3

Origins and development of grassland communities in northwestern Europe

Herbert H.T. Prins
Tropical Nature Conservation and Vertebrate Ecology Group, Department of Environmental Sciences, Wageningen Agricultural University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands

3.1 INTRODUCTION

Most of the countryside of northwestern Europe is characterized by an absence of forest. Indeed, forest covers only about 25% of France, 27% of Germany, 10% of The Netherlands and 8% of England and Wales; in western Europe only 1% is considered to be 'old-growth' forest (Dudley, 1992). This quintessence was captured by many seventeenth century painters, who emphasized the sky with its clouds over near-treeless landscapes. To many a citizen of today, heaths, downs, limestone grasslands and other open vegetation types are viewed as original, natural and ancient. Yet many of these vegetation types are artificial and, as such, are as unnatural as most forests of northwestern Europe.

This chapter will elucidate the origins of open vegetation dominated by grasses, and will pay particular attention to the effect of human influences on vegetation composition and development, and to the impact of large herbivores on the vegetation. Grass and humanity – there is more to their interrelation than is often surmised when one is sitting on a well kept lawn, since grasses form the mainstay of domesticated herbivores. Grasses form the production basis for milk, meat and wool and grasses were the fuel that made the first semi-intensive agriculture possible through ploughing by oxen and horse. Indeed, through human manipulation of vegetation over the last millennia, Europe's present landscape, including most of its nature reserves, came into being. The question of which of today's open vegetation types are least disturbed and most akin to natural vegetation, and which ones are to be viewed as culturally derived, has important implica-

Grazing and Conservation Management. Edited by M.F. WallisDeVries, J.P. Bakker and S.E. Van Wieren. Published in 1998 by Kluwer Academic Publishers, Dordrecht. ISBN 0 412 47520 0.

tions for the management of these vegetation types and, thus, for the management of nature reserves.

3.2 OPEN VEGETATION BEFORE THE PLEISTOCENE

The basis for understanding the present open vegetation in northwestern Europe lies in understanding the Pleistocene. The study of vegetation development during interglacial periods allows human influence to be teased apart from natural development during the Holocene, in which we live. This section briefly describes vegetation development prior to the Pleistocene.

Grasses (Gramineae, about 8000 species) and sedges (Cyperaceae, about 4000 species) belong to the Order Cyperales which, together with other monocotyledons, probably derived from dicotyledons during the beginning of the Cretaceous – 135 million years before present (BP) (Cronquist, 1968; Von Denffer *et al.*, 1976; Doyle, 1978). There is good evidence that the first angiosperms lived in locally disturbed habitats, such as stream margins, away from closed forests dominated by conifers and ferns (Doyle, 1978) and that until the end of the Cretaceous (65 million years ago), monocotyledons grew mainly in swamps (Von Denffer *et al.*, 1976). During this epoch there is very little evidence for open vegetation, and the Earth was covered to a large extent by forests dominated by woody species (Cronquist, 1968; Kurtén, 1972; Von Denffer *et al.*, 1976; Webb, 1977, 1978). Evidence for this stems both from the types of plants that have been found and from the absence of remains of grazing animals. During the early Tertiary (Eocene, 45 million years BP) the average temperature in northwestern Europe was about 22°C and the area was covered with forests resembling present tropical monsoon forests. Yet on Spitsbergen and Greenland the first representatives of the species that would later dominate Europe were already established: representatives of *Castanea*, *Juglans*, *Fagus*, *Quercus*, *Acer*, *Betula*, *Populus*, *Salix*, *Tilia*, *Ulmus* and *Alnus* were growing, as well as *Picea* and *Pinus* (Mai, 1965; Hess *et al.*, 1967). During the Miocene (20 million years BP) the average temperature dropped to about 20°C and Europe was covered by evergreen subtropical forests. These forests comprised about one-third a temperate element (131 higher plant species) and two-thirds a subtropical element (226 species) although the mosses that occurred all have a tropical distribution at present (Hess *et al.*, 1967; Schmidt, 1969). During the following epoch the general cooling continued, and during the Pliocene (2 million years BP) the average annual temperature dropped to 15–18°C and in Switzerland even to 10–17°C (Schmidt, 1969). At that time European forests were characterized by temperate species but included species that until the present only survived outside Europe in East Asia or North America (*Ginkgo*, *Liriodendron*, *Magnolia*, and *Metasequoia*) (Hess *et al.*, 1967; Walter, 1968; Schmidt, 1969).

As well as cooling during this period, the climate became much drier because new mountain ranges arose with rain-shadows in their lee. This was mainly caused by orogenesis of the Alps, the Pyrenees and mountain ranges on the Balkan, and elsewhere the Himalayas, the Andes and the Rocky Mountains (Kurtén, 1972; Webb, 1977, 1978). It should be realized that at that time montane plant species had disappeared from Europe because the mountain ranges that had formed during the Hercynian orogeny (about 300 million years BP: Gotthard-Aar Massif, Black Forest, Vosges, Ardennes, Massif Armoricain) had eroded long before the Pliocene (Hess *et al.*, 1967). This desiccation did not result in the disappearance of the European forests – in contrast to North and South America and Central Asia, where steppe formations developed (Webb, 1977, 1978), although in Europe and North Asia many plant species became extinct during the cooling and desiccation in the course of the Miocene and later. During the Pliocene the occurrence of the first modern plant species can be demonstrated (Reid and Chandler, 1915): in Reuverian deposits from Reuver, Swalmen and Brunssum 214 species were identified, of which 98 are still extant and of which 22 occur at present in Europe:

> *Alisma plantago-aquatica*, *Carpinus betulus*, *Cicuta virosa*, *Corylus avellana*, *Ilex aquifolium*, *Larix decidua*, *Lycopus europaeus*, *Malus sylvestris*, *Myriophyllum verticillatum*, *Najas marina*, *Picea abies*, *Prunus spinosa*, *Quercus robur*, *Ranunculus nemorosus*, *Sagittaria sagittifolia*, *Scirpus lacustris* ssp. *glaucus*, *S. lacustris* ssp. *lacustris*, *S. mucronatus*, *Sparganium erectum*, *Trapa natans*, *Urtica dioica*, *Urtica urens*.

The newly developed mountain ranges in Europe derived their typical cold-adapted mountain flora mainly from two sources: the Mediterranean and the high Asian mountains (Table 3.1). Many herbs that came to dominate the vegetation were derived from woody species, and Cronquist (1968) stressed the point that herbaceous groups of angiosperms relate not directly to each other, but separately to the 'woody' core of the division (see also Doyle, 1978). The result of both evolution and temperature changes was that the flora of Europe became gradually more modern, and during the Pleistocene nearly all species were apparently identical to those of the present (Table 3.2).

In North America, in the rain-shadow of the Rocky Mountains, open grassland communities developed but not (at that stage) the associated fauna. The first herbivorous ungulates date back to the Palaeocene (65 million years BP) but these were apparently still browsers rather than grazers. It appears that the first mammals adapted to feeding on grasses developed in Asia, where the first finds of hypsodontic mammals date back to the Oligocene (40 million years BP). Hypsodontism refers to the type of cheek-teeth: high-crowned with clear enamel ridges well suited for grinding the siliceous plant material that is typical in grasses. These mammals penetrated North America, but even during the Miocene no steppes had developed. The open landscape was savanna-like, interspersed with gallery forests. However, tough grasses such as *Stipa* date back to this epoch and typical

Table 3.1 Plant genera from which some species have colonized the Alps (Hess *et al.*, 1967)

Species from Asian mountains	Species from the Mediterranean
Aconithum	*Allium**
Androsace	*Anthyllis*
*Artemisia**	*Biscutella*
Astragalus	*Campanula*
Crepis	*Cerinthe*
Delphinium	*Colchicum*
Gentiana	*Crocus*
Oxythrophis	*Dianthus*
Pedicularis	*Globularia*
Primula	*Gypsophila*
Rhododendron	*Helianthemum*
	Herniaria
	Linaria
	Narcissus
	Ononis
	Saponaria
	Sesleria
	Silene

* Species from these genera are also considered to have originated in the steppe area of eastern Europe (Szafer, 1966, cited in Godwin, 1975).

Table 3.2 The modernization of the European flora since the Miocene (after Szafer, 1946, cited in Godwin, 1975)

Epoch and fossil deposit arranged by geological age	*N* species investigated	% Species local at present
Miocene (*c.* 20 million BP)		
Salzhausen	22	4.5
Herzogenrath	39	12.8
Wieliczka	27	18.5
Niederlausitz	62	22.6
Sosnice	46	31.1
Pliocene (*c.* 2 million BP)		
Pont-du-Gail	36	25.0
Frankfurt	89	29.2
Kroscienko	113	33.8
Reuver	116	35.0
Willershausen	44	41.2
Castle Eden	41	61.0
Pleistocene (*c.* 1 million BP)		
Tegelen	85	75.2
Schwanheim	47	78.9
Vogelheim	55	94.6
Cromer	132	98.4

grazing ruminants had developed by the end of the Miocene (Webb, 1977, 1978). Modern associations between grasslands and herbivores could now start to evolve, and during the following Pliocene period herd-forming grazing ungulates reached their highest species diversity (Kurtén, 1972; Webb, 1977, 1978) to be followed by a continuing loss of diversity during the Pleistocene. However, during this long time span from the Cretaceous until the Pliocene, there is no evidence for grasslands in northwestern Europe. Most of Europe was covered in forest, with the exception of the peaks of the new mountain ranges.

3.3 OPEN VEGETATION DURING THE PLEISTOCENE

The Pleistocene period was characterized by the occurrence of widespread glaciations in the northern hemisphere. During these periods woody vegetation disappeared to a large extent (Table 3.3; Figure 3.1). It should be noted at this point that the reconstruction of prehistoric vegetation is largely based on fossil remains. One of the main sources of information about the vegetation at that time is through the study of fossil pollen. From these pollen assemblages it is clear that woody species gave way to Gramineae and Ericales (Table 3.4) although it should be realized that the pollen of many herb species is strongly underrepresented because it is not dispersed by wind. The use of fossil plant remains, whether they are macroscopic plant parts or whether they are pollen, to gain an insight into palaeovegetation is fraught with difficulties but the basic methods appear valid (Janssen, 1979).

The glacial periods during the Pleistocene alternated with interglacial periods. During glacial periods the average temperature dropped to about 0°C or even lower (Atkinson *et al.*, 1987) and plant species that were adapted to cold and dry conditions dominated the vegetation. During the interglacials, temperatures increased to present values, or became even higher, and present-day species dominated the vegetation. The first cool period at the junction of the Pliocene and the Pleistocene was the Pre-Tiglian (Table 3.4), which can perhaps be characterized as a glacial period (Zagwijn, 1960).

Table 3.3 Decline of woody species in western Europe (after Reid and Chandler, 1933; Godwin, 1975)

Epoch	Location	% Woody species
Lower Eocene	London Clay	97
Upper Eocene	Hordle	85
Middle Oligocene	Bembridge	57
Late Pliocene	Reuver	57
Early Pleistocene	Tegelen	28
Middle Pleistocene	Cromer	22

Table 3.4 Dominance of graminean species in the Pleistocene (after Zagwijn, 1960; data from the following locations: Meinweg, Bouwberg, Waubach, Herkenbosch, Susteren and Zeeuws-Vlaanderen)

Epoch and deposit	Percentage of pollen sum Woody species	 Ericales	 Gramineae
Pliocene			
Susterian	85	10	5
Brunssumian	85	10	5
Reuverian	85	10	5
Pleistocene			
Pre-Tiglian	50	10	40
Tiglian[a]	70	15	15
Eburonian	45	15	40
Menapian	20	20	60
Late Pleistocene	20	1	80

[a] The Tiglian was a comparatively warm period.

3.3.1 Interglacial periods

After the Pre-Tiglian, the Tiglian (about 2 million years ago) in northwestern Europe was again a warm period, which can be considered as the first interglacial. Elephants, rhinoceroses, a wild pig species and possibly even tapirs (see Table 3.6) lived in a landscape that was dominated by riverine woodlands and swamps floristically similar to those that nowadays occur in the Caucasus (Van den Hoek Ostende, 1990). Most modern plant species that lived during the Tiglian are now affiliated with marshy plant communities and open water; a few species are affiliated with forest communities, but only very few with present-day grassland communities (Table 3.5). Grassland communities as they occur at present were still very rare in Europe, though steppe formation worldwide had its widest distribution during the Pliocene and grazing mammal species reached peak variety at that time (Kurtén, 1972; Webb, 1977, 1978).

Figure 3.1 The Mongolian steppe. Natural grasslands such as these dominated Europe during the Ice Age.

