainage has been compromised by river engineering operations, then subsurface drainage is occasionally used. Where this is the case, the species richness of the grassland may depend on the continued operation of the pipe system.

The desilting of rivers to aid the drainage of surrounding land was a common practice in the period 1960-1980 and was a potentially damaging operation for any associated MG4 meadows (eg the River Churn at North Meadow NNR.) The intensity with which rivers were managed during the 1970s and 1980s in order to maintain standards of surface for land drainage has now been reduced (EA 2000), and it is expected that rivers will slowly return by geomorphological processes to their natural depth and width. The recent changes in river management in favour of more natural processes is destined to continue under the auspices of the European Water Framework Directive.

2.6.5 Mineral extraction

As mentioned earlier, many floodplains are currently being exploited for the coarse sediments (sands and gravels) which underlie them. This will have direct impacts on any meadows on an extraction site that are not protected within the planning system, and indirect effects on surrounding sites which are reliant on the same gravel terrace for subirrigation or drainage. The fragmentation of the shallow aquifer may disrupt its function and disconnect the floodplain from the river (Longley 1998). It also limits the scope for restoration of the habitat, which in some areas may depend on the river terraces for the maintenance of an appropriate hydrological regime.

2.6.6 River restoration

Where rivers have been hydrologically disconnected from their floodplains through embankment or straightening, it is often possible to reverse the intervention and partially restore the river to a more natural state. An example of this practice of river restoration, which has relevance to potential habitats for MG4 grassland is the River Cole at Coleshill in Oxfordshire (Holmes & Nielsen 1998). In part of the restored reach, the floodplain holds a species-rich meadow containing the snakes-head fritillary (*Fritillaria meleagris.)* Restoration of the river involved the re-instatement of former meanders and the raising of the riverbed by the addition of gravels. The goal of reconnecting the river to its floodplain has been considered a success from a hydraulic perspective (Kronvang *et al* 1998). The duration of floodplain inundation has increased 12 fold.

Although river restoration is a practical technique by which areas of former floodplain meadow may be restored, there are several constraints to its use. The original objectives of a river-engineering project often relate to the protection of property from floods. Where flood-management structures have been installed to protect urban developments on the floodplain, the constraint is a socio-economic one. Relocation of developments would tend to be too unpopular and/or expensive in most cases.

In cases where defence of property is not important, there are other difficulties to be faced in restoring lowland rivers. The area of impact is usually large and the riparian ownership is often complex leading to difficulties, if some parties do not wish to co-operate. Even if the river itself can be returned to a more natural state, it does not follow that the floodplain will return to its former state. If it has been under intensive agricultural use, its soils may be compacted and nutrient-enriched and its natural micro-topography levelled. In particular, it should be noted that hydrological restoration of a river and its associated floodplain would not be straightforward where mineral extraction has fundamentally altered the composition of the floodplain sediments.

3. Nutrient dynamics

3.1 Ecosystem productivity

River floodplains are unique among wetland types in that they have a linear form along rivers and streams. When not modified by ditching, the linkage between the river, its riparian zone and the adjacent upland is a continuum. Although river floodplains are known to be relatively nutrient-rich compared to other semi-natural habitats and to be important for their role in regulating nutrient import and export, there are surprisingly few studies that have addressed the nutrient dynamics of the floodplain ecosystem (Verhoeven *et al* 1998). Many of these studies are in the Netherlands, where numerous wetland communities have been lost due to nutrient enrichment, drainage, or flood control, and where the partial restoration of the connection between the river and its floodplain areas by the removal of embankments is a new conservation management option.

The availability of nutrients, particularly of nitrogen and phosphorus, is known to directly influence primary productivity, plant species composition and food chain integrity of these ecosystems. Knowledge of the nutrient status of the floodplain community is also necessary to understand the potential effects of any restoration measures on their nutrient dynamics, and thus to evaluate the potential for restoration of typical floodplain plant communities.

The current paradigm for understanding the biogeochemistry of floodplain wetlands can be encompassed in the 'Flood-pulse concept' (Junk *et al* 1989). This emphasises the overriding effects of seasonal floods on the functioning of the floodplain as well as the river channel. Floodplains receive sediment inputs through each flooding event and have long been recognised as nutrient-rich, fertile environments. However, it is becoming more obvious that it is not simply the duration of the flood pulse, but also (and sometimes overridingly) the quality of the river water that is important for nutrients, especially P (Spink & Sparks 1998).

Several researchers have addressed the assumption that high species diversity is related to low nutrient supply. Janssens *et al* (1998) found in a study of 281 permanent grassland sites (covering a range of soil types, soil fertility, pH and water supply) that all sites with a relatively high species richness were found on soils containing less than 50 mg P (extractable by acetate+EDTA) kg^{-1} dry soil, and 250 mg K (extractable by acetate+EDTA) kg^{-1} dry soil. No relationship between species-richness and soil nitrogen was found, possibly because of the additional effect of microbial population dynamics in controlling N availability.

In common with other wetland ecosystems, floodplain communities are some of the most productive semi-natural systems. However, highly productive communities are generally not species-rich: maximum species diversity in wet grasslands occurs at intermediate levels of total biomass production in the range. 400 - 700 g m^{-2} yr^{-1} (Verhoeven *et al* 1996). One potential explanation for changes in the species composition of formerly diverse floodplain grasslands is, therefore, that nutrients have increased to the point where productivity has exceeded the 700 g m^{-2} yr^{-1} threshold (equivalent to 7 tonnes ha^{-1} yr^{-1}). The productivity of floodplain meadows could be increasing either as a result of increasing atmospheric deposition of nitrogen compounds (INDITE 1994) or due to the increasing amount of phosphorus bound to flood-deposited sediments (Walling *et al* 2000). The relative importance of these processes is dependent on which of the major nutrients is currently limiting productivity within the meadows.

3.2 Limiting nutrients

Plant growth in moist grasslands is usually limited by the availability of N, P, or, less frequently, K, or a combination of these elements (Verhoeven *et al* 1996). A low availability of one or more of these nutrients is crucial for maintaining diverse vegetation. Nutrient availability is the net result of nutrient inputs, nutrient recycling, and nutrient exports. These processes vary greatly for different elements.

For phosphorus (P), in natural systems the main source is weathering of rocks, but in wet grasslands, inflow of phosphates is predominantly through sediment deposition. The main input of soluble phosphates to rivers is from point sources such as urban sewage works: these inputs peaked in the 1960s-1980s and have been declining in most major European catchments since, as a result of improved waste-water treatment techniques. The main input of particulate phosphate, however, is from agriculture (Mainstone *et al* 2000).

For nitrogen (N), the main sources are:

1 atmospheric inputs of NO_3^- and NH_4^+,
2 microbial fixation of atmospheric N_2, and
3 particulate N in flood waters.

Atmospheric inputs of oxidised N (NO_3^-) are primarily due to incomplete combustion of fuel in motor vehicles, whereas the primarily source of reduced N (NH_4^+) is volatilised ammonia from agriculture. Atmospheric N deposition ranges from about 5 to 50 kg N ha^{-1} yr^{-1} in the UK. Levels of N in deposition have declined in Europe over the last 5-10 years, but only slightly. Microbial fixation is partly a function of vegetation community composition (MG4 communities contain several species of the family Fabaceae (legumes), which host N-fixing bacteria, eg *Trifolium pratense, Lathyris pratensis, T. repens, Lotus corniculatus, Vicia cracca*) and partly of soil conditions such as pH. The nitrogen contribution to the soil from legumes may be as much as 100 kg N ha^{-1} yr^{-1} and may therefore be a major component of the nitrogen budget (Stevenson & Cole 1999). Nitrogen derived from floodwater is primarily in the form of organic matter, such as leaf litter from vegetation higher in the catchment deposited on the floodplain.

It is theoretically possible to construct budgets for inputs and outputs of the major nutrients. However, grassland vegetation does not respond to the total store of nutrient in the soil, but to its availability. It is therefore necessary to understand what controls the availability of nutrients, such as N and P, in floodplain meadows and to identify which nutrient, if any, is limiting. Soil chemical and physical characteristics affect the availability of N and P through nutrient recycling in different ways. Prolonged wetness results in the release of P, since under anoxic conditions, phosphate bound to Iron (III) compounds is released as the iron is reduced to Iron (II). Long wet periods also strongly stimulate denitrification, whilst limiting both nitrification and mineralisation. Both of these factors mean that, in theory at least, prolonged anoxic conditions in riparian grasslands promote N limitation of productivity. Rewetting can therefore be an important tool for reducing nutrient availability in N-enriched sites (Van Duren Petgel 2000).

Conversely, P limitation should occur in better drained sites, with P retained as insoluble phosphates (P bound to the oxidised Iron, Fe (III)). Thus, enhanced soil oxygen supply through, for example, the maintenance of surface drainage systems could be a management tool for temporarily reducing P availability in P-enriched sites. It must be remembered, however, that unlike N, which is permanently lost from the system through denitrification, lowering water tables will only reduce the *availability* of P, but not the *store* of P. The ability to *lock up* P in this way is also dependent on soil pH. In soils of high pH, P is bound to calcium rather than iron and its availability is then less variable with respect to the soil's redox status.

Another potential factor controlling availability of nitrogen and phosphorus is vegetation management. Koerselman *et al* (1990) showed in the Netherlands that harvesting creates a strong net loss of P from the system and a relatively small net loss of N. Thus, wet grasslands with a long history of mowing may be expected to be P limited, whereas irregularly or only recently mown fens would be N limited. This has been confirmed in experimental fertilization studies (Verhoeven *et al* 1996).

Another difference between N and P release is the extent to which it is affected by other biological processes. Experiments suggest that microbially-mediated processes such as nitrogen-fixation, nitrification and organic matter mineralisation exert a key effect on N availability in the soil, with no analogue existing for P (Van Oorschot *et al* 1998). The reason is that, unlike N, mineralisable P does not accumulate in forms that are readily available to the microbes. Instead, PO_4^{3-} is quickly immobilized by several organic and inorganic adsorption mechanisms, making its availability more directly related to physical and chemical environmental conditions such as pH, redox and presence of iron and calcium.

From a qualitative standpoint, one would expect stands of the MG4 community to be P- rather than N-limited in comparison to other wetlands, because they are:

- Regularly mown and hence nutrients are stripped from the site as biomass.
- On soils of higher than average pH with higher than average levels of free calcium.
- On soils with good surface drainage resulting in aerated soils and high redox status.

This is supposition, however, as no evidence from controlled fertilizer experiments is available to confirm whether MG4 vegetation is either N or P limited.

One practical way of assessing the degree of limitation of plant growth by nutrients is by assaying the N and P concentrations of herbaceous plant material. Critical values for N and P limitation are 14 mg N g^{-1} and 0.7 mg P g^{-1}, respectively (Verhoeven *et al* 1996). Even more useful has been combining these into ratios, eg the vegetation N:P ratio at end of the growing season. Verhoeven *et al* (1996) suggested that an N:P molar ratio >36 was characteristic of P-limited community, those <31 are N-limited, and those in-between may be co-limited or share limitations with other elements. Using these criteria they were able to almost perfectly divide about 40 sites taken from the literature.

The data available from hay analysis from MG4 or related communities is summarised in Table 3.1. Interpretation of the samples from the Derwent Ings suggests that the N:P molar ratio is just 22. This would indicate a limitation in N rather than P. The absolute nitrogen content of the herbage was almost at the critical value published by Verhoeven *et al* (1996) see Table 3.2.

Table 3-1 Hay mineral analysis from unfertilised MG4 flood meadows, with comparison to other mesotrophic grasslands occupying similar sites. DOMD = % pepsin cellulase digestibility.

Community	Site	N%	P%	K%	Na%	Ca%	Mg%	DOMD	Reference:
MG4	Cricklade	1.10						61.5	English Nature records
MG13	Cricklade	1.47						58.7	English Nature records
SOM3	Meuse	1.6	0.16	1.79	0.1	0.72	0.21		Krebs *et al* 1999
M22equivalent	Meuse	1.1	0.1	1.12	0.03	0.82	0.34		Krebs *et al* 1999
MG4/13	Derwent Ings TatA	1.38	0.14	1.11		0.40	0.13	61	English Nature records
MG6/7 fertilised	North Wyke, Devon	2.22	0.27	1.78	0.38	0.28	0.13	62	BD1425 IGER (7&8)

Table 3-2 A comparison of the nutrient analysis performed on hay samples from the Derwent Ings with published critical values (Verhoeven *et al* 1996)

	Derwent Ings Hay sample	Critical values
N content / mg g^{-1}	13.8	14.0
P content / mg g^{-1}	1.4	0.7
N:P molar ratio	21.8	31

Therefore this quantitative analysis suggests nitrogen-limitation whilst the qualitative view suggested P-limitation. Gilbert (2000) questioned whether the extrapolation of Verhoeven's critical values, which were largely derived from low productivity grasslands, to more productive, mesotrophic systems is valid. Unfortunately, there are no experiments of controlled fertilisation in parallel with yield analysis on any stand of MG4 grassland, to unambiguously discriminate between N versus P-limition. Co-limitation by both nutrients is also a possibility. Conclusions about the actual limiting nutrient in floodplain meadows cannot be drawn, given our current state of knowledge.

Other nutrients besides N and P should also be considered. Only a few studies reveal potassium (K) limitation to vegetation; this is restricted to sites that have been severely drained in the past and mostly used for hay cropping as well, which resulted in K removal (Oomes *et al* 1996; Van Duren & Petgel 2000). The available data from the Derwent Ings samples suggest K is a candidate for being the limiting nutrient there, because the K-content of the herbage is at the bottom end of the range observed in other grasslands. K-availability may not be as important as P in determining species richness, but it is believed to have a significant impact on species composition. At the Park Grass experiment, for example, in plots receiving K, *Taraxacum officinale* agg. was 60 times more abundant than plots in which K was not replaced (Tilman *et al* 1994).

3.3 Mitigation of high nutrient availability

Having demonstrated that nutrient supply has a major influence on species diversity, this raises the possibility that nutrient availability might be reduced and/or controlled at a site in order to restore (or maintain) species diversity in wet meadows. In theory, the strategy would be to focus on a macronutrient (N, P or K) whose availability could be most easily reduced so that it becomes limiting relative to the other macronutrients (in line with the Verhoeven ratios for example.) In practice, it may be difficult to regulate the supply of a particular nutrient through controlling inputs and nutrient cycling (eg by regulating the redox status) and/or by controlling nutrient exports (eg through hay removal.)

Nutrient-availability depletion studies have been conducted in the Netherlands, where nutrient inputs were dramatically reduced to wet meadows through sod removal (Berendse *et al* 1992). Species diversity, however, was not necessarily restored to pre-enrichment levels. It was more successful on sites close to a seed source and on sandy soils rather than clay-rich soils or soils with high organic matter. The reason for the difference between soil composition is that clay-rich and organic soils had a higher capacity to retain nutrients through the soil profile i.e. below the level removed by sod cutting, and these nutrients became available through desorption or mineralisation long after nutrient inputs were reduced. Thus, because of both abiotic and biotic factors, there may be a considerable lag time before restoration measures are successful.

Compared to English wet grasslands, the well-studied Dutch floodplains of the Rhine have been more heavily enriched with P. This has led to higher rates of P release and N mineralisation than other less polluted grasslands. There have been few such detailed studies with other wetland ecosystems, but there are suggestions that much higher carbon:phosphorus (C:P) ratios occur in floodplain grasslands in the UK than in the Netherlands. Van Oorschot (1996) found grasslands along the Torridge River in Devon, UK those along the Shannon River, Ireland to have C:P ratios in excess of 100, in comparison to Dutch floodplain grasslands with values of 50-80. Occasional flooding with polluted Rhine water, high in particulate P, in the 1960s-1990s is the most probable cause. In contrast, carbon:nitrogen (C:N) ratios of soils in all 3 areas were similar, in the range 11-20. The degree to which nutrients are bound in organic versus inorganic forms will be a factor determining their distribution in terms of depth in the profile. Sod removal assumes a concentration of available nutrients in the surface layers.

Other mitigation techniques for reduction of available nutrients such as soil inversion of soil mixing to dilute nutrient-rich top-soil with nutrient-poor sub-soil, are also dependent on clear stratification in the distribution of nutrients.

Chemical amendments to the soil to chemically immobilise nutrients have been suggested (Gilbert 2000). Phosphorus availability can be reduced by altering pH in either direction. Acidifying soils to pHs below 5.0 will promote the binding of phosphorus by iron and aluminium, but this is not appropriate for the MG4 situation where many of the component species are not found on such acid soils, presumably as a result of sensitivity to either iron or aluminium toxicity. Phosphorus may also be immobilised by increasing soil pH above 7.0. In this case it becomes bound to free calcium ions. This is more compatible in the context of MG4 grassland, where some stands already have soil pHs above 7.0 (as high as 8.3 according to Jefferson, 1977) and liming may be a tool for combating the effects of excess P deposition, though such amendment should be done with care on sites with pH below 7.0, as it may have other impacts on community composition.

The use of hydrological management to affect soil redox status was discussed in section 3.1 above. However, options are again limited if working with an existing grassland sward as the imposition of anoxia to strip N from the soil will itself eliminate many of the target species for MG4 conservation. Drainage of soils to promote P immobilisation may be more compatible hydrologically, but not effective in high pH soils where calcium rather than iron is the metal controlling P solubility.

Whichever technique is considered, mitigation on nutrient-enriched sites requires an understanding of the nutrient's chemical and physical distribution within the soil profile.

3.4 Nitrogen budget

A quantified budget is difficult to achieve for N because of the complex interaction with the atmosphere. The fluxes involved in nitrogen-deposition, nitrogen-fixation, volatilisation of ammonia and denitrification of nitrate are all potentially significant yet difficult to quantify. Leaching losses may also be significant, and again hard to quantify.

Nitrogen is important, however, because it is frequently a limiting nutrient in terrestrial ecosystems, and its availability has a profound impact on plant growth. The availability on nitrogen in a soil is not the same as the soil's reserve of the element. The readily available pool of nitrogen is often very small compared to the total N-content of the soil. Very large quantities of N are stored under permanent grasslands, such as floodplain meadows, in organically-bound forms. The readily available pool (NO_3^- and NH_4^+) is rapidly cycled, with the products of N-mineralisation being rapidly absorbed by plants during the growing season. Spot measurements of the available pool are therefore not a reliable guide to the site's nitrogen status. A small pool may be detected where there is in fact a high flux (Jamieson & Barraclough 1999.) Over the long-term, however, increased N deposition can shift the nutrient limitation of grasslands from nitrogen to another element, most often phosphorus (Kooijman *et al* 1998).

3.4.1 Sources of nitrogen

The major sources of N to floodplains are atmospheric N, nitrogen fixation, and nitrogen from the river. Inorganic N from the atmosphere is deposited in oxidised and reduced form. Oxidised N (NO_x), primarily from incomplete combustion in vehicle engines, can be deposited as NO_2 in dry deposition and NO_3^- in wet deposition; reduced N is primarily ammonia volatilised through agriculture, animal housing etc. which forms NH_4^+ in wet deposition. Similar to the rest of Europe, the pattern of NO_x deposition in the UK tends to generally follow major population concentrations, being highest in the Midlands and the south-east of England. NH_4^+ is deposited more closely to the point of emission than NO_3^-, resulting in a very heterogeneous 'patchy' distribution, with high levels directly downwind from point sources. Overall in the UK, the highest NH_4^+ deposition occurs in areas of intensive agriculture, such as the South-west, Welsh borders and East Anglia. The net result of the patterns of NO_3^- and NH_4^+ deposition is overall high N deposition in W. England and Wales, and the highest deposition over areas of high population concentration. Much lower N deposition occurs over Scotland, although orographic effects mean that deposition can be relatively high in mountainous areas even where local sources of N are low.

In floodplains, nitrogen (primarily organic forms and soluble NO_3^-) can also be deposited by floodwater. This feature of floodplain soils means that they participate in 'nutrient spiralling', by which nutrients such as nitrogen are continuously cycled through the ecosystem as they move downstream, through recycling flood deposits of nitrogen (Pinay *et al* 1999). Streams and rivers draining agricultural land in the UK can have high nitrate concentrations: in a recent study of a riparian ecosystem in East Anglia the drainage stream (a tributary of the River Ouse) was measured to exceed EU limits of 11 g N m^{-3} more than 25% of the time over a 1-year period (Machefert *et al* in review). The relative contribution of NO_3^- from the river in relation to atmospheric N is a function of the nitrate concentration of the river and the flooding frequency, and would be vary considerably between different floodplains and be difficult to predict from year to year.

A recent review of water quality in the context of habitat restoration (Lamberth & Haycock 2001) cites values for the nitrogen content of river water regarded as eutrophic. In the case of nitrogen, values of 1.5 g m^{-3} of total oxidised nitrogen (TON) and 1 g m^{-3} of reduced nitrogen (ammonium) are given. If we calculate the nutrient loading that would be applied to the floodplain if 0.2 m depth of water were left following the recession of a flood (or infiltrated the soil during the flood), which would be a representative figure for some areas within floodplain depressions, the total N-load would be in the order of 5 kg ha^{-1}. If we assume 3 such flood events per year (Table 2.2), then the annual load would be 15 kg ha^{-1}. This is of the same order as the atmospheric deposition and would be further supplemented by organically bound N deposited as allochthonous leaf litter (Xiong & Nilsson 1998). Such deposition would tend to be spatially variable and amounts as high as those calculated here would only occur in depressions able to retain water on recession of the flood or along the "strandline." A spatially averaged mean would be lower and therefore floodwater-source N is likely to be lower than atmospheric deposits except in cases of heavily polluted rivers.

3.4.2 Sinks for nitrogen

Nitrogen is lost from a site in a number of ways; primarily through harvesting of vegetation (and animals), denitrification and leaching.

Grassland vegetation can remove significant amounts of nutrients, especially N and K; offtake values in hay for unfertilised species-rich hay meadows on the Somerset Levels were measured at 70.1 kg N ha^{-1}, 5.5 kg P $ha^{-1}$and 39.4 kg K ha^{-1} (Kirkham & Wilkins 1994b). Grasslands that are N-limited may increase the uptake and storage of N if nitrogen deposition increases, to a point, before invasion of more N-tolerant species takes place. Microbial saturation must also occur before significant N leaches from the system. For forests, microbial immobilisation generally takes place at a organic horizon molar C:N ratio greater than 27 (Gundersen *et al* 1998).

Wet grasslands have an additional microbial removal mechanism for N: denitrification. Denitrification is a facultative anaerobic process that occurs most efficiently under fluctuating aerobic-anaerobic conditions. A source of labile C and NO_3^- are also required. The loss of N through denitrification can occur as gaseous N_2, upon complete denitrification, or the intermediary products NO or N_2O (a powerful greenhouse gas) under sub-optimal conditions. In a review of 33 field studies, Machefert *et al* (2001) found that 'threshold' conditions of 10^oC and 60% water-filled pore space (WFPS) are required for a significant loss of N as N_2O. They also determined that, on average, about 0.5-2 kg N ha^{-1} y^{-1} are lost through denitrification by unfertilised riparian grasslands, and found broad patterns between N_2O fluxes and the mean annual rainfall, the depth of the organic horizon, and the soil bulk density. These results are in agreement with more detailed studies of N gaseous losses along a single river; eg Pinay (1995) in the Garrone river, France found that in-situ denitrification was significantly correlated to the proportion of fine particles (silt+clay) in the soil, with >70% as the threshold at which significant denitrification is observed. On a monthly basis, over the course of a year, silty or loamy sites always showed significantly higher denitrification rates than sandy soils.

There is, however, no evidence that denitrification rates are correlated with flood duration, at least for inundation events lasting under a week. Pinay (1995) hypothesised this is not long enough to alter the long-term redox status of a site to significantly affect gaseous N losses. The existence of a given time before there is a measurable microbial response to a change in hydrology is in agreement with a number of studies on methane (CH_4) emission (reviewed in Dise, 2001) showing a lag of 1-6 weeks between inundation of a wetland and significant increases in the flux of methane. This may be due to time required to deplete reserves of soil oxygen, build up significant microbial populations, saturate methane-binding sites, reduce other electron acceptors, or any combination of these reasons.

Flooding can exert a strong *indirect* influence on soil redox status, however, by depositing fine-textured soils in depressions close to the water table, allowing optimal conditions for anaerobic processes to occur (Pinay *et al* 1999). Although irregular, flooding is essential to providing the 'pulses' of soil and nutrients, and maintaining the landscape features conducive to redox processes (Junk *et al* 1989; Pinay *et al* 1999).

Although flood pulses of short duration do not significantly affect redox status, it is well-documented that major pulses of N_2O and other reduced gases can occur after intensive rain events (eg Clayton *et al* 1994; Mattson and Likens, 1993). It is highly likely that this is due to emission of gases that are trapped in pore spaces rather than an actual increase in production - this may be due to both changes in air pressure and the physical displacement of soil gases by water.

In unfertilised grasslands, uptake, immobilisation and denitrification normally remove nearly all of the nitrogen, such that nitrate leaching is minimal. Leaching is more important for potassium (K) than either N or P, which is mainly lost by surface runoff as particulate P in these environments.

3.4.3 Critical loads

The European Union has adopted the 'critical loads' concept to address pollution abatement strategies. A critical load is defined as 'a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge' (Hettelingh *et al* 1995).

In some ecosystems, such as peatlands and coniferous forests, a change in ecosystem function, such as N-leaching or N-accumulation are used as a 'detectable change' for determining critical loads. In grasslands, however, current critical load estimates are based on biological indicators: the reduction of species diversity as communities become dominated by nitrophilic species such as certain tall grasses. Critical loads for calcareous species-rich grasslands, at 25-35 kg N ha^{-1} yr^{-1}, are slightly higher than those for neutral to acid, species-rich grasslands, at 20-30 kg N $ha^{-1}yr^{-1}$. (Bobbink *et al* 1996). The reason is that calcareous soils tend to be well-buffered, and also bind phosphate, so that many of these sites are more P than N-limited. The critical load for grasslands that are managed by cutting (which removes N) can also be higher than those in which biomass is not regularly removed. Still, when total N-deposition is assessed, critical loads for neutral to acid species rich grasslands are exceeded in many parts of the UK, including much of the west of England, the Midlands and Yorkshire. This suggests that some grassland community shifts toward more N-tolerant species may have already occurred in the UK due to excess nitrogen deposition. There is some evidence, from comparing the results of countryside surveys 20 years apart, that this is indeed the case (Chalmers *et al* 2000).

3.5 Phosphorus budget

Phosphorus is more amenable to budgets than is nitrogen. It enters a floodplain meadow system primarily in a particulate form attached to sediment and leaves primarily in the hay crop. Relatively small amount will be removed by grazing animals. It is also important to know whether a given site is storing P or exporting it. Indication of P accumulation may not be obvious in terms of short-term changes to the vegetation composition of a site, but once the soil has become heavily loaded with the nutrient, restoration of a P-limited system is likely to be an extremely difficult and protracted process (Richardson and Qian 1999).

Whilst it is easier to construct an input/output budget for phosphorus than it is for nitrogen, its internal cycling once in the site is even more intractable. That is to say the availability of the nutrient to plants does not necessarily reflect the total amount present. Soils can store large amount of P as insoluble compounds (both organic and inorganic) and conversion between the available and unavailable forms of the nutrient are at least as important in describing phosphorus status as the overall mass budget. Studies at Tadham Moor in Somerset have suggested that there is a net export of P from the site leading to a decline in the total P reserve, yet the availability of P is increasing and vegetation is responding to this (J.R.B. Tallowin, pers. comm.)

There has been no attempt at a P-budget for a MG4 grassland, but using information from other sources an outline can be constructed. The amount of sediment deposited at a site is inherently variable from year to year depending on flood frequency and water quality. However, a number of river floodplains in southern England have been extensively studied (Walling & He 1998) and so an estimate of mean sediment rate can be approximated. Data presented in their paper for 5 separate rivers suggest a mean silt deposition rate at a distance of 50 m from the river is 2 kg m^{-2} yr^{-1}. The phosphorus content of such sediments is not easily defined. The total phosphorus content of river sediments in lowland floodplains is of the order of 1000 mg kg^{-1} (Walling *et al* 2000), whilst plant-available phosphorus in samples of fresh sediment taken from an MG4 site (North Meadow NNR) and extracted using Olsen's bicarbonate reagent, gave values of 220 mg kg^{-1} (J.C. Gilbert, pers. comm.). If we take the latter value, which is probably the more relevant in terms of floodplain vegetation, we can estimate a influx of available phosphorus at 4.4 kg P ha^{-1} yr^{-1}. Phosphorus is also present in a dissolved phase, but at much lower levels. If we take the value of 0.1 g m^{-3} cited in Mainstone *et al* (2000) as being a representative figure for the concentration of dissolved phosphate in a eutrophic lowland river, and use the same assumptions as for the nitrogen budget in section 3.4.2 above, then the P-loading to the floodplain from a dissolved source would be in the order of 0.6 kg P ha^{-1} yr^{-1}. This gives a total loading of available phosphorus of 5 kg ha^{-1} yr^{-1} . In terms of removal we have a typical hay yield of 4 tonnes ha^{-1} yr^{-1} and a P content of 0.14%. This gives an export of 5.6 kg P ha^{-1} yr^{-1} in the hay alone. This simple calculation points to a system approximately in balance, but there are major caveats associated with it:

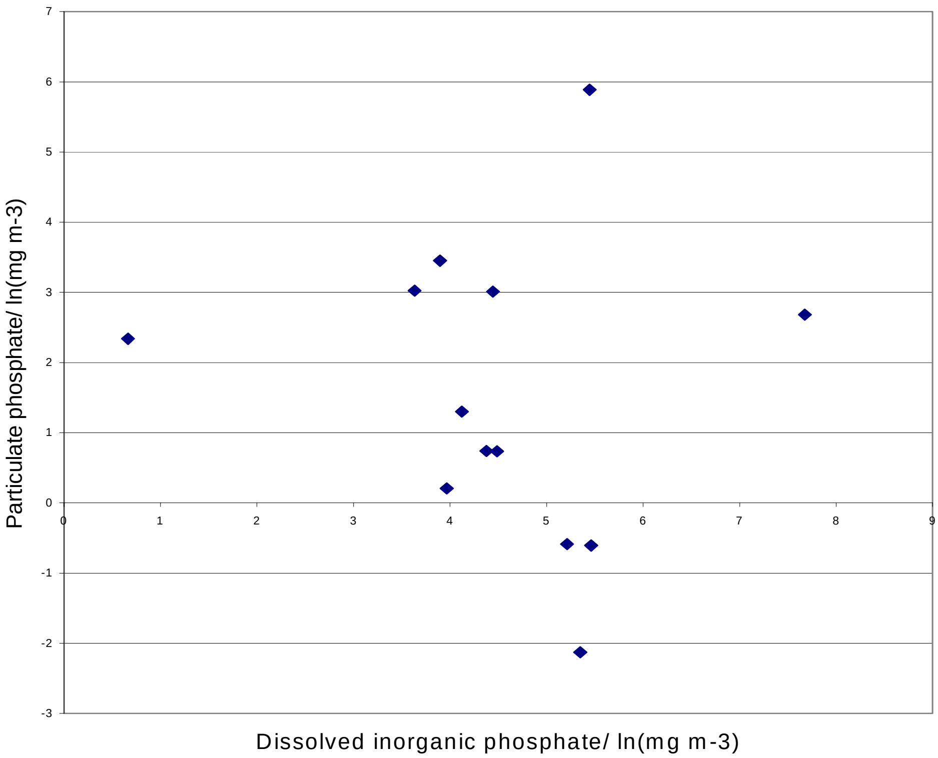
- the sedimentation rate was a very generalised mean, and the assumptions about floodwaters rather coarse;
- the P-availability assumes that the estimated 800 mg kg^{-1} of P that was not extracted by Olsen's reagent remains in an unavailable form; and

- no account was taken of P removed from the site by animals (though this is likely to be small).

It would be useful to perform such a budget using site-specific data to analyse net P accumulation or loss over a number of years. Mass budgets on a short timescale are not likely to reflect phosphorus availability because the internal cycling factors such as redox status will overwhelm small changes on an annual basis. A site being a net importer or exporter of P may only become relevant to the vegetation after many years, even decades.

In terms of spatial distribution within a site, Walling and He (1998) make the point that sediment deposition is very variable, with depressions that hold floodwater receiving the greatest amount of sediment. The action of grazing animals by distributing their dung over the field will perhaps counteract this concentration effect to some extent by creating a finer-scale heterogeneity (Herriot & Wells 1963; Putman *et al* 1991.) Soil analysis at North Meadow (Payne *et al* 1998) has shown that soil phosphorus availability is highest within depressions. The result may be due to enhanced silt deposition or to the increased mobilisation of phosphorus in anoxic soils. This signals that sampling of meadow soils must be performed carefully in order to obtain a valid estimate for nutrient availability across the site. (see section 5.3 for discussion of effect of P-variability on plant community composition.)

In terms of seasonal variation in the phosphorus loadings of rivers, there are two factors to consider, one relating to the soluble phase the other to particulate P. In lowland catchments dominated by waste-water discharges, the loading of soluble phosphorus is relatively constant through the year. The concentration of soluble P is therefore largely a function of river flow. In summer, low flows result is less dilution of the discharged P and therefore higher concentrations are recorded (Mainstone *et al* 2000). The concentration of particulate P, meanwhile, is largely a function of the proportion of the river's flow, which originates from overland flow following rain. This is because surface water carries a much higher suspended sediment load than groundwater and increase in river flow will re-suspend material from its bed and banks. Concentrations of particulate P are therefore highest following storm events. The sum of these two parts gives the total P concentration, whose seasonal trend depends on the geology of the catchment (determining overland flow) and the amount of waste-water being discharged (Mainstone *et al* 2000). In terms of its relevance to floodplain situations, it is particulate P that is of greater relevance (see calculation above.) The implications for the hydrological management of floodplain meadows are not clear. The deposition of P will be driven primarily by unpredictable storm events creating both overland flow higher in the catchment and floodplain inundation lower down. On most sites there is limited ability to influence these events. Allowing water to leave the site rapidly, following the recession of the flood will prevent P in the soluble phase being absorbed by the meadow soil and may result in some of the finest suspended material being returned to the river. Indeed in an agricultural catchment studied by Brunet and Astin (2000), there was a net loss of soluble P from the floodplain during flood events. If there are options to deliberately flood a meadow, even when river flows are low, then these should be exercised with care in summer and autumn when the concentration of soluble P is likely to be high. The concentration of soluble P in natural floods is perhaps less of a concern as so little of it (if any) seems to be retained. Another useful point from the paper by Brunet and Aston (2000) is that there is no consistent relationship between concentrations of soluble and particulate P (Figure 3.1). This illustrates that river chemistry is so dynamic that internal equilibrium is rarely attained. River water quality is usually expressed in terms of soluble P, which is not necessarily a good guide to likely rates of P deposition on floodplains. Therefore, whilst the concentration of soluble phosphate in the River Thames has been reported to have risen 8-fold over the period 1940-



1980 (Heathwaite *et al*. 1996), it does not necessarily indicate an equivalent rise in the phosphorus load being delivered to the floodplain.

Figure 3-1 Correlation between soluble and particulate phases of P carried in the River Adour, France (after Brunet & Aston 2000).

It appears that the two measures bear little relation to one another and therefore estimates of soluble P in a river are not a reliable guide to levels of particulate P.

3.6 Sulphur budget

High sulphur deposition and its noxious effects have been a feature of densely populated areas since the Industrial Revolution, but acid rain only became an international issue with the introduction of tall stacks in the 1960s and 1970s to reduce local pollution. Increasing concerns about acid rain effects gave rise to a series of EU sulphur protocols in the 1980s, which resulted in increased efficiency, installation of scrubbers on tall stacks, and phasing out of obsolete plants.

As a direct result of this legislation in the UK, sulphur deposition has declined dramatically by 50-60% in the last 20 years. Current deposition of SO_4^{2-} across the UK averages around 15 kg S ha^{-1} yr^{-1}, ranging from about 3 to 35 kg S ha^{-1} yr^{-1}. The major decline in SO_4^{2-} deposition has had the rather bizarre effect that some crops in the UK are becoming S deficient, requiring S-containing fertilisers for optimal yield (Chalmers *et al* 2000; McGrath *et al* 1996). There have been no studies on whether this is an issue for MG4 grasslands, although from the few element ratios available it does not appear that S-deficiency is an immediate problem.

The sulphur deposition also has a role in the acidification of the surface soil. This has not been widely investigated for floodplain grasslands, which are normally well-buffered as a result of sediment deposition restoring cations such as calcium, magnesium and potassium to the soil, which are lost by leaching in other environments. However, floodplains that have become separated from the river through the construction of embankments may be at risk from acidification, because they have lost their supply of sediment. Whilst sulphur loads from the atmosphere are declining, their role as acidifying agents is being taken by nitrogen compounds which may also act to strip cations from surface soil. Surface acidification is perhaps not an immediate threat to MG4 conservation, but it is another potential problem to be considered if the normal functioning of the floodplain is disrupted.

3.7 Source of floodwater

In natural floodplain systems, floodwaters tend to be a combination of water leaving the main river, when the channel's capacity is exceeded, and water draining from the immediate catchment onto the floodplain. The quality of these two water types may be quite different. The water spilling from the channel will tend to have a high suspended sediment load as the carrying capacity of water is related to its velocity. Differences between the two sources will also reflect variation in land use between the local and the higher catchments. Catchments with a high proportion of tilled land and with clay geology will tend to produce higher loads of suspended sediment (eg Steegen *et al* 2000), compared to catchments with permanent plant cover (eg Hill & Peart 1998).

When the flood routing within the floodplain is manipulated using embankments, these two water sources are kept separate and the sedimentation regime experienced by different parts of the floodplain could vary considerably. There have been no quantitative studies comparing the effect of different floodwater sources on floodplain meadows, but it would be expected that areas receiving water only from the local catchment would have a much reduced sedimentation rate and hence nutrient supply. Water from a local agricultural catchment may carry considerable quantities of dissolved nutrients, but as discussed above, it is unlikely that these nutrients would be retained by the floodplain once floods recede, unless infiltration rates were very high. One would hypothesize therefore that the nutrient supply to an area of floodplain protected from river-sourced floods by an embankment would decline, in spite of intermittent flooding from its local catchment.

In areas with a significant human influence, land use can play an overriding role in the chemistry of certain ions, especially nitrate and phosphate. Thornton and Dise (1998) found in a survey of 55 streams in the English Lake district, that the proportion of agricultural land explained between 40 and 55% of the variability in the streamwater fluxes of alkalinity, calcium and nitrate. Johnes (1996) used a simple export coefficient model (in which the total N and P load to a water body is modelled empirically as the sum of the individual loads on a catchment-area basis) to predict total N and P fluxes in 38 UK catchments within 5% of observed values. The approach has recently been extended to allow application to the entire land area of England and Wales, predicting total N and total P export from land to adjacent waters on a parish basis. The model is constructed using data collected on the spatial distribution of land use, fertilisers applied to each land use type, the numbers and distribution of livestock and human populations in the catchment, and the input of nutrients to the catchment through nitrogen fixation and atmospheric deposition. It also takes account of spatial variations in the intrinsic nutrient retention capacity of each landscape unit. Such approaches are potentially powerful tools for evaluating the impact of land use and land management on surface water quality. In the context of floodplain meadows, however, it is the deposition of nutrients back to land that is important and these models are less well developed. The isotope methods described in Walling and He (1998) show considerable promise for improving our understanding of this area.

3.8 Hay mineral content

Hay mineral contents are presented in Table 3.1 for a limited range of MG4 and MG4-related sites, where data were available. The sites are remarkably similar to each other, which is unexpected given that the vegetation communities they support may be quite different, eg species-rich MG4 versus species-poor grassy MG13. This may reflect the paucity of the data set, but also the fact that these communities form a continuum that is difficult to sample separately. However, communities of conservation importance do differ markedly from an improved MG6/7 grassland that stands on a gravelly river floodplain at North Wyke, Devon. This shows markedly higher contents of nitrogen, sodium, and phosphorus, and reduced levels of calcium. Surprisingly, potassium, magnesium and digestibility (DOMD) do not differ greatly between the two groups.

3.9 Trends in nutrient deposition

The deposition of N compounds from the atmosphere was discussed above. The rate of deposition increased sharply during the last century, nitrates in rainfall increased 5-fold in the period 1930-1970 (Brimblecombe & Stedman 1982). As a result, it is possible that some communities which were previously limited by N, may now become P limited instead (Wilson *et al* 1995). There is insufficient data from MG4 stands or related sites to determine whether this is an issue for floodplain grasslands, but nutrient addition experiments on other species-rich swards (section 3.4) suggest that it probably is. Changes in ammonium deposition have been less marked and the increased nitrate to ammonium ratio that results is a significant factor in the increased acidity and therefore leaching potential of rainfall (Brimblecombe & Stedman 1982).

Phosphorus trends were considered by Walling *et al* (2000), who have reconstructed the sediment deposition record on 20 floodplain sites in southern England, using soil cores and caesium-137 as a tracer. They have used these data to estimate the rate of phosphorus accumulation over the past forty years. A mean value of 5.6 kg P ha^{-1} yr^{-1} was obtained. This figure refers to total phosphorus in any chemical form and therefore does not give a true picture of the phosphorus available for uptake by plants. The majority of the phosphorus will probably remain bound to the sediment particles and will not enter the soluble phase. See the discussion of nutrient budgets above (section 3.2) for a consideration of plant-available phosphorus.

One interesting outcome of the research is that an estimate of the increase in phosphorus concentration, in sediments deposited on the floodplain, between 1950 and 1992 was possible. The results varied from 9% for an upland catchment dominated by sheep pasture to 170% for a lowland catchment supporting intensive agriculture including a substantial proportion of arable cultivation. The authors concluded that fertiliser application and the discharge of effluent to rivers was responsible for this trend.

There has been no long-term study to show the impact of phosphorus-loading on an MG4 community. The survey of Gilbert (2000) showed available phosphorus (as measured by the

Olsen method) of MG4 grasslands to fall in the range 5 – 15 mg kg^{-1}, which equates to a P Index of zero or one (MAFF, 1994). Her results suggest that MG6 or MG7 communities would replace the MG4 community when soil P availability (Olsen) rises above 15 mg kg^{-1}, but this transition has not been documented. The work of Richardson and Qian (1999) suggests that many wetlands in North America can accumulate up to 10 kg P ha^{-1} yr^{-1} from silt without an adverse impact on their vegetation diversity. It is not clear whether this level of deposition would be compatible with the MG4 situation where soils are better aerated and organic matter (capable of locking up P) tends not to accumulate. There is a gap in our knowledge of this type of floodplain situation that needs to be addressed, in order to conserve the community effectively.

3.10 Impact of nutrient supply on vegetation production

Most studies agree that the factor controlling nutrient availability and therefore productivity on wet meadows is the magnitude and timing of flooding or raised water tables (section 2). This has two main implications for nutrient cycling:

1 Supply of nutrients in sediment deposited by flood waters.

2 The effect of high water table, and consequent anoxia of soil horizons on nutrient availability.

Annual hay cropping removes nutrients from the soil, which need to be replaced to maintain productivity. Treweek *et al* (1997) suggest that both flooding (i.e. nutrient and water supply) and the timing of flooding is crucial for a meadow. Plants that may tolerate winter flooding may not be able to survive a late flood in the growing season " The optimal period of growth of the grasses coincided with the slow subsidence of the water and the drying out of these flats…[in April-June] (Baker 1937). Control of flooding, by locks, dams, weirs and sluices inevitably disrupts this flooding regime and in particular the supply of nutrient-rich silt (Baker 1937, van Oorschot *et al* 1998). John Beever's yield records from East Cottingworth, Dewent Ings, for the period 1975-2000 are presented in Figure 3.2. The adjacent River Derwent was embanked in 1972 as part of a flood-defence scheme. From 1977 until present, yields from these fields have steadily declined. No nutrient input is allowed under the terms of a management agreement, which has followed the site's designation as a SSSI in 1983.

A multiple regression analysis of these yield data was undertaken to determine if the observed trend was explicable in terms of relevant weather variables (D. Gowing, pers. comm.) Smith (1960) showed that much of the variation in hay yield across the country could be explained by a term he called "Actual transpiration" during the growing season (March-June). Another generally used variable for predicting crop yield is accumulated temperature (day degrees). Broad and Hough (1982) suggested 5.5^{o}C was the appropriate threshold temperature for grass growth in the UK and this figure was used to calculate day degrees until end of June for each year that yield data were available. These two variables plus the length of time since the embankment was raised were used in the multiple regression. Accumulated temperature did not explain a significant amount of the variation in yield, but actual transpiration did ($P = 0.01$). After allowing for the effect of this weather variable, a very strong underlying downward trend in yield remained, which was largely explained by the length of time since the embankments were raised ($P < 0.0001$). There is a confounding factor in the analysis that must be considered before drawing any conclusions. The meadows did receive nitrogen fertiliser (approx 70 kg ha^{-1} yr^{-1}) during the period prior to site notification. Further analysis is required to verify whether the fall in yields is due to the raising of the embankment (with an implied loss of nutrients from silt) or the cessation of fertiliser application.

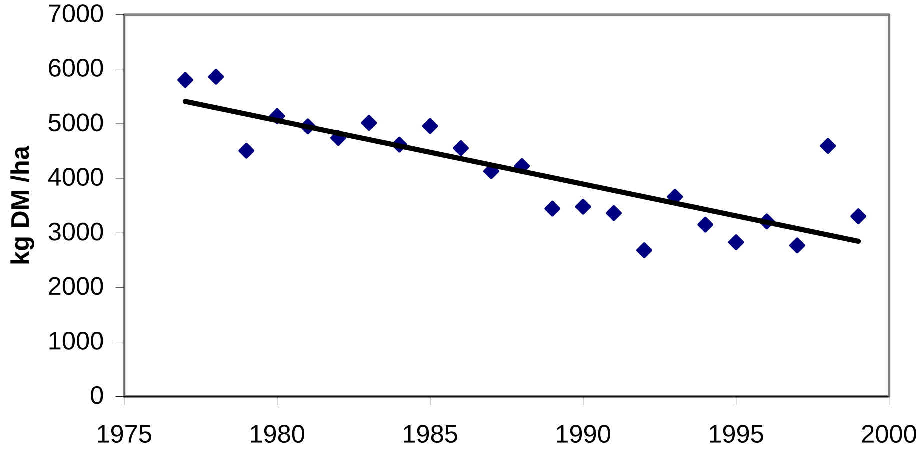


Figure 3-2 Mean hay yield from East Cottingworth flood meadows (Derwent Ings, Yorkshire).

The linear trend line gives a correlation coefficient of 0.69.

A separate data set from Cricklade North Meadow (David Massen, pers. comm.) indicates that northern areas of the site, which now rarely flood following the deepening of the River Churn in the 1980s, have significantly lower hay yields (3.2 t ha^{-1}) compared to southern areas, which are still regularly flooded by the River Thames (5.3 t ha^{-1}).

For other meadows that are no longer flooded, Crofts & Jefferson (1999) suggest that a light dressing (20 t ha^{-1} over 5 years) of farm-yard manure (FYM) may be applied if hay yields are falling or below 2.5 t ha^{-1}. While annual removal of a hay crop reduces the nutrients available in meadows, such a nutrient deficit is not found in pastures, where most nutrients are recycled via grazing animals. However, where sites are grazed year-round and gain nutrients from floods (or FYM) as well, it is possible that the sites may become eutrophicated and this has implications for the floral composition of the meadow, as at Port Meadow (see section 4.3.4). Another potential problem is if the deposited silt has been washed off agricultural land and contains high levels of nutrients derived from fertiliser use, which, when deposited on floodplain meadows, can alter their species composition (eg Smith *et al* 1996a; Tallowin *et al* 1998). While the yearly supply of silt is not quantified here, it clearly plays an important part in maintaining nutrient levels and safeguarding the productivity and therefore survival of these meadows.

High water-table levels caused by flooding or impeded drainage cause the upper soil horizons to become anoxic and alter the rates of nitrification and denitrification processes. Many studies have found that nitrogen mineralisation is reduced when water levels are raised (eg Berendse *et al* 1994, Oomes *et al* 1997, Krebs *et al* 1999). In contrast, van Oorschot *et al* (1998) found that N mineralisation , nutrient uptake and hay yield increased in wetter floodplains. Nitrogen losses due to denitrification are similar between dry and wet grasslands, but depend on a lower water table, tending to be highest during the summer for wet grasslands (Berendse *et al* 1994; Tallowin 1997). Reduced nitrogen mineralisation leads to reduced uptake in the above ground biomass, which limits nitrogen lost to the system through harvesting. This has implications for the quality of forage and hay from these meadows.

High water-table levels also affect other soil nutrients. Data from Cricklade North Meadow NNR show that the wetter areas (supporting MG13) that are more frequently flooded have higher soil P contents (29 g P m^{-3}) than drier MG4 communities (7.5 g P m^{-3}), and also raised potassium levels (EN data 2000). This agrees with other studies (Krebs *et al* 1999). Van Oorschot *et al* (1998) found that soil P availability and carbon (and nutrient) content was higher where flood meadows received alluvium in flood water, than on controlled rivers where silt transport was reduced. The soils of many MG4 flood meadows differ from other mesotrophic wet grasslands by their relatively high pH and calcium contents (Baker 1937; Rodwell 1992) which, together with their common history of annual vegetation harvesting, would suggest that they are P rather than N limited communities (Van Duren & Pegtel 2000). Janssens *et al* (1998) found that levels above 50 mg P kg^{-1} dry soil (as determined by EDTA/acetate extraction) limits vegetation diversity to a maximum of 20 spp per 100 m^2, and we would expect lower yields in diverse MG4 communities than in species-poor MG13 grasslands.

Lastly, nitrogen inputs from atmospheric deposition play a role in raising nutrient status in wet grasslands. In the Netherlands, Berendse *et al* (1994) quantified aspects of the nitrogen balance for unfertilised non-flooding grasslands and found that atmospheric deposition was the main form of N input into the system, and equivalent to a fertiliser application of about 60 kg N ha^{-1} yr^{-1}. However, this amounted to just 44% of the nitrogen removed by annual harvesting of vegetation, so the system has a net nitrogen loss. Shifts in vegetation community are likely, however, if hay cutting ceased and was replaced by continuous grazing.

4. Agronomy and vegetation management

4.1 Introduction

This section aims to quantify agronomic outputs (eg hay yields) from agriculturally unimproved and improved flood meadows.

Many aspects of modern grassland management, the use of fertilisers, herbicides and pesticides, re-seeding, drainage and silage production have resulted in the reduced botanical diversity of grasslands. The vast majority of mesotrophic floodplain grasslands on moderate- to nutrient-rich mineral soils are now species-poor and considered to be of little conservation value. Mesotrophic grasslands unaffected by agricultural improvement such as the MG4 floodplain meadows are now rare and threatened.

Agronomic data from periodically flooded meadows on alluvial soils in lowland floodplains containing the *Alopecurus pratensis – Sanguisorba officinalis* (MG4) grassland (Rodwell 1992) were sought. In addition any data from other categories of floodplain grassland types found close to MG4 communities, such as the *Lolium perenne - Alopecurus pratensis – Festuca pratensis* (MG7C) flood-pasture, the *Cynosurus cristatus – Caltha palustris* (MG8) water meadow, *Holcus lanatus – Deschampsia cespitosa* (MG9) grassland, the *Holcus lanatus – Juncus effusus* (MG10) rush pasture, *Festuca rubra – Agrostis stolonifera – Potentilla anserina* (MG11) grassland and the *Agrostis stolonifera – Alopecurus geniculatus* (MG13) grassland, were sought for comparative purposes. In addition to searching the available literature, inquiries were made of managers of MG4 flood meadows for current management information.

4.2 Traditional management

Traditionally, MG4 flood meadows were managed by cutting once for hay in mid-summer with the hay aftermath grazed in the late summer and autumn (Brian 1993). Some meadows were grazed through much of the winter. Traditionally cattle but also horses or ponies and sheep were grazed on these meadows. Before the Enclosure Acts of the 18th century, flood meadows formed part of a mixed farm. Stock were grazed on marginal land during the day, folded on unenclosed arable land at night and essential stock (breeding and draught animals) were kept alive through the winter on hay and aftermath grazing from the meadows (Green 1990). With most animal dung targeted at maintaining fertility on arable land, only meadows that were regularly flooded with river silt could maintain their productivity under a long-term hay regime. At this time most land was collectively managed, each family was assigned a strip of meadow to maintain and harvest (often by casting lots each year), with communal grazing rights on meadows after the hay cut (Baker 1937; Brian 1993). Aftermath grazing started on or around Lammas Day (1 August; hence “Lammas Meadows”) and on meadows which were not completely flooded could continue through the winter until Candlemass (2 Feb) or even as late as Lady day (25th March), when the meadow was closed for hay (Brian 1993). Hay cuts tended to be around mid-July (Baker 1937) although in some years fields were cut in September or not at all (Crofts & Jefferson 1999). While most communal meadows have been enclosed and improved, a few still operate this medieval system, particularly Lugg Meadow, Herefordshire (Brian 1993). Sites with complex multi-ownership patterns have been more resistant to change and have thereby maintained their diverse flora, as at Derwent Ings (Jefferson 1997) and Cricklade North Meadow NNR, Wiltshire.

Not all floodplain grasslands are cut for hay. There are records of some, such as Port Meadow Oxon, being grazed over a long period of time (Baker 1937) and others are treated as pasture today. The effect on the flora of these areas will be assessed in the section 4.3.4. However, continuous grazing was certainly never the normal usage of most of these meadows. Duffey *et al* (1974) states that "hay cutting is the principal management for flood-meadows, and that the aftermath is rarely grazed, in contrast to wet alluvial meadows [MG13-type] which are generally grazed in summer and occasionally cut for hay". This quote appears to be at odds with management information that has been obtained for this review from a number of floodplain sites with MG4 meadows, all of which have been traditionally aftermath grazed.

Baker (1937) reported that there was no input of nutrients (eg cattle cake, artificial fertilisers) additional to those supplied by alluvial sediment and excreta from grazing animals on Oxfordshire flood meadows. We found no positive mention of manure or other nutrients being added to flood meadows, but this does not rule out the practice altogether. However, animal manure was a scarce resource and it is likely that it would have been saved for the arable fields, rather than applied to already rich flood meadows.

4.3 Agronomic data

4.3.1 Dry matter yield

Primary measures of lowland semi-natural grassland productivity that have agronomic relevance are the yields of herbage harvested either by cutting machinery or the output achieved by grazing livestock. In this review yields of cut herbage, unless stated otherwise, refer to the yield of herbage dry matter and to the amount of herbage harvested above a cutting height of *c*. 5cm above ground level, this being the average cutting height of most conventional cutter bar and agricultural mowers. Cutting species-rich meadows in this way removes c. 70% of the dry matter yield at a July hay cut, leaving the remainder as aftermath to be grazed (Kirkham & Wilkins 1994a; Tallowin 1997). There is no evidence to suggest that this proportion differs significantly with vegetation community, but will be diminished by a later cut date. The harvested yield information will, therefore, be of limited value for estimating the net productivity of the grasslands as Weigert and Evans (1964) and Williamson (1976) pointed out.

In addition, the data presented here are a mixture of scientific studies and yields taken by farmers. In the former case, the figure is the yield at cutting, while the latter is generally the yield at baling (often given in numbers of bales, the yield in weight terms has therefore had to be estimated). It is important to distinguish between yields at cutting and baling, as up to 15% of the yield can be lost in the process of haymaking, eg by fragmentation and respiration (Tallowin 1997.) In addition, significant loses in nutrient content can be caused by rain while the cut hay lies in the field. However, the economic productivity of the field is limited to that portion of the herbage dry matter the farmer can remove as bales and as liveweight gain in his stock. By using these measurements we can form an accurate picture of the difference between income possible from the meadow and the expenditure necessary to maintain its conservation value, and hence the level of agri-environmental support that may be offered to a farmer.

Topographical variation in floodplain meadows result in hydrological gradients that allow a mixture of different plant communities rather than a single dominant community to exist at many sites. The meadows for which yield data were available contain varying proportions of

MG4 grassland, with MG4 stands generally occurring in the drier parts of the meadow. Therefore some caution in interpreting these data as being largely derived from the MG4 community should be exercised. Where possible we have recorded all communities contributing to a particular yield in Table 4.1. Yields for vegetation communities typically found in flood meadows alongside MG4, such as MG5, MG8, MG10 and MG13, are also given.

Dry matter yields obtained from a single hay cut in mid-summer from the sample of semi-natural grasslands containing the MG4 community ranged from about 3.0-6.0 t ha^{-1} (Table 4.1). At the low end of this range, the yield represents approximately only one third of the yields that might be obtained from intensively managed agriculturally improved grass cut twice for silage (Tallowin 1997). The higher-yielding floodplain meadows produced about 60% of the yield that would be expected from agriculturally managed grassland. Based on Verhoeven's estimates of total productivity compatible with high species diversity, hay yields between 2.8 and 4.9 t ha^{-1} yr^{-1} would be optimal (this assumes the hay cut represents approximately 70% of the annual production of a grassland.)

The yields of hay from meadows containing the MG4 community are compared with typical values from other floodplain communities in Table 4.1. Other unfertilised species-rich unimproved communities fall within the range of MG4 sites. For example, agriculturally semi-improved grasslands, such as MG6, and those where drainage is impeded, such as MG10, tend to have relatively high yields of around 6 t ha^{-1}. While we cannot draw too much from such a small sample, it is clear that floodplain meadows containing the MG4 community can be relatively productive, certainly compared with some other species-rich grasslands, such as the MG5 community, under drier soil conditions where yields of around 2 t ha^{-1} have been recorded. Farmers have observed considerably lower yields from the more species-rich areas compared to the more grass-dominated (and generally species poorer) parts of the same floodplain meadow system. However, yield data from Portholme meadow for 2001 suggest that lots with more species-rich MG4 have higher yields (60-90 small bales $acre^{-1}$ equivalent to 3.7-5.6 t ha^{-1}) than areas with more species-poor MG4/MG13 vegetation (50 bales $acre^{-1}$) (data taken from unpublished NVC survey by S. Lambert 1997 and Portholme hay sale catalogue). This single observation cannot be confirmed without longer-term data from specific community types on a number of floodplain meadows. If species-rich areas have a lower or more variable yield than the grassy ones, this should perhaps be reflected in support payments.

It is possible to assess the proportion of sites managed in a traditional manner (i.e. July hay cut and aftermath grazed) from large data sets made up of many small sites managed by different people, such as the Derwent Ings data set (appendix 2). From this we have found that of those farmers returning management data as per their SSSI agreement in 1999, 80.6% cut hay in July and 71.6% grazed the aftermath. The figures are similar for 2000, and agree closely with Jefferson's 1997 findings of 77% of MG4 in favourable management, i.e. hay cut and aftermath grazed.

Table 4-1 Hay yields from MG4 communities, and of other unfertilised communities found or associated with flood meadows for comparison.

Only data from sites with June/July cutting dates are quoted to eliminate differences due to cut date. Where one figure is given for a site, it is the mean of several years' data. Where data is drawn from sites with intimate mixtures of communities, all communities are listed.

Community	**Site**	**Area Site (ha)**	**Yield of 1st hay cut (kg/ha)**	**Date of cut**	**Aftermath grazing?**	**Reference**
MG4/MG13	Derwent Ings		~4000	July	70%	English Nature, York
MG4	Cricklade	34.04	3617	July	Yes	David Massen, English Nature
MG13	Cricklade	10.57	5313	July	Yes	David Massen, English Nature
MG4	Mottey Meadow	18.5	4600	July	Yes	Tim Coleshaw, English Nature
MG4	Portholme	103.2	4191	July	Yes	Jo Oldacre, English Nature
MG4	Seeton Meadow	11.3	180 big round bales	July	Yes	Plantlife
MG4	Upton Hams	61	5768	End July	Yes	David Goodwin, pers. comm.
MG4/6	Lugg Meadows	132.3	6000 4500-5600	End July	Yes	Mr Skerritt pers. comm. Mr C. Griffiths pers comm
MG4	River Ray, Oxon		3700-5000	July	Yes	R. Lambourne, pers comm
MG5	Bratoft		2219	July	No	Silvertown *et al* 1994b
MG5	Park Grass 2d,3d,12d	0.6	1467	June	No	Crawley *et al*
MG8	Tadham		3024	June	Yes	Tallowin 1997
MG10	North Wyke, Devon		6083	July	Yes	Tallowin 1997
MG6	Colt Park		5676.7	21 July	Yes	Smith *et al* 1996b
MG7 fert	North Wyke, Devon		7147	July	Yes	BD1425 IGER (7&8)
MG13	Netherlands		4218	June	No	Korevaar 1986
SOM3	Meuse, France		4200	July 1997	No	Krebs *et al* 1999
M22 equiv	Meuse, France		4600	June 1997	No	Krebs *et al* 1999

*Part of MG4 on Mottey Meadows has FYM applied at 3 t ha^{-1} occasionally.

Table 4-2 Stocking data for sites with aftermath grazing

** based on 1LU = 1 bovine animal >24months, 1.66 bovine animals 12-24 months, 2 bovine animals<12 months or 6.66 sheep.

Community	Site	Area grazed	Stock type	No. stock	Grazing period	No. days grazed	Avg LU/ha (range) **	Reference
MG4/6	Upper Lugg Meadows	63 ha	Cattle	69	02/08-02/02 2000/1	Varies	1.1	D Merriman pers comm
		63	Cattle Sheep	79 46	02/08-02/02 1990/1	Varies	1.36	
MG4/6	Lower Lugg	69.4 ha	Sheep	300	02/08-02/02	Varies	0.65	D. Merriman
		69.4	Cattle Sheep	47 630	02/08-02/02 1990/1	Varies	2.04	
MG4/13	Derwent Ings		Cattle or Sheep	Varies	01/08-31/10 but 7 sites April-Oct	Varies	3.25 (0.29-9.89)	
MG4	River Ray		Sheep		No information	70	1.2-1.7	R Lambourne
MG4	Seaton Meadow	11.3 (8.1)	Cattle + followers	10 10	01/09-30/11	56	1.33	Joe Costley Plantlife
MG4	Mottey Meadows	18.5 ha	Sheep	40	01/09-31/10	21	0.325	Tim Coleshaw, EN
MG4	Portholme	103.2ha	Cattle Sheep	40-100 300	01/09-30/11 01/09-28/02	91 <181	0.82-1.41	David Hicks (Alexanders)
MG4	Upton Ham	61 ha	Sheep or Cattle	~1000 90	12/08-31/01 12/08-31/12	Varies Varies	2.46 1.48	David Goodwin pers. comm
MG4+MG13	Cricklade	44.7 ha	Cattle Horses	11 - 30 11 - 29	12/09 - < 12/02	<153	0.4 – 1.1	Vince Foley (Court Leet)

Data were available for over twenty years from John Beever's diaries (unpublished) giving outputs from meadows in the Derwent Ings. These data showed a significant decline in dry matter yield with time (Figure 3.2). The value of averaging the yields when year to year variation does not appear to be largely due to differences in weather/rainfall is questionable. Such time series data need to be viewed in conjunction with botanical information so that the yields can be related to botanical "quality" (from a nature conservation perspective) of a meadow.

The decline shown in Figure 3.2 matches those recorded from various restoration experiments where fertilisation has stopped but hay cropping has continued (eg Baker & Olff 1995; Oomes *et al* 1996). The river banks along East Cottingworth were raised in 1972 to prevent flooding, and the reduction in yields since that time implies that there may have been a reduced nutrient input by silt or other means during this period. The relationship between flooding and fertility was explored in section 3.

4.3.2 Hay mineral content and effects on animal nutrition

Hay mineral contents are presented in Table 3.1 for a limited range of sites where data were available. The MG4-type sites are remarkably similar to each other, which is unexpected given that the vegetation communities they support may be quite different eg species-rich MG4 versus species-poor grassy MG13. This may reflect the paucity of the data set, but also that they form a continuum that is difficult to sample separately. However, these communities of conservation importance do differ markedly from an improved MG6/7 that stands on a gravelly river floodplain at North Wyke, Devon. This shows markedly higher contents of nitrogen, sodium, and phosphorus, and reduced levels of calcium.

Calcium, phosphorus, potassium and sodium are the four most abundant mineral elements in animal tissue (ADAS 1975) and their availability in forage is of major importance for the nutrition of animals grazing these grasslands. We assessed the mineral content of hay from MG4 grasslands with regard to the minimum forage content necessary to maintain an animal's health and body condition, rather than that necessary for growth and reproduction. Adequacy of mineral content in the diet depends of the digestibility of the forage, intake rate and the type, age and physiological condition of the animal. Additionally, losses of both dry matter and nutrient content during hay making mean that fresh herbage from these meadows are likely to contain higher nutrient contents than the hay samples that were analysed.

The lowest calcium content found in the MG4 hay samples was around 4g kg^{-1} DM. Although this content would be sub-optimal for most productive ruminants given an *ad libitum* intake (AFRC 1991), some studies indicate that cattle may be able to tolerate this apparent inadequacy (Wallis De Vries 1994). Such a low calcium content would, however, be too low for sheep, especially lactating ewes (AFRC 1991). Deleterious effects on the growth and health of livestock fed on hays from species-rich grasslands may arise because of a relatively high calcium-to-phosphorus ratio of the forage. The absorption and utilization of both calcium and phosphorus depends upon supplying a correct Ca:P ration in the diet and also on the presence of adequate amounts of vitamin D3. There is, however, uncertainty over what constitutes an optimum Ca:P ratio, the general guidance being that a 1:1 to 2:1 ratio is safe. The MG4 grasslands sampled had hay Ca:P ratios of 2.8:1 to 4:1. An unusually wide ratio can be as harmful as a deficiency of either mineral inducing, for example, inadequate utilization of certain essential trace elements (ADAS 1975).

The phosphorus contents of cut herbage from MG4 grasslands were below the estimated minimum metabolic requirement for growing cattle, which is 1.8 g kg^{-1} DM (Cohen 1975; ADAS 1983). Without any change in liveweight (i.e. growth) a forage diet of about 1.0 g kg^{-1} DM appear to be required by cattle. This suggests that the MG4 grasslands sampled supply sufficient phosphorus to maintain livestock, but not enough to support high growth rates. Where forage phosphorus content falls below 0.9g kg^{-1} DM adverse affects on growth and body condition are likely (Tallowin & Jefferson 1999). Low soil nutrient availability, particularly extractable phosphorus content, is now recognised as a key requirement for the development of grasslands with high species-richness (Marrs 1993; Janssens *et al* 1997). Janssens *et al* (1997) have shown that when the amount of phosphorus (extractable with EDTA-acetate[2]) exceeds 50 mg kg^{-1} of dry soil the number of grassland species that can co-

[2] Note that estimates of P-availability depend on the extractant and methodology used. There are several standard methods in general usage. The one involving EDTA-acetate tends to give higher estimates than the method using the Olsen bicarbonate extractant cited elsewhere in this report (see Gilbert 2000.)

exist falls dramatically. These authors also demonstrated that associated with this low soil phosphorus availability there was a very low yield of this mineral in the hay.

Forage levels of potassium were sufficient for both cattle and sheep, while levels of sodium would sustain cattle but not sheep, which require >2 g Na kg^{-1}DM. All MG4 hay magnesium contents were slightly sub-adequate for ruminant livestock, which require 2-2.5 g Mg kg^{-1} DM (ADAS 1983).

4.3.3 Grazing animal output

While almost all of the sites for which data are available had aftermath grazing, few managers kept records of stock numbers on the site, and none had complete records that would enable the calculation of animal production, such as liveweight gained over the grazing period. This information is necessary to complete the economic assessment of the meadow, and so should be a priority for further research.

Sites containing MG4 were grazed by cattle, sheep and horses or combinations thereof. The data collated gives stocking densities of between 0.29 and 9.89 livestock units (LU) ha^{-1}, with most sites carrying between 0.5 and 2.5 LU ha^{-1} in the autumn. The exception is the wide range of stocking levels found on the Derwent Ings area, with very high stocking levels of sheep on small sites in some cases. Additionally, seven of the farmers in this area manage their floodplain grassland as pasture, grazing from April to October in most cases at stocking rates below 2.5 LU ha^{-1}. Portholme Meadow SSSI is managed under a Countryside Stewardship agreement, which allows a maximum of 281 cattle to graze between September and November, i.e. 3.1 LU ha^{-1}. This suggests that the meadows are not being over grazed and, in the case of the Lugg Meadows, the intensity of grazing has fallen in the last 10 years as smallholders move out of farming. In the long-term this may threaten the survival of many commonly grazed meadows.

There appears to be little difference in impact on grassland community composition between cattle and horse grazing (Gibson 1996; Putman *et al* 1991). Patterns of animal use (and dunging) are aggregated and tend to be non-random and seasonally restricted by flooding. Both cattle and horses appear to graze similar areas, but at different times reflecting that the two species do not graze together (Putman *et al* 1991). Seasonally inundated areas had significantly shorter sward heights than dry areas (Putman *et al* 1991) implying that they were preferred grazing areas. Latrine sites tend to develop a distinctive flora, but grazing of these areas is only avoided when there are high dung densities (Gibson 1996).

Sheep are not traditionally used to graze wet sites, as they are more prone to liver fluke infestation and foot rot than cattle (Haslam 1973). However, they have been used on several sites in this survey, such as Lugg Meadows. Anecdote suggests that sheep are more suitable grazers for this site as cattle, and particularly large breeds such as Charolais can poach the meadow badly. Since sheep grazing on the Upper Lugg Meadow has been prevented by dog-walkers, Mr Skerritt, who farms this area, claims to have seen visible changes in the site – but unfortunately there are not data to quantify this change. Joe Costly (Plantlife, pers. comm.) suggests that this site has deteriorated since classification and should be considered to have MG6 and MG7 characteristics, possibly due to nutrient input from phosphorus-enriched silt than the change in grazing, but see discussion of Port Meadow in 4.3.4.

It should be noted that most areas of a site supporting MG4 grassland are well-drained and surface saturation would not normally persist for more than a few days after the recession of a flood (section 2). Therefore the sites may be more suitable for sheep grazing than is generally believed, if their forage intake is suitably supplemented (section 4.3.2).

4.3.4 Grazing versus cutting

The traditional management of MG4 floodplain meadows is a hay cut in June or July, followed by aftermath grazing (of varying duration). Pixey Mead in Oxfordshire, for example, has a long documented history of being mown. However, some floodplain grasslands are not classified as MG4. Examples include Staines Moor and Port Meadow. The latter is adjacent to Pixey Mead and has been managed for centuries by being grazed (i.e. it is a pasture rather than a meadow) (Baker, 1937, Ratcliffe 1977.) Grazing was found to be the prevalent recent management of Hampshire floodplain grassland by Hazel (1984) and of Staines Moor (Putman *et al* 1991), although this may show agricultural expediency (eg no local demand for hay, and/or a perceived low agricultural value of such “marginal land”) rather than preferred management.

Baker (1937) provides species lists for different areas of Port Meadow and Pixey Mead, which enables a rough comparison of their community types to be made (using MATCH; Malloch 1999). As expected, the drier areas of Pixey Meads are characteristic MG4 communities, while those on Port Meadow graded from MG6 at the driest end to MG10 at the wettest. This is not to say that Port Meadow is species poor – 56 species were recorded and 30 of those were also found on Pixey Mead. However, *Lolium perenne* was dominant on the drier areas of Port Meadow, giving it an improved character – Hopkins (in Fuller 1987), for instance, defines improved grassland as containing over 20% *L. perenne* in the sward. Rodwell (1992) and Gibson (1996) suggest that very heavy grazing can convert species-rich mesotrophic grasslands to semi-improved MG6 communities by encouraging species tolerant of grazing like *Lolium perenne*. The mechanism may be also related to enhanced nutrient cycling under grazing.The amount of nutrients removed by grazing livestock is relatively small, < 15 percent of nitrogen inputs removed in milk and body mass in grazed dairy pastures (Jarvis, 1999) and < 10 percent of total N input in pastures grazed by beef cattle (Garwood, 1988). Additionally, nitrogen mineralization rates may be greater under grazing than under mowing (eg Hassink 1992) due to poaching creating bare ground. Total standing crop is increased under grazing compared to cutting due to enhanced recycling and availability of nitrogen (Lantinga *et al* 1999). This means that under grazing-only management systems any annual influx of nutrients from alluvial deposits is likely to lead to eutrophication and eventual dominance by nutrient-demanding plants. On hay meadows subject to the same level nutrient input via flooding the high relative removal of nutrients in the harvested hay (approximately 70%) avoids nutrient accumulation (section 3).

Grazing tends to favour species that have their growing points close to the ground and readily reproduce vegetatively, as is the case with most grasses. Most dicotyledonous species (forbs) that have an elevated growing point (eg *Sanguisorba officinalis* and *Filipendula ulmaria*) and particularly annual species which rely on seed production for continued survival in a sward (eg *Rhinanthus minor* and *Bromus racemosus*) tend to be severely disadvantaged by close grazing (Treweek *et al* 1997). Hence such forbs and annuals are confined to meadows cut for hay, or which are subjected to only light grazing pressure. Vegetative increase of grasses tends to be stimulated by frequent grazing or mowing, which also delays or inhibits flowering and results in a denser, more leafy sward (Treweek *et al* 1997.) Return of seed is higher under a late mowing or light grazing regime (Smith *et al* 1996c). Greater burnet (*Sanguisorba officinalis*), a constant species of MG4 flood meadows, is particularly inhibited by grazing (Treweek *et al* 1997) and it is therefore inappropriate to manage an MG4 flood meadow without hay cutting. The Snakes-head Fritillary (*Fritillaria meleagris*) is a particularly characteristic species of MG4 stands. It completes the above-ground part of its annual cycle between March and May, and grazing in this season can be detrimental to its survival (Corporaal *et al* 1993).

Aftermath grazing tends to produce more diverse grasslands than those subject to cutting alone (Smith *et al* 1996b.) Late winter – early spring grazing can significantly reduce hay yield, particularly where cutting occurs in early July. Such grazing practice however can be important for new plants to establish in that it grazing opens up the sward and, where poaching occurs, creates bare ground and niches for seedling recruitment.

The standing crop on unmanaged grassland tends to be considerably higher, due to the accumulation of dead vegetation and litter, compared with grasslands that are cut or grazed (Smith 1994). Species richness decreases as the total standing crop of all species increases (section 3.1). Oomes and Mooi (1981) found that species were lost from a community within 8 years of abandoning management. Therefore any management is preferable to abandonment, but mowing with aftermath grazing appears to be preferable to grazing only for the maintenance of plant species diversity of floodplain grasslands. Where large competitive species such as as hogweed (*Heracleum spondylium*), cow parsely (*Anthriscus sylvestris*) and tall oat-grass (*Arrhenatherum elatius*) have begun to invade a meadow, earlier cutting dates may be necessary to reverse the trend (Huhta *et al* 2001). Earlier cutting will reduce the amounts of nutrient returned to the soil as litter and thereby avoid nutrient accumulation in the system.

4.4 Summary

Our agronomic knowledge of MG4 flood meadows is limited, by a lack of data recorded from these grasslands. In contrast, our understanding of the processes of nutrient cycling that are common to many wetlands appears to be more substantial. This review presents, to our knowledge, the first published yields from these grasslands, however, the agronomic database is far from complete, particularly where flood meadows are grazed in common. Long-term data sets such as those recorded by John Beevers are invaluable in providing evidence of unsustainable management systems, but such agronomic data sets need to be linked to changes in floral diversity and community structure. More research and assiduous data gathering by those who manage these grasslands is urgently needed.

5. Vegetation response to hydrology and nutrient availability

5.1 Community composition

The MG4 community is a product of consistent management (both cutting and grazing), site hydrology and soil nutrient availability (Rodwell 1992). All three of these factors need to be in place to generate a plant community that is recognisable as an *Alopecurus pratensis-Sanguisorba officinalis* meadow. The plant association described by Rodwell (1992) as MG4 is a distinct one. Although much reduced in extent, it is still to be found at approximately 100 separate sites scattered over a large part of England, though still centered upon the major river valleys in the south (Jefferson 1997), and at all of them it displays a distinct phytosociological character. That is not to say it is a monolithic community of conservative composition. There is variation within it. Since the community was first described in 1992, from a limited number of samples from 22 sites, it has been more extensively studied and a much larger data set has been amassed (eg Gowing *et al* 1998; Benyon, 1998.) Analysis of several thousand samples spread over 20 sites (some of which were not in the original analysis) has suggested that the composition of the typical community is consistent with the description as originally published (J. S. Rodwell pers. comm.; M.V. Prosser, pers. comm.). What the new data have revealed is a more detailed, complex relationship between the MG4 association and other alluvial grasslands.

Rodwell (1992) recognised that there was a gradation between MG4 on the better-drained parts of the floodplain and other communities, such as MG9 *Holcus lanatus – Deschampsia cespitosa* grassland and the *Holco-Juncetum* (MG10), where the drainage was impeded, culminating in stands of S6 *Carex acutiformis* swamp or MG13 *Agrostis stolonifera – Alopecurus geniculatus* inundation grassland, where water was held on the surface for prolonged periods. Furthermore, he noted that more intensive agricultural use of MG4 and the cessation of hay cutting could convert it to the *Lolium perenne-Alopecurus pratensis-Festuca pratensis* flood pasture (MG7C) or to MG6 *Lolio –Cynosuretum.* Recent data imply that the transition to MG7C is probably an intrinsic part of semi-natural flood meadows, which can persist under hay-cutting management and is not necessarily a sign of deliberate intensification of agricultural use (J.S. Rodwell, pers. comm.; R.N. Humphries, pers. comm.; M.V. Prosser, pers. comm.). The MG7C community appears to be associated with those parts of the floodplain which are less well drained than the MG4 stands. These may reflect a soil composed of finer sediments and less developed structure. Such finer, possibly newer, soils may also be richer in available nutrients than the older, often higher, soils. Soil data collected from North Meadow NNR and cited in its management plan (Payne *et al* 1998) are consistent with this view, showing areas of the meadow with affinities to MG7C to be richer in available phosphorus. The driving variable behind the MG4/MG7C transition could be primarily hydrological, primarily nutritional or an interaction between the two factors. Since both factors are linked to topography and to patterns of sediment deposition, this question is difficult to resolve. Our current understanding of these issues is summarised in the following sub-sections.

The recently collected data also show large areas which are transitional between MG4 and MG7C (eg several of the Derwent Ings and Upton Ham SSSI). The vegetation tends to have a low frequency of many of the classic MG4 herb species (*Sanguisorba officinalis, Leontodon autumnalis*), whilst retaining the grass assemblage. Species such as *Poa trivialis* and *Agrostis stolonifera* are often at higher constancy than in the published floristic table for the community. This has been termed species-poor MG4, but is not considered to be sufficiently distinctive to warrant sub-community status (J.S. Rodwell, pers. comm.). Observation of the vegetation type over time will reveal whether it is a stable community or a transitional stage toward the MG7C community.

5.2 Effect of hydrology on community composition

Alluvial floodplain grasslands have been extensively studied worldwide in an attempt to discover how their composition relates to their physical environment. The early work from the Netherlands (eg Grootjans & Ten Klooster 1980; Smeets *et al* 1980) has been supplemented by studies from Sweden (Zhang 1983), France (Grevilliot *et al* 1998), Germany (Schrautzer *et al* 1996), Czech Republic (Prach 1992), North America (Allen-Diaz 1991) and Japan (Yabe & Oniumaru 1997). All concur that depth to water table is a dominant environmental factor, though methods of interpreting it vary. All report zonation of the vegetation in response to depth of the water-table below ground surface, but most refer to within-site studies. The methods used to quantify water regime are often not easily transferred between sites. Many do not explicitly account for the soil type or the climate of the studied site.

An interesting paper by Kotowski *et al* (1998) investigates the differences in species tolerance to water regime between two sites, one Dutch, one German, which differ in their species richness. They find there are consistent differences between sites in terms of the range of water-table depths tolerated by each species. They conclude that the different competitive environments are the cause, though they do concede that subtle differences in soil type and climate may also play a role.

Gowing *et al* (1998) compared a number of different methods for interpreting water-table depth regimes to determine which gave most explanatory power in terms of species distributions within floodplain and water meadows. The most reliable method for the majority of species was a Dutch concept, referred to as Sum Exceedence Values (Siebens 1965). This is a peak-over-threshold technique for cumulating the degree of potential stress experienced by vegetation over an annual cycle (Figure 5.1). The method has the advantage of being responsive to varying soil and climatic environments by adjusting the threshold depths to suit the individual site. This gives the possibility, at least in theory, of deriving tolerances, which are transferable between sites. Gowing *et al*. (1997) published tolerance ranges for 67 species, which were derived from information gathered on 7 independent sites. The tolerance range is defined in two dimensions, one reflecting the species response to waterlogging and low soil aeration, the other to soil drying. This allows more information to be conveyed than was possible under the one-dimensional rankings of Ellenberg (1988) or Londo (1988) as some species showed themselves to be tolerant of both waterlogging and soil drying, whilst others tolerate neither. It is not possible to make that distinction on a linear scale. This issue is discussed in Gowing and Spoor (1998).

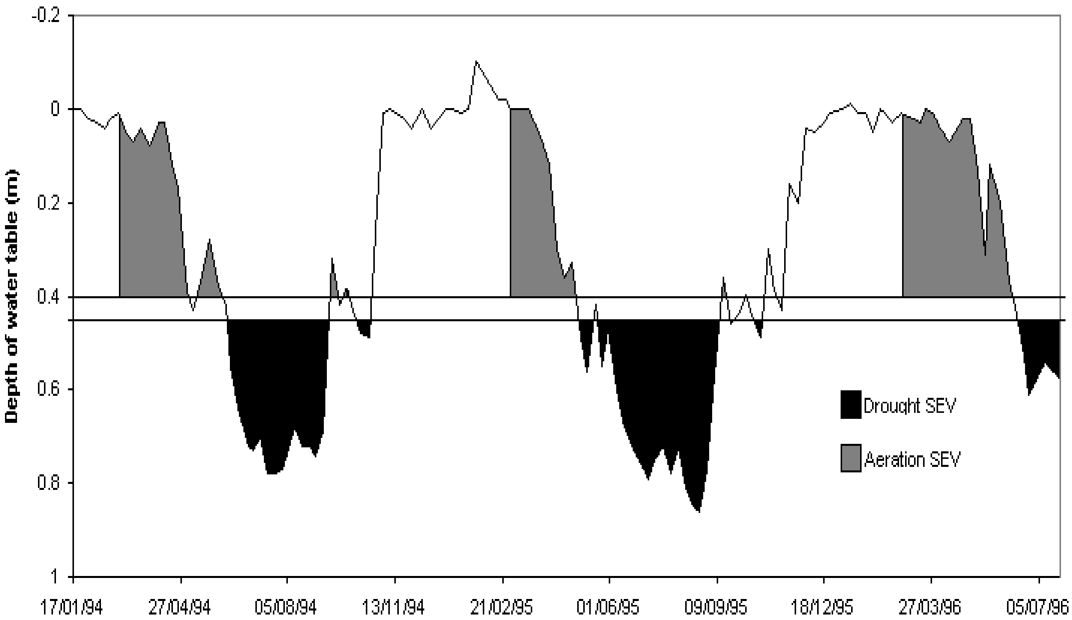


Figure 5-1 A hydrograph showing soil water tables as distance below surface from a floodplain grassland.

The horizontal lines represent thresholds for potential plant stress and the shaded area represent the Sum Exceedence Values.

Using the SEV methodology, Gowing and Youngs (1997) interpreted the water regime of the floodplain meadow vegetation at North Meadow NNR. The water-regime tolerance range of the MG4 community fell between that of the *Centaureo-Cynosuretum cristati* (MG5) and the inundation community described in their paper as MG13, but subsequently reassigned to the *Agrostis stolonifera – Ranunculus repens* (OV28) inundation grassland. The methodology is currently being applied to 20 sites in England, all with damp meadow plant communities in order to derive robust estimates of community water-regime tolerances (Lawson & Gowing 2001). This information will be more applicable for conservation purposes than the species-level data, as provisional results suggest community tolerances are more tightly defined, than those of individual species, which often occur in several community types and have broad tolerances to water regime.

SEVs as a description of soil water regime consider only quantitative hydrology. They do not account for either water source or water movement (Wheeler & Shaw 2001). Where lateral water movement within the root zone is substantial (eg in soligenous mires), oxygen and nutrients are being made more available to the plants and the relationship between species distribution and water depth, observed in a more static system, is often disrupted. MG4 grasslands, however, rarely display such high rates of lateral water movement in the root zone. Typically in floodplain systems, water movement is by vertical flux near the surface, though lateral movement in underlying aquifers may be substantial (Gowing *et al* 1998.) Recent publications by Dutch workers investigating the ecohydrology of poor fen communities, put much emphasis on water source and its nutrient and pH status as determinants of plant community type (Grootjans *et al* 1996; Olde Venterinck *et al* 2001). This is clearly justified in oligotrophic vegetation, but Gilbert (2000) has shown that these variables are sub-ordinate to quantitative hydrology in an experimental, mesotrophic system. Provisional results from the SEV project are shown in Figure 5.2, though it must be stressed that data analysis is not yet complete. The figure is useful in emphasising the hydrological position of the MG4 community with respect to other floodplain grasslands. It shows tolerance of soil drying in summer, but not to waterlogging in spring.

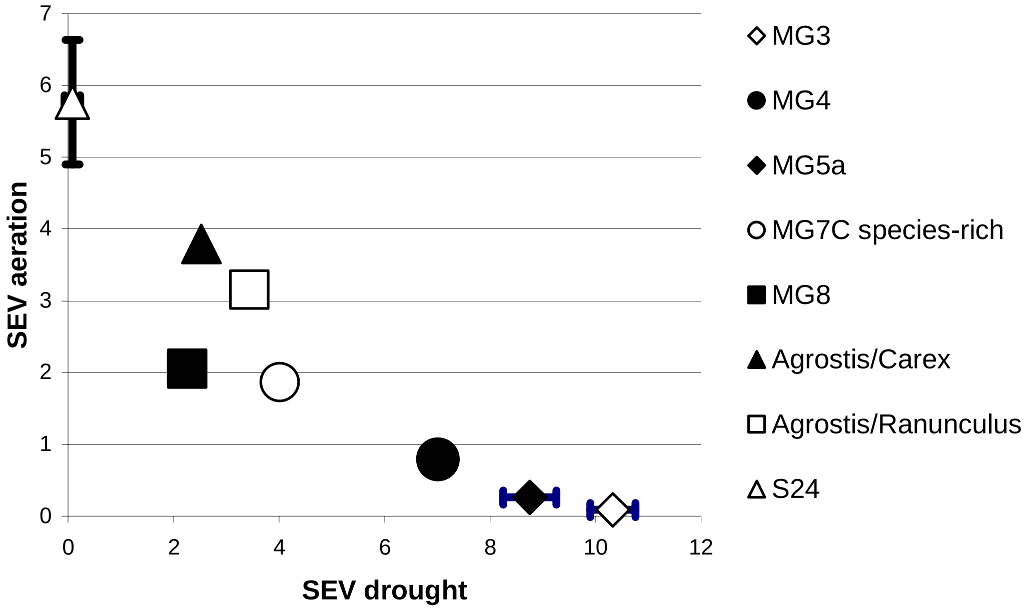


Figure 5-2 The water regime preferences of some wet grassland plant communities.

(One fen community is included for comparison). The data were gathered across 20 independent sites. The points represent mean values and the error bars represent standard errors for those means, where no error bars are visible it is because they are smaller than the symbol.

An alternative source of information with respect to species' water-regime requirements was published by Newbold and Mountford (1997). This gives minimum, maximum and "preferred" water-table depths for wetland plants. The listings do not specify the seasonality of these descriptions, however, which is a limitation in applying the information to floodplain meadows, where timing of water-table elevation, rather than its absolute height appears critical (Grevilliot *et al* 1998.) Only 6 species typical of MG4 grassland are listed in the booklet. There is no consensus in terms of their preferred water table depth, but they are all listed as not being found on sites with surface water.

5.3 Effect of nutrient availability on community composition patterns

The literature revealed no experimental study of nutrient manipulation in MG4 grassland. therefore any information has to be inferred from studies performed on drier MG5 grassland (eg the Bratoft experiment, Silvertown *et al* 1994b; Park grass experiment, Williams 1978) MG3 grassland (Smith 1994, 1997) and MG5/MG8 transition grassland (Tadham experiment, Mountford *et al* 1993). In none of these cases was silt deposition a variable in the study, so the results have to be viewed with some caution when extrapolating to a floodplain situation.

Many such studies both in Britain and on the continent (Bobbink 1991) have focussed on rates of nitrogen addition and a notional critical load has been derived, which for neutral grasslands is believed to be in the range 20-30 kg N ha^{-1} yr^{-1} (Bobbink *et al* 1996). Such detailed experiments have not been performed with phosphorus, but as discussed in section 3, the critical load is in the region of 10 kg P ha^{-1} yr^{-1} (Verhoeven *et al* 1996). If critical loads are exceeded, it is argued that species diversity and nature conservation interest will decline.

The best studied MG4 site in terms of its soil nutrient status is Cricklade North Meadow NNR (Gilbert 2000; Lawson & Gowing 2001). Depressions within the meadow have higher P availability than the rest of the area. The vegetation within these depressions is species-poor inundation grassland (in terms of the NVC it is most closely related to the OV28 *Agrostis stolonifera-Ranunculus repens* community.) In this situation, it is not easy to distinguish the roles of nutrient availability and of waterlogging in creating pockets of this community in an otherwise fairly homogenous matrix of MG4.

Sites supporting the closely allied MG5 *Cynosurus cristatus-Centaurea nigra* community have been better studied in terms of soil nutrient availability. The almost 150-year history of MG5 at the Park Grass Experiment allows a number of long-term trends of possible relevance to MG4 to be observed both in species composition and yield. Dodd *et al* (1994a) showed that addition of moderate levels of P+K fertilizer, but no nitrogen, changed the species composition somewhat and in the direction of an MG1e community, a tall ranker grassland. However this took in the region of 100 years. Plots receiving just 48 kg ha^{-1} yr^{-1} nitrogen and no other fertilizers have remained almost constant in their species composition as MG5a whereas the 'control' plots receiving no fertilizer at all, except atmospheric deposition, have changed from their original MG5a to MG5b. It should be noted that this site is not aftermath grazed, but receives a second cut in autumn, so any extrapolation of the results to MG4 meadows should be with caution.

The species composition of plots may not have altered much even after 140 years with no fertilizers and annual hay removal, but the yield certainly has changed. Dodd *et al* (1994b) showed the summer hay yields starting off around 2.5-3.0 t ha^{-1}, then the control unfertilized plot slowly decreasing in first-cut yield for the first 50 years, then remaining fairly constant at around 1 t ha^{-1} biomass for the next 50 years. A plot receiving P, K, sodium (Na) and magnesium (Mg), but no nitrogen yielded approximately 3 t ha^{-1} throughout the period and a plot with P, K, Na, Mg and nitrogen yielded approximately 5 t ha^{-1}. This very long-term data shows that both N and P are required for the highest yields, supplying P without N only partially restored yields and it also changed the species composition with additional legumes coming in, which then supplied the nitrogen themselves. It is perhaps unfortunate that in this experiment the treatment supplying high levels of N with no P, which may have shown the most dramatic effects of stripping out the P and causing the yield to collapse over the long-term, supplied the N in a form that caused severe soil acidification, so confounding any purely nutrient effects. Once this acidification was eventually corrected on part of the plot, the yield stabilized at about 2.5 t ha^{-1} again indicating that the yield was limited by both N and P.

5.4 Rates of community change

Very few studies have followed permanent plots within alluvial meadows over time in order to estimate rates of change. Permanent quadrats in North Meadow NNR have been monitored since 1998 and have revealed marked changes in vegetation composition in response to the heavy rainfall and floods experienced in the winters of 1999/2000 and 2000/2001. Plots which were typical MG4 stands have moved to become typical examples of MG7C in just 2 years (Lawson & Gowing, pers. comm.). This emphasises how dynamic this vegetation type can be even in response to natural variations in the climate. Similar short-term changes in response to flood events have been observed in vegetation composition of the Derwent Valley floodplain meadows in Yorkshire (P. Benyon & R.N. Humphries, pers. comm.)

It is assumed that the community can recover from flooding episodes, as they must have occurred in many of the sites holding the community. The rate of recovery can only be guessed at however without the benefit of field observation. It is known that many MG4 species do not have a persistent seedbank (McDonald *et al* 1993), so a rate-limiting step would be the re-colonisation of the area by external propagules. The long-term experiment at Cricklade North Meadow NNR has been set up to address this issue (Lawson and Gowing, 2001.)

The effect of droughts on the community cannot be directly determined, as there appears to be a dearth of data which chronicles the vegetation through a drought period such as the one experienced in the south of England in 1989-1991. A large data set from North Meadow NNR has been analysed to ascertain how many of years of water-regime data prior to the date of vegetation sampling is required to best explain the spatial pattern observed. Provisional results of this analysis suggest at least seven-years data are required (T. Sparks, pers. comm.)

In terms of response to a change in the nutrient regime, this has been observed in fields where fertiliser applications have ceased. In a study of the Drentse Aa valley in the Netherlands, Berendse *et al* (1992) reported that species richness increased by 50% over a period of 16 years following cessation of fertiliser application. Mountford *et al* (1996) made predictions for the recovery of MG5/MG8 grassland at Tadham Moor, Somerset following the cessation of fertiliser treatments, suggesting that it would take up to 30 years for some plots to recover their original diversity after having had high annual doses (200 kg ha^{-1}) of artificial nitrogen fertiliser over a 4-year period.

The other change that threatens the MG4 community is the cessation of agricultural management. Significant changes to the species composition can occur in just 2 years without cutting and grazing, with the nature of the vegetation changing considerably within a decade (Joyce 1998.)

5.5 Restoration of the MG4 community

The literature details two attempts at restoration of the meadow type in England. Both involved the sowing of former arable fields, one known as Somerford Mead near Oxford has been documented by McDonald (1993, 1996) and the other bordering an established MG4 site at Long Herdon meadow was reported by Manchester *et al* (1997) and Manchester *et al* (1999). Both resulted in partial success with some target species establishing from seed, but indicate that the reassembly of the community will be a lengthy process. The sites continue to be monitored and will hopefully give a more complete picture of restoration viability in due course.

Studies of the seedbank at Somerford Mead, which had been a MG4 grassland prior to arable cultivation, revealed few of its component species to have a persistent seedbank and therefore restoration schemes will need to rely on natural dispersal from neighbouring stands of the community or on artificially imported seed. Prospects of floodwaters delivering the necessary seeds have not been confirmed. A study in Germany (Holzel & Otte 2001) suggested that regular flooding had little if any impact on the seedbank of a floodplain grassland. However, for at least one constituent species, *Fritillaria meleagris,* seed transport by flood water is known to be important (Corporaal *et al* 1993.)

6. Deficiencies in our understanding of floodplain meadow ecology

6.1 Botanical data on vegetation change

A chrono-sequence of botanical data, ideally from permanent quadrats, within MG4 meadows would greatly assist in determining the resilience of the plant community to external perturbations of its environment. Much of the discussion in this review has been based on inference from studies of grasslands related to MG4, but not from the community itself. Given the high priority afforded to its conservation, more long-term monitoring of MG4 sites should be instigated. At present, on-going monitoring of permanent quadrats is taking place at just 3 established sites (North Meadow, Wilts, Oxley Mead, Bucks and Mill Crook, Northants.) and one restoration site (Somerford Mead, Oxon.)

6.2 Nutrient budgets

A full nutrient budget for a floodplain site holding an MG4 community is lacking. Modern techniques of estimating sediment deposition using isotope signatures should make this feasible. At present we cannot say with certainty whether the majority of floodplain meadows are accumulating or losing phosphorus. In addition to a mass balance budget, more knowledge is required in terms of the internal cycling of nutrients within a site. Chemical analysis of soils for nutrient availability and vegetation for nutrient content would help construct a model of nutrient fluxes.

6.3 Community reassembly

Observation of MG4 community re-assembly following species lost during flood events is needed. Although there are now reports (not yet in the public domain) of MG4 grasslands losing species richness and trending toward MG7C communities as a result of prolonged flooding, the reverse trajectory has not been studied and so our estimates of recovery time are necessarily vague. Restoration attempts have highlighted that arrival of propagules for MG4 species at new sites and their survival in the seed bank are very poor. We do not know to what degree these constraints operate within a site. When part of a MG4 site loses its MG4 character as a result of prolonged inundation, how long does that patch take to recover, given a return to an appropriate water regime? Long-term monitoring data could answer this, but in parallel, modern techniques in ecological genetics could determine the degree of genetic diversity within the constituent populations of isolated MG4 communities and estimate the gene flow between sites. If individual sites are genetically isolated, their long-term sustainability may be threatened.

6.4 Drivers of community change

The relative importance of the ecological drivers which control the equilibrium between MG4 and MG7C in floodplain meadows needs to be better understood. It is known that both wetter soils and higher nutrient availability favour the MG7C community. In order to manage sites in favour of the MG4 component of the vegetation, it would be helpful to know which of these drivers is the more significant or whether it is the interaction between them that is critical. The information would help determine whether MG7C is a dynamic component of floodplain communities or an indicator of species loss.

6.5 Impacts of eutrophication and climate change

Management techniques to mitigate against increased nitrogen deposition from the atmosphere and higher spring temperatures need to be investigated in case these landscape-scale processes are threatening the integrity of floodplain meadows. There is evidence that grassland communities are accumulating nitrogen as a result of atmospheric deposition. This favours the grass component of the sward at the expense of the herbs. Another contributory factor is the higher frequency of warm springs in the past decade, which may be a feature of climate change in the future, and which encourages an early burst of nitrogen mineralisation again favouring grass species. One of the conclusions from Silvertown *et al* (1994a) was that factors stimulating grass growth such as early N mineralisation, caused assymetric competition for light and had a large effect in suppressing other components of the sward. Our understanding of the processes of nitrogen cycling within the grassland is not currently sufficiently complete to assess the merits of mitigation strategies, such as earlier or additional hay cuts.

6.6 Economic analysis of floodplain management

Maintenance of floodplain meadows requires regular and timely management by farmers. To assess the economic benefit that farmers may expect to gain from the meadow and hence any subsidy that is necessary to ensure appropriate management, a reliable measure of grazing stock performance is required. There are no published data sets relating the liveweight gain of cattle or sheep to a period of grazing on MG4 meadow. This information is necessary to make a full agronomic assessment of the system.

6.7 The role of flood water in maintaining surface pH

It is accepted that a circum-neutral to slightly alkaline soil reaction (pH 6 – pH 8) is conducive to species richness (Grime 1979) and the circumstantial evidence is that floodplain meadows are maintained at a neutral pH by flood deposits, which offset the effects of acid rain. The regularity and extent of such sedimentation has not been quantified however. It needs to be related to the buffer capacity and leaching potential of the soil to determine the flood frequency required to avoid surface acidification.

6.8 Physiological ecology

The physiological ecology of the component species of MG4 grasslands is poorly understood. Some were included in the Comparative Plant Ecology text of Grime *et al* (1988), but the components of the community as a whole were poorly represented, due to the geographic emphasis of that work. Although plant responses to soil drying, nutrient availability and soil redox state are known at a general level, the vast majority of the underlying research has been with crop species. The relative sensitivities of semi-natural grassland species have been rarely investigated (eg Milnes *et al* 1998). If sites are to be managed for particular species or a target composition, then the relative competitive abilities of species in the context of their physical environment need to be better understood.

7. Conclusions

The floodplain meadow community known as *Alopecurus pratensis-Sanguisorba officinalis* grassland (MG4) is a rare and threatened plant community, which occupies less than 1500 ha in total. It was once a widespread and important cultural part of the English landscape, but is now almost entirely confined to nature reserves. The reason for its vulnerability is that it has distinct and precise requirements in three separate areas. These will be summarised in turn.

7.1 Hydrology

The community requires a soil, which can supply moisture throughout the year by virtue of a high water holding capacity and/or a natural sub-irrigation system. The community is not tolerant of soil anoxia brought about by waterlogging for more than a few days during the growing season. This makes the community's presence on a river floodplain somewhat precarious and the community is reliant on an adequate surface drainage system, capable of removing surface water from the site promptly following the recession of the flood.

7.2 Nutrition

The community is relatively productive in comparison to other semi-natural vegetation types. It typically yields 4 t ha^{-1} yr^{-1} in hay in addition to up to 6 months of grazing for stock (total production may be c. 6 t dry matter ha^{-1} yr^{-1}.) To support this productivity it requires a mesotrophic soil. That is one with moderate availability of all the major nutrients. If these availabilities decline the community may move toward the composition of old hay meadow community (MG5). If they increase the community will tend toward the less diverse grasslands (MG6a and MG7C). Therefore the availability of each nutrient needs to be managed to keep it within an appropriate range (see section 5.3 for range of P status). Traditional management achieved this goal, but in the modern era with rivers carrying phosphorus-enriched silt, the atmosphere depositing considerable quantities of nitrogen and the climate leading to warmer springs and the earlier mineralisation of organic matter, maintaining a balance is more challenging. In terms of management options, supplying farmyard manure to sites, which no longer receive silt may be an option, but it has not been tested. For sites with excess nutrients, reducing inputs is the first option to try, but a second hay cut in autumn is a possible alternative.

7.3 Vegetation management

The community is usually the product of several hundred years of consistent management involving both a summer hay cut and aftermath grazing. Both of these aspects are important for conserving the floristic diversity of the sward. Current wisdom promotes the maintenance of traditional practices, yet there is a need to recognise that the wider environment is changing as described in 7.2 above. Holding to the dogma of traditional management may no longer be the ideal and new departures such as a second hay cut may need to be considered in order to counteract increased nutrient loadings and thereby maintain the floristic composition of the community. Increasing cover of large competitive species such as as hogweed (*Heracleum spondylium*), cow parsley (*Anthriscus sylvestris*) and tall oat-grass (*Arrhenatherum elatius*) suggest earlier cutting dates should be considered.

7.4 Conservation management

Although the response to the questionnaire relating to perceived threats at each of the remaining sites pointed to water management being the main concern, this may be more a perception than reality at some sites. Hydrology of wildlife sites has received a lot of attention recently, alerting people to changes and such changes are often readily visible. If the change involves more prolonged inundation of the site, then it certainly is a concern, which needs to be addressed by the re-instatement of traditional surface drainage systems. Drainage of the site by local ditches is less likely to be a threat as the community does not require soil saturated to the surface, as many mires and fens do. The risk from altered hydrology is perhaps more likely to be an indirect one through the change in sediment deposition. The community could be more at risk from changes to its nutrient supply and its surface pH, than from changes to its hydrology *per se*.

8. Recommendations for further research

In order to address the current deficiencies in our understanding of floodplain meadows and their management (listed in section 6), further research is required. Having consulted a number of researchers interested in this area, the following topics have been proposed:

1 The construction of a nutrient budget for a floodplain meadow site (primarily for phosphorus) is seen as a priority. Determining the fate of particulate phosphorus is necessary to estimate what proportion of it becomes available to the vegetation. In addition, a survey of a range of sites is needed to determine the extent to which P-availability determines yield and to identify the most important environmental factors controlling the internal cycling of phosphorus within the meadow.

2 Controlled nutrient addition experiments within floodplain meadows are necessary to demonstrate which (if any) of the major nutrients are limiting productivity of the sward.

3 Quantification of nutrient ratios in meadow vegetation (primarily N:P) should be determined to assess whether they are reliable indicators of nutrient limitation. Their potential as early warning indicators of nutrient enrichment should be explored.

4 Controlled amounts of farmyard manure (and possibly lime) should be applied to floodplain meadows, which no longer flood, to assess whether it restores their former yield, without an adverse impact on species composition.

5 Long-term monitoring of restoration and rehabilitation trials is needed to assess the time scale required for creating and enhancing the community on suitable sites. This should include a study of the dispersal mechanisms and invasive capacity of key MG4 species.

6 A further development of the condition assessment methodology should be considered involving the identification of indicator species within the meadow's flora, whose altered frequency may serve as an early warning of increasing nutrient availability, increasing wetness, inadequate management or overgrazing.

7 An assessment of the importance of microtopography within meadows in maintaining high species diversity would be valuable. Microtopographic variation can increase the fine-scale heterogeneity of a site and promote its diversity. The preservation and possible enhancement of a meadow's microtopography could be used as a conservation tool.

8 The exclusion of flood waters and hence silt from an area of floodplain that currently supports the MG7C community would be useful to assess if and how rapidly the vegetation changes and whether species characteristic of MG4 grassland colonise. Hydrological monitoring over such a period would allow the question of whether MG7C supplants MG4 due to higher nutrient availability, greater aeration stress in spring or a combination of these factors.

9. An investigation into whether consistent traditional management is the ideal prescription for maintaining species diversity would be timely. Questions to be addressed include:

   Would variation in cutting dates or not cutting occasionally enhance diversity? Does earlier cutting and/or a second cut in autumn improve diversity by removing more nutrients and therefore reversing any trend toward eutrophic nutrient status? Can earlier cutting alone rehabilitate poorly managed meadows in which coarse species have become abundant?

10 The range/variability in nutritional quality of the hay from MG4 grassland needs further evaluation both through chemical analysis but also through feeding trials in order for the most effective agronomic use of this forage to be promoted. This database would be an important component in the development of sustainable management systems for MG4 grasslands within a landscape context.

11 Background experience and behavioural traits of livestock used to graze MG4 grassland could have important implications on the structure and composition of these grasslands. We need to assess whether the use of pre-adapted livestock (and/or particular types of livestock) should be used on such species-rich grassland. We also need to assess the potential role that such livestock could have, if moved between MG4 sites, in promoting dispersal/gene flow between isolated sites.

12 Studies in gene ecology to determine to what extent species populations at individual sites are genetically isolated from other metapopulations. Key conservation questions include the following:

   What size of site (or complex of sites) is necessary to support populations with sufficient genetic diversity for long-term sustainability?

   What are the important dispersal processes and are they still functional within metapopulations?

13 Studies into the autecology of important constituent species in the community such as *Fritillaria meleagris* and *Sanguisorba officinalis,* would inform our understanding of the environmental requirements of the community as a whole and its sensitivity to change.

14 The identification of key species, which control the structure and nutrient relations, of the meadow.

15 An investigation into the reliance of short-lived annual and biennial species within the community on cutting date and intensity of aftermath grazing.

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10. Bibliography

ADAS, 1975. *The Important Mineral Elements in Animal Nutrition and their Optimum Concentration in Forages*. ADAS Advisory Paper no. 16. London: HMSO. Ministry of Agriculture, Fisheries and Food.

ADAS, 1983. *Mineral, traces element and vitamin allowances for ruminant livestock*. Report of an Interdepartmental Working Party on the ARC (1980): Technical Review: 'the Nutrient Requirements of Ruminent Livestock'. London: HMSO. MAFF, DAFS, DANI, UKASTA, BVA.

AFRC, 1991. Technical committee on responses to nutrients. A reappraisal of the calcium and phosphorus requirement of sheep and cattle. *Nutritional Abstracts and Reviews (Series B).* CAB International. 61, pp. 573-612.

ALLEN-DIAZ, B.H., 1991. Water-table and plant-species relationships in Sierra Nevada meadows. *American Midland Naturalist*, **126**, 30-43.

ARMSTRONG, W., 1979. Aeration in higher plants. *Advances in Botanical Research*, **7**, 226-332.

ATWELL, B.J. & STEER, B.T., 1990. The effect of oxygen deficiency on uptake and distribution of nutrients in maize plants. *Plant Soil*, **122**, 1-8.

AVERY, B.W., 1973. Classification in the soil survey of England and Wales. *Journal of Soil Science*, **24**, 324-334.

BAKER, H., 1937. Alluvial meadows: A comparative study of grazed and mown meadows. *Journal of Ecology*, **25**, 408-420.

BAKKER, J.P. & OLFF, H., 1995. Nutrient dynamics during restoration of fen meadows by haymaking without fertiliser application. *In:* Wheeler, ed. *Restoration of Temperate Wetlands.* pp. 143-166.

BENYON, P.R., 1998. *Lower Derwent Valley: MG4 grassland boundary survey. Report to Environment Agency*. Leeds.

BERENDSE, F., OOMES, M.J.M., ALTENA, H.J. & DEVISSER, W., 1994. A Comparative-study of nitrogen flows in 2 similar meadows affected by different groundwater levels. *Journal of Applied Ecology*, **31**, 40-48.

BERENDSE, F., OOMES, M.J.M., ALTENA, H.J. & ELBERSE, W.T., 1992. Experiments on the restoration of species-rich meadows in the Netherlands. *Biological Conservation*, **62**, 59-65.

BLACKSTOCK, T.H., RIMES, C.A., STEVENS, D.P., JEFFERSON, R.G., ROBERTSON, H.J., MACKINTOSH, J. & HOPKINS, J.J., 1999. The extent of semi-natural grassland communities in lowland England and Wales: a review of conservation surveys 1978-96. *Grass and Forage Science*, **54**, 1-18.

BOBBINK, R., HORNUNG, M. & ROELOFS, J.G.M., 1996. Empirical nitrogen critical loads for natural and semi-natural ecosystems. *In: Manual on Methodologies and Criteria for Mapping Critical Levels/Loads*. Berlin: Federal Environment Agency.

BRIAN, A., 1993. Lammas Meadows. *Landscape History*, **15**, 57-69.

BRIMBLECOMBE, P. & STEDMAN, D.H., 1982. Historical evidence for a dramatic increase in the nitrate component of acid rain. *Nature*, **298**, 460-462.

BROAD, H.J. & HOUGH, M.N., 1982. The growing season and grazing season in the United Kingdom. *Grass and Forage Science*, **48**, 26-37.

BRUNET, R.C. & ASTIN, K.B., 2000. A 12-month sediment and nutrient budget in a floodplain reach of the River Adour, southwest France. *Regulated Rivers-Research & Management*, **16**, 267-277.

BUCKLEY, J., 1988. *The water relations and distribution of selected species, above shallow ground water on Yarnton Mead, Oxfordshire*. BSc project report. Coventry Polytechnic.

CHALMERS, A., KIRKHAM, F., MCLAREN, R., SMITH, K., DOWNIE, L. & GOODLASS, G., 2000. A review of the use of organic manures on lowland grassland pastures in the U.K. Peterborough: *English Nature Research Reports*, No. 368.

CLAYTON, H., ARAH, J.R.M. & SMITH, K.A., 1994. Measurement of nitrous oxide emissions from fertilised grassland using closed chambers. *Journal of Geophysical Research*, **99**, 16599-16607.

COHEN, R.D.H., 1975. Phosphorus and the grazing ruminant. *World Review of Animal Production*, **11**, 27-43.

CORPORAAL, A., HORSTHUIS, M. A. P. & SCHAMINEE, J. H. J., 1993. Oecologie, verspreiding en planten sociologische postie van de kievitsbloem (*Fritillaria meleagris L.*) in Nederland en Noordwest-Europa. *Stratiotes*, **6**, 14-39.

COUNCIL OF THE EUROPEAN COMMUNITIES., 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities*, **L206**, 7-50.

CRAWFORD, R. M. M., 1982. Plant life in aquatic and amphibious habitats. *In: Encyclopaedia of plant physiology*. Berlin: Springer Verlag. 12B. pp. 453-477.

CRAWFORD, R.M.M., 1993. Plant survival without oxygen. *Biologist*, **40**, 110-114.

CROFTS, A. & JEFFERSON, R.G., 1999. *The lowland grassland management handbook. 2nd edition*. Peterborough: English Nature and the Wildlife Trusts.

DAVIES, W. J. & GOWING, D. J. G., 1999. Plant responses to small perturbations in soil water status. *In:* Press, M., Scholes, J. & Barker, M., eds. *Physiological Plant Ecology*. British Ecological Society Symposium 39. pp. 67-89.

DAVIES, W.J. & ZHANG, J., 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual review of plant physiology and molecular biology*, **42**, 55-76.

DEMPSEY, P. & CODLING, I., 2001. *Ouse and Nene strategic studies: Ecological Risk Assessment. Report to Anglian Water plc*. Swindon: WRc plc.

DISE, N. B., 2001. Biogeochemical dynamics III: Carbon. *In:* Maltby, E., ed. *The Wetlands Handbook*. Oxford: Blackwell Science.

DODD, M., SILVERTOWN, J., MCCONWAY, K., POTTS, J. & CRAWLEY, M., 1994. Biomass stability in the plant communities of the Park Grass Experiment: The influence of species richness, soil pH and biomass. *Philosophical Transactions of the Royal Society B*, **346**, 185-193.

DODD, M. E., SILVERTOWN, J., MCCONWAY, K., POTTS, J. & CRAWLEY, M., 1994. Application of the British national vegetation classification to the communities of the park grass experiment through time. *Folia Geobotanica & Phytotaxonomica*, **29**, 321-334.

DUFFEY, E., MORRIS, M.G., SHEAIL, J., WARD, L.K., WELLS, D.A. & WELLS, T.C.E., 1974. *Grassland Ecology and Wildlife Management*. London: Chapman and Hall.

ENVIRONMENT AGENCY., 2000. *The action plan for flood defence*. Bristol: Environment Agency.

ELLENBERG, H., 1988. *The vegetation ecology of central Europe*. Cambridge University Press.

FREAM, 1888. On the flora of water meadows, with notes on their species. *Journal of the Linnean Society (Botany)*, **24**, 279-288.

FULLER, R.M., 1987. The changing extent and conservation interest of lowland grasslands in England and Wales - a review of grassland surveys 1930-84. *Biological Conservation*, **40**, 281-300.

GARWOOD, E.A., 1988. Water deficiency and excess in grassland: the implications for grass production and for the efficiency of use of N. In: Wilkins, R.J., ed. *Nitrogen and water use by grassland*. Proceedings of Colloquium at North Wyke Research Station, Devon, March 1987. Hurley: AFRC Institute for Grassland and Animal Production.

GIBSON, C. W.D., 1996. The effects of horse and cattle grazing on English species-rich grasslands. Peterborough: *English Nature Research Reports*, No. 210.

GILBERT, J. C., 2000. *High soil phosphorus availability and the restoration of species-rich grassland*. PhD thesis. Cranfield University.

GOWING, D.J.G., 1998. *Oxley Mead SSSI - moisture retention properties of the soil*. Maidstone. Report prepared for Weeks Technical Services.

GOWING, D.J.G., GILBERT, J.C., YOUNGS, E.G. & SPOOR, G., 1997. *Water regime requirements of the native flora - with particular reference to ESAs*. Project BD0209. London: Final Report to Ministry of Agriculture, Fisheries and Food.

GOWING, D.J.G., GILBERT, J.C., YOUNGS, E.G. & SPOOR, G., 1997. *The water requirements of the native flora. Final report*. MAFF project BD0209. London: Ministry of Agriculture, Fisheries and Food.

GOWING, D.J.G. & YOUNGS, E.G., 1996. The effect of the hydrology of a thames flood meadow on its vegetation pattern. *In:* Large, A. ed. *Floodplain rivers: hydrological processes and ecological significance.* Newcastle: University of Newcastle. Newcastle. British Hydrological Society Occasional Paper No. 8. pp. 69-80.

GOWING, D.J.G., YOUNGS, E.G., GILBERT, J.C. & SPOOR, G., 1998. Predicting the effect of change in water regime on plant communites. In: *Hydrology in a changing environment*. Chichester: John Wiley and Sons. Chichester. Vol. I.H.,

GREEN, B.H., 1990. Agricultural Intensification and the Loss of Habitat, Species and Amenity in British Grasslands - a Review of Historical Change and Assessment of Future-Prospects. *Grass and Forage Science*, **45**, 365-372.

GREVILLIOT, F., BROYER, J. & MULLER, S., 1998. Phytogeographical and phenological comparison of the Meuse and the Saone valley meadows (France). *Journal of Biogeography*, **25**, 339-360.

GRIEG, J.R.A., 1988. *Some evidence of the development of grassland plant communities*. BSBI conference report no. 19. Oxford University Committee for Archaeology.

GRIME, J.P., 1979. *Plant strategies and vegetation processes*. Chichester: Wiley.

GRIME, J.P., HODGSON & HUNT, 1988. *Comparative Plant Ecology*. London: Unwin.

GROOTJANS, A.B., VANWIRDUM, G., KEMMERS, R. & VANDIGGELEN, R., 1996. Ecohydrology in The Netherlands: Principles of an application- driven interdiscipline. *Acta Botanica Neerlandica*, **45**, 491-516.

GROOTJANS, A.P. & KLOOSTER, T., 1980. Changes of ground water regime in wet meadows. *Acta Botanica Neerlandica*, **29**, 541-554.

GROOTJANS, A.P., VANDIGGELEN, R., WASSEN, M.J. & WIERSINGA, W.A., 1988. The effects of drainage on groundwater quality and plant-species distribution in Stream Valley meadows. *Vegetatio*, **75**, 37-48.

GUNDERSEN, P., CALLESEN, I. & DE VRIES, W., 1998. Nitrate leaching in forest ecosystems in controlled by forest floor C/N ratio. *Environmental Pollution*, **102**, 403-407.

HADDON, S.W., 1998. *The effect of soil nutrient status of river flooding on the Derwent Ings*. York. Report to English Nature.

HASLAM, S.M., 1973. The management of British wetlands. *Journal of Environmental Management*, **16**, 308-309.

HASSINK, J., 1992. Effect of grassland management on N-mineralisation potential, microbial biomass and N-yield in the following year. *Netherlands Journal of Agricultural Science*, **40**, 173-185.

HAZEL, V., 1984. *Hampshire's Countryside Heritage: Meadows*. Hampshire County Council.

HEATHWAITE, A.L., JOHNES, P.J. & PETERS, N.E., 1996. Trends in nutrients. *Hydrological Processes*, **10**, 263-293.

HENSON, I., JENSON, C. & TURNER, N., 1989. Leaf gas exchange and water relations of lupins and wheat. I. Shoot response to soil water deficits. *Australian Journal of Plant Phsiology*, **16**, 401-413.

HERRIOT, J.B.D. & WELLS, D.A., 1963. The grazing animal and sward productivity. *Journal of Agricultural Science*, **61**, 89-99.

HETTELINGH, J.-P., POSCH, M., DESMET, P.A.M. & DOWNING, R.J., 1995. The use of critical loads in emission reduction agreements in Europe. *Water, Air & Soil Pollution*, **85**, 2381-2388.

HILL, R.D. & PEART, M.R., 1998. Land use, runoff, erosion and their control: a review for southern China. *Hydrological Processes*, **12**, 2029-2042.

HOLMES, N.T.H. & NIELSEN, M.B., 1998. Restoration of the Rivers Brede, Cole and Skerne: a jount Danish and British EU-LIFE demonstration project, I - setting up and delivery of the project. *Aquatic conservation: Marine and Freshwater Ecosystems*, **8**, 185-196.

HOLZEL, N. & OTTE, A., 2001. The impact of flooding regime on the soil seed bank of flood meadows. *Journal of Vegetation Science*, **12**, 209-218.

HOPKINS, A., MATKIN, E.A., ELLIS, J.A. & PEEL, S., 1985. Southwest England grassland survey 1983. 1. Age structure and sward composition of permanent and arable grassland and their relation to manageabililty fertiliser nitrogen and other management features. *Grass and Forage Science*, **40**, 348-360.

HUHTA, A., RAUTIO, P., TUOMI, J. & LAINE, K., 2001. Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. *Journal of Vegetation Science*, **12**, 677-686.

INDITE, 1994. *Impacts of nitrogen deposition in terrestrial ecosystems*. London: Department of the Environment.

JACKSON, D.L. & MCLEOD, C.R., 2000. *Handbook on the UK status of EC Habitats Directive interest features.* Peterborough: Joint Nature Conservation Committee.

JAMIESON, N., MONAGHAN, R. & BARRACLOUGH, D., 1999. Seasonal trends of gross N mineralization in a natural calcareous grassland. *Global Change Biology*, **5**, 423-431.

JANSSENS, F., PEETERS, A., TALLOWIN, J.R.B., BAKKER, J.P., BEKKER, R.M., FILLAT, F. & OOMES, M.J.M., 1998. Relationship between soil chemical factors and grassland diversity. *Plant and Soil*, **202**, 69-78.

JANSSENS, F., PEETERS, A., TALLOWIN, J.R.B., SMITH, R.E.N., BAKKER, J.P., BEKKER, R.M., VERWEIJ, G.L., FILLAT, F., CHOCARRO, C. & OOMES, M.J.M., 1997. Relationship between soil nutrients and plant diversity in grassland: definition of limits for the maintenance and the reconstruction of species-rich communities. *In: Management for Grassland Biodiversity*. Warsaw, Poland. Proceedings of the International Occasional Symposium of the European Grassland Federation. pp. 315-322.

JARVIS, S.C., 1999. Accounting for nutrients in grassland: challenges and needs. *In*: Corrall, A.J., ed. *Accounting for Nutrients, a challenge for grassland farmers in the 21st century*. Reading: British Grassland Society Occasional Symposium No 33.

JEFFERSON, R.G., 1997. Distribution and status of Alopecurus pratensis - Sanguisorba officinalis floodplain meadows in England. Peterborough: *English Nature Research Reports*, No. 249.

JEFFERSON, R.G. & ROBERTSON, H.J., 1998. *Review of hay meadow management:organic nutrient additions to semi-natural grassland*. Internal paper tabled to the general Committee of English Nature Council.

JOHNES, P.J., 1996. Evaluation and management of the impact of land use change on the nitrogen and phosphorus load delivered to surface waters: the export coefficient modelling approach. *Journal of Hydrology*, **183**, 323-349.

JONES, R. & ETHERINGTON, J.R., 1971. Comparative studies of plant growth and distribution in relation to waterlogging. *Journal of Ecology*, **59**, 793-801.

JOYCE, C.B., 1998. Plant community dynamics of managed and unmanaged floodplain grasslands: an ordination analysis. *In:* Joyce, C. & Wade, M., eds. *European Lowland Wet Grasslands: Biodiversity, Management and Restoration*. Chichester: Wiley. pp. 173-191.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E., 1989. The flood pulse concept in river-floodplain systems. *In:* Dodge, D.P., ed. *Proceedings of the Large River Symposium.* Canadian Special Publication of the Fisheries and Aquatic Sciences. 106, pp. 110-127.

KIRKHAM, F.W. & WILKINS, R.J., 1994a. The productivity and response to inorganic fertilizers of species-rich wetland hay meadows on the Somerset Moors: the effects of nitrogen under hay cutting and aftermath grazing. *Grass and Forage Science*, **49**, 159-162.

KIRKHAM, F.W. & WILKINS, R.J., 1994b. The productivity and response to inorganic fertilizers of species-rich wetland hay meadows on the Somerset Moors: the effect of nitrogen phosphorus and potassium on herbage production. *Grass and Forage Science*, **49**, 163-175.

KOERSELMAN, W., BAKKER, S.A. & BLOM, M., 1990. Nitrogen, Phosphorus and potassium mass balances for two small fens surrounded by pastures. *Journal of Ecology*, **78**, 428-442.

KOOIJMAN, A.M., DOPHEIDE, J.C.R., SEVINK, J., TAKKEN, I. & VERSTRATEN, J.M., 1998. Nutrient limitations and their implications on the effects of atmospheric deposition in coastal dunes; lime-poor and lime-rich sites in the Netherlands. *Journal of Ecology*, **86**, 511-526.

KOREVAAR, H., 1986. *Production and feeding value of grass from grassland with restrictions in use and fertilization for nature conservation.* Lelystad: The Netherlands Research and Advisory Institute for Cattle, Sheep and Horse Husbandry (PR). Doctoral Thesis, Report 101.

KREBS, L., CORBONNOIS, J. & MULLER, S., 1999. The impact of hydrological fluctuations on shallow groundwater hydrochemistry under two alluvial meadows. *Hydrobiologia*, **410**, 195-206.

KRONVANG, B., SVENDSEN, L.M., BROOKES, A., FISHER, K., MOLLER, B., OTTOSEN, O., NEWSON, M. & SEAR, D., 1998. Restoration of the rivers Brede, Cole and Skerne: A joint Danish and British EU-LIFE demonstration project, III - Channel morphology, hydrodynamics and transport of sediment and nutrients. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 209-222.

LAMBERTH, C. & HAYCOCK, N.E., 2001. *Water quality constraints on the creation and management of wetland habitats.* Sandy: Report to the Royal Society for the Protection of Birds.

LANTINGA, E.A., DEENEN, P.J.A.G. & VAN KEULEN, H., 1999. Herbage and animal production responses to fertilizer nitrogen in perennial ryegrass swards. II Rotational grazing and cutting. *Netherlands Journal of Agricultural Science*, **47**, 243-261.

LARGE, A.R.G. & PETTS, G.E., 1996. Historical channel-floodplain dynamics along the River Trent Implications for river rehabilitation. *Applied Geography*, **16**, 191-209.

LAWSON, C.S. & GOWING, D.J.G., 2001. *The water-regime requirements and rate of response to hydrological change of grassland plant communities*. Annual report to DEFRA. Project BD1310. Cranfield.

LONDO, G., 1988. Nederlandse freatofyten. *PUDOC*. Wageningen. pp. 108.

LONGLEY, A.J., 1998. *Modelling the impact of gravel extraction on the hydrology of the Cotswold Water Park, near Cirencester*. MSc Thesis. University of Newcastle upon Tyne.

MACHEFERT, S.E., DISE, N.B., GOULDING, K.W.T. & WHITEHEAD, P.G., 2001. *Nitrous Oxide emission from a range of land-uses across Europe*. Science of the Total Environment, in press.

MAFF, 1994. *Fertilizer recommendations for agricultural and horticultural crops. Sixth edition. Ministry of Agriculture*. Fisheries and Food Reference Book 427. London.

MAINSTONE, C.P., PARR, W. & DAY, M., 2000. *Phosphorus and river ecology - tacking sewage inputs*. Report to English Nature. Swindon: WRc plc.
MALLOCH, A.J.C., 1999. *MATCH version 2 for WINDOWS NT/95/98*. Lancaster: Unit of Vegetation Science, University of Lancaster.

MANCHESTER, S.J., MCNALLY, S., TREWEEK, J.R., SPARKS, T.H. & MOUNTFORD, J.O., 1999. The cost and practicality of techniques for the reversion of arable land to lowland wet grassland - an experimental study and review. *Journal of Environmental Management,* **55**, 91-109.

MANCHESTER, S.J., TREWEEK, J.R., MOUNTFORD, J.O. & PYWELL, R.F., 1997. The success of nurse crops in the establishment of species-rich lowland wet grassland. *In:* Sheldrick, R.D., ed. *Grassland management in ESAs.* British Grassland Society Occasional Symposium no 32, pp. 260-261.

MARRS, R.H., 1993. Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. *Advances in Ecological Research*, **24**, 241-300.

MATTSON, M.D. & LIKENS, G.E., 1993. Air pressure and methane fluxes. *Nature*, **347**, 718-719.

MCGRATH, S.P., ZHAO, F.J. & WITHERS, P.J.A., 1996. *Development of sulphur deficiency in crops and its treatment*. No 376. London: Proceedings of the Fertiliser Society.

MILNES, K.J., DAVIES, W.J., RODWELL, J.S. & B.J., F., 1998. The responses of *Briza media* and *Koeleria macrantha* to drought and re-watering. *Functional Ecology,* **12**, 665-672.

MOUNTFORD, J.O., LAKHANI, K.H. & HOLLAND, R.J., 1996. Reversion of grassland vegetation following the cessation of fertilizer application. *Journal of Vegetation Science,* **7**, 219-228.

MOUNTFORD, J.O., LAKHANI, K.H. & KIRKHAM, F.W., 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *Journal of Applied Ecology*, **30**, 321-332.

NEWBOLD, C. & MOUNTFORD, J.O., 1997. *Water level requirements of wetland plants and animals*. English Nature Freshwater Series No 5. Peterborough: English Nature.

OLDE VENTERICK, H., WASSEN, M.J., BELGERS, J.D.M. & VERHOEVEN, J.T.A., 2001. Control of environment variables on species density in fens and meadows: importance of direct effects and effects through community biomass. *Journal of Ecology*, **89**, 1033-1040.

OOMES, M.J.M., KUIKMAN, P.J. & JACOBS, F.H.H., 1997. Nitrogen availability and uptake by grassland in mesocosms at two water levels and two water qualities. *Plant and Soil*, **192**, 249-259.

OOMES, M.J.M. & MOOI, H., 1981. The effect of cutting and fertilizing on the floristic composition and production of an Arrhenatherion-elatioris grassland. *Vegetatio*, **46-7**, 233-239.

OOMES, M.J.M., OLFF, H. & ALTENA, H.J., 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of Applied Ecology*, **33**, 576-588.

PAYNE, K., KNOTT, A. & MASSEN, D., 1998. *Cricklade North Meadow Management Plan*. Devizes: English Nature (Wiltshire Team).

PEZESHKI, S.R., 2001. Wetland plant responses to soil flooding. *Environmental and Experimental Botany*, **46**, 299-312.

PINAY, G., DECAMPS, H. & NAIMAN, R.J., 1999. The spiralling concept and nitrogen cycling in large river floodplain soils. *Large Rivers*, **11**, 281-291.

PINAY, G., RUFFINONI, C. & FEABRE, A., 1995. Nitrogen cycling in two riparian forest soils under different geomorphic conditions. *Biogeochemistry*, **430**, 9-29.

PONNAMPERUMA, F.M., 1972. The chemistry of submerged soils. *Advances in Agronomy*, **24**, 29-96.

PRACH, K., 1992. Vegetation, microtopography and water table in the Luznice River floodplain, South Bohemia, Czechoslovakia. *Preslia*, **64**, 357-367.

PUTMAN, R.J., FOWLER, A.D. & TOUT, S., 1991. Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. *Biological Conservation*, **56**, 329-347.

RATCLIFFE, D.A., 1977. *A Nature Conservation Review*. Cambridge University Press.

RICHARDSON, C.J. & QIAN, S.S., 1999. Long-term phosphorous assimilative capacity in freshwater wetlands: a new paradigm for sustaing ecosystem structure and function. *Environmental Science and Technology*, **33**, 1545-1551.

ROBERTSON, H.J. & JEFFERSON, R.G., 2000. Monitoring the condition of lowland grassland SSSIs. Part 1 - English Nature's rapid assessment method. Peterborough: *English Nature Research Reports*, No. 315.

RODWELL, J. S., 1992. *British plant communities. Volume 3. Grasslands and montane communities.* Cambridge: Cambridge University Press.

ROSS, S. M., 1995. Overview of the hydrochemistry and solute processes in British Wetlands. *In:* Hughes, J. M. R. & A.L., eds. *Hydrology and Hydrochemistry of British Wetlands*. Chichester: H. John Wiley.

SEAR, D.A., 1994. River restoration and geomorphology. *Aquatic conservation: Marine and Freshwater Ecosystems*, **4**, 169-177.

SIEBEN, W.H., 1965. Het verband tussen outwatering en opbrengst bij de jonge zavelgronden in de Noordoostpolder. *Van Zee tot Land*, **40**, 1-117.

SILVERTOWN, J., DODD, M., McCONWAY, K., POTTS, J. & CRAWLEY, M., 1994a. Rainfall, biomass viration, community composition in the Park Grass Experiment. *Ecology*, **75**, 2430-2437.

SILVERTOWN, J., DODD, M.E., GOWING, D.J.G. & MOUNTFORD, J.O., 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature*, **400**, 61-63.

SILVERTOWN, J.W., WELLS, D.A., GILLMAN, M.P., DODD, M.E. & LAKHANI, K.H., 1994b. Short-term effects and long-term after-effects of fertiliser application on the flowering population of green-winged orchid Orchis morio. *Biological Conservation*, **69**, 191-197.

SIMPSON, N.A. & JEFFERSON, R.G., 1996. Use of farmyard manure on semi-natural (meadow) grasslands. Peterborough: *English Nature Research Reports*, No. 150.

SMIRNOFF, N. & CRAWFORD, R., 1983. Variation in the sturcture and response to flooding of root aerenchyma in some wetland plants. *Annals of Botany*, **51**, 237-249.

SMITH, L.P., 1960. The relation between weather and meadow-hay yields in England. *Journal of the British Grassland Society*, **15**, 203-208.

SMITH, L.P. & TRAFFORD, B.D., 1976. *Climate and drainage*. Technical Bulletin no. 34. London: MAFF.

SMITH, R.S., 1997. Upland meadow grasslands in the Pennine Dales ESA. *In:* Sheldrick, R. D., ed. *British Grassland Society Occasional Symposium.* Grassland management in ESAs.32, pp. 80-90.

SMITH, R.S., BUCKINGHAM, H., BULLARD, M.J., SHIEL, R.S. & YOUNGER, A., 1996a. The conservation management of mesotrophic (meadow) grassland in norther England.1. Effects of grazing, cutting date and fertilizer on the vegetation of a traditionally managed sward. *Grass and Forage Science*, **51**, 278-291.

SMITH, R.S., CORKHILL, P., SHIEL, R.S. & MILLWARD, D., 1996b. The conservation management of mesotrophic (meadow) grassland in Northern England .2. Effects of grazing, cutting date, fertilizer and seed application on the vegetation of an agriculturally improved sward. *Grass and Forage Science*, **51**, 292-305.

SMITH, R.S., PULLAN, S. & SHIEL, R.S., 1996. Seed shed in the making of hay from mesotrophic grassland in a field in northern England: Effects of hay cut date, grazing and fertilizer in a split-split-plot experiment. *Journal of Applied Ecology*, **33**, 833-841.

SMITH, R.S. & RUSHTON, S.P., 1994. The effects of fertilisers on plant species composition and conservation interest of U.K. grassland. *In:*. Haggar, R.J. & S.P., eds. *Grassland management and nature conservation.* Reading: British Grassland Society. Occasional Symposium No. 28, pp. 64-73.

SNOWDEN, R.E.D. & WHEELER, B.D., 1993. Iron toxicity to fen plant species. *Journal of Ecology*, **81**, 35-46.

SPINK, A., SPARKS, R.E., VAN OORSCHOT, M. & VERHOEVEN, J.T.A., 1998. Nutrient dynamics of large river floodplains. *Regulated Rivers-Research & Management*, **14**, 203-216.

STANFORD, G. & EPSTEIN, E., 1974. Nitrogen mineralisation - water relations in soils. *Soil ScienceSociety of America Proceedings*, **38**, 103-107.

STEEGEN, A., GOVERS, G. & NACHTERGAELE, J., 2000. Sediment export by water from an agricultural catchment in the Loam Belt of central Belgium. *Geomorphology*, **33**, 25-36.

STEVENSON, F.J. & COLE, M.A., 1986. *Cycles of soil*. Chichester: Wiley.

TALLOWIN, J.R.B., 1997. The agricultural productivity of lowland semi-natural grassland: a review. Peterborough: *English Nature Research Reports*, No. 233.

TALLOWIN, J.R.B. & JEFFERSON, R.G., 1999. Hay production from lowland semi-natural grasslands: a review of implications for ruminant livestock systems. *Grass and Forage Science*, **54**, 99-115.

TALLOWIN, J.R.B., KIRKHAM, F.W., R.E.N., S. & MOUNTFORD, J.O., 1998. Residual effects of phosphorous fertilisation on the restoration of floristic diversity to wet hay meadows. *In:* C.B., J. & P.M., W., eds. *European lowland wet grasslands:biodiversity, management and restoration*. London: John Wiley & Sons Ltd. pp. 249-263.

TAYLOR, S. A., 1952. Oxygen diffusion in pourous media as a measure of soil aeration. *Soil Science Socity of America Proceedings*, **14**, 55-61.

THORNTON, G.J.P. & DISE, N.B., 1998. The influence of catchment characteristics, agricultural activities and atmospheric deposition on the chemistry of small streams in the English Lake District. *Science of the Total Environment*, **216**,

TILMAN, D., DODD, M.E., SILVERTOWN, J., POULTON, P. & CRAWLEY, M.J., 1994. The park grass experiment: insights from the most long-term ecological study. *In:* Leigh, R.A. & Johnston., A.E., eds. *Long-term experiments in agricultural and ecological sciences*. Wallingford: CAB International. UK. pp. 287-303.

TREWEEK, J., JOSE, P. & BENSTEAD, P., 1997. *The Wet Grassland Guide: Managing floodplain and coastal wet grasslands for wildlife*. Sandy, Bedfordshire. Royal Society for the Protection of Birds.

TROUGHT, M.C.T. & DREW, M.C., 1980. The development of waterlogging damage in wheat seedlings (*Triticum aestivum L.*) I. shoot and root growth in relation to changes in the concentration of dissolved gases and solutes in the soil solution. *Plant Soil*, **54**, 77-94.

VAN DER PEIJL, M.J. & VERHOEVEN, J.T.A., 2000. Carbon, nitrogen and phosphorus cycling in river marginal wetlands; a model examination of landscape geochemical flows. *Biogeochemistry*, **50**, 45-71.

VAN DUREN, I.C., BOEYE, D. & GROOTJANS, A.P., 1997. Nutrient limitation in an extant and drained poor fen: implications for restoration. *Plant Ecology*, **133**, 91-100.

VAN DUREN, I.C. & PEGTEL, D.M., 2000. Nutrient limitations in wet, drained and rewetted fen meadows: Evaluation of methods and results. *Plant and Soil*, **220**, 35-47.

VAN OORSCHOT, M., HAYES, C. & VAN STRIEN, I., 1998. The influence of soil desiccation on plant production, nutrient uptake and plant nutrient availability in two French floodplain grasslands. *Regulated Rivers: Research and Management*, **14**, 313-327.

VAN OORSCHOT, M., ROBBEMONT, E., BOERSTAL, M., VAN STRIEN, I. & VAN KERKHOVEN-SCHMITZ, M., 1997. Effects of enhanced nutrient availability on plant and soil nutrient dynamics in two English riverine ecosystems. *Journal of Ecology*, **85**, 167-179.

VARTAPETIAN, B.B., 1978. *Introduction - life without oxygen*. ed. Hook, D. D. & Crawford, R. M. M. Plant life in anaerobic environments. Ann Arbor Science Publications. pp. 1-11.

VERHOEVEN, J.T.A., BOGAARDS, H., VAN LOGTESTIJN, R.S.P. & SPINK, A., 1998. Initial estimates of nutrient-related process rates in floodplains along modified rivers in the Netherlands. *New Concepts For Sustainable Management of River Basins*. pp. 229-240.

VERHOEVEN, J.T.A., KOERSELMAN, W. & MEULEMAN, A.F.M., 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: Relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution*, **11**, 494-497.

WALKER, L., 1995. *Water-table management in wildlife habitats*. Cranfield University.

WALLING, D.E. & HE, Q., 1998. The spatial variability of overbank sedimentation on river floodplains. *Geomorphology*, **24**, 209-223.

WALLING, D.E., HE, Q. & BLAKE, W.H., 2000. *River floodplains as phosphorus sinks*. *In:* Stone, M., ed. *The role of erosion and sediment transport in nutrient and contaminant transfer.* IAHS publication no. 263, pp. 211-218.

WALLIS DE VRIES, M.F., 1994. *Foraging in a landscape mosaic. Diet selection and performance of free-ranging cattle in heathland and riverine grasslant.* Netherlands: University of Wageningen.

WEIGERT, R.G. & EVANS, F.C., 1964. Primary production and the disappearance of dead vegetation on an old field in Southeastern Michagan. *Ecology*, **45**, 49-63.

WESSELING, J. & VAN WIJK, W.R., 1957. Soil physical conditions in relation to drain depth. *In:* Luthin, J.N., ed. *Drainage of agricultural lands*. Madison. pp. 461-504.

WHEELER, B.D. & SHAW, S.C., 2001. *Wetland monitoring*. Peterborough: Report to the Environment Agency (Anglian Region).

WILLIAMS, E. D., 1978. *Botanical composition of the park grass plots at Rothamsted*. Rothamsted: Rothamsted Experimental Station.

WILLIAMSON, P., 1976. Above-ground primary production of chalk grassland allowing for leaf death. *Journal of Ecology*, **64**, 1059-1075.

WILSON, E.J., WELLS, T.C. E. & SPARKS, T.H., 1995. Are calcareous grasslands in the UK under threat from nitrogen deposition - an experimental-determination of a critical load. *Journal of Ecology*, **83**, 823-832.

XIONG, S. & NILSSON, C., 1998. Dynamics of plan litter in riparian meadows: setting a reference for management. *In:* Joyce, C. & Wade, M., eds. *European Lowland Wet Grasslands: Biodiversity Management and Restoration*. Chichester: Wiley. pp. 193-200.

YABE, K. & ONIMARU, K., 1997. Key variables controlling the vegetation of a cool-temperate mire in northern Japan. *Journal of Vegetation Science*, **8**, 29-36.

ZHANG, L., 1983. Vegetation ecology and population biology of *Fritillaria meleagris L*. at the Kungsangen Nature Researve, Eastern Sweden. *Acta Phytogeographica Suecica*, **73**, 1-95.

ZHANG, L. & HYTTEBORN, H., 1985. Effect of ground water regime on development and distribution of *Fritillaria meleagris*. *Holartic Ecology,* **8**, 237-244.

Appendices

Appendix 1 List of MG4 sites in England

Site name	County	Gridref	Catchment	Area ha	Status
Acaster South Ings	North Yorkshire	SE594437	Ouse	37	SSSI
Aubert Ings	North Yorkshire	SE453538	Ouse	9.6	SSSI,NNR
Bolton Percy Ings	North Yorkshire	SE534401	Ouse	6.8	SSSI
Breighton Meadows	North/East Yorkshire	SE704330	Ouse	26.04	SSSI,NNR pSAC RAM SPA
Burr Closes	North Yorkshire	SE596340	Ouse	1.2	SSSI
Church Ings	North Yorkshire	SE594456	Ouse	4.7	SSSI
Derwent Ings	North/East Yorkshire	SE 695410	Ouse	190	SSSI,NNR pSAC RAM SPA WT VCO
Clifton Ings	North Yorkshire	SE582532	Ouse	61.25*	NS
Fulford Ings	North Yorkshire	SE608491	Ouse	3.7	SSSI
Naburn Marsh	North Yorkshire	SE600479	Ouse	8	SSSI
Fen Carr Meadows	West Yorkshire	SE656156	Trent	4.25	NS, WT
Arncott Bridge Meadows	Oxfordshire	SP609185	Thames	7.2*	SSSI
Cassington Meadows	Oxfordshire	SP463101	Thames	7.03*	SSSI,pSAC
Ducklington Mead	Oxfordshire	SP363077	Thames	5.6	SSSI
Grafton Lock Meadow	Oxfordshire	SU273991	Thames	11.1	SSSI,NT
Hook Meadow and the Trap Grounds	Oxfordshire	SP500089	Thames	11.3*	SSSI
Iffley Meadows	Oxfordshire	SP524038	Thames	36.2*	SSSI,WT
Langleys Lane Meadow	Oxfordshire	SP391015	Thames	3.5*	SSSI
Wolvercote Meadows	Oxfordshire	SP484096	Thames	9.2	SSSI,pSAC
New Marston Meadows	Oxfordshire	SP520076	Thames	44.42*	SSSI
Chimney Meadows	Oxfordshire	SP352000	Thames	49.38*	SSSI, NNR
Pixey & Yarnton Meads	Oxfordshire	SP480105	Thames	85.6	SSSI,pSAC, CL
Castor Flood Meadows	Cambridgesire	TL123973	Nene	42*	SSSI
Portholme	Cambridgeshire	TL238708	Great Ouse	104	SSSI,pSAC
Mottey Meadows	Staffordshire	SJ840134	Trent	44.6*	SSSI,NNR pSAC
Bosworth Mill Meadow	Northamptonshire	SP628822	Severn	5.2*	SSSI,WT
Bugbrooke Meadows	Northamptonshire	SP672586	Nene	9.8*	SSSI,WT
Mill Crook	Northamptonshire	SP773464	Great Ouse	5.7*	SSSI,WT
River Ise and Meadows	Northamptonshire	SP882832	Nene	14*	SSSI, WT
Wadenhoe Marsh & Achurch Meadow	Northamptonshire	TL008828	Nene	47.4*	SSSI
Wollaston Meadows	Northamptonshire	SP898650	Nene	14.6	SSSI
Barn Hill Meadows	East Yorkshire	SE734285	Ouse	8.5	SSSI
Bishop Wilton Poorland	East Yorkshire	SE778558	Ouse	2.1	SSSI
Hotham Meadow	East Yorkshire	SE895351	Ouse	0.9	SSSI
Lambwath Meadows	East Yorkshire	TA208398	Hull	22	SSSI
Melbourne & Thornton Ings	East Yorkshire	SE745450	Ouse	17.5*	SSSI,NNR pSAC RAM SPA VCO
Newton Mask	East Yorkshire	SE707500	Ouse	16.5*	SSSI,pSAC RAM SPA
White Carr Meadow	East Yorkshire	SE787457	Ouse	1.1	SSSI
Clattinger Farm	Wiltshire	SU012933	Thames	60.3*	SSSI,p.SAC WT
North Meadow Cricklade	Wiltshire	SU094946	Thames	44.4	SSSI,NNR p.SAC,CL

Site name	County	Gridref	Catchment	Area ha	Status
Upper Waterhay Meadow	Wiltshire	SU068937	Thames	2.8	SSSI
Eakring & Maplebeck Meadows	Nottinghamshire	SK705622	Trent	16.03*	SSSI,WT
Besthorpe Meadows	Nottinghamshire	SK817643	Trent	9.23*	SSSI, WT
Barrow Gravel Pits	Leicestershire	SK568166	Trent	35.9*	SSSI
Loughborough Meadows	Leicestershire	SK538218	Trent	63.5	SSSI,WT
Newton Burgoland Marshes	Leicestershire	SK381084	Trent	8.1*	SSSI
Kendalls Meadow	Leicestershire	SP394981	Trent	2.7*	SSSI
Muston Meadows	Leicestershire	SK824367	Trent	8.77*	SSSI,NNR
Seaton Meadows	Leicestershire	SP915979	Welland	11.43*	SSSI
Sheepy Fields	Leicestershire	SK332025	Trent	5.3*	SSSI
Lea Marsh	Lincolnshire	SK816868	Trent	27.24	SSSI
Allington Meadows	Lincolnshire	SK871398	Witham	4.1*	SSSI
Birches Barn Meadows	Warwickshire	SK282021	Trent	10.74	SSSI
Brook Meadow	Warwickshire	SP180743	Trent	1.73	SSSI,WT
Racecourse Meadow	Warwickshire	SP186537	Severn	1.5	SSSI
Packington Meadows	Warwickshire	SP228858	Trent	1.04	NS
Railway Meadow, Langley	Warwickshire	SP199632	Severn	0.96	SSSI
Anker Meadows, Atherstone	Warwickshire	SP327961	Trent	3.25	NS
Oak Tree Farm Meadows	Warwickshire	SP189666	Severn	2.5	SSSI
Sherbourne Meadows	Warwickshire	SP242618	Severn	21.53*	SSSI
River Itchen Meadows	Warwickshire	SP403561	Severn	45.3*	NS
Long Meadow, Thorn	Hereford & Worcester	SP015553	Severn	5.1*	SSSI,WT
Marshlands Meadow	Hereford & Worcester	SO812324	Severn	1.08	SSSI
Poolhay Meadows	Hereford & Worcester	SO829308	Severn	2.75*	SSSI
Rectory Farm Meadows	Hereford & Worcester	SO922382	Severn	8	SSSI
Burley Dene	Hereford & Worcester	SO814324	Severn	13*	NS
Hooze Meadows	Hereford & Worcester	SO820335	Severn	3.2	NS
Shurnock Meadow	Hereford & Worcester	SP018609	Severn	1.2*	NS
Marsh End Meadows	Hereford & Worcester	SO817356	Severn	1	NS
The Sturts	Hereford & Worcester	SO338480	Wye	14	SSSI
Upton Ham	Hereford & Worcester	SO860400	Severn	56.6*	SSSI
Hunsdon Mead	Hertfordshire/Essex	TL418110	Thames	34*	SSSI
Long Herdon Meadow	Buckinghamshire	SP648202	Thames	4.5	SSSI
Oxley Mead	Buckinghamshire	SP819348	Great Ouse	3.7	SSSI
Went Ings Meadows	South Yorkshire	SE650183	Ouse	6.4*	SSSI
Ashleworth Ham	Gloucestershire	SO833263	Severn	10	SSSI
Chessels Meadow, Dikler Brook	Gloucestershire	SP187230	Thames	2.6*	NS
Chaceley b	Gloucestershire	SO855305	Severn	0.3	NS
Yew Tree Inn Meadows	Gloucestershire	SO866301	Severn	3.5	NS
Chaceley a	Gloucestershire	SO856303	Severn	1.2	NS
Hyde Hill Meadows	Gloucestershire	SP178244	Thames	0.5	NS
Elmlea Meadows	Gloucestershire	SU079948	Thames	6.9*	SSSI
Roding Valley Meadows	Essex	TQ436953	Thames	19.8*	SSSI
Cuttle Brook Meadow	West Midlands	SP202757	Trent	2	NS
Fen End Meadows	West Midlands	SP229758	Trent	1.2	NS
Parkfield	West Midlands	SP170741	Trent	0.6	NS

Site name	County	Gridref	Catchment	Area ha	Status
Sheldon Country Park	West Midlands	SP160851	Trent	1.5	NS
Blythe Fields	West Midlands	SP155765	Trent	22*	NS
Great Hytail	West Midlands	SP160784	Trent	3	NS
Ford Meadow & Pasture	West Midlands	SP222763	Trent	1	NS
Henwood Mill Meadow	West Midlands	SP182794	Trent	0.3	NS
Bickenhill Meadows	West Midlands	SP188816	Trent	7.2*	SSSI
River Blythe Meadows	West Midlands	SP112733	Trent	2	SSSI
Great Blencow Meadows & Fen	Cumbria	NY459326	Eden	7.6*	SSSI
Broad Dales	Cumbria	NY253524	Wampool	16.4*	SSSI
Lord's Meadow, Albrighton	Shropshire	SJ822036	Severn	2.6	NS
Billingham Beck Meadow	Middlesborough	NZ448234	Tees	c.2	NS

Key

SSSI:	Site of Special Scientific Interest
NNR:	National Nature Reserve
pSAC:	Special Area of Conservation
RAM:	Ramsar Site
SPA:	Special Protection Area
WT:	Local Wildlife Trust Reserve
NT:	National Trust Reserve
VCO:	Other voluntary conservation organisation reserve
CL:	Registered Common Land
NS:	Non-statutory site

* Site area includes plant communities in addition to MG4

Appendix 2 Hay yields from North and East Yorkshire flood meadow SSSIs

– Assume square bales = 20kg and round bales =150. *=hay nutrient content analysed, Green = haylage, e = estimated
Stock type, No, dates for 2000 only

SSSI name	Field	Area/ha	Yield (t/ha) 1999	Yield (t/ha) 2000	Grazed?	Stock No	Dates
Acaster South Ings	1	4.57	4.81	No data	Sheep	5	Aug-Sept
	2	7.97	4.64	1.51	Sheep	40	10/08-20/09
	3	10.4	5.46	2.31	Sheep	?	?
	4	4.12	4.37	2.67	Yes		
	5	2.5	5.4	2.2	sheep	?	?
	6	11.42	4.94	2.76	Cattle sheep	40 120	15/08-12/10 14/08-20-09
	7	4.07	4.91	2.46	Let - cattle	85	05/08-07/10
Breighton Meadows	1	2.68	5.58	4.29	No		
	2	8.59	0.99	1.16	No		
	3	1.77	2.82	2.83	No		
	4	4.89	2.66	2.78	Yes		
Burr Closes	1	1.38	1.99	1.27	No		
Derwent Ings	1	7.36	3.8	No data	No		
	2	3.84	3.58	No data	Yes		
	3	9.15	0.11	No data	Yes		
	4	8.27	3.69	No data	Yes		
	5	10.12	3.42	No data	Yes		
	6	6.59	2.20	No data	Yes		
	7	2.43	1.88	No data	Yes		
	8	9.98	2.63	No data	Yes		
	9	2.66	6.46	No data	Yes		
	10	0.61	7.53	No data	No		
	11	4.11	6.57	No data	Yes		
	12	7.64	9.97	No data	Yes		
	13	10.63	2.38	No data	Yes		
	14	1.83	6.24	No data	Yes		
	15	26.93	4.46	1.49	Yes		
	16	6.66	3.44	3.8	Yes		
	17	7.45	3.68	1.34	No		
	18	2.03	2.47	4.93	No		
	19	14.89	4.46	4.75	Yes		
	20	11.88	5.50	6.78	Yes		
	21	4.05	6.17	5.68	Yes		
	22	12.94	4.55	No data	Yes		
	23	13.27	5.28	2.64	Yes		
	24	2.5	4.88	No data	Yes		
	25	14.98	3.0	No data	Yes		
Lambwath Meadows	1	3.47	5.76	1.44	Yes/no		
	2	4.12	7.28	3.16	No		
	3	7.82	8.5	7.033	Yes	90s	01/10-29/10
	4	1.89	3.76	3.44	Yes/no		
	5	2.43	4.73	4.32	Yes	160s	30/09-24/10

SSSI name	Field	Area/ha	Yield (t/ha) 1999	Yield (t/ha) 2000	Grazed?	Stock No	Dates
Melbourne & Thornton Ings	1	10.04	4.05	5.18	Yes	70s	09-30/10
	2	10.1	2.01	No data	Yes	100s	01/09-22/09
	3	5.06	1.19	0.89	Yes	20suc	11/08-24/10
	4	4.18	2.19	2.63	Yes	160s	28/09-08/10
	5	6.59	8.34	No data	No		
	6	3.67	6.28	No data	No		
	7	2.06	5.09	No data	No		
	8	4.13	18.16	No data	Yes		
	9	4.53	4.49	No data	No		
	10	16.64	1.08	No data			
Newton Mask	1	1.21	4.6	4.13	No	?sheep	
	2	9.81	1.73	1.51	Yes	150s	01/09-01-10
Kirkby Wharfe	1	?		91 round	Steers	11	25/07-10/10
	2	5.5		No data	May 5 cows +	8cows	1/06-31/10
	3	2.5		4.2e	No		
Pocklington canal	1	1.26		No data		6s	01/05-31/10

Year	Total Area With available information (ha)	No agreement holders	No reportees	No farms with hay data	Area of reported hay cut (ha)	No farms grazed
1999	374	83	67 (80.7%)	54 (80.6% of report)	360.63	48 (71.6%)
2000	199	68	54 (79.4%)	45 (83.3%)		36 (66.7%)

Appendix 3 Site questionnaire for English Nature Local Teams

1. Do you think any of the following issues threaten the site:
    - Altered water management (eg changes to river engineering or maintenance, local mineral extraction, changes in upstream land-use)
    - Increased nutrient availability (eg deposition of enriched silt from rivers, fertiliser application)
    - Decreased nutrient availability (eg exhaustion of soil by hay cropping)
    - Habitat fragmentation (eg loss of other unimproved grasslands in the area)
    - Other (please specify, eg unusual weather conditions)

2. If there has been an alteration to the site's hydrology in the past 30 years, can you categorise it as one of the following:
    - Surface ditching
    - Straightening of adjacent river
    - Deepening of adjacent river
    - Changes to control structure(s) in river (eg locks, weirs, sluices)
    - Embanking of the river (inc. bank repair with gabions, piling etc.)
    - Change in management of locks, sluices etc.
    - Change in frequency/magnitude of river maintenance (weed cuts / desilting)

3. Have there been any records kept of, or studies into, any of the following issues on the site (perhaps by NNR site managers, farmers, higher education centres or statutory bodies such as FRCA or EA)?
    - Hay yields (counts of hay bales)
    - Grazing regime (eg stocking density, length of grazing season)
    - Nutrient analysis of hay
    - Nutrient analysis of soil
    - Nutrient analysis of river water (we are aware of routine river data from the Environment Agency, but has there been a particular study in the locality)

4. Are you aware of any fertilisers having been applied to the site in the past 30 years?
    - Farm-yard manure
    - Slurry
    - Inorganic fertiliser (Nitrogen/Phosphorus/Potassium)
    - Lime/ basic slag
    - Other

4a. Is it still being applied? If not, when did fertiliser application cease?

4b. Are there any records of the amounts applied?

5. Has the vegetation of the site been recorded by means of vegetation quadrats at any time in the past 30 years?

5a. Were any of the quadrats marked and re-visited?

6. Are there any people whom you would recommend we contact to explore the above points in more detail?