

Eco-hydrological guidelines for wet woodland - Phase I

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Eco-hydrological guidelines for wet woodland – Phase I

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Executive summary

The implementation of the EU Habitats Directive through the Conservation (Natural Habitats, &c.) Regulations 1994 requires all competent authorities to assess plans and projects that could affect the nature conservation value of designated sites (SACs and SPAs) in order to ensure that their ecological integrity will not be adversely affected. This requires a greater understanding of the potential impact of a range of human activities on the condition of these sites and on the specific ecological requirements of the designated habitats and species. An essential element of any assessment is the need to gauge impacts against ecological targets. The Environment Agency, English Nature, the Countryside Council for Wales and Sheffield University recently collaborated in a number of projects to provide data for setting scientifically robust targets for lowland wetland plant communities. Following the success of this work, it was decided to extend the approach to cover the two Annex 1 wet woodland habitats; residual alluvial forests and bog woodlands.

The aim of this project is to provide an overview of the current state of the science relating to the eco-hydrological requirements of wet woodlands, to facilitate ecological target setting. There were two objectives:

- i. To review relevant information on the ecological characteristics of wet woodland habitats.
- ii. To critically evaluate the information, identifying any gaps/requirements for further data collection, and assessing whether on the basis of currently available information, it is possible to provide interim guidance for ecological target setting.

The findings are presented in two main sections. The first reviews the current scientific and practitioner understanding of the basic eco-hydrological characteristics and resource requirements of the two Annex I wet woodland types; residual alluvial forest and bog woodland. Each habitat is considered in turn, starting with a general description of the component NVC types and their eco-hydrological requirements. This is followed by an assessment of the distribution, nature and classification of existing wet woodland habitats in the UK. Finally, information is presented on the specific eco-hydrological requirements of key component species, including water regime and nutrition. A detailed reference section and list of key national and international contacts are also provided.

The second section assesses the adequacy of the available literature for setting robust eco-hydrological targets for the two wet woodland types. The starting point is to evaluate the knowledge base regarding the floristic composition, distribution, landscape setting and substratum type for each habitat. This information is then used to formulate a number of conceptual models describing our current understanding of the main water supply mechanisms that underpin the different NVC wet woodland types. The extent of our knowledge on their specific water, nutrient/hydrochemistry and management regime needs is then considered, followed by an assessment of their vulnerability to eco-hydrological changes. Finally, potentially useful methodologies for deriving eco-hydrological guidelines are identified and discussed.

Attached in Appendix 1 is a draft management plan for an alluvial forest (Hurcott and Podmore Pools SSSI). The outputs of the Phase 1 contract are assessed as material that can be drawn upon to develop site-specific guidelines on the management and hydro-ecological

regime for conservation purposes. From this evaluation, a generic methodology is outlined as an aid to conservation staff wanting to apply the project output.

Key words: Wet woodland, residual alluvial forest, bog woodland, eco-hydrology, guidelines

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1 Introduction

The implementation of the EU Habitats Directive through the Conservation (Natural Habitats, &c.) Regulations 1994 requires all competent authorities to assess plans and projects that could affect the nature conservation value of designated sites (SACs and SPAs) in order to ensure that their ecological integrity will not be adversely affected. This requires a greater understanding of the potential impact of a range of human activities on the condition of these sites and on the specific ecological requirements of the designated habitats and species. An essential element of any assessment is the need to gauge impacts against ecological targets. The Environment Agency, English Nature and the Countryside Council for Wales have recently collaborated in a number of projects to provide data for setting scientifically robust targets for lowland wetland plant communities (Wheeler & Shaw 2001; Atkins & Entec 2003; Wheeler and others 2004). Following the success of this work, they decided to extend the approach to cover the two Annex 1 wet woodland habitats; residual alluvial forests and bog woodlands. Unfortunately, relatively little data appeared to be available on these habitats and thus the first step was to clarify the current state of knowledge on their basic ecological characteristics.

The aim of this project is to provide an overview of the current state of the science relating to the eco-hydrological requirements of wet woodlands. There were two objectives:

- (i) To review relevant information on the ecological characteristics of wet woodland habitats.
- (ii) To critically evaluate the information, identifying any gaps/requirements for further data collection, and assessing whether on the basis of currently available information, it is possible to provide interim guidance for ecological target setting.

This report presents the findings of the review and critical evaluation. It comprises two parts:

- (i) A review of current scientific and practitioner understanding of the basic eco-hydrological characteristics and resource requirements of Annex I wet woodland types and their component NVC types.
- (ii) A critical evaluation of gaps in knowledge and further research requirements concerning the eco-hydrological characteristics and resource requirements of Annex I wet woodland types and their component NVC types.

Attached in Appendix is a draft management plan for an alluvial forest (Hurcott and Podmore Pools SSSI). The outputs of the Phase 1 contract are assessed as material that can be drawn upon to develop site-specific guidelines on the management and hydro-ecological regime for conservation purposes. From this evaluation, a generic methodology is outlined as an aid to conservation staff wanting to apply the output of the Phase 1 contract.

1.1 References

ATKINS & ENTEC. 2003. *Habitat and species summary guidance notes*.

WHEELER, B.D., & SHAW, S.C. 2001. *A wetland framework for impact assessment at statutory sites in Eastern England*. Environment Agency R&D Note W6-068/TR1 and TR2.

WHEELER, B.D. and others 2004. *In*: BROOKS, A.W., JOSE, P.V., & WHITEMAN, M.I., eds. *Ecohydrological guidelines for lowland wetland plant communities*. Peterborough: Environment Agency (Anglian Region).

2 Review of current scientific and practitioner understanding of the basic eco-hydrological characteristics and resource requirements of Annex I wet woodland types and their component NVC types

2.1 Introduction

This chapter provides an in-depth review of current knowledge relating to the basic ecological characteristics and resource requirements of two wet woodland habitats recognised within Annex 1 of the EU Habitats Directive; these include ‘Residual alluvial forests’ (NVC types W5, W6, W7) and ‘Bog woodland’ (NVC types M18, M19, W4). Effective conservation and management of these wetland habitats are hindered at present by a lack of readily accessible and directly transferable information that can be used by responsible agencies to:

- (i) Set robust ecological targets incorporating the specific eco-hydrological requirements of these habitats; and
- (ii) assess likely impacts of current and proposed management activities (water/ sediment/ peat abstraction, stream diversion, discharge of effluents and nutrient loading from agricultural activities) that may threaten or have a negative impact on habitat quality.

The review builds on a previous attempt to assess our understanding of the eco-hydrological requirements of wet woodlands in the UK (Atkins & Entec 2003). It draws on published and unpublished material and informal communications with experts to try to determine the sensitivity of these habitats to anthropogenic influences. Information from peer-reviewed publications were prioritised in the search for source material as this information was considered to provide a more solid grounding from which to formulate (and defend) eco-hydrological guidelines for wet woodlands.

The review is split into two main sections to cover first ‘Residual Alluvial Forests’ and secondly ‘Bog Woodlands’. Each of these sections is sub-divided into five subsections with the following headings:

- (i) General description of wet woodland and eco-hydrological factors relevant to habitat type

Included within the general description are the following: (a) key physical, geomorphological, hydrological and biological processes operating in each wet woodland system, (b) functioning of key processes affecting wet woodlands within the wider landscape context and (c) how each wet woodland habitat might be affected where drivers of key processes are altered; eg expected trajectories of wet woodland structure, composition and function in response to the spread of invasive species, increased grazing intensities, water abstraction etc.

- (ii) Distribution and description of wet woodland habitat in the UK

It was considered to be important to get a general overview of existing wet woodland habitat in the UK in order to assess inter-site variability in key physical (eg basic geological setting,

sediment textural properties), geomorphological, hydrological and biological processes operating in each system as well as key threats to habitat integrity. With limited time to complete such a task and sparse information that was readily available on each wet woodland, information was collected from only a selection of wet woodlands. This information will be used to aid the critical evaluation of wet woodlands (Section 3).

(iii) Vegetation classification of wet woodland

In proceeding with the literature search, it was felt that there was a need to define the wet woodland habitats that were under review, not only as they are described within the NVC system, but also as they are recognised under different vegetation classification systems, including those pre-dating the NVC and equivalent European (or other) classification systems. In this section there is some discussion of expected vegetation community trajectories according to shifts in hydrological conditions.

(iv) Eco-hydrological requirements of key component species of each wet woodland type

Information on the specific eco-hydrological requirements of dominant vegetation species typically occurring in the different wet woodland types is presented in the form of a list. A number of headings (ie nutrition & pH, substrate, flooding, drought, hydroperiod, effects of grazing & inter-specific competition) highlight species-specific requirements of (and responses to) key eco-hydrological variables.

(v) References lists

These include: (a) a reference list of literature detailing wet woodland ecosystem characteristics and eco-hydrological requirements at the whole ecosystem scale, (b) a reference list of literature examining the specific water resource and nutrient requirements of key species in Annex 1 wet woodland habitats, (c) a list of key national and international contacts (academics, practitioners) with relevant expertise relating to Annex 1 wet woodland habitats and (d) other relevant references and web page links.

2.2 Methods

Bibliographic databases already held on wet woodlands were reviewed and supplemented using the *ISI Web of Knowledge* which primarily allowed for journal article searches on three directories (ie *Science Citation Index Expanded* 1975-present, *BIOSIS Previews*®: 1969-present, *Current Contents Connect*®). A number of recent conference proceedings were also reviewed (eg INTECOL 7th International Wetlands Conference, Utrecht 2004, Holland; "River Restoration 2004" conference, Zagreb, Croatia) and relevant experts contacted by e-mail. Attempts were made to contact persons responsible for the management of specific bog or residual alluvial forests for site specifications. In addition, literature (and contact details of authors) was sought that described national (eg 'Wetland Framework') and international methodologies in existence that might be adopted to facilitate the development of guidelines for the management of wet woodlands in the UK.

2.3 Residual Alluvial Forests

2.3.1 General description of Residual Alluvial Forests (W5, W6, W7) and eco-hydrological factors relevant to this habitat type.

The alluvial forests existing today in Britain occur on moderately base-rich, eutrophic mineral or peat soils that are subject to periodic inundation and/or permanently, or seasonally high water table levels (JNCC web site). They can be found in various landscape situations throughout a river valley (Figure 1).

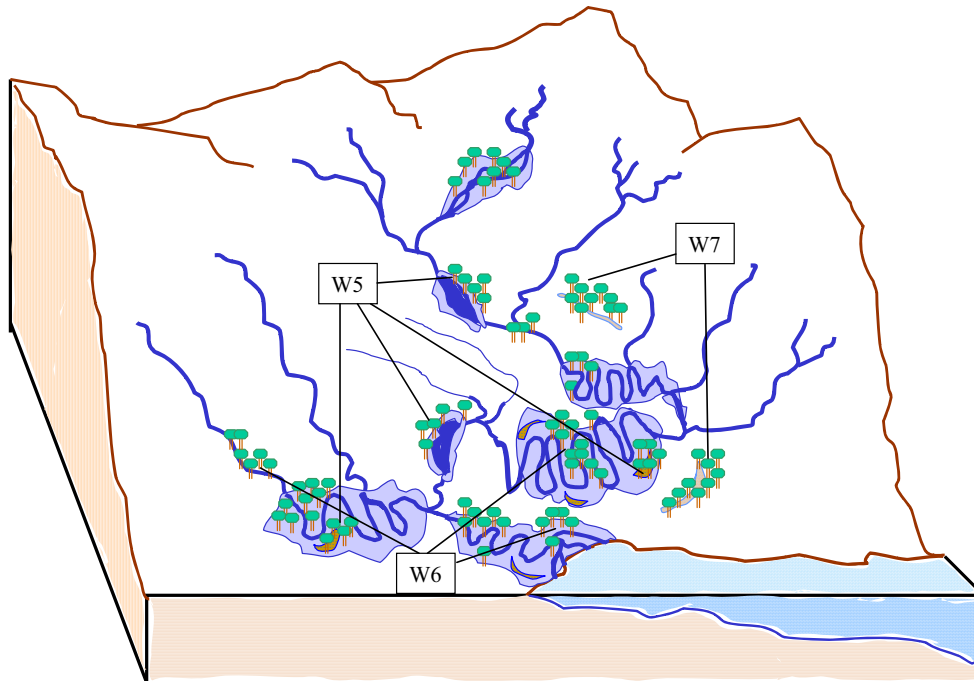


Figure 1 Landscape situations of *Alnus glutinosa*–*Carex paniculata* (W5), *A. glutinosa*–*Urtica dioica* (W6) and *Alnus glutinosa*–*Fraxinus excelsior*–*Lysimachia nemorum* (W7) alluvial forest communities.

Alnus glutinosa – *Carex paniculata* (W5) and *A. glutinosa*–*Urtica dioica* (W6) alluvial forest communities tend to occur in areas of low relief. Water is derived from surface flow and/or groundwater sources (eg spring-fed from a shallow aquifer, subsurface percolation of water from a river, overbank flooding). W5 alluvial forest communities typically occur on the edges of standing, or very slow-moving freshwater bodies/courses. That is, along lakes and ponds, or damp depressions on the floodplain at some distance from the main water course/body (eg in former side-channels and backswamps) which remain permanently wet and water-logged. With limited disturbance from floodwaters (ie there may be occasional water inputs from surface flows following a major flooding event), organic material tends to accumulate where this alluvial forest type is located, resulting in the formation of superficial deposits of organic material of varying thickness that overlie mineral alluvial deposits (see conceptual model Figure 11, Chapter 3 – section 3.2.2). W6 communities are distinct from W5 alluvial forests in that they occur along mobile watercourses (eg fast or slow flowing rivers and streams) as either wide or narrow strips of vegetation along the stream banks and/or on in-stream islands. The size of the W6 alluvial forest will depend on (i) how confined the river valley is and (ii) the degree of human occupation of the floodplain and encroachment into riparian zones. At low elevations the vegetation is regularly subject to the physical impacts of floodwaters and

inundation. The vegetation is otherwise adapted to rapid fluctuations in water table levels and significant seasonal variations in water availability that reflect a favoured hydroperiod. With the frequent remobilisation of sediments (and particularly along faster flowing streams) during flooding events, there is a constant threat of significant degradation or aggradation of riverbanks that is not present in the other two alluvial forest types. Also unique to this alluvial forest type, is clear sub-community zonation which is determined by depth to the water table and frequency of disturbance at varying elevations within the riparian zone (see conceptual model Figure 12, Chapter 3 – section 3.2.2).

Unlike W5 and W6 alluvial forests, *A. glutinosa* – *Fraxinus excelsior*- *Lysmachia nemorum* (W7) communities are present on higher ground along river valleys and can be found along the edges of the wider wooded valley, well beyond the main river course, and in areas of sharper relief (eg common on the fringes of the uplands in the north and west of the UK and areas such as the Weald in south-east England) (Figure 2) (Atkins & ENTEC 2003). With no reliance on surface water originating from rivers, this alluvial wet woodland type depends chiefly on groundwater supplied (i) from subsurface (and surface) flows down valley slopes and and/or (ii) laterally as springline flow from rock strata either along the slopes of middle-aged rivers, or along ‘brook channels’ which are not inundated by flooding, but where the groundwater emerges and maintains the soils in a semi-saturated state (Rodwell & Dring 2001) (see conceptual model Figure 13, Chapter 3 – section 3.2.2).

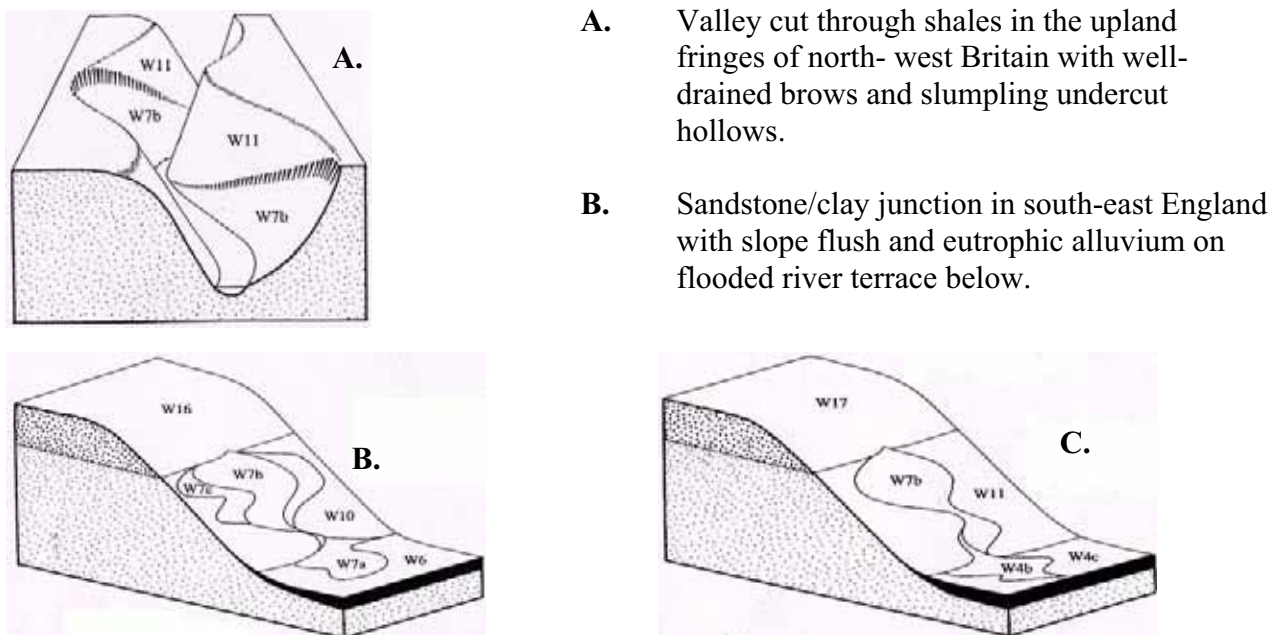


Figure 2 Different landscape situations of W7 alluvial forests, showing mosaic of successional stands adjacent to one another on hill-slope (Rodwell 1991a).

The complexity of sediment and hydro-geomorphological processes in *A. glutinosa*-*U. dioica* (W6) alluvial forests requires further elaboration as discussed in the following sections. Descriptions in the following sections of the importance of seasonally high (and low) water table levels are, nevertheless, of equal relevance to W5 and W7 alluvial forests.

2.3.1.1 Floods as important exogenous disturbances affecting the structure and composition of *Alnus glutinosa-Urtica dioica* W6 Alluvial Forests

The composition and rejuvenation of vegetation in W6 alluvial forests at any given time is fundamentally related to the magnitude, frequency and timing of recent flooding events (the hydroperiod) as well as the local geomorphology (Hughes 1994). These physical processes are in turn functions of the size and structure of the drainage network, the sediment load and both local and catchment level climatological conditions. Nanson and Croke (1992) recognize three classes of floodplain which differ in terms of levels of disturbance to the vegetation community (Gurnell 1995). The three classes of floodplains are defined according to a range of typical geomorphological features (eg sediment texture) and river processes (eg water velocity) and are classified as:

Class A - high-energy non-cohesive floodplains. These floodplains are typically located in steep headwater areas where channel migration is prevented by valley confinements. They are unstable floodplains which erode in response to extreme flooding events.

Class B - medium-energy non-cohesive floodplains. These floodplains have regular (seasonal) flood events and occur in relatively unconfined valleys (eg braided and meandering rivers).

Class C - low-energy cohesive floodplains. These floodplains are formed by regular flow-events in an unconfined valley. The floodplain either has a single laterally stable channel, or an anastomosing low-gradient channel. The scale of geomorphological disturbance is limited compared to the total floodplain area so that even prolonged floods will cause only slight physical disturbances.

High-energy floodplains (class A) experiencing high magnitude and unpredictable flood events would be expected to have a very short turn-over time for sediments. They are thus likely to be characterized by vegetation at a pioneer stage of development which can survive damage by floodwaters and severe degrees of erosion and sediment deposition. Medium and low energy floodplains (classes B and C), in contrast, are expected to support diverse vegetation communities across large environmental gradients. Typically, the active channel margins on these floodplains are frequently reworked by low-magnitude and high-frequency (often seasonal) floods to support short-lived pioneer communities which favour physical disturbance, while mature vegetation stands with species typical of later successional stages occupy levees and terraces on the floodplain; here inundation occurs less frequently and channel change is slower.

When attempting to predict, or understand the composition of vegetation on Class B and C floodplains it is important to also consider geomorphic type. Meandering and braided river systems will have very different proportions of the active floodplain exposed and available for plant colonization and, therefore, very different coverage by mature riparian vegetation stands. On single thread, meandering rivers, flood peaks will erode established communities on the outside of river bends and create point bars through sedimentation on the inside of river curves. Here pioneer communities will become established and encourage further sedimentation and vegetation establishment. Braided river systems, on the other hand, typically have wider and shallower riverbeds ensuring a large colonizable area during periods of low flow (Johnson 1994). The uneven and less predictable direction of river flow on

braided river floodplains also means, however, that the distribution of vegetation in different seral stages will be scattered and highly variable throughout the floodplain.

2.3.1.2 Frequency and magnitude of floods

Alluvial forests of the W6 type (also known as sequential successional, or mosaic forests) typically comprise fast-growing, early successional woody species in the overstorey (eg willow, alder, birch) and as such, rely on periodic disturbances for the replacement of suitable regeneration sites for these species. The pioneer woodland species making up residual alluvial forests often do not survive more than 60-80 years (Rood & Mahoney 1990; Décamps 1996) and thus, medium to high-magnitude floods are needed at least every 50 years for the forest renewal (Cordes and others 1997). According to Brinson's conceptual model (1990), where the frequency and magnitude of floods are inversely proportional, low-frequency high-magnitude floods affect the whole floodplain and significantly alter the landscape (eg create oxbow lakes). Extensive regeneration of riparian communities can be associated with these flooding events, as reported along the Red Deer River in Alberta, Canada following a 1 in 100-year event (Cordes and others 1997). Medium-power intermediate-frequency floods are also important for the creation of suitable sites for regeneration. For example, along the Red Deer River, Alberta it is estimated that 1 in 20-year floods are necessary to maintain historical levels of riparian regeneration; these medium-sized floods act to clear away vegetation and contribute fine sediments to create regeneration niches (Cordes and others 1997). Low-magnitude, high frequency floods do not play a significant role in terms of the creation of regeneration sites, but are important for the replenishment of underground water sources, sediment deposits and for the maintenance of the establishment sites of pioneer communities (eg removal of aggressive competitors) (Stromberg & Patten 1990).

Where the timing, intensity, frequency and (or) duration of flood disturbances are disrupted and become insufficient to maintain typical early successional woody riparian species assemblages, there will either be a gradual transformation of the floodplain woodland towards a climax hardwood community, regenerated through autogenic processes (eg competition and gap formation) (Pautou and others 1988; Amoros and others 1987a), or a complete loss of the riparian woodland community to simpler systems (eg on North American prairie rivers, poplars tend to be the main and sometimes the only tree species; Cordes and others 1997; Bradley & Smith 1986) (Figure 3).

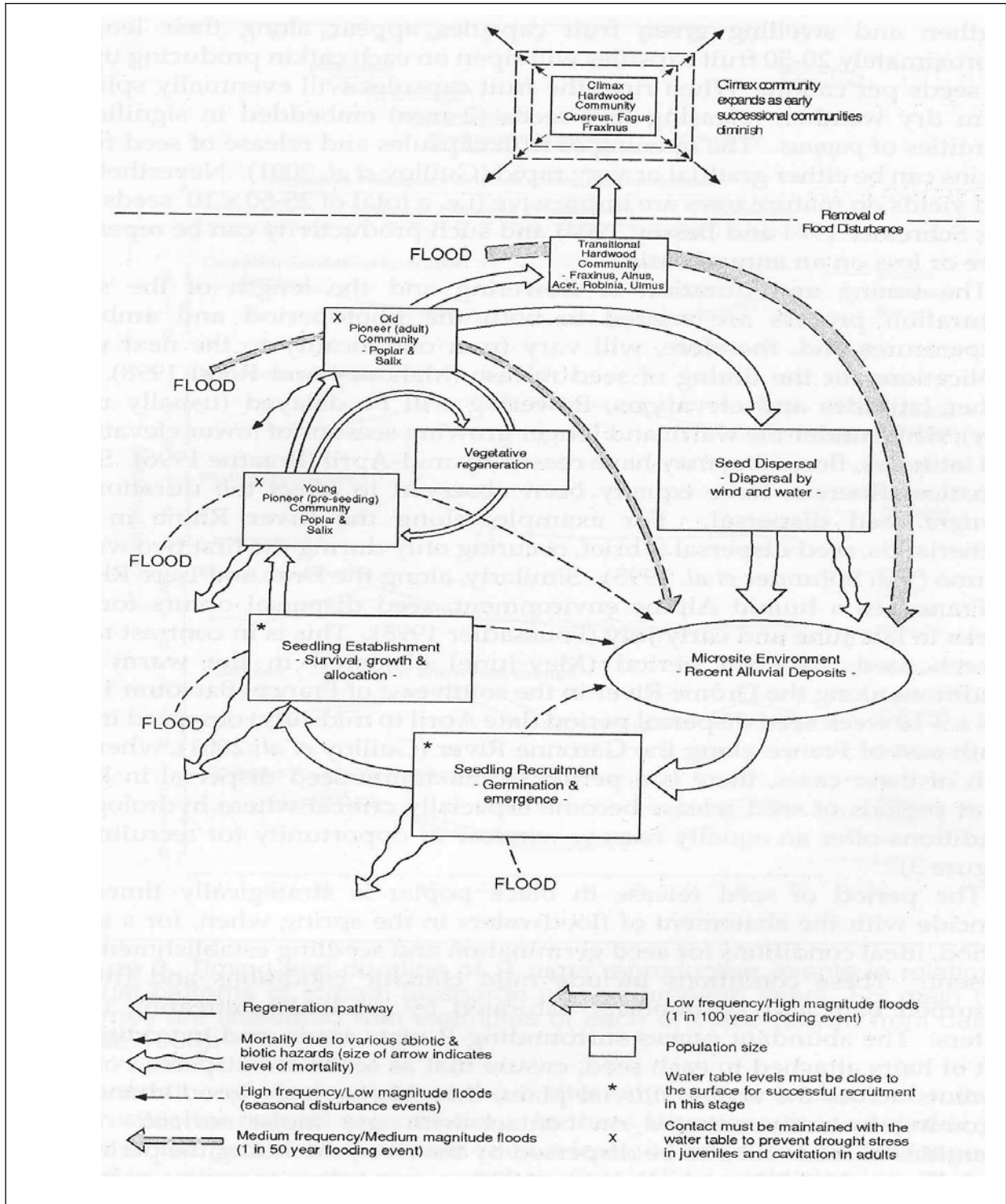


Figure 3 Conceptual model of the regeneration of Salicaceae woodland showing the importance of natural disturbance for rejuvenation (Barsoum 2001).

Décamps and Tabacchi (1994) refer to the length of the recovery phase compared with the time interval between flood disturbances as a means of gauging the influence of flood disturbance regimes on successional riparian plant communities. Their observations along the Garonne and Ardour Rivers in southern France show that where the time interval between floods is greater than the post-flood recovery phase, the vegetation is able to develop towards later successional stages. Less stable systems will be characterized by a recovery phase that is equal to, or greater than the time interval between flood disturbance events (Figure 4). Generally, the recovery period of riparian vegetation communities tends to be shorter on floodplains in semi-arid regions compared with those in temperate and humid regions. This is because rivers in semi-arid areas tend to have more friable, non-cohesive banks which act to reduce the overall turnover time of sediments and thus a greater percentage of short-lived pioneer communities is supported on this type of floodplain. For example, along the Tana River in semi-arid south-eastern Kenya, there is an estimated floodplain turnover of 150 years, compared with a floodplain turnover of 700 years in the wetter climatic conditions found along the Beatton River in British Columbia (Hughes 1994). It is important to recognize, nevertheless, the complexity of vegetation responses on floodplains especially when considering species with long life cycles; there will inevitably be lag effects between biotic and abiotic variables on a floodplain during the post-flood period (Hughes 1997).

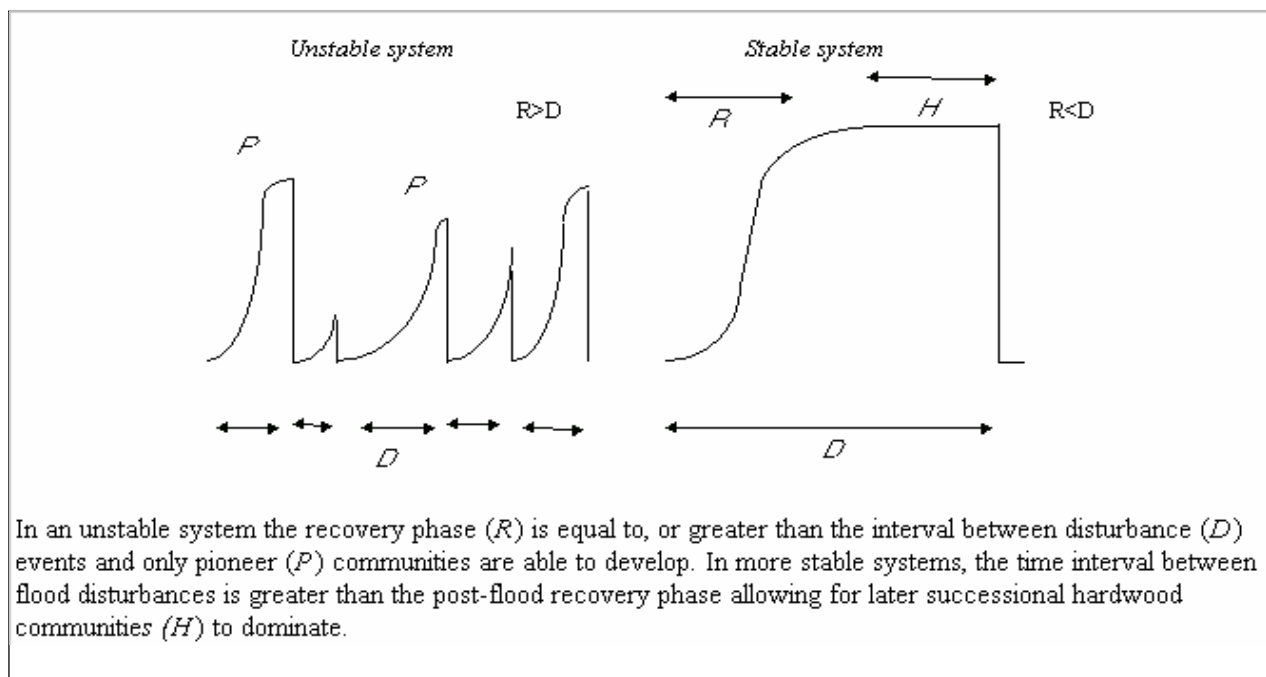


Figure 4 Flood disturbance regimes and recovery by riparian vegetation (Modified from Décamps & Tabacchi 1994).

2.3.1.3 Seasonality of flood disturbances

W6 alluvial forest vegetation species are responsive to not only the frequency and scale of floods, but also to the seasonality of floods and the shape of the flood attenuation hydrograph. For example, members of the Salicaceae family and other pioneer species are vulnerable to flood and drought stress during the establishment phase of their life cycles and thus, require specific hydrological regimes for successful dispersal and establishment of propagules.

Ideally, floods occur prior to seed release to (i) create exposed and competitor-free regeneration niches, (ii) generate and disperse vegetative fragments and (iii) recharge the water table. Field observations (Johnson 1994; Streng and others 1989; Stromberg & Patten 1992) and experimental work (Mahoney & Rood 1991; 1992; Segelquist and others 1993) emphasize the subsequent need by these pioneer species for a gradual abatement of water levels during the establishment phase. A gradually declining water table ensures continuous root contact with the water table, a 'connection' which must be maintained throughout the life cycle of these species to meet high water demands and prevent cavitation (ie the introduction of air bubbles into xylem vessels) (Mahoney & Rood 1993; Tyree and others 1994). A generalized flood attenuation hydrograph, ideal for poplar seedling establishment in southern Alberta is illustrated in Figure 5A; the relatively predictable seed dispersal patterns of regenerating Salicaceae defines a constant recruitment box in both space and time. Hydrological patterns are less predictable over time and, as illustrated (Figures 5 B-C), can lead to unsuccessful regeneration in certain years. It should be stressed that the model is a simple one and does not consider the effects of other abiotic (eg rainfall, temperature) and biotic factors (eg competition, herbivory) which might otherwise affect the survival of regenerating plants.

2.3.1.4 Floodplain topography and sediments

Rates of sedimentation and erosion will affect the proportions of colonizable microsites at given elevations (Harris 1987) and the range of bio-geomorphic features which can provide protected microsites (eg sites of aggradation downstream of debris dams) on the active alluvial plain. Moreover, differences in edaphic properties (eg sediment texture, percentage of organic material) between floodplains, or even on the same floodplain, have an important and determining role on the final composition of W6 alluvial forest vegetation which becomes established by affecting drainage rates and nutrient availability (Kalliola & Puhakka 1988; Frye & Quinn 1979; Buchholz 1981). The greater water retention capacity of finer sediments, for example, can be potentially limiting of plant growth if rates of water table decline are slow following a flooding event and water-logged conditions develop. Within the active zone, geomorphic units typically colonised by alluvial forest species include islands, intermittently flooded side channels and point bars. These geomorphic units all differ in terms of the relative proportions of fine and coarse sediments and amount of organic material present.

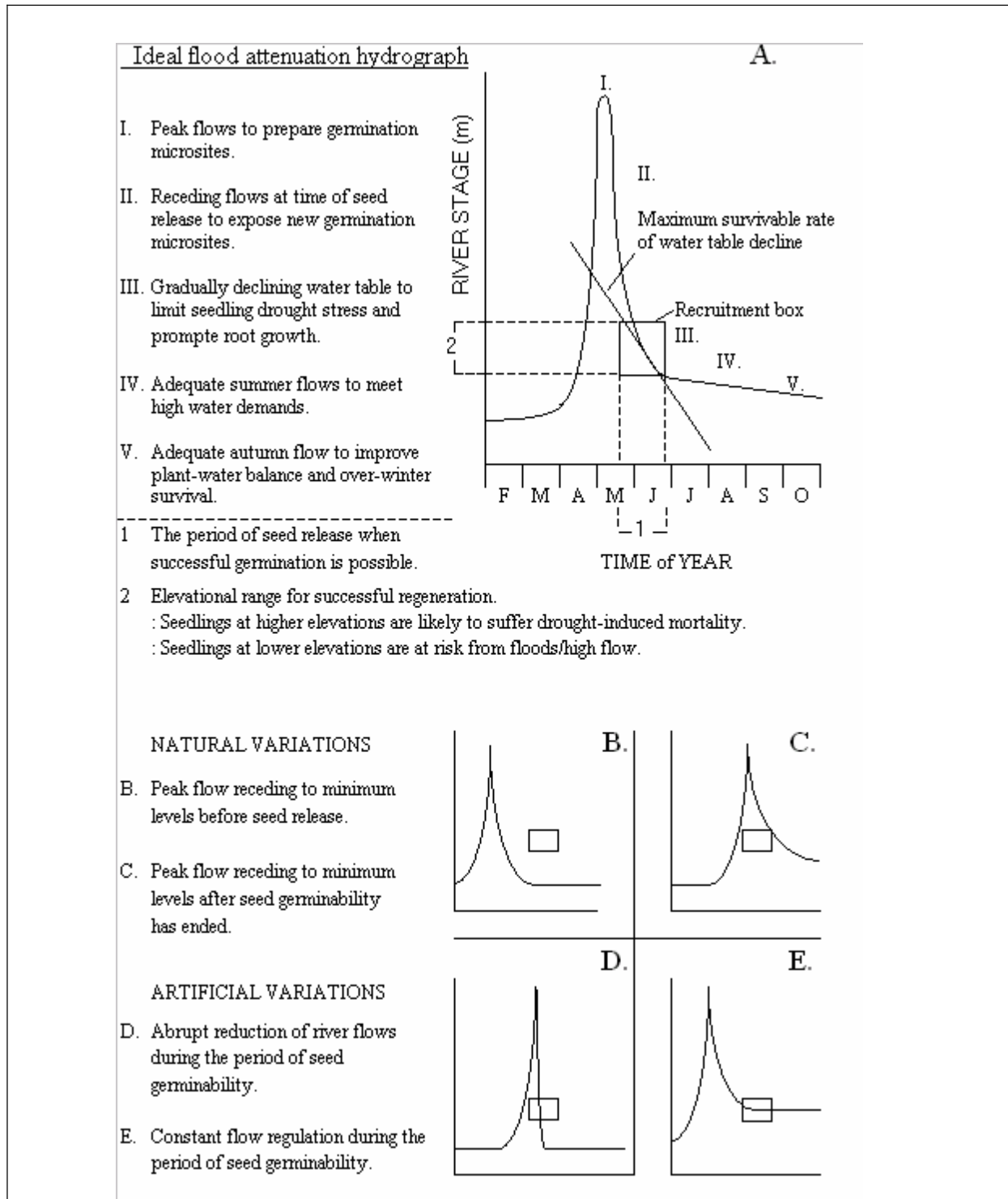


Figure 5 Generalised hydrographs: variations on stream flow and their relation to the 'recruitment box' (modified from Mahoney & Rood 1993).

2.3.1.5 The changing face of floodplains today – current threats to Alluvial Forests

The hydrological and geomorphological characteristics of river courses and floodplains in the UK have changed dramatically since the beginning of the 18th century with important ecological consequences for early successional woody riparian communities (Petts 1989). The first significant modifications to river flow involved the construction of navigation training works and flood embankments. These activities, while allowing for the reclamation of land for human settlement and for agricultural purposes, have led gradually to the channelization of the greater part of major river systems in the UK. From the 1950's, there has been an intensification of river management practices as hydroelectric development, gravel extraction and the construction of reservoirs and river diversions have become widespread (Bravard and others 1994; Roux and others 1989). The combined effect of these activities has had a profound effect on the geomorphology and hydrology of rivers and has greatly reduced the surface areas of floodplains and their associated vegetation communities.

Managed rivers today are typically characterized by several if not all of the alterations to flow and geomorphology listed below:

- (i) Altered discharge rates: Channelization and gravel extraction lead to incision which, in turn, generally contributes to faster flow and a reduction in the lateral migration of channels. Faster flow also has the effect of increasing rates of sediment deposition in some areas (e.g. on islands, gravel/sand bars and channel edges), but just as frequently, can cause serious erosion of recently established geomorphological features, thereby reducing the overall stability of in stream habitats. In the summer months, extraction of water for irrigation, or as drinking water can significantly reduce flow rates (Bravard & Peiry 1993; Peiry and others 1994).
- (ii) Disruption of 'natural' water table fluctuations and the flood attenuation hydrograph: Generally, downstream of impoundments there is an overall drop in water table levels and unnatural pulses also often result in frequent and abrupt drops, or increases in water table levels at weekly, daily, or even hourly intervals; in some cases, water table levels may remain high over extensive periods leading to anaerobic conditions. Incision of channelized rivers and water extraction can also significantly lower water table levels.
- (iii) Altered patterns and rates of sedimentation: Large quantities of sediment become trapped behind dams and weirs which has the effect of reducing the amount of suspended alluvial material carried by the river downstream. Trapped sediment is only released with surplus discharges in excessive quantities, leading to irregular fluxes of eroded material; the result is either burial of vegetation in the main channel when released or limited turnover of sediment/habitat creation when not released (Bravard & Peiry 1993).
- (iv) Altered periodicity and magnitude of flow: Discharges are generally increased downstream of dams in the winter months and early spring for the production of electricity, but significantly reduced thereafter as reservoirs are filled during the summer and autumn. Reservoirs buffer flood peaks and, therefore, remove large-scale disturbance events which are otherwise important in terms of the turnover of sediment and in the creation of freshly exposed and colonizable patches (Bravard and others 1994).

In the UK, threats to alluvial forests also include a number of biotic variables. Browsing by deer/rabbits and grazing by livestock is very common on UK floodplains and the influences

exerted by grazers/browsers on the structure and composition of alluvial forests should not be under-estimated. Coppice management has its own effects on alluvial forest structure and composition often related to significant changes to microclimatic conditions (Holscher and others 2001). The same can be said for exotic invasive species. Riparian zones commonly provide habitat and dispersal corridors for alien species (DeFarrari & Naiman 1994); physical disturbance caused by flooding, resource availability and habitat diversity in riparian zones are considered to be contributing factors explaining high rates of invasion by alien species (Hobbs & Huennke 1992; Stohlgren and others 1999; Lonsdale 1999).

2.3.2 Distribution and description of Residual Alluvial Forests in the UK.

While at one time floodplain forests covered vast tracts of land along Britain’s river systems, the pre-historic wide-spread clearance of floodplains for settlement and agriculture, has eliminated most of our natural alluvial forest (Peterken 1996). Only fragments of alluvial woodland now survive, frequently in association with drier woodland communities, or as isolated stands within herbaceous wetland vegetation. Over the past century the intensification of riparian and river management activities has seen a steep decline of even these surviving fragments (Petts 1989; Peterken & Hughes 1998).

The JNCC estimates that currently only 4,500 – 8,000 ha of residual alluvial forests remain in the UK, predominantly located in the wetter regions of the country as illustrated in Figure 6a.

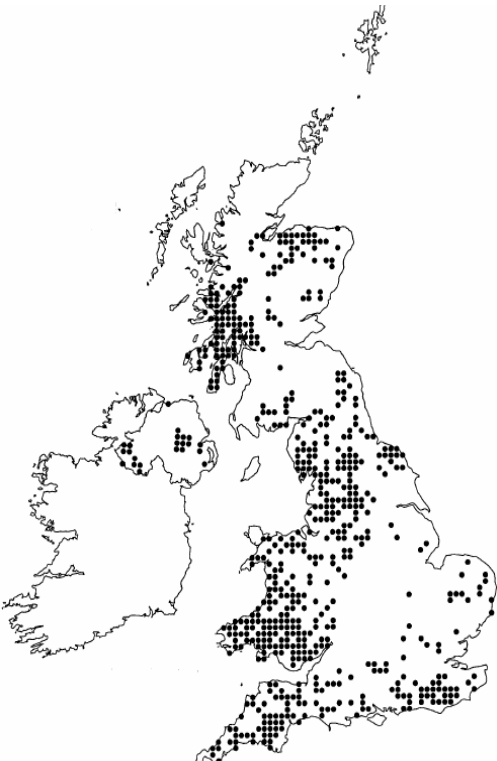


Figure 6(a) Distribution of all known stands of 91E0 residual alluvial forests. Rodwell & Dring (2001)

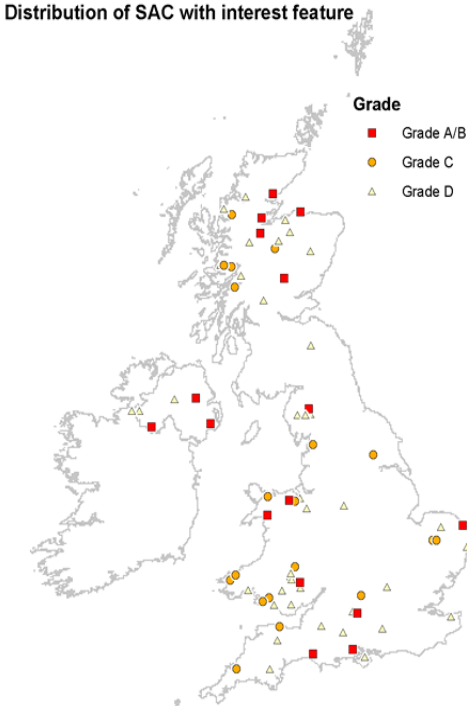


Figure 6(b) The location of SACs with 91E0 residual alluvial forests habitat *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, and Salicion albae). JNCC web site.

Residual alluvial forest has been identified as a priority habitat requiring protection in the UK and due to their rarity and value many of these alluvial woodlands have been selected as Special Areas of Conservation (SACs). Table 1 provides some details of the best sites (those graded as A/B) and Figure 6b shows the distribution of all SACs with 91E0 habitat. From Table 1 it can be seen that the most extensive areas of alluvial forest occur in The Broads and New Forest, although these are severely impacted by anthropogenic pressures such as eutrophication and overgrazing. The most natural sites, those with all the successional stages of vegetation communities from open fen to woodland, presently occur in northern Scotland.

Table 1 Summary of site characteristics of SAC sites with alluvial forest habitat graded as A or B for quality.

	Area (ha)	pH	Nutrient status	Soil texture	Geology	Landscape character
Coed y Cerrig	7.3	basic - neutral		alluvium and peat	sandstone	floodplain valley
Meirionnydd oakwoods and bat sites	191	acidic	poor		sandstone and metamorphic	dynamic floodplain
Conon Islands	55.2	neutral		alluvium mud and sand		unmodified dynamic coastal floodplain
Hollymount	8.7	neutral	rich	alluvium mud and peat		lowland floodplain
Kennet Valley Alderwoods	57	basic		alluvium and peat		lowland riparian floodplain
Llwyn	13.4	neutral	poor - rich	alluvium clay and peat	sedimentary sandstone	lowland riparian floodplain
Lower River Spey – Spey Bay	65.3	neutral - acidic	poor	mosaic of alluvial substrates		lowland riparian floodplain
Mound Alderwoods	208	basic		alluvium mud, sand and peat	sedimentary sandstone	estuarine floodplain
Rea's Wood and Farr's Bay	26	neutral	rich	alluvium sand and shingle		lowland lake shore floodplain
River Eden	59	basic - acidic	poor - rich	alluvium clay - shingle	igneous, metamorphic and sedimentary	riparian floodplain,
Shingle Islands	39.7	basic?	rich	shingle	metamorphic calc-schists	riverine shingle islands.
The Broads	762.5	basic	poor - rich	alluvium clay and peat		lowland floodplain valley
The New Forest	293	basic - neutral	poor	alluvium clay, sand and peat	sedimentary sandstone	lowland riparian floodplain
Upper Lough Erne	132	basic	rich	alluvium clay and peat	Sandstone	lowland lake shore floodplain and islands
Urquhart Bay Wood	43	basic	poor - rich	alluvium sand and shingle	metamorphic	lowland riparian floodplain and riverine islands
West Dorset Alder Woods	144	basic	poor - rich	shallow silty peats		issues

2.3.3 Vegetation classification of Residual Alluvial Forests

Floodplain woodlands are floristically diverse as they reflect the variation in site topography, hydrology, substrate, nutrient status and management. Additionally being part of a natural succession, they are subject to changes through time. It can be seen from Table 1 that alluvial woodland develops on soil of varying acidity and nutrient status. The natural vegetation community structure reflects the site conditions; various classification schemes have been devised to describe and define the different plant communities in the UK. When compiling information on the eco-hydrological requirements of floodplain woodlands from the literature, it is essential to ensure that similar vegetation communities are being compared. In recent literature from the UK the NVC system is commonly used to identify the vegetation community being studied. However, earlier papers and European studies refer to different vegetation classification systems and it is important to understand how these equate to the NVC system.

2.3.3.1 UK classification of Residual Alluvial Forests pre-dating the NVC system

Many early papers used the classification defined by Moss and others (1910) for English woodlands, which was based on dominant tree species and soil characteristics. The scheme identified three woodland series the Alder-Willow series, the Oak and Birch series, and the Beech and Ash series. The Alder-Willow thickets and carrs of the first series and the damp oak woods of the Oak and Birch series would cover residual alluvial forest stands.

McVean (1956) defined nine alder woodland communities after an extensive survey of wet woodlands in various stages of succession in Sutherland, Glen Nevis, north Wales, Norfolk and the New Forest. His scheme has been widely referred to by later authors. Table 2 illustrates how McVean placed his communities within a matrix of soil wetness and acidity, and the subsequent NVC communities in which they were assigned.

Table 2 The soil conditions associated with nine Alder communities identified by McVean (1956) and the subsequent NVC community to which they were assigned.

		Increasing water		
		—————→		
		1	2	3
Increasing bases	↓	a	W4b	W4c
		b	W6, W7b	
		c	W2, W5	W5

Another widely used classification scheme is that developed by Peterken (1993) for ancient and semi-natural woodland in Britain. He identified 12 groups of woodland stands, one of which was alder woodland (Group 7). He then sub-divided the group based on topography, water regime and base status. Table 3a illustrates his classification system and Table 3b summarises the soil properties of each sub-community based on field observations at 79 sites across the UK.

Table 3 (a) The classification of Group 7 stand types of ancient and semi-natural British alder woodland, and the subsequent NVC community to which they were assigned (Peterken 1993).

7A <i>Valley alder woodland on mineral soil</i>	
a.	Acid valley alder woods (pH <5) lack calcicole species; accumulated peat and humus; water table remains below 30cm [W6e, W7c].
b.	Valley alder woods on neutral-alkaline soils (pH > 5) [W6d, W7a & c]
7B <i>Wet valley alder woods</i>	
a.	Sump alder woods [W5a – c]
b.	Base-rich spring line alder woods
c.	Base-poor spring line alder woods [W7a & b]
7C <i>Plateau alder woods</i>	
7D <i>Slope alder woods</i> [W7c]	
7E <i>Bird cherry alder woodland</i>	
a.	Lowlands [W7c]
b.	Uplands [W7b & c]

Table 3 (b) Comparison of soil properties at 79 UK sites with Group 7 alder stands (Peterken 1993).

Peterken Stand Type	7Aa	7Ab	7B	7C	7D	7Ea	7Eb
NVC community	W6e, W7c	W6d, W7a&c	W5a-c, W7		W7c	W7c	W7b/c
Number of sites sampled	10	17	20	12	9	6	5
Median pH	3.9	6.0	6.3	5.3	5.1	5.3	5.6
Drainage Free (no impeded drainage)	0.6	0.35			0.55	0.5	
Imperfect (20 cm)	0.3	0.47	0.1	0.66	0.22	0.17	
Poor (11 – 20 cm)		0.12	0.05	0.17		0.33	
Very poor (0 - 10 cm)	0.1	0.06	0.85	0.17	0.22		1.0
Mean sediment texture class	1.1	2.4	2.1	1.7	2.2	0.7	2.8

Sediment texture class:

0 = sand or loamy sand

1 = sandy loam

2 = sandy clay loam, loam sandy clay and silty loam

3 = silt, clay loam and silty clay loam

4 = silty clay and clay

2.3.3.2 UK classification of Residual Alluvial Forests according to the NVC system

The NVC includes five woodland types considered to be typical of floodplain woodland by Brown and others (1997). The following section summarises details of the *Alnus* dominated communities W5, W6 and W7, and those most closely associated with them in natural successions from open water to drier climax woodland (W2, W8 and W10); community details are taken from Rodwell (1991a;b).

***Salix cinerea* - *Betula pubescens* – *Phragmites australis* woodland**

***Alnus glutinosa* – *Filipendula ulmaria* sub community.** These include fen carr woodlands of topogenous fen peats and floodplain mires that are largely confined to East Anglia, Cheshire and Shropshire. The community is subject to fluctuating water table levels and often develops as primary woodland after direct invasion of herbaceous fens, when accumulated litter raises the ground surface above the winter floods. The species composition is determined by the timing of the spring fall in soil water table, residual surface moisture levels and the germination requirements the pioneer shrub community. The establishment of shrubs and trees depends on the creation of bare soil patches as *Alder* and *Salix cinerea* seedlings are unable to survive even a thin covering of soil, and require high light intensities throughout the seedling establishment phase. Seedlings often become established on top of *Carex paniculata* tussocks, but are then susceptible to subsidence of the unconsolidated substrate.

Fens in the Broads are typical of these types of wet woodlands; here the water is fairly eutrophic with a pH range of 6.5 – 7.5 and dissolved calcium concentration [Ca] of 60 – 120 mg/l. When the soil surface dries out in the summer oxidation may occur, resulting in a flush of nutrients. Leaf litter turnover is enhanced during these periods and leads to the gradual development of a peaty, mull soil. In time, the W2a sub-community typically develops into *Alnus-Utica* (W6) woodland, although in less fertile sites and in stagnant water *Alnus-Carex* woodland (W7b) and *Salix-Carex* woodland (W3) are likely to develop, respectively. This habitat type is often severely degraded by human activities such as draining, peat extraction and mowing.

***Alnus glutinosa* – *Carex paniculata* woodland**

These woodlands occur on waterlogged organic soils on topogenous floodplain mires where there is a strong influence of calcareous ground water and periodic deposition of allochthonous mineral material in winter floods. They are often the pioneering woodland community after fens are invaded by *Salix cinerea* and *Alnus glutinosa*; as the stands age alder will exclude willow.

***Phragmites australis* sub-community.** Occurs on flat winter-flooded terraces beside small, slow moving rivers and as fragments of mire within agriculturally improved landscapes on mineral soils. Typically the field layer has low species diversity and it is often further impoverished due to human disturbance.

***Lysimachia vulgaris* sub-community.** Occurs as large stands on fen peat in the Broads and along the margins of sluggish rivers in the eastern lowlands. On recently colonised river terraces, conditions tend to be waterlogged throughout the year; in older stands the substrate may be sinking under the weight of maturing trees. The species within this sub-community are tolerant of tidal water-level fluctuations.

***Chrysosplenium oppositifolium* sub-community.** Not typical of alluvial soils. Tends to occur at springs and seepages in small-incised valleys.

***Alnus glutinosa* – *Urtica dioica* woodland**

These woodlands occur on substantial, active alluvial deposits along mature rivers and on remnants of undrained floodplains. The soils tend to be moist and eutrophic. There may be

marked seasonal fluctuations in water table levels, and the community can tolerate low soil-moisture levels where the substrate dries in the summer or becomes elevated due to continued flood deposits with an associated drop in water table. Fen valley alder woods also occur in open water transitions on floodplain mires where strongly enriched waters regularly flood fen peats. It can develop as secondary woodland where there is eutrophication of substrates under other kinds of wet woodland.

Typical sub-community. Typical of naturally eutrophic mineral soils created by the deposition of rich particulate matter in slacker reaches of rivers, abandoned meanders and floodplains. The ground is often submerged for several weeks in winter and hollows may remain wet throughout the summer. Fertiliser runoff and sewage effluents often add to the plentiful supply of nutrients. Also occurs on floodplain mires where peats have begun to dry out and become surface-oxidised, with a flush of nutrients.

***Salix fragilis* sub-community.** Small isolated stands of pioneer community on raw alluvium on levees of small river terraces, river bends and uncultivated floodplains, on naturally eutrophic mineral soils. Subject to anthropogenic eutrophication as described in W6a. In narrow valleys, W6a & b often form the riparian margin to upslope mixed deciduous woodland.

***Salix viminalis*/ *S. triandra* sub-community.** Typical community of managed and derelict osier beds on freshly colonised alluvium such as river islands; often-sloppy mud. Osier species dominate over alder ground flora, similar to W6a and W6b.

***Sambucus nigra* sub-community.** Drier sites than W6a-c, such as typically very fertile brown alluvial soils or alluvial gleys on old river terraces. Includes pools over peat in floodplain and basin mires removed from the influence of flooding. Although soil moisture wet enough to sustain dominance of alder in canopy, soils may dry out in summer.

***Betula pubescens* sub-community.** Heavy, base-poor, gleyed mesotrophic soils.

***Alnus glutinosa* - *Fraxinus excelsior* – *Lysimachia nemorum* woodland**

Typical of moist to very wet mineral soils in which there is no tendency for accumulation of fen peat or acidic organic matter; sites tend to be moderately base-rich and mesotrophic. Locally distributed across wetter parts of north and west Britain, but with some sites in the Weald and the New Forest. The sub-communities differ in the nature of the water supply and extent of waterlogging.

***Urtica dioica* sub-community.** Occurs on light textured alluvial soils on flat or gently sloping terraces on young river systems. Soils free draining but kept moist by high water tables or by flooding/flushing from above. Inundation water not as eutrophic as in W6 communities.

***Carex remota* sub-community.** Associated with springs or seepages lines where groundwater emerges on shedding slopes.

***Deschampsia cespitosa* sub-community.** Associated with seepages on valley sides, within other woodland types, on soils with impeded drainage.

***Fraxinus excelsior* – *Acer campestre* – *Mercurialis perennis* woodland**

Occurs on calcareous mull soils derived from calcareous parent material in warm dry lowlands of southern Britain. Frequently found in transition with other wet woodlands (W5 – W7). Soils tend to be clays or clay-loam subject to seasonal waterlogging. There are three wet sub-communities, which differ in the extent and duration of their seasonal waterlogging and are commonly found in transition with some form of alder woodland:

***Primula vulgaris* – *Glechoma hederacea* sub-community.** Occurs on gentle slopes where soils are gleyed at depth.

***Anemone nemorosa* sub-community.** Typical of surface hollows and flatter plateau where soils are seasonally gleyed to the base of the A horizon.

***Deschampsia cespitosa* sub-community.** Typical of stream sides on gentle slopes around flushes and springs where soils are waterlogged for most of the year. Often gives way to more eutrophic *Alnus-Urtica* woodland on flatter ground and *Alnus-Carex* woodland on fen peats below springs.

***Quercus robur* – *Pteridium aquilinum* – *Rubus fruticosus* woodland**

Base-poor (Typical pH 4 - 5.5) brown soils including drier alluvium and river terraces.

***Anemone nemorosa* sub-community.** Found on winter or spring waterlogged soils such as along the sides of streams or heavy clays present in hollows in undulating topography. Often found in close association with *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland around slope flushes. Occurs in transition with *Alnus-Carex* woodland where peat accumulates in small river valleys and on alluvial flats with *Alnus – Urtica* woodland.

It is worth noting that while *Alnus* communities (W5, W6 and W7) are presently the most common wet woodlands on British floodplains, pollen surveys suggest that a wider range of wet woodland forest types existed before widespread deforestation (Brown and others 1997). Across much of the lowlands and the colline region of north-west Europe, *Salix alba* is the most important early colonist of river alluvial deposits following the initial invasion by osiers. In the UK, although *Salix alba* is frequently planted it is only dominant along lowland rivers such as the Great Ouse; *Salix fragilis* is usually more abundant elsewhere (Harper and others 1997).

2.3.3.3 European vegetation classification systems of the Residual Alluvial Forest communities found in the UK

Residual alluvial forests including wet willow, alder and ash woodlands are classed as being *Alnion glutinosae-incanae* in the EU habitat Directive. This broad and complex class includes the non-alluvial woodlands occurring on flushes and in valleys, which are never flooded, but not pioneer alluvial willow woodland.

Due to our oceanic climate some British woods should be considered as being distinct alliances or sub-alliances of the European vegetation groupings, which European authors have not yet described. Klötzli (1970) divided the valley alder woods of Britain into *Osmundo-Alnetum* and *Pellio-Alnetum*. Prieditis (1997) identified all alder-dominated wetland forest

across an extensive area of Europe to be a single community, *Carici elongatae – Alnetum*. He considered the community's range to extend from the UK to Belorussia, and Norway to Austria. He identified another alluvial community called *Salicion-Albae*, which is typical of dynamic colonising sites.

Residual alluvial forests are recognised under the EU Habitats Directive as '91E0-Residual Alluvial Forests'. Under the CORINE-biotype (EC 1991) and Palaeartic classification systems (DeVilliers & DeVilliers-Terschuren 1993), 'residual alluvial forests' as recognised in the UK can be found in the following categories: 44.1 'riparian willow forests' and 44.3 'medieurop. woods' (various sub-types in this category). In the EUNIS classification they are known as G1.1 'riparian woodlands - *Salix, Alnus*' (various sub-types in this category) and G1.2 'fluvial woodlands – *Fraxinus, Alnus, Ulmus*' (several sub-types in this category). Table 4 summarises the key European classifications of alder dominated alluvial woodlands.

Table 4 Summary of key European and British definitions and classification schemes of wet and riparian woodlands.

Current name as adopted in Directive 97/62/EC	91E0 Alluvial forests with <i>Alnus glutinosa</i> and <i>Fraxinus excelsior</i> (<i>Alno-Padion Alnion incanae, Salicion Albae</i>)		
CORINE code as given in Directive 92/43/EEC	44.3 Residual alluvial forests (<i>Alnion glutinoso-incanae</i>)		
BAP Priority Habitat	Wet Woodlands		
FC Guide	8 Wet Woodlands		
Vegetation Map of Europe	U Woodlands of flood plains, estuaries and freshwater polders p.p.		
EUNIS Habitat	G1.1 Riparian woodland	G1.2 Fluvial woodland	G1.1 Riparian woodland
Palaeartic Classification (Devillers & Devillers-Terschuren 1993)	44.2?	44.13	44.3
Klotzli (1970)	<i>Osmundo-Alnetum</i>		<i>Pellio-Alnetum</i>
Prieditis (1997)	<i>Carici elongatae - Alnetum</i>	<i>Salicion Albae</i>	<i>Alno – Ulmion (Alno – Padion)</i>
NVC Community Rodwell 1991	W5 <i>Alnus glutinosa – Carex paniculata</i> woodland	W6 <i>Alnus glutinosa – Urtica dioica</i> woodland	W7 <i>Alnus glutinosa – Fraxinus excelsior-Lysimachia nemorum</i>
Nutrient Status	Deep very wet peats	Seasonally dry nutrient rich soils often coarse free draining sediments	Flushed perennially wet soils mainly humic gleys or shallow peats. Poor
Base status	Basic - Neutral	Basic - Neutral	Acidic
Substrates	Wet peats	Mineral deposits with peat	Mineral soils
Distribution	Norfolk/New Forest mires	Raw alluvial deposits/ estuaries	north and west of Britain

2.3.3.4 Evolution of Residual Alluvial Forests with shifting environmental conditions

There are a number of publications that describe the evolution of residual alluvial forests as a result of natural succession (Piegay and others 2000) and in response to anthropogenic pressures such as changes to water table levels (Marston and others 1995), altered hydroperiods (Sanchez-Perez and others 1993) and eutrophication. A number of these references refer to actual observed changes through time (Bernadzki and others 1998; Tapper 1993), while others describe expected trajectories based on surveys of alluvial forests of different ages within a region and a general understanding of the ecology of species within each community (Schnitzler 1995; Piegay and others 2000). Few of the studies investigating shifts in vegetation community composition provide comprehensive details of the soils of the sites being surveyed. Usually this has been inferred by the authors through assessments of the herbaceous vegetation communities.

The most obvious environmental gradient in floodplains is from high-slope, coarse-sediment, high-energy systems, which are often braided, to low-slope, fine substrate, low-energy floodplains, which generally have meandering and anastomosing rivers. Geomorphological complexity is the key to floodplain habitat diversity (Brown and others 1997) and alluvial woodlands lend themselves to the study of vegetational succession, occurring as they do in such a dynamic ecotone with strong ecological gradients of water level, nutrient availability and disturbance. The various types of riparian woodland are considered separately; however, in the first instance, papers concerning vegetation succession within and along rivers will be reviewed here, followed by those dealing with vegetation succession from open water transitions to woodlands in wetland areas, and finally, peat-based systems occurring around flushes and springs.

The woodland vegetation communities within a river basin are naturally diverse reflecting the patterns in valley morphology and the dynamics of fluvial metamorphosis (Piegay and others 2000). A typical floodplain should exhibit patch-scale variation ordered along a gradient from species-poor pioneer communities on frequently disturbed ground to more diverse alder-dominated woodland on older stable deposits and in abandoned channels which, in time, is invaded by ash. In poorly drained areas the disturbance-dependant alder-swamp communities will persist, however on better drained alluvial soils where flooding has become infrequent due to stabilisation of the river channel, terrestrial succession will lead to mixed broadleaf woodland, including oak, ash and sycamore. In addition to this natural diversity, anthropogenic pressures have altered the course of natural succession and vegetation development. Naturally multi-braided rivers are frequently constrained to a single channel and are often entrenched by embankments, which isolate the floodplain from the river, leading to reduced flood frequency and duration and a lowering of the water table. The disturbance-dependent vegetation community is often replaced by later successional stages.

Among the most pertinent descriptions of observed (and expected) shifts in vegetation community trajectories is Pearsall's 1938 investigation of the characteristics of wet woodland soils from sites subject to waterlogging. Figure 7 illustrates observed alluvial forest vegetation community successions (continuous lines) and expected community successions (broken lines) according to gradients in soil redox potential and pH with no expected availability of nitrates in reduced conditions (eg waterlogged soils).

In the following section, reports of the development of alluvial forest vegetation through autogenic succession are summarised. The successional phases of alluvial forest stands are related to hydrological and edaphic gradients. Willow and poplar dominate pioneer communities, and under natural conditions these pioneer soft woods are replaced by hardwood species such as oak, elm and ash in less than 100 years (Schnitzler 1995).

Marston and others (1995) studied the River Ain in south east France where increased horizontal stability of the river has led to incision of the channel and decreased floodplain disturbance, a decline in sedimentation rates and a drop in water table levels by 1m. The development of high-forest vegetation (elm, ash and alder) in the floodplain created a negative feedback loop as the bank-side vegetation restricted channel migration and over-bank flows. The alluvial forest gradually expanded into the abandoned channels and on poorly drained soils, the shrub-swamp communities of willow and herbaceous plants were replaced by mixed forests comprising ash, alder, black poplar and oak. On well-drained soils, ash and oak declined in favour of mesophytic stands of black poplar.

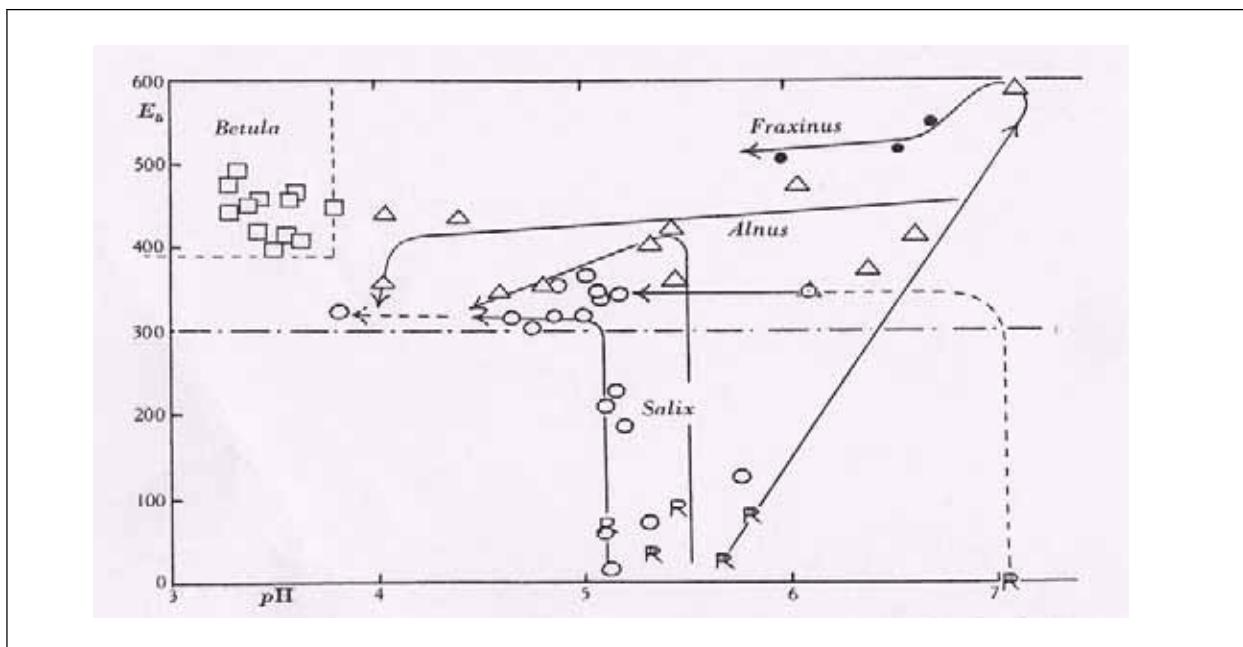


Figure 7 Observed and expected alluvial forest community succession along gradients of pH and soil redox potential (Pearsall 1938).

The symbols used are (1) *Salix cinerea* series on fen peat – circles, (2) Mixed willow and alder on alluvial silt – triangles, (3) *Betula* > 60% fen peat – squares and (4) reed-swamp – R shaded loops indicating *Alnus* series

Willow colonises areas of fen habitat where accumulated organic matter reduces the vertical fluctuations of the water table creating less reduced conditions favourable for seed germination (Southall and others 2003a). On impoverished tin mining spoil in Cornwall, there was a clear relationship between the age and structure of willows and the ground flora of W1 pioneer woodland. The ground flora under invading willow influenced the composition and structure of the field layer of the future woodland. Willows are capable of growing in waterlogged soils due to an internal oxygenation system, which allows for root respiration and results in oxygen leakage at the root surface.

Many wet woodlands develop after the abandonment of mowing or grazing on traditional wet meadows. The seed bank of later successional stages of alluvial forests often contains seeds of many herbaceous species that have been lost from the vegetation community. Seedling densities tend to decrease exponentially through successional stages and rare or endangered species are scarcely ever found in the seed bank. The seed rain of later successional stages reflects above ground vegetation, which is dominated by invasive species such as, nettle, alder, birch and willow. The restoration of earlier stages from the seed bank is unlikely to succeed (Jensen 1998). Alder can quickly invade eutrophic swamps; rates of 100 – 150 m in 15 years were observed by Cluzeau (1992) in the Rhine. In natural successions from open water to high forest it is possible for there to be cyclical succession, with alternations between an open carr fen and alder fen woodland, which can be observed in the pollen and macrofossil record (Pokorny and others 2000).

The mechanisms by which *Alnus glutinosa* is replaced by *Fraxinus excelsior* during primary succession have been studied by Tapper (1993; 1996) on a small, uninhabited and ungrazed island. Alder was often the most abundant tree species at the coast or along the riparian margin, but was replaced by ash inland, or at higher elevations further away from flood disturbance. Alder did not regenerate under the forest canopy. No seedlings survived longer than 3 years, even after the experimental thinning of the canopy and removal of the field layer. Most seedlings died within the first year. In contrast survival of ash was 35% after 10 years. Annual height increments of juvenile ash were small under a closed canopy (<8mm y⁻¹), but growth of the juveniles increased rapidly when a fallen tree created a gap. Ash colonised canopy gaps created by dead alders; where no gaps were present some ash managed to compete for light resources with mature alder. Over the 10 year survey period, 25% of the alders that were initially present died off. Alder mortality was preceded by a reduction in crown size and was significantly associated with over-topping by ash. Ash expands horizontally above alder crowns when ash heights exceed those of mature alder.

Where flooding frequency is insufficient enough to remove an extensive herb layer, slow-growing herb species will tend to be out-competed, as would the seedlings of tree species. Where flooding is removed from the system, regeneration of *Fraxinus* occurs where shading in summer prevents the formation of a dense herb cover (Siebel & Blom 1998).

2.3.4 Eco-hydrological requirements of key component species of Residual Alluvial Forests

Information describing the ecohydrological requirements of a selection species commonly found in W5, W6 and W7 alluvial forests was collated following a thorough literature review (primarily of peer-reviewed scientific articles) and a synthesis of this information is outlined below for each of the selected species. Literature searches uncovered many relevant studies such that only a partial review was possible here. Thus, the species-specific ecohydrology information that is provided in this document should not be regarded as a comprehensive review of all that is known on the species at present in this respect. The information provided serves rather to indicate the sort of information that might be available for each species; the ways in which this information might be used is assessed in Task 2.

Additional species could have been reviewed for each alluvial forest type, but the species lists initially proposed in the tender document (Table 5) were considered sufficient in this first scoping study to cover a range of dominant over-storey and understorey species that are known: (i) to differ widely in their tolerance to flooding and drought (eg *Salix* vs. *Crataegus*),

(ii) to be well-studied (eg *Urtica*, *Phragmites*, *Iris*, *Salix*), (iii) to be transient or more ‘long-term’ members of the alluvial forest community (eg *Urtica* vs. *Carex*), (iv) to differ in terms of their success and mode of regeneration (eg presence/absence of a seed bank; capable; ability to regenerate by asexual strategies), (v) to have very similar ecohydrological requirements, but subtle differences that allow for co-existence (eg *Carex* spp., *Salix* spp.) and (vi) to differ in their occurrence along disturbance and successional gradients (eg *Salix* vs. *Alnus* vs. *Fraxinus*)

Table 5 List of species selected for literature review.

W5	<i>Alnus glutinosa</i> , <i>Betula pubescens</i> , <i>Carex paniculata</i> , <i>Salix cinerea</i> , <i>Carex acutiformis</i> , <i>Phragmites australis</i> , <i>Dryopteris dilatata</i> , <i>Angelica sylvestris</i> , <i>Filipendula ulmaria</i> , <i>Urtica dioica</i> , <i>Iris pseudacorus</i>
W6	<i>Alnus glutinosa</i> , <i>Betula pubescens</i> , <i>Crataegus monogyna</i> , <i>Salix caprea</i> , <i>S. cinerea</i> , <i>S. fragilis</i> , <i>S. purpurea</i> , <i>S. triandra</i> , <i>S. viminalis</i> , <i>Sambucus nigra</i> , <i>Urtica dioica</i>
W7	<i>Acer pseudoplatanus</i> , <i>Alnus glutinosa</i> , <i>Betula pubescens</i> , <i>Fraxinus excelsior</i> , <i>Salix caprea</i> , <i>S. cinerea</i> , <i>Corylus avellana</i> , <i>Crataegus monogyna</i>

2.3.4.1 Nutrition

The potential to buffer instream habitats from diffuse pollution has led to a considerable body of work, which attempts to determine the effect of changing water regimes on the biochemical processes within floodplain woodlands. The transfer and storage of materials in floodplains are largely under the control of flood duration; flood frequency and magnitude collectively create a mosaic of geomorphic surfaces that influence the spatial pattern and successional development of the riparian vegetation.

The mode of nitrogen delivery affects alluvial forest ecosystem functioning. Leaf litter is the primary source of nitrogen in small headwater streams. Alder litter has a high N content (1.6 – 2.2 % dry mass) and can supply 8 - 14 kg N ha⁻¹ y⁻¹ (Chauvet 1987; Busse & Gunkel 2002). In floodplains of large rivers the main input of nitrogen is via the supply of sediments and organic matter in surface flow, mobilised from upstream catchments and deposited during flooding. As a result, floodplain soils are very fertile and possess a high capacity for nutrient cycling. The surface water of a German Alder-Carex fen was estimated to receive 24.6 kg N ha⁻¹ y⁻¹ from litter fall and sediment mineralization. The nitrogen cycle is driven by processes that occur on or at the surface of particulate material. In flooded forests the high contact duration between water and sediment increases the biological use and total amount of nitrogen processed.

Floods and droughts are natural events that affect the nitrogen cycling pathways with important implications for floodplain productivity. Flood duration influences the biogeochemical processes that are sensitive to the oxidation-reduction status of the soil. Nitrification requires oxygen and can only occur in aerated soils. Under permanently anaerobic conditions the organic nitrogen mineralization process results in the accumulation of NH₄. Despite the presence of a large potential nitrate reducing bacterial population in the soil, floodplain soils often show no significant denitrification activity (Busse & Gunkel 2002). In fine-textured floodplain soils, annual denitrification rates have been measured at ~50% of the nitrogen deposited during floods (Pinay and others 2002). Waterlogged soil quickly become nitrate depleted when nitrification is inhibited by the anaerobic conditions. The soil nitrogen capital can therefore accumulate in conditions of prolonged flooding. However, higher denitrification rates of 14 kg N ha⁻¹ y⁻¹ (Mogge 1995) have been reported from alder fens with lower water tables where aerobic soil conditions

favour mineralization. Natural fluctuations in the water table is a key driver of soil fertility, the annual flood cycle creates alternate aerobic and anaerobic conditions, enhancing organic matter decomposition and nitrogen loss. Flood regime also affects nutrient cycling by influencing soil structure and texture through the removal and deposition of sediments. Sediment texture influences denitrification rates; eg fine sediments such as clays provide the greatest surface area and microbial habitat, and measured denitrification rates are most rapid in fine textured sediments (<65% silt and clay), (Pinay and others 2002). Alluvial sediments contain a large proportion of the ecosystem's phosphorus capital but only a small proportion is available to plants. Phosphates are not easily available in calcareous waters because of their low solubility and adsorption to soil colloids. In regularly flooded sites however plants receive soluble phosphate, which is available for plant uptake in the floodwater and via the temporary release of adsorbed phosphates through the reduction of FeIII to Fe II. The measured soluble phosphorus in a forest soil that became isolated from flooding behind a dyke was 50% less than the soil of island forests receiving regular inputs from floodwaters (Tremolières and others 1999).

Flooding has been shown to contribute a significant proportion of the annual phosphorous and nitrogen budget to an alluvial forest ecosystem. However, for most other nutrients (K, Mg, Ca and S) the rate of mineralization of soil stocks exceeds the input from sedimentation or atmospheric deposition. After 30 years without flooding, the nutrient content of alluvial soils is close to that of flooded sites, except for nitrogen. Complex hardwood forests are efficient at taking up bioavailable nutrients resulting in nutrient poor ground water under alluvial hardwood forests (Sanchez-Perez and others 1993).

Gusewell & Koerselman (2002) reviewed how nitrogen and phosphorus concentrations and the N: P ratio of European non-forested wetland plants varied among species and sites, and how they were related to nutrient availability and limitation. The field data revealed that N concentration varied more among species than between sites, while the opposite tended to be the case for N:P ratios. Both concentrations and ratios were poorly correlated to various measures of nutrient availability in the soil, and other limiting and stress factors were shown to influence N:P ratios.

***Acer pseudoplatanus* L.: W7**

This species shows best growth in fertile soils and is probably to some extent a nitrophilous species. Soils where the species occur are almost invariably ones where humus decay is rapid and nitrification free (Jones 1944).

***Alnus glutinosa* L: W5, W6, W7**

Drainage of alder fen peats resulted in a 50% loss of the nitrogen content of the top 10cm of the soil, a decline in soil pH due to H⁺ production related to nitrogen mineralization, and a reduction in the concentrations of Ca and Mg (Kazda 1995). In addition to changes brought about through desiccation, eutrophication has also been demonstrated to significantly inhibit ectomycorrhizal development in alder, with implications for nutrient uptake (Baar and others 2002). Eutrophied forests had lower soil water pH and reduced concentrations of Mg and Fe compared to an undisturbed forest.

The accumulation of peat within an alder floodplain forest is highly dependent on the flood regime and nitrogen status of the inundation water. Dissimilation of nitrogen by denitrification

produces oxygen, which can sustain microbial degradation of organic matter via the Krebs cycle under anaerobic conditions. However, where the annual N loss from denitrification is less than the nitrogen input from litter fall, organic matter accumulates in soil (Pinay and others 1993). Similarly, Dilly and others (1999) report that peat accumulated in an *Alnus glutinosa* forest in the permanently wet soil adjacent to the shore of a eutrophic lake in Germany. However, they noted that in the intermittently wet soils, the eutrophic lake water intensified the microbial transformations, resulting in humus degradation within the histosols. In contrast, further upslope the acidic runoff reduced the carbon and nitrogen cycling within the soil.

Agricultural run-off typically leads to increases in nitrate concentrations in the alluvial sediments of floodplain woodlands. Eutrophication of naturally sulphate-rich ground water has been shown to cause chlorosis in alder-carr vegetation due to iron deficiency. This is because nitrate is an energetically more favourable electron acceptor in anaerobic sediments than iron and sulphate, so that high nitrate concentrations function as a redox buffer preventing the reduction of oxidised iron and sulphur. Low sulphate, in turn, limits the mobilisation of phosphate from iron-phosphate complexes. The result is an inability for alder carr to take up phosphate and iron, resulting in mineral deficiency (Lucassen and others 2004).

Alnus improves the soil condition for other species, thereby facilitating forest succession on alluvial floodplains. In salt affected floodplains in Alaska, salt crusts formed on the early successional mineral soils due to low rainfall and high potential evaporation (Yarie 1993; Yarie and others 1993). The successional development from the pioneer willow vegetation to an intermediate poplar-alder stage was slow due to the high cation content of the soil. The alder augmented the physical, chemical and biological soil environment through the inclusion of N-rich leaf litter, resulting in the disappearance of the salt crusts and a reduction of the soil mineral salt content in the later successional stages.

In his review of the literature relating to the habitats and successional trends of the alder dominated wetland forests of the Baltic regions, Predities (1997) reports that the range of values for soil pH, C/N ratio and humus content are so considerable that these factors cannot be reliably used to predict vegetation communities. Table 6 summarises the edaphic conditions of floodplain alder swamps from oligotrophic and eutrophic sites in the Baltic region.

Table 6 Summary of edaphic conditions characteristic of floodplain alder swamps.

	<i>Circaeo – Alnetum</i>	<i>Carici elongatae – Alnetum</i>
	Meso-trophic/eutrophic sites	Oligotrophic sites
Humus content	29 – 94	29 – 88; 86 – 90
C/N ratio	12 - 17	16 – 24
PH	5.5 – 7.6	4 – 6.5 [3.0- oligotrophic site]

***Angelica sylvestris* L. W5**

***Betula pubescens* L. W5, W6, W7**

Optimum proportions for mineral nutrients needed for maximum growth were observed to be 100 N: 65 K: 13 P: 7 Ca: 8.5 Mg (Ingestad 1971). The total concentration of the solution had

an optimum range of 400 - 800 $\mu\text{S cm}^{-1}$ conductivity, corresponding to 55 - 110 mg l^{-1} of nitrogen, although the concentration had only a small effect on growth when the optimal proportions of nutrients were present (Ingestad 1970). Studies using radioactive isotopes have shown that phosphate was extracted from the first 10 cm of a freely draining brown podzolic soil, with less than 1% coming from a depth of below 50 cm (Harrison and others 1988). Birch had a higher demand for phosphorus than spruce, but both species had similar proportions of Ca-45 and Rb-86 (an analogue of potassium) in their foliage after application of the radioactive isotopes to the forest floor (Brandtberg and others 2004).

Birch is widely considered to be a 'soil improver' giving rise to deacidified soils (Gardiner 1968). Miles (1988) recorded a change from a mor to a mull humus type under birch stands, increases in pH, exchangeable calcium and total phosphorous, increased rates of cellulose decomposition and nitrogen mineralization, and a decrease in C/N, C/P and C/K quotients from the critically high levels that were present in moorland soils. There was also a tendency for organic material to be incorporated into the bleached horizon of podzols.

***Carex acutiformis* L. : W5**

Where the flood regime or water table depth is altered through river management, intensive peat mineralization can deplete the soil N status of Alder fens. This can lead to a loss of typical fen species such as *Carex acutiformis* and a succession towards other woodland communities, as reported in the lower Rhine, Germany (Kazda 1995) and the Netherlands (Baar and others 2002).

Photosynthetic rates within a dense stand of *Carex acutiformis* were only 7% less than the theoretical maximum (Schieving and others 1992). *Carex acutiformis* could achieve this high photosynthetic capacity due to the high nitrogen content of the stand. A relatively high minimum leaf N content is necessary to maintain the physiological function of the shaded basal parts of the leaves within dense stands.

C. acutiformis can adequately meet ion demands under oligo- and mesotrophic conditions through efficient metabolic uptake processes. Under eutrophic and saline conditions, *Carex* species including *C. acutiformis* are capable of regulating ion absorption through the exclusion of soil ballast ions such as Na^+ , Ca^{2+} and heavy metals, which prevent the accumulation of toxic concentrations of nutrients (Choo & Albert 1999).

C. acutiformis consistently grew best in pot experiments comparing the response of species from mesotrophic and eutrophic fens to differing nutrient supply (Aerts and others 1992, Perez-Corona & Verhoeven 1996; 1999). *Carex acutiformis* had greatest biomass in soils irrespective of N supply or soil P status. The success of the smaller *Carex* species (*C. lasiocarpa* P-limited sites and *C. diandra* N-limited sites) in nutrient poor sites was not due to higher relative growth rate, biomass production or nutrient uptake. Other factors such as interstitial water chemistry, resource allocation, clonal reproduction, and faster seed germination or seedling establishment must confer a competitive advantage and determine the field distribution of fen carr species.

***Carex paniculata* L.: W5**

***Corylus avellana* L.: W7**

***Crataegus monogyna* L.: W6, W7**

***Dryopteris dilatata* L.: W5**

***Fraxinus excelsior* L.: W7**

Ash prefers fertile soils and this is reflected by the high nutrient content of its leaves and rapid leaf litter decay rates; eg leaves shed in autumn are mostly completely decayed by the following June (Wardle 1961).

The resorption of nutrients (N, P, K, Ca and Mg) from ash foliage to perennial organs before abscission was similar between flooded and unflooded forests on the upper Rhine, despite the soils having very different levels of available phosphorus. This may be due to the improved conditions for fungal mycorrhiza at the unflooded site, which compensated for the loss of soluble phosphate inputs from flooding. Ash is known to have a high potassium requirement and potassium resorption in the unflooded forest was greater than at the flooded site (Tremolières and others 1999).

***Iris pseudacorus* L.: W5**

This species has a high nitrogen requirement (Ellenberg 1979). It tolerates and can absorb heavy metals (Piccardi & Clauser 1983).

Mean mineral content (K, Na, Ca, Mg, Fe, C, N, P) of roots, rhizome, and shoots of this species is given by Ho (1979a, b), while leaf concentrations (Na, K, Ca, Mg, Fe, Mn, Cu, Zn, P, N) in late July-early August are given by Sutherland (1990) for a range of habitats in Britain.

***Phragmites australis* L.: W5**

***Salix caprea* L.: W6, W7**

***Salix cinerea*: W5, W6, W7**

***Salix fragilis*: W6**

***Salix purpurea*: W6**

***Salix triandra*: W6**

***Salix viminalis*: W6**

***Sambucus nigra* L.: W6**

S. nigra is a species typical of disturbed, base-, nitrogen- and phosphate-rich soils with high levels of available P, K and N. At different locations on the Tyne floodplain, *S. nigra* derived nutrition from periodic flooding episodes (Table 7). Tolerant of high N loads and occasional flooding by brackish water, this species has high foliar nutrient contents and exhibits extremely rapid litter decomposition (ie at rates similar to that of *Urtica dioica*) (Atkinson & Atkinson 2002).

Table 7 Summary of edaphic conditions characteristic of *S. nigra* dominated wet woodlands.

Site	Habitat	pH fresh soil	Loss on ignition (%)	K ($\mu\text{g/g}^{-1}$)	P ($\mu\text{g/g}^{-1}$)	N ($\mu\text{g/g}^{-1}$)
Mean	11 English sites	6.9	9.6	310.9	43.0	118.1
<i>SD</i>		1.4	5.0	229.9	56.1	97.3
3	Sandy flood-plain	7.6	1.2	24.0	nd	20.0
4	Sandy flood-plain	7.8	4.0	53.5	7.1	46.8
5	Stabilised flood-plain	7.7	7.5	34.8	14.9	124.8

S. nigra was resistant to severe pollution from a phosphate fertiliser factory. Soil pH was raised from 6.5-7.5 to 8.0-9.0, soil fluoride increased to 200 p.p.m. above normal levels, and the soil sodium content was more than 500 mg per 100 g soil (Heinrich & Schaller 1987).

Urtica dioica L.: W5, W6

The nutrient requirements of the species are not clear. One study suggests a frequent association with soils that have a high nitrate content, resulting in increasingly improved growth, although ammonium is toxic (Olsen 1921). Another study reports good growth of *Urtica* in sediment with low nitrate content; eg sand and gravel (Bates 1933).

Urtica is typical of less acid soils and grows best with a nitrate source, reflecting its preference for the aerobic conditions of well drained soils Falkengrengrerup (1995). However, *Urtica* is tolerant of acid soil conditions and required management to control its spread during the restoration of lowland heath vegetation on acidified arable soils Dunsford and others (1998).

2.3.4.2 Regeneration & seedling establishment

Differences or similarities among alluvial forest plant species in their requirements for successful germination and establishment has important implications for the maintenance of species diversity. On the one hand, under the assumption that community composition is at equilibrium (Tilman 1982), species diversity may be maintained if regeneration requirements vary among species such that each species is either a better competitor in, or more tolerant of, a distinct set of micro-environmental conditions within a heterogeneous habitat (Grubb 1977). Alternatively, similar requirements for regeneration may be shared by many species within a given habitat, with diversity maintained by stochasticity of dispersal and colonization events (and/or disturbances) and with local community composition in a continuous state of flux, or non-equilibrium (Chesson & Case 1986; Van der Maarel, & Sykes 1993). Both of these 'mechanisms' may be operating at the same time in alluvial forests and need to be considered when seeking to understand both how species diversity is maintained and factors that contribute towards the local distributions of co-occurring species.

Acer pseudoplatanus L.: W7

A. pseudoplatanus seedlings become established on bare ground in open sites (Williams & Buxton 1989) on a wide range of soil types, although usually it does not regenerate on podsols, or on heavy clay where gleying comes close to the soil surface, resulting frequently in root rot. Regeneration may be profuse on shallow rendzinas on solid chalk, though subsequent growth is poor; on the other hand, on rendzinas over chalk rubble growth can be excellent (Jones 1944). Seedlings (24 weeks +) have significantly lower root:shoot ratios and a greater proportion of dry weight in leaves in 16% daylight compared with 66% daylight;

shoot growth rates are also significantly faster in 66% daylight conditions. Fast and monopodial growth of shoots is considered to be a shade-avoidance mechanism, allowing seedlings to out-compete herbaceous plants. Common maximum height of trees is 15-20 m (Williams & Buxton 1989).

***Alnus glutinosa* L.: W5, W6, W7**

Seedling establishment is slow on raw peat, but abundant in sphagnum fens (optimal growth where the water table is 10-30 cm below the surface), although growth slows in the second and third growing seasons, possibly due to excessively damp soil-moisture conditions and a lack of phosphate (McVean 1955).

***Angelica sylvestris* L.: W5**

***Betula pubescens* L.: W5, W6, W7**

Flowering in birch usually starts at 5-10 years and seed production can best be described as irregular rather than continuous; it is affected by spring air temperatures, cold springs leading to massive loss of male catkins (Pichugina 1972; Gimingham 1984). Seeds are short lived and must quickly colonise suitable open areas free even of low-growing vegetation before seeds lose viability (Granström & Fries 1985; Hill & Stevens 1981). Germination is common on cushions of Sphagnum, but seedling establishment is rare at these microsites (Miles & Kinnaird 1979a). In southern England, germination in the field begins in March and peaks in April, whilst in the Scottish Highlands it begins in April and peaks in June (Miles & Kinnaird 1979a). A light requirement for germination (eg maximal germination observed with a 20-h photoperiod at 15⁰C) can be overcome by scarification of the pericarp, or reduced by aqueous leaching. It can also be overcome by a period of chilling at 5⁰C in damp conditions (Black & Wareing 1954).

Seedlings commonly suffer mortalities of 80-90% during their first growing season; they are susceptible to drought, damping off in wet sites with low irradiance, or frost heaving (Miles & Kinnaird 1979a; Vaartaja 1962). Mean soil temperatures should be approximately 12⁰C or higher for effective nitrogen uptake and rapid growth of seedlings during the first winter (Karlsson & Weih 2001). The root systems of seedlings are, however, very susceptible to drying as they tend to remain in the top 10 cm of the soil, even where well-watered. A mortality rate of 47% was obtained when subjecting *B. pendula* seedlings to a soil water potential of -1.6 bars for seven days (Humphries and others 1982).

83% of the variation in *B. pendula* seedling weight was found to be predictable from soil chemical variables and particularly the phosphate content (Helliwell 1974). Enriching soils with P, K and N increased the numbers and first year growth of *B. pubescens* seedlings, while liming resulted in increased seedling mortality and poor growth (Kaunisto, 1981). Seedlings grown under conditions of reduced nitrogen supply continued to grow slowly for at least 6 weeks compared with the control, but did not form lateral buds and had a chlorophyll deficiency (Horgan & Wareing 1980).

Vegetative reproduction by sprouting from the base occurs in response to damage and results from the presence of basal buds, usually found underground (Kauppi and others 1987).

***Carex acutiformis*: W5**

***Carex paniculata*: W5**

***Corylus avellana*: W7**

***Crataegus monogyna* Jacq.: W6, W7**

Seedlings of this species become established on bare ground in open sites. Seedlings (24 weeks +) have significantly lower root:shoot ratios and a greater proportion of dry weight in leaves in 16% daylight compared with 66% daylight; shoot growth rates are also significantly faster in 66% daylight conditions. Fast and monopodial growth of shoots is considered to be a shade-avoidance mechanism, allowing seedlings to out-compete herbaceous plants. Common maximum height of trees is 5-8 m (Williams & Buxton 1989).

***Dryopetris dilatata*: W5**

***Filipendula ulmaria*: W5**

***Fraxinus excelsior* L.: W7**

Regular fruit-bearing in ash usually begins at 30-40 years (Wardle 1961). This species is a prolific seed-former, a single tree producing about 100,000 seeds every second year (Rohmeder 1949), although there may be longer gaps between masting years. Seedlings will become established wherever the field layer is reduced in density (whether by overhead shade, dryness, waterlogging or disturbance), but late frost is a hazard in open habitats (eg the opening buds of seedlings were observed to be killed by -3°C [for 17.5 hours] and instantly at -10°C) (Wardle 1961).

Seedlings need only a small depth of well-drained soil on which to become established; subsequent growth will depend on a decline in water table levels (Kassas 1951). Seedlings have a high degree of tolerance to shading cast by deciduous trees, but at the same time they do not tolerate shading by their own species or vernal field layer plants such as *Mercurialis perennis* (Wardle 1961; Boyd 1992). Where there is shade overhead or from intra- and inter-specific competitors in the field layer, seedling growth will be suppressed until a gap opens up in the canopy. Most seedling growth under canopy will be in the spring and early summer. Suppressed seedlings may not progress beyond the trifoliate stage for many years (Wardle 1961).

***Iris pseudacorus* L.: W5**

This species produces an average of 6 seed-yielding pods per plant and the mean number of seeds per capsule will vary (eg 30-50) (Sutherland 1990). The hard-coated seeds of this species are released in the autumn. Dispersed by water, the seeds can float for 7 months and will remain viable even if shallowly buried for sometime (Coops & Vandervelde 1995). It has been estimated that 20% of seeds shed in October germinate in February-June the next year; 20% more germinate in the following spring (Dymes 1920).

Germination of *I. pseudacorus* is dependent upon temperature; ie germination is 5% at 20°C , 22% at 25°C and 52% at 30°C , with no germination below 15°C (Sutherland 1990).

Germination will also not occur in saturated or flooded conditions (ie water level at surface, or

5 cm above sediment surface for 6 weeks in fine-grained sand); rather, it is restricted to exposed soil conditions. Following germination, seedlings require prolonged periods of exposure for rapid growth and establishment. Submergence (water level 5 cm above sediment surface) for a period of 6 weeks did not lead to seedling mortality, but was observed to significantly slow the leaf growth of 1 week-old seedlings. Recovery, however, was rapid with growth rates of submerged seedlings rapidly equalling non-submerged seedling growth rates once flooded conditions were removed (Coops & Vandervelde 1995). Seedlings are rare in the field in most habitats, with mortality of seedlings mainly occurring in the first two months. Although between 28% and 72% of seedlings survive the first year, only 3.6% of seedlings grow to a size at which the clone becomes fragmented (Falińska 1986).

During early seedling development, there is a high proportion of root relative to shoot and almost all seed reserves are used in producing a considerable root system (Whitehead 1971).

***Phragmites australis* L. : W5**

The plumed seed of *P. australis* are released in massive quantities in the winter and are borne by the air and/or water (floating periods of 2-3 days). Best conditions for germination are damp, exposed sediment (water level just below sediment surface); percentage germination is significantly reduced in saturated or flooded conditions (ie water level at surface, or 5 cm above sediment surface for 6 weeks in a fine-grained sand). Best leaf growth of 1 week-old seedlings was observed on drained substrates (water level just below sediment surface) for 6 weeks, compared with 5 weeks drained + 1 week flooded (water level 10 cm above the water surface), 5 weeks flooded + 1 week drained, or 6 weeks flooded. Under submerged conditions seedling growth stopped and re-started after drainage, resulting in significantly lower biomass for seedlings exposed to flooding compared with those in drained conditions. These results suggest that while seedlings can survive floods, there is a need for prolonged periods of substrate exposure for rapid growth to improve the chances of successful establishment (Coops & Van der Velde 1995). Comparable results have been reported in various studies demonstrating the range of water level or soil-moisture conditions required for successful germination of *P. australis* (Van der Toorn 1972; Haslam 1973).

In young, three month-old plants, total submergence for up to 17 days was responsible for severely restricted the photochemical efficiency of leaves and no recovery was observed following re-exposure to air. The effects of shorter periods of total submergence, or only partial submergence, however, were found to be reversible (Mauchamp & Methy 2004). Armstrong and others (1999) reported that any degree of complete submergence (40 - 120 mm above sediment surface) of young seedling shoots of *P. australis* (height of 20-30 mm) in a sandy substrate greatly reduced (by 75-100%) the chances of their becoming emergent. Seedling leaves that became covered in epiphytic algae (this was especially frequent in P-enriched water) lost their chlorophyll and had even less chance of emergence. When water table levels dropped to the sediment surface after a 25-day flooding period, all seedlings recovered quickly except for those covered in algae.

***Salix caprea* L.: W6, W7**

There is no dormancy period as seed is essentially only a large embryo surrounded by a transparent thin coat. 99% of seed will germinate directly following dissemination and contact with a damp surface. Epicotyl development occurs after 2 weeks (Simak 1980).

Salix cinerea: W5, W6, W7

Salix fragilis: W6

Salix purpurea: W6

Salix triandra: W6

Salix viminalis: W6

Sambucus nigra L.

Elder usually flowers in its third or fourth year, rarely in its second (Bolli 1994). Most shrubs produce copious amounts of fruit and viable seed each year, the exception being shrubs growing in deep shade; in woodlands shrubs produce few or no flowers (Atkinson & Atkinson 2002).

Elder will not establish where there is a turf. It is capable, however, of establishing in a closed shrub canopy (Gilbert 1991). Large even-aged stands of elder often occur where it has colonised open areas.

Urtica dioica L.

While the age of first flowering is not known, flowering is known not to occur in the first field season. Seed production thereafter is abundant and occurs on an annual basis. Fruits are single-seeded (no information on the number of fruits per plant) and seeds are dispersed by the wind or animals (eg deer, magpies, cattle). Seeds can remain viable for 2+ years and demonstrate high percentage germination (98%) if kept dry (Greig-Smith 1948). Seeds germinate in the field at sites that are very wet, exposed to full sunlight and subject to temperature fluctuations. Under similar conditions, germination percentages of different batches of seeds can vary widely (eg 26-94%). Growth of seedlings is achieved in full daylight (optimum at 11-20% full daylight conditions and minimum at 5-10% of full daylight) with high levels of flowering in well-lit conditions compared with very limited flowering, but abundant vegetative growth, in deep shade (Olsen 1921; Greig-Smith 1948).

Vegetative spread is by means of rhizomes (incremental rate of spread estimated at 35-45 cm per annum (Kerner, 1895)). New rhizomes are produced in late summer or autumn either from older rhizomes, or from the base of aerial shoots. They continue to grow at or just beneath the soil surface until the death of aerial shoots, when they turn up to form new shoots; in very loose soils rhizomes may be found at greater depths (30 cm or deeper). New shoots produced in the autumn survive the winter in most years and resume growth the following spring (Greig-Smith 1948).

2.3.4.3 Sediment

Given two different sediments with a similar percentage of soil moisture, more of the water held in a coarser sediment will be available to plants than in a finer sediment since soil-suction in coarser sediment will be lower than in finer sediment. This suggests that plants with high water demands, such as *Salix* spp., should grow fastest in coarser sediments than finer sediments if water is abundantly available in both, assuming that nutrients are not a

limiting factor. Experimental work has demonstrated, however, that the use of water by plant species in different sediment types is not so clear cut (Mahoney & Rood 1991; 1992; Barsoum & Hughes 1998). Significantly higher soil-porosity in finer sediments (eg sediment with high proportions of fine sand, silts and/or clay) compared with coarser sediments (coarse sand, gravel) will inevitably have a disproportionate influence on the aerobic status of the substrate and increase the number of contact points between roots and soil water. Measurements of root dry weights and root ramification in particular show a subtle interplay between these factors and the availability of soil water to explain growth (Barsoum & Hughes 1998).

***Acer pseudoplatanus* L.: W7**

A. pseudoplatanus establishes in a wide range of soils, although usually it does not regenerate on podsoles, or on heavy clay where gleying comes close to the soil surface, resulting frequently in root rot (Jones 1944). The best growth is attained in deep, moist soils, freely drained and of relatively high base status; ie on constantly moist deep loamy sands and on light to medium loams (Nisbet, 1893; Jones 1944).

***Alnus glutinosa* L.: W5, W6, W7**

A. glutinosa grows throughout Britain on permanently and seasonally wet soils that are characteristic of stream-sides, depressions and swampy ground; it also occurs on terraces and sloping ground in oceanic regions. More specifically, *A. glutinosa* is restricted to unstable mineral sediments along stream and lake margins comprising recent alluvia, flush soils and those of impeded drainage or seasonally wet hill slopes (ie occurs in deep fen peats and acid bog peats, but not in blanket or raised bogs) (McVean 1955). The species can grow in strongly acid to alkaline soils (pH 3.4 - 7.2) and appears to tolerate acidic peats best in eastern England. Alder woodland occurs at base rich flushes in the uplands, but is absent from base poor flushes which tend to develop into bog communities (Peterken 1993).

Best growth of young trees (eg 5-8 years old) has been observed in continuously damp organic soils, compared with clays or free-draining alluvial sediments; in these latter sediment types, water availability for plant uptake can be limiting. Among older trees (28+ years), best growth was observed in free-draining alluvial sediment; here with access to the water table, the roots can grow in a well-aerated substrate (Claessens & Thibaut 1994) (Figure 8). Thibaut and others (2004) demonstrated that soil factors have a more important influence on *A. glutinosa* growth than climatic variables; while growth in the species was found to be very sensitive to soil-moisture differences occurring in different substrate types (inter-site variation), it was comparatively unaffected by significant climatic differences between study sites located, as far apart as Sweden, Hungary and Belgium.

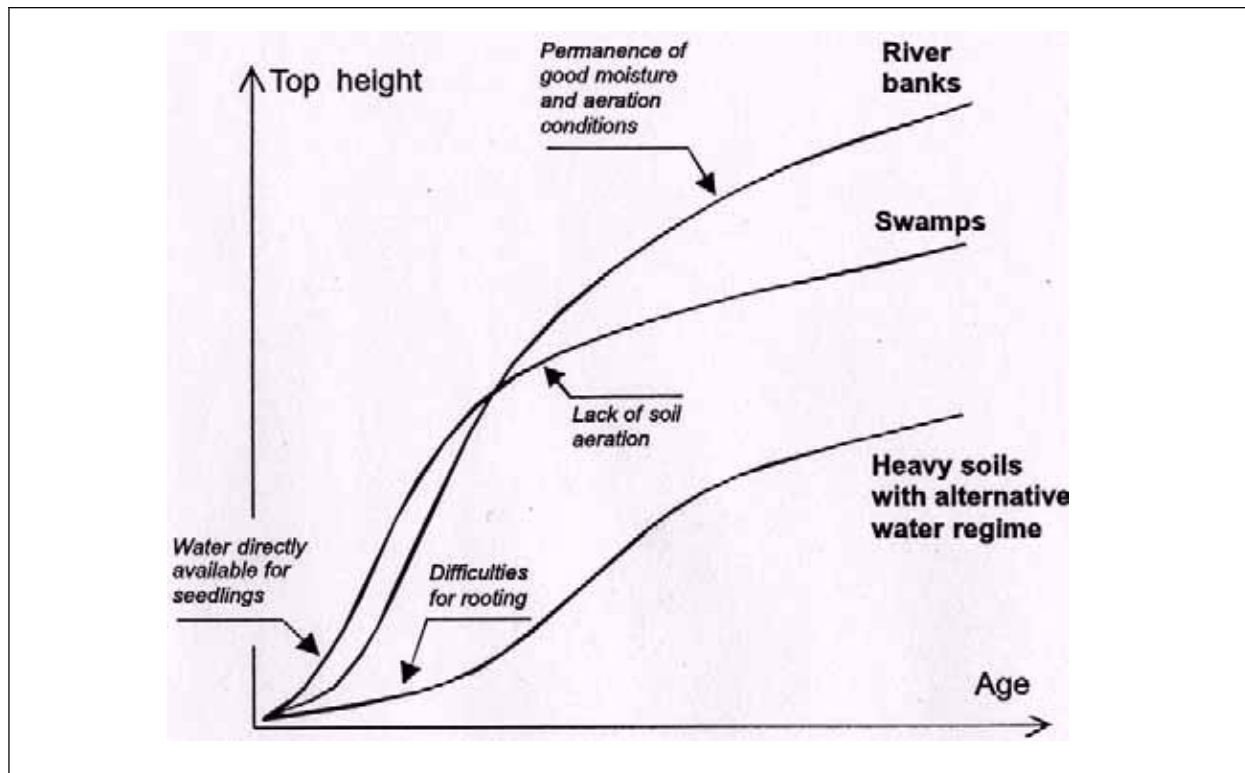


Figure 8 Hypothetical growth curve shapes of black alder (*Alnus glutinosa*) for three major site types – adapted from Spurr and Barnes (1980) by Thibaut and others 2004.

Angelica sylvestris L.: W5, W6, W7

Betula pubescens L.: W5, W6, W7

This species is tolerant of a wide range of soil conditions and has been found growing in soils with groundwater pH values of 7.8, 6.6 and 3.5 (Gill & Davy 1983).

Carex acutiformis: W5

Carex paniculata: W5

Corylus avellana: W7

Crataegus monogyna Jacq.: W6, W7

This species occurs as adult trees on weakly to moderately leached soils (Williams & Buxton 1989).

Dryopteris dilatata: W5

Filipendula ulmaria: W5

Fraxinus excelsior L.: W7

Ash is absent where surface soil pH's are lower than 4.2 and is most abundant in calcareous substrates (ie chalk, oolite, Montain limestone, Old Red Sandstone) where the pH ranges from

5 to 8; in very basic soils young plants may suffer, however, from lime chlorosis. In substrates with low levels of pH, ash can still occur on lower slopes, hollows and along stream banks where percolating water has increased sediment pH levels (Wardle 1961).

Highest densities of ash roots are found in fen peat and in slightly acidic sand (1000-1500 cm of roots less than 1 mm in diameter in soil samples of 85 cc volume). On heavier loam soils, where root penetration is more difficult, values ranged from 230 to 400 cm. Roots may be sparsely distributed to great depths, but the permanent water table sets a lower limit. Growth of ash roots will only take place between limits of 4^oC and 29^oC. The roots are of two types. 'Coarse' roots (over 0.5 mm diameter at the tip) persist indefinitely and appear able to withstand long periods of poor aeration. 'Fine' roots are more numerous, mostly abscised after 1 year and are killed if the water table rises temporarily (Wardle 1961).

***Iris pseudacorus* L.: W5**

I. pseudacorus typically occurs on soils of continuously high water content, but the soil does not need to be submerged and the plant is capable of surviving in dry sandy soil (Dykes 1974). This species can be found over a variety of soil types ranging from shingle, thin layers of organic matter on gravel or sand, to orthodox gleys; it is also present on peats as well as permanently submerged organic and inorganic soils at the edge of freshwater bodies. It tolerates considerable soil and water acidity (eg plant can survive in water with a pH of 2.0-3.5 (Seidel 1973a)) and occurs from pH 3.6 to 7.7, although it is less frequent in areas of chalk. The rhizomes may grow over submerged bare rocks with roots penetrating through gaps to underlying soil, or may survive as floating mats. A favoured microhabitat includes depressions in the riparian landscape (Sutherland 1990).

***Phragmites australis*: W5**

***Salix caprea* L.: W6, W7**

***Salix cinerea*: W5, W6, W7**

***Salix fragilis*: W6**

***Salix purpurea*: W6**

***Salix triandra*: W6**

***Salix viminalis*: W6**

***Sambucus nigra* L.**

***Urtica dioica* L.: W5, W6**

U. dioica develops well on recently disturbed, nutrient rich, fine-textured sediment (Siebel & Bouwma 1998), although it can also be found growing on most other soil types (pH range of 3.6-7.3), except possibly on acid peat (Greig-Smith 1948). Once established, the texture of the sediment is probably important in determining vegetative extension; young rhizomes are considered to be incapable of penetrating (or only very slowly) a compact substratum. The species occurs occasionally as an epiphyte on willow and ash (Greig-Smith 1948).

2.3.4.4 Drought/temperature

‘A continuum of possible drought-resistance strategies exists among vascular plants. At one end of this range there are species facing a wide variation in water potential (anisohydric species), and at the other end there are those that experience consistent xylem pressure (isohydric species). Often, anisohydric species tend to be drought-tolerant whereas isohydric species buffer their water potential on a diurnal and seasonal time scale by different drought avoidance strategies’ (Vogt 2001).

Among the range of adaptations allowing for acclimation to soil drying, typically many plants will: 1) shift the allocation of assimilates from shoots to roots and therefore increase root growth and extension, usually at the expense of shoot growth; ie the results are reductions in leaf expansion rates, leaf production and stem elongation and thus, reduced transpirational demand relative to water absorption (Molyneux & Davies 1983; Barsoum 1998) and 2) demonstrate an osmotic adjustment via increased concentration of solutes in the symplast, allowing turgor to be maintained at low water potential; ie lower water potential in tissues enables water to continue to be extracted from the drying soil while maintenance of turgor allows for stomatal opening, cell expansion, root growth and increases in productivity. The speed of on-set and duration of drought stress are important because acclimation to drought stress in plants is a time-requiring process; ie it takes time for plants to make necessary changes to growth and translocation patterns (Davies & Zhang 1991).

It is very common in many riparian plant species for ‘cavitation’ to occur where water draw down rates are too rapid and contact is lost with the water table wetting front. According to the widely accepted cohesion–tension theory of sap ascent, xylem sap present in the vessels of transpiring plants flows under tension caused by evaporation from the leaves. ‘Cavitation is the abrupt change from liquid water under negative pressure to water vapour (under vapour pressure) leading to an air-filled (embolized) vessel under atmospheric pressure. The quantity of cavitation events depends on the amount of cavitation-causing factors in the sap or the cell walls. As a result of cavitation and embolism formation, stem hydraulic conductivity is reduced, which may be critical for a plant under drought stress’ (Vogt 2001). ‘Loss of hydraulic conductivity is a direct measure of cavitation and embolism formation in the xylem vessels’ (Tyree & Sperry 1989).

Acer pseudoplatanus L.: W7

A. pseudoplatanus trees are comparatively vulnerable to drought-induced xylem cavitation and have high hydraulic conductance. It appears when comparing *A. pseudoplatanus* with a related drought resistant species (*Acer opalus*), that the vulnerability of *A. pseudoplatanus* to cavitation is at the expense of hydraulic efficiency (Lemoine and others 2001; Tissier and others 2004).

82-day old *A. pseudoplatanus* seedlings showed reduced transpiration rates in drought situations, with indications of xylem cavitation and enhanced root growth following the withdrawal of water and gradual drying of a sediment mixture comprising a mixture of loam, sand and peat compost in a ratio of 2:1:1. However, despite signs of drought stress, leaf growth was maintained for up to six weeks following the withdrawal of water, whereby leaf production and expansion dropped significantly (Khalil & Grace 1992).

***Alnus glutinosa* L. Gaertn.: W5, W6, W7**

For high nitrogenase activity, alder root nodules require a continuous supply of photoassimilates and strict regulation of oxygen levels in the nodules (Huss-Danell 1985; Wheeler & Bowes 1974; Silvester and others 1990). Drought stress can disrupt these balances and *A. incana* has been observed to display reduced translocation of photoassimilates to nodules and 70% reduced nitrogenase activity at the start of a prolonged period of drought-stress (ie after 2-3 days in a sandy sediment, water potential [Ψ nodules] was -1.1 to -1.6 MPa). Absorption was possible where at least part of the root system was supplied with sufficient water that allowed for continued effective transportation of assimilates to nodules (Sundström & Hussdanell 1995).

In *A. glutinosa*, no relationship was observed between vessel diameter of branches, petioles, or roots and vulnerability to cavitation. Petioles were more vulnerable than branches to cavitation in *A. glutinosa* trees and this occurred where water potential fell below -1.2 MPa. Roots were the most vulnerable plant organ to cavitation with likely effects on stomatal conductance and hence, noticeable reductions in growth (Hacke & Sauter 1996), although the root systems of drought stressed alders (*A. incana*) can persist for some time regardless of clear reductions in nitrogenase activity (Sundström and Hussdanell 1995). Reversal of embolism is assumed to be possible when conditions are favourable; eg prolonged periods of rain. The metabolic activity and consumption of photoassimilates in the nodule are a pre-requisite for both the import of photoassimilates to the nodule and the export of nitrogen compounds from the nodule (Raven and others 1989).

Drought-stressed *A. glutinosa* trees/seedlings became susceptible and weakened by the fungal parasite *Phomopsis alnea* (a microscopic coelomycete) that causes stem cankers and die-back (Moricca 2002).

***Betula pubescens* L.: W5, W6, W7**

***Carex acutiformis* L.: W5**

***Carex paniculata* L.: W5**

***Corylus avellana*: W7**

***Crataegus monogyna* Jacq.: W6, W7**

C. monogyna showed high stomatal conductance and low stomatal sensitivity to increases in atmospheric evaporative demand. This indicates poor stomatal control and thus poor water-use efficiency during periods of drought. Observations of declining pre-dawn water potentials throughout the growing season were linked to premature leaf abscission in the summer (Mediavilla & Escudero 2003).

***Dryopteris dilatata*: W5**

***Filipendula ulmaria* L.: W5**

***Fraxinus excelsior* L.: W7**

Soil dryness reduces the rate of height and diameter growth of ash saplings and under extreme conditions, an ash tree may not develop beyond a shrub phase (Wardle 1961).

Ash will, however, become acclimated to dry sites. The species was shown to have low hydraulic conductance and low xylem vulnerability to embolism (Lemoine and others 2001). Another study reports on diurnal and seasonal variation in sap flow rates and stem water potential of ash saplings subjected to drought conditions (Kerr & Cahalan 2004). A deficit of water in shoots, due either to soil drought or desiccation by wind, has been observed to result in their dying back, in yellow coloration, in abscission of leaves and in failure of the apical buds to open in the following spring. Annual growth of trees is clearly influenced by rainfall in the early summer (May and June) (Wardle 1961).

***Iris pseudacorus* L.: W5**

The rhizome of this species appears to be tolerant of long periods in dry soils (eg 3 months). Roots are fairly shallow and are usually 10-20 cm long, but can be up to 30 cm long (Sutherland 1990). Plants are restricted to low altitudes, suggesting that it is intolerant of low temperatures (Sutherland 1990).

***Phragmites australis* L.: W5**

***Salix caprea* L.: W6, W7**

***Salix cinerea*: W5, W6, W7**

***Salix fragilis*: W6**

***Salix triandra*: W6**

***Salix purpurea*: W6**

***Salix viminalis*: W6**

Stem and leaf growth decreased during periods of water deficit. Exceptionally high stem growth rates (twice the potential growth rates) were recorded following a drought period, probably caused by root allocated assimilates being sent above-ground (Lindroth and others 1994).

***Sambucus nigra* L.**

S. nigra is extremely vulnerable to xylem cavitation (90% loss of conductivity at -2.2 MPa compared with loss of conductivity at -6 MPa in the drought adapted shrub species *Sorbus aucuparia* L.) (Vogt 2001; Vogt & Lösch 1999) and shows similar hydraulic vulnerability curves to various *Populus* and *Salix* species (eg *P. fremontii*, *P. balsamifera*, *Salix gooddingii*). Nearly total blockage of sap flow could potentially occur at -2.2 MPa and only small fluctuations of field water potential are tolerable for this species to maintain its internal water potential. While there is evidence that *S. nigra* can refill embolized vessels (eg during periods of rain) and has sensitive stomatal control of transpiration (shows isohydric water

potential patterns which includes daily and seasonal variations in stem water potential), these adaptations provide only limited avoidance of drought stress (Vogt & Lösch 1999); eg when compared with various drought resistant shrub species, *S. nigra* shows poorer recovery following xylem cavitation (Vogt 2001; Salleo and others 1997).

Specific Leaf Areas (leaf area over leaf dry weight) of *S. nigra* bushes growing in dry conditions were significantly greater than bushes growing in saturated conditions; this indicates a greater investment in leaf expansion rather than per unit of foliage mass in dry conditions and thus, a greater efficiency/capacity to photosynthesize under these conditions (Atkinson & Atkinson 2002).

Shoots that arise late in the growing season are often killed by cold winter weather (Metcalf 1948).

***Urtica dioica* L.: W5, W6**

Transpiration rates of *U. dioica* decline where water table levels are low (50-60 cms below the sediment surface) (Šrútek 1997). This is confirmed by Boot and others (1986) who observed the maintenance of water potentials (-0.2 to -0.4 MPa) by 17 day-old *U. dioica* seedlings under 0-, 1-, 2- and 3-h drought treatments per day for a period of 6 weeks, but severe wilting after 5 h and 7 h of drought stress per day over the same experimental period. Although prolonged drought (5 h and 7 h day⁻¹) also resulted in inhibited vegetative growth and flowering, this drought treatment had no significant effect on the partitioning of dry matter between shoots and roots, and seedlings that had initially wilted during the first week of drought stress, rapidly recovered indicating a process of drought-hardening which probably involved stomatal closure (Boot and others 1986). In very dry conditions, stunted growth resulted in plants averaging 30-60 cm compared with heights of 160 cm in favourable growing conditions (Greig-Smith 1948). Early frosts in the autumn cause shoot die-back (Greig-Smith 1948).

2.3.4.5 Flooding

(i) Flooding effects as related to elevation, geomorphic context on floodplain and flooding periodicity

While the risk of drought-induced mortality in W6 (and even W5) alluvial forests may be significant at high elevations on the floodplain (and especially for new recruits), at lower elevations the probability of partial, or even complete inundation is a major risk during periods of high flow. Floods are inevitable cyclical disturbances along rivers and streams subject to natural flows. Generally they affect the majority of low-lying landforms (eg gravel and sand bars) and submerge, over short periods (several days), any plants colonizing these zones. Longer periods of raised water levels typically occur in the spring and autumn when water tables are replenished; prolonged saturated soil conditions or complete submergence of plants at low elevations often develop over these periods.

Along dynamic streams and rivers, frequent lateral migration of the main channel and side-channels may result in the sudden long-term submergence of plants previously only periodically submerged. In cut-off side-channels, plants may be either partially, or completely submerged in stagnant water that, within hours of flooding, can become anoxic as static conditions bring about a reduction in the diffusion of oxygen (plant roots and micro-

organisms also rapidly deplete oxygen reserves). The utilization of oxygen supplies by respiring microflora and plant roots will be especially rapid when water temperatures are highest in the summer months (Vartapetian & Jackson 1997; Russell 1977).

Often plant species occurring at low elevations are adapted to the anoxic conditions that develop, especially if flooding/raised water table levels occurs during periods of dormancy or water table levels are fluctuating frequently, thereby replenishing oxygen in the substrate. The development of stagnant, waterlogged conditions and/or flooding that occurs outside of the dormant period (ie in late spring and summer) is more problematic. Even among the more tolerant species, the timing of flooding is critical for successful plant establishment and most species have lower tolerance of flooding during growth periods (eg Siebel & Blom 1998). Duration and timing of summer flooding in particular have been documented as the most influential variables affecting plant persistence on floodplains (Johansson & Nilsson 2002). As a general rule, soil inundation should not last longer than 40% of the growing season each year (Kozlowski 1984; Crawford 1982).

Along flooding gradients, depth and duration of flooding are the main environmental variables determining a zonation in vegetation and this is most evident in W6 alluvial forests (Blom & Voesenek 1996). Individual plants may be affected directly due to their germination requirements with regards to soil-moisture (Keddy & Ellis 1985; Coops & Van der Velde 1995), or different tolerances to flooding as seedlings and adults (Welling and others 1988). The establishment phases are known to be the most sensitive of a plants life cycle to flooding (Lenssen and others 1991; Rood & Mahoney 1990). Characteristics related to seed dispersal, seed bank formation, germination and seedling survival determine the establishment success of any given species (Harper 1977; Coops & Van der Velde 1995).

(ii) Specific impacts of flooding and adaptations to flooding in alluvial forest species

Apart from the potential for mechanical damage to plants from floods (eg burial from sediment, dislodgement), which has obvious implications for their health and survival, secondary effects of flooding include: (i) altered plant metabolism and reduced photosynthesis (eg a suppression of oxygen-dependant pathways, carbon assimilation processes and photosynthate utilization), (ii) altered stomatal closure, (iii) altered photochemical balances, (iv) the disruption of functional relationships between roots and shoots resulting in altered nutrient uptake and water absorption, (v) the production by roots of toxic waste substances such as ethanol and cyanogenic compounds and (vi) the build-up of soil toxins (eg iron and manganese) due to the reduced conditions (Kozlowski 1984; Russell 1977; Kramer 1951; Vartapetian & Jackson 1997). Accumulation of toxic fermentation products and a lack of the enzyme superoxide dismutase (SOD) make plants susceptible to 'post-anoxic injury' when plant tissues are not protected against oxygen damage on return to air (Monk and others 1987). Metabolic and morphological adaptations helping to minimize damage to plants from these secondary flood stresses generally reside in shoots of plants rather than the roots and include the following:

- 1) An indication of resilience to episodic floods is the ability of shoots to tolerate submergence in a semi-dormant state by relying on carbohydrate reserves in the absence of the basic materials required for photosynthesis (ie carbon dioxide and water, the latter of which is less available as roots become depleted of oxygen).
- 2) There might be an ability to elongate shoots rapidly to increase the chances of contact with the atmosphere, or well-oxygenated layers of water.

- 3) A capacity for adventitious root formation and hyper-trophied lenticils at the base of shoots to replace flood-damaged roots, which permits a certain amount of water and oxygen to be absorbed directly from the surroundings and translocated via aerenchyma (enlarged air spaces) to roots and shoots.
- 4) Pressurised gas transport, or ‘thermo-osmosis’ is a trait that has been adapted by many distantly related species subject to oxygen deficit in wet soils; it involves the accumulation of air in the inter-cellular spaces of the stem which is then transported under differential partial pressure towards the roots, thereby substantially improving the oxygen supply to roots. More specifically, pressurised gas transport occurs when the darkly pigmented bark on tree trunks absorbs radiant energy, warming up air within the stem by a couple of degrees compared to the surrounding air. The temperature differences promote a flow of gas from the atmosphere to the stem which subsequently creates a positive pressure in the stem’s intercellular system and promotes the flow of air to the roots. The flow increases not only the oxygen partial pressure in the roots, but also the rate of oxygen loss to the rhizosphere. Localised in the phellogen layer of lenticels might be a thermo-osmotically active partition which serves to increase pressurization of the air in stems (Grosse and others 1992; Büchel & Grosse 1990).
- 5) To curtail the demand by shoots for root-derived resources; morphological escape mechanisms might include stomatal closure, leaf epinastic curvature and a reduction in leaf expansion.
- 6) The accumulation of SOD during anoxia is a highly effective biochemical adaptation to survive long-term flooding and post-anoxic injury (Monk and others 1987).

Vegetation species typically associated with wet woodlands are known to have most, if not all of these morphological adaptations, although certain species are seemingly better adapted to episodic flooding than others. This differentiation will define where a species occurs along a hydric gradient; for example, Krasney and others (1988) observed a clear relationship between the adventitious rooting ability of *Salix interior*, *Salix alaxensis*, *Populus balsamifera* and *Populus tremuloides* seedlings and their distribution on the Tanana River in interior Alaska. Variations among species will also define a species survival and growth response in the event of a flood or continuously waterlogged conditions. Van Splunder and others (1996), for example, suggest that the higher frequency of *Salix alba* seedlings at low elevations on the floodplain in a clay-sand substrate, compared with *Populus nigra*, can be explained by the ability of *S. alba* seedlings to extend their roots into saturated soils.

***Acer pseudoplatanus* L.: W7**

In freely draining sandy sediment, one year-old *A. pseudoplatanus* seedlings demonstrated reduced survival (15% mortality) and highly significant reductions in height growth when subjected to a flooding regime (standing water, 10 cm above sediment surface) for 120 days compared with control seedlings subjected to no flooding. Recovery was very good, however, in the second growing season (Frye & Grosse 1992).

Although this species favours moist soils, it does not tolerate waterlogging (Jones 1944). Unlike *Alnus glutinosa* and *Betula pubescens*, *A. pseudoplatanus* is not able to avoid anaerobic stress by pressurised gas transport; this trait is absent in this species, suggesting that it favours drier soil conditions (Grosse and others 1992).

***Alnus glutinosa* L.: W5, W6, W7**

Increased oxygen conductivity of roots in waterlogged soil is achieved by aerenchymatous root tissues (Köstler and others 1968). As in other species of alder (*A. incana*, *A. japonica*, *A. hirsuta*), *A. glutinosa* is able to avoid anaerobic stress by pressurised gas transport improving oxygen transport into roots (Büchel & Grosse 1990). Added protection from flooding-induced anoxia and post-anoxic stress is derived from the accumulation of the enzyme superoxide dismutase (SOD) in root tissues during inundation (Monk and others 1987).

In *Alnus incana* flooding was found to severely arrest N-fixation, photosynthesis and growth in two year-old saplings with 100% mortality where flooding occurred in the late spring/summer compared with lower rates of mortality in the autumn (Kaelke & Dawson 2003). In *Alnus rubra* Bong. and *Alnus viridis* ssp. *sinuata* (Regel) Love & Love, flooding (20/50 day flood + 20-day recovery) lead to: (i) a reduction in nitrogenase activity, (ii) a decline in the relative growth rates, or increased mortality of roots, (iii) the formation of adventitious roots and (iv) increased stomatal conductance (Batzli & Dawson 1997). Growth in two year-old saplings of *A. japonica*, on the other hand, was not affected by flooding (mid-June till early November), except for a slight decrease in height growth. Some morphological signs of adaptation to flooding were observed: stem base hypertrophy, hypertrophied lenticels, the formation of adventitious roots and the development of new roots (Terazawa & Kikuzawa 1994).

***Angelica sylvestris*: W5**

***Betula pubescens* L. Ehrh.: W5, W6, W7**

B. pendula is known to avoid anaerobic stress to some extent by pressurised gas transport of oxygen from shoots into roots; oxygen uptake rates by pressurised gas transport are affected strongly, however, by the level of irradiation of the stem, decreasing by 67-76% in the dark (Monk and others 1987; Grosse and others 1992). Nevertheless, moderate degrees of flooding results in reduced growth and survival; ie 30 days flooding resulted in marked reductions in survival and growth of 11-12 week-old seedlings (Rinne 1990; Johansson & Nilsson 2002).

In freely draining sandy sediments 20% of one year-old *B. pubescens* seedlings did not survive a flooding treatment of 120 days (standing water, 10 cm above sediment surface). Surviving seedlings demonstrated a marked reduction in height growth when subjected to this flooding regime compared with seedlings exposed to no flooding. The reduced growth persisted into a second growing season, with average biomass production declining by 34% compared with the control. It is expected that one of the indirect consequences of flooding on seedlings is an impeded competitive ability (Frye & Grosse 1992).

***Carex acutiformis* L.: W5**

***Carex paniculata* L.: W5**

***Crataegus monogyna* Jacq.: W6, W7**

In freely draining sandy sediment, one year-old *C. monogyna* seedlings demonstrated a marked reduction in stem diameters and a reduction in height growth when subjected to a flooding regime (standing water, 10 cm above sediment surface) for 120 days compared with

control plants subjected to no flooding. Recovery was very good, however, in the second growing season (Frye & Grosse 1992).

***Dryopteris dilatata*: W5**

***Filipendula ulmaria* L.: W5**

This herbaceous species is considered to be among the more anoxia-tolerant temperate herbaceous species and can thus tolerate waterlogged conditions for extended periods (Studer-Ehrensberger and others 1993). Rather than produce aerenchyma when flooded, the species endures oxygen deprivation in a quiescent state (Barclay & Crawford 1982; Smirnov & Crawford 1983; Brändle & Crawford 1987).

Survival and growth of 11-12 week-old seedlings showed marked reductions after 200 days continuous flooding. Growth was significantly better along free-flowing compared with regulated rivers where flooding duration was shorter (Johansson & Nilsson 2002).

***Fraxinus excelsior* L.: W7**

Unlike *Alnus glutinosa* and *Betula pubescens*, *F. excelsior* is not able to avoid anaerobic stress by pressurised gas transport; while this trait is absent in this species, ash is nevertheless able to grow in wet soils on account of its naturally high diffusion rate in the dark (Grosse and others 1992).

In waterlogged habitats (may be W5b), ash saplings dominate because young seedlings are shallow-rooted. Subsequent growth is often checked, however, unless the site is drained. On waterlogged sites, ash may in fact suffer seasonal water shortage because roots are unable to penetrate to sufficient depths and root systems become too small to support the growing tree (Wardle 1961).

In freely draining sandy sediment, one year-old *F. excelsior* seedlings demonstrated 100% survival and a significant increase in diameter (but not height) growth when subjected to a flooding regime (standing water, 10 cm above sediment surface) for 120 days. Growth was retarded, however, in the second growing season (biomass production rate decline of 40%) compared to seedlings that had received no flooding treatment in the previous year (Frye & Grosse 1992). The increased stem diameter of ash seedlings in the flooded situation is likely to be due to the formation of aerenchyma, allowing for the continuous diffusion of oxygen to roots and thus the maintenance of shoot growth under flooded conditions.

***Iris pseudacorus* L.: W5**

I. pseudacorus can survive long periods of natural waterlogging and experimental anoxia (eg it occurs in water up to 25 cm deep), although no growth occurs during this period (Barclay & Crawford 1982; Hetherington and others 1983). Survival is effected by the transfer of oxygen from leaves in air through to aerenchymatous rhizomes, enabling aerobic respiration. *I. pseudacorus* rhizomes without leaves exposed to the air (eg submerged) can also tolerate approximately two months of total absence of oxygen at +20°C without any apparent damage to tissues and can resume growth when placed under normal oxic conditions (Brändle & Crawford 1987). The high tolerance to anoxia is attributed specifically to the high storage carbohydrate content of rhizomes, which maintains glycolysis and ethanolic fermentation

during oxygen deficiency (Hanhijärvi & Fagerstedt 1995). It appears, however, that substrate type will have an important influence on resistance to anoxic conditions; i.e. *I. pseudacorus* showed a 40% decline in growth in waterlogged, compared to drained conditions, when growing in an organic sediment with a decomposing litter layer comprised mostly of *Phragmites australis* litter; growth was less inhibited in waterlogged mineral sediments (Lenssen and others 1999).

***Phragmites australis* L.: W5**

Floods can lead to significant declines in *P. australis* coverage (Dienst and others 2004). Where damage from flooding is severe, secondary shoots replace a complete die-back of primary shoots in surviving plants. Less severe damage can lead to increased insect infestation of primary shoots (Ostendorp and others 2003). Warren and others (2001) and Blanch and others (2000) suggest that *P. australis* is more sensitive to hydroperiods (magnitude, timing and frequency of flooding events) and fluctuations in water levels than to continually high water-table levels. Amsberry and others (2000) observed, however, that even waterlogged conditions at the lowest elevations in marshes are not always survivable by *P. australis*. It is known to avoid anaerobic stress to some extent by pressurised gas transport of oxygen from shoots into roots (Armstrong & Armstrong 1991).

***Salix caprea* L.: W6, W7**

Up to 13 weeks of waterlogging had little effect on form and growth rates of above-ground parts. Belowground, waterlogged plants developed hypertrophied lenticels within four weeks, followed by significant increases in stem diameter. Most of the root system died by the end of the waterlogging treatment and mycorrhiza were lost. New roots that developed were long, branched and floated on or near the water surface; these originated from pre-existing woody roots and hypertrophied lenticels (Good and others 1992).

***Salix cinerea*: W5, W6, W7**

Up to 13 weeks of waterlogging had little effect on form and growth rates of above-ground parts. Belowground, waterlogged plants developed hypertrophied lenticels within four weeks, followed by significant increases in stem diameter. One clone showed a significant increase in its leaf area and stem dry weight. Most of the root system died by the end of the waterlogging treatment and mycorrhiza were lost. New roots that developed were short, fine and highly branching; these grew vertically upwards until they reached the water surface. They originated from pre-existing woody roots and from hypertrophied lenticels on submerged portions of stems (Good and others 1992).

***Salix fragilis*: W6**

After 16 days in waterlogged conditions, severe root die-back was compensated for by many new roots growing from old root bases. No such recovery was observed following 32 days of waterlogging. Total submersion caused more severe damage to aerial parts than waterlogging. After 8 days, shoot tips started to rot (Good and others 1992).

***Salix purpurea*: W6**

In freely draining sandy sediment, 1 year-old *S. purpurea* demonstrated 85% survival of seedlings and marked reductions in height (but not diameter) growth when subjected to a flooding regime (standing water, 10 cm above sediment surface) for 120 days compared with control seedlings subjected to no flooding. Recovery was very good, however, in the second growing season; seedlings that received the flooding treatment showed significantly increased height growth compared to seedlings that received no flooding (Frye & Grosse 1992).

***Salix triandra*: W6**

***Salix viminalis*: W6**

The growth of this species is minimally affected by soil flooding and oxygen shortage. Shoot and root tip extension were shown to slow down during a four week period of flooding. This was immediate for roots at depths of 100-300 mm, but delayed for 20 days for shoots. In the upper 100 mm of the soil, flooding enhanced adventitious root and aerenchymatous development. Root and shoot growth recommenced and was even stimulated following flooding (Jackson & Attwood 1996).

After 16 days in waterlogged conditions, severe root die-back was compensated for by many new roots growing from old root bases. No such recovery was observed following 32 days of waterlogging. Total submersion caused much more severe damage to aerial parts than waterlogging. After 25 days, shoot tips started to rot (Good and others 1992).

***Sambucus nigra*: W6**

***Urtica dioica* L.: W5, W6**

High water table levels (10-20 cm below the surface) and prolonged flooding rapidly limits *U. dioica* growth and vegetative spread (Šrůtek 1997). Spring flooding halted growth and caused high mortality of young (3 to 5 day-old) seedlings at the end of the flooding period, indicating post-anoxic injury. Mortality increased with increasing duration of flooding (10-30 days). Summer flooding of *U. dioica* had more severe consequences, with no young plants surviving more than four weeks of flooding; leaves of submerged plants fell off and new ones started to grow. Adventitious roots appeared on the nodes of submerged parts of their stems, while fine roots decomposed. Autumn flooding proved to be the least destructive flooding period; young seedlings were taller by this point and were able to survive (semi-submerged) nine weeks of flooding, although they demonstrated declines in dry mass and displayed leaf and root mortality. Leaves fell off flooded plants and these were replaced by new ones, but stem, leaf, root and rhizome dry weights were significantly less than for unflooded control plants, leaving some doubt over the likelihood of flooded plants surviving the subsequent winter months (Klimesšová 1994).

Despite abundant seed in seed banks at low and high elevations along river banks, *U. dioica* seedling numbers quickly dropped off at low elevations during the growing season, indicating that it is restricted to higher elevations on the floodplain and is sensitive to inundation (Lenssen and others 1999; Lenssen and others 1998).

2.3.4.6 Biotic disturbances

(i) Grazing

Typically, herbivores remove less than 10% of the above ground primary production from any natural community and large herbivores, as distinct from smaller rodent or invertebrate herbivores, are responsible for consuming far less than this. In the UK, densities of grazing stock are artificially high due to the absence of natural predators and the pasturage of domestic livestock alongside native species. In areas where alternative suitable habitat is restricted, grazing pressure may have significant impacts on the vegetation community composition and structure (Putman 1996). Riparian woodland can become a hot spot of activity as stock tend to concentrate around water and the consequences of grazing within wet woodlands can be considerable. If grazing pressure is heavy by a single herbivore, selective feeding may alter the species composition of alluvial forests, especially where there is differential palatability of herbaceous species, which may alter successional development within the stand (McInnes and others 1992).

Direct effects of grazing include predation of seed and the consumption of seedlings, checked growth, nutrient stress, and resource allocation being diverted to defensive chemicals. Indirect effects comprise the release from shrub/bramble canopy shade, removal of competing sward, creation of bare ground, increased incorporation of leaf litter into the soil, and the burial of seeds.

Grazing is not always detrimental to the structure or biodiversity of a woodland. Many papers report that the woodland can become degraded following livestock exclusion. The timing of grazing is important since trees are more likely to be browsed in the winter when alternative food sources are scarce. The removal of apical buds from dormant saplings may encourage vigorous re-growth, resulting in changes to leaf form and nutrient status. Light grazing during the summer is beneficial to tree growth through the reduction of herbaceous competition.

Robertson & Rowling (2000) report that grazing alters the structure and function of riparian woodlands. After 50 years without grazing the vegetation community composition was significantly different between grazed and ungrazed areas. In the areas with no stock access the above ground biomass was greater; seedling and sapling densities were higher and leaf litter and fine woody debris accumulated on the ground. The impact of grazing on riparian function was dependent on stream size. The in-stream fine and coarse woody debris were more plentiful in areas without stock on the larger rivers but not in tributaries.

Acer pseudoplatanus L.: W7

Sycamore appears to be very palatable to sheep and was effectively controlled by grazing without affecting the regeneration success of oak and rowan in an upland alder woodland in north Wales (Linhart & Whelan 1980). The authors recommend the reintroduction of light winter grazing to encourage the sheep to eat bramble and sycamore, which had become invasive within fenced enclosures.

***Alnus glutinosa* L.: W5, W6, W7**

Woodland regeneration in response to the exclusion of livestock was studied in an upland oak/ash/alder woodland in north Wales by Linhart & Whelan, (1980). Sheep and cattle were excluded using fences and the relative abundance of seedlings and /saplings recorded after 16 years. They found that seedling and sapling populations did not reflect the relative abundance of mature canopy species. Oak and alder were the most common mature species but both produced few seedlings. In the unfenced plots few seedlings survived >2 years. In fenced areas saplings of sycamore and ash would probably fill gaps created in the alder canopy. In the unfenced grazed areas saplings of hawthorn and ash were most likely to replace mature alder trees.

Livestock (sheep and ponies) exclusion over a 20-year period in another upland alder woodland (W7) in north Wales caused dramatic differences in the composition and structure of the vegetation community. Within the fenced area shrub, tree and bryophyte species coverage all increased, while the cover of grasses and forbs declined. The exclusion of stock led to increases in palatable (*Rubus fruticosus*) and shade tolerant woodland species (*Carex laevigata* and *Eurhynchium praelongum*). Leaf litter and deadwood accumulated on the surface rather than being incorporated into the soil by trampling. The presence of accumulated litter favoured species that were able to germinate and become established under this organic layer (Latham & Blackstock 1998).

In coppiced areas, first-year seedlings densities were in the order of 20 m². Within fenced areas, ash regeneration was prolific. The authors suggest that a rapid successional development towards ash woodland will probably occur within fenced enclosures (Latham & Blackstock 1998).

***Betula pubescens* L.: W5, W6, W7**

Grazed/clipped birch trees grew larger leaves with higher K, Ca and N content compared with untreated plants. Clipped trees were preferred by snails and large herbivores suggesting they are more palatable. The authors suggest that the removal of apical dominance in clipped trees releases many growing points, which compete for nutrients such as nitrogen (Danell and others 1997).

Grazing of upland tree species in Cumbria resulted in soil disturbance and improved regeneration of birch and ash. Recruitment rates did not limit regeneration in any plot although sapling/seedling ratios were higher for birch than ash; this could be attributed to the greater palatability of ash leaves to sheep. Ash was restricted to nutrient rich flushes within the alluvial woods owing to a higher soil phosphorus requirement and was able to survive complete defoliation four times within a single growing season. A greater proportion of tree seedlings reached sapling height in winter grazed plots despite more saplings being damaged by grazing. Growth increment was greatest in ash in summer grazed plots and it responded quickly to the removal of competition by herbaceous swards (Hester and others 1996).

Woodland regeneration in the New Forest reflects periods in which grazing pressure was relaxed due to the removal of deer in 1851 and reduced populations of cattle and ponies (Peterken & Tubbs 1965).

Voies (*Microtus agrestis* L.) have been reported to feed on seed/seedlings of birch and damage trees following the enclosure of ground (Miles & Kinnaird 1979b). Grazing of seedlings by deer, sheep and hares prevents regeneration of birch, although at the same time the continuous trampling by animals creates suitable conditions for birch regeneration (Lähde & Raulo 1977; Miles & Kinnaird 1979b). However, only 4 years after removal of grazing animals from a *B. pubescens* wood, the mean moss and litter depth had increased from 2 to 8 cm and birch seedling growth was minimal (Miles & Kinnaird 1979b). Kinnaird (1974) found that saplings survived browsing for up to 10 years in grass swards, but up to 31 years in longer heather swards with substantial alterations to the growth and appearance of browsed plants. Bark stripping by red deer, horses, cattle and squirrels has been noted by Miles & Kinnaird (1979b). Deer display a preference for birch at bud burst (Miller 1971), although palatability of birch for insects and other herbivores declines with intensity of grazing (Edwards & Wratten 1982).

***Dryopteris dilatata*: W5, W6, W7**

The presence/absence of indicator species in plant associations can be used as a descriptive and predictive management tool for understanding successional patterns across the landscape. *Dryopteris dilatata* is a good indicator of grazing pressure (Gillingham and others 2000); when sheep (*Ovis aries*) were excluded from pasture in North Wales *Dryopteris dilatata* emerged as a dominant species in the sward (Hill and others 1992).

Vigour and abundance of *Dryopteris dilatata* is affected by deer foraging (Oct.-April). Removal of any portion of the rhizome by deer greatly reduced vegetative growth during the following summer. Plants with more than 25% of rhizomes removed produced no growth, while removal of 1-25% greatly retarded growth; sometimes with abundant foliage being produced late in the growing season (Gillingham and others 2000).

***Fraxinus excelsior* L.**

Grazing of upland tree species in Cumbria resulted in soil disturbance and improved regeneration of birch and ash. Recruitment rates did not limit regeneration in any plot although sapling/seedling ratios were higher for birch than ash; this could be attributed to the greater palatability of ash leaves to sheep. Ash was restricted to nutrient rich flushes within alluvial woods due to their higher soil phosphorus requirement and was able to survive complete defoliation four times within a single growing season. A greater proportion of tree seedlings reached sapling height in winter grazed plots despite more saplings being damaged by winter grazing. Growth increment was greatest in ash in summer grazed plots and ash responded quickly to the removal of competition by herbaceous swards (Hester and others 1996).

Grazing of grass swards by rabbits improved the establishment of ash seedlings, but can also result in seedling mortality if too intensive. Deer frequently damage saplings by rubbing. Mice and voles can cause high seedling mortality by severing roots while tunneling or eating seed (Wardle 1961).

***Iris pseudacorus* L.: W5**

Seeds of this species are not mentioned in the recorded diet of any bird (Witherby and others 1938-41). Damage by vertebrate and invertebrate grazers is negligible (ignored by cattle,

sheep, ponies, goats and rabbits) and ingestion of leaves by cattle is known to be harmful (Forsyth 1976). There is a report of it been eaten down to the rhizomes by cattle if herbage is short in the autumn, and the early season leaves may be nibbled by sheep (Sutherland 1990). However, leaves are brittle and susceptible to damage by trampling, and thus the species is absent from areas of pronounced disturbance from grazers (Sutherland 1990).

***Salix* spp.**

Wild ungulates significantly reduce height growth and reproductive output of willow, poplar and alder species. When domestic stock, elk and deer are excluded from the riparian zone, the riparian shrubs quickly recover (Case & Kauffman 1997).

Salix cinerea and *Betula pendula* saplings respond to water shortage by increasing soluble nitrogen in tissues. This indirectly leads to an improvement in the feeding efficiency of Lepidopteran herbivores (*Smerinthus ocellatus*, *Phalera bucephala*, and *Mimas tiliae*) by increasing digestive efficiency and growth rates of Lepidopteran larvae in situations where plants are growing in soils of low nitrogen status. Thus, *S. cinerea* and *B. pendula* are vulnerable to increased rates of Lepidopteran herbivory following drought stress (Thomas & Hodkinson 1991).

***Sambucus nigra* L.**

Elder leaves contain cyanogenic glycosides from which hydrogen cyanide is released by enzyme action. This renders the leaves unpalatable which is reflected by the low numbers of insects on elder compared with other woody species. Deer, however, have been reported to browse preferentially on elder (Bobek and others 1979).

***Urtica dioica* L.**

Avoided by rabbits and cattle, but eaten by other herbivores. May be destroyed by continued trampling (Greig-Smith 1948).

(ii) Coppicing / mowing

The fertile soils of alluvial forests produce woodlands with high potential productivity and traditionally stands of alder and willow have been managed as coppice. Coppice management reduces the ecosystem biomass and soil nutrient pool, although soil nutrient availability is generally unaffected. This is due to warmer soil temperatures, invasion by broom, frequent soil disturbance and burning, which accelerate nutrient turnover and maintain soil nutrient supply. Reduced nutrient pools in the soil organic layers are likely to limit the capacity of coppice wood ecosystems to regenerate if heavy disturbance such as soil erosion occurs (Holscher and others 2001). Many other broadleaf species coppice strongly after felling, particularly ash and hazel (Wardle 1961), Elder will re-sprout from stumps following cutting (Metcalf 1948).

Alluvial forests can become established on seasonally flooded fens when mowing or grazing is abandoned. Mowing and removal of biomass on a regularly flooded fen did not prevent establishment of *Alnus glutinosa*, although it hindered sapling growth. The small patches of bare ground created by mowing activities facilitated succession (Gusewill & Le Nedic 2004).

The restoration of an abandoned species rich fen-meadow in Denmark was assessed by (Vinther & Hald 2000). Removal of alder scrub followed by either mowing or grazing increased species diversity and encouraged the establishment of biennials and hemicryptophytes. Grazing lead to the development of sedge and rush communities with geophytes, whereas mowing resulted in the dominance of grasses, primarily with phanerophytes and chamaephytes. *Urtica* will not withstand repeated cutting (Greig-Smith 1948).

(iii) Invasion by weeds

Competition is considered to be a determining factor in the zonation of a species along a flooding gradient. Species richness on a frequently flooded riparian shore is principally controlled by abiotic factors such as flooding depth and duration, however at higher elevations plant interactions are more significant (Buttery & Lambert 1965; Lenssen and others 1999). Several foreign species introduced to the UK in the 19th Century for ornamental reasons are aggressively dominant and have created a serious problem in some areas. Japanese Knotweed, Himalayan Balsam and Giant Hogweed are rapidly spreading along river systems and currently pose a threat to wetland habitats, including alluvial forests.

Introduced from Japan, the Giant Knotweeds (*Fallopia japonica* and *F. sachalinensis*) is highly invasive where soils are acidic and well-drained, inundation is by eutrophic water, and when river fluctuations are altered by human activities (eg embankments, deforestation). On granite substrates, *F. japonica* will invade deforested river margins and softwood forests of willow and poplar, but will not manage to invade later successional stages of riparian forest in the presence of oak, elm or ash. On calcareous floodplains, *Fallopia* species are scattered and expansion is checked by competition with native species (Schnitzler & Muller 1998).

Buddleia davidii seedlings can withstand a soil water potential of -2.8 bars compared to *B. pendula* at -1.6 bars (Humphries and others 1982).

(iv) Pests / diseases

A range of insect, nematode, fungal and bacterial parasites affecting birch is given by Atkinson, (1992). An insignificant number of ash seedlings tend to die from insect attack, but widespread damage to leaf surfaces caused by Lepidopterous larvae reduces the ability of seedlings to survive the winter. A list of insect, nematode, fungal and bacterial parasites affecting ash is given by Wardle (1961). The range of parasites for *Iris pseudacorus* is given by Sutherland (1990).

2.3.5 References

2.3.5.1 Literature detailing Residual Alluvial Forest characteristics and eco-hydrological requirements at the whole ecosystem scale

AMOROS, C. and others. 1987a. The reversible process concept applied to the environmental management of large river ecosystems. *Environmental Management*, 11, 607-617.

ATKINS & ENTEC. 2003. *Habitat and species summary guidance notes*.

- BARSOUM, N. 2001. Regeneration: requirements and promotion measures. *In*: F. LEFÈVRE, and others, eds. *EUFORGEN Technical Bulletin: In situ conservation of Populus nigra*, 16-24. Rome: International Plant Genetic Resources Institute.
- BERNADZKI, E. and others. 1998. Compositional dynamics of natural forests in the Bialowieza National Park, northeastern Poland. *Journal of Vegetation Science*, 9(2), 229-238.
- BISSARDON, M., GUIBAL, L., & RAMEAU, J-C. *Corine biotopes: Version originale Types d'habitats français*. Available from:
http://www.natura2000.espaces-naturels.fr/biotope/pdf/corine_biotopes_chapitre_4.pdf
- BRADLEY, C.E., & SMITH, D.G. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany*, 64, 1433-1442.
- BRAVARD, J.-P. and others. 1994. The Rhône River: a large alluvial temperate river – Chapter 20. *In*: CALOW, P., & PETTS, G.E., eds. *The rivers handbook 2*, 426-447.
- BRAVARD, J.-P., & PEIRY, J.-L. 1993. La disparition du tressage fluvial dans les Alpes françaises sous l'effet de l'aménagement des cours d'eau (19-20^{ème} siècle). *Zeitschrift Geomorph.*, 88, 67-79.
- BROWN, A.G., HARPER, D., & PETERKEN, G.F. 1997. European floodplain forests: structure, functioning and management. *Global ecology and biogeography letters*, 6, 169-178.
- BRINSON, M.M. 1990. Riverine forests. *In*: LUGO, A.E., BRINSON, M., & BROWN, S., eds. *Ecosystems of the World 15. Forested Wetlands*, 87-141 Amsterdam: Elsevier.
- BUCHHOLZ, K. 1981. Effects of minor drainages on woody species distributions in a successional floodplain forest. *Canadian Journal of Forest Research*, 11, 671-676.
- BUSSE, L.B., & GUNKEL, G. 2002. Riparian alder fens - source or sink for nutrients and dissolved organic carbon? 2. Major sources and sinks. *Limnologia*, 32(1), 44-53.
- CLUZEAU, C. 1992. Dynamique de colonisation de l'Aulne glutineux, *Alnus glutinosa* (L) dans un marais eutrophe de la plaine alluviale du Rhone. *Annals Science Forestier*, 49, 539-548.
- CORDES, L.D., HUGHES, F.M.R., & GETTY, M. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: The Red Deer River, Alberta, Canada. *Journal of Biogeography*, 24, 675-695.
- CORINE. 1988. *Corine biotopes project. Technical handbook Volume 1*.
- DÉCAMPS, H. 1996. The renewal of floodplain forests along rivers : a landscape perspective. *Verh. Internat. Verein. Limnol.* 26, 35-59.

- DÉCAMPS, H., & TABACCHI, E. 1994. Species richness in vegetation along river margins. *In: GILLER, P.S., HILDREW, A.G., RAFAELLI, D.G., eds. Aquatic Ecology: Scale, Pattern and Process*, 1-12. London: Blackwell.
- DE FARRARI, C.M., & NAIMAN, R.J. 1994. A multi-scale assessment of the occurrence of exotic plants in the Olympic Peninsula, Washington. *Journal of Vegetation Science*, 5, 247-258.
- DEVILLERS, P., & DEVILLERS-TERSCHUREN, J. 1993. *A classification of Palaearctic habitats*. Strasbourg: Council of Europe.
- EC ENVIRONMENT. 1991. *Biotopes Manual*. A method to identify and describe consistently sites of major importance for nature conservation (Data specifications, part 2, vol. 3). Corine Luxembourg: Commission of the European Communities, EUR 12587/3.
- EC 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*, L 206 (22/7/92): 7-49.
- EC ENVIRONMENT. 2003. *Interpretation manual of European Union Habitats*. European Commission DG Environment, Brussels EUR-25. Available from: http://europa.eu.int/comm/environment/nature/nature_conservation/useful_info/documents_publications/index_en.htm
- ELLENBERG, H. and others. 1992. Ziegerwerte von Pflanzen in Mitteleuropa (indicator values of plants in Central Europe). *Scripta Geobotanica*, 18, 1-258.
- EUNIS European Nature Information System habitat classification. Available from: <http://eunis.eea.eu.int/habitats.jsp>
- FRYE, R.J., & QUINN, J.A. 1979. Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. *Bull. of the Torrey Bot. Club*, 106(4), 334-345.
- GURNELL, A. 1995. Vegetation along river corridors: Hydrogeomorphological interactions. *In: A.M. GURNELL., & G.E. PETTS, eds. Changing River Channels*, 237-260. Chichester: Wiley.
- HARPER, D. and others. 1997. The distribution and abundance of riparian trees in English lowland floodplains. *Global ecology and biogeography letters*, 6, 297-306.
- HARRIS, R.R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a Californian alluvial stream. *American Midland Naturalist*, 118(2), 393-405.
- HOBBS, R.J., & HUENNEKE, L.F. 1992. Disturbance, diversity and invasion: implications for conservation. *Conservation Biology*, 6, 324-337.
- HOLSCHER, D., SCHADE, E., & LEUSCHNER, C. 2001. Effects of coppicing in temperate deciduous forests on ecosystem nutrient pools and soil fertility. *Basic and Applied Ecology* 2(2), 155-164.

- HUGHES, F.M.R. 1994. Environmental change, disturbance and regeneration in semi-and floodplain forests Chapter 17. *In: A.C. MILLINGTON, & K. PYE, ed. Environmental change in drylands: Biogeographical perspectives*, 321-345. John Wiley & Sons Ltd..
- HUGHES, F.M.R. 1997. Floodplain biogeomorphology. *Progress in physical geography*, 21(4), 501-529.
- JENSEN, K. 1998. Species composition of soil seed bank and seed rain of abandoned wet meadows and their relation to aboveground vegetation. *Flora*, 193, 345-359.
- JOHNSON, C.A. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. *Ecol. Monogr.*, 64, 45-84.
- JNCC web site
<http://www.jncc.gov.uk/protectedsites/sacselection/habitat.asp?FeatureIntCode=H91E0>.
 Protected sites habitat accounts – Forests. 91E0 Residual alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, and *Salicion albae*).
- KALLIOLA, R., & PUHAKKA, M. 1988. River dynamics and vegetation mosaicism: A case study of the River Kamajonka, northernmost Finland. *Journal of Biogeography*, 15, 703-719.
- KLÖTZLI, F. 1970. Eichen-, Edellaub- und Bruchwälder der Britischen Inseln. *Schweiz, Zeit. F. Forstwes*, 121, 329-366.
- LONSDALE, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522-1536.
- MAHONEY, J. M., & ROOD, S.B. 1991. A device for studying the influence of a declining water table on poplar growth and survival. *Tree Physiology*, 8, 305-314.
- MAHONEY, J.M., & ROOD, S.B. 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management*, 54, 141-156.
- MAHONEY, J.M., & ROOD, S.B. 1993. A model for assessing the effects of altered river flows on the recruitment of riparian cottonwoods. *In: Riparian management, common threads and shared interests. USDA Forest Service General Technical Report RM, 226, 228-232.*
- MARSTON, R.M. and others. 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology* 13, 121-131.
- McVEAN, D.N. 1956. Ecology of *Alnus glutinosa* (L.) Gaertn. V Notes on some British alder populations. *Journal of Ecology*, 44, 321-330.
- MOSS, C.E., RANKIN, W.M., & TANSLEY, A.G. 1910. The woodlands of England. *New Phytologist*, 9, 113-149.
- NANSON, G.C., & CROKE, J.C. 1992. A generic classification of floodplains. *Geomorphology*, 4, 459-486.

- PAUTOU, G., GIREL, J., & BOREL, J.-L. 1988. Initial repercussions and hydroelectric developments in the French Upper Rhône Valley: A lesson for predictive scenarios, propositions. *Environ. Management*, 16(2), 231-242.
- PEARSALL, W.H. 1938. The soil complex in relation to plant communities II. Characteristic woodland soils. *Journal of Ecology*, 26, 180-194.
- PEIRY, J.-L., SALVADOR, P.G., & NOUGUIER, F. 1994. L'incision des rivières dans les Alpes du Nord: Etat de la question. *Rev. de Geog. Alp. De Lyon*, 69, 47-56.
- PETERKEN, G. F. 1993. *Woodland Conservation and Management 2nd Edition*. London: Chapman & Hall.
- PETERKEN, G.F. 1996. *Natural woodland. ecology and conservation in northern temperate regions*. Cambridge: Cambridge University Press.
- PETERKEN, G. F., & HUGHES, F.M.R. 1998. Limitations and opportunities for restoring floodplain forest in Britain. In: R.G. BAILEY., P.V. JOSÉ & B.R. SHERWOOD, eds. *United Kingdom Floodplains*, 197-215. West Yorkshire: Westbury Academic & Scientific Publishing.
- PETTS, G.E. 1989. Historical analysis of fluvial hydrosystems. In: G.E. PETTS, ed. *Historical Change of Large Alluvial Rivers: Western Europe*, 1-18. Chichester: John Wiley & Sons Ltd.
- PIEGAY, H., SALVADOR, P-G., & ASTRADE, L. 2000. Réflexions relatives à la variabilité spatiale de la mosaïque fluviale à l'échelle d'un tronçon. *Z. Geomorph. N. F.* 44, 3, 317-342
- POKORNY, P., KLIMESOVA, J., & KLIMES, L. 2000. Late holocene history and vegetational dynamics of a floodplain alder carr: A study from eastern Bohemia, Czech Republic. *Folia Geobotanica*, 35(1), 43-58.
- PRIEDITIS, N. 1997. *Alnus glutinosa* – dominated wetland forests of the Baltic region: community structure, syntaxonomy and conservation. *Plant Ecology*, 129, 49-94.
- RODWELL, J.S. 1991a. *British plant communities. Volume 1: Woodlands and scrub*. Cambridge University Press, Cambridge.
- RODWELL, J.S. 1991b. *British Plant Communities. Volume 2. Mires and heaths*. Cambridge: Cambridge University Press.
- RODWELL, J.S. (ed.) and others. 1991. *British Plant communities Volume 1. Woodlands and Scrub*. Cambridge: Cambridge University Press.
- RODWELL, J., & DRING, J. 2001. European significance of British woodland types. *English Nature Reports*, No. 460. Peterborough: English Nature.

- ROOD, S.B., & MAHONEY, J.M. 1990. The collapse of riparian poplar forests downstream from dams on the western prairies: Probable causes and prospects for mitigation. *Environmental Management*, 14, 451-464.
- ROUX, A.L. and others 1989. Ecological changes of the French Upper Rhône River since 1750 – Chapter 18. In: G.E. PETTS, ed. *Historical change of large alluvial rivers: Western Europe*, 323-350. John Wiley & Sons.
- SANCHEZ-PEREZ, J.M. and others. 1993. Nutrient content in alluvial soils submitted to flooding in the Rhine alluvial deciduous forest. *Acta Oecologica*, 14(3), 371-387.
- SCHNITZLER, A. 1995. Successional status of trees in Gallery forest along the river Rhine. *Journal of Vegetation Science*, 6(4), 479-486.
- SEGELQUIST, C.A., SCOTT, M.L., & AUBLE, G.T. 1993. Establishment of *Populus deltoides* under simulated alluvial groundwater declines. *Am. Midl. Nat.*, 130, 274-285.
- SIEBEL, H.N., & BLOM, C.W.P.M. 1998. Effects of irregular flooding on the establishment of tree species. *Acta Botanica Neerlandica*, 47, 231-240.
- SOUTHALL, E.J., DALE, M.P., & KENT, M. 2003a. Floristic variation and willow carr development within a southwest England wetland. *Applied Vegetation Science*, 6, 63-72.
- STOHLGREN, T.T. and others 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, 69, 25-46.
- STRENG, D.R., GLITZENSTEIN, J.S., & HARCOTBE, P.A. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs*, 59, 177-204.
- STROMBERG, J. C., & PATTEN, D.T. 1990. Riparian vegetation instream flow requirements: A case study from a diverted stream in the eastern Sierra Nevada, California, USA. *Environmental Management*, 14, 185-194.
- STROMBERG, J. C., & PATTEN, D.T. 1992. Mortality and age of black cottonwood stands along diverted and undiverted streams in the eastern Sierra Nevada, California. *Madroña*, 39(3), 205-233.
- TAPPER, P.-G. 1993. The replacement of *Alnus glutinosa* by *Fraxinus excelsior* during succession related to regenerative differences. *Ecography*, 16(3), 212-18.
- TAPPER, P.-G. 1996. Tree dynamics in a successional *Alnus-Fraxinus* woodland. *Ecography*, 19, 237-244.
- TYREE, M.T. and others. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta – a possible factor in the decline of the ecosystem? *Tree Physiology*, 14, 455-466.

2.3.5.2 Literature examining the specific water resource and nutrient requirements of key component species of Residual Alluvial Forests

- AERTS, R., DECALUWE, H., & KONINGS, H. 1992. Seasonal allocation of biomass and nitrogen in 4 *Carex* species from mesotrophic and eutrophic fens as affected by nitrogen supply. *Journal of Ecology*, 80(4), 653-664.
- AMSBERRY, L. and others. 2000. Clonal integration and the expansion of *Phragmites australis*. *Ecological Applications*, 10(4), 1110-1118.
- ARMSTRONG, J., & ARMSTRONG, W. 1991. A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. ex Steud. *Aquatic Bot.*, 39, 75-88.
- ATKINSON, M.D. 1992. Biological Flora of the British Isles: *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. *Journal of Ecology*, 80, 837-870.
- ATKINSON, M.D., & ATKINSON, E. 2002. Biological Flora of the British Isles: *Sambucus nigra* L. *Journal of Ecology*, 90, 895-923.
- BAAR, J. and others. 2002. Ectomycorrhizal root development in wet Alder carr forests in response to desiccation and eutrophication. *Mycorrhiza*, 12(3), 147-151.
- BARCLAY, A.M., & CRAWFORD, R.M.M. 1982. Plant survival under strict anaerobiosis. *Journal of Experimental Botany*, 33, 541-549.
- BARSOUM, N. 1998. A comparison of vegetative and non-vegetative regeneration strategies in *Populus nigra* and *Salix alba*. PhD Thesis. Department of Geography, University of Cambridge.
- BARSOUM, N., & HUGHES, F.M.R. 1998. Regeneration response of black poplar to changing river levels. In: H.WHEATER & C. KIRBY, eds. *Hydrology in a changing environment - Vol. 1*, 397-412. Wiley.
- BATES, G.H. 1933. The great stinging nettle. *J. Minist.Agri.*, 39, 12.
- BATZLI, J.M., & DAWSON, J.O. 1997. Physiological and morphological responses of Red alder and Sitka alder to flooding. *Physiologia Plantarum*, 99(4), 653-663.
- BEKKER, R.M. and others. 1998. Soil nutrient input effects on seed longevity: a burial experiment with fen-meadow species. *Functional Ecology*, 12(4), 673-682.
- BERRY, A.M., & TORREY, J.G. 1985. Seed germination, seedling inoculation and establishment of *Alnus* spp. in containers in greenhouse trials. *Plant and Soil*, 87(1), 161-73.
- BLACK, M., & WAREING, P.F. 1954. Photoperiodic control of germination in seed of birch (*Betula pubescens* Ehrh.). *Nature*, 174, 705-706.
- BLANCH, S.J., WALKER, K.F., & GANF, G.G. 2000. Water regimes and littoral plants in four weir pools of the River Murray, Australia. *Regulated Rivers and Management*, 16(5), 445-456.

- BLOM, C.W.P.M., & VOESENEK, L.A.C.J. 1996. Flooding: the survival strategies of plants. *Trends in Ecology and Evolution*, 11, 290-295.
- BOBEK, B. and others. 1979. Deer pressure on forage in a deciduous forest. *Oikos*, 32, 373-380.
- BOLLI, R. 1994. Revision of the genus *Sambucus*. *Dissertationes Botanicae*, 223, 1-227.
- BOOT, R., RAYNAL, D.J., & GRIME, J.P. 1986. A comparative study of the influence of drought stress on flowering in *Urtica dioica* and *Urtica urens*. *Journal of Ecology*, 74(2), 85-95.
- BOYD, J.M. 1992. Sycamore - a review of its status in conservation in Great Britain. *Biologist*, 39(1), 29-31.
- BRÄNDLE, R., & CRAWFORD, R.M.M. 1987. Rhizome anoxia tolerance and habitat specialization in wetland plants. In: R.M.M. CRAWFORD, ed. *Plant Life in Aquatic and Amphibious Habitats*, 397-410. Oxford: Blackwell Scientific Publications.
- BRANDTBERG, P.O., BENGTSSON, J., & LUNDKVIST, H. 2004. Distributions of the capacity to take up nutrients by *Betula* spp. and *Picea abies* in mixed stands. *Forest Ecology and Management*, 198(1), 193-208.
- BÜCHEL, H.B., & GROSSE, W. 1990. *Tree Physiology*, 6, 247-256.
- BURDON, J.J., ERICSON, L., & MULLER, W.J. 1995. Temporal and spatial changes in a metapopulation of the rust pathogen *Triphragmium ulmariae* and its host, *Filipendula ulmaria*. *Journal of Ecology*, 83(6), 979-989.
- BUSSE, L.B., & GUNKEL, G. 2002. Riparian alder fens - source or sink for nutrients and dissolved organic carbon? 2. Major sources and sinks. *Limnologia*, 32(1), 44-53.
- BUTTERY, B.R., & LAMBERT, J.M. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. I. The competition mechanism. *Journal of Ecology*, 53, 163-181.
- CASE, R.L., & KAUFFMAN, J.B. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in Northwest Oregon. *Northwest Science*, 71(2), 115-126.
- CHAUVET, E. 1987. Changes in the chemical composition of alder poplar and willow leaves during decomposition in a river. *Hydrobiologia* 148, 35-44.
- CHESSON, P.L., & CASE, T.J. 1986. Overview: Nonequilibrium community theories: chance, variability, history and coexistence. In: J. DIAMOND & T.J. CASE, eds. *Community Ecology*, 229-239. New York: Harper and Row.

- CHOO, Y.S., & ALBERT, R. 1999. Mineral ion, nitrogen and organic solute pattern in sedges (*Carex* spp.) - a contribution to the physiotype concept. II Culture experiments. *Flora*, 194(1), 75-87.
- CLAESSENS, H., & THIBAUT, A. 1994. Ou peut-on cultiver l'aulne glutineux avec succes? *Silva Belgica*, 101, 7-12.
- COOPS, H., & VAN DER VELDE, G. 1995. Seed dispersal, germination and seedling growth of 6 helophyte species in relation to water-level zonation. *Freshwater Biology*, 34(1), 13-20.
- CRAWFORD, R.M.M. 1982. In: O.L. LANGE and others, eds. *Encyclopedia of Plant Physiology*, Vol. 12B, 453-477. Berlin: Springer-Verlag.
- DANELL, K., HAUKIOJA, E., & HUSSDANELL, K. 1997. Morphological and chemical responses of mountain birch leaves and shoots to winter browsing along a gradient of plant productivity. *Ecoscience*, 4(3), 296-303.
- DAVIES, W.J., & ZHANG, J. 1991. Root signals and the regulation of growth and development of plants in drying soils. *Annual Review Plant Physio. Mol. Biol.*, 42, 55-76.
- DIENST, M., SCHMIEDER, K., & OSTENDORP, W. 2004. Effects of water level variations on the dynamics of the reed belts of Lake Constance. *Limnologica*, 34(1-2), 29-36.
- DILLY, O. and others. 1999. Microbial processes and features of the microbiota in histosols from a black alder (*Alnus glutinosa* (L.) Gaertn.) forest. *Geomicrobiology Journal* 16(1), 65-78.
- DUNSFORD, S.J., FREE, A.J., & DAVY, A.J. 1998. Acidifying peat as an alternative to the reconstruction of lowland heath on arable soil: a field experiment. *Journal of Applied Ecology*, 35(5), 660-672.
- DUVIGNEAUD & DENAYER DE SMET. 1970.
- DYKES, W.R. 1974. *The Genus Iris*. Cambridge: Cambridge University Press.
- DYMES, T.A. 1920. Notes on the life-history of *Iris-pseudacorus*, Linn., with special reference to seeds and seedlings. *Proceedings of the Linnean Society of London*, 132, 59-63.
- EDWARDS, P.J., & WRATTEN, S.D. 1982. Wound-induced changes in palatability in birch (*B. pubescens* ssp. *pubescens*). *American Naturalist*, 120, 816-818.
- ELLENBERG, H. 1979. Zeigerwerte von Gefässpflanzen Mitteleuropas. *Scripta Geobotanica*, 9, 1-122.
- FALIŃSKA, K. 1986. Demography of *Iris pseudacorus* L. populations in abandoned meadows. *Ekologia Polska*, 34, 583-613.
- FALKENGRENGRERUP, U. 1995. Interspecies differences in the preference of ammonium and nitrate in vascular plants. *Oecologia* 102(3), 305-311.

- FORSYTH, A.A. 1976. *British Poisonous Plants*. London: HMSO.
- FRYE, J., & GROSSE, W. 1992. Growth responses to flooding and recovery of deciduous trees. *Zeitschrift für Naturforschung C - A Journal of Biosciences*, 47(9-10), 683-689.
- GARDINER, A.S. 1968. *The reputation of birch for soil improvement. A literature review*. Forestry Commission Research and Development Paper 67. London: HMSO.
- GILBERT, O.L. 1991. *The Ecology of Urban Habitats*. London: Chapman & Hall.
- GILL, J.A., & DAVY, A.J. 1983. Variation and polyploidy within lowland populations of the *B. pendula*/*B. pubescens* complex. *New Phytologist*, 94, 433-451.
- GILLINGHAM, M.P., PARKER, K.L., & HANLEY, T.A. 2000. Partial consumption of shield fern, *Dryopteris dilatata*, rhizomes by black-tailed deer, *Odocoileus hemionus sitkensis*, and its potential implications. *Canadian Field Naturalist*, 114(1), 21-25.
- GIMINGHAM, C.H. 1984. Ecological aspects of birch. *Proceedings of the Royal Society of Edinburgh*, 85B, 65-72.
- GRANSTRÖM, A., & FRIES, C. 1985. Depletion of viable seeds of *Betula pubescens* and *Betula verrucosa* sown onto some north Swedish forest soils. *Canadian Journal of Forest Research*, 15, 1176-1180.
- GOOD, J.E.G. and others. 1992. Species and clonal variation in growth responses to waterlogging and submersion in the genus *Salix*. *Proceedings of the Royal Society of Edinburgh Section B - Biological Sciences*, 98, 21-48.
- GREIG-SMITH, P. 1948. Biological flora of the British Isles: *Urtica dioica* L. *Journal of Ecology*, 36, 339-355.
- GRIME, J.P., HODGSON, J.G., & HUNT, R. 1989. *Comparative Plant Ecology. A functional Approach to Common British Species*. London: Unwin Hyman.
- GROSSE, W., BODDENBERG, A., & FUJITA, H. 1992. *Ecological Research* (submitted)
- GROSSE, W. FRYE, J., & LATTERMANN, S. 1992. Root aeration in wetland trees by pressurized gas-transport. *Tree Physiology*, 10(3), 285-295.
- GRUBB, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*, 52, 107-145.
- GUSWELL, S., & KOERSELMAN, M. 2002. Variation in nitrogen and phosphorus concentrations of wetland plants *Perspectives in Plant Ecology Evolution and Systematics*, 5(1), 37-61.
- GUSWELL, S., & LE NEDIC, C. 2004. Effects of winter mowing on vegetation succession in a lakesore fen. *Applied Vegetation Science*, 7(1), 41-48.

- HACKE, U., & SAUTER, J.J. 1996. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus basamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology*, 111(2), 413-17.
- HANHIJARVI, A.M., & FAGERSTEDT, K.V. 1995. Comparison of carbohydrate utilization and energy-charge in the yellow flag iris (*Iris pseudocorus*) and garden iris (*Iris germanica*) under anoxia. *Physiologia Plantarum*, 93(3), 493-497.
- HARPER, J.L. 1977. *Population Biology of Plants*. London: Academic Press.
- HARRISON, A.F., MILES, J., & HOWARD, D.M. 1988. Phosphorous uptake by birch from various depths in the soil. *Forestry*, 61, 349-358.
- HASLAM, S.M. 1973. Some aspects of the life history and autecology of *Phragmites communis* Trin.: A review. *Polskie Archiwum Hydrobiologii*, 20, 79-100.
- HEINRICH, W., & SCHALLER, G. 1987. Veränderungen von Ökosystemstrukturen im Einflussbereicheines Düngemittelwerkes. *Hercynia*, 24, 328-334.
- HELLIWELL, D.R. 1974. *The growth of sycamore (Acer pseudoplatanus L. and Betula verrucosa Ehrh.) seedlings in different soils*. Merlewood Research and Development Paper 58.
- HESTER, A.J., MITCHELL, F.J.G., & KIRBY, K.J. 1996. Effects of season and intensity of sheep grazing on tree regeneration in a British upland woodland. *Forest Ecology and Management*, 88(1-2), 99-106.
- HETHERINGTON, A.M., HUNTER, M.I.S., & CRAWFORD, R.M.M. 1983. Survival of *Iris* species under anoxic conditions. *Ann. Bot.*, 51, 131-133.
- HILL, M.O., & STEVENS, P.A. 1981. The density of viable seed in soils of forest plantations in upland Britain. *Journal of Ecology*, 69, 693-709.
- HILL, M.O., EVANS, D.F., & BELL, S.A. 1992. Long-term effects of excluding sheep from hill pastures in north Wales. *Journal of Ecology*, 80(1), 1-13.
- HO, Y.B. 1979a. Chemical composition studies on some aquatic macrophytes in three Scottish lochs. Part 1. Chlorophyll, ash, carbon, nitrogen and phosphorous. *Hydrobiologia*, 63, 161-166.
- HO, Y.B. 1979b. Chemical composition studies on some aquatic macrophytes in three Scottish lochs. Part 2. Potassium, sodium, calcium, magnesium, and iron. *Hydrobiologia*, 64, 209-214.
- HOLSCHER, D., SCHADE, E., & LEUSCHNER, C. 2001. Effects of coppicing in temperate deciduous forests on ecosystem nutrient pools and soil fertility. *Basic and Applied Ecology* 2(2), 155-164.
- HORGAN, J.M., & WAREING, P.F. 1980. Cytokinins and the growth responses of seedlings of *Betula pendula* Roth and *Acer pseudoplatanus* L. to nitrogen and phosphorous deficiency. *Journal of Experimental Botany*, 31, 525-532.

- HUMPHRIES, R.N., JORDAN, M.A., & GUARINO, L. 1982. The effect of water stress on the mortality of *Betula pendula* Roth and *Buddleia davidii* Franch. seedlings. *Plant and Soil*, 64, 273-276.
- HUSS-DANELL, K., & SELLSTEDT, A. 1985. Nitrogenase activity in response to darkening and defoliation of *Alnus incana*. *Journal of Experimental Botany*, 36, 1352-1358.
- INGESTAD, T. 1970. A definition of optimum nutrient requirements in birch seedlings. I. *Physiologia Plantarum*, 23, 1127-1138.
- INGESTAD, T. 1971. A definition of optimum nutrient requirements in birch seedlings. II. *Physiologia Plantarum*, 24, 1127-1138.
- JACKSON, M.B., & ATTWOOD, P.A. 1996. Roots of willow *Salix viminalis* L. showed marked tolerance to oxygen shortage in flooded soils and in solution culture. *Plant and Soil*, 187(1), 37-45.
- JOHANSSON, M., & NILSSON, C. 2002. Responses of riparian plants to flooding in free-flowing and regulated boreal rivers: an experimental study. *Journal of Applied Ecology*, 39, 971-986.
- JONES, E.W. 1944. Biological flora of the British Isles *Acer pseudo-platanus* L. *Journal of Ecology*, 32, 215-252.
- KAELKE, C.M., & DAWSON, J.O. 2003. Seasonal flooding regimes influence survival, nitrogen fixation and the partitioning of nitrogen and biomass in *Alnus incana* ssp. *rugosa*. *Plant and Soil*, 254(1), 167-177.
- KARLSSON, P.S., & WEIH, M. 2001. Soil temperatures near the distribution limit of the mountain birch (*Betula pubescens* ssp. *czerepanovii*): Implications for seedling nitrogen economy and survival. *Arctic, Antarctic and Alpine Research*, 33(1), 88-92.
- KASSAS, M. 1951. Studies in the ecology of Chippenham Fen. II. Recent history of the Fen, from evidence of historical records, vegetational analysis and tree-ring analysis. *Journal of Ecology*, 39, 19-32.
- KAUNISTO, S. 1981. Birch regeneration in a peat cut-away area. *Suo*, 32, 53-60.
- KAUPPI, A., RINNE, P., & FERM, A. 1987. Initiation, structure and sprouting of dormant basal buds in *Betula pubescens*. *Flora*, 179, 55-83.
- KAZDA, M., 1995. Changes in alder fens following a decrease in the ground-water table - results of a geographical information system application. *Journal of Applied Ecology*, 32(1), 100-110.
- KEDDY, P.A., & ELLIS, T.H. 1985. Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct responses? *Canadian Journal of Botany*, 63, 1876-1879.

- KERNER, A. 1895.
- KERR, G., & CAHALAN, C. 2004. A review of site factors affecting the early growth of ash (*Fraxinus excelsior* L.). *Forest Ecology and Management*, 188, 225-234.
- KHALIL, A.A.M., & GRACE, J. 1992. Acclimation to drought in *Acer pseudoplatanus* L. (Sycamore) seedlings. *Journal of Experimental Botany*, 43, 1591-1602.
- KINNAIRD, J.W. 1974. Effect of site conditions on the regeneration of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.). *Journal of Ecology*, 62, 467-473.
- KLIMESOVA, J. 1994. The effects of timing and duration of floods on growth of young plants of *Phalaris-arundinacea* L. and *Urtica-dioica* L. - an experimental-study. *Aquatic Botany*, 48(1), 21-29.
- KÖSTLER, J.N., BRUCKNER, F., & BIBELRIETHER, H. 1968. *Die Wurzeln der Waldbäume*. Hamburg:Verlag Paul Parey.
- KOZLOWSKI, T.T. 1984. *BioScience*, 34,162-167.
- KRAMER, P.J. 1951. Causes of injury to plants resulting from flooding of the soil. *Plant Physio.*, 26(4), 722-736.
- KRASNEY, M.E., VOGT, K.A., & ZASADA, J.C. 1988. Establishment of four Salicaceae species by seed and vegetative reproduction on river bars in interior Alaska. *Holarctic Ecology*, 11, 210-219.
- LÄHDE, E., & RAULO, J. 1977. Development of silver birch (*Betula pendula* Roth) seedlings outplanted at different developmental stages on ploughed reforestation areas in North Finland. *Comunicationes Instituti Forestalis Fenniae*, 91, 1-30.
- LATHAM, J., & BLACKSTOCK, T.H. 1998. Effects of livestock exclusion on the ground flora and regeneration of an upland *Alnus glutinosa* woodland. *Forestry*, 71(3), 191-197.
- LEMOINE, D., PELTIER, J.P., & MARIGO, G. 2001. Comparative studies of the water relations and the hydraulic characteristics in *Fraxinus excelsior*, *Acer pseudoplatanus* and *A. opalus* trees under soil water contrasted conditions. *Ann. For. Sci.* 58, 723-731
- LENSSEN, J..P.M., MENTING, F.B.J., & BLOM, C.W.P.M. 1998. The effect of flooding on the recruitment of reed marsh and tall forb plant species. *Plant Ecology*, 139, 13-23.
- LENSSEN, J.P.M. and others. 1999. Effects of sediment type and water level on biomass production of wetland plant species. *Aquatic Botany*, 64(2), 151-165.
- LENSSEN, J.P.M. and others.. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos*, 86(3), 523-534
- LINDROTH, A., VERWIJST, T., & HALLDIN, S. 1994. Water-use efficiency of willow – variation with season, humidity and biomass allocation. *Journal of Hydrology*, 156(1-4), 1-19.

- LINHART, Y.B., & WHELAN, R.J. 1980. Woodland regeneration in relation to grazing and fencing in Coed Gorswen, North Wales. *Journal of Applied Ecology*, 17, 827-840.
- LUCASSEN, E.C.H.E.T. and others. 2004. High ground water nitrate concentrations inhibit eutrophication of sulphate-rich freshwater wetlands. *Biogeochemistry*, 67(2), 249-267.
- MAHONEY, J. M., & ROOD, S.B. 1991. A device for studying the influence of a declining water table on poplar growth and survival. *Tree Physiology*, 8, 305-314.
- MAHONEY, J.M., & ROOD, S.B. 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management*, 54, 141-156.
- MAUCHAMP, A., & METHY, M. 2004. Submergence-induced damage of photosynthetic apparatus in *Phragmites australis*. *Environmental and Experimental Botany*, 51(3): 227-235.
- McINNES, P.F. and others. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, 73, 2059-2075.
- McVEAN, D.N. 1955. Ecology of *Alnus glutinosa* (L.) Gaertn. III Seedling establishment. *Journal of Ecology*, 43, 195-225.
- MEDIAVILLA, S., & ESCUDERO, A. 2003. Stomatal responses to drought at a Mediterranean site: a comparative study of co-occurring woody species differing in leaf longevity. *Tree Physiol.*, 23(14): 987-96.
- METCALFE, C.R. 1948. The elder tree (*Sambucus nigra* L.) as a source of pith, pegwood and charcoal with some notes on the structure of the wood. *Kew Bulletin*, 1948, 1, 163-169.
- MILES, J., & KINNAIRD, J.W. 1979a. The establishment and regeneration of birch, juniper and Scots pine in the Scottish highlands. *Scottish Forestry*, 33, 102-119.
- MILES, J., & KINNAIRD, J.W. 1979b. Grazing: with particular reference to birch, juniper and Scots pine in the Scottish highlands. *Scottish Forestry*, 33, 280-289.
- MILES, J. 1988. Vegetation and soil changes in the uplands. In: M.B. Usher & D.B.A. Thompson, eds. *Ecological change in the uplands*, 57-70. British Ecological Society Special Publication 7. Oxford: Blackwell.
- MILLER, H.G. 1971. Grazing and the regeneration of shrubs and trees. *Range Ecology and Research, 1st Progress Report*, 27-40. Nature Conservancy, Edinburgh.
- MOGGE, B. 1995. N₂O Emmissionen und enitrifikationsabgaben von Böden einer Jungmoränenlandschaft in Schleswig-Holstein. *Ecosys. Beiträge zur Ökosystemforschung Suppl. Bd. 9 Kiel*.
- MOLYNEUX, D.E., & DAVIES, W.J. 1983. Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia*, 58: 220-224.

- MONK, L.S., FAGERSTEDT, K.V., & CRAWFORD, R.M.M. 1987. *Plant Physiol.*, 85, 1016-1020.
- MORICCA, S. 2002. *Phomopsis alnea*, the cause of dieback of black alder in Italy. *Plant Pathology*, 51(6), 755-64.
- NISBET, J. 1893. *British Forest Trees*. London & New York: MacMillan & Co.
- OLSEN, C. 1921. Ecology of *Urtica dioica* L. *Journal of Ecology*, 9, 1.
- OHLSON, M. 1995. Growth and nutrient characteristics in bog and fen populations of Scots pine (*Pinus sylvestris*). *Plant and Soil*, 172, 235-245.
- OSTENDORP, W., DEINST, M., & SCHMIEDER, K. 2003. Disturbance and rehabilitation of lakeside *Phragmites* reeds following an extreme flood in Lake Constance (Germany). *Hydrobiologia*, 506(1-3): 687-695.
- PEREZ-CORONA, M.E., & VERHOEVEN, J.T.A. 1996. Effects of soil P status on growth and P and N uptake of *Carex* species from fens differing in P-availability. *Acta Botanica Neerlandica*, 45(3), 381-392.
- PEREZ-CORONA, M.E., & VERHOEVEN, J.T.A. 1999. Biomass allocation and phosphorus productivity of *Carex* species in relation to soil phosphorous status. *Israel Journal of Plant Sciences*, 47(2), 97-102.
- PETERKEN, G.F. 1993. *Woodland Conservation and Management 2nd Edition*. London: Chapman & Hall.
- PETERKEN, G.F., & TUBBS, C.R. 1965. Woodland regeneration in the New Forest, Hampshire, since 1650. *Journal of Applied Ecology*, 2, 159-170
- PICCARDI, E.B., & CLAUSER, M. 1983. Absorption of copper by *Iris pseudacorus*. *Water, Air and Soil Pollution*, 19, 185-192.
- PICHUGINA, N.P. 1972. Effects of ecological factors upon seed formation of certain interspecies hybrids of birch. *Ekologiya*, 6, 89-91.
- PINAY, G., ROQUES, L., & FABRE, A. 1993. Spatial and temporal patterns of denitrification in a riparian forest. *Journal of Applied Ecology*. 30, 581-591.
- PINAY, G., CLEMENT, J.C., & NAIMAN, R. 2002. Basic principles and ecological consequences of changing water regimes on nitrogen cycling in fluvial systems. *Environmental Management*, 30(4), 481-491.
- PRIEDITIS, N. 1997. *Alnus glutinosa* – dominated wetland forests of the Baltic region: community structure, syntaxonomy and conservation. *Plant Ecology*, 129, 49-94.
- PUTMAN, R.J. 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. *Forest Ecology and Management*, 88, 205-214.

- RAVEN, J.A. and others. 1989. Water balance of N₂-fixing root nodules: Can phloem and xylem transport explain it? *Plant Cell Environ.*, 12, 683-688.
- RINNE, P. 1990. Effects of various stress treatments on growth and ethylene evolution in seedlings and sprouts of *Betula pendula* Roth. and *Betula pubescens* Ehrh. *Scandinavian Journal of Forest Research*, 5, 155-168.
- ROBERTSON, A.I., & ROWLING, R.W. 2000. Effects of livestock on riparian zone vegetation in an Australian dryland river. *Regulated Rivers: Research and Management*, 16, 527-541.
- ROOD, S.B., & MAHONEY, J.M. 1990. Collapse of riparian poplar forest downstream from dams in western prairies: probable causes and prospects for immigration. *Environ. Manag.* 14, 451-464.
- RUSSELL, R.S. 1977. *Plant root systems: their function and interaction with the soil*. New York: McGraw Hill.
- SALLEO, S., NARDINI, A., & LO GULLO, M.A. 1997. Is sclerophylly of Mediterranean evergreens an adaptation to drought? *New Phytologist*, 135, 603-612.
- SANCHEZ-PEREZ, J.M. and others. 1993. Nutrient content in alluvial soils submitted to flooding in the Rhine alluvial deciduous forest. *Acta Oecologica*, 14(3), 371-387.
- SCHIEVING, F. and others. 1992. The vertical- distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant and Soil*, 142(1), 9-17.
- SCHNITZLER, A., & MULLER, S. 1998. Ecology and biogeography of highly invasive plants in Europe: giant knotweeds from Japan (*Fallopia japonica* and *F. sachalinensis*). *Revue d'ecologie – la terra et la vie*, 53(3), 3-38.
- SEIDEL, K. 1973a. Zu Biologie und Gewässer-Reinigungsvermögen von *Iris pseudacorus* L. *Naturwissenschaften*, 60, 158.
- SIEBEL, H.N., & BLOM, C.W.P.M. 1998. Effects of irregular flooding on the establishment of tree species. *Acta Botanica Neerlandica*, 47, 231-240.
- SIEBEL, H.N., & BOUWMA, I.M. 1998. The occurrence of herbs and woody juveniles in a hardwood floodplain forest in relation to flooding and light. *Journal of Vegetation Science*, 9, 623-630.
- SILVESTER, W.B., HARRIS, S.L., & TJEPKEMA, J.D. 1990. Oxygen regulation and haemoglobin. - In: C.R. SCHWINTZER & J.D. TJEPKEMA, eds. *The Biology of Frankia and Actinorhizal Plants*, 157-176.
- SIMAK 1980.
- SMIRNOFF, N., & CRAWFORD, R.M.M. 1983. Variation in the structure and response to flooding of root aerenchyma in some wetland plants. *Annals of Botany*, 51, 237-249.

- SRUTEK, M. 1997. Growth responses of *Urtica dioica* L to different water table depths. *Plant Ecology*, 130(2), 163-169.
- STUDER-EHRENSBERGER, K. STUDER, C., & CRAWFORD, R.M.M. 1993. Competition at community boundaries – mechanisms of vegetation structure in a dune slack complex. *Functional Ecology*, 7(2), 156-68.
- SUNDSTRÖM, K.R., & HUSSDANELL, K. 1995. Long-term drought stress alters nitrogenase activity and carbon translocation in split-root cultured *Alnus incana*. *Physiologia Plantarum*, 94(2), 181-186.
- SUTHERLAND, W. 1990. Biological Flora of the British Isles. *Iris pseudacorus* L. *Journal of Ecology*, 78, 833-848.
- TERAZAWA, K., & KIKUZAWA, K. 1994. Effects of flooding on leaf dynamics and other seedling responses in flood-tolerant *Alnus japonica* and flood-intolerant *Betula platyphylla* var *japonica*. *Tree Physiology*, 14(3), 251-261.
- THIBAUT, A., CLAESSENS, H., & RONDEUX, J. 2004. Site index curves for *Alnus glutinosa* (L.) Gaertn. in southern Belgium: effect of site on curve shape. *Forestry*, 77(2), 157-171.
- THOMAS, A.T., & HODKINSON, I.D. 1991. Nitrogen, water-stress and the feeding efficiency of Lepidopteran herbivores. *Journal of Applied Ecology*, 28(2), 703-720.
- TILMAN, D. 1982. Resource competition and community structure. New Jersey: Princeton University Press.
- TISSIER, J. and others. 2004. Relationships between hydraulic traits and habitat preference for six *Acer* species occurring in the French Alps. *Annals of Forest Science*, 61(1), 81-86.
- TREMOLIERES, M. and others. 1999. Changes in foliar nutrient content and resorption in *Fraxinus excelsior* L., *Ulmus minor* Mill. and *Clematis vitalba* L. after prevention of floods. *Annals of Forest Science*, 56(8), 641-650.
- TYREE, M.T., & SPERRY, J.S. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 19-38.
- VAARTAJA, O. 1962. The relationship of fungi to survival of shaded tree seedlings. *Ecology*, 43, 547-549.
- VAN DER MAAREL, E., & SYKES, M.T. 1993. Small-scale plant species turn-over in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science*, 4, 179-188.
- VAN DER TOORN, J. 1972. Variability of *Phragmites australis* (Cav.) Trin. ex Steudel in relation to the environment. *Van Zee tot Land*, 48, 1-122.
- VAN SPLUNDER, I. and others. 1996. Morphological responses of seedlings of four species of Salicaceae to drought. *Canadian Journal of Botany*, 74, 1988-1995.

- VARTAPETIAN, B.B., & JACKSON, M.B. 1997. Plant adaptations to anaerobic stress. *Ann Bot (Lond)* 79: 3–20.
- VERHOEVEN, J.T.A., BELTMAN, B., & DE CALUWE, H. 1996. Changes in plant biomass in fens in the Vechtplassen area, as related to nutrient enrichment. *Neth. J. Aquat. Ecol.* 30, 227-237.
- VINTHER, E., & HALD, A.B. 2000. Restoration of an abandoned species-rich fen meadow in Denmark: changes in species richness and dynamics of plant groups during 12 years. *Nordic Journal of Botany*, 20(5), 573-584.
- VOGT, U.K. 2001. Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L. *Journal of Experimental Botany*, 52(360), 1527-1536.
- VOGT, U.K., & LOSCH, R. 1999. Stem water potential and leaf conductance: A comparison of *Sorbus aucuparia* and *Sambucus nigra*. *Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere*, 24(1-2), 121-123.
- WARDLE, P. 1961. Biological Flora of the British Isles: *Fraxinus excelsior* L. *Journal of Ecology*, 49, 739-751.
- WARREN, R.S. and others. Rates, patterns and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. *Estuaries*, 24(1), 90-107.
- WELLING, C.H., PEDERSON, R.L., & VAN DER VALK, A.G. 1988. Recruitment from the seedbank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. *Journal of Ecology*, 76, 483-496.
- WHEELER, C.T., & BOWES, B.G. 1974. Effects of light and darkness on nitrogen fixation by root nodules of *Alnus glutinosa* in relation to their cytology. *Z. Pflanzenphysiol.*, 71, 71-75.
- WHITEHEAD, F.H. 1971. Comparative autecology as a guide to plant distribution. In: E. DUFFEY & A.S. WATT, eds. *The Scientific Management of Animal and Plant Communities for Conservation*, 167-176. Oxford: Blackwell Scientific Publications.
- WILLIAMS, P.A., & BUXTON, R.P. 1989. Response to reduced irradiance of 15 species of native and adventive shrub and tree seedlings from eastern Canterbury. *New Zealand Journal of Ecology*, 12, 95-101.
- WITHERBY, H.F. and others 1938-41. *The Handbook of British Birds*. London: Witherby.
- WOLTERS, D.J., AKKERMANS, A.D.L., & VAN DIJK, C. 1997. Ineffective Frankia strains in wet stands of *Alnus glutinosa* L. Gaertn. in the Netherlands. *Soil Biology & Biochemistry*, 29(11-12), 1707-1712.

YARIE, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana river floodplain, interior Alaska. *Canadian Journal of Forest Research*, 23(5), 1001-1014.

YARIE J. and others. 1993. Soil-solution chemistry in relation to forest succession on the Tanana river floodplain, interior Alaska. *Canadian Journal of Forest Research*, 23(5), 928-940.

2.3.5.3 Key national and international contacts (academics, practitioners) with relevant expertise relating to Residual alluvial forests

Amoros, Claude. Senior Researcher. Riverine Wetland Succession & Restoration Group (*Ecologie des Eaux Douces et des Grands Fleuves*), Université Claude Bernard, LYON I / C.N.R.S. 5023, Lyon, France. amoros@cismisun.univ-lyon1.fr

Influence of disturbances on the functioning and dynamics of aquatic ecosystems; resilience mechanisms; predictive models on recovery processes (role of geomorphological and hydrological processes, and life-traits of aquatic species); ecological successions and ecosystem connectivity within alluvial floodplains (landscape ecology); interactions between physical and biological mechanisms.

Anderson, Russell. Forest Ecologist. Forest Research, Northern Research Station, Roslin, Midlothian. russell.anderson@forestry.gsi.gov.uk

Research background in the soils and hydrology of peatlands, heathlands and wet woodlands. Undertook research on bog woodlands as part of the LIFE Wet Woods project and has worked with Scottish Natural Heritage to develop their Site Condition Monitoring Protocol for bog woodland. Maintains close contact with many groups involved in wetland ecology across the UK through visiting restoration sites and regularly attending conferences, most recently the 'Integrating Wetland Hydrology and Ecology in the UK' meeting in London in March this year. MSc thesis (2003) consisted of a review of heathland management and restoration.

Angold, Penelope. Lecturer. Geography, Earth and Environmental Sciences, University of Birmingham. p.g.angold@bham.ac.uk

Research interests include the dynamics of river margin riparian vegetation, the effects of disturbance and pollution on plant species and communities, biodiversity and community ecology, plant community ecology; seed banks.

Supervision of a PhD project started in 2002: Joanne Goodson (joint with Prof. A. Gurnell) *Environmental controls on the colonisation and establishment of riparian vegetation on river banks subject to varying grazing pressure.*

Baird, Andrew. Professor of Physical Geography. Hydrological, Hydrochemical and Fluvial Processes Research Group, Queen Mary – University of London. a.j.baird@qmul.ac.uk
Research focuses on wetland soils and uses a variety of research approaches, including laboratory mesocosm experiments, field survey and experimentation, and computer modelling. Particular interest in northern peatlands and how carbon 'cycles' within them; ie peatlands as an important global store of carbon and source of atmospheric methane. Assistant editor of *Wetlands* and co-edited *Eco-Hydrology: Plants and Water in Terrestrial and Aquatic Environments* (1999).

Barsoum, Nadia. Floodplain Woodland Ecologist /Long Term Forest Monitoring Programme Leader. Forest Research, Alice Holt, Farnham, Surrey. nadia.barsoum@forestry.gsi.gov.uk.

Floodplain woodland ecologist with post-doctoral research experience in riparian woodland ecology in the UK, France and Sweden. Active member of the two consecutive EU projects entitled 'Floodplain Biodiversity and Restoration' (FLOBAR 1 & 2). Within FLOBAR research focussed on the influences of contrasting hydrological and sedimentological conditions on the regeneration, survival, growth, balance of sex ratios and/or balance of regeneration strategies (sexual and asexual) in various species of *Populus*, *Salix* and *Alnus*. Research has also involved linking riparian landscape structure and processes to the genetic structure of hydrochoric and clonal riparian plant populations. Co-authored two separate floodplain woodland manuals with detailed guidelines.

Bornette, Gudrun. Senior Researcher. Riverine Wetland Succession & Restoration Group (*Ecologie des Hydrosystemes Fluviaux*), Université Claude Bernard, LYON I / C.N.R.S. 5023 Lyon, France. bornette@avosnes.univ-lyon1.fr

Measuring the inputs and outputs of physical and biological variables and their influence on riverine wetland dynamics; particularly the role of flood disturbances in ecological successions. Hypotheses are tested through 1) comparative analysis of chronological series of data at several temporal scales and 2) field experiments at several spatial scales (from individual species to whole ecosystem experiments). Research findings are applied to wetland restoration projects.

Bradley, Chris. Lecturer. Geography, Earth and Environmental Sciences, University of Birmingham. c.bradley@bham.ac.uk

Research interests include monitoring and modelling of floodplain wetland hydrology (eg Narborough Bog, Leicestershire; Insh Marshes, Speyside) including numerical analysis of water-table fluctuation and unsaturated water flow, experimental studies of hydrological properties; the effects of climate change and river control on wetland hydrology.

Broadmeadow, Samantha. Researcher in riparian woodland and freshwater ecology. Forest Research, Alice Holt, Farnham, Surrey. samantha.broadmeadow@forestry.gsi.gov.uk

Research interests include the role of native woodland within the riparian zone of forest plantations and the impact of forest management on the ecology of low order streams.

Brown, Tony. Professor. Leader of the Late Quaternary Palaeoenvironments Research Group. Department of Geography, University of Exeter. a.g.brown@exeter.ac.uk

Two overlapping research interests: (i) floodplain geomorphology and palaeoecology and (ii) alluvial geoarchaeology. In floodplain geomorphology, revision of geomorphological models of floodplain formation and investigations into the use of floodplain sediments as proxy environmental indicators (eg use of palaeochannels for the generation of pollen and other palaeoecological data). Also, studies into the effects of vegetation on modern channels, particularly of multiple channel rivers. In alluvial geoarchaeology, a focus on floodplain vegetation change and archaeology in lowland England and alluviation and human history in the Mediterranean. Research is ongoing in the Gearagh alluvial woodlands in SW Ireland and

in the New Forest with a particular interest in linking beetle faunas and alluvial history at these sites.

Coops, Hugo. Senior Aquatic Ecologist. Institute of Inland Water Management and Waste Water Treatment (RIZA), Holland. h.coops@RIZA.RWS.minvenw.nl.

Relevant research experience relates to the regeneration of floodplain forest (field and greenhouse experimental work). Work otherwise includes co-ordinating research and policy support for water management at the national level.

Davenport (Boitsidis), Angela. Research Fellow. Flood Hazard Research Centre, Middlesex University. A.Boitsidis@mdx.ac.uk

Research is focussed at the interface of geomorphology, hydrology, engineering and ecology. An interest in how urban river channels adapt under different engineering regimes, how to assess the physical quality of urban and modified rivers, and how this can be translated into simple and effective river management tools. Research experience on riparian vegetation seed banks and hydrochory.

Edwards, Peter. Professor and Head of Department. Geobotanisches Institut, Swiss Federal Institute of Technology, Zürich, Switzerland. peter.edwards@env.ethz.ch

Riparian vegetation ecology. Research has been undertaken along the Tagliamento River, Italy, linking spatio-temporal patterns in riparian vegetation distribution and physical processes.

Elliot, Maxine. New Forest LIFE 3 River Restoration Project Manager. Environment Agency, Winchester. maxine.elliott@environment-agency.gov.uk

Gilvear, David. Senior Lecturer. Department of Environmental Science, University of Stirling. d.j.gilvear@stir.ac.uk

Research focuses on an understanding of river and floodplain systems from a hydro-geomorphological perspective. Areas of interest include river channel change, wetland hydrology, instream flow requirements, instream and floodplain vegetation patch dynamics and the application of airborne remote sensing to river and floodplain environments. Currently research includes, airborne remote sensing of river corridors, geomorphic response and biotic recovery of engineered channels, instream flows and habitat hydraulics, floodplain landscape diversity and hydrological-ecological interactions on floodplain wetlands.

Girel, Jacky. Laboratoire d'Ecologie Alpine (LECA), Université Joseph Fourier, France. jacky.girel@ujf-grenoble.fr

Riparian woodland ecologist. Studies the impacts of man along French rivers (landscape ecology) and the effects of historical land-uses and civil engineering works on the present riparian landscape (land cover).

Gowing, David. Senior Lecturer in Ecohydrology, Cranfield University, Silsoe, Bedfordshire. d.gowing@cranfield.ac.uk

Research experience in the field of plant/water relationships, specialising in the ecohydrology of floodplain systems. Has experience of working for the Environment Agency (EA,) assessing wetland implementation options and helping with the implementation of the Habitats Directive. Has been involved in the preparation of a number of Water Level Management Plans and has convened a course on behalf of several environmental organisations, entitled "Hydrological management for conservation." Particular research interest is the relationship between soil water regime and the distribution of semi-natural plant communities. Has published a number of papers on the topic and has acted as a ecohydrological consultant for RSPB, WWT, EA, English Nature, Countryside Council for Wales, local government and private land owners.

Gurnell, Angela. Professor / Head of Geography Department. King's College London, University of London. angela.gurnell@kcl.ac.uk

Research investigates (i) the ways in which vegetation can control fluvial processes (eg influence of woody debris), (ii) vegetation establishment and river margin dynamics (eg patterns of sedimentation, hydrochory, invasive species) and (iii) the hydroecological characteristics of urban rivers.

Supervision of a PhD project started in 2002: Joanne Goodson (joint with Dr. P. Angold) Environmental controls on the colonisation and establishment of riparian vegetation on river banks subject to varying grazing pressure.

Hedges, Pete. Environmental Systems Research Group, Aston University, Birmingham. P.D.Hedges@aston.ac.uk

Research activities centred on the hydrology and establishment of wetland systems, with current activity focussed on determining the water use of wetland habitats; design, restoration and management of wetlands; and, phytoremediation.

Current projects include:

Water use rates of wet woodlands. Aim is to refine water budget design methodology for wet woodland habitats and builds upon the work of Read (PhD 2003). Will result in the publication of evapotranspiration rates and nationally applicable monthly water use coefficients for this habitat. Research involves monitoring the water budget of two 2 m diameter lysimeters at each of two sites, both of which were planted in October 2000.

- Cherry Holme Wood is an established wet woodland adjacent to the River Trent; 5-year old *Salix caprea* trees were transplanted into the lysimeters and the understorey turves were reinstated.
- Leam Valley Local Nature Reserve is a mosaic of wetland habitats (including open water; reedbed, marsh; wet grassland wetland, wet woodland) created by the Warwickshire Wildlife Trust in the washlands of the River Avon at Leamington Spa. 3-year old *Salix caprea* were purchased as bare-root stock and planted in the lysimeters. Understorey vegetation was established using turves from the adjacent terrestrial woodland and plug planting of target species.

Cherry Holme is representative of a mature wet woodland habitat with a developed canopy, whilst the Leam Valley lysimeters allow the progress of a developing wet woodland to be monitored.

The response of the biodiversity of wet woodlands to differing management practices. Aim is to assess the biodiversity of wet woodlands in response to different management practices. This assessment should result in the development of a methodology for predicting the outcome of management practices to obtain an optimum degree of biodiversity in a given situation.

Supervision of 2 PhD projects related to these projects is ongoing. A number of related publications in press.

Holmes, Nigel. Alconbury Environmental Consultants, Huntingdon
NigelHolmes@aecw.demon.co.uk

Hughes, Francine. Senior Lecturer in Ecology and Conservation. Department of Life Sciences, Anglia Polytechnic University. f.hughes@apu.ac.uk

Plant ecologist with research interests relating to the ecology, hydrology and restoration of European floodplain forest ecosystems. Current focus on developing 'environmental flows' for riparian ecosystems and integrating these into river management practices. Joint co-ordinator of a series of EU-funded research projects, based in the Geography Department at the University of Cambridge. The most recent one is known as 'Floodplain Biodiversity and Restoration' FLOBAR2 funded under the European Union's 5th Framework Programme. Research projects within FLOBAR programme were conducted on floodplain ecosystems in France, Sweden, Germany, the UK and Canada and involved manipulation experiments, field survey and field experimental research. Currently chairing the Management Committee for Wicken Fen National Nature reserve in Cambridgeshire, UK.

Johansson, Mats. Assistant Professor. Landscape Ecology Group, University of Umeå, Sweden Mats.Johansson@ac.lst.se

Research is concentrated on processes that control the distribution and abundance of plants along rivers. Main topics of interest are: mechanisms controlling plant zonation on riverbanks, floodplain restoration and temporal and spatial dynamics in riparian plant communities. Research is conducted using empirical and experimental methods within the fields of population, community as well as landscape ecology. Presently co-ordinates and implements the Water Framework Directive in the Umeå region with links to the EU Life project "Forests for Water" (adapting forestry to the WFD).

Johnson, Carter. Professor of Ecology. Department of Horticulture, Forestry, Landscape & Parks, South Dakota State University, USA. Carter_Johnson@sdstate.edu

Research interests in streamflow regulation and riparian ecosystems.

Kollmann, Johannes. Associate Professor. Botanical Section of the Department of Ecology, The Royal Veterinary and Agricultural University, Denmark. jok@kvl.dk

Plant ecologist with a strong interest in population ecology and community ecology. Research focuses on the ecology of seed dispersal (especially fleshy-fruited species), invasive alien plants (eg *Impatiens glandulifera*) and riparian ecology (eg participation in a large interdisciplinary project on riparian woodland island dynamics in a near-natural braided river in the Italian Alps, the Tagliamento River).

Lambs, Luc. Senior Researcher. LABORATOIRE DYNAMIQUE DE LA BIODIVERSITÉ (LADYBIO) CNRS/Université Paul Sabatier, Toulouse, France. lambs@ecolog.cnrs.fr

Sap flow and water transfer in riparian woodland species such as poplar and willow.

Large, Andrew. Senior Lecturer in Geography. University of Newcastle.
a.r.g.large@ncl.ac.uk

Research interests include the relationships between hydrology, geomorphology and ecology in fluvial systems, and recent and long-term change in fluvial and wetland systems (focusing particularly on floodplain and in-channel environments).

Leech, Kim. SAFER (Strategies and Actions/Implementations for Flood Emergency Risk Management) Project Manager, Forestry Commission, Scotland.

Kim.leech@forestry.gsi.gov.uk

Maltby, Ed Professor. Royal Holloway University of London, Director of the Royal Holloway Institute for Environmental Research (RHIER) and Head of the Wetland Ecosystem Research Group. e.maltby@rhul.ac.uk

Environmental management and research experience in various wetland types (moorland, peatlands, marshes, swamps, estuaries and coasts) in the UK and world-wide (particularly Europe, United States, SE Asia). Pioneered the development of the functional approach to wetlands. Co-ordinator of a sequence of EU projects from 1988 to present linking wetland science to the changing needs of policy. Diverse projects with English Heritage, English Nature, Environment Agency, Countryside Agency involving translation of wetland science into better decision making and policy support (eg a study of the effect of raised water levels in the Somerset Levels, South West England, funded by English Nature - 1990). Author and co-author of 8 books and over 150 publications and reports, focusing on the importance of wetland ecosystems at all scales from global to local, and on the results of fundamental and applied wetland ecosystem research; presentation of more than 50 invited lectures/addresses at international conferences.

McEwen, Lindsey. Principal Lecturer in Physical Geography. Head of Geography and Environmental Management Research Unit, University of Gloucestershire.

lmcewen@glos.ac.uk

Supervision of a PhD project started in 2000: Kineavy, B. *Interaction of geomorphology and ecology in riparian woodland* (part funding through Countryside Council for Wales).

Mountford, Owen. Senior Researcher, Centre for Ecology and Hydrology, Monks Wood.
om@ceh.ac.uk

Research focusses on the relationship between water-management and the composition of wetland vegetation. This approach has included historical investigations, experiments and surveys, and the socio-economic context of wetland management. Direct links between ecology and hydrology have become increasingly central to research activities, with studies of rivers and sedimentation, grassland/forest composition and floods or waterlogging; and catchment-based approaches. Wetland restoration (at a site and regional level) is a key application of such research.

Morrissey, I.P. Research Assistant. Hydroecology Research Group, School of Geography, Earth & Environmental Sciences, University of Birmingham i.p.morrissey@bham.ac.uk

Muller, Etienne. Senior Researcher. Laboratoire DYnamique de la BIODiversité (LADYBIO) CNRS/Universite Paul Sabatier, Toulouse, France. emuller@cict.fr

Sap flow and water transfer in riparian woodland species such as poplar and willow. Recruitment dynamics of poplar and willow species.

Murphy, Dierdre. Project Officer for Ripon (Laver-Skell) Multiobjective Pilot Project looking at ways of benefiting the wider environment through better integration of wildlife and habitat improvements, land management changes, including agri-environment agreements, and river restoration with flood defence works. deirdre.murphy@DEFRA.GSI.GOV.UK

Naiman, Robert. Professor. Aquatic & Fishery Sciences, College of Ocean and Fishery Sciences, University of Washington, USA. naiman@u.washington.edu

Research interests are focused on the structure and dynamics of streams and rivers, riparian vegetation, and the role of large animals in influencing system dynamics. He has written and edited nine books on aquatic ecology and watershed management, in addition to over 130 journal articles.

Nilsson, Christer. Professor. Leader of Landscape Ecology Group, University of Umeå, Sweden. christer.nilsson@eg.umu.se

Very broad range of research related to riparian vegetation communities. Topics include: (i) floodplain Biodiversity and Restoration, (ii) control of plant species diversity in riparian corridors, (iii) biodiversity in riparian and seepage forests: approaches to ecologically sustainable forestry, (iv) fragmentation and regulation of southern rivers, (v) effects of forest biomass removal on plant biodiversity, (vi) the relative importance of dispersal and local site conditions for plant species diversity in riparian zones.

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Has participated in a range of national and international research projects assessing the effects of forestry on water flows and water quality. Also been involved in evaluations of the potential benefits and threats posed by the restoration of floodplain woodlands. Played a central role in the development of national Forest and Water Guidelines, and maintains strong links with the national agencies, private industry and other end users. Regularly approached for expert advice on floodplain riparian woodland and hydrology (catchment management plans) and is involved in several key stakeholder groups.

Patterson, Gordon. Environment Policy Advisor, Forestry Commission Scotland, with a specific interest in wet woodland. Forestry Commission, Edinburgh. gordon.patterson@forestry.gsi.gov.uk

Petts, Geoff. Professor / Director of the Centre for Environmental Research & Training / Pro-Vice Chancellor. University of Birmingham. g.e.petts@bham.ac.uk

Research interests are at the interface of hydrology, geomorphology and ecology with particular interests in regulated rivers, the analysis of environmental flows, and conservation applied to the sustainable development of water projects.

Piégay, Hervé. Senior Researcher. *Eco-Geographie et Geo-morphologie des Systemes Fluviaux*, Department of *Environnement - Ville - Société* CNRS 5600, Lyon, France. piegay@univ-lyon3.fr

Supervision of PhD. Dufour, S. (2001) *Riparian vegetation responses to flooding and sedimentation*.

Pinay, Gilles. Senior Researcher. Laboratoire d'Evolution des Systemes Naturelles et Modifies, Universite de Rennes, Rennes, France. gilles.pinay@univ-rennes1.fr

Research focuses on the biogeochemical processes in river floodplains. Main research topics include the cycling and availability of nitrogen and phosphorus in riverine wetlands along river networks and the role of these land-water ecotones on the regulation of diffuse nitrogen fluxes from the drainage basin. Coordinator of a European Programme called NICOLAS (Nitrogen Control by Landscape Structures in Agricultural Environments) supported by the Environment & Climate Direction (DG XII).

Reed, Katy. Environmental Consultant, Middlemarch Environmental Limited katy@middlemarch-environmental.com

Currently producing a Best Practice Guide for Severn Trent Water / The National Forest Company partnership associated with 'The Design, Creation, Establishment and Management of Wet Woodlands'. The report will detail research carried out over the past 3 years in The National Forest Area and should be available mid-2005.

Richards, Keith. Professor. Department of Geography, University of Cambridge. ksr10@cam.ac.uk Specialised in fluvial geomorphology. Interests include river and floodplain restoration and inter-relationships between hydrological and ecological processes in the floodplain environment. Co-ordinator of a series of EU-funded research projects, based in the Geography Department, University of Cambridge. The most recent one is known as 'Floodplain Biodiversity and Restoration' FLOBAR2 funded under the European Union's 5th Framework Programme (see web page - <http://www-flobar.geog.cam.ac.uk/>). Research projects within FLOBAR programme were conducted on floodplain ecosystems in France, Sweden, Germany, the UK and Canada and involved manipulation experiments, field survey and field experimental research.

Roberts, John. Senior Researcher. Centre for Ecology and Hydrology, Wallingford. jro@ceh.ac.uk

Project Leader on NERC-funded project entitled 'Influence of woodlands on recharge in the Pang catchment' Within this project there is a component related to wet woodlands addressing the following questions: (i) what are the transpiration rates of tree species common in wet woodlands ? (ii) what are the environmental and soil water controls on transpiration ? (iii) does the structure of the wet woodland stand (i.e block as opposed to linear/narrow strip)

influence water use ? The species of interest are alder, ash, willow and poplar. Although the Pang catchment figures in the title the wet woodland sites are selected on the basis of species composition, scientific relevance and the security of the site. The work involves a NERC research studentship held by Nathan Callaghan (co-supervised with David Gowing) at the Department of Biological Sciences, Open University.

Rood, Stewart. Professor. Biological Sciences Department, University of Lethbridge, Canada. rood@uleth.ca

Research interests include: 1) Plant physiology with emphasis on gibberellins, 2) Ecophysiology of river valley cottonwoods and 3) River regulation and restoration.

Sadler, Jon. Senior Lecturer. University of Birmingham j.p.sadler@bham.ac.uk

Research interests include the biogeography of invertebrates on patchy habitats in riverine environments

Supervision of PhD project started in 2001. Bates, A. *The dynamics of Invertebrates of Exposed Riverine Sediments in Wales*. (joint with Adrian Fowles CCW) and EU funded - 1997-2000. Bell, D. *Carabids from riparian habitats in Britain in relation to inundation*.

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D.Sear@soton.ac.uk

Specialises in fluvial geomorphology. Research interests include river and floodplain management and restoration.

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Spencer, Jonathan. Forestry Commission Forest Ecologist with an interest in floodplain Woodland. Forestry Commission, England. jonathan.spencer@forestry.gsi.gov.uk

Stromberg, Julie. Associate Professor, Arizona State University, Arizona, USA. jstrom@asu.edu

Research specialty is in the study of ecosystem processes, with the purpose of aiding managers in applying an understanding of these processes to restoration and management decisions in endangered ecosystems. Most of work concerns applied bihydrology, the relationships between hydrology, hydrologic modifications, and riparian (streamside) ecosystems. These studies have examined relationships of physical system components such as groundwater levels, stream flows, and flooding regimes, to biological phenomena such as plant population dynamics and plant community structure. Some studies are conducted at reference sites where human influence is minimal. Others are carried out at hydrologically altered sites and in at-risk ecosystems.

Specific goals of previous and ongoing studies include: (i) describing the ecological consequences of hydrologic modifications on riparian plant species and communities; (ii) understanding the biological and physical processes that maintain species biodiversity in riparian landscapes; (iii) identifying site conditions and processes that favor native species over exotic plant species; (iv) obtaining the ecological information needed to implement

successful riparian restoration projects; and (v) understanding the influences of flood and fire disturbance on ecosystem structure and function.

On the editorial board of *Restoration Ecology* and serves as a member of the Southwestern Willow Flycatcher Endangered Species Recovery team (appointed by USFWS).

Tabacchi, Eric. Senior Researcher. Laboratoire DYnamique de la BIOdiversité (LADYBIO) CNRS/Universite Paul Sabatier, Toulouse, France. tabacchi@ecolog.cnrs.fr

Riparian plant ecologist. Key areas of riparian vegetation research: (i) riparian landscapes and ecosystems, (ii) plant diversity dynamics and disturbance regimes, (iii) plant diversity dynamics and spatial heterogeneity, (iv) riparian plant communities and global change, (v) plant succession, hydraulics and geomorphology, (vi) propagule (seed) bank dynamics, (vii) biological invasions, (viii) spatial modelling of plant diversity and (ix) ecoregions.

Supervision of PhD project started in 2001 Corenblit, D.: *Reciprocal Relationships between Vegetation Dynamics and Riverbed Stability : the Case Study of the Tech River (S. France)*.

Thomas, Huw. Forest Hydrologist, Forest Research, Talybont Research Office, Talybont-on-Usk, Brecon. huw.thomas@forestry.gsi.gov.uk

Conducts research into the hydraulic impact of floodplain woodland restoration and represents the Forestry Commission in various groups involved in flood defence; catchment planning and land use management and has strong links with floodplain woodland/river restoration schemes throughout the UK, particularly in Wales. Uses hydraulic river models to assess the effect of woodland size, density, shape and positioning on the physical properties of floods including water level, velocity, travel time and storage.

Tickner, David. Freshwater Policy Officer. Research Centre-Freshwater, World Wide Fund for Nature-UK (WWF-UK), Panda House, Weyside Park, Godalming. info@wwf.org.uk

Research background into ecohydrological requirements of riparian vegetation species using field survey and water table level manipulation experiments. PhD thesis (2000): *Hydro-geomorphological influences on the growth of, and competition between, alien and native riparian plant species*.

Tockner, Klement. Senior researcher. Leader of Floodplain ecology and biodiversity research group. Department of Limnology, Swiss Federal Institute for Environmental Science and Technology (EAWAG), Switzerland. klement.tockner@eawag.ch

Research interests cover the following topics: (1) Floodplain and wetland ecology (inundation dynamics, geomorphic dynamics, biodiversity, and ecosystem processes), (2) Linking biodiversity with ecosystem processes, (3) Landscape ecology and community ecology, (4) Interaction between fluvial dynamics, ecosystem processes and biodiversity, (5) Linking aquatic and terrestrial communities, (6) Development of conservation strategies for river corridors, and (7) Metapopulation dynamics of floodplain species.

Present research projects:

- Ecology of a glacial floodplain (Val Roseg, Switzerland) (since 1996),
- Comparative ecology and biodiversity of floodplains (Tagliamento, Val Roseg, Danube) (since 1997)
- Life of the edge: Linking aquatic and terrestrial communities (since 2000)

- Ecology of floodplain ponds (since 1999)
- Geomorphic, hydrologic and ecological dynamics along a large river corridor: the role of connectivity and scale (Tagliamento-project, since 1998)
- Role of island dynamics in maintaining biodiversity (since 1999)
- Development of indicators to assess restoration projects (since 2000)
- TempQsim: Evaluation and improvement of water quality models for application to temporary waters in Southern European catchments (since 2002)
- Metapopulation dynamics of amphibians in dynamic floodplains (since 2004)

Tyree, Melvin. Adjunct Professor of Botany. University of Vermont, USA. mtyree@aol.com
Involved in research in the following areas: 1) Water stress physiology of plants, specifically hydraulic architecture and 2) Role of nutrient stress, drought and insect damage on health of maple trees.

Wheeler, Bryan. Senior Lecturer, Department of Animal and Plant Sciences, University of Sheffield. b.d.wheeler@sheffield.ac.uk

Research centres on wetland ecology. Activities form part of a 'Wetland Research Centre'. Research is broadly concerned with identifying factors and processes influencing the composition and distribution of distinctive vegetation types in wetlands (including ontogenic influences as well as current environmental, hydrological and management conditions). An extensive field data resource (FenBASE and BogBASE databases) provides a focus for experimental studies, which have been particularly concerned with the tolerance of wetland plants to waterlogged conditions, especially with regard to reduced phytotoxins. It also provides a basis for much 'applied' research, which is primarily concerned with wetland conservation and, especially, the restoration of wetlands damaged by peat extraction and groundwater abstraction.

Current research is concerned with the identification of generic water supply mechanisms to, and within, wetlands in England and Wales and the relationship of this to vegetation patterns.

Wheeler, Nicky. Project officer for floodplain forest restoration site at Milton Keynes, Milton Keynes Park Trust, Milton Keynes. mstreet@mkparks.co.uk

Wilson, Caterine. Co-director of the Hydroenvironmental Research Centre specialising in eco-hydraulics at the University of Cardiff. WilsonCA@Cardiff.ac.uk

2.3.5.4 Other references and web page links relevant to Residual alluvial forests

HALL, J. 1997. An analysis of National Vegetation Classification survey data. *JNCC Report*, No. 272.

INTECOL 7th International Wetlands Conference, Utrecht 2004, Holland. Available at: <http://www.bio.uu.nl/intecol/mission/themes.php>

JNCC web site - http://www.jncc.gov.uk/protectedsites/sacselection/SAC_habitats.asp.

PEAT, H., & FITTER, A. 2005. *The Ecological Flora of the British Isles at the University of York*. Available from:

<http://www.york.ac.uk/res/ecoflora/cfm/ecofl/index.cfm>

River Restoration 2004 conference, Zagreb, Croatia. Available from:

<http://www.minvenw.nl/rws/riza/home/ecrr/>

WEIFERS, J. 1990. Forested wetlands in Europe. *In*: A.E. LUGO and others, eds. *Ecosystems of the world 15. Forested wetlands.*, 413-414. Amsterdam: Elsevier.

WHITBREAD, A.M., & KIRBY, K.J. 1992. *Summary of National Vegetation Classification woodland descriptions*, No. 4. Peterborough: Joint Nature Conservation Committee.

WILDFOWL & WETLANDS TRUST. 1994. *Wetlands, industry & wildlife – a manual of principles and practices.*

2.4 Bog woodlands

2.4.1 General description of bog woodlands (M18, M19, W4) and eco-hydrological factors relevant to this habitat type

There are two distinct types of bog woodland. Both are woodlands of low productivity on peat. An ombrotrophic type consists of stunted Scots pine or downy birch scattered or growing in sparse, open stands on raised, ombrotrophic, bogs. Ombrotrophy (ie the supply of water and nutrients to a convex bog surface solely via rain and other forms of atmospheric deposition) is thought to be the sole water replenishment mechanism in ombrotrophic wet woodlands (Figure 9). Ground-water mound theory can help relate drainage to change in depth to the water table for raised bogs, but the effects of changes in regional groundwater levels is unclear. A second minerotrophic type of bog woodland is groundwater-dependent and consists of closed-canopy stands of downy birch, goat willow, grey willow or common alder on fen peat. Minerotrophic situations include spring fens on valley mires, central flow lines of valley mires and lagg fens around raised bogs. The spring-fed minerotrophic bog woodlands seem to be fed by groundwater welling up through the peat, presumably originating from underlying springs (Figure 9). The presence of plants requiring a degree of minerotrophy supports this assumption. Minerotrophic bog woodland restricted to the central flow lines of valley mires presumably receives nutrients by irrigation with drainage water. Flooding is likely to irrigate the surface during the winter, while during summer there may be some sub-surface irrigation through moderately porous peat. The drainage water presumably carries minerals from mineral soil further upstream so its chemistry will depend on local rock and drift types.

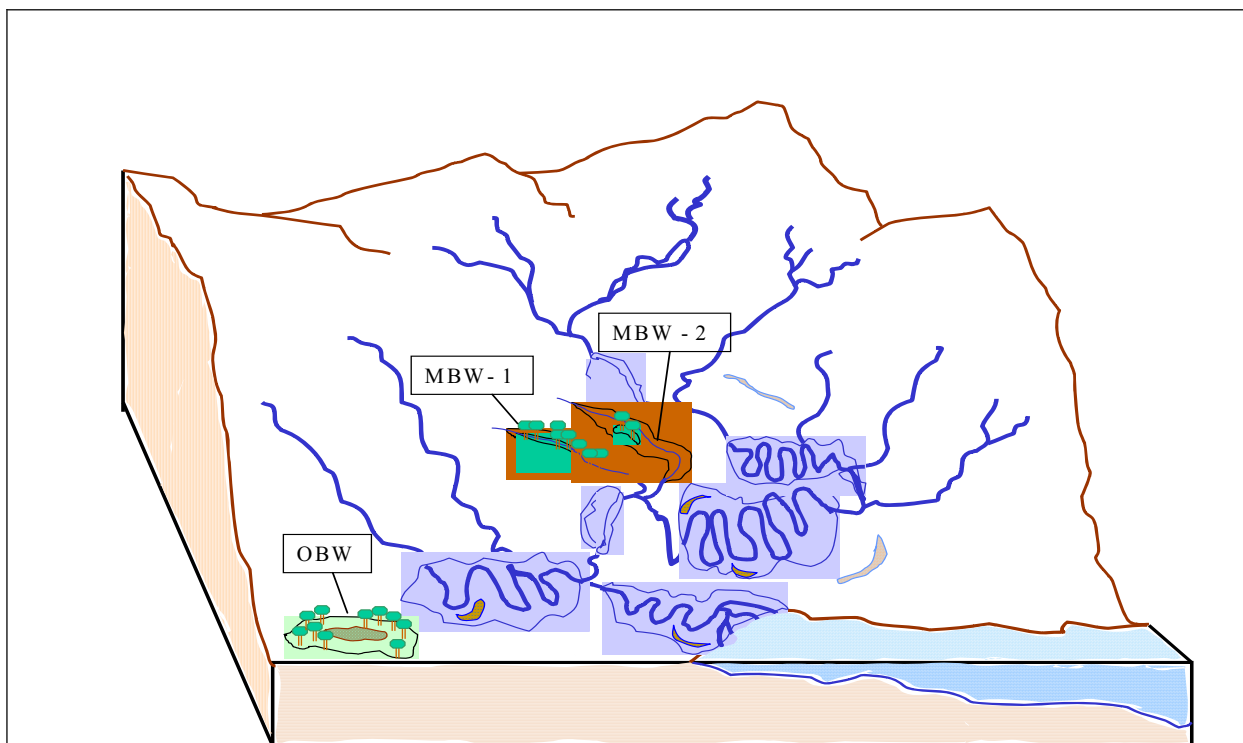


Figure 9 Landscape situations of ombrotrophic and minerotrophic bog woodlands in a catchment.

OBW - Ombrotrophic bog woodland growing on the edges and outer part of a plateau, but not in its centre.
MBW - 1: Minerotrophic bog woodland growing along central flow line of a valley mire. **MBW - 2:** Minerotrophic bog woodland growing where groundwater upwelling is occurring in a valley mire.

Trees in marginal conditions for growth are the key characteristic of the ombrotrophic type. A sufficiently low browsing pressure, at least for a long enough period to allow tree establishment, is crucial, and given that productivity is inherently low, the required period may be 20-30 years. A relatively continental climate may be important in Britain but there is no proof of this. The current distribution of the type may be influenced more by browsing pressure than climate. Nutrient availability is the main factor limiting tree growth sufficiently for the retention of bog vegetation. Phosphorus is probably the most limiting element for this ombrotrophic type so nitrogen deposition may not stimulate tree growth and succession. Lowering of the water table by drainage allows access to a thicker layer of oxic peat and releases additional nutrients from it, stimulating tree growth and altering the habitat beyond the range accepted as bog woodland.

A degree of minerotrophy is the key characteristic of the groundwater-dependent type. The bog woodland often ends abruptly where the ground flora indicates a transition to oligotrophic or ombrotrophic conditions. The trees are less nutritionally constrained than those in the ombrotrophic type so a wider range of tree species can be present. Tree growth may still be constrained by the high water table limiting access to oxic peat and tree stability may be poor because the root systems are disproportionately shallow. A ground flora with fen species well represented is characteristic.

In theory, various hydrological changes can threaten bog woodland habitats. Bog woodland on raised peat represents a delicate balance between open bog and closed-canopy woodland so an increase or, as occurs more commonly, a decrease in site wetness could cause a loss of the habitat. Increased wetness would tend to favour bog vegetation and reduce the competitive ability of the trees, provided that the water quality remained the same. Decreased wetness would favour growth and expanded coverage of trees and in time, provided their regeneration were not compromised, would encourage canopy closure, leading to the shading out of bog species. Examples of changes in both directions are described in the literature (Banner and others 1983; Legg and others 2001; Turunen & Turunen 2003).

Bog woodlands on raised peat are unlikely to be affected by changes in groundwater chemistry. However, other types of bog woodland certainly could be affected. Spring-fed woods might gradually change their composition, with more nutrient-demanding tree species likely to out-compete the dominant over-storey tree species, *Betula pubescens*. The resultant change in canopy density and light levels could affect some of the specialist lower plants inhabiting these woods. In theory, changes in artesian pressure could also affect spring-fed woods, in that a reduction in pressure might reduce the supply of minerals to the rooting zone.

Bog woodland growing on lagg fen around raised bogs could be affected by quantitative and particularly qualitative changes in lagg streams, either in the lagg or further upstream. The extent to which raised mire water tables are affected by regional groundwater lowering is uncertain. Bragg (2004) speculated that nearby groundwater abstraction might increase vertical leakage from Kirkconnel Flow, a damaged lowland raised bog colonized by woodland. Limited piezometer measurements suggested that there was no vertical leakage although further work to confirm this is required.

2.4.1.1 Depth to water table

Tree growth in bog peat is related to depth to the water table. It has been amply demonstrated in a forestry context that lodgepole pine (*Pinus contorta*) height (Boggie & Miller 1976) and

root growth (Boggie 1972) on deep peat are reduced by a high water table. Trees were grown in small isolated plots on deep bog peat, in which the water table was maintained at the surface and at 11, 19, 24 and 34 cm below it. To ensure that any effect was not due to paucity of nutrients in the peat, NPK fertiliser was applied at planting and again two years later. By seven years after planting, fewer than half of the trees in the waterlogged plot survived but in the other treatments, roots grew to a depth of 10, 15, 20 and 40 cm respectively. Roots appeared to have formed mycorrhizas except in the waterlogged treatment, ruling out mycorrhizal inhibition as the cause of the difference between the other treatments. After 12 growing seasons, 38 percent of the trees survived in the waterlogged treatment. Mean tree heights were 0.65, 1.25, 1.29, 2.19 and 3.05 m in the five treatments respectively.

2.4.1.2 Nutrient concentrations in soil water

The growth of downy birch on bog peat may be constrained by the availability of nitrogen or phosphorus, depending on which is most limiting. Tomassen and others (2004) found that, unlike in Holland, where birch invasion of bogs has occurred in areas with high N deposition, birch on bogs in Ireland did not respond to N fertilization because P availability continued to limit growth.

2.4.1.3 pH

Changes in pH, unless very marked, may not affect plants in bog woodlands directly but may do so indirectly by altering the availability of the nutrients already present. A rise in pH caused by a change in hydraulic pathways in the peat will generally be accompanied by an increased influx of base cations and perhaps also of other nutrients. Similarly a drop in pH would usually be accompanied by a decrease in base cation and nutrient influx.

2.4.1.4 Flooding

Bog woodlands on bog peat are unlikely to be subjected to anything other than very shallow and ephemeral floods because bog peat normally forms only after a mire surface becomes slightly raised above the level of the surrounding ground. Mires in flood-prone situations are unlikely to have undergone the succession from fen to bog. Willow (and occasionally birch) carr woods, sometimes found on lagg fen areas around raised bogs, may be prone to more prolonged flooding.

Prolonged flooding might occur on sites where management has included measures to raise the water table. Drain blocking is unlikely to cause floods except very locally. Construction of linear structures, such as bunds, could result in more extensive waterlogging.

Flooding can affect vegetation in two main ways: direct physical effects, particularly oxygen availability in the rooting zone; and indirect chemical effects, whereby floods supply significant amounts of nutrients and/or bases. Prolonged flooding can hinder tree development. Seedlings of downy birch (*Betula pubescens*) and silver birch (*Betula pendula*), subjected to flooding for 120 days show markedly reduced growth compared to controls growing in freely drained conditions (Frye & Grosse 1992). The latter species also becomes frost-sensitive during the flooding period and remains vulnerable into the next growing season. Goat willow (*Salix caprea*) and Grey willow (*S. cinerea*) seedlings survived waterlogging for up to 13 weeks (Good and others 1992), although there is almost complete die-back of roots; loss of the rooting system is compensated for, to some extent, by new roots

that grow either upwards (towards aerobic conditions), or from the stems of seedlings. One grey willow clone continued to grow while waterlogged.

2.4.2 Distribution and description of bog woodlands in the UK

The distribution of known bog woodlands (ie EU Habitats Directive category 91D0) in Great Britain was presented by Rodwell & Dring (2001) but the source of the information is not known (Figure 10). This distribution does not reflect the finding of Hall (1997) for W4 woodland, based on a collection of surveys, that the type is particularly common in the Scottish Highlands, especially in the west.

Inclusion in the W4 category of other woodlands not fitting the bog woodland definition may account for this discrepancy.

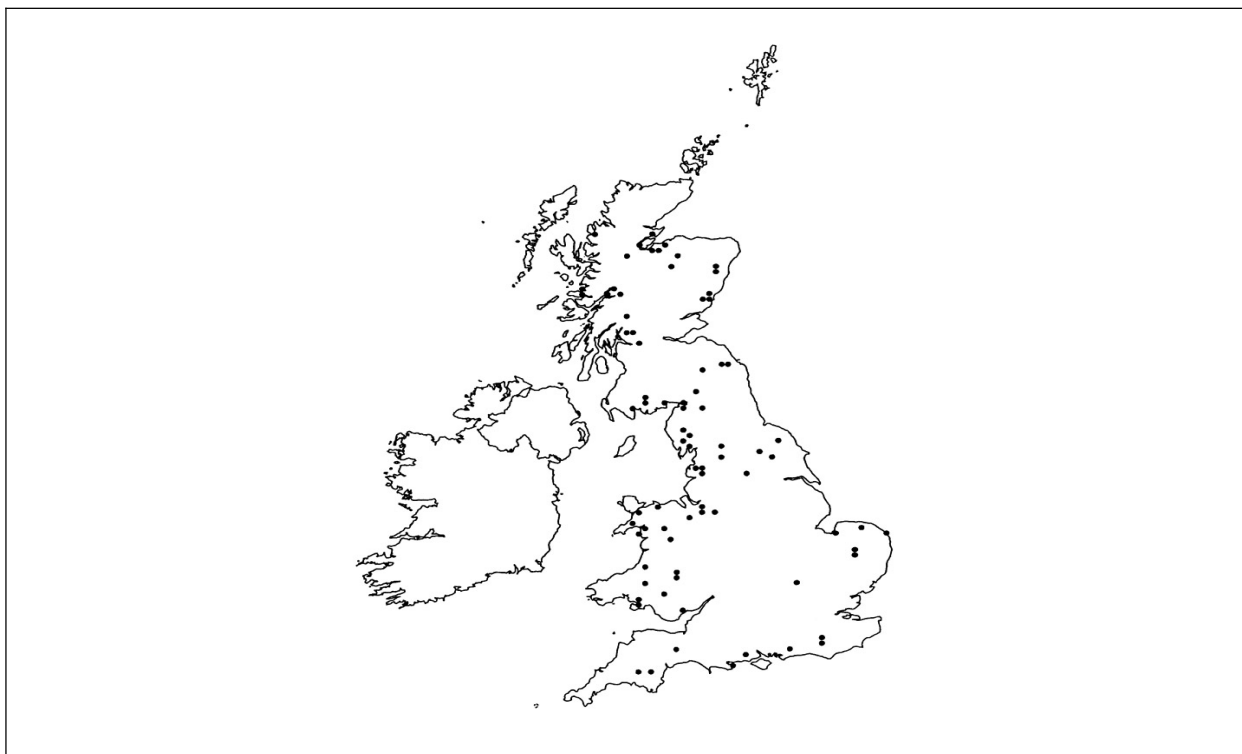


Figure 10 Distribution of bog woodland in Great Britain (Rodwell & Dring 2001).

In Great Britain as a whole we have used the broader definition given in the EU Interpretation Manual to identify and notify sites for this habitat type. Fifteen SACs in England and Wales and ten in Scotland contain bog woodlands (Table 8).

Table 8 SACs in England, Wales and Scotland with bog woodland.

Grades are from (JNCC 2004) (A = best, D = worst). Descriptions were compiled from (JNCC 2004) and from information received from English Nature (A. Nicholson, *pers. comm.*), Neil Sanderson and CCW (J. Latham, *pers. comm.*).

SAC name	Grade	Type
Dorset Heaths (Purbeck and Wareham) and Studland Dunes	A or B	Ancient, closed-canopy birch on fen island (spring-fed?) in bog (Morden Bog)

SAC name	Grade	Type
New Forest	A or B	Ancient, closed-canopy birch/sallow/ alder on flushed, firm peat (eg Church Moor, Dibden Bottom) Closed canopy sallow/birch, swampy, fringing flushed stands or along very wet valley mire flow lines (eg Denny Bog)
Shortheath Common	C	No info
Borrowdale Woods	C	No info
West Midlands Mosses	D	No info
River Wye/Afon Gwy	D	No info
Clean Moor and Holme Moor	D	No info
Dorset Heaths	D	No info
Cors Caron	C	Low, closed-canopy(?) W4 downy birch/grey willow on edge (lagg fen?) of raised bog. Also W1 on same site?
Rhos Goch	C	Low downy birch/grey willow W4 on inner edge of wooded lagg of raised bog damaged by drainage and cutting. W1, W2, W5 also on same site? No info
Merionnydd Oak Woods and Bat Sites	C	No info
Corsydd Eifionydd	D	No info
Cors Fochno	D	No info
Mynydd Epynt	D	No info
River Usk/Afon Wysg	D	
Ballochbuie	A or B	Forest mires in Caledonian pinewood. M18 and M19 mires with a sparse to open cover of variably stunted Scots pine. Also bog woodland on fen at Mòine Chruinn.
Cairngorms	A or B	In Caledonian pinewood. M18 and M19 mires with a scattering of stunted Scots pine trees and saplings. Some bog woodland apparently ancient and stable.
Monadh Mor	A or B	Stunted Scots pine on peat-filled hollows of complex glacial moraine area. Apparently stable although possibly of recent origin following peat cutting.
Pitmaduthy Moss	A or B	Scattered stunted Scots pine on complex of poor fen and bog. Possibly of relatively recent origin (history of peat cutting suspected).
Kinveachy Forest	C	Scots pine bog woodland in Caledonian pinewood.
Loch Maree Complex	C	Small-scale examples of relatively undisturbed Scots pine bog woodland in wettest areas of Caledonian pinewood with low level of disturbance.
Strathglass Complex	C	Scattered Scots pine bog woodland on wetter peatland areas in Caledonian pinewood.
Glen Tanar	D	No info
Loch Lomond Woods	D	No info
Sunart	D	

These bog woodlands occur in several distinct hydrological settings, most of the English and Welsh examples having at least some groundwater influence and therefore, strictly speaking, fen rather than bog woodlands. The wood on Morden Bog seems to be growing on fen peat, supplied with groundwater from below by artesian pressure. Some of the New Forest bog woods are fed with mineral-charged water flowing laterally down the central flow-lines of valley mires. Bog woodland at Cors Caron and Rhos Goch is probably on lagg fen and therefore receiving both surface water and ground water. At Rhos Goch the wood is also spreading up the damaged raised bog surface, where there is no groundwater influence but nutrients come from rain and oxidising peat.

2.4.3 Vegetation classification of bog woodlands

Before the 1992 Habitats Directive (EC 1992) the term bog woodland had no widely known and accepted definition. It was used by different people to mean different things (and to some extent, still is). In the run-up to the drafting of the Habitats Directive, bog woodland was proposed as a natural habitat type for inclusion. The proposers intended the class to cover two habitat types: (i) raised bogs with a natural cover of stunted trees and (ii) somewhat-wooded, terrestrialising, former glacial hollow lakes in bog-lake complexes (R. Lindsay, *pers. comm.*). During the process of formalising legislation, the definition of the habitat class got broadened well beyond what was originally intended. The Directive used the Corine Biotope Classification (Corine 1988) to list in Annex 1 the natural habitats requiring SAC designation. It uses the Corine habitat codes 44.A1 to 44.A4 to define bog woodland.

The Corine classification includes four types (44.A1 *Sphagnum* birch woods, 44.A2 Scots pine bog woods, 44.A3 Mountain pine bog woods and 44.A4 *Sphagnum* spruce woods) within the class 44.A. Corine does not name this class 'Bog woodland', as does the Directive. Instead it uses the term 'Birch and conifer swamp woods', which it describes as 'woods of *Betula pubescens*, *Pinus spp.* or *Picea abies* colonizing bogs and acid fens'. Only the first two subclasses (*Sphagnum*-birch woods and Scots pine bog woods) occur naturally in Britain and only the former is found in England and Wales. *Sphagnum*-birch woods are described in Corine as 'Forests of *Betula pubescens* or *B. carpatica* on peaty, humid and very acid soils, colonizing bogs of reduced peat building activity and acid fens, with *Molinia caerulea*, *Vaccinium uliginosum*, *V. mytilus*, *Empetrum nigrum*, *Trientalis europaea* and many *Sphagnum*s, mosses and liverworts'. The phrase 'bogs of reduced peat building activity' presumably includes bogs altered by drainage and/or peripheral peat cutting. This definition of bog woodland therefore includes woods colonizing damaged bogs, at least up to the time when the tree canopy shades out the bog species mentioned.

Before the Habitats Directive was formally adopted, the Corine classification was revised, causing some ambiguity and confusion among those interpreting the Annex 1 habitats list. The European Commission clarified the habitat definitions by issuing an interpretation manual with definitions, lists of characteristic species and other useful information on the habitats (EC 2003). It defines bog woodland as 'Coniferous and broad-leaved forests on a humid to wet peaty substrate, with the water level permanently high and even higher than the surrounding water table. The water is always very poor in nutrients (raised bogs and acid fens). These communities are generally dominated by *Betula pubescens*, *Frangula alnus*, *Pinus sylvestris*, *Pinus rotundata* and *Picea abies*, with species specific to bogland or, more generally, to oligotrophic environments, such as *Vaccinium spp.*, *Sphagnum spp.*, *Carex spp.*'

For Britain, JNCC has published a narrower definition of bog woodland for the selection of candidate SACs (JNCC 2004). It recognises **true** bog woodland as ‘scattered trees occurring across the surface of a bog in a relatively stable ecological relationship as open woodland, without the loss of bog species’. This it distinguishes from ‘the progressive invasion of bogs by trees, through natural colonisation or afforestation following changes in the drainage pattern, which leads eventually to the loss of the bog community’. JNCC states clearly that ‘secondary birch woodland on degraded bogs, and woodland encroachment resulting from falling water-tables, are excluded from the Annex-1 definition’. The definition covers most of the recognised bog woodland sites in Scotland but not some of the English and Welsh sites (N. Sanderson, *pers. comm.*).

A detailed study of vegetation and tree cover of Scots pine wooded bogs at Abernethy Forest, Strathspey, recognised three distinct types (Woodland bog, Wooded bog and Bog woodland), differing in the degree to which tree cover is constrained by a high watertable (McHaffie, Legg, Amphlett, Worrell & Cowie 2002). The term ‘woodland bog’ is used for essentially open bog with abundant tree seedlings and a few stunted trees, and with full tree development prevented by the permanently high water table. ‘Wooded bog’ has a high water-table and stunted trees with an open canopy. ‘Bog woodland’ describes woodland with relicts of bog vegetation beneath a closed canopy that has resulted from a lowering of the water-table on formerly open bog. Legg and others (2001) showed that the vegetation of these Abernethy sites included NVC communities M15, M17, M18 and M19, but that they all represented the more continental end of the range of vegetation for the NVC classes. They concluded that the bogs support a dynamic system in which the vegetation can change among the three categories of density of woodland, with disturbances, including water-table fluctuation, causing the changes.

For sites on raised peat (ie ombrotrophic sites), stability of the habitat over time is a necessary qualification, separating true bog woodland from colonising woods on damaged bogs. As lowering of the water-table encourages the development of closed canopy woodland, leading to the disappearance of almost all bog plant species, we could say that on raised bogs it is an eco-hydrological threshold that distinguishes between bog woodland and more productive woodland.

2.4.4 Eco-hydrological requirements of key component species of bog woodlands

Efforts were concentrated on some key species from NVC communities W4, M18 and M19 as given in the Table 9. It is now clear that some SAC bog woodland sites in England and Wales support NVC communities other than these.

Table 9 List of species for which literature reviews were completed.

M18	<i>Calluna vulgaris</i> , <i>Erica tetralix</i> , <i>Eriophorum angustifolium</i> , <i>E. vaginatum</i> , <i>Sphagnum papillosum</i> , <i>S. tenellum</i> , <i>S. capillifolium</i>
M19	<i>Calluna vulgaris</i> , <i>Rubus chamaemorus</i> , <i>Eriophorum vaginatum</i> , <i>E. angustifolium</i> , <i>Sphagnum capillifolium</i>
W4	<i>Betula pubescens</i> , <i>Pinus sylvestris</i> , <i>Salix cinerea</i> , <i>Molinia caerulea</i> , <i>Sphagnum fallax</i>

2.4.4.1 Nutrition

W4 (*Betula pubescens* – *Molinia caerulea* woodland)

Species composition of the vegetation is influenced by soil moisture, base-richness of the soils and nutrient status of the system (Rodwell 1991a). Some of the W4 sub-communities extend into soligenous situations with nutrient poor peaty gleys. In base rich flushes with mineral soil it is replaced by W7 (*Alnus-Fraxinus-Lysimacha*).

Downy birch (*Betula pubescens*) (Atkinson 1992)

Mycorrhizal symbiosis is required for birch to grow on bogs (Weigers 1990), but mycorrhizal fungi require aerated soil and may suffer from phosphorus deficiency on bogs (MacKenzie & Worrell 1995). Tolerant of very infertile soils, downy birch prefers more minerotrophic sites, either shallow peat suffused with minerals from the underlying substrate or in basin situations with roots accessing groundwater (MacKenzie & Worrell 1995).

Scots pine (*Pinus sylvestris*)

Scots pine is known to be tolerant of very infertile soils (Carlisle & Brown 1968; Ohlson 1995).

Purple moor grass (*Molinia caerulea*) (Taylor, Rowland & Jones 2001)

Molinia prefers infertile to very infertile soils (<http://www.york.ac.uk/res/ecoflora/cfm/ecofl/>,).

Ling heather (*Calluna vulgaris*)

Calluna tolerates low nutrient concentrations and is said to be calcifugous (Gimingham 1960).

Common cottongrass (*Eriophorum angustifolium*)

This species prefers infertile soil and is normally found on deep peat but occasionally elsewhere. Calcium concentration is important (Phillips 1954).

Hare's-tail cottongrass (*Eriophorum vaginatum*)

Hare's-tail tolerates very infertile soils. It can concentrate mineral nutrients, particularly phosphorus, under ombrogenous conditions (Wein 1973).

2.4.4.2 pH

pH ranges tolerated by bog woodland species are given in Table 10. Data are from various sources, collected at (<http://www.york.ac.uk/res/ecoflora/cfm/ecofl/>).

Table 10 Indicative pH range tolerated by key bog woodland species.

Species	pH range	
<i>Betula pubescens</i>	3.1	7.5
<i>Salix cinerea</i>	3.9	7.8
<i>Molinia caerulea</i>	3.1	7.8
<i>Calluna vulgaris</i>	3.2	7.4
<i>Erica tetralix</i>	3.1	7.4
<i>Eriophorum angustifolium</i>	2.2	7.6
<i>Eriophorum vaginatum</i>	3.0	5.6
<i>Rubus chamaemorus</i>	-	4.5

2.4.4.3 Flooding

Downy birch (*Betula pubescens*)

Prolonged inundation for the growing season can kill downy birch (Weigers 1990).

Purple moor grass (*Molinia caerulea*)

Molinia adapts to waterlogging by horizontal root development (Taylor, Rowland & Jones 2001).

Ling heather (*Calluna vulgaris*)

Calluna roots require oxidising soil conditions, even in very wet peat. This can restrict roots to the upper 5-10 cm on very wet sites. It can root at least 85 cm down into well-aerated soil (Gimingham 1960).

Crossleaved heath (*Erica tetralix*)

Although it grows in waterlogged peat, it is unclear whether the roots can exploit anaerobic peat (Bannister 1966). It tolerates waterlogged, poorly aerated peat. Depth to water table determines distribution, and presumably competitive balance, between *E. tetralix* and *Calluna*. *E. tetralix* communities are found where the water table is permanently high and *Calluna* communities are found where there is a fluctuating water table.

Common cottongrass (*Eriophorum angustifolium*)

Common cottongrass is capable of rooting down into permanently anaerobic lower peat layers (Weigers 1990).

Hare's-tail cottongrass (*Eriophorum vaginatum*)

Hare's-tail can tolerate the water table at the surface in spring and lower in summer but requires a peat water content of >5 kg water per kg dry matter (Wein 1973).

2.4.4.4 *Sphagnum* mosses

The two major factors influencing the distribution of *Sphagnum* species are the height of the surface relative to the local general water level and the chemical status of water in the peat (Daniels & Eddy 1990). In bog woodland, shade tolerance must also be a key factor since canopy closure can increase shade markedly and lead to the disappearance of most *Sphagnum* species.

The species differ in their ability to withstand desiccation and therefore in the height above the water table at which they can survive. At the two extremes, *S. cuspidatum* usually grows in standing water or in places that hold standing water for most of the year, whereas *S. austinii* can form hummocks reaching up to one metre above the water table, no mean feat for a plant without any internal vascular system. The latter species has distinct pendent branches, which conduct water externally by capillary action, and branch leaves tightly pressed against the branch and overlapping one another to reduce evaporation. It grows in tight cushions, which maintain a humid internal environment.

Precise information on ecological amplitudes of *Sphagnum* species in terms of height above water table and water chemistry is not available but the species have been assigned ‘Ellenberg numbers’ (Ellenberg, Weber, Dull, Wirth, Werner & Paulsen 1992). Relative ecological amplitudes for height above the local general water level and nutrient availability were given by (Daniels & Eddy 1990) (Table 11).

Table 11 Published indices of ecological preference (Ellenberg and others 1992) and ranges inferred by R. Anderson from published diagrams (Daniels & Eddy 1990) for some key *Sphagnum* species found in bog woodlands.

	Ellenberg Moisture ¹	Ellenberg Reaction ²	Ellenberg Light ³	D&E Ht algwl ⁴	D&E Trophy ⁵
<i>Sphagnum papillosum</i>	6	1	9	0.4-0.9 m	O-Me
<i>Sphagnum capillifolium</i>	7	2	-	0.4-1.0 m	O-Me
<i>Sphagnum fallax</i>	7	2	7	0.2-0.6 m	O-Mi
<i>Sphagnum tenellum</i>	8	2	9	0.2-0.9 m	O

¹ Moisture index: 6=constantly moist or damp sites, 7=damp to wet sites, 8=wet sites

² Reaction (pH) index: 1=never above pH 5, often below pH 3, 2=mostly well below pH 5

³ Light index: 7=generally in well-lit places but can bear partial shade, 9=in full light, mostly in full sun

⁴ Height above local general water level: Ranges taken from diagrams showing relative ecological amplitudes, figures are my invention and assume linearity of the diagram’s wetness scale.

⁵ Trophy or nutrient availability requirements: O=oligotrophic or nutrient-poor, Me=mesotrophic or middling in nutrient levels, Mi=minerotrophic or nutrient-rich.

2.4.4.5 Eco-hydrological vulnerability based on component species

A far greater range of species would have to be included to determine eco-hydrological thresholds for bog woodland communities and this requires better information on species composition than we have been able to obtain. The range of bog woodland types included, even within the Natura sites supporting the habitat, is large. Prediction of thresholds based on individual species would have to be done separately for the distinct types.

Bog woodland supporting *Rubus chamaemorus* (if such exists) would presumably lose this species if the site were to become irrigated with groundwater so that the pH rose above 4.5. The same may be said about two species definitely found in some bog woodlands, *Sphagnum papillosum* and *Eriophorum vaginatum*, with pH thresholds of 5 and 5.6, respectively. The opposite effect might be seen in *Salix cinerea*. If peat pH were to fall below 3.9, for example by lowering of the groundwater table, this species might be lost from an existing site. Ombrotrophic mire species, including the subset found in this type of bog woodland, are stress-tolerant, adapted to low-nutrient, high water table, conditions. Any hydrological activities which reduce the severity of these conditions will shift the competitive balance in favour of more strongly competitive but less stress-tolerant species and might result in the loss of mire species. *Sphagnum tenellum*, for example, might be lost if nutrient supply is increased since it prefers oligotrophic conditions.

The biggest changes are likely to result from changes in suitability of sites for the dominant tree species.

2.4.5 References

2.4.5.1 Literature detailing bog woodland characteristics and eco-hydrological requirements at the whole ecosystem scale

- BANNER, A., POJAR, J., & ROUSE, G.E. 1983. Postglacial palaeoecology and successional relationships of a bog woodland near Prince Rupert, British Columbia. *Canadian Journal of Forest Research*, 13, 938-947.
- BRAGG, O.M. 2004. The restoration of Kirkconnel Flow: searching for a bog amongst the trees. *International Peat Journal*, 12.
- CORINE. 1988. Corine biotopes project. *Technical handbook Volume 1*.
- EC. 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*, L 206(22/7/92), 7-49.
- EC. 2003. *Interpretation manual of European Union Habitats*. Brussels: European Commission DG Environment.
- ELLENBERG, H. and others. 1992. Ziegerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe). *Scripta Geobotanica*, 18, 1-258.
- HALL, J. 1997. An analysis of National Vegetation Classification survey data. *JNCC Report*, No. 272.
- JNCC. 2004. SAC selection website.
- LEGG, C.J. and others. 2001. *The status of wooded bogs at Abernethy, Strathspey, Restoring Natural forest habitats, Fort William*, 12-16.
- MACKENZIE, N.A., & WORRELL, R. 1995. *A preliminary assessment of the ecology and status of ombrotrophic wooded bogs in Scotland*, 40. Battleby: Scottish Natural Heritage.
- RODWELL, J.S. 1991a. *British plant communities. Volume 1: woodlands and scrub*. Cambridge: Cambridge University Press.
- RODWELL, J.S. 1991b. *British Plant Communities. Volume 2. Mires and heaths*. Cambridge: Cambridge University Press.
- RODWELL, J., & DRING, J. 2001. European significance of British woodland types. *English Nature Research Reports*, No. 460.
- TOMASSEN, H.B.M. and others. 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? *Journal of Applied Ecology*, 41(1),139-150.
- TURUNEN, C., & TURUNEN, J. 2003. Development history and carbon accumulation of a slope bog in oceanic British Columbia, Canada. *The Holocene*, 13(2), 225-238.

WEIGERS, J. 1990. Forested wetlands in Europe. In: A.E. LUGO, M. BRINSON, & S. BROWN, Eds. *Ecosystems of the world 15. Forested wetlands*. Amsterdam: Elsevier.

2.4.5.2 Literature examining the specific water resource and nutrient requirements of key component species of bog woodland

ATKINSON, M.D. 1992. *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. *Journal of Ecology*, 80, 837-870.

BANNISTER, P. 1966. *Erica tetralix* L. *Journal of Ecology*, 54, 795-813.

BOGGIE, R. 1972. Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland. *Oikos*, 23, 304-312.

BOGGIE, R., & MILLER, H.G. 1976. Growth of *Pinus contorta* at different water-table levels in deep blanket peat. *Forestry*, 49(2), 123-131.

CARLISLE, A., & BROWN, A.H.F. 1968. *Pinus sylvestris* L. *Journal of Ecology*, 56, 269-307.

DANIELS, R.E., & EDDY, A. 1990. *Handbook of European Sphagna*. London: HMSO.

FRYE, J., & GROSSE, W. 1992. Growth responses to flooding and recovery of deciduous trees. *Zeitschrift fur Naturforschung C – A Journal of Biosciences*, 47(9-10), 683-689.

GIMINGHAM, C.H. 1960. *Calluna* Salisb. *Journal of Ecology*, 48, 455-483.

GOOD, J.E.G. and others. 1992. Species and clonal variation in growth-responses to waterlogging and submersion in the genus *Salix*. *Proceedings of the Royal Society of Edinburgh Section B - Biological Sciences*, 98, 21-48.

MCHAFFIE, H. and others. 2002. Scots pine growing on forested mires in Abernethy Forest, Strathspey, Scotland. *Botanical Journal of Scotland*, 54, 209-219.

OHLSON, M. 1995. Growth and nutrient characteristics in bog and fen populations of Scots pine *Pinus sylvestris*. *Plant and Soil*, 172, 235-245.

PHILLIPS, M.E. 1954. *Eriophorum angustifolium* Roth. *Journal of Ecology*, 42, 612-622.

TAYLOR, K., ROWLAND, A.P., & JONES, H.E. 2001. *Molinia caerulea* (L) Moench. *Journal of Ecology*, 89, 126-144.

WEIN, R.W. 1973. *Eriophorum vaginatum* L. *Journal of Ecology*, 61, 601-615.

2.4.5.3 Key national and international contacts (academics, practitioners) with relevant expertise relating to Bog Woodland

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2.4.5.4 Other references and web page links relevant to bog woodland

ATKINS & ENTEC. 2003. *Habitat and species summary guidance notes.*

<http://www.york.ac.uk/res/ecoflora/cfm/ecofl/> University of York ecological database website.

3 Critical evaluation of gaps in knowledge and further research requirements concerning eco-hydrological characteristics and resource requirements of Annex I wet woodland types and their component NVC types

3.1 Introduction

This critical evaluation follows from a review of information currently available describing the ecohydrological requirements of residual alluvial forests and bog woodland in the UK (Chapter 2). Its purpose is to provide a critical assessment of the adequacy of current knowledge as a basis for issuing guidance on the management of these habitats (ie the production of ecohydrological guidelines that principally ensure that the nutrient and hydrological requirements of the habitat are met). The two habitat types are considered separately, although both adopt the same reporting as drawn up in the production of ecohydrological guidelines for lowland wetland plant communities (Wheeler and others 2004¹). This structure was deemed to be useful as a means of highlighting under previously identified areas of interest where information might be lacking and to go through the process of considering, at this early stage, the feasibility of writing up each section as part of a set of comprehensive ecohydrological guidelines for alluvial forest and bog woodlands. The first section deals with alluvial forest/bog woodland **context** and critically considers the information available detailing their floristic composition and distribution, as well as the landscape situation & topography within which these wet woodlands are found and the substratum that the community is commonly associated with. This is followed by a section on current understanding of the **supply mechanisms & conceptual models** that provide information on the main water supply mechanisms of alluvial forest/bog woodland communities. The third section describes the extent of our knowledge of their water, nutrient/hydrochemistry and management **regime** requirements. The **implications for decision-making** are covered in the final section and address both the vulnerability and restorability of the community; potentially useful methodologies that might be used to set guidelines are identified and discussed.

3.2 Critical evaluation of eco-hydrology information for Residual Alluvial Woodland

In order to avoid repetition, all residual alluvial forest communities (W5, W6 and W7) are treated in a single evaluation, although where appropriate particular sub-types are referred to separately.

3.2.1 Context

3.2.1.1 Floristic composition

The level of adherence of existing UK alluvial forests to the three main alluvial forest categories (W5, W6, W7) described in Rodwell's (1991) NVC system (see Section 3, Task 1)

¹ WHEELER, B.D. and others. 2004. In: Brooks, A.W., José, P.V. and Whiteman, M.I., eds. *Ecohydrological Guidelines for Lowland Wet Plant Communities*. Environment Agency (Anglia Region).

remains unclear. The singular adoption of the NVC as a system that comprehensively defines the floristic composition of all alluvial forests in the UK is also questionable.

Residual alluvial forests are frequently subject to eco-hydrological conditions that have been altered to a greater or lesser degree by human interference in the landscape (eg altered patterns of river flow, fertiliser run-off and increased levels of browsing and grazing). This is likely to result in significant diversity in floristic composition between alluvial forests depending on the nature, intensity and frequency of human 'interference'. Time-lags in vegetation community development following disturbance further complicates the interpretation of vegetation response, and to some extent, probably explains the inconsistent descriptions of successional development of W5, W6 and W7 alluvial forest stands in the literature. In addition, there are a number of alluvial forest species that were likely to have been common in former times, but may now be less prominent, or may have disappeared from alluvial forest communities altogether. Based on observations of remnant alluvial woodland, Peterken (1981) suggests that these once contained *Populus canescens*, and *P. nigra* in association with *Alnus glutinosa*, *Fraxinus excelsior*, *Quercus robur*, *Salix alba*, *S. fragilis*, *S. triandra* and *S. viminalis*. Huntley and Birks (1983) also propose, based on pollen analysis, that *P. nigra*, *P. alba* and *P. canescens* were all occurring in riparian habitats in Britain before the intervention of humans in the landscape, although there is some question as to whether *P. alba* and *P. canescens* are truly native to Britain (Tabbush 1996).

The black poplar *Populus nigra* certainly is a species that has been disappearing from the British landscape for a long time with some 2000-3000 genetically distinct trees remaining in England and Wales today. These often occur now as lone trees in hedgerows and on riverbanks. Once widespread south of a line from the Mersey to the Wash (and as far as the Thames basin and River Severn), the black poplar has suffered from a loss of natural floodplain woodland habitat and, in the past, a systematic policy of removal of these trees and particularly female specimens due to the copious production of fluffy seeds (whether fertilised or not). Relict populations occur today in the Vale of Aylesbury, parts of Herefordshire and Worcester, the river valleys of Suffolk (Spencer 1994) and on the east side of Yorkshire as far north as the Tees (White 1993). The decline of the black poplar and the associated, but less well-publicised decline in white willow *Salix alba* from English lowland floodplains, signals a likely complete loss of *P. nigra* - *S. alba* alluvial forest mixtures characteristic of recently deposited mineral soils close to major river channels, as in mainland Europe (Peterken & Hughes 1998). However, since no 'unaffected' alluvial forests remain in Britain today, it is unlikely that it will ever be possible to verify whether remaining or restored alluvial forest truly reflect the original native species composition.

In order to address the knowledge gaps discussed above, a first requirement is to assess the degree to which vegetation in existing alluvial forests truly corresponds to the NVC categories and their component sub-categories. Floristic data from alluvial forests is likely to exist mostly in unpublished formats. There is, therefore, a need to compile this information and (i) make assessments of adherence to NVC categories and sub-categories and (ii) make an estimate of the relative proportions of vegetation communities pertaining to each NVC category (information which is not currently available).

Secondly, decisions need to be made regarding the strict use of NVC categories since they actually reflect the impoverished, truly 'residual', condition of the remnants of alluvial forests in the UK today, rather than the **potential** floristic composition of these forests as they may have been in the past and could be restored in the future. The stands in existence today are

small and fragmented compared to formerly extensive and continuously distributed forests along river courses throughout Britain. This change in status alone undoubtedly has affected the floristic composition of residual alluvial forest. Edge effects, for one, are increased, but the reduced potential for effective dispersal of pollen and seed between disparate and smaller patches of alluvial forest has probably also influenced floristic composition with consequences for species (and genetic) diversity.

3.2.1.2 Distribution

No comprehensive data are available describing the extent of residual alluvial forest cover in the UK today and thus current coverage of W5, W6 and W7 alluvial forests. Inventories that have been produced by statutory nature conservation agencies in England, Scotland and Wales, and by the governmental Department of the Environment in Northern Ireland are incomplete and chiefly only provide limited descriptive information (eg floristic composition, local topography, geology, substrate etc.) for sites designated as Special Areas of Conservation. The Joint Nature Conservation Committee (JNCC) to some extent co-ordinates data between these agencies (eg The woodland NVC atlas for Great Britain (1998)), but while its web site (<http://www.jncc.gov.uk/protectedsites/sacselection/habitat.asp?FeatureIntCode=H91E0>) provides a map showing the location of residual alluvial forests that are currently recognised as Special Areas of Conservation and non-SAC alluvial forests, this information does not appear as comprehensive as distribution maps provided by Rowell & Dring 2001 (see Figure 6 a+b, Chapter 2). Minimal descriptive information is given on site characteristics such as floristic composition, substrate, geology, hydrology etc. (see summary of information provided by JNCC for alluvial forest SAC's in Table 1, Chapter 2). To obtain more detailed information on each site, it is necessary to first establish the names of component SSSI(s) of each SAC and then obtain the contact addresses of the conservation officers responsible for each SSSI (via English Nature). In some cases where the alluvial forest SSSI's comprise, or are located within, a large nature reserve detailed information may be available via the nature reserve web page (eg Bure Marshes National Nature Reserve; http://www.english-nature.org.uk/about/teams/team_photo/Buremarshes.pdf). Other information pertaining to each SSSI (mostly relating to habitat management) can be obtained via the English Nature web site at: <http://www.english-nature.org.uk/special/sssi/search.cfm>. Consultation of this site requires prior knowledge of the alluvial forest location (to county level) and the SSSI name designated to it.

Additional alluvial forest distribution data may be available for Scotland from the Land Cover Survey (LCS88) completed in 1988. Based on the interpretation of 1:25000 mainly monotone stereo paper aerial photographs (with the addition of colour through the central belt of Scotland), the LCS88 recognizes the following relevant categories of landcover: "Wetlands: drains trees" and "Blanket bog/peatland veg.: erosion trees". Another potential source of UK data is the *National Inventory of Woodland and Trees* (NIWT1 and NIWT2) undertaken at present by Forest Research; this inventory comprises repeated surveys based on 1 ha sample squares rather than on whole woodland areas and thus it is not possible to determine the extent of different habitat types.

3.2.1.3 Landscape situation and topography

The landscape situation and topography of residual alluvial forests within a catchment is understood only in general terms and is based on fairly scant descriptions in the wider literature (eg Atkins & ENTEC 2003; Peterken 1996; Peterken & Hughes 1998; Rodwell &

Dring 2001). Site-specific information is both very vague and incomplete at easily accessed sources (e.g. JNCC web pages), or is scattered and not readily available (ie requires direct contact to be made with local conservation officers). Significant differences can be expected between the landscape situations and topography of W5, W6 and W7 communities (see section 2.3.2, Chapter 2), although further clarification is necessary. The first need is to verify *expected* compared with **actual** landscape situations and topography of the three communities and in so doing, to elaborate on the very general descriptions that are presently available for each vegetation community – a single table and/or distributional map would help to highlight the relative proportions of alluvial forests in the range of possible topographic and landscape situations. Secondly, in order to better appreciate the geographical situation of a particular alluvial forest (and the degree of inter-site variability in terms of geographic situation), there is a need to provide details that will help to set each site in some sort of hydrological and geomorphological context; this is particularly true of W6 alluvial forests which occur along watercourses of varying description. In particular, information is required on stream order, stream type (meandering, braided, anastomosing) and flow regimes (managed, free-flowing, hydroperiods) of the main watercourses along which alluvial forests are present or could hold potential for restoration. Eco-hydrological guidelines will need to take into account inter-site variability so it is vital that information of this kind is available from the outset.

3.2.1.4 Substratum

Published descriptions and site-specific information available on the JNCC webpage for alluvial forests classed as SAC's, provide only a general picture of the substratum on which Britains alluvial forests are growing (see Table 1, Chapter 2). Available information on pH and nutrient status is too vague to be useful in setting eco-hydrological guidelines (eg poor/rich; acidic-neutral-basic) and the same applies for sediment textural descriptions which give little indication of the ratios of fine to coarse material.

Rough distinctions in substrate preferences are recognised for the different alluvial forest vegetation community types (W5, W6, W7) (see Section 2.3, Chapter 2) (Atkins & ENTEC 2003; Rodwell 1991), but details on inter-site variability both among and within these (eg in terms of depth of the organic layer, sediment textural properties in profile, soil pH, nutrients) are missing. It is thus not possible to distinguish a range of substrate conditions favoured by each alluvial forest type. Detailed information on substratum may be available for alluvial forests designated as SACs in records collected and kept by regional conservation offices. Collation of such data will be helpful not only to define the range of substrate conditions linked to different alluvial forest types, but also in order to set site-specific guidelines (eg water level thresholds can only be set where there is some indication of proportions of fine to coarse sediments and thus, likely water availability to vegetation). Substrate 'preferences' of plant species associated with each alluvial forest type may also help to reveal further details on W5, W6 and W7 alluvial forest substratum. This has been attempted in Table 12, however the information is scattered and further work is required to summarise the substrate preferences of individual species as reported in the literature. Nevertheless, Table 12 reveals a fairly wide range of sediment types that are linked to a number of dominant vegetation species in each alluvial forest type. The pH ranges tolerated are quite wide, but according to Ellenberg the majority of species growing in the three alluvial forest types have a preference for more basic conditions.

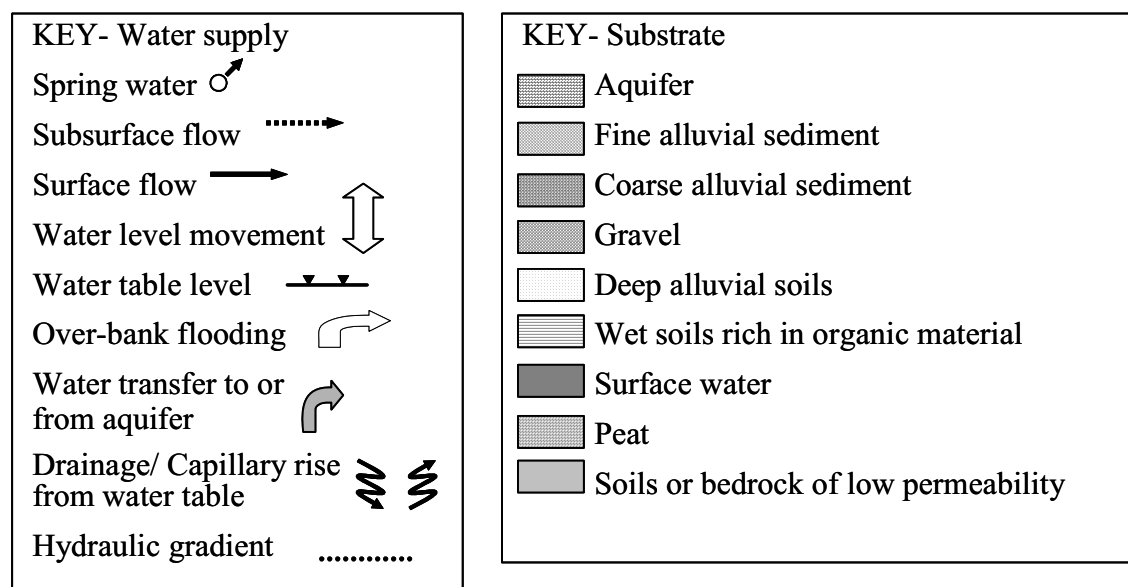
Table 12 Substrate conditions favoured by plant species that are common in W5, W6 and W7 alluvial forests.

Plant species	NVC community type			Substrate								
	W5	W6	W7	Sediment type (range)	Organic layer	Best growth	Tolerance range	pH Ellenberg	Best growth	Heavy metal tolerance ^{Alt.ref. 11}	Salinity tolerance ^{Alt.ref. 11}	
<i>Acer pseudoplatanus</i>				Sandy sediment - clays ¹		Deep loamy sands and light to medium loams ¹		6	soils of relatively high base status ¹⁰	None	0	Tolerates salt spray
<i>Alnus glutinosa</i>				Sandy sediment - clays ²	Occurs in deep fen peat ⁷	Organic soils when young trees; sandy, free-draining sediment when older ²	3.4 - 7.5 ¹¹	6		None	0	'Brackish'
<i>Angelica sylvestris</i>				Slow to free-draining ¹¹				6		None	0	'Affected'
<i>Betula pubescens</i>							3.5 - 7.8 ⁴	4		None	0	'Affected'
<i>Carex acutiformis</i>								7		None	0	
<i>Carex paniculata</i>								6		None	0	
<i>Corylus avellana</i>								6		None	0	
<i>Crataegus monogyna</i>						Moderately leached soils ¹⁰		7		None	0	
<i>Dryopteris dilatata</i>								4			0	
<i>Filipendula ulmaria</i>							4.4 - 8.0 ¹¹	6			0	'Affected'
<i>Fraxinus excelsior</i>				Free-draining ¹¹			4.2 - 8 ⁹	7		None	0	
<i>Iris pseudacorus</i>				Shingle and thin layers of organic matter on gravel-orthodox gleys; rhizomes may grow over submerged bare rock (penetrating through gaps to underlying soil). May also survive as floating mats. ³	Occurs on peat and permanently saturated organic soils	Depressions in riparian zone	2.0 - 7.7; less frequent in areas of chalk	6		'Good'	1+	Fresh to brackish
<i>Phragmites australis</i>							2.9 - 8.6	7		Metallophyte Cu, Fe, Pb & Zn	2+	Fresh to brackish
<i>Salix caprea</i>								7+			0	'Affected'
<i>Salix cinerea</i>							3.6 - 7.7	6		None	0	
<i>Salix fragilis</i>								7		None	0	
<i>Salix purpurea</i>								7+		None	0	
<i>Salix triandra</i>								7		None	0	
<i>Salix viminalis</i>								6		None	0	
<i>Sambucus nigra</i>								7		None	0	Tolerant of salt spray and occasional flooding by brackish water
<i>Urtica dioica</i>				Most soil types ¹¹	Will not grow on acid peat ³	Fine sands and silts ⁸	3.6 - 7.3 ¹¹	7		None	0	'Affected'

1 Nisbet, 1893
 2 Claessens & Thibaut 1994
 3 Dykes 1974
 4 Gill & Davy 1983
 5 Greig-Smith 1948
 6 Jones 1944
 7 McVean 1955
 8 Siebel & Bouwma 1998
 9 Wardle 1961
 10 Williams & Buxton 1989
 11 Peat & Fitter 2005

3.2.2 Water supply mechanism and conceptual model

No conceptual models of water supply mechanisms exist specifically for W5, W6 and W7 alluvial forest communities, although some general descriptions can be found in the literature for each type and also for related wetland ecosystems (Lloyd and others 1993; Rodwell & Dring 2001; Atkins & Entec 2003). These very basic descriptions (and an understanding of the basic functioning of alluvial forest ecosystems) have been used to construct generalized conceptual models illustrating assumed water supply mechanisms for the three different alluvial forest types. Keys to symbols used in the illustrations are given below:



In *Alnus glutinosa* – *Carex paniculata* (W5) alluvial forest communities, water is derived from surface flow and/or groundwater sources (eg spring-fed from a shallow aquifer, subsurface percolation of water from a nearby river, or over-bank flooding) (Figure 11). As W5 alluvial forest communities typically occur on the edge of standing, or very slow-moving freshwater bodies/courses (eg along lakes and ponds, or former side-channels and back-swamps), they are usually characterised by permanently wet and waterlogged conditions. With limited disturbance from floodwaters (ie there may be occasional water inputs from surface flows following a major flooding event), organic material tends to accumulate where this alluvial forest type is located, resulting in the formation of superficial deposits of organic material of varying thickness that overlie mineral alluvial deposits.

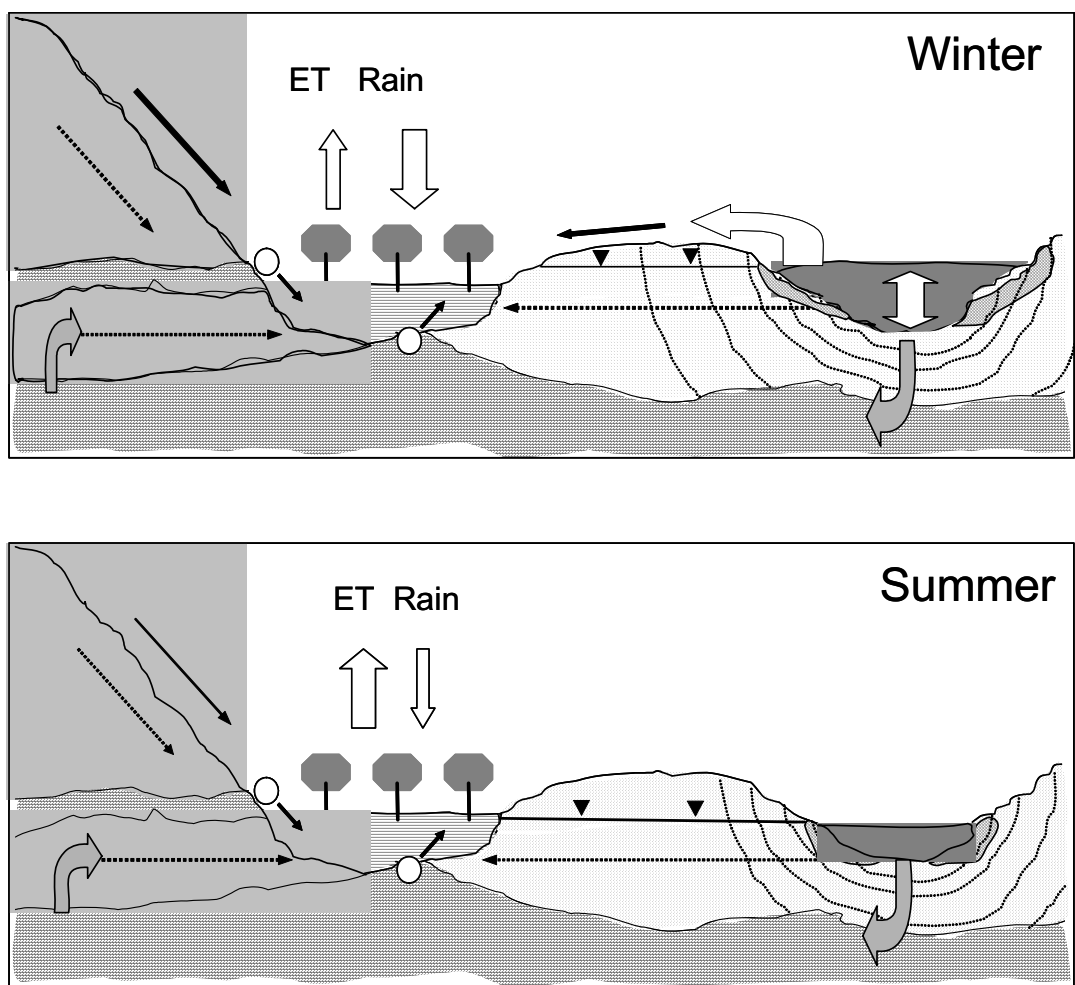


Figure 11 Conceptual model of water supply mechanisms in *Alnus glutinosa* – *Carex paniculata* (W5) alluvial forest communities in the winter and summer.

In *A. glutinosa-Urtica dioica* W6 communities, the vegetation is regularly subjected to the physical impacts of floodwaters and inundation from the nearby river. There is a clear zonation of vegetation communities determined by depth to the water table and frequency of disturbance at varying elevations within the riparian zone (Figure 12). The vegetation is adapted to rapid fluctuations in water table levels and significant seasonal variations in water availability that reflect a favoured hydroperiod. With the frequent remobilisation of sediments (and particularly along faster flowing streams) during flooding events, there is a constant threat of significant degradation or aggradation of riverbanks. A well structured profile favours drainage in the wetter winter months while finer alluvial sediments (fine sands and silt) ensure the upward movement of water in the summer months by capillary forces. Deep tap roots of riparian tree species allow contact to be maintained with this ‘capillary fringe’.

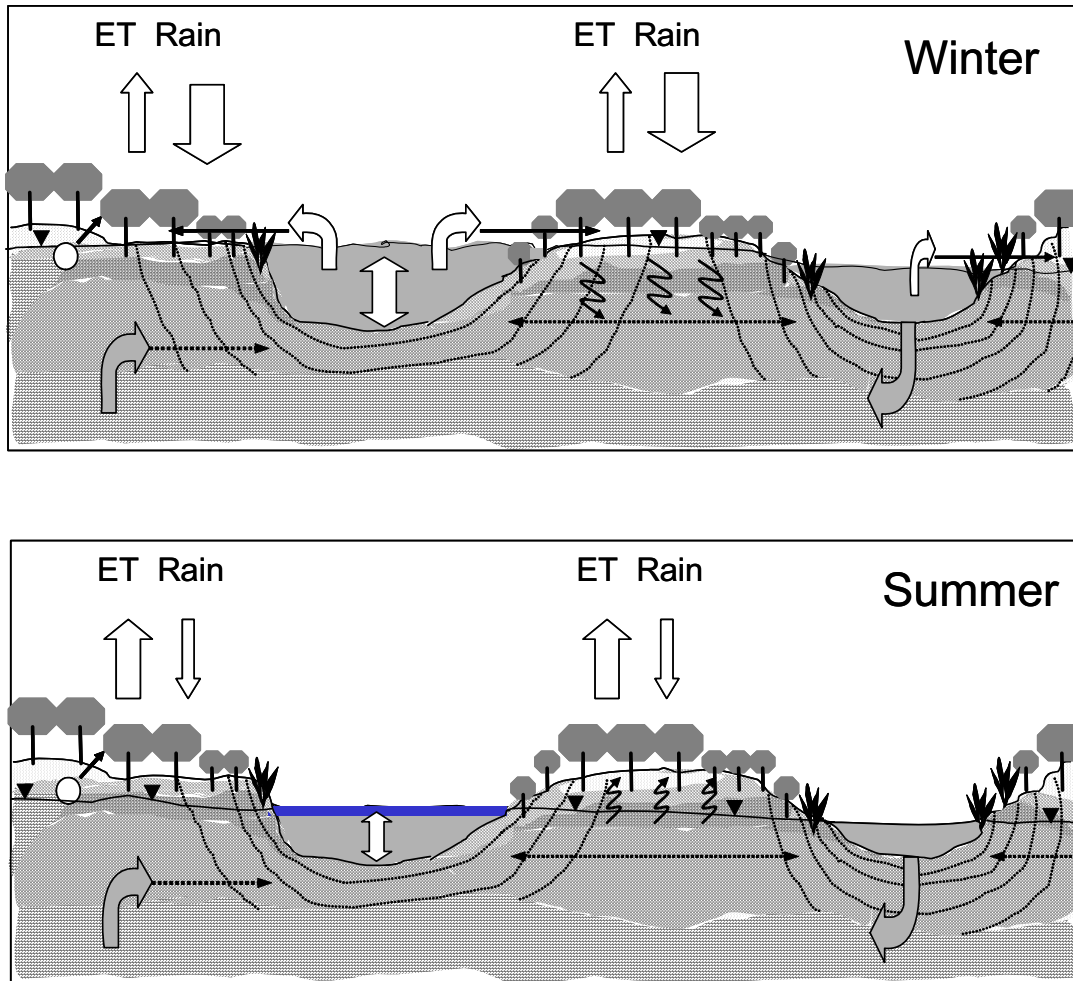


Figure 12 Conceptual model of water supply mechanisms in *A. glutinosa-Urtica dioica* (W6) alluvial forest communities in the winter and summer.

With no reliance on surface water originating from rivers, *A. glutinosa – Fraxinus excelsior-Lysmachia nemorum* (W7) communities depend chiefly on groundwater supplied (i) from subsurface (and surface) flows down valley slopes and/or (ii) laterally as springline flow from rock strata either along the slopes of middle-aged rivers, or along ‘brook channels’ which are not inundated by flooding, but where the groundwater emerges and maintains the soils in a semi-saturated state (Rodwell & Dring 2001) (Figure 13).

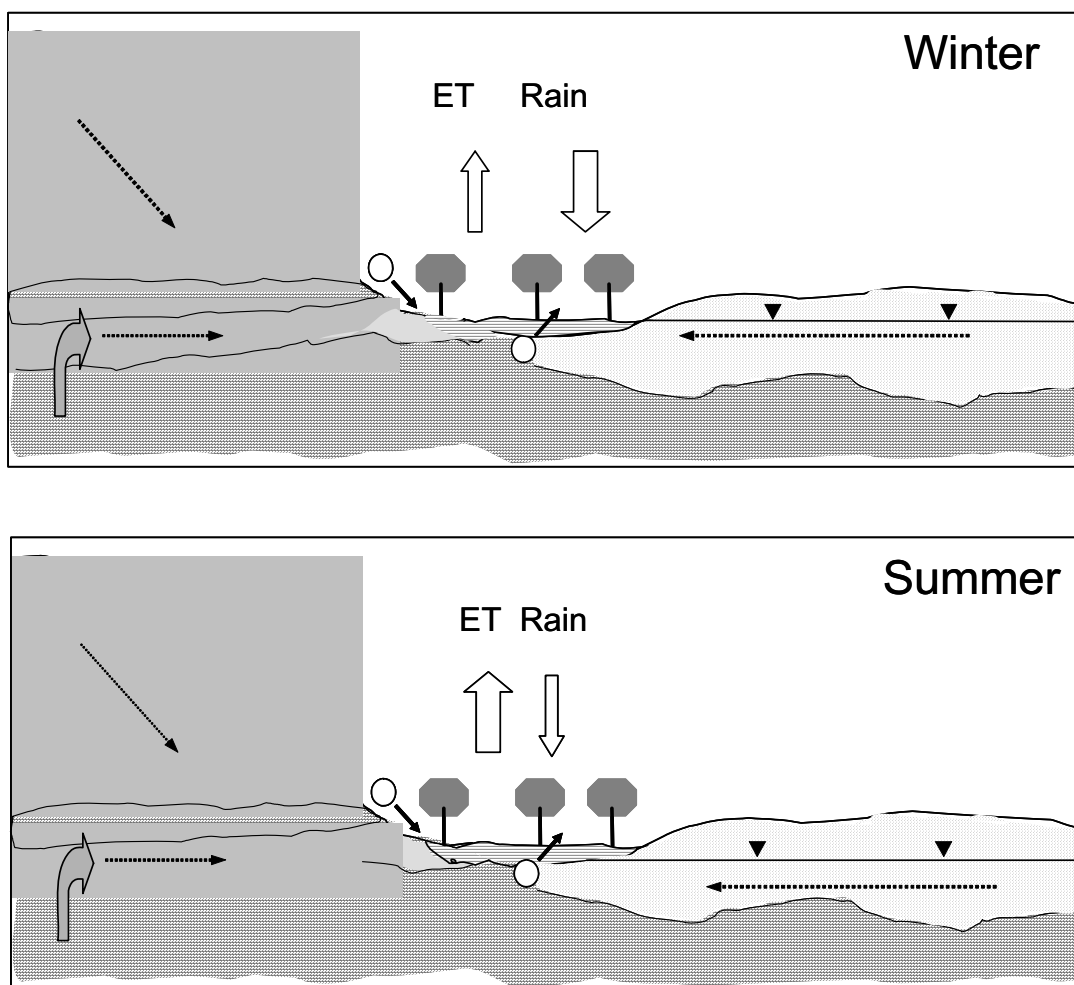


Figure 13 Conceptual model of water supply mechanisms in *A. glutinosa* – *Fraxinus excelsior*-*Lysmachia nemorum* (W7) alluvial forest communities in the winter and summer.

3.2.3 Regimes

3.2.3.1 Water regime

No information on water regime requirements exists specifically for W5, W6, W7 alluvial woodland communities; although some general descriptions can be found in the literature for each separate community and generalisations can be made from similar communities found in mainland Europe. There is some scope for producing guidelines by extrapolating from studies detailing the specific water requirements of component species, although this information is scattered and requires much additional work (following the literature search completed in Chapter 2) to summarise the water regime preferences of individual species. An effort has been made in this direction and the following tables attempt to define species responses to (i) flooding and anoxic conditions (Table 13), (ii) drought and preferred water table levels (Table 14) and also regeneration strategies and environmental requirements (Table 15); understanding ideal recruitment conditions will contribute to an understanding of the impact of drought/flooding in terms of their timing, magnitude and frequency. Ultimately a whole community water regime requirement will be needed and extrapolation from species-specific information is potentially a useful approach.

3.2.3.2 Nutrient regime / hydrochemistry

No information on nutrient requirement exists specifically for W5, W6, W7 alluvial woodland communities; although some general descriptions can be found in the literature for each separate community and generalisations can be made from similar communities found in mainland Europe. There is some scope for producing guidelines by extrapolating from studies detailing the specific nutrient requirements of component species (Table 16), although this information is scattered, requiring further significant effort (following the literature search completed in Chapter 2) to summarise nutrient regime preferences of individual species. An understanding of whole community nutrient regime requirements is ultimately needed and the species-specific approach may be one way of providing this information. A conceptual model has been produced that illustrates the expected positions of alluvial forest vegetation communities along soil moisture-nutrient gradients (Figure 14).

Table 13 Responses of plant species common in W5, W6 and W7 alluvial forests to flooding and waterlogged conditions.

Plant species	NVC community type			Flooding		Tolerance All ref. ²⁶	Physical damage	
	W5	W6	W7	Anoxic conditions			Seedlings	Adults
				Seedlings	Adults			
<i>Acer pseudoplatanus</i>				At 12 months, 15 % mortality and significant reductions in height growth when water level is 10cm above sediment surface for 120 days in a free-draining sandy sediment. Very good recovery in second growing season ¹ .	Intolerant of water-logging ¹⁰ . Unable to avoid anaerobic stress by pressurised gas transport ¹¹ .			
<i>Alnus glutinosa</i>				Flooding arrests N-fixation, photosynthesis and growth in 2-year old <i>A. incana</i> saplings with 100% mortality if flooding occurs in late spring/summer compared with lower rates of mortality in the autumn ² .	Able to avoid anaerobic stress and post-anoxic stress by pressurised gas transport and accumulation of the enzyme superoxide dismutase (SOD) ¹² . Increased conductivity of roots in water-logged soils also achieved by aerenchymatous root tissues ¹³ .	***		
<i>Angelica sylvestris</i>				Marked reductions in survival and growth of 11-12 week old seedlings during 30-day flooding period ^{3,4} . In freely draining sediments, 20% of 1 year-old seedlings did not survive a flooding treatment of 120 days (10 cm standing water above sediment surface) and surviving seedlings demonstrated a marked reduction in height growth. Reduced growth persisted into the second growing season; 34% decline in biomass production rate impeded competitive ability ⁵ .	Some avoidance of anaerobic stress by pressurised gas transport of oxygen from shoots to roots which is significantly affected by levels of irradiation of the stem ^{11,12} .	**		
<i>Carex acutiformis</i>								
<i>Carex paniculata</i>								
<i>Corylus avellana</i>						*		
<i>Crataegus monogyna</i>				In free-draining sediment, marked reduction in stem diameters and height growth of 1 year-old saplings when subjected to flooding (10 cm standing water above sediment surface) for 120 days. Excellent recovery in second growing season ⁵ .		**		
<i>Dryopteris dilatata</i>								
<i>Filipendula ulmaria</i>				Marked reductions in survival and growth of 11-12 week-old seedlings after 200 days continuous flooding ⁴ .	Can tolerate water-logged conditions for extended periods by entering a quiescent state ^{14,15,16} .			
<i>Praxinus excelsior</i>				In free-draining sediment, 100% survival and marked increase in stem diameters of 1 year-old saplings when subjected to flooding (10 cm standing water above sediment surface) for 120 days. Growth was retarded in second growing season (40% decline in biomass production rate). The increased stem diameter of flooded seedlings was likely to be due to the formation of aerenchyma, allowing for continuous diffusion of oxygen to roots ⁵ .	Does not benefit from pressurised gas transport, but high diffusion rate allows for growth in wet soils ¹¹ . In water-logged habitats (may be W5b) plant may suffer seasonal water shortage because roots do not develop well (remain in upper layers of substrate) and are too small to support growing tree ¹⁷ .			*
<i>Iris pseudacorus</i>				Tolerates 6 weeks of submergence, but slowed leaf growth; rapid recovery post-flooding ¹¹ .	Can survive long periods of water-logging and experimental anoxia (eg occurs in water up to 25 cm deep) in a quiescent state ^{18,19} . Survival effected by transfer of oxygen from leaves in air through to aerenchymatous rhizomes, enabling aerobic respiration. Completely submerged plants can tolerate approximately 2 months of total absence of oxygen at +20°C without any apparent damage to tissues and resumption of growth when normoxic conditions resume ¹⁶ . Substrate type has an important influence on resistance to anoxic conditions; ie significantly greater reductions in growth in waterlogged organic sediment with a decomposing litter layer of <i>P. australis</i> , than waterlogged mineral sediments ²⁰ .			
<i>Phragmites australis</i>				1 week-old seedlings tolerate 6 weeks of submergence, but seedling growth stops during flooding and leaves loose chlorophyll; growth resumes post-flooding ^{6,7,8} . In 3 month old plants submerged for 17 days severely restricted photochemical efficiency of leaves and no recovery post-flooding ⁹ .	Some avoidance of anaerobic stress by pressurised gas transport of oxygen from shoots to roots ²¹ . Prolonged flooding can lead to significant declines in <i>P. australis</i> coverage ^{22,23} . More sensitive to hydroperiods (magnitude, frequency and timing of flooding events) and fluctuations in water levels than high water table levels that result in waterlogged conditions ^{24,25} .			
<i>Salix caprea</i>					Up to 13 weeks of water-logging has little effect on form and growth rates of above-ground parts of plant. Belowground, hypertrophied lenticels develop within four weeks, followed by significant increases in stem diameter. Most of the root system dies by the end of 13 weeks and mycorrhiza is lost. New roots developing from pre-existing root bases and hyper-trophied lenticels, were long, branched and floated on or near the water surface ²⁶ .	**		

Plant species	NVC community type			Seedlings		Adults		Tolerance All ref. ²⁶	Physical damage	
	W5	W6	W7	Seedlings	Adults	Seedlings	Adults			
<i>Salix cinerea</i>					Up to 13 weeks of water-logging has little effect on form and growth rates of above-ground parts of plant. Belowground, hypertrophied lenticels develop within four weeks, followed by significant increases in stem diameter and in certain cases significant increases in leaf area and stem dry weight. Most of the root system dies by the end of 13 weeks and mycorrhiza is lost. New roots, developing from pre-existing root bases and hypertrophied lenticels, were short, fine and highly branching; these grew vertically upwards until they reached the water surface ²⁹ .			***		
<i>Salix fragilis</i>					After 16 days in waterlogged conditions, severe root die-back was compensated for by many new roots growing from old root bases. No such recovery after 32-days of waterlogging. Total submersion caused severe damage to aerial parts of plant; after 8 days shoot tips started to rot ²⁵ .			***		
<i>Salix purpurea</i>				In free-draining sandy sediment, 85% survival, but marked reductions in height (but not stem diameter) growth of 1 year-old saplings when subjected to flooding (10 cm standing water above sediment surface) for 120 days. Excellent recovery in second growing season (saplings receiving flooding treatment showed significantly better height growth, compared with non-flooded controls) ¹ .						
<i>Salix triandra</i>										
<i>Salix viminalis</i>					After 16 days in waterlogged conditions, at depths of 10-30 cm, rapid and severe root die-back was compensated for by many new roots growing from old root bases. No such recovery after 32-days of water-logging. In upper 10 cm of substrate, flooding enhanced adventitious root and aerenchymatous development. Shoot growth slowed after a 20-day delay. Total submersion caused severe damage to aerial parts of plant; after 25 days shoot tips started to rot. Root and shoot growth recommenced and was stimulated following flooding ^{29, 30} .			***		
<i>Sambucus nigra</i>								*		
<i>Urtica dioica</i>				Despite abundant seed in seed banks at low and high elevations along river banks, seedling numbers quickly drop off at low elevations during the growing season indicating a restriction to higher elevations on the floodplain and sensitivity to inundation ^{20, 27} . Spring flooding observed to halt growth and cause high mortality of several day-old seedlings. Mortality increased with increasing flood duration (10-30 days). Summer flooding has the most severe consequences with no survival where flooding duration is longer than 4 weeks. Able to survive 9 weeks of autumn flooding, although significantly reduced biomass (stem, root, leaf and rhizome dry weights) may handicap over-winter survival ²⁸ .	High water table levels (10-20 cm below the surface) and prolonged flooding rapidly limits growth and vegetative spread ³¹ .					

Increasing tolerance to waterlogging from: * brief winter flooding only; ** prolonged winter flooding; *** spring flooding.

- 1 Frye & Grosse 1992
2 Kaelke & Dawson 2003
3 Rinne 1990
4 Johansson & Nilsson 2002
5 Frye & Grosse 1992
6 Ingestad 1971
7 Van der Toorn 1972
8 Haslam 1973
9 Mauchamp & Methy 2004
10 Van der Toorn 1972
11 Grosse and others 1992
12 Monk and others 1987
13 Köstler and others 1968
14 Studer-Ehrenberger and others 1993
15 Smimoff & Crawford 1987
16 Brändle & Crawford 1987
17 Wardle 1961
18 Barclay & Crawford 1982
19 Hetherington and others 1983
20 Lennsen and others 1999
21 Armstrong & Armstrong 1991
22 Dienst and others 2004
23 Ansberry and others 2000
24 Warren and others 2001
25 Blanch and others 2000
26 Wildfowl & Wetlands Trust 1994
27 Lennsen and others 1998
28 Klimesová 1994
29 Good and others 1992
30 Jackson & Attwood 1996
31 Vogt 2001

Table 14 Responses of plant species common in W5, W6 and W7 alluvial forests to drought and some notes on preferred water table levels.

Plant species	NVC community type			Optimal water table depth (m below soil surface)		Ellenberg Moisture Alt.ref.4	Susceptibility (given for spring, summer and autumn where possible)		
	W5	W6	W7	spring	summer		autumn	Drought	
								Seedlings	Adults
<i>Acer pseudoplatanus</i>									
<i>Alnus glutinosa</i>				Continuous supply required ¹	Water level close to surface when young trees, but deeper when fully grown ² .	5	In loam:sand:peat mixture (2:1:1) 2.5 month old seedlings show reduced transpiration rates, signs of xylem cavitation and enhanced root growth. Shoot growth is maintained for up to 6 weeks, but leaf production and expansion subsequently drops significantly ² .	Vulnerable to xylem cavitation ^{9,10} .	
<i>Angelica sylvestris</i>						8		Vessels are vulnerable to cavitation. In increasing order of vulnerability are branches, petioles and roots. Root system can persist for 'some time' despite clear reductions in the translocation of photo-assimilates, in nitrogenase activity and in plant growth ^{11,12} . Reversal of embolism is assumed to be possible upon re-wetting of soils ¹³ .	
<i>Betula pubescens</i>						7	47% mortality when subjected to 70 days of drought (soil water potential -1.6 bars) ⁶ .		
<i>Carex acutiformis</i>				Tolerate submergence; slight to no flow ¹	Tolerate submergence; slight to no flow ¹	8			
<i>Carex paniculata</i>				Tolerate submergence; slight to no flow ³	Tolerate submergence; slight to no flow ³	9			
<i>Corylus avellana</i>						5			
<i>Crataegus monogyna</i>						5		Shows poor stomatal control and thus, poor water-use efficiency during periods of drought. Drought results in pre-mature leaf abscission in the summer ⁴ .	
<i>Dryopteris dilatata</i>						6			
<i>Filipendula ulmaria</i>						8			
<i>Fraxinus excelsior</i>				Dry to water-logged conditions ¹	Dry to water-logged conditions ¹	6	Reduced height and diameter growth. Sapling may not develop beyond shrub phase ⁷ .	Not vulnerable to xylem embolism, but displays die-back, discoloration of leaves and failure of apical buds to open in following spring ^{7,9}	
<i>Iris pseudacorus</i>				Continuous supply ¹	Continuous supply ¹	9		The rhizome of this species is tolerant of long periods (3 months +) in dry soil. The roots are shallow (up to 30 cm long) ⁵ .	
<i>Phragmites australis</i>				Periodically high water levels and short periods of submergence ¹ .	Periodically high water levels and short periods of submergence ¹ .	10+			
<i>Salix caprea</i>				Permanently high water levels ¹ .	Permanently high water levels ¹ .	7			
<i>Salix cinerea</i>				Permanently to periodically high water levels ¹ .	Permanently to periodically high water levels ¹ .	8			
<i>Salix fragilis</i>				Permanently to periodically high water levels ¹ .	Permanently to periodically high water levels ¹ .	8			
<i>Salix purpurea</i>				Permanently to periodically high water levels ¹ .	Permanently to periodically high water levels ¹ .	9			
<i>Salix triandra</i>				Periodically high water levels ¹ .	Periodically high water levels ¹ .	8			
<i>Salix viminalis</i>				Permanently to periodically high water levels ¹ .	Permanently to periodically high water levels ¹ .	8			
<i>Sambucus nigra</i>						5		Extremely vulnerable to xylem cavitation (90% loss of conductivity at -2.2MPa), thus only small fluctuations of field water potential are tolerable for this species to maintain water potential. Evidence that embolized vessels can refill and that species has sensitive stomatal control of transpiration, but these adaptations provide limited avoidance of drought stress ^{16,17,18} .	

Plant species	NVC community type	Optimal water table depth (m below soil surface)			Ellenberg Moisture ^{Allref.4}	Susceptibility (given for spring, summer and autumn where possible)	
		spring	summer	autumn		Drought	
						Seedlings	Adults
<i>Urtica dioica</i>	W5 W6 W7	Not waterlogged ¹			6	<p>Seedlings</p> <p>17 day-old seedlings displayed severe wilting after 5 h and 7 h of drought stress per day over for a period of 6 weeks, but maintenance of water potentials (-0.2 to -0.4 MPa) after 0-, 1-, 2- and 3-h drought treatments per day over the same experimental period. Although prolonged drought (5 h and 7 h per day) also resulted in inhibited vegetative growth and flowering, this drought treatment had no significant effect on the partitioning of dry matter between shoots and roots and the seedlings that had initially wilted during the first week of drought stress, rapidly recovered indicating a process of drought-hardening which probably involved stomatal closure.⁸</p>	<p>Adults</p> <p>Transpiration rates decline where water table levels are low (50-60 cms below the sediment surface)¹⁹. In very dry conditions, stunted growth yields plants averaging 30-60 cm compared with heights of 160 cm in favourable growing conditions.²⁰.</p>

- 1 Grime and others 1989
- 2 Claessens & Thibaut 1994
- 3 Lenssen and others 1989
- 4 Peat & Fitter 2005
- 5 Khalil & Grace 1992
- 6 Humphries and others 1982

- 7 Wardle 1961
- 8 Boot and others 1986
- 9 Lemoine and others 2001
- 10 Tissier and others 2004
- 11 Hacke & Sauter 1996
- 12 Sundström & Hussdaneil 1995

- 13 Raven and others 1989
- 14 Mediavilla & Escuero 2003
- 15 Sutherland 1990
- 16 Vogt 2001
- 17 Vogt & Losch 1999
- 18 Seidel 1973a

- 19 Struik 1997
- 20 Greig-Smith 1948

Table 15 Regeneration conditions favoured by plant species common in W5, W6 and W7 alluvial forests.

Plant species	NVC community type	Asexual				Sexual						
		Dispersal				Seedling establishment						
		Period of seed release (E-England, W-Wales, S-Scotland)	Peak of seed release	Mechanism(s)	Seedbank typical density (m ² Alt. ref. 2)	Longevity of seed	Light conditions	Substrate	Water table levels			
<i>Acer pseudoplatanus</i>	W5 W6 W7		None ²			'transient' ²						
<i>Alnus glutinosa</i>			Sprouting from the basal buds at base of plant (usually below-ground) in response to damage ¹			'transient - persistent' ²				Optimal growth where water level is 10-30cm below surface ¹		
<i>Angelica sylvestris</i>						47						
<i>Betula pubescens</i>			Sprouting from the basal buds at base of plant (usually below-ground) in response to damage ¹	March - April (E,W); April-June (S) ⁶	April (E,W); June (S) ⁶	300	wind; water ⁸	300	'short-lived' ^{2,9} years ⁷	Maximal germination observed with a 20-h photoperiod at 15°C. ¹³	Prolonged periods of damp, but not water-logged conditions. Seedling roots tend to remain in the top 10cm of soil ^{7,8} .	
<i>Carex acutiformis</i>			Common ²									
<i>Carex paniculata</i>			Common ²									
<i>Corylus avellana</i>			None ²									
<i>Crataegus monogyna</i>												
<i>Dryopteris dilatata</i>												
<i>Filipendula ulmaria</i>												
<i>Fraxinus excelsior</i>			None ²									
<i>Iris pseudacorus</i>			Common ²		Autumn ⁷	62	water ⁷	14	7+ months ⁷	None to medium shading ² Semi-exposed; where small gaps occur in field layer, suppressed growth if excessive shading. ¹³ Exposed conditions for prolonged periods. ⁷	Damp, but well-drained soil conditions. ¹⁷ Prolonged periods of damp, but not water-logged soil conditions. ⁷	
<i>Phragmites australis</i>			Common ²				wind; water ⁷		20% of seeds shed in Oct. germinate in Feb.-June the next year; 20% more germinate the following spring. ¹⁰ no dormancy period ²	None to medium shading ²	Fine to coarse alluvium ²	
<i>Salix caprea</i>			Common ²		May-June ²				no dormancy period ²	No to light shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Salix cinerea</i>			Common ²		May-June ²				no dormancy period ²	No shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Salix fragilis</i>			Common ²		May-June ²				no dormancy period ²	No to light shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Salix purpurea</i>			Common ²		May-June ²				no dormancy period ²	No shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Salix triandra</i>			Common ²		May-June ²				no dormancy period ²	No shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Salix viminalis</i>			Common ²		May-June ²				no dormancy period ²	No shading ²	Fine to coarse alluvium ²	Damp, but well-drained soil conditions. ¹⁷
<i>Sambucus nigra</i>								69	'transient - persistent' ²	Will not establish where there is turf, but		

Table 16 Nutrient conditions favoured by plant species common in W5, W6 and W7 alluvial forests.

Plant species	NVC community type			Tolerance range soil nutrients ^{All.ref.2}	Ellenberg Nitrogen ^{All.ref.2}	Nutrient levels (seedlings + adults)				Effects of nutrient loading
	W5	W6	W7			N (mg g ⁻¹ and mg g ⁻¹ soil nutrient content; mg l ⁻¹ soil water concentration)	P	K	Ca	
<i>Acer pseudoplatanus</i>				'Fertile'	6	4.7 mg l ^{-1.1} 5 mg g ^{-1.4} 21 mg g ^{-1.5} 3.8 mg l ^{-1.5}	0.5 mg l ^{-1.1} 0.9 - 14.9 mg g ^{-1.8} 1.14 mg g ^{-1.3} 0.39 mg l ^{-1.5}	20 - 485 mg g ^{-1.8} 39 mg g ^{-1.4}	1.0 - 2.3 mg g ^{-1.8} 4 mg g ^{-1.4}	Significantly inhibits ectomycorrhizal development ¹
<i>Alnus glutinosa</i>										
<i>Angelicca sylvestris</i>				'Fertile - very fertile'	5					
<i>Betula pubescens</i>				'Infertile - very fertile'	4	100 mg l ^{-1.3}	13 mg l ^{-1.3}	65 mg l ^{-1.3}	7 mg l ^{-1.3}	
<i>Carex acutiformis</i>				'Infertile [eutrophic water]'	6					
<i>Carex paniculata</i>				'Infertile [eutrophic water]'	6x					
<i>Corylus avellana</i>				'Fertile'	6					
<i>Crataegus monogyna</i>				'Very infertile - very fertile'	6x					
<i>Dryopteris dilatata</i>					5x					
<i>Filipendula ulmaria</i>				'Fertile'	5					
<i>Fraxinus excelsior</i>				'Fertile'	6	3.5 mg g ^{-1.6}	0.04 mg g ^{-1.6}	0.1 mg g ^{-1.6}	9.4 mg g ^{-1.6}	
<i>Iris pseudacorus</i>				'Infertile - very fertile'	6					
<i>Phragmites australis</i>				'Infertile'	6					
<i>Salix caprea</i>				'Fertile'	7+					
<i>Salix cinerea</i>				'Fertile'	5					
<i>Salix fragilis</i>				'Fertile'	7					
<i>Salix purpurea</i>				'Infertile - very fertile'	5					
<i>Salix triandra</i>				'Infertile - fertile'	5					
<i>Salix viminalis</i>				'Fertile'	6					
<i>Sambucus nigra</i>				'Fertile'	7x	20 - 125 mg g ^{-1.7}	n.d. - 15 mg g ^{-1.7}	24 - 54 mg g ^{-1.7}		
<i>Urtica dioica</i>				'Fertile'	8+					

1 Baar and others 2002

2 Peat & Fitter 2005

3 Williams & Buxton 1989

4 Du vignaud & Denayer de Smet 1970

5 Verhoeven 1996

6 Tremolieres and others 1999

7 Atkinson & Atkinson 2002

8 McVean 1955

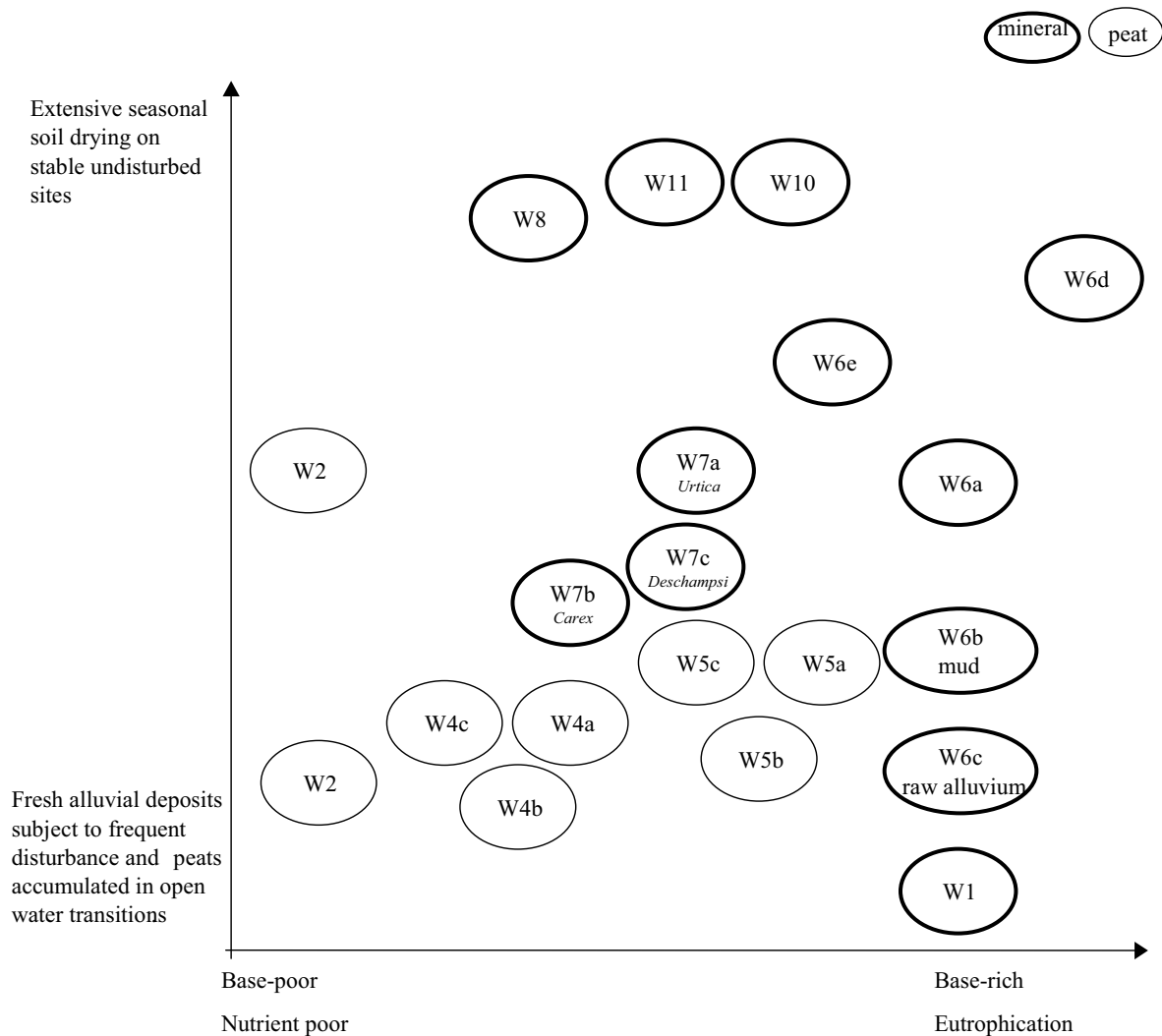


Figure 14 Conceptual model illustrating the expected position of alluvial forest communities along soil moisture and nutrient availability gradients.

3.2.3.3 Management regimes

There are no specific management regimes that are required to maintain alluvial forests, although coppicing of alder and willow is known to occur in some alluvial forests and may be a helpful management strategy where flood disturbances are removed from the system; ie coppicing activities (in conjunction with clearing of undergrowth) can open up stands, encouraging natural regeneration of early successional woody riparian tree species. It is not clear whether coppice activities as a conservation strategy in alluvial forests is sometimes linked to the active selection of species for wildlife value (Table 17).

Table 17 Wildlife value of plant species common in W5, W6 and W7 alluvial forests.

Plant species	NVC community type			Wildlife value All Ref. 1	Number of insect species supported All Ref. 1
	W5	W6	W7		
<i>Acer pseudoplatanus</i>					
<i>Alnus glutinosa</i>				Moderate. Cones eaten by Siskin and Redpoll.	90
<i>Angelica sylvestris</i>					
<i>Betula pubescens</i>				High. Seeds and buds eaten by birds.	229
<i>Carex acutiformis</i>					
<i>Carex paniculata</i>					
<i>Corylus avellana</i>				High. Nuts	107
<i>Crataegus monogyna</i>				Very high. Berries. Nest sites for small birds.	230
<i>Dryopteris dilatata</i>					
<i>Filipendula ulmaria</i>					
<i>Fraxinus excelsior</i>				Moderate.	41
<i>Iris pseudacorus</i>					
<i>Phragmites australis</i>					
<i>Salix caprea</i>				High	260+
<i>Salix cinerea</i>				High	260+
<i>Salix fragilis</i>				High. Older specimens often develop holes used by nesting birds.	260+
<i>Salix purpurea</i>					260+
<i>Salix triandra</i>					260+
<i>Salix viminalis</i>				High. Nest sites for Coots and Grebes.	260+
<i>Sambucus nigra</i>				Moderate. Berries.	19
<i>Urtica dioica</i>					

1 Wildfowl & Wetlands Trust 1998.

3.2.4 Implications for decision making

3.2.4.1 Vulnerability

(i) Grazers

While grazers are frequently present in alluvial woodlands in Britain, an understanding of their influence on the floristic composition and community structure remains limited. Information that is available tends to report on species-specific responses to grazing (as well as responses to browsing and granivory) with impacts reported in terms of degree of damage to plants and to regeneration potential.

(ii) Mowing / coppicing

Only a very limited number of studies report on the impact of mowing/coppicing on alluvial woodland floristic composition and structure, and it is not clear how widespread these management activities might be.

(iii) **Invasive species**

A number of invasive species of alluvial woodlands are recognised, although for most there is no information available that provides an indication of how widespread and aggressive they might be.

(iv) **Pests / diseases**

Pests and diseases affecting the dominant species of alluvial woodlands are well-documented, although the information is scattered and would require compilation prior to inclusion in management guidelines. Ideally, symptoms of diseases (signs of the presence of a pest species) would be needed in addition to a simple listing of potentially harmful parasites.

The following conceptual models (Figures 15-17) attempt to outline the main eco-hydrological threats to W5, W6 and W7 alluvial forest communities.

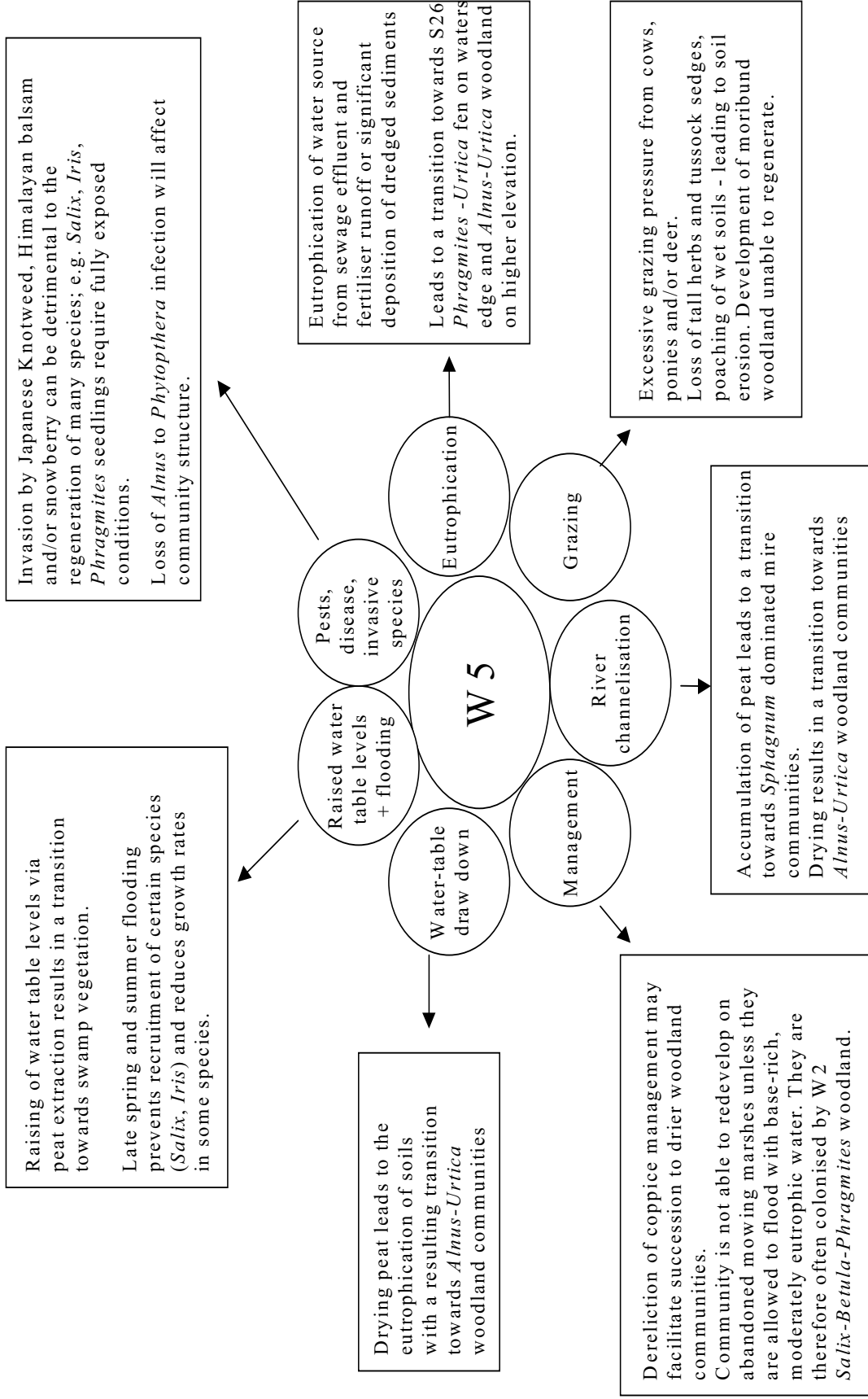


Figure 15 Vulnerability of *Alnus glutinosa* – *Carex paniculata* (W5) alluvial forest communities to environmental and management changes.

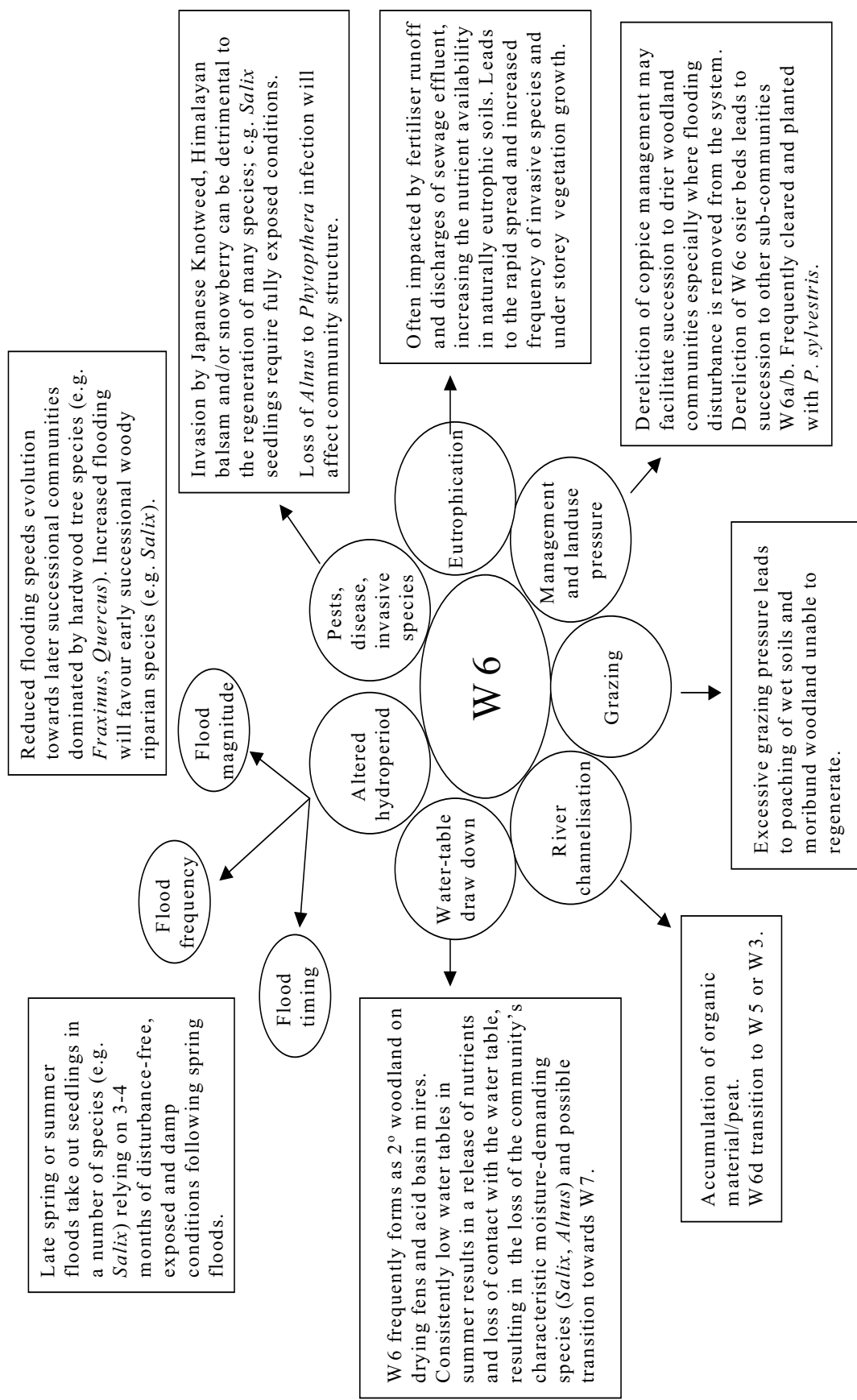


Figure 16 Vulnerability of *A. glutinosa-Urtica dioica* (W6) alluvial forest communities to environmental and management changes.

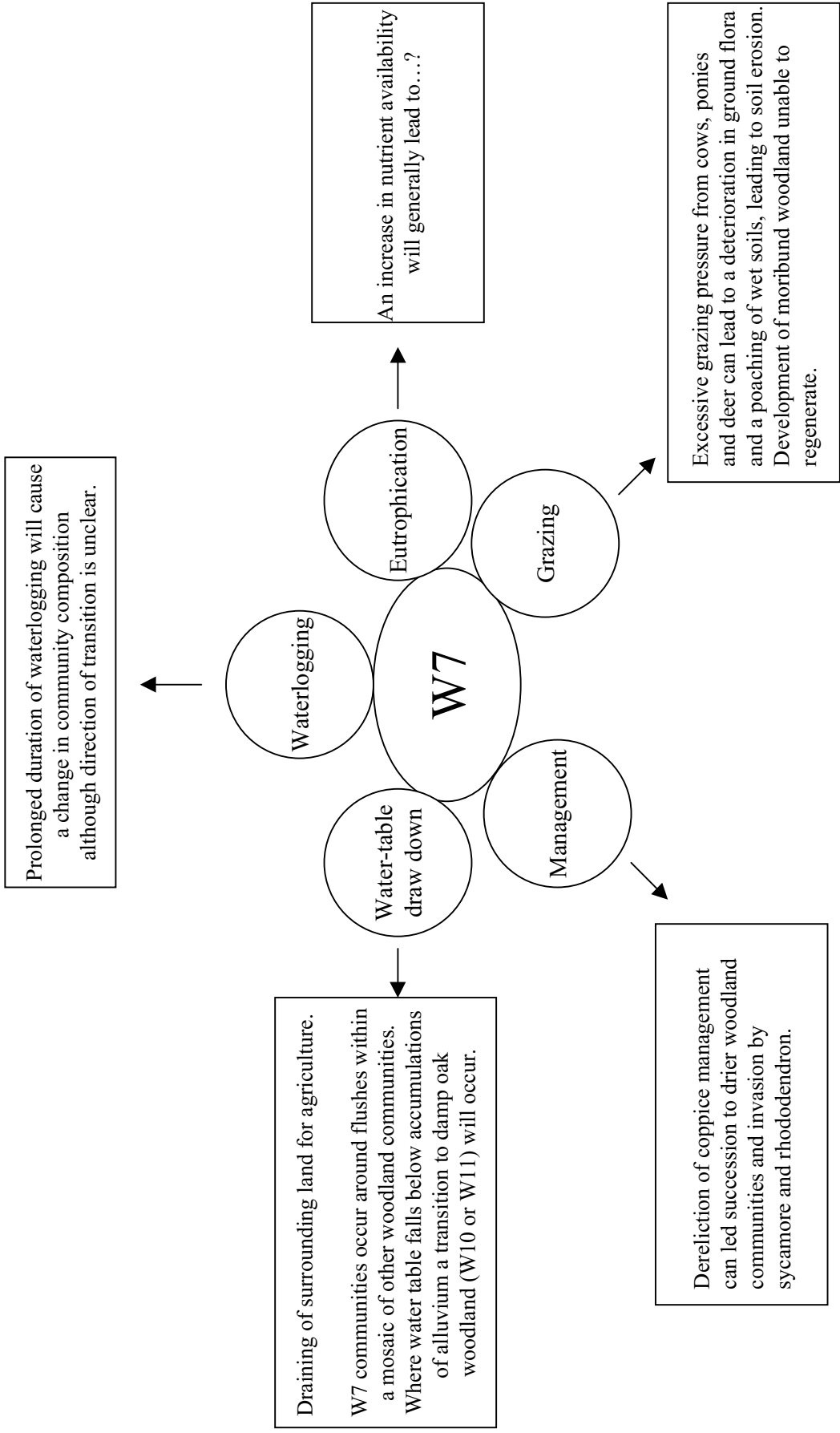


Figure 17 Vulnerability of *A. glutinosa* – *Fraxinus excelsior*- *Lysmachia nemorum* (W7) alluvial forest communities to environmental and management changes.

3.2.4.2 Restorability

Over the last decade alluvial woodland restoration projects have become increasingly common in North America, mainland Europe and in Britain. The majority of restoration projects involve alluvial woodland growing along river edges and as such, are relevant to W6 rather than W5 and W7 alluvial forest types. Many of the restoration projects in Britain are on a small scale (along small streams) and information on these is provided by the River Restoration Centre (<http://www.therrc.co.uk/>). Larger restoration projects have been conducted mostly on a reach basis (eg along the River Danube) although a number of floodplain woodland restoration projects have been undertaken on a whole river catchment basis (North America). The relatively recent attempts at restoring alluvial woodlands means that lessons are still being learned in this area. A number of international conferences specifically devoted to river restoration (eg River Restoration 2004: Principles, Processes & Practices in Zagreb, Croatia) and the formation of the European Centre for River Restoration (<http://www.rws.nl/rws/riza/home/ecrr/>) provide forums for information exchange in this field.

3.2.4.3 Useful methodologies

Methodologies developed for advising on the management and conservation of wetland habitats can have one of two approaches; they can either be 'prescriptive', or 'interactive'. Prescriptive approaches seek to conserve a wetland habitat in a given state through the development of habitat-specific recommendations that advise on appropriate water, nutrient and/or management regimes for the maintenance of habitat condition. Because the focus is on the eco-hydrological requirements of a single wetland habitat type, only one interpretation of 'acceptable' regimes is offered. Herein lies a difficulty for decision-makers who typically need to take into account a wide variety of competing needs for resources and in particular, for water resources. Interactive (also known as holistic, or multicriteria) approaches have wider ecosystem (even landscape), rather than habitat-specific objectives and aim to identify and quantify relationships between multiple components of the ecosystem and altered water, nutrient and management regimes.

In a river ecosystem, for example, an interactive approach might consider relationships between changes in river flow and the condition of floodplain woodlands and/or aquatic communities, as well as impacts on wildfowl and various other water users (eg anglers, producers of hydroelectricity). Examples of this approach include one of the latest holistic methodologies that has been developed to date for river ecosystems, described by King and others (2003); ie DRIFT (Downstream Response to Imposed Flow Transformation), and the Catchment Abstraction Management Strategies currently being developed by the Environment Agency in order to allocate water to a range of users, including abstractors and the environment (for further examples see Arthington 1998; Swales & Harris 1995; <http://www.lk.iwmi.org/ehdb/EFM/efm.asp>). Interactive approaches are arguably better suited (than prescriptive approaches) for creating scenarios that can be used in negotiation (Brown & Joubert 2003), particularly those where socio-economic and other landscape wide factors are important.

In the UK, The Habitats Regulations and Water Framework Directive are proving to be important drivers for the development of robust targets for hydroecological requirements of various water dependent habitats. The 'Wetland Framework' (originally developed as a partnership project between the Environment Agency, English Nature and the University of

Sheffield - Wheeler & Shaw 2000) is a methodology being developed for wetlands in England and Wales, that identifies main distinctive wetland habitats and classifies them on the basis of recurrence of repeated sets of ecohydrological conditions. The methodology uses a 'bottom-up' approach based on analysis of a substantial set of field data. Derived from this work, and also research by Gowing (2002) in summer dry grasslands, are a series of NVC community-specific 'Ecohydrological Guidelines' that have been developed for the Environment Agency (Wheeler and others 2004). These are based on an understanding of water supply and habitat conditions required by wetland communities gained from the earlier detailed studies. The ecohydrological guidelines seek to provide a 'user friendly' framework to assess and predict the impact of specific environmental changes (eg water level draw down, nutrient enrichment etc.) on a range of wetland NVC communities. Ecohydrological Guidelines are developed for individual NVC communities and therefore follow a prescriptive approach.

The Wetland Framework approach provides valuable information on water supply mechanisms to wetlands in a range of hydrological, topographical and landscape settings. The Ecohydrological Guidelines provide generic regimes on an NVC-type basis and therefore do not have the sensitivity to address the site-specific needs of wetland habitats (as defined not only by the local, but also the regional context).

3.2.5 References

ARTHINGTON, A.H. 1998a. *Comparative evaluation of environmental flow assessment techniques: review of holistic methodologies*. Land and Water Resources Research and Development Corporation Occasional Paper No. 26/98. Canberra, Australia.

ATKINS & ENTEC. 2003. *Habitat and species summary guidance notes*.

BROWN, C.A., & JOUBERT, A. 2003. Using multi-criteria analysis to develop environmental flow scenarios for rivers targeted for water resource management. *Water SA*, 29(4), 365-374.

GOWING, D.J.G. and others. 2002. *The water regime requirements and the response to hydrological change of grassland communities*. Final Report for DEFRA – commissioned project BD1310. Silsoe: Cranfield University.

HALL, J. 1997. An analysis of National Vegetation Classification survey data. *JNCC Report*, No. 272.

HUNTLEY, B., & BIRKS, H.J.B. 1983. An atlas of past and present pollen maps for Europe: 0-13,000 years ago. Cambridge: Cambridge University Press.

KING, J., BROWN, C., & SABET, H. 2003. A scenario-based holistic approach to environmental flow assessments for rivers. *River Research & Applications*, 19, 619-639.

LLOYD, J.W. and others. 1993. Wetland vulnerability in East Anglia: a possible conceptual framework and generalised approach. *Journal of Environmental Management*, 37, 87-102.

PETERKEN, G. 1981. *Woodland conservation and management*. London: Chapman and Hall.

PETERKEN, G. 1996. *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge: Cambridge University Press.

PETERKEN, G. & HUGHES, F. 1998. Limitations and opportunities for restoring floodplain forest in Britain. *In: R.G. BAILEY, P.V. JOSÉ AND B.R. SHERWOOD*, eds. *United Kingdom Floodplains*, 423-436. Westbury Publishing.

RODWELL, J., & DRING, J. 2001. European significance of British woodland types. *English Nature Research Reports*, No. 460. Peterborough: English Nature.

SPENCER, J. 1994. *The native black poplar in Britain: An action plan for its conservation*. English Nature (Newbury) report produced on behalf of the Black Poplar Working Group.

SWALES, S. & HARRIS, J.H. 1995. The expert panel assessment method (EPAM): a new tool for determining environmental flows in regulated rivers. *In: HARPER, D.M., FERGUSON, A.J.D.*, eds. *The Ecological Basis for River Management*, 125-134. New York: John Wiley & Sons.

TABBUSH, P. 1996. Native poplars and the restoration of floodplain forests. *Quarterly Journal of Forestry*, 128-134.

WHEELER, B.D., & SHAW, S.C. 2001. *A wetland framework for impact assessment at statutory sites in Eastern England*. Environment Agency R&D Note W6-068/TR1 and TR2.

WHEELER, B.D. and others. *In: BROOKS, A.W., JOSE, P.V. & WHITEMAN, M.I.*, eds. *Ecological guidelines for lowland wetland plant communities*. Peterborough: Environment Agency (Anglian Region).

WHITE, J. 1993. *Black poplar: The most endangered native timber tree*. Forestry Commission - Research Information Note 239.

3.3 Critical evaluation of ecohydrology information for bog woodland

This evaluation could have dealt with ombrotrophic and minerotrophic bog woodland separately because there are fundamental hydrological differences between the two. Likewise, minerotrophic bog woodland could have been separated into groundwater-fed and surface water-fed types. However there is so little pertinent literature that we have treated all types in a single evaluation but referred to the particular sub-types where appropriate.

3.3.1 Context

The relationship between bog woodland and NVC classes is not clear. Best matching NVC classes are known for some examples, such as those at Abernethy and the best English and Welsh SAC sites.

The Abernethy study (Legg and others 2001; McHaffie and others 1999; McHaffie and others 2002) showed that the wooded bogs there best matched four different mire types. It is unclear what degree of tree cover is required before a site constitutes bog woodland. The Abernethy study proposed a 3-class terminology including 'bog woodland' but it could only

have limited applicability (ie to Scots pine wooded bogs) and might be unacceptable because it would exclude examples without a closed canopy and could include transient examples on drained sites.

Analogous to the degree of tree cover, there are no accepted thresholds in terms of productivity or stability.

3.3.1.1 Floristic composition

Rodwell (1991) provided floristic tables for wet woodland NVC communities and sub-communities but none corresponds exactly with bog woodland generally or eco-hydrological sub-types thereof.

Several studies have provided floristic composition data for wooded bogs in Scotland (Legg and others 2001; MacKenzie & Worrell 1995; McHaffie and others 1999; McHaffie and others 2002; Wells 2002). These have mainly focused on Scots pine sites and have included ombrotrophic and weakly minerotrophic sites.

Floristic data from bog woodland sites in England and Wales is not readily available but some undoubtedly exists in unpublished form. For example, for wooded areas of Rhos Goch and Cors Caron we obtained site and NVC summary quadrat records by NVC woodland type, an NVC communities map and woodland record sheets (Jim Latham, pers. comm.). These contained detailed floristic data but they were recorded by NVC community and sub-community. It was not clear what areas were regarded as bog woodland as opposed to other woodland types. For English sites, the SSSI citations and unit details can be accessed on the web but these generally do not use the term bog woodland and are insufficiently detailed to be useful for our purpose. Any really useful data that exist are probably held only at local offices of the nature conservation agency or land manager.

Judging from the very limited site data obtained during this contract, the range of floristic variation among sites is large. Floristics may be a useful indicator of eco-hydrological sub-type and better knowledge about existing sites might allow the guidelines to distinguish sub-types on the basis of their composition.

3.3.1.2 Distribution

The JNCC website includes a map of the UK distribution of the habitat at <http://www.jncc.gov.uk/publications/JNCC312/habitat.asp?FeatureIntCode=H91D0b>. This includes only candidate and possible SAC sites and is identical to the map of SACs with bog woodland as an interest feature. The accompanying text states that no data are available for sites not proposed as an SAC and that the habitat is likely to occur on more SACs in Scotland than are shown on the map. For the UK as a whole and particularly for Scotland it is likely that there are also examples not in SACs.

MacKenzie and Worrell (1995) included a map of the distribution of wooded bogs in Scotland as recorded by the Land Cover of Scotland 1988. It showed sites in the LCS88 category 183, 'blanket bog and other peatland vegetation, no erosion, with scattered trees'. Around 200 sites are marked. Presumably these are not all bog woodlands; some may represent woodland colonising drained bogs and some may have such scattered trees that they don't represent woodland at all. We know of no equivalent data-set for England and Wales. Thus the distribution of the habitat is very uncertain.

3.3.1.3 Landscape situation and topography

This information may exist locally in unpublished form for some SAC sites but is not readily available. At most sites, there may not have been any formal assessment of landscape situation or topography because until now there has been no need for this information. Even for a site that has been the subject of research studies such as the bog woodland on Morden Bog in the New Forest, only a very sketchy description of its landscape situation (Haskins 1978) and, as far as we know, no topographic data are available. An air photo of this site (Andrew Nicholson pers. comm.) helps to illustrate the landscape setting but the topography cannot be discerned.

3.3.1.4 Substratum

We assume that all the SAC bog woodlands are on deep peat, which may have been used as a defining characteristic in identifying bog woodlands, but the range of peat depths is not known. Nor is information on peat type or nutrient status available.

Palaeoecological studies have been conducted at some sites, such as Morden Bog (Haskins 1978) and Abernethy (Sandra Pratt PhD, Colin Legg, Pers. comm.), and these might yield useful data on present and former substrates. We think that the results of this type of specialist study are generally not known about or are overlooked by ecologists working in the field of habitat conservation.

3.3.2 Water supply mechanism and conceptual model

Several different water supply mechanisms support bog woodlands. Knowing the supply mechanism is the key to understanding the hydrology of a site, identifying its eco-hydrological tolerance ranges and giving guidance on water activities that may affect it. Conceptual models for three water supply mechanisms supporting bog woodlands are presented on the following pages. The legend is in Section 3.2.2.

Ombrotrophy (ie the supply of water and nutrients to a convex bog surface solely via rain and other forms of atmospheric deposition) is thought to be the sole mechanism at some sites (Figure 18). Groundwater mound theory can help relate drainage to change in the depth to water table for raised bogs but the effects of changes in regional groundwater levels is unclear.

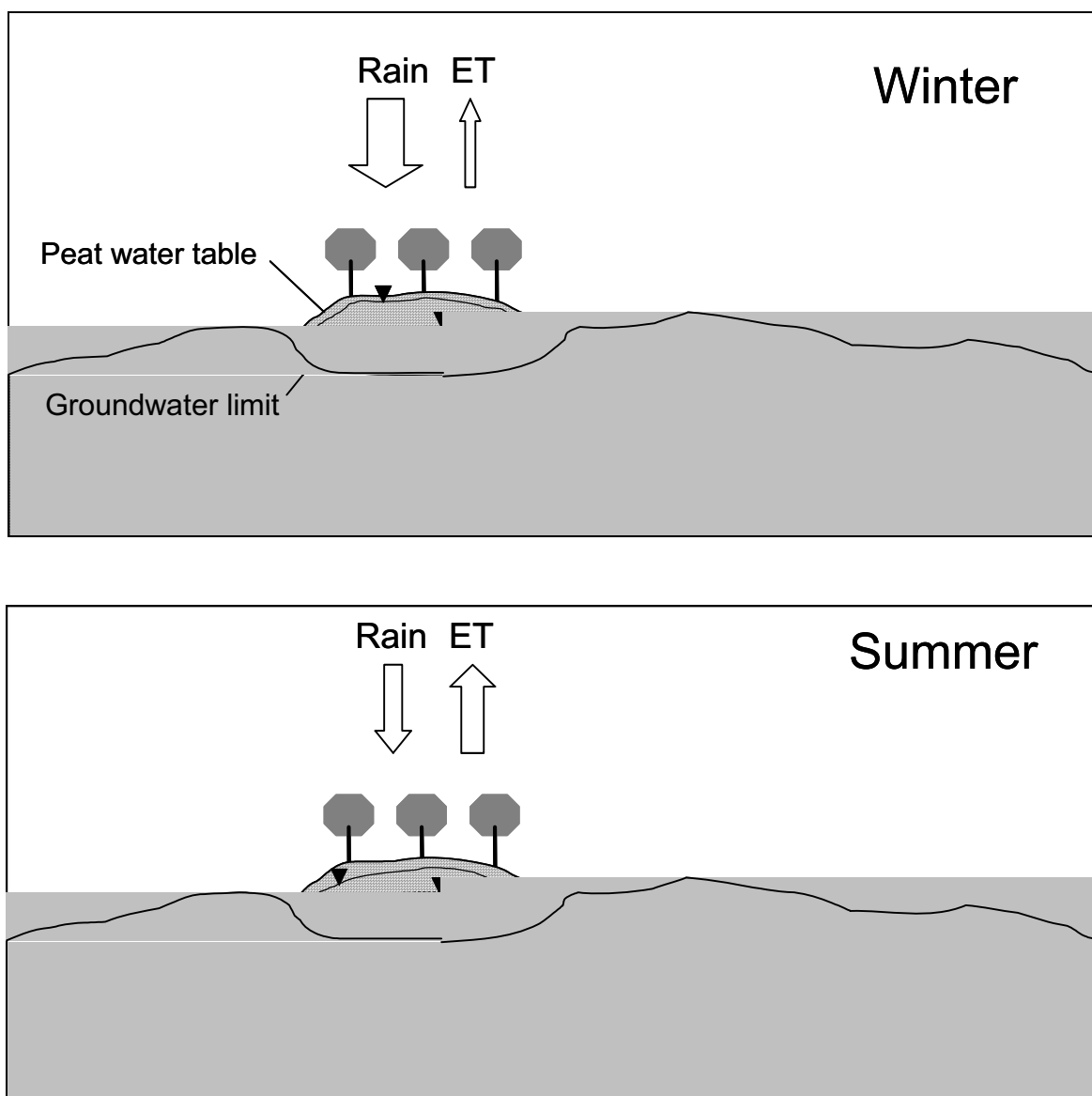


Figure 18 Conceptual model of W4 ombrotrophic bog woodland in the winter and summer.

Some bog woodlands seem to be fed by groundwater welling up through the peat, presumably originating from springs under the peat (Figure 19). The presence of plants requiring a degree of minerotrophy supports this assumption.

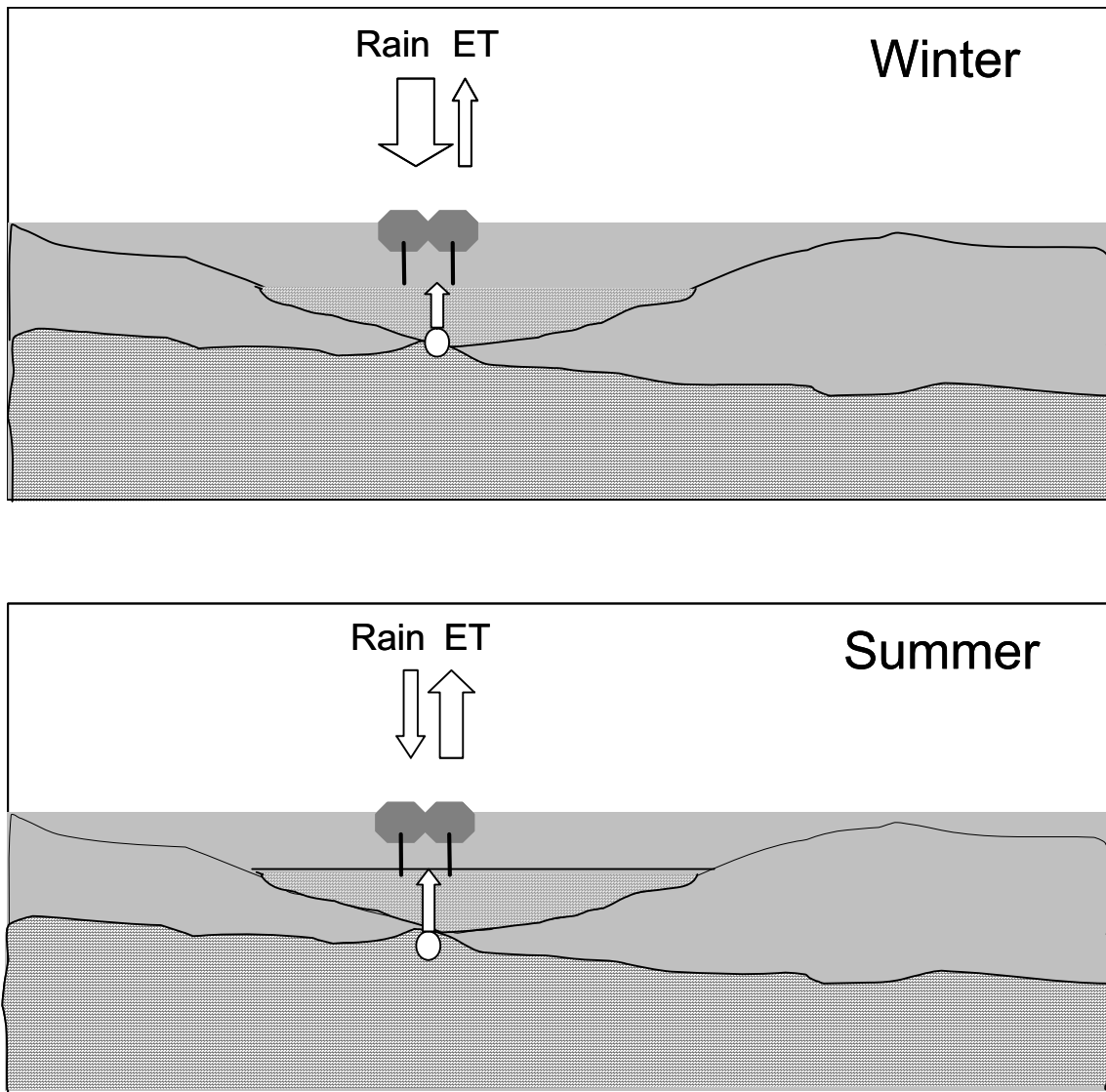


Figure 19. Conceptual model of W4 Spring-fed bog woodland in the winter and summer.

Bog woodland restricted to the central flow lines of valley mires presumably receives nutrients by irrigation with drainage water (Figure 10). Flooding presumably irrigates the surface during the winter and during summer there may be some sub-surface irrigation through moderately porous peat. The drainage water will probably carry minerals from mineral soil further upstream so its chemistry will depend on local rock and drift types.

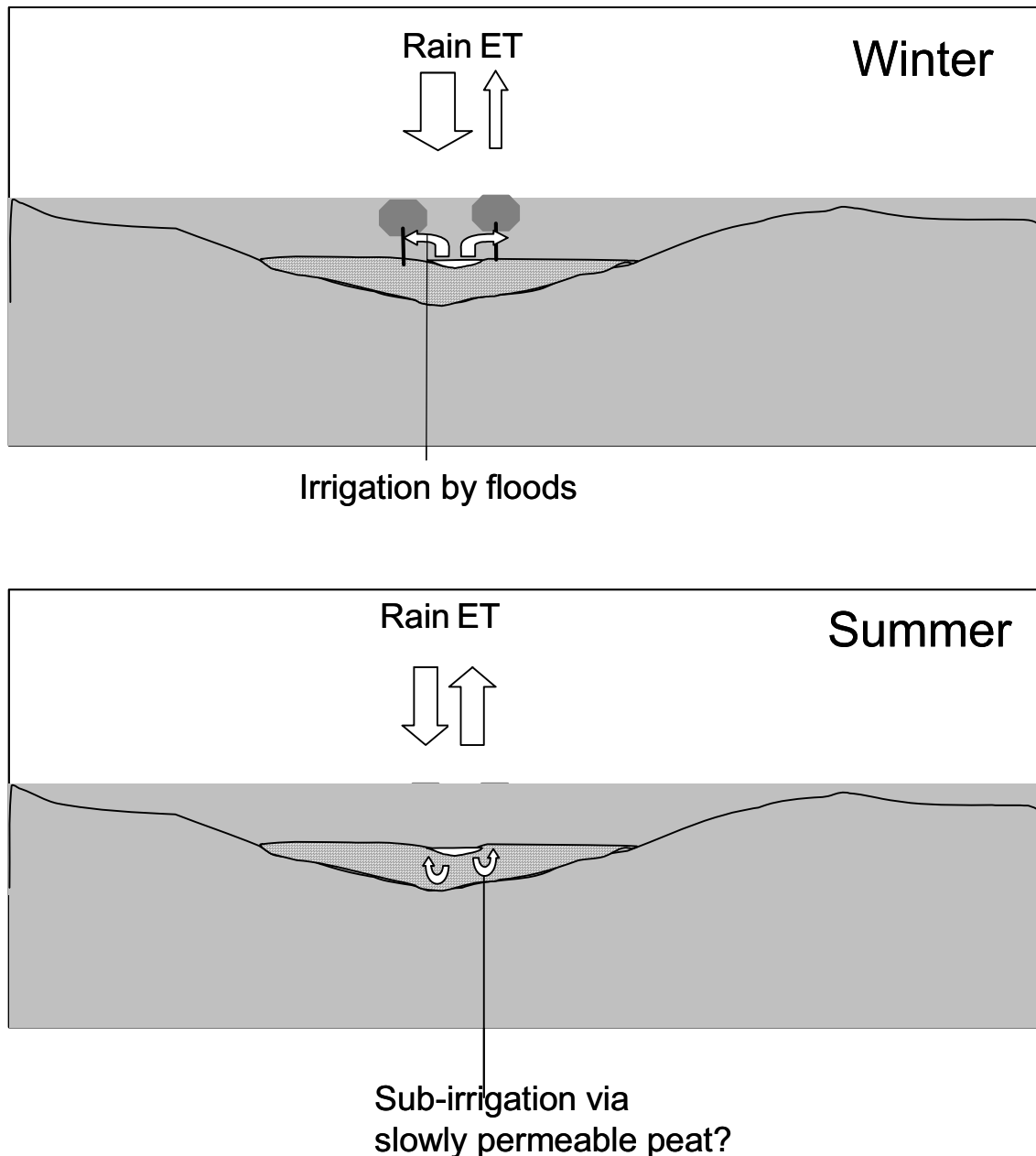


Figure 20. Conceptual models of W4 Valley mire flow-line bog woodland in the winter and summer.

3.3.3 Regimes

3.3.3.1 Water regime

We found no information on the range of water regimes tolerated by bog woodland habitats. The component species approach to determining the preferences and tolerances of bog woodland habitats would be difficult to adopt without better information on the floristic composition of the main bog woodland sub-types.

Information on water regime requirements of the component plant species is generally only available as vague, qualitative statements of the preferred or optimum conditions. Quantitative preference and/or tolerance ranges may be available for *Sphagnum* species but we did not find any and instead took the dubious course of attempting to quantify the

qualitative ranges given by Daniels and Eddy (1990). A separate, dedicated search would be required to confirm the availability of quantitative ranges for *Sphagnum* species.

The work on lodgepole pine growth in relation to various fixed water table levels (Boggie 1972; Boggie & Miller 1976) is difficult to translate to a bog woodland context. This is because, unlike Scots pine and downy birch, lodgepole pine has aerenchymatous roots and is presumably better adapted physiologically to growing in peat with the water table close to the surface.

3.3.3.2 Nutrient regime / hydrochemistry

Wheeler and Proctor (2000) provide a schematic arrangement of categories of expected mire climax vegetation in the absence of human disturbance in relation to water pH and substratum fertility (their Figure 3d). It differentiates a zone with open bog from one with herbaceous or sparsely wooded vegetation and zones for various wet woodland NVC communities. The authors admit that the diagram is speculative, which is unfortunate as it has the potential to be a useful conceptual model. Without validation it would be unwise to use it. It would be important to determine whether other factors, such as depth to water table, browsing pressure and fire frequency affect the climax vegetation directly (ie not just by altering pH and/or fertility).

3.3.3.3 Management regimes

We found no information on management regimes tolerated by bog woodland or about changes to bog woodland communities resulting from management or lack of it. This lack of information is perhaps inevitable for a habitat that exists mainly as unmanaged examples.

The existence of bog woodland on islands in Loch Maree in the north-west Highlands indicates that relative continentality of climate is not a pre-requisite for its occurrence. It also suggests that grazing and/or browsing may have generally prevented bog woodland establishment on UK bogs. Control of grazing/browsing pressure seems likely to be crucial yet no research on the subject was found in our review.

3.3.4 Implications for decision making

3.3.4.1 Vulnerability

Anderson and Harding (2002) reported that some Scots pine bog woodland examples in Scotland had survived tree cutting, peat cutting or fire. However we cannot conclude that bog woodlands are not vulnerable because we do not know whether other examples have been lost due to these or other anthropogenic activities.

Stable ombrotrophic bog woodland is ecologically intermediate between bog and woodland, supposedly representing a delicate balance, and could therefore be expected to be vulnerable to impacts that alter the balance. Damage to raised bogs has commonly triggered the succession from bog to woodland but how such colonising woodland compares to bog woodland is not known. Figure 21 outlines the main eco-hydrological threats to ombrotrophic bog woodlands. Figures 22 and 23 set out the main eco-hydrological threats to spring-fed bog woodlands and valley mire flow line bog woodlands but there is little information on the hydrology of these types and so the diagrams are more speculative.

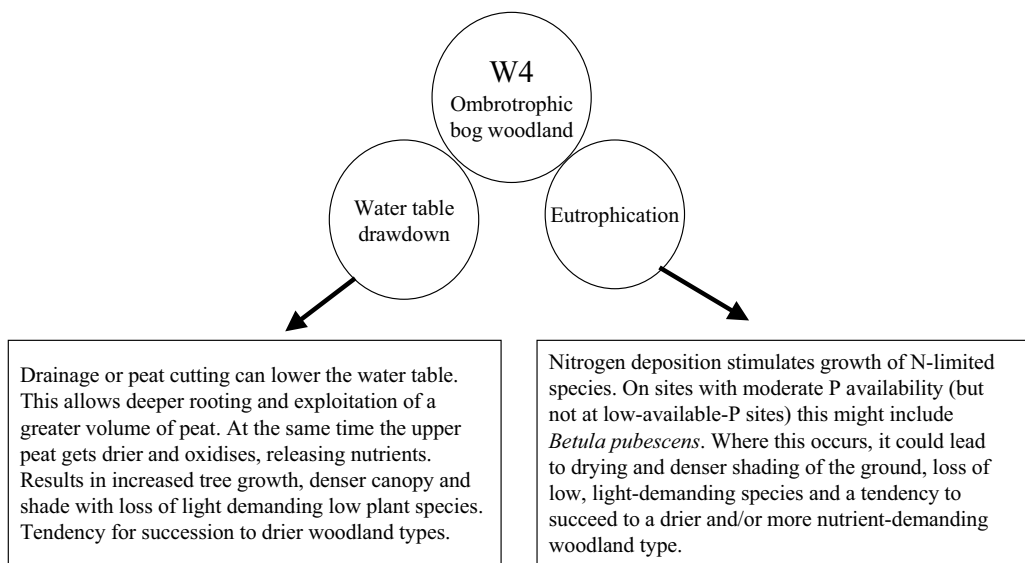


Figure 21. Vulnerability of ombrotrophic bog woodlands to environmental and management changes.

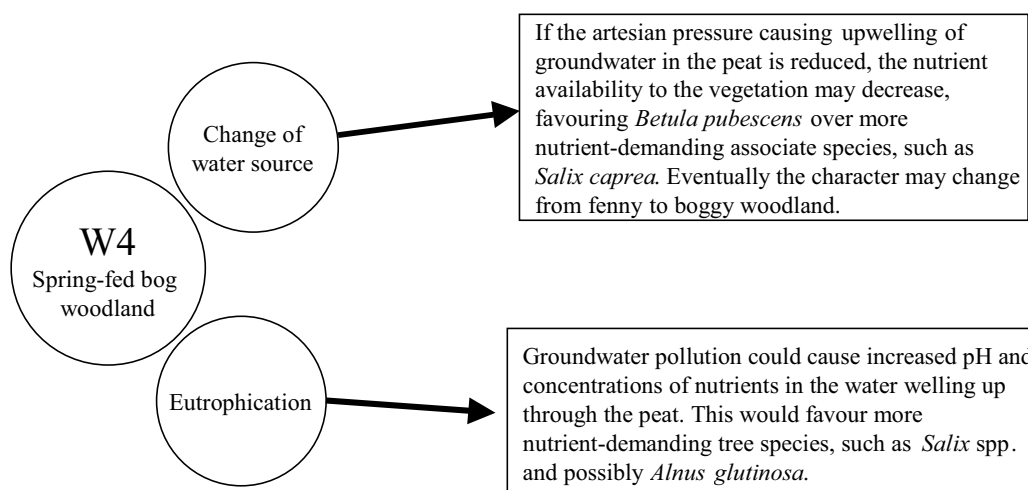


Figure 22. Vulnerability of spring-fed bog woodlands to environmental and management changes.

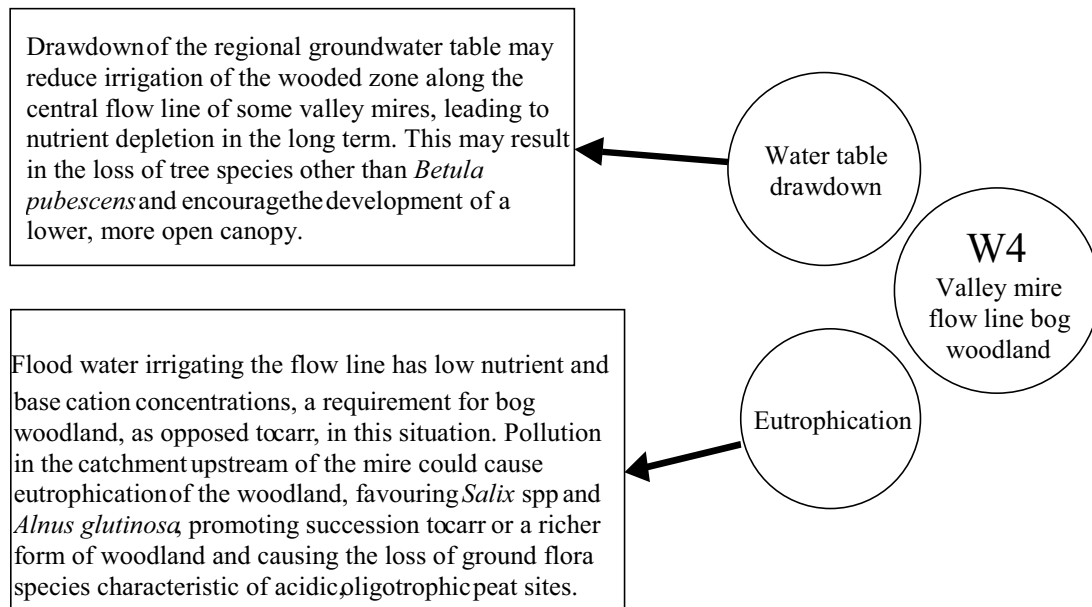


Figure 23. Vulnerability of valley mire flow-line bog woodlands to environmental and management changes.

3.3.4.2 Restorability

Little is known about the restorability of bog woodland. There have been restoration attempts under the LIFE Wet Woods and LIFE New Forest projects. The focus has been on safeguarding the future of existing bog woodland by sympathetic management of adjoining land. We can only speculate on whether some of this adjoining land formerly supported bog woodland and therefore whether the management constitutes restoration. Both these projects are too recent for success to be judged yet.

3.3.4.3 Useful methodologies

See Section 3.2.4.3 in critical evaluation of eco-hydrology information for alluvial woodland.

3.3.5 References

- ANDERSON, A.R., & HARDING, K.I.M. 2002. The age structure of Scots pine bog woodlands. *Scottish Forestry*, 56(3), 135-143.
- BOGGIE, R. 1972. Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland. *Oikos*, 23, 304-312.
- BOGGIE, R., & MILLER, H.G. 1976. Growth of *Pinus contorta* at different water-table levels in deep blanket peat. *Forestry*, 49(2), 123-131.
- DANIELS, R.E. & EDDY, A. 1990. *Handbook of European Sphagna*. London: HMSO.
- HASKINS, L.E. 1978. The vegetational history of South-East Dorset. PhD Thesis. Southampton.

LEGG, C.J., MCHAFFIE, H., AMPHLETT, A. & WORRELL, R. 2001. *The status of wooded bogs at Abernethy, Strathspey, Restoring Natura forest habitats, Fort William*, 12-16.

MACKENZIE, N.A., & WORRELL, R. 1995. *A preliminary assessment of the ecology and status of ombrotrophic wooded bogs in Scotland*, 40. Battleby: Scottish Natural Heritage.

MCHAFFIE, H. and others. 2002. Scots pine growing on forested mires in Abernethy Forest, Strathspey, Scotland. *Botanical Journal of Scotland*, 54, 209-219.

MCHAFFIE, H., LEGG, C.J., & WORRELL, R. 1999. Classification of bog woodland habitat and review and analysis of restoration management at RSPB Abernethy Forest Reserve. Edinburgh: RSPB.

RODWELL, J.S. 1991. *British plant communities. Volume 1: woodlands and scrub*. Cambridge: Cambridge University Press.

WELLS, C. 2002. A survey of peat stratigraphy of seven 'bog woodland' sites in Scotland. Life Wet Woods Project.

WHEELER, B.D. & PROCTOR, M.C.F. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology*, 88, 187-203.

4 Appendix. DRAFT Management Plan for Hurcott and Podmore Pools SSSI

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A site visit / walk over survey of the Hurcott Pool part of the Hurcott and Podmore Pools SSSI was conducted on February 28, 2005 by N. Barsoum and H. Thomas who were accompanied by John Bingham (English Nature conservation officer). Available information (Table 18) was subsequently reviewed prior to drafting a management plan for the SSSI. Site specific guidelines are given first in terms of the hydrology of the site and this is followed by guidelines suggesting measures that can be taken to manage the wet woodland. Subsequent sections assess the possibilities for drawing upon the outputs of the Phase 1 contract to develop site-specific advice on the management and hydro-ecological regime for conservation purposes. From this evaluation, a generic methodology is outlined as an aid to conservation staff wanting to apply the output of the Phase 1 contract.

Table 18. Information on which hydrology and wet woodland management plans for Hurcott and Podmore Pools SSSI site are based.

Vegetation Survey 1978
Vegetation Survey 1998
Notes on boreholes and piezometer installations
« <i>Review of Wetland SSSIs 1998/99 (Ten Point Action Plan) : Report 4-Hurcott & Podmore Pools Environment Agency</i> ». Includes Site Description (setting, SSSI designation, geology, hydrogeology, perceived vulnerability to abstraction), Review of Abstraction Licences, Impact Assessments, Conclusions and Recommendations.
Hydrology data (groundwater levels [Podmore 1998-2005 ; Hurcott 1997-04], rainfall [1980-2004], mean daily flow Hurcott wood [1999-present], mean daily stage Hurcott pool [2000-05]).

Hydrology Management Plan

Review

Hurcott and Podmore SSSI is located on the Wildmoor Sandstone Formation which forms part of the Sherwood Sandstone Group, and is a major aquifer. This major aquifer has high conductivity, storage and transmissivity values. The groundwater gradient is mainly from east to west, with groundwater levels at 48mAOD at the eastern end and 38mAOD at the western end. This can be compared to ground elevations of 52mAOD and 40mAOD from east to west respectively. Historical data suggests that Hurcott and Podmore Pools were fed partly by groundwater, indicating that the pools are in hydraulic continuity with the groundwater. The artificial lowering of the Hurcott Pool in 1982/83 in response to the Reservoirs Act (1975) would have led to a limited drawdown of the local water table. However, data from the Environment Agency indicates that it is the subsequent over-abstraction of the Sherwood Sandstone aquifer that has led to the longer-term drop in

groundwater levels. The groundwater level data for the past 5 years suggests that the water table is continuing to fall.

Over-abstraction of groundwater in the area and its subsequent reduction in level has also caused a reduction in baseflow to both watercourses and pools, leading to a reduction in surface water inflow. A large proportion of the inflow is now derived from the Hagley Wastewater Treatment Works (WTW) and Blakedown WTW, both operated by Severn Trent Water.

As a consequence of lowered groundwater levels and depleted surface water inflow it is believed that Hurcott Pool is suffering from a net loss of water from the system. This loss is partly from evaporation and surface discharge, but more significantly, by infiltration to groundwater due to the water levels in the pool being a few metres higher than local groundwater levels.

The combined effect of reduced surface water baseflow, reduced groundwater levels feeding the pool and the semi-detachment of the pools from the local groundwater has led to a degradation of the Hurcott Pool SSSI area. Areas of semi-permanent or permanently wet ground have now become dry, resulting in the oxidation of peat deposits. The exposure of the tree root systems, which is up to 50 cm in places, is further evidence that the ground is drying and shrinking in places. The site appears to be shifting from a mainly anaerobic environment (waterlogged) to a drier, more oxygen rich aerobic state.

Management solutions

In order to compensate for the overall loss of water from the system a number of solutions could be offered both for the short term and long term. Adding woody debris (>10cm diameter and minimum 2m length) to the river system can be an effective technique for increasing pool area and numbers in some river channels. Woody debris also significantly increases the hydraulic roughness of the channel and adjacent floodplain; it slows down the passage of the flood flows and effectively creates a small flood control reservoir (i.e. increases storage) within the woodland area. The use of strategically placed woody debris within the woodland, approximately perpendicular to the flow could help hold water during periods of high out of bank flows, in order to increase the storage potential of the woodland. This would create ponded areas within the woodland, which could help increase local groundwater levels and offer longer periods of wet ground. The construction of woody debris dams within the main channel of the watercourse would encourage out of bank flows and help reinstate the hydraulic complexity of a woodland watercourse and increase surface water levels within the wooded area.

Adding or keeping fallen logs with branches and roots attached would be more effective than straight, clean trunks as they would offer more stability during high flows as well as maximising the hydraulic roughness. Fallen trees can be attached or anchored to stationary objects if there is a risk of mobilisation during high flows, especially in high-energy environments. There are numerous methods of doing this including anchoring using locally available ballast (e.g. boulders or gravel), pilings, cabling, chaining, or pinning together large woody debris, or a combination of these. The method used would be site dependent and an assessment would be required in order to evaluate the suitability of each technique.

Whenever possible, woody debris should be placed in locations and configurations where it would be expected to occur naturally. In this case, the main aim of woody debris placement would be to maximise the hydraulic effect on flows, therefore careful assessment would need to be carried out to identify the main areas of flow during flood conditions. Placement of woody debris should first be focused within the main channel. A tree felled into the main channel with roots and branches intact would encourage the accumulation of smaller woody debris travelling downstream. The build up of smaller debris behind the main trunk would eventually form an effective barrier to the flow and encourage out of bank flows. Further secondary woody debris dams could be placed in the flood channels in order to increase the hydraulic complexity of the system and increase the lateral extent of the flood, from a mainly single channel to a more dendritic/braided system during flood flows.

Best placement of woody debris dams along the watercourse and associated floodplain could be evaluated using hydraulic modelling techniques. This could help ensure that the dams would have maximum hydraulic effect along the reach, and a more accurate assessment could be made of the existing flooding regime and the effect that woody debris placement would have on the system. It is unlikely that materials would need to be imported onto the site as there appeared to be a sufficient source of woody debris already available, including large trees and smaller branches.

The reduction in the surface water level of the pond has led to a reduced backwater effect within the woodland, increasing the proportion of dry areas. The construction of a small bund just upstream of Hurcott Pool could help increase this effect during high flows, thus increasing water levels within the woodland area. The channel would remain open although water levels could be raised by a debris dam at the inlet into the pool (Figure 24).

Refilling Hurcott Pool to historical levels thus reinstating the hydraulic continuity of the pool with the groundwater would offer a long-term solution to the continuing degradation of the site. Reviewing the licensed groundwater abstractions within the Sherwood Sandstone Group aquifer is required to achieve a more sustainable balance between water demand and the needs of the Hurcott Pool SSSI. Reducing the amount of over abstraction would lead to a long-term restoration of groundwater levels. Raising water levels in the pool by simply increasing the sill height would have a limited effect on groundwater levels until abstractions are reduced.

Wet woodland Management Plan

Review

Hurcott and Podmore Pools SSSI supports the largest area (23.5 ha) of alder carr wet woodland in Worcestershire. Despite its significant wildlife value and high species diversity (at least prior to the recent over-abstraction of groundwater in the area), this wet woodland cannot be considered to be representative of wet woodland communities that would otherwise naturally be growing along Blakedown Brook. The alder-dominated wet woodland that exists today is instead the product of an artificial ‘wetting’ of the valley floor along an approximately 2 km stretch of Blakedown Brook following the construction of dams, artificial pools and, within the Hurcott section, a bund that transects the narrow valley. These constructions have also contributed to the development of bulrush-dominated swamp habitat along the pool edges (Photo 1).



Photo 1

Photo 1: View over Hurcott Pool.

While the Hurcott and Podmore SSSI site is dominated by artificial structures (and as such, is subject to highly modified natural physical processes and wetland habitat), these have been in place over significant periods of time (e.g. records suggest that the Hurcott pool and dam have been in existence since 1600, as a water supply for a paper mill). Sediment cores, for example, reveal the existence of thick peat layers (up to 7 metres in places) overlying sandy alluvial sediment deposits, suggesting that water-logged conditions have persisted over long periods in the Hurcott and Podmore stretches of wet woodland. The extensive coverage of old alder coppice in the lower Hurcott section also attests to the age of the wet woodland.

Prior to the recent over-abstraction of groundwater in the area, the wet woodland that developed (following the installation of the dam and pools in medieval times) shared a greater resemblance to W5 *Alnus glutinosa*- *Carex paniculata* swamp communities than the W6 *A. glutinosa* - *Urtica dioica* alluvial forest community that might otherwise be expected to occur in such a stream side setting. There were, nevertheless, some traces of the W6 community still occurring/blending with this artificial swamp community prior to the significant abstraction of ground water and lowering of pool levels in the area; i.e. a vegetation survey conducted in 1978 highlights, for example, the presence of several species that are more commonly found in W6 NVC communities (e.g. *Sambucus nigra*).

Significant lowering of groundwater levels, as described in the previous section has led to an impoverishment of the ground flora and particularly in the downstream section of the Hurcott reach. Here significant mortality of alder trees is evident and this may be due to drought-induced cavitation of xylem vessels following a loss of contact with the water table during dry periods (Photos 1 & 2). *Alnus glutinosa* is known to be vulnerable to cavitation (Hacke & Sauter, 1996; Raven *et al.*, 1989) and significant drops in water table levels during the lifetime of the alder trees in the lower Hurcott section of the site is clearly happening as evidenced by significant shrinkage of the ground around the trees (Photos 3 & 4).



Photos 2 & 3 show the high mortality rates of alder trees in the downstream section of the Hurcott site.



Other indications of shifts in the ground flora that reflect a gradual drying-out of the habitat include the presence of *Carex* tussocks (indicative of previously very wet conditions) that are now in poor condition. Also, an invasion of nettles in the understorey indicates that water-logged conditions, if they still occasionally occur during periods of high surface flow, are not sufficiently prolonged to kill-off this otherwise flood-intolerant species (Vogt, 2001). The presence of species more typically found in a wetter W5 community suggests that the alluvial forest in the Hurcott section of the SSSI is presently at a crucial turning point – rapid intervention (halting abstraction activities and raising of water table levels) is likely to still enable a reversal of current trends.

Photos 4 & 5 illustrate the shrinking of the ground level from alder coppice bases as it dries out.



Consistently low water tables and, as a consequence, the oxidation of the thick organic layers (particularly during the summer months) is likely to also be contributing to a significant

release of nutrients with a likely depletion of soil N status. The eutrophication of soils in such systems typically results in the transition that is evidenced (shift towards *Alnus-Urtica* wet woodland communities). Species commonly occurring in a W5 NVC community (e.g. *Carex* species, *Phragmites*) will not perform well in the new nutrient enriched conditions (Kazda, 1995; Baar *et al.*, 2002). There is also evidence of significant inhibition of ectomycorrhizal development in *A. glutinosa* where nutrient loading occurs which may further explain the decline of this species in the lower Hurcott section (Baar *et al.*, 2002).

Of particular concern in the Hurcott section of Hurcott and Podmore Pools SSSI, is the complete lack of evidence of any recruitment from softwood species, although some vegetative sprouting was observed from fallen trunks. The dense coverage of nettle and the invasive Himalayan balsam are likely to hinder recruitment from seed by shading out seedlings; both willow and alder require damp, exposed conditions during the first growing season. In addition, a likely consequence of the lowered water table levels in the area are rapid drawdown rates following flooding events; willow and alder seedlings are highly sensitive to a rapid drying of soils and must be able to track receding water table levels following floods. It is unclear how the timing of periods of high surface flow might have been affected by the Hagley and Blakedown Wastewater Treatment Works (discontinuous records commence only in 1999 for Hurcott wood), but this is an additional factor that may be affecting recruitment as specific timing of seed release in the spring and limited seed longevity in both alder and willow provide only a short window of opportunity for recruitment. The daily mean flow records that do exist suggest that surface flows do not vary significantly through the year (0.05-0.2 m³/sec), although daily mean flow peaks reached 0.2 in June and July of 2001 when active seedling recruitment would normally be occurring.

Management solutions

A number of wet woodland management measures can be introduced to improve the current degraded status of the alluvial forest stands in the Hurcott and Podmore Pools SSSI site. It must first be recognised, however, that these management measures cannot and do not seek to reinstate the 'original' swamp-like W5 alluvial forest communities that existed prior to significant water abstraction in the area. Where it is accepted that the alluvial forest of today is a transitional alluvial forest type (W5 transforming into a W6 NVC community), and hence contains species that are common in both W5 and W6 community types, the aim is to enhance the species diversity of this transitional community and attempt to create ideal conditions that allow for the natural, self-sustained recruitment of alluvial forest species.

To encourage natural regeneration of alder and willow, clearing of nettle and Himalayan balsam and the creation of exposed earth by raking surface layers (or sod removal where vegetation and root material is very dense) is likely to be necessary on a regular basis prior to periods of seed release (Friedman *et al.*, 1995). Where there is the possibility of manipulating the timing of daily flow rates from the Hagley and Blakedown Wastewater Treatment Works, ideally a period of high flow and flooding should also precede periods of willow and alder seed release in the spring. Encouraging localised flooding with log jams may be sufficient to hold back enough water to keep sediments damp during the period of seedling development. Drops in groundwater levels by some 3-4 metres suggests that seedlings may, nevertheless, have some difficulty tracking the water table and becoming established, although this water depth problem might be compensated for in the Hurcott section by the apparent shrinking of ground levels as peat layers dry out. Experimental planting of rooted saplings can help to determine the extent of the groundwater lowering

problem to alder and willow recruitment at the site. Where planted saplings survive, there is a good chance that seedlings can also become established, with some care taken to retain sufficiently damp conditions in surface layers over the establishment period (possibly by some artificial irrigation – see Cooper & Haveren, 1994; Friedman *et al.*, 1995). Where grazing from deer and rabbits is problematic, it may be necessary to go as far as installing exclosures to maximise recruitment success.

The nutrient loading problems of the site are likely to be exacerbating the invasion of the undergrowth by nettle and Himalayan balsam. Run-offs and atmospheric deposition from an adjacent chicken farm (Photos 6 & 7) and possible high nutrient loads from the Hagley and Blakedown Wastewater Treatment Works may be further adding to the likely eutrophic conditions of the site. While, nutrient inputs from effluents can be addressed, it is unlikely that much can be done to reduce the nutrient loading that is occurring as a consequence of the breakdown of previously water-logged peat layers. Slowing the process may, however, be possible where log jams are effective at retaining water in the system. Planting of alder and willow saplings (e.g. rooted cuttings from trees on site) along the stream edge may similarly encourage localised flooding by increasing the hydraulic roughness of the channel.

Photos 6 & 7 : Effluent discharge into lower Hurcott section from nearby chicken farm.



In order to enhance the species diversity of the site, and in particular to favour the less common species typical of W5/W6 transitional communities, it is likely that regular mowing of the groundlayer will be necessary to remove invasive species (e.g. nettle, Himalayan balsam, *Rubus*). Regular mowing would act to mimic the ‘natural’ disturbances (i.e. extensive periods of water-logging/periods of high surface flow) that would otherwise limit the spread of invasive species. Particular attention should be paid to areas of previously high species diversity which may have become over-run by invasive species, but nevertheless still retain conditions that favour diversity (e.g. highly heterogeneous substrate and hydrological conditions in a confined area); detailed notes identifying such areas can be found in the 1998 vegetation survey. Removal of exotic conifer stands from the site would provide new recruitment gaps and temporarily increase heterogeneity of the wet woodland stands.

Application of Phase 1 contract to guide the development of site-specific advice

The flow diagram below (Figure 25) illustrates the recommended pathway that can be followed to help: 1) define the context and current status of an alluvial forest and 2) guide conservation efforts/make reasoned decisions on how to manage a given alluvial forest. Input from the Phase 1 contract occurs at all stages of the defined pathway and acts primarily as a reference source to help identify key variables to be considered (e.g. range of possible water supply sources to a particular wet woodland type) and likely scenarios (e.g. likely evolution of wet woodland community) where artificial disturbances are added to the system. The principal concept behind the flow diagram is that the natural physical processes of a site define the natural vegetation community that persists there (unless the physical processes have been disturbed in some way). In order to identify how to conserve a wet woodland site, it is thus important to recognise the impacted compared with the unimpacted woodland and from here to identify a realistic/locally acceptable starting point for conservation action; this may involve the restoration of natural physical processes to achieve a natural woodland, or preservation of modified physical processes to preserve an existing 'modified', but highly valued wet woodland community. Equally, a similar procedure can be used to predict (based on information in the Phase contract) likely shifts in an alluvial forest as a consequence of proposed/anticipated disturbances.

The generic methodology formulated here to guide conservation staff suggests that the starting point for a wet woodland site evaluation is to define first the setting and basic underlying physical processes that define the site (i.e. steps 1. and 2. of the data collection procedure - top right hand corner of Figure 25). Information required includes the **geology** of the site, **substratum in profile** prior to significant human interference (e.g. proportion of coarse to fine alluvial deposits) and **topography** (e.g. slope across and along a river valley where wet woodland is situated). The **basic hydrology** of the site (prior to any human intervention) and its **setting in the wider catchment** should also be reviewed, using the diagrams and conceptual models provided in the Phase 1 document as aids.

The main objective in collecting this basic information is get a picture of the main sources of water and infiltration rates according to local substratum and topography. A second flow diagram (Figure 26) provides examples of this information as collected for the Hurcott and Podmore SSSI. Where local and/or regional hydrology has been altered by humans (Question 1), information giving an historical account of specific factors that may have altered the regional and/or local site hydrology and geomorphology should be collected next (step 3 in Figure 25). This should be in sufficient detail to help explain the current composition and structure of existing vegetation communities. Examples of this are given in Figure 26 for the Hurcott and Podmore Pools SSSI. A similar review of other biotic and abiotic disturbances *significantly* affecting wet woodland structure and composition should be given as suggested in step 4 in response to Question 2. The conceptual models that have been formulated in the Phase 1 contract (section entitled 'Implications for Decision Making – Vulnerability') can serve to highlight potential biotic and abiotic disturbances that can cause substantial changes to wet woodland structure and composition. The final steps in the information collection process (Steps 5. and 6.) should aim to identify the current structure and composition of vegetation in wet woodland stands and determine the likely 'unimpacted wet woodland' composition and structure (historical surveys prior to disturbances would be invaluable in this latter respect). Again the descriptions and conceptual models developed in the Phase 1 contract can help to identify these (e.g. Figure 14- 'Conceptual model illustrating

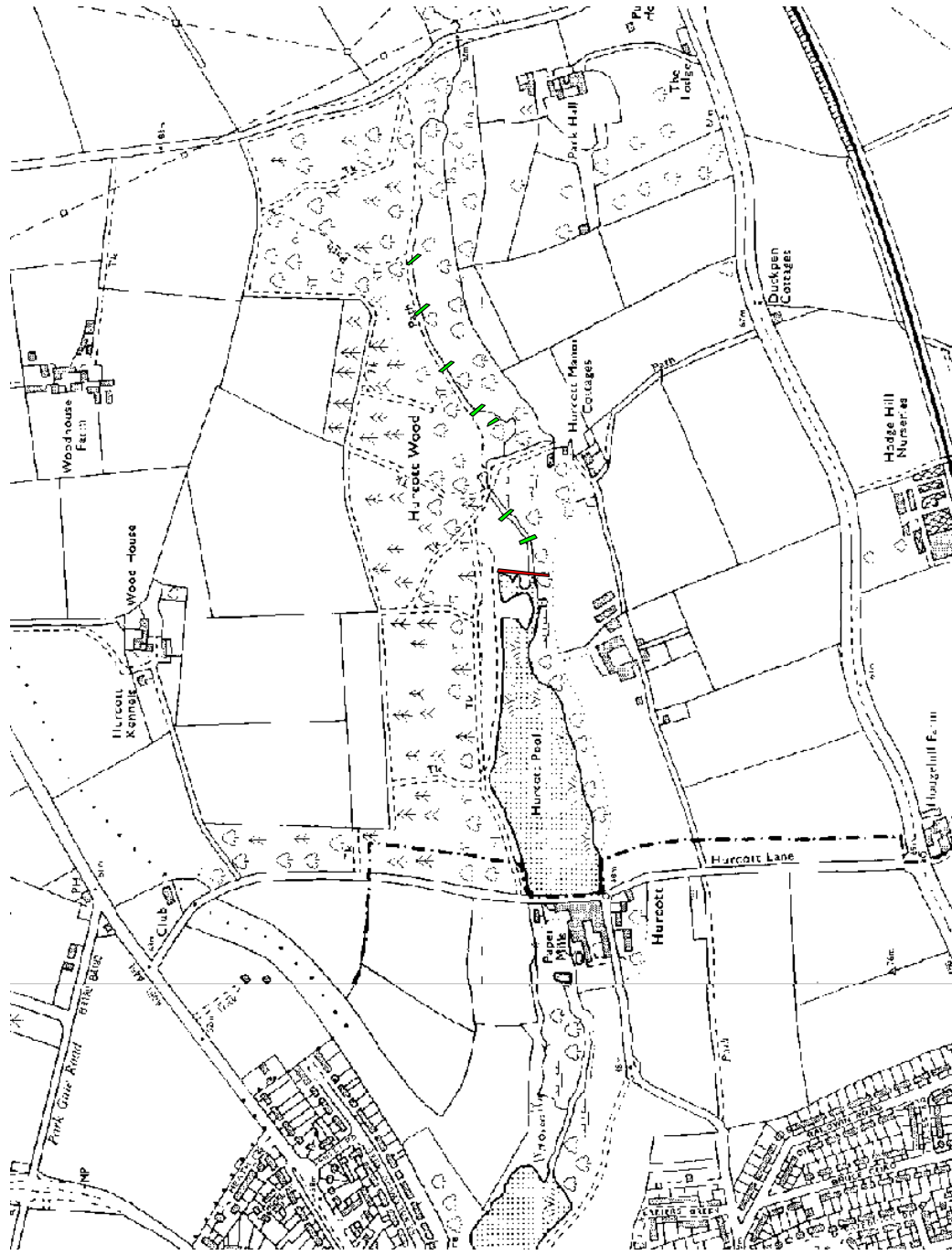
the expected position of alluvial forest communities along soil moisture and nutrient availability gradients’).

Once all information has been gathered as outlined above, the question (Question 3) of the possibility, and indeed, the desirability of reinstating natural processes/removing any biotic and abiotic disturbances must be addressed. The wet woodland that is in existence today may be considered to be less valuable where it is the product of significant modification of natural physical processes and there may be a preference to recover a more ‘natural’ wet woodland community by removing the artificial elements in the system. In certain cases this may not be possible or desirable and the objective might be to attempt to enhance the current community by preserving the elements that allow for it to function (e.g. key, albeit artificial water sources). The Phase 1 document provides certain relevant species-specific information that can be used to help manage a site in favour of missing/affected species. More complete information of this kind for a wider number of dominant or particularly sensitive species (in table format) could be useful in this respect.

In the case of anticipated or proposed disturbances to a wet woodland site, the generic methodology developed here can equally be applied as an aid that will help to identify likely scenarios.

References

- BAAR, J. and others. 2002. Ectomycorrhizal root development in wet Alder carr forests in response to desiccation and eutrophication. *Mycorrhiza*, 12(3), 147-151.
- COOPER, D.J., & VAN HAVEREN, B.P. 1994. Establishing Felt-Leaf Willow from seed to restore Alaskan, U.S.A., floodplains. *Arctic and Alpine Research*, 26(1), 42-45.
- FRIEDMAN, J.M., SCOTT, M.L., & LEWIS, W.M. 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. *Environmental Management*, 19(4), 547-557.
- HACKE, U., & SAUTER, J.J. 1996. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus basamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology*, 111(2), 413-17.
- KAZDA, M. 1995. Changes in alder fens following a decrease in the ground-water table - results of a geographical information system application. *Journal of Applied Ecology*, 32(1), 100-110.
- RAVEN, J.A., and others. 1989. Water balance of N₂-fixing root nodules: Can phloem and xylem transport explain it? *Plant Cell Environ.*, 12, 683-688.
- VOGT, U.K. 2001. Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L. *Journal of Experimental Botany*, 52(360), 1527-1536.



N ↑

Not to Scale

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Figure 24. Suggested locations of bund and strategic debris dams.

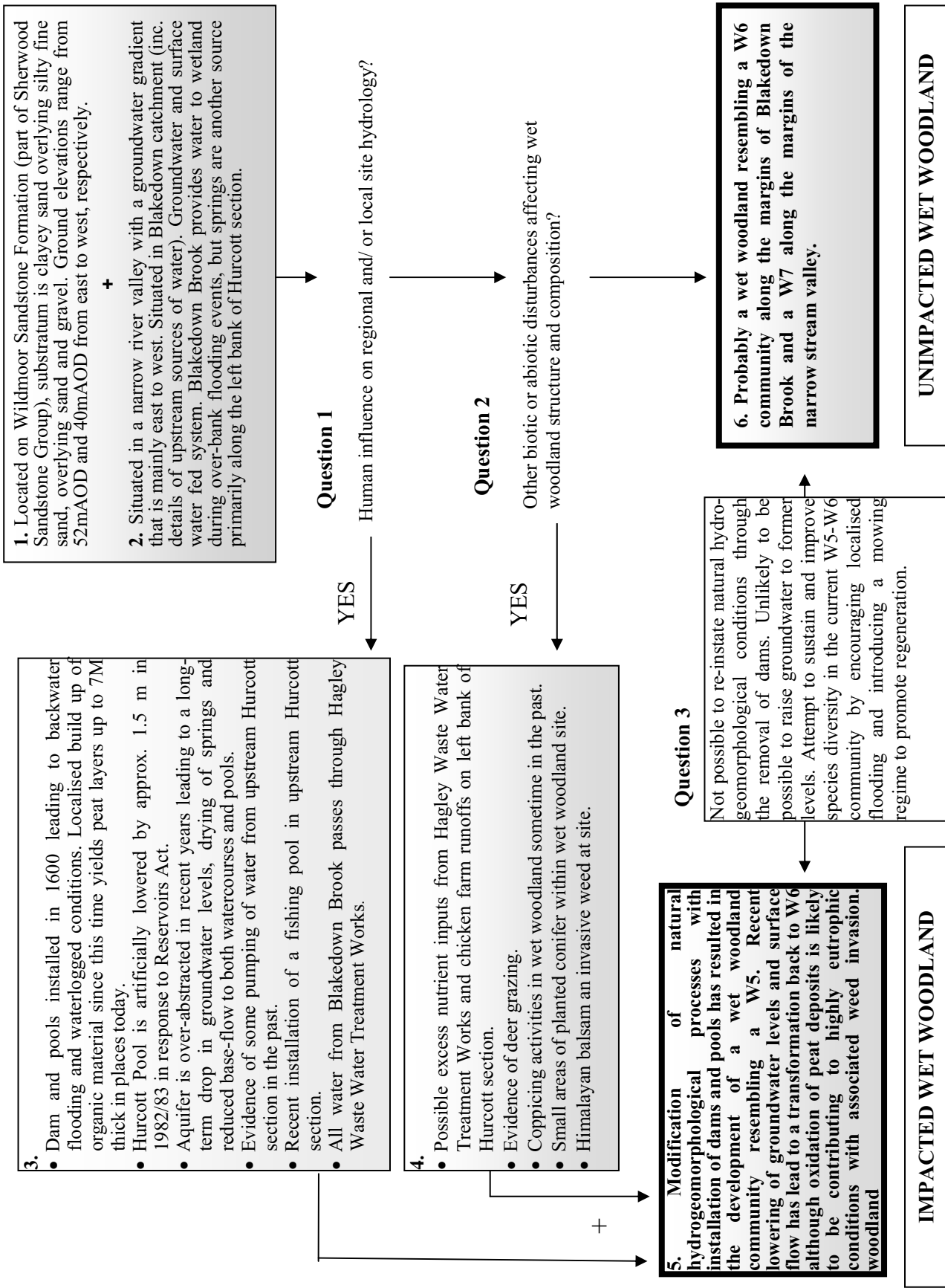


Figure 26. Example of information to be collected using generic methodology designed to guide conservation staff in the production of wet woodland site-specific management guidelines.



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