Table 3.5 Vegetation during Early and Middle Pleistocene, deduced from flora of Tegelen (Dutch Limberg) and Cromer, respectively

Vegetation formation and class	N character species (Pleistocene) Early[a]	 Middle[b]
Open water		
Potametea	11	14
Total	11 (= 20%)	14 (= 11%)
Marshes		
Phragmitetea	8	7
Bidentetea tripartiti	7	–
Parvocaricetea	1	4
Littoreletea	–	2
Isotea–Nanojuncetea	–	2
Oxycocco-Sphagenetea	–	4
Total	16 (= 29%)	26 (= 21%)
Ruderal vegetation		
Chenopodietea	4	9
Artemesietea vulgaris	3	13
Plantaginetea majoris	3	6
Secalietea	2	2
Total	12 (= 22%)	30 (= 24%)
Forest		
Querco-Fagetea	4	16
Rhamno-Prunetea	3	6
Quercetea robori-petraeae	1	4
Trifolio-Geranietea sanguinei	1	3
Alnetea glutinosae	–	8
Franguletea	–	4
Epibolietea angustifolii	–	1
Total	9 (= 16%)	42 (= 34%)

Table 3.5 *(continued)*

Vegetation formation and class	N character species Pleistocene)	
	Early[a]	Middle[b]
Grassland		
Koelerio-Corynephoretea	3	2
Molinio-Arrhenatheretea	3	9
Festuco-Brometea	1	–
Total	7 (= 13%)	11 (= 9%)

[a] Of 55 species that still occur in northwestern Europe, the present-day associations (classified after Westhoff and Den Held, 1969) give some indication that grasslands could have already occurred in the Early Pleistocene to some extent. If these formations occurred, then their species composition was so different from the modern ones that it is difficult to suggest what the vegetation looked like. Many other forest species occurred that are now extinct, such as *Alnus viridis, Acer opulifolium, Acer limburgensis, Magnolia* spec., *Phellodendron* spec., *Pterocarya limburgensis.*

[b] During a Middle Pleistocene interglacial (Cromer flora based on Reid and Chandler, 1933), the flora was already more modern, with 123 recognizable species, but the distribution over the different formations did not differ ($\chi^2 = 7.867$, df = 4; NS) from that of Tegelen.

With the alternations of glacials with interglacials during the Pleistocene, the proportion of plant species living in Europe became increasingly similar to the present, and during the Middle Pleistocene the number of species that can be used for a vegetation reconstruction on the basis of character species for present-day plant communities increases (Table 3.5). It appears safest not to try to identify plant communities from the fossil material from before the end of the Pleistocene, but to limit the reconstruction to formations (that is, physiognomic units such as forest, grassland, bog) (Janssen, 1979; see also Delcourt and Delcourt, 1991). Quite a lot of information is available for the Cromerian (Voigtstedtian) interglacial (about 1 million years ago) but from the available data there is very little indication of the occurrence of grasslands during that interglacial period (Table 3.5). Also fossils of mammals, such as straight-tusked elephant (or forest elephant, *Elephas antiquus*, also known as *Palaeoloxodon antiquus*), extinct deer (*Cervus accronatus*), wild boar (*Sus scrofa*) and extinct rhinoceroses (*Dicerorhinus kirchbergensis* and *D. etruscus*) (Stuart, 1991; Kahlke, 1994) indicate the presence of forests. The hippo species at that time, *Hippopotamus* cf. *major,* could indicate riverine floodplains but the ecology of this species may have been different from the present hippo species: its occurrence appears to be associated with coniferous forest (*Pinus*, *Picea* and *Abies*) mixed with alder and a rich marsh community without much evidence for real grasslands (Stuart and Gibbard, 1986).

The last major interglacial was the Eemian (Ipswichian), about 130 000 to 110 000 years ago. This period is quite well understood. At that time the straight-tusked elephant occurred in northwestern Europe again, together with fallow deer (*Dama dama*), red deer (*Cervus elaphus*), the ancestor of the wisent (that is, Steppe bison, *Bison priscus*) and a rhinoceros (*Dicerorhinus kirchbergensis*) akin to the Sumatran rhino (Table 3.6). The Eemian interglacial was warmer than today and the period was characterized by an early development of climax forest, where *Quercus* had its culmination before *Corylus*. The period ended with dominance by spruce and *Pinus*. Also the beaver (*Castor fiber*) lived here during this period. When the climate became colder during the Early Weichselian, the vegetation changed from birch and pine forest to one characterized by *Betula nana*, *Juniperus* and herbaceous vegetation. This sequence is a near mirror-image of the vegetation development during the reforestation in the Holocene (Aaris-Sørensen *et al.*, 1990). The Eemian interglacial is perhaps the best example of the potential appearance of northwestern Europe today had there been no human interference.

Are there reliable indications of the occurrence of open grasslands at that time? A species of particular interest is the hippo (*Hippopotamus amphibius*), of which fossils have been found that date from the Eemian interglacial (Table 3.6) (Stuart and Gibbard, 1986). Hippo was typically found together with fallow deer, steppe rhino (*Dicerorhinus hemitoechos*), spotted hyena (*Crocuta crocuta*) and the straight-tusked (forest) elephant, while the vegetation could be characterized as mixed oak forest (*Quercus*, *Pinus*, *Acer*, *Alnus* and *Corylus*) or as temperate forest with hornbeam (*Carpinus*). Quite often hippo fossils have been found in association with giant deer (*Megaceros giganteus*), aurochs (*Bos primigenius*) and red deer. Investigations on pollen spectra from hippo bones reveal a preponderance of tree pollen but with indications of herb-dominated riverine floodplain plants (grasses, sedges, *Plantago*, Compositae and a few aquatics) (Stuart and Gibbard, 1986). Judging from the present-day effect of hippo on African vegetation, it has been concluded that during the warmest period of the Eemian large herbivores were maintaining, and possibly even initiating, herb-dominated areas on the floodplains (Turner, 1975; Stuart and Gibbard, 1986). However, it is not clear whether these riverine grasslands have to be viewed as grazing swards or as *Phragmites* reedlands, since the pollen of Gramineae includes those of *Phragmites* (Turner, 1975). The presence of fallow deer would suggest real grazing swards and thus the occurrence of grasslands in the strict sense of the word during the Eemian. These grasslands then occurred within the mixed forest, and could have been used by aurochs, red deer, giant deer, steppe rhino and hippo. It thus appears justified to conclude that most of northwestern Europe was covered by closed forests and swamps and by riverine grassy floodplains during previous interglacial periods (Kurtén, 1972).

Table 3.6 Large mammals occurring in Europe since the Pliocene (based on Anderson, 1984; but for Proboscids on Mol and Van Essen, 1992)

Species	Pliocene	Pleistocene			Holocene
		Early	Middle	Late	
Primates					
Macaca florentina[T]	+	–	–	–	–
Wolves					
Cuon (alpinus) (dhole)	–	–	+	+	–
Canis (lupus) (wolf)	–	+	+	+	+
Bears					
Ursus etruscus[T]	+	–	–	–	–
Ursus spelaeus (cave bear)[1]	–	–	+	+	–
Ursus arctos (brown bear)	–	–	+	+	+
Ursus maritimus (polar bear)	–	–	–	+	+
Large cats					
Dinofelis (sabertooth)	+	+	–	–	–
Machairodus (sabertooth)	+	+	–	–	–
Meganteron (sabertooth)	+	+	–	–	–
Aciconyx pardinensis (giant cheetah)	–	+	–	–	–
Aciconyx jubatus (cheetah)	–	–	–	+	–
Homotherium latidus (scimitar cat)	–	–	–	+	–
Panthera schreuderea[T,2]	+	–	–	–	–
Panthera leo (lion) (incl. cave lion ssp. *spelaea)*	–	–	–	+	+[3]
Panthera pardus (leopard)	–	–	–	+	–
Hyenas					
Euryboas (hunting hyena)	+	+	–	–	–
Chasmaporthes (hunting hyena)	–	+	–	–	–
Crocuta crocuta (spotted hyena) (incl. cave hyena ssp. *spelaea)*	–	–	–	+[4]	–
Hyaena perrieri[T]	+	–	–	–	–
Hyaena brevirostris (short-faced hyena)	–	+	+	–	–
Hyaena hyaena (striped hyena)	–	–	–	+	–
Beavers					
Trogontherium[T] (Eurasian giant beaver)	+	+	+	+	–
Castor fiber (beaver)	–	–	–	?	+
Proboscids					
Deinotherium (deinothere)	+	–	–	–	–
Anancus arvernensis (straight-tusked gomphotere)	+	+	–	–	–
Mammut borsoni (Borson's mastodont)	+	+	–	–	–
Elephas namadicus[5]	+	+	+	+	–
Mammuthus meriodionalis[T] (southern mammoth)	+	+	–	–	–
Mammuthus throgonterii[6] (steppe mammoth)	–	–	+	–	–
Mammuthus primigenius (woolly mammoth)	–	–	–	+	+[7]
Rhinoceroses					
Diceros bicornis (black rhino)	+	–	–	–	–
Dicerorhinus etruscus[T]	+	+	–	–	–
Dicerorhinus kirberchensis (cf. Sumatran rhino)	?	+	+[8]	–	–
Dicerorhinus hemitoechus (steppe rhino)	+	+	+	+	–
Elasmotherium (giant rhino)	–	+	+	+	–
Coelodonta antiquitatus (woolly rhino)	–	–	+	+[9]	–
Tapirs					
Tapirus spp.[10] (tapir species)	(+)[T,11]	+	+	–	–
Horses					
Hipparion spp. (three-toed horse species)	+	–	–	–	–
Equus spp.[12] (horse species)	+[T]	+	+	+	+
Hippopotamus					
Hippopotamus cf. *major* (extinct hippo)	–	–	–	+[13]	–
Hippopotamus amphibius (hippo)	–	–	+[14]	+[14]	–
Pigs					
Sus spp. (boar – different species)	+[T,15]	+	+	–	–
Sus scrofa (wild boar)	–	+	+[16]	+	+
Deer					
Eucladocerus (bush-antlered deer)	+[T,17]	+	+	–	–
Libralces gallicus (extinct moose)	–	+	–	–	–
Alces latifrons (giant moose)	–	–	+	–	–
Alces alces (moose)	–	–	–	+	+
Capreolus capreolus (roe deer)	–	–	+	+	+
Cervus rhenanus[T]	+	–	–	–	–
Cervus elaphus (red deer)	–	+	+	+	+
Dama dama (fallow deer)	–	+[18]	+[18]	–	–
Megalocerus giganteus (giant deer)	–	–	+	+	+[19]
Rangifer tarandus (reindeer)	–	–	+	+	+
Bovids					
Soergelia (primitive musk ox)	–	–	+	–	–
Praeovibos (extinct musk ox)	–	–	+	–	–
Ovibos moschatus (musk ox)	–	+	+	+	+[20]
Gazella spp. (gazelle species)	+	–	–	–	–

Table 3.6 *(continued)*

Species	Pliocene	Pleistocene			Holocene
		Early	Middle	Late	
Rupicapra rupicapra (chamois)	–	–	–	+	+
Hippotragus (cf. sable and roan antelope)	+	–	–	–	–
Saiga tatarica (saiga antelope)	–	+	+	+	–
Leptobos[T,21]	+	–	–	–	–
Bison priscus (steppe bison)	–	–	+	+[22]	–
Bison bonasus (wisent)	–	–	–	–	+[23]
Bos primigenius (aurochs)	–	–	–	+[24]	+
Capra spp. (goat and ibex)	–	+	+	+	+
Ovis (sheep)	–	+	?[25]	?[25]	–
Large carnivores (excl. bears)	6	8	3	8	2
Large herbivores (excl. bears)	19	21	25	21	14

[T] Late Pliocene mammals from Tegelen (The Netherlands), after Van den Hoek Ostende (1990).
[1] The cave bear was a strict vegetarian (Anderson, 1984) and became extinct about 15 000–11 000 BP (Stuart, 1991).
[2] *Panthera schreuderea* may be identical to *P. schaubi* and/or *P. toscana*.
[3] Lion became extinct about 11 000 BP (Stuart, 1991).
[4] Spotted hyena apparently became extinct *c.* 20 000 BP in England and 14 000 BP in southern France (Stuart, 1991).
[5] *Elephas namadicus* is also known as *Palaeoloxodon antiquus* (Mol and Van Essen, 1992); it was a browsing species living in broad-leaved forests, and continued to live during the Weichselian (about 100 000 BP in Italy (Stuart, 1991).
[6] Also known as *Mammuthus armeniacus* (Mol and Van Essen, 1992).
[7] Extinct in Europe 10 000 BP (Lister, 1991).
[8] The rhinoceros *Dicerorhinus hemitoechus* was more a grazer, *D. kirchbergensis* more a browser; these species became extinct quite early in northwestern Europe but continued to live in the Levant till about 20 000 BP (Stuart, 1991).
[9] Woolly rhinoceros was a grazer; it was extinct 12 000 BP (Stuart, 1991).
[10] Tapir systematics needs revision and is not clear (Anderson, 1984).
[11] The dating of *Tapirus arvernensis* is not certain (Van den Hoek Ostende, 1990).
[12] Horse systematics in state of confusion (Anderson, 1984) but, for the Late Glacial, I only find references to *Equus ferus*. There is, *inter alia*, no evidence that it survived in the wild state in Britain.
[13] *Hippopotamus* cf. *grandis* is known from the Cromer Forest Bed series (Stuart and Gibbard, 1986); it might have been a different species than *H. amphibius*.
[14] Hippopotamus lived in Europe during interglacials only (Anderson, 1984); Stuart (1991) considers *H. antiquus* a subspecies of *H. amphibius*.
[15] The boar species reported for Tegelen is *Sus strozzii*.
[16] Wild boar had a refugium in Italy during the Last Glacial (Stuart, 1991).
[17] The bush-antlered deer of Tegelen is reported to be *E. teguliensis*.
[18] Fallow deer lived in northwestern Europe during the Eemian interglacial (Anderson, 1984) but it occurred during the Weichselian in Italy (Stuart, 1991).
[19] Giant deer survived until about 10 500 BP (Stuart, 1991).
[20] Musk ox survived until the Early Dryas (about 12 000 BP) in southern Germany and 15 000 BP in southern France, and became extinct on Taymir Peninsula 3000 BP (Stuart, 1991).
[21] *Leptobos* was ancestral to both *Bison* and *Bos*.
[22] Steppe bison survived until about 12 000 BP in southern France but appears to have been absent from northwestern Europe during the Late Glacial; before that time it was apparently common (Stuart, 1991).
[23] Wisent appears to be a recent immigrant from North America (Anderson, 1984).
[24] Aurochs is first recorded from the Holstein interglacial.
[25] I have not been able to find records of sheep or ibex from the Middle or Late Pleistocene.

Climatic fluctuations were a recurrent phenomenon during the Pleistocene, and several interstadials took place during which forest vegetation returned after a glacial period. However, the pattern of forest development over time varied: different patterns of tree species immigration rates resulted in slight differences in species assemblages during the different warm periods (Delcourt and Delcourt, 1991). This makes it difficult to use previous warm periods as exact models of natural vegetation development during the Holocene – that is, the period in which we now live. On the other hand, Bennet *et al.* (1991) showed that in Europe the beginning of a warm period is generally characterized by the occurrence of *Betula* and *Pinus*, followed by *Ulmus* and *Quercus*, with a final stage characterized by *Carpinus* and *Abies*. With the onset of colder conditions, populations of most tree species became extinct again, with *Pinus* and *Betula* replacing the other species; *Salix* populations may have continued to exist north of the Alps during a glacial period. Bennet *et al.* (1991) stressed the point that (with the possible exception of *Betula* and *Pinus*) there was no southward migration of trees at the end of a warm period. Instead, all evidence points to relict populations of broad-leaved trees and apparently species such as *Taxus* and *Picea* survived glacial periods in the mountains of the Balkans, Italy and Greece, from where recolonization of northwestern Europe took place during warm climatic conditions. Frequently, interstadial vegetation was characterized by steppe–tundra, not forest, and the next section focuses on this steppe–tundra.

3.3.2 Glacial periods

During glacial periods it appears that although the average annual temperature dropped considerably, the summer temperatures were moderate though still below 10°C (Atkinson *et al.*, 1987). Low winter temperatures (about –25°C; Atkinson *et al.*, 1987) prevented tree growth (Bell, 1969). The July wind directions were from east to northeast (not from the southwest as is the present normal pattern), which may have resulted in lower precipitation than today. The resulting vegetation in northwestern Europe can best be characterized as steppe–tundra, i.e. a vegetation that had an affiliation both with modern tundra vegetation and with the steppe. Typical species indicating an affiliation with steppe vegetation are (Bell, 1969; Godwin, 1975):

> *Ajuga reptans*, *Androsace septrentionales*, *Aphanes arvenis*, *Artemisa* spp., *Blysmus* (*Scirpus*) *rufus*, *Carex arenarea*, *Coryspermum* spec., *Demasonium alisma*, *Diplotaxis tenuifolia*, *Festuca rubra*, *Filipendula ulmaria*, *Groenlandia densa*, *Helianthemum canum*, *Linum perenne*, *Lycopus europaeus*, *Medicago sativa falcata*, *Onobrychis viciifolia*, *Potentilla fruticosa*, *Ranunclus sardous*, *Rumex maritimus*, *Rhinanthus* spp., *Stipa* spp.

The large herbivore assemblage from this environment is discussed below.

During the last glaciation (Weichselian), the steppe–tundra covered southern England and Ireland, southwestern France, The Netherlands, northern Germany to central Poland and from there to Siberia and Beringia. Real steppes appear to have covered most of the loess soils. They occurred in northern France, central and southern Germany, the Rhone area in France, northern Italy, and Hungary; from there the steppe stretched to the Black Sea and the Caspian Sea. A park-tundra, physiognomically perhaps like the open savannas of East Africa, covered Spain and Portugal, most of Italy and the Balkan Peninsula; it also covered the area north of the Caspian Sea and from there north of the Mongolian Plateau further to the east. Coniferous forests covered Corsica and Sardinia, Sicily and southern Italy, Greece, and the southern shores of the Black Sea and the Caspian Sea (Kurtén, 1972).

On the basis of radiocarbon-dated finds of woolly mammoth (*Mammuthus primigenius*), Aaris-Sørensen *et al.* (1990) concluded that an ice-free period occurred during the Weichselian (Devensian) glacial period between 45 000 and 20 000 years ago (see also Lister, 1991). Mammoth disappeared from northwestern Europe when the ice advanced: the vegetation became very sparse and plant cover discontinuous, while soil surface layers were unstable (Aaris-Sørensen, 1990). Large herbivores, apparently, could no longer find food here and disappeared from the record, though a few woolly mammoth finds date from this period (Lister, 1991). The ice-free period, however, was characterized by a steppe-like biome: the steppe–tundra. Because this steppe–tundra, which stretched from northwestern Europe to Beringia, was characterized everywhere by the mammoth, this vegetation type has been termed 'mammoth steppe' by Guthrie (1990). It was dominated by sedges and grasses, and only a few shrubs and herbs (Aaris-Sørensen *et al.*, 1990). Mammoth typically fed on grasses and sedges, but herbs and even mosses and ferns were consumed and occasionally browse from shrubs and trees (Lister, 1991; see also Guthrie, 1990). These steppe–tundras, steppes and park-tundras were ideally suited for large herbivores. Apart from species that are now extinct, such as mammoth, predators that are now considered typical of Africa – such as spotted hyena, lion (*Panthera leo*) and leopard (*Panthera pardus*) (Guthrie, 1990; see the rock paintings discovered in France in 1994) – preyed upon the large herbivores (Table 3.6). Besides the woolly mammoth, the herbivore species of the Weichselian mammoth steppe were giant deer, reindeer (*Rangifer tarandus*), saiga antelope (*Saiga tatarica*), musk ox (*Ovibos moschatus*), woolly rhinoceros (*Coelodonta antiquitatis*) and steppe bison (Figure 3.2; Table 3.6) (Aaris-Sørensen, 1999). Typical also were wild horse (*Equus ferus*) (Figure 3.3) and wild sheep (*Ovis* spec.) (Klein, 1974) but also steppe rhinoceros (*Dicerorhinus hemitoechus*), common hamster (*Cricetus cricetus*) and steppe pika (*Ochotona pusilata*) (Roebroeks, 1990) – all indicative of steppe-like vegetation. It should be stressed that this steppe-like landscape was not identical to present-day steppes of Eurasia: the mammoth steppe has no parallel today.

With the continuing cycle of glacial periods alternating with interglacial periods, and with the subsequent alternation of open vegetation and forests, the number of herd-forming herbivore species dwindled not only in Europe

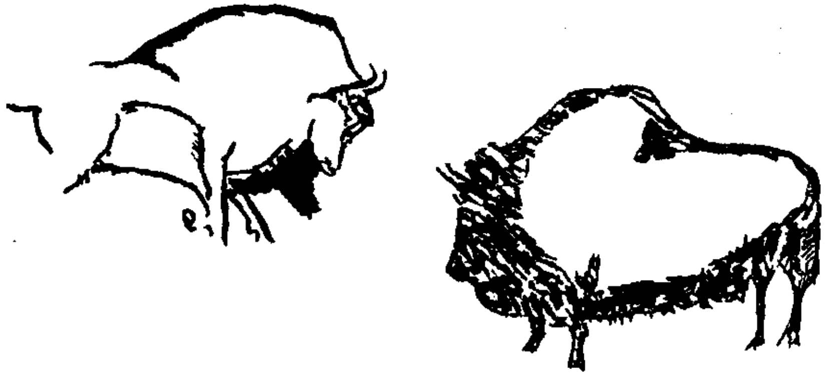

Figure 3.2 Steppe bison are frequently portrayed in Paleolithic art. These examples are from Front-de-Gaume (left) and Le Portel (right) (redrawn after Guthrie, 1990).

Figure 3.3 In the late Pleistocene, many large herbivores became extinct. The Przewalski horse (or *takhi*) escaped this fate but nearly became extinct in historical times. It is now being reintroduced into Mongolia.

but also in North America (Webb, 1977) and South America (Webb, 1978). In fact, at the end of the Pliocene 30 species of this type of herbivore, with a social organization typical of grazers (Estes, 1991), lived in Europe but only six remained there at the very end of the Pleistocene (Good, 1964) (Table 3.6). Thus, it is likely that the potential for keeping the vegetation open through grazing diminished during the Pleistocene. Other herbivores, more typical for a shrub vegetation, were moose (*Alces alces*), red deer, giant deer and wild goat (*Capra* spec.) (Klein, 1974). The main effect of the remaining wild herbivores, with a predominance of browse in their diet, will have been on structuring the species composition of woody species. Indeed, moose and hare (*Lepus* spec.) can have quite a considerable impact on nutrient cycling and on woody species composition in the forest-steppe of southern Russia (Zlotin and Khodashova, 1980). This has also been described for moose in boreal forest (Pastor *et al.*, 1993) and a significant herbivore influence on woodland structure has been observed in African savanna systems (Prins and Van der Jeugd, 1993).

Structuring of the woody species composition does not imply that the balance cover between woody species and the herbaceous layer was influenced towards a higher percentage cover of herbs and grasses or that browsers would have facilitated the development of grassland vegetation. Perhaps with the extinction of the 'bulldozer herbivores' (elephant, mammoth) this was no longer possible in northwestern Europe.

3.4 THE TRANSITION FROM PLEISTOCENE TO HOLOCENE

After the last retreat of the ice from northwestern Europe (Late Weichselian period, 13 000 to 10 000 years ago), woolly mammoth again immigrated to England, Denmark and southern Sweden about 13 000 years ago together with the associated mammoth-steppe 'disharmonious' faunal assemblage (Aaris-Sørensen *et al.*, 1990; Lister, 1991). One thousand years later mammoth became extinct in Europe – in France, England (Lister, 1991), Denmark and southern Sweden (Aaris-Sørensen *et al.*, 1990) – but survived another few thousand years in Siberia.

The Late Weichselian steppe–tundra was characterized by a mixture of floral elements from several modern biomes: tundra, steppe and even mediterranean vegetation (Table 3.7 and above). Likewise, the faunal assemblage is considered to be disharmonious (Table 3.8). Disharmonious species assemblages are characterized by the coexistence of species that today are allopatric and presumably ecologically incompatible (Graham and Lundelius, 1984). Typical examples of such species combinations are spotted hyena–red deer, spotted hyena–lynx (*Lynx lynx*)–brown bear (*Ursus arctos*)–hippopotamus, spotted hyena–reindeer, or spotted hyena–wolverine (*Gulo gulo*); all these combinations have been found in France (Graham and Lundelius, 1984) (Table 3.8). The disharmony may have caused a disequilibrium between species which was created by the disruption of coevolutionary interactions between plants and animals at the end of the Pleistocene, and this may have been a cause of many extinctions of large herbivores at the beginning of the Holocene (Graham and Lundelius, 1984). Late Pleistocene extinction of large mammals is certainly real (Table 3.6) (Graham and Lundelius, 1984). Much of the so-called unusually high mortality of the Pleistocene is best regarded as a natural consequence of high faunal turnover caused by major oscillations during the Pleistocene and the Holocene in climate and environmental heterogeneity (Gingerich, 1984). There is no convincing evidence for overkill of large herbivore populations by early humans (Anderson, 1984; Graham and Lundelius, 1984). When the climate changed during the transition from the Pleistocene to the Holocene 10 000 years ago, different species showed individual readjustments to environmental change. This implies that community structure would not have been stable over long periods of time; thus, modern communities cannot be used as direct analogues in the reconstruction of Pleistocene environments or Pleistocene communities.

The improvement of the climate after 13 000 BP was deduced originally from the palynological record. It was assumed that the occurrence of plant species was a good reflection of the climate and from the palynological record it appeared that the transition was rather slow. However, based on *Coleoptera* data, it appears there was a rapid climatic amelioration around 13 000 BP. This leads to the conclusion (Tipping, 1991) that:

> The lag between climate and vegetation in the [Late Weichselian] makes estimates from palynological data of the rates of thermal improvement unwise ... The detection of climatic deterioration from palynological data might have a firmer basis, provided the deterioration is sufficiently pronounced to have disrupted the vegetation.

From these observations it can be concluded that the vegetation and the associated large mammal fauna were not in equilibrium with climatic conditions. There was an important time lag of about 1000 years in the vegetation response to the climatic improvement in, for example, southern Sweden; this confirms the idea that plant species cannot be used directly as palaeoclimatic indicators at that time (Berglund *et al.*, 1984) (see Figure 3.4). Insects, because of their quick colonization of newly available habitats, are much more reliable (Coope, 1994). Also, *Coleoptera* assemblages are remarkably 'harmonious' during the last million years or so, indicating that their physiological adaptation to climatic factors, for example, has not changed: a time lag between *Coleoptera* assemblage structure and climate has not been observed (Coope, 1987).

During the Pleniglacial (22 000–18 000 BP) the average temperature in July was about 10°C and in January about –16°C. When the ice retreated the coldest winter months even became as cold –20 to –25°C and the climate was

Table 3.7 Steppe–tundra species assemblage during the Older Dryas (*c.* 13 000 BP): the assemblage was different from modern tundra and modern steppe; trees were almost absent, and broad-leaved trees were only present in northern Yugoslavia (area 7)

	Area												
Vegetation	1	2	3	4	5	6	7	8	9	10	11	12	13
Grasses and herbs													
Poaceae	+	+	–	+	+	+	–	+	u	+	+	–	–
Cyperaceae	+	+	–	+	+	+	–	+	u	+	+	–	–
Compositae	–	+	+	+	+	–	–	–	u	–	–	–	–
Artemisia	–	+	+	+	+	–	–	–	u	–	+	+	+
Centaurea	–	+	–	–	–	–	–	–	u	–	+	–	+
Chenopodiaceae	–	+	+	+	–	–	–	+	u	–	+	–	–
Rumex	–	+	–	–	–	–	–	–	u	–	+	–	–
Plantaginaceae[1]	–	+	+	–	–	–	–	–	u	–	+	–	+
Caryophyllaceae[2]	–	–	–	–	–	–	–	–	u	–	–	–	+
Ranunculaceae	–	+	+	–	+	–	–	–	u	–	–	–	–
Thalictrum	–	+	+	–	–	–	–	–	u	–	+	–	–
Saxifragaceae													
Saxifraga	–	+	+	–	–	–	–	–	u	+	+	–	–
Parnassia	–	–	–	–	–	–	–	–	u	+	–	–	–
Cystaceae[3]	–	+	+	–	+	–	–	–	u	–	+	–	+
Plumbaginaceae[4]	–	–	–	+	–	–	–	–	u	–	+	+	–
Rosaceae	–	+	–	–	–	–	–	–	u	–	–	–	–
Sanguisorba	–	–	–	–	–	–	–	–	u	–	–	+	–
Filipendula	–	+	–	–	+	–	–	–	u	–	–	–	–
Polygonaceae[5]	–	+	–	+	+	–	–	–	u	–	–	–	–
Rubiaceae	–	+	+	–	–	–	–	–	u	–	–	–	–
Umbelliferae	–	+	+	–	–	–	–	–	u	–	–	–	–
Spore plants													
Selaginella	–	+	+	+	–	+	–	–	u	+	+	–	+
Botrychium	–	+	+	–	–	–	–	–	u	–	+	–	–
Shrubs and dwarf trees													
Hippophaë	+	–	+	+	–	+	–	–	u	+	+	–	+
Salix[6]	+	+	+	+	+	+	–	+	u	+	+	–	–
Betula nana	+	+	–	+	+	–	+	+	u	–	+	–	–
Ephedra[7]	+	+	+	+	–	+	–	+	u	–	–	–	–
Juniperus	–	+	+	+	–	+	–	+	u	+	+	–	–
Pinus	–	+	–	+	+	+	–	+	u	+	–	–	–
Trees													
Larix	–	–	–	–	–	–	–	–	u	+	–	–	–
Corylus	–	–	–	–	–	–	+	+	u	–	–	–	–
Populus	–	+	–	–	–	–	–	–	u	–	–	–	–
Broad-leaved[8]	–	–	–	–	–	–	+	–	u	–	–	–	–

Table 3.7 (*continued*)

u = unvegetated
[1] *Plantago*
[2] *Gypsophilla repens*
[3] *Helianthemum*
[4] *Armeria*
[5] *Polygonum*
[6] *Salix polaris* or *S. repens*
[7] *Ephedra* cf. *dystachia*
[8] includes besides *Quercus* also *Acer*, *Carpinus*, *Fraxinus*, *Tilia* and *Ulmus*.
Area 1: Western Alps (Wegmüller, 1972)
Area 2: Northern Alps in Switzerland (Welten, 1972)
Area 3: Bayerische Voralpen (Schmeidl, 1972)
Area 4: Northern Alps, near Salzburg (Klaus, 1972)
Area 5: Lower Austria (Perschke, 1972)
Area 6: Basin of Vienna, Austria (Klaus, 1972)
Area 7: Southeastern Alps and northern Jugoslavia (Serceli, 1972)
Area 8: Karnische Alpsa, Austria (Fritz, 1972)
Area 9: Dachstein, central Austria (Krasl, 1972)]
Area 10: Western Carpathians (Ralska-Jasiewiczowa, 1972)
Area 11: Lowlands of northern and central Europe (Firbas, 1949)
Area 12: Northwestern Germany (Behre, 1967)
Area 13: The Netherlands (Waterbolk, 1954)

much more continental. The temperature range between the warmest and coldest month was about 30–35°C in the period between 14 500 until just before 13 000 BP, compared with 14°C at present (Atkinson *et al.*, 1987). The evidence now points to a very fast climatic improvement around 13 000 BP (with a rise in temperature of 7–8°C in summer and 25°C in winter), a slow cooling between 12 500 and 10 500 BP (with summer temperature of about 10°C and winter temperatures of about –15 to –20°C during the Younger Dryas around 10 500 BP) and again a fast warming around 10 000 BP (Atkinson *et al.*, 1987) (Figure 3.4). There were short-term climatic deteriorations in the period from 13 000 to 10 000 BP during the Older Dryas, Dryas 2, and the Younger Dryas (Figure 3.5) (Cordy, 1991). Recently it was shown that the final transition of a glacial climate to the present temperate climate took only 50 years at the end of the Younger Dryas (Dansgaard *et al.*, 1989). Indeed, plants typical of tundra conditions were growing while the July temperature had already increased to 18°C and the January temperature to –5°C. This time lag underscores the point made about plant and animals assemblages that were not harmonious, or in equilibrium with the prevailing climatic conditions at the end of the Late Glacial. In the face of such a major change it cannot be expected that regional floras and mammalian faunas (in contrast to insects) were indicative of the climate after such a sudden transition (Coope, 1994): colonization rates would have precluded this.

Whether the disharmony of faunal assemblages was a fact and not an artefact from admixture of different layers or the lack of a fine enough stratigraphy is not very easy to clarify. The detailed Cordy (1991) study of

Table 3.8 Presence of Late Glacial mammal species indicative of a 'disharmonious' mammal assemblage (A–C) and of mammal species from the Boreal period indicative of a 'harmonious' assemblage (D)

	Late Glacial			Boreal
Species	A	B	C	D
Sorex araneus (common shrew)	+	–	–	–
Desmana moschata (desman)	–	–	+	–
Erinaceus europaeus (hedgehog)	–	–	–	+
Spermophilus spp. (suslik, groundsquirrel)	+	–	+	–
Sciurus vulgaris (squirrel)	–	–	–	+
Castor fiber (beaver)	+	+	+	–
Clethrionomys glareolus (bank vole)	+	–	–	–
Arvicola terrestris (water vole)	+	+	–	–
Microtus agrestis (field vole)	+	–	+	–
Microtus oeconomus (northern vole)	+	+	–	–
Microtus gregalis (tundra vole)	+	+	–	–
Apodemus sylvaticus (woodmouse)	+	–	–	–
Dicrostonyx torquatus (Arctic lemming)	+	+	–	–
Lemnus lemnus (Norway lemming)	+	+	–	–
Lepus spp. (hare)	+	+	+	+
Ochotona pusilla (steppe pika)	+	+	–	–
Canis lupus (wolf)	+	+	+	+
Alopex lagopus (Arctic fox)	+	+	–	–
Vulpes vulpes (red fox)	+	+	–	+
Ursus arctos (brown bear)	+	+	+	+
Ursus spelaeus (cave bear)	+	–	–	–
Crocuta crocuta (spotted hyena)	+	–	–	–
Gulo gulo (wolverine)	+	–	+	–
Martes martes (pine marten)	–	–	–	+
Mustela putorius (polecat)	–	–	–	+
Meles meles (badger)	–	–	–	+
Lutra lutra (otter)	–	–	–	+
Panthera leo (lion)	+	–	+[1]	–
Felis sylvestris (wild cat)	+	–	–	+
Lynx lynx (lynx)	+	+	–	+
Mammuthus primigenius (woolly mammoth)	+	+	+	–
Coelodonta antiquitatis (woolly rhinoceros)	+	–	–	–
Sus scrofa (wild boar)	–	–	–	+
Equus ferus (wild horse	+	++	+	–
Megalocerus giganteus (giant deer)	+	–	+	–
Alces alces (moose)	+	–	+	+
Capreolus capreolus (roe deer)	–	–	–	+
Rangifer tarandus (reindeer)	+	+	+	–
Cervus elaphus (red deer)	–	++	–	+
Saiga tatarica (saiga antelope)	–	+	–	–
Ovibos moschatus (musk ox)	+	–	–	–
Bos primigenius (aurochs)	+[2]	+	+	+
Bison bonasus (wisent)	–	–	+	–

Table 3.8 (*continued*)

---

[1] This record is from the Late Dryas (about 10 000 BP), The Netherlands (Housley, 1991).

[2] It is likely that this was aurochs and not wisent, since the latter is considered a post-glacial immigrant from North America (Anderson, 1984).

A. 18 000 to 14 000 BP, Wales (David, 1991).

B. 13 000 to 11 000 BP (Bølling to Younger Dryas), Somerset (Currant, 1991); the fauna was dominated by red deer and wild horse.

C. 13 000 to 10 000 BP, Denmark (Aaris Sørensen *et al.*, 1990); a number of species appear to have become (locally) extinct already, such as woolly rhinoceros and musk ox.

D. 9000 to 8000 BP, Denmark (Aaris Sørensen, 1988); the species composition is typical for the rest of the holocene until Recent, when many species went locally extinct due to the spreading of cultivation.

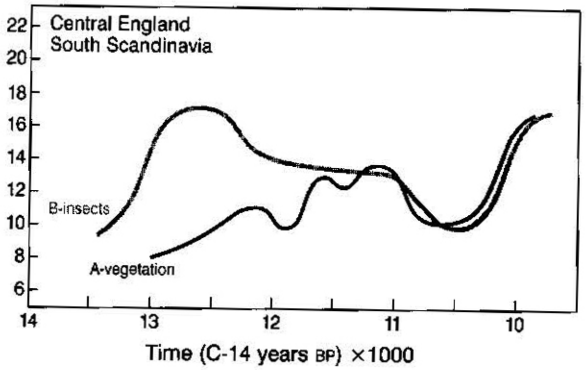

Figure 3.4 Average July temperatures for the time span 13 000–10 000 BP reconstructed from (A) palaeobotanical evidence and (B) palaeoentomological evidence. Both are supposed to be representative for areas with similar climatic regimes (central England and southern Scandinavia). (After Berglund *et al.*, 1984.)

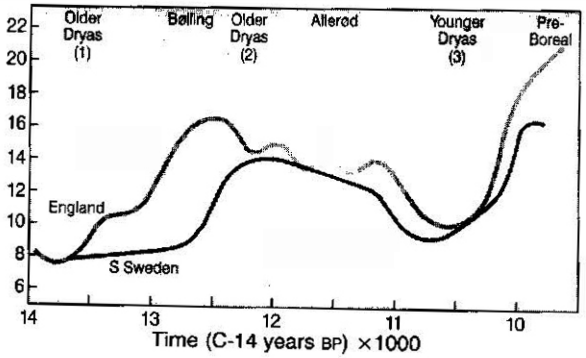

Figure 3.5 Correlation between average July temperatures for the time span 13 500–9500 BP. (After Lemdahl, 1988, referred to in Larsson, 1991.)

microtines during the rapid alterations of the climate during the period 13 000 to about 9000 BP may serve as a warning. From this evidence it is clear that arctic lemming and other vole species that are typical for more temperate conditions alternated in abundance and tracked the changes in climate well (Cordy, 1991). However, it may very well be that large herbivores could not track changes as rapidly as the vole species and, thus, that large mammal assemblages were really disharmonious. By the same token, it is unlikely that the vegetation could respond so quickly to the improved conditions, and it is therefore likely that plant communities were transient and very unstable in time during the transition from the Pleistocene to the Holocene. If the Late Pleistocene faunal and floral assemblages had responded to environmental changes as communities, rather than as individual species, then the large herbivore communities should have been able to track the changes in vegetation communities. Given the expansion of the grassland biome and the decline of the forest biome at the end of the Pleistocene (because of increased continentality of the climate), ecological theory would predict lower mammal extinction rates in the expanding grasslands than in the shrinking forests; this was not the case in North America, where numerous grazing taxa became extinct (Graham and Lundelius, 1984). Alternatively, the evidence points to loss of the coevolutionary adaptations because of drastic changes in the plant communities; hence it appears that the grazing sequence as established for East African savanna ecosystems (De Boer and Prins, 1990) and postulated for the Pleistocene mammoth steppe (Guthrie, 1990) became disrupted. This disruption could have resulted in increased competition between the grazers, causing some species to go extinct, while other species could not assemble the diets they needed for reproduction; this also could have led to extinction (Graham and Lundelius, 1984).

A disruption similar to that of the link between grazers and food plants has been suggested for the link between browsers and trees in the case of the mastodon (*Mammut americanum*), which primarily fed on coniferous trees. During the Pleistocene, large areas were characterized by open *Pinus*-dominated parklands. When pine and spruce forests collapsed into island-like distributions, the mastodon went extinct; apparently, mastodons were not able to adapt to the deciduous forests that succeeded spruce and pine (King and Saunders, 1984). Alternatives to extinction for large herbivores were migration to other communities, as was shown by reindeer, thus causing segregation of species that had once lived together. However, migration also needed adaptation to the new plant communities that emerged. These phenomena may explain the transition from disharmonious assemblages to modern assemblages, and may also explain the high species loss at the beginning of the Holocene.

It is not fully clear when the disharmony of plant communities came to an end, and when 'normal' (i.e. modern) plant communities can be reconstructed or recognized from the fossil record with any degree of precision. While mammal communities were disharmonious during the very last part of the Pleistocene (13 000 to 10 000 BP), they were apparently already harmonious during the Boreal (about 8500 BP) (Table 3.8), and, again, it can be assumed that this also applied to plant communities. The same 'date of transition' can be observed from the North American assemblages (Graham and Lundelius, 1984) and from the African ones (Klein, 1984). Numerous species of the modern North American grassland communities were residents of the Late Pleistocene grasslands (*Stipa comata*, *S. spartea*) but some floral (and faunal) species immigrated into the central grasslands from the eastern forest, western mountains (*Stipa viridula*, *S. agropyron*, *Elymus* spp.) and northern subarctic and by autochthonous evolution (present-day prairie species from the families *Andropogon*, *Bouteloua*, *Buchloe*, *Schizachirium* and *Sorghastrum*). These processes were intrinsically linked with (local) extinction. The culmination of all these events was reached during the transition of the Pleistocene to the Holocene, when the modern grassland communities emerged in North America (Graham and Lundelius, 1984). However, emergence of modernity of these communities does not imply that they remained unchanged, and this will be considered later when discussing chalk grasslands. Taking all the evidence together, it appears reasonable to suggest that from about 10 000 BP plant species and plant assemblages were able to track the climatic change, since from then onward data on the ecology of insect taxa agree with those on plant taxa (Figure 3.4).

The general picture of the vegetation development is that the steppe–tundra expanded when the climate ameliorated at the end of the Pleistocene. Both plant species typical for a modern tundra (such as *Dryas octopetala*, *Saxifraga oppositifolia* and *Salix polaris*) and species typical for steppes (such as *Ephedra*, *Hippophaë* and *Helianthemum*) were growing in most of northwestern Europe (Table 3.7) (see also Welten, 1972) and only in Ireland were there plants that were typical for heaths, such as *Calluna*, *Erica* and *Empetrum* (Firbas, 1949). In the north of Britain the vegetation mainly comprised grasses, *Artemisia* (*norvegica*, *campestris*, *maritima*), *Empetrum*, together with Chenopodiaceae and Caryophyllaceae, *Juniperus* and *Betula* (Tipping, 1991). Tall trees were absent from the landscape of northwestern Europe but *Hippophaë* was present. It is thought that delayed immigration and possibly also insufficiently developed soils were the reason for the lack of deciduous trees (Kolstrup, 1991).

Between the Older Dryas and the Younger Dryas two warmer periods occurred (Bølling and Allerød), interspersed with a very short colder period, Dryas 2 (Figure 3.2), with *Populus*, *Prunus* and *Sorbus* and with grasses mainly on dry sites (Kolstrup, 1991). Most of northwestern Europe became covered by forest dominated by *Pinus* and *Betula* (Table 3.9). Perhaps these forests were not very dense, as the palynological record shows high pollen sums for grasses and sedges, but most of the reported herbs belong to the Umbelliferae, which is an indication that conditions were no longer optimal for large grazers – very few species of this plant family are included in their diet.

During the Younger Dryas (about 10 500 BP), the change towards more reduced tree growth was probably caused by colder conditions. *Betula nana* replaced *B. pubescens* again but this has also been ascribed to drier conditions during this period as compared with the Older Dryas (Kolstrup, 1991). Further south, in southern Germany and northern Italy, pine (*Pinus sylvestris*) and birch forest began to spread over the riverine floodplains during the Older Dryas, to be replaced by oak and mixed oak forest at the end of the Pre-Boreal (9000 BP) (Becker and Kromer, 1991).

In northwestern Europe, the Pre-Boreal starts with the final disappearance of Arctic lemmings which were replaced by rodents typical for grasslands, such as Norway lemming (*Lemnus lemnus*), steppe pika and common hamster. Reindeer and wild horse occurred again during the Younger Dryas and the first part of the Pre-Boreal, but then about 10 000 BP the modern woodland rodent assemblage replaced the grassland assemblage completely (Cordy, 1991). Likewise, reindeer were still present in Schleswig-Holstein about 10 000 BP, apparently in large numbers (Bratlund, 1991), but are gone from the record only 1000 years later in both Denmark (Aaris-Sørensen, 1988) and southern Sweden (Larsson, 1991). The disappearance of reindeer took place at the same date in southern England, coinciding with the disappearance of wild horse (Lewis, 1991). Grassland indicator species disappeared and apparently the dominant vegetation in northwestern Europe became forest.

Table 3.9 Vegetation during the Allerød period (*c.* 11 500 BP) (see Table 3.7 for areas and references)

	Area										
Vegetation	1	2	3	4	5	6	7	8	9	10	11
Grasses and herbs											
Poaceae	+	+	+	+	–	+	–	+	u	+	+
Cyperaceae	+	+	+	+	–	+	–	+	u	+	+
Herbs[1]	–	+	+	+	–	–	–	+	u	+	+
Shrubs and trees											
Hippophaë	–	–	–	+	–	–	–	–	u	+	–
Salix	–	–	–	–	–	–	–	–	u	+	+
Betula	+	+	+	+	+	–	–	+	u	+	+
Pinus	+	+	+	+	+	+	–	+	u	+	+
Picea	–	–	–	–	–	–	–	–	u	+	–
Corylus	–	–	–	–	–	–	–	+	u	–	–
Broad-leaved[2]	–	–	–	–	–	–	+	–	u	–	–

u = unvegetated

[1] Mainly Umbelliferae, such as *Heracleum sphondylium*.

[2] This includes *Carpinus*, *Fagus*, *Quercus*, *Tilia* and *Ulmus*.

3.5 VEGETATION DEVELOPMENT DURING THE HOLOCENE

The present period, the Holocene, began 10 000 BP. Currently it is characterized by the occurrence of many grassland communities, which is in apparent contrast to the previous warm periods during the Pleistocene when forests dominated the landscape. Because the impact of human activities on the landscape became so much more important, it is not unlikely that many of the present grassland communities are the result of these activities. It is important to study the evidence for this during the Holocene.

The first evidence of human occupation in northwestern Europe is from artefacts that can be classified as belonging to the Middle Palaeolithic (about 300 000 to 35 000 BP). Most of these date back to the previous glacial period, the Weichselian, but also to the last interglacial period, the Eemian (130 000 to 110 000 BP). Even during the second-last glacial period, the Saalian, and the preceding interglacial periods (Hoogeveen, about 250 000 BP) humans were already present in, for example, The Netherlands. Even older finds date back to about 400 000 BP from Cagny in northern France and from Boxgrove in southern England and to about 350 000 BP from Bilzingsleben in Germany (Roebroeks, 1990). All ancient sites are from people that lived in northwestern Europe during interglacial periods and the first evidence for survival during a glacial period is from La Cotte de St Brelade, on Jersey (240 000 BP) (Roebroeks, 1990). All evidence so far points to a human culture focused on hunting, scavenging, and gathering during the Palaeolithic. This continued until after the end of the last glaciation and the beginning of the Holocene, and even during the Mesolithic period this was the sole mode of 'production'.

As was shown above, the second part of the Pre-Boreal (10 000 to 9000 BP) coincided with a major change from a fauna and flora typical of grasslands to those of woodland. This period marks the beginning of the Holocene, and forests again dominated the landscape (Table 3.10), with the most important tree species again being *Pinus* and *Betula*. An increasing number of broad-leaved species began to become established (Table 3.10). During the next period, the Boreal (9000 to 8000 BP), *Corylus* (mixed with *Alnus*) and *Picea* increased in importance (Table 3.11), with *Fagus* appearing in Lower Austria. The climax was reached with the Atlanticum (8000 to 5000 BP), when forests dominated by *Quercus robur*, *Q. pubescens*, *Q. petraea*, *Ulmus glabra*, *U. minor*, *U. laevis*, *Tilia platyphyllos*, *T. cordata*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *A. platanoides*, *A. campestre* and *Betula pendula* became widespread in northwestern Europe (Firbas, 1949). Human culture – the Mesolithic – was still characterized by hunting and gathering and the human impact on the landscape was still minimal (Waterbolk, 1985). The Atlanticum, then, is the critical epoch in which to find out whether natural grasslands occurred in the forests of that time or not: the general picture is that of a closed forest in which humans played and had played a minimal role. This hinges critically on the definition of the term 'grassland', which is clearly a physiognomic one (as are forest, bog, etc.) and should be used at the landscape level. This implies that it should be used for units with an area of at least several hectares and with a tree and shrub cover of less than 2% (Loth and Prins, 1986). In the context of this chapter, therefore, the term does not include grassy woodlands, or forests in which small patches of grass occur.

An important corollary to the conclusion that species disequilibrium may have been the major cause of extinction, as discussed above, is that one cannot deduce from the extinction of large mammalian grazing herbivores that grasslands disappeared and that forests became closed (i.e. not offering feeding opportunities to large grazers). However, it may be assumed that, with the near-absence of large grazers during the Holocene after the faunal collapse described above, the forests could become closed since large grazers were no longer present in sufficient variety to maintain grazing swards within these forest. Indeed, during the Boreal only one true grazing large herbivore species was still present in northwestern Europe – namely, the aurochs (*Bos primigenius*). This species was apparently common in the lower Rhineland during the transition of the Late Pleistocene open steppe–tundra to the forests of the Pre-Boreal (Street, 1991). Perhaps it could have become a dominant ungulate of northwestern Europe if agriculture and hunting had not swept it into extinction, just as the African buffalo apparently became dominant in eastern and southern Africa after the demise of *Elephas recki* (Prins, 1996). Additional mixed feeders (i.e. not true grazers) were red deer, wild boar and wisent (*Bison bonasus*). Under present climatic conditions, the latter three species are not able to maintain open swards and it is doubtful whether aurochs would have been able to do so: from a long-term study of African buffalo in East Africa it is clear that buffalo cannot prevent bush encroachment (Prins and Van der Jeugd, 1993). Other grazing species – woolly mammoth, wild horse, giant deer and (to some extent) reindeer – were not able to maintain viable populations in northwestern Europe and thus could not assist the surviving species in maintaining open swards. It is doubtful whether even the aurochs would have been able to maintain itself in the northwestern European forest if open grasslands had not occurred along coasts and large rivers (see below). The American bison (*Bison bison*), even though it survived from the Pleistocene, was not able to maintain open areas in the oak–chestnut (*Quercus–Castanea*) forests of the Appalachians to the east of the Mississippi river, and did not maintain viable populations there, but deer could do so (Guildhay, 1984). The North American data suggest that some of the Late Pleistocene forests were more open and perhaps more patchy than those of today (Graham and Lundelius, 1984), again suggesting that closed forests were the normal climax forests of the Holocene.

Table 3.10 Vegetation during the Pre-Boreal (*c.* 9500 BP) (see Table 3.7 for areas and references)

	Area										
Vegetation	1	2	3	4	5	6	7	8	9[a]	10	11
Trees											
Betula	+	ND	+	+	+	–	–	+	–	+	+
Pinus	+	ND	+	+	+	+	–	+	–	+	+
Picea	–	ND	–	–	+	–	–	+	–	–	+
Corylus	+	ND	+	–	+	–	+	+	–	+	+
Alnus	–	ND	–	–	–	+	–	+	–	–	+
Quercus	+	ND	–	–	+	–	–	+	–	–	+
Ulmus, Tilia, Carpinus	–	ND	–	–	+	–	–	+	–	+	–
Populus	–	ND	–	–	–	–	–	–	–	+	+

ND = no data (area 2, Bayerische Voralpen)
[a] In area 9 (Dachstein, central Austria) vegetation spread but was still cold-adapted steppe-like, with *Artemisia*, *Ephedra* and *Juniperus*.

Table 3.11 Vegetation during the Boreal (*c.* 8500 BP) (see Table 3.7 for areas and references)

	Area										
Vegetation	1	2	3	4	5	6	7	8	9	10	11
Trees											
Betula	+	ND	+	+	–	–	ND	ND	+	–	+
Pinus	+	ND	+	+	–	+	ND	ND	–	+	+
Picea	+	ND	+	+	+	+	ND	ND	+	–	+
Corylus	+	ND	+	–	+	+	ND	ND	–	+	+
Alnus	+	ND	–	–	–	+	ND	ND	+	+	+
Quercus	+	ND	–	–	+	+	ND	ND	–	–	–
Ulmus, Tilia, Carpinus	+	ND	–	–	+	+	ND	ND	+	+	–
Fagus	–	ND	–	–	+	–	ND	ND	–	–	–

ND = no data (area 2, Bayerische Vorlapen; area 7, Southeastern Alps; area 8, Karnische Alps)

Although the occurrence of large herbivores such as roe deer (*Capreolus capreolus*), red deer, aurochs and wild boar and the absence of open grassland species, such as saiga antelope, is normally interpreted as indicating a near-closed forest, some arguments plead against it. The major one is that seedling and establishment ecology, especially of *Quercus* species, indicates that light must have penetrated the forest floor at least occasionally (Vera, 1997). A personal conclusion is that open grasslands will have been restricted to areas above the tree-line, areas above salt domes, salt marshes (Figure 3.6) and some floodplains. Many individual species that are, at present, typical for grasslands will have found their habitat there, while others could survive in small patches or as understorey in the forests (this will be discussed later). The conclusion is that biotic factors appear to have played a minimal role for keeping forests open during the Atlanticum. For this reason, the experiments as conducted with introduced cattle in forest reserves in The Netherlands are of major importance in establishing whether or not large grazers were, at least potentially, able to open forest or to maintain large grassy patches in these forests (WallisDeVries, 1994; Van Wieren, 1995).

It is often assumed that along the large lowland rivers, the floodplains were covered by grassland because the long duration of floods would have prevented tree growth. It is more likely that these plains in the broad-leaved tree zone were forested. These riparian forests (German *Auenwald*, Dutch *ooibos*) (Figures 3.7 and 3.8) can tolerate prolonged flooding even during the growing season (Dister, 1983; Gerken, 1988; Späth, 1988). Three main types are known: *Populus* forest (included in *Alno-Padion*), *Fraxinus–Ulmus* forest (*Alno-Padion*) and *Alnus–Fraxinus* (*Circaeo-Alnion*) forest (names of syntaxa follow Westhoff and Den Held, 1969). *Fraxinus–Ulmus* forests in particular can survive flooding well, for up to 60% of the growing season, and are even resistant to drifting ice (Schmidt, 1969). The *Alno-Padion* communities include the *Salix* communities along rivers. Because of the highly dynamic environment, open places can be found with *Phalaris arundinacea*, *Poa trivialis*, *P. palustris* and many herbs that are known to occur at present in wet meadows used for haymaking (type *Molinio-Arrhenatheretea*) (Ellenberg, 1978):

> *Angelica sylvestris*, *Anthriscus sylvestris*, *Dactylis glomerata*, *Filipendula ulmaria*, *Galium uliginosum*, *Heracleum sphondylium*, *Lathyrus pratensis*, *Lythrum salicaria*, *Lysimachia vulgaris*, *L. nummularia*, *Myosotis palustris*, *Poa trivialis*, *Stachys palustris*, *Taraxacum officinale*.

Genuinely treeless communities along rivers are dominated by reeds (*Phragmitetum* and *Phalaridetum*) or by tall herbs (*Lolio-Potentillion anserinae* = *Agropyro-Rumicion crispi*) and ruderals (*Polygono-Chenopodietum* and *Chondrilletum*) (Figures 3.7 and 3.8). It is surmised that especially the tall herb community was the vegetation type where the remaining large herbivores concentrated during the Holocene when forests were not offering feeding opportunities for wild grazers on a large scale any more (Westhoff and Van Leeuwen, 1966). Especially when grazed, *Lolio-Potentillion anserinae* communities can develop into grasslands that are considered normal at present; relevant plant associations are *Potentillo-Festucetum arundinacea* (with *Festuca arundinacea*) and *Rumici-Alopecuretum geniculati* (with *Alopecurus geniculatus*, *Inula britannica* and *Lysimachia nummularia*), both belonging to the *Arrhenatherion* alliance. With heavy grazing and input from fertilizers these associations develop into *Poo-Lolietum* (with *Lolium perenne*, *Plantago major*, *Poa trivialis*, *P. pratense*, *Taraxacum officinale* and *Trifolium repens*) (Westhoff and Den Held, 1969). This association is nowadays widely distributed over northwestern Europe.

Vegetation types not dominated by trees definitely occurred on salty soils above salt domes in the interior of northwestern Europe (Central Germany, Poland, Czechoslovakia, Hungary and Rumania) (Ellenberg, 1978). The German and Polish salt-dome vegetation shows affinity with the salt marshes along the North Sea and the Baltic, the other with the area from the Aral to the Caspian Seas (Vicherek, 1973).

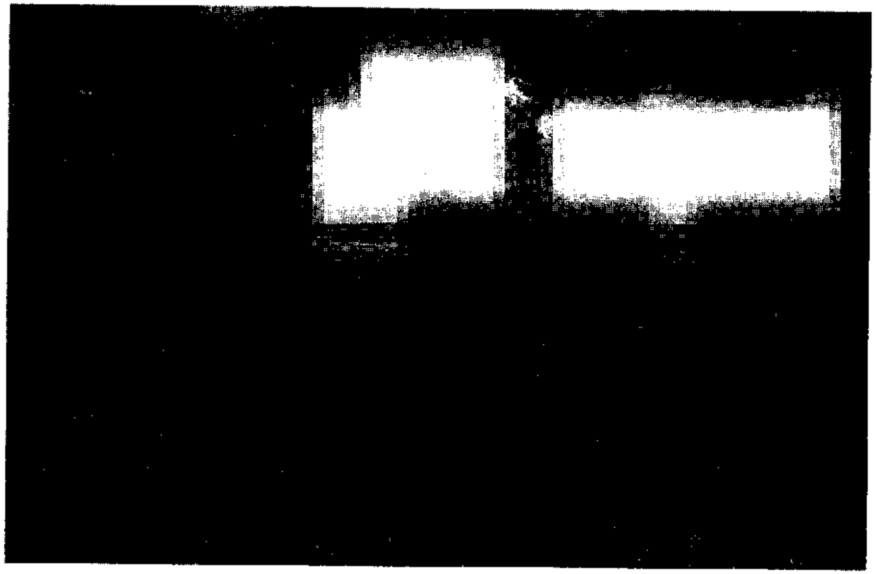

Figure 3.6 Under present climatic conditions, natural grasslands such as this salt marsh on one of the Friesian islands are uncommon in northwestern Europe.

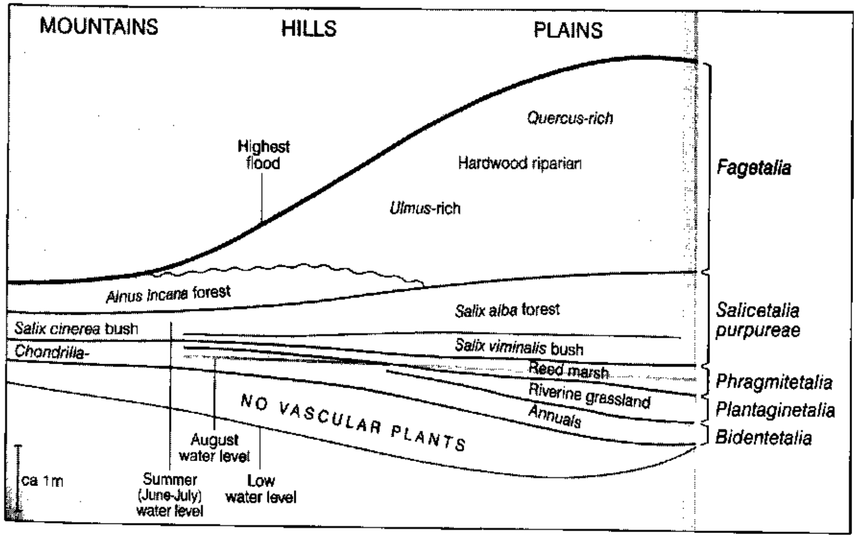

Figure 3.7 The different plant communities along a river course from high (left) to low (right) altitude. (After Ellenberg, 1978.)

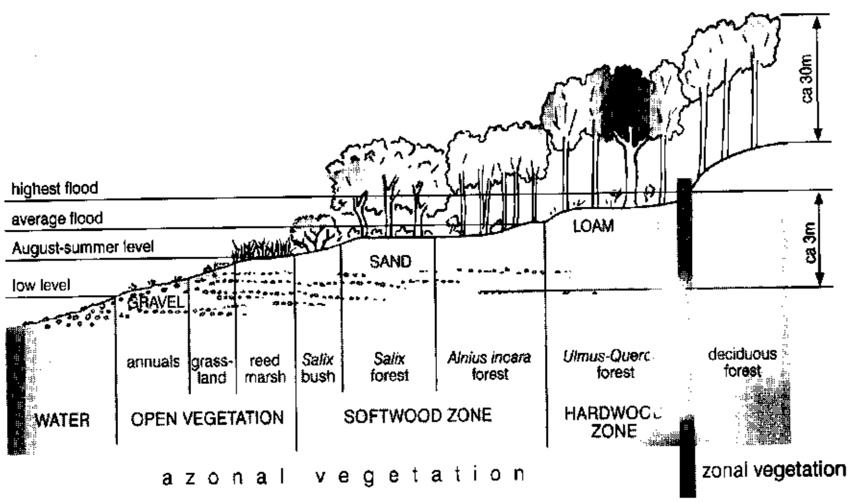

Figure 3.8 A vegetation zonation alongside a river in a montane area. (After Ellenberg, 1978.)

The northwestern European salt marshes have a striking number of species in common with the southeastern steppes; for example:

> *Armeria maritima, Artemisia maritima, Aster tripolium, Atriplex hastata* (= *A. prostrata*), *Blysmus rufus, Festuca rubra, Juncus maritimus, Limonium vulgare, Plantago maritima, Puccinellia distans, Salicornia brachystachya, S. stricta, Spergularia marina, Triglochin maritima.*

Many of these species will have found their niche in the Pleistocene open steppe–tundra, as is known for *Armeria maritima* and *Plantago maritima* (Pennington, 1969), and were restricted with the advance of the forests. Other littoral vegetation types developed on dunes along the coast. The modern plant communities from the *Koelerio-Corynephoretea* (dunes and downs) also have many plant species in common from the more humid steppes of continental Europe (German: *Wiesensteppe*). These are, for example:

> *Achillea millefolium, Anthyllis vulneraria, Arenaria serpyllifolia, Carex praecox, Erigeron acer, Galium verum, Hieracium pillosella, Helictotrichon pubescens, Helichrysum arenarium, Koeleria cristata, Potentilla argentata, Trifolium campestre*, and *Hippophaë rhamnoides*.

Again, a number of these species are known to have occurred in the Pleistocene steppe–tundra. However, these communities also gave way to forest – that is, to *Fraxino-Ulmetum* or to *Querco-Betuletum*. Whether this happened everywhere is not certain, but in the Sub-Boreal period (about 5000 BP) it appears to have been the normal pattern and only with the advance of human occupation did the *Koelerio-Corynephoretea* grasslands develop again (Zagwijn, 1971; Doing and Doing-Huis in 't Veld, 1971). Some types of these dry grasslands, especially those on soils with a low calcium carbonate content, have a strong affinity with natural grasslands that developed on glacial sand deposits along the large European rivers, such as the Rhine, Ems, Weser, Aller, Elbe, Oder, Netze and Weichsel. Normal vegetation development resulted in *Querco-Betuletum* forests there too, but tree growth was prevented on sands with a very high infiltration capacity (Ellenberg, 1978). Typical for these grasslands are species such as (Ellenberg, 1978):

> *Agrostis canina, Calluna vulgaris, Carex arenaria, Corynephorus canescens, Festuca ovina, Filago minima, Hieracium pilosella, Hypochoeris radicata, H. glabra, Jasione montana, Rumex acetosella, Spergularia morisonii, Teesdalea nudicaulis.*

Large grazing herbivores could not maintain physical condition on these grasslands, as is shown by the WallisDeVries (1994) experiments with cattle. However, where these grasslands were in close proximity to the *Lolio-Potentillion anserinae* communities along the large rivers, it is likely that large grazing herbivores, such as aurochs, could persist if they could exploit both communities within a year (WallisDeVries, 1994).

To summarize, natural grasslands at the beginning of the Neolithic period (i.e. when agriculture started in Europe) will have been restricted to areas where tree growth was prevented by high salinity (above salt domes and on salt marshes), by high water infiltration rates of soils on glacial sand deposits or by long inundations along the lowland rivers. Other types of open vegetation could be maintained where the temperature was too low for tree growth, i.e. above the tree-line in mountains or in the far north. Another niche for grassland species may have been on cliffs (Knapp, 1979/1980), as was also surmised for North America (Marks, 1983).

When the cultural transition of the Mesolithic to the Neolithic took place in northwestern Europe, around 6500 BP (in the Atlanticum), the general picture is one of extensive forests that covered close to 100% of the area. In these forests there was some hunting but its impact will have been rather low since the human density was in the order of about 0.05 humans/km^2 (Waterbolk, 1985). Hunting camps have been found in marshy grounds where people were fishing and fowling. Evidence for human impact on the vegetation is slight but it has been suggested that in order to facilitate hunting, and perhaps even to increase game densities, a form of forest management took place that facilitated the growth of hazel (*Corylus avellana*) or heather (*Calluna vulgaris*) (Simmons *et al.*, 1981). Around camps there is evidence for the increase of *Plantago major* and *Rumex* species and other

Chenopodiaceae (Waterbolk, 1954); and in some forested areas, tree removal may have caused blanket-peat to develop (Simmons, 1981). Manipulation of the vegetation for an increased hunting success has been suggested even for the end of the Pleistocene, in line with the Pleistocene overkill hypothesis (Simmons, 1981). Evidence for the first seems extremely weak (*pace* Bush, 1993), and the postulated Pleistocene overkill of large herbivores does not make sense in the light of hunting strategies that, of necessity, would have conformed with optimal foraging theories.

3.6 HUMAN IMPACT

3.6.1 Neolithic and Bronze Age

In a large part of northwestern Europe, the transition from the Mesolithic to the Neolithic, i.e. with the start of farming and making of pottery, took place during the transition from the Atlantic to the Sub-Boreal period, around 5000 BP (Van Zeist, 1959). Farming is defined as the production of primary foodstuffs and raw materials by means of deliberate cultivation of plants and keeping of animals. Farming started in the Middle East and spread at an average rate of about 2 km per year to northwestern Europe, where it was mainly restricted to loess soils during the Neolithic (Van Zeist, 1980). Humans selected forests on these soils, and started with a slash-and-burn cultivation (for a description from Russia at the end of the last century, see Smith, 1959). This cultivation technique gave quite good results in forests but not in steppes. Soils could be cultivated for some six years before they had to be left fallow. Although hoes have been found, the normal cultivation practice appears to have been use of the ard (scratch-plough), and no evidence for digging sticks has been encountered. Pigs played an important role in the economy and they may have influenced the structure of the surrounding forest. Cattle were becoming important but were not yet used for labour, and there is no evidence of haymaking to maintain them over the winter (Smith, 1959; Ten Cate, 1972; Knörzer, 1975; Ellenberg, 1978; Van Zeist, 1980). In this forest environment there was no place for sheep and goats: they came slightly later and did not become important until the Bronze Age (Clason, 1980). Hunting and fishing remained important in marshy areas, as demonstrated by the very revealing excavations at Bergschenhoek, Swifterbant and Hazendonk (all about 5500 BP) in The Netherlands (Louwe Kooijmans, 1980).

The first farmers cultivated mainly cereals and, because of the small size of the fields and correlated shady conditions, the use of ards, the likely absence of fertilization and the apparent harvesting of ears only, the associated weed community was different from the modern *Secalietea*. The resulting '*Bromo-Lapsanetum praehistoricum*' consisted of species originating from adjacent forests (*Lapsanum communis*, *Poa nemoralis*, *Rumex sanguineus*), species from river sides (*Chenopodium album*, *Polygonum persicaria*) and plant species that had migrated from the southeastern steppes (*Galium spurium*, *Polygonum convolvulus* and *Vicia hirsuta*) (Knörzer, 1971; see also Smith, 1959). Also *Plantago major* became important but *P. lanceolata*, indicative of grasslands, remained very rare (Van Zeist, 1959). The cultivated cereals were einkorn (*Triticum monococcum*) and emmer wheat (*T. dicoccum*). From later finds, it is clear that seeds of some 'weeds' were harvested too, such as from *Chenopodium album*, *Polygonum lapathifolium* and *Spergula arvensis* (Van Zeist, 1980). The advance of farming has been associated with the decline of *Ulmus* in the palynological record (Waterbolk, 1954; Van Zeist, 1959; Oldfield, 1967; Godwin, 1975). Because of the absence of evidence for grasslands and haymaking (e.g. Knörzer, 1975), it has been suggested that cattle were fed leaves of elm (*Ulmus*) and ash (*Fraxinus*), and perhaps leaves of lime (*Tilia*), maple (*Acer*) and oak (*Quercus*) as well. The so-called elm decline has been taken as evidence for the Neolithic opening-up of the forest (*landnam*) (for an extensive discussion, see Smith *et al.*, 1981). Evidence for feeding cattle with browse at that time is weak or absent (e.g. Knörzer, 1975) even though broad-leaved tree-fodder feeding has been observed in the last few hundred years (Troels-Smith, 1960 and Iversen, 1973; cited in Peglar and Birks, 1993). However, elm disease has been identified as the very likely cause of the prehistoric elm decline (Perry and Moore, 1987), and the recent work of Peglar (1993) in particular elegantly shows that disease was the most likely cause. Pollarding of trees, perhaps for the production of fodder, may have influenced the rate of transmission of the disease since pollarding instruments could have been contaminated with the fungus (Moe and Rackham, 1992); however, this is linking two assumptions into a chain, if one were to take fodder use as a causal explanation of the elm decline during the Neolithic. This is not to deny the fact that the forest was opened up at the time and that the species composition changed (Peglar and Birks, 1992; Peglar, 1993). Rackham (1980) had already pointed out that for Neolithic man to have an impact on elm, as deducted from the 50% pollen reduction of *Ulmus* during the elm decline, 'requires a human population much larger and more elm-centred than any archaeologist has hitherto proposed' (Rackham, 1980; Peglar and Birks, 1993).

Human density during the Neolithic and the Bronze Age was still very low – for example, in the order of 0.5 humans/km^2 in Drenthe (northern Netherlands) (Waterbolk, 1985): this is about 10 times higher than during the Mesolithic but about 10 times lower than during the Middle Ages. The resultant effect on the vegetation appears to have been mainly the expansion of shrubs. From England, there is evidence that *Crataegus* species, *Prunus spinosa* and *Sambucus nigra* became more important, while new species became established, such as *Acer campestre*, *Buxus sempervirens*, *Euonymus europaeus*, *Malus sylvestris*, *Prunus avium*, *Rhamnus catharticus*, *Salix fragilis*, *Sorbus aria* and *Ulex europaeus* (Godwin, 1975). This 'shrub phase' is also evident from sub-fossil mollusc faunas in southern England (Evans, 1972).

The estimated 0.5 human/km^2 mentioned above is an even lower population density than that of modern Gabon in equatorial Africa. Although the comparison is fraught with difficulties, it is noticeable that in Gabon such a density results mainly in an increased percentage of secondary forest but not in the disappearance of forest (Prins and Reitsma, 1989). Stock-grazing in the secondary forests of northwestern Europe led to good conditions for the establishment of light-demanding tree species such as *Betula* (Turner, 1981; see also Reuter, 1920; Gundermann and Plochmann, 1985) but also *Quercus* (Vera, 1997).

Grass pollen grains are found in increasing numbers with the advance of farming from about 4500 BP. There is evidence from about 5000 BP (beginning of Late Neolithic) that cattle were kept in barns, and *Plantago lanceolata*, indicative of grasslands, becomes increasingly important in the pollen record (Van Zeist, 1959). From about 4000 BP evidence for cattle kraals has been found (Waterbolk, 1954; Brongers and Woltering, 1978), and apparently cattle were used as draught animals with the invention of the plough in eastern Europe (Smith, 1959) but not yet in western Europe. When the Bronze Age began, around 4000 BP, the climate became a bit cooler and especially wetter. Heaths dominated by *Calluna vulgaris* developed, through heavy grazing by livestock, from natural grasslands growing on sandy soils (*Koelerio-Corynephoretea* grasslands) and could spread because shifting agriculture started now on soils other than loess as well, resulting in the demise of forests on higher grounds.

Shifting agriculture – that is, permanent abandonment of farmland on cleared forests after loss of soil fertility – appears to have replaced rotational farming with fallow (shifting cultivation, outfield) that was the norm during the preceding period. Evidence for the absence of fallow has been concluded from the presence of Compositae, Chenopodiaceae, *Spergula* and *Spergularia* in the fossil record (Waterbolk, 1954). Farming practice will have remained more or less the same because of the continuation of the *Bromo-Lapsanetum praehistoricum* (Knörzer, 1971). Baudais-Lundstrom (1978) concluded from excavations in Switzerland that meadows and hayfields were developing around 4000 BP, but her species list contains too many species from forests for such a conclusion. Also, there has been no evidence that forests on heavy soils were felled during the Bronze Age, when soil-tilling was probably too difficult with the available technology.

There is good evidence that chalk grasslands started to develop during the Bronze Age from about 3500 BP onwards. Plant species that were to find a niche in grasslands on chalk uplands (downs; *Mesobromion*) found their original niche in forest fringes, also along cliffs. These forest fringe communities are the *Lithospermo-Quercetum*, *Geranio-Peucedanetum*, and *Seslerio-Fagetum* with species such as (Knapp, 1979/1980):

> *Anthericum liliago*, *Bupleurum falcatum*, *Carlina vulgaris*, *Centaurea scabiosa*, *Cirsium acaulon*, *Euphorbia cyparissias*, *Gentianella ciliata*, *G. germanica*, *Leucanthemum vulgare*, *Linum catharticum*, *Origanum vulgare*, *Pimpinella saxifraga*, *Ranunculus bulbosus*, *Salvia pratensis*, *Sanguisorba minor*, *Teucrium chamaedrys*, *T. montanum*, *Thymus praecox*.

Down types in northern France (*Mesobrometum–Seslerio-Polygatelosum*) could date back to the Pleistocene (Stott, 1971), just as the open vegetation from the Upper Teesdale with its many arcto-alpine species (Pennington, 1969) and the *Caricion austroalpinae* from calcareous highlands in northern Italy (Pignatti and Pignatti, 1975). It has been claimed that grasslands on limestone cliffs in England also date back to the Pleistocene ('*Brometalia erecti*': Tansley cited in Shimwell, 1971) but evidence for this does not seem to be available (see also Moore, 1987). Bush (1993) concludes that at least some British chalklands had open grassland habitats continuously from the end of the Pleistocene, but his palaeoecological record shows a gap between 8000 and 4400 BP. This is exactly the time period that is supposed to have known the least human disturbance and Bush's inference that the ensuing vegetation had enough open space for grassland taxa to survive *in situ* does not appear warranted from his data. His conclusion (Bush, 1993) that 'it is clear that chalk grassland is more a landscape type ... than an identifiable community as its component species have changed through time, apparently in response to climatic change' is well supported and important. Evidence for development of the downs of southern England for the Neolithic is weak, and even for the Bronze Age not much proof is available (Smith *et al.*, 1981) because conditions for pollen fossilization were not good (Tinsley and Grigson, 1981). Yet most data point to the development of rather extensive grasslands at that time (Turner, 1981). Some time ago it was thought that in continental Europe a nomadic pastoralist society had already developed by the end of the Neolithic (Standvoetbeker Culture, about 4800 BP) (Waterbolk, 1954; Van Zeist, 1959; Godwin, 1975) but more recently this has been rejected (Brongers and Woltering, 1978). The evidence for such a society appears to be limited to the Celtic Iron Age in Great Britain and Ireland, which is several centuries later (Pennington, 1969; Godwin, 1975); and sagas appear to reflect this life style (see the eighth century Irish *Tain Bo Cuailge*; Kinsella, 1969). Later, during the Iron Age, Julius Caesar would report a similar economy for the Germanic tribes (see below).

Even though the fossil records shows a preponderance of evidence for a pastoral economy during the Bronze Age in southern England (Turner, 1981) this, of course, is not evidence of a pastoral society. Evidence of a purely pastoral society in the British highlands during the Bronze Age is not strong (Tinsley and Grigson, 1981) but extensive clearings developed at that time into heath (moor) and bog which replaced the original oak forest; livestock may have grazed these grassy heaths but cereal cultivation took place as well. A concurrent change from a pig-centred economy to a cattle and sheep economy took place at that time. The end result of the forest clearings, perhaps together with a deteriorating climate, was extensive soil leaching and acidification. This then led to the disappearance of grazing lands, which were replaced by heaths and bogs (Tinsley and Grigson, 1981), but the same happened under forest grazing where forests also became replaced by bogs (Turner, 1981). The same processes were observed on nutrient-poor soils in The Netherlands (Waterbolk, 1954; Van Zeist, 1959).

3.6.2 Iron Age and Middle Ages

During the following Iron Age period, which started about 3000 BP, there was a change in agricultural practice. Arable fields became permanent and were bordered by embankments. Complexes of these fields are called celtic fields, and such complexes can cover more than 100 ha. Firm evidence for soil tilling also dates from this period, because traces of ards are known from the soil in celtic fields (Van Zeist, 1980), and even humus fertilization took place (Brongers and Woltering, 1978). Individual arable fields became larger, and cereal harvesting was now at ground level. Barley (*Hordeum vulgare* and *H. distichum*) and millet (*Panicum miliaceum*) were included in the agricultural practice, possibly as an adaptation to deteriorating soil fertility due to long-term farming but also due to an increased climatic humidity (Van Zeist, 1980). This change in practice led to the disappearance of the *Bromo-Lapsanetum prehistoricum* and species better adapted to the new situation became weeds in the arable fields, such as *Alopecurus myosuroides*, *Anthoxanthum aristatum*, *Apera spica-venti*, and *Poa annua*. This points to the development of modern weed communities associated with cereal production, i.e. the *Secalietea*. It is possible that the first meadow-like vegetation developed at this time (Knörzer, 1971). Indeed, species like *Bromus sterilis*, *Phleum pratense*, *P. nodosum*, *Poa nemoralis*, *P. trivialis* and *P. pratense* found a place in the original cereal weed association, the *Bromo-Lapsanetum prehistoricum* (Knörzer, 1971), but not in the *Secalietea*. During the Iron Age in England, settled agriculture and permanent grazing developed for the first time between 400 BC and AD 100; the open landscape, as we know it, developed at that time (Turner, 1981). Sheep became more important than cattle over most of Britain, which has been taken as evidence for further deterioration of pasture quality (Clark, 1952; Godwin, 1975). These observations from The Netherlands and from England that permanent agriculture developed during the Iron Age have an important corollary: under permanent agriculture, the persistent weed problem increases. This implies that a different cultivation technique had to be used, and, in fact, the ard was replaced by the plough. Good evidence for the use of the plough, i.e. turning of the soil, has been found in, for example, Oudemolen (northern Netherlands) from the Late Iron Age (Waterbolk, 1985). Ploughing can hardly be done without the aid of draught animals, such as cattle (Godwin, 1975), and the result was that there was no place left for grasses in the cereal fields.

More or less simultaneously, the harrow was invented, the function of which is to break clods and to remove grassy weeds. So, stubble fields became less attractive for cattle because of the disappearance of grass from these fields and simultaneously the need for grasslands increased because of the higher demand for labour from draught animals (for which only cattle were used). Hence, it is likely that grasslands became much more important, because now there was an economic need for them. It should be realized that ploughing was often needed in spring, in order to grow summer cereals, which means that peak labour demand was also in spring because that was when the fields had to be prepared. As cattle would have suffered a serious loss of physical condition over the winter (WallisDeVries, 1994), it became of paramount importance to develop a system of storing fodder during winter. This must have led to haymaking, since harvesting grass is a relatively efficient way of collecting food and storing it over winter. Most browse species do provide enough energy to roughage grazers such as cattle in summer but time budgets of labour for the collection of willow leaves and twigs for animal fodder (S.E. Van Wieren, personal communication) show that harvesting grass is at least 10 times more efficient than collecting willow fodder from dense stands of young trees, if efficiency is expressed as dry weight of fodder collected per unit time. Preliminary observations also show that the intake rate of cattle is much higher on hay than on dried leaves of shrubs or trees (S.E. Van Wieren and M.F. WallisDeVries, personal communication). With the invention of the heavy plough in the early Middle Ages the need for an energy source for draught oxen became even more acute (see below). In comparison with horses, cattle are better adapted to work hard on a relative low quality diet and they do not need cereals to do this. Indeed, good quality hay was a prerequisite to cereal production for the human population (Slicher van Bath, 1976). Tüxen (1974) makes mention of mowed *Molinietalia* grasslands dated as 5000 BP, but this is a wrong citation of Janssen (1972): there seems to be no evidence for haymaking from before the Roman occupation in northwestern Europe (e.g. Knörzer, 1975). On calcareous soils in southern England, however, the relative importance of grasslands (as percentage of totally cleared grounds) became less important and the arable field proportion increased concurrent with intensified forest clearance during the Iron Age (Turner, 1981).

Stalling of cattle, which could be taken as evidence for haymaking, is known from the northern part of The Netherlands from the Middle Bronze Age (Emmerhout) but also from the Iron Age (Hijken, Ezinge) (Brongers and Woltering, 1978). Evidence for Iron Age cattle stables has also been found in Jutland (Jankuhn, 1969, cited in Knörzer, 1975). However, the presence of stables may merely indicate that cattle were kept indoors at night and it does not necessarily prove winter feeding. Before the Late Iron Age (about 300 BC) houses were not permanent and they were moved with the shifting agriculture, apparently through the village territory; but during the Late Iron Age and later, houses were permanently located close to the permanent agriculture on the celtic fields (Waterbolk, 1985). In at least some areas of northwestern Europe, human population density had increased to some 10–15 humans/km^2 (calculated from Van Es, 1994, for the areas of the Cananefati and Batavi along the lower Rhine in The Netherlands), which explains the need for novel agricultural techniques. From the Roman period Columella's instructions (in *De Rustico*, about AD 75) are available about how to manage hayland, which includes re-sowing, removal of moss, fertilization with dung and ashes, and exclusion of cattle from the land to preclude sod destruction under wet conditions (Lange, 1976). Even if the Romans had followed this advice in practice, their influence would have been small, as is indicated by the estimate that in the southern Netherlands the total area under cultivation for feeding half the Roman army that occupied Germania Inferior was only 10 000 ha (Van Es, 1972); this is less than 1% of the area. Indeed, Appolinaris Sidonius in his letter to Heronius (AD 476), describes the river banks of a number of rivers in southern Europe as having sandbanks, bordered by reeds, thorn shrubs and *Acer* and *Quercus* (Ter Kuile, 1976) but he does not mention grasslands. Horace (23 BC in his Odes II-5) even mentions heifers 'to play with the calves in marshy willow-brooks' (Shepherd, 1983). Fossil evidence for the occurrence of haylands is very meagre indeed, and plant species typical of the moist, nutrient-rich *Arrhenatheretalia* grasslands have not been identified from the central European excavations (Lange, 1976).

The first evidence for haymaking is known from around AD 200 for the area along the Lower Rhine near Utrecht: haymaking took place in the wet floodplains of the river (Kooistra, 1994). These areas were originally *Phragmitetum* and *Lolio-Potentillion anserinae* communities and not *Alno-Padion* brook forests or other types of forest. Hence hay-making in this first case did not imply felling of trees. Also Körzer's (1975) study on fossil remains of plant taxa indicative of grasslands in the Rhineland area of Germany reveals that the variety of these taxa is so large that, according to him, it can be concluded that grazing grounds developed during the Roman occupation for sufficiently long duration to set the stage for the formation of modern grassland communities. Plant species in these communities originated mainly from forest floor communities, salt marshes and small open areas on steep slopes, and were even introduced by long-distance dispersal through livestock from steppes and alpine areas. Indeed, all character species of the *Arrhenaterion* grasslands appeared then for the first time in the fossil material and some evidence for dry chalk grassland (*Festuco-Brometea*) has been found, with species such as *Salvia pratensis*, *Scabiosa columbaria*, *Sanguisorba minor*, *Pimpinella saxifraga* and *Carex caryophyllea*. Character species of the nutrient-rich *Arrhenatherion* grasslands and moist *Molinietalia* grasslands were, however, still very rare or even absent (Knörzer, 1975).

During the Iron Age, the salt marshes of northwestern Europe also became occupied. Fossil material from the artificial floodhills (*terpen* or *wierden*) clearly show that the Dutch salt marshes were intensively grazed some 2000 years ago because many species of the *Juncetum gerardii* community, subassociation *leontodontetosum autumnalis*, were found (Van Zeist, 1974). Human occupation of these salt marshes started in only about 500 BC; excavations at Ezinge showed that stables could house over 50 head of cattle (Waterbolk and Boersma, 1976). Caesar's description of the Suebi, a Germanic tribe, as living mainly off milk and off meat obtained through hunting (*Gallic War*, IV-1; Handford, 1951) seems exaggerated when considering the palaeobotanical record (Knörzer, 1975). Likewise Caesar's observation that near the Rhine the Germanic tribes 'are not agriculturalists and live principally on milk, cheese, and meat' (VI-22; Handford, 1951) is refuted (cf. Kooistra, 1994): the observations from the area of the Frisii shows that they grew foodplants, and the experiments of Van Zeist *et al.* (1976) on Dutch salt marshes show that agriculture was possible even without dikes.

Very good evidence for the occurrence of grasslands (*Koelerio-Corynephoretea* and *Festuco-Brometea*) and for moist grasslands possibly used for haymaking (*Molinio-Arrheneatheretea*) dates back to the early Middle Ages, namely from Czech villages from the *Burgwallzeit* (AD 700–900) (Opravil, 1978) and from storage barns from Wrocklaw cathedral (AD 1000) (Kosina, 1978; see also Knörzer, 1975) (Figure 3.9). Written sources also mention haymaking at that time in northern France: 'Sixteen *bonniers* [20 ha] of cropland ... There are 4 bonniers of meadow, from which 30 loads of hay can be taken. There are 3 bonniers of copse' (Pounds, 1974). There is no fossil evidence for real meadows from Germany from before AD 1000 (Willerding, 1978) but evidence becomes increasingly common afterwards (Lange, 1976).

During this period the heavy plough replaced the light plough that was in use during the Roman period. These heavy ploughs needed teams of people and oxen: the coulter made a vertical cut through the soil, while the share cut horizontally, and the mouldboard turned the soil, burying the weeds (Pounds, 1974). In the early Medieval period only oxen were used for ploughing, but with the introduction of the padded collar to the harness, horses could be used additionally in the late Medieval period (Pounds, 1974). 'A chief restraint on animal rearing was the shortage of winter fodder ... [and] there was nothing except hay on which to feed the animals through the winter. Ploughing oxen had a prior claim on the food supply' (Pounds, 1974). Dairy cows were few, except in low-lying lands of Belgium, The Netherlands and northern Germany (Pounds, 1974). Much of the pasture will have been provided by salt marshes until embankments against the sea caused fresh water to replace the salt or brackish water and to alter the vegetation towards ordinary inland grassland dominated by species as *Lolium perenne*.

The fossil evidence thus coincides with historical data, which show that between AD 800 and 1000 and from the year 1400 onward, forests on heavy or wet soils were increasingly cleared (Walter, 1927). This was made possible,

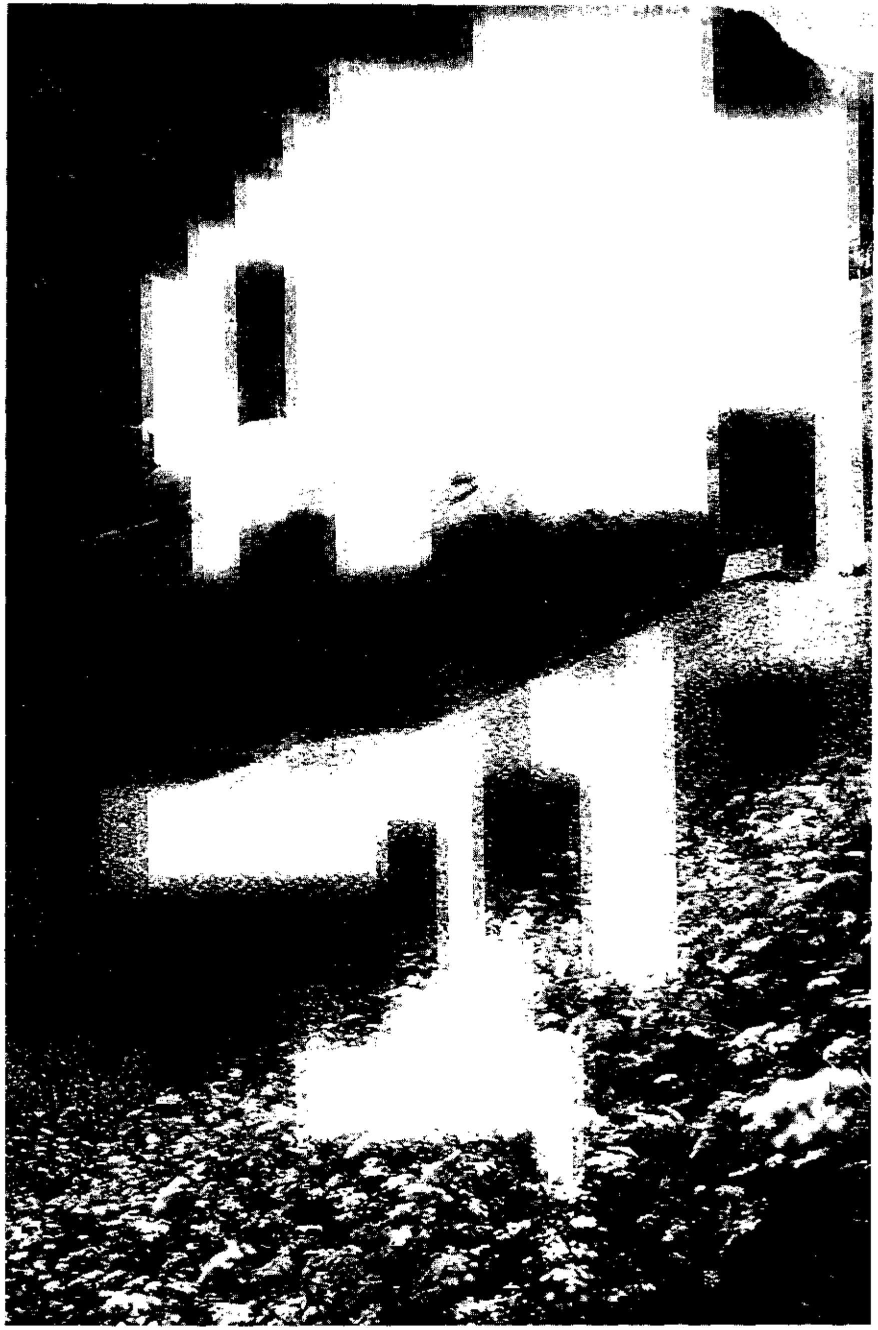

Figure 3.9 Most existing grasslands are 'replacement communities', such as this abundantly flowering, semi-natural hay-meadow in the montane Swiss Alps.

or perhaps necessary, by the increased human density and by better techniques for draining the soils (Pounds, 1974). Since the *Molinietalia* grasslands are a subdivision of the *Molinio-Arrheneatheretea* class, the group of communities that replaced the alder forest and willow stands (namely, the *Calthion palustris*, *Filipendulion* and *Junco subuliflori–Molinion* communities) have developed only since the Middle Ages. The forests from wetter sites were then felled as a result of the development of appropriate technology and a growing demand for land with the rising human population (Pound, 1974). A more detailed account of human impact on plant communities, particularly with respect to grazing by livestock, is given in Chapter 4.

3.7 CONCLUSIONS AND CONSEQUENCES FOR NATURE CONSERVATION

It can thus be concluded that grassland communities in northwestern Europe belong only to a small extent to the natural landscape, in contrast to *Phragmitetea* reed and sedge communities (*Phragmition*, *Oenanthion aquaticae* and *Magnocaricion* communities) which had undoubtedly developed during the previous interglacial periods and perhaps even before the Pleistocene (Table 3.12). The oldest anthropogenic grasslands belong to the *Mesobromion* which started developing in the Bronze Age alongside the *Calluna* heaths. The *Arrhenatherion* grasslands may be seen as a derivative from the natural *Lolio-Potentillion anserinae* communities along the larger rivers, which could spread due to intensified grazing by domestic stock. Moist grasslands used for haymaking, especially the *Molinietalia* grasslands, are of recent origin and date back only to the Middle Ages when forests on poorly drained soils were felled. These anthropogenic grasslands belong to the semi-natural landscape (Chapter 2).

These observations and conclusions have important implications for nature conservation. If nature is defined as the combination of wild native species and the action of natural processes on these wild species, then the aim of nature conservation should only be to maintain the integrity of natural communities and even ecosystems. Nature conservation of grassland communities could then be restricted to the natural grassland types (Table 3.12). Nature management of this latter class should then be aimed at preventing nutrient input but also at the removal of dominance by *Calluna vulgaris*, and grazing as a management technique to suppress grass growth would be inappropriate. To maintain salt marshes one needs flooding by salt water, and grazing or mowing are not necessary as long as mudflats can develop into new salt marshes. Management techniques to maintain the *Mesobromion*, which often include grazing, would be inappropriate, since the natural vegetation there would be broad-leaved forest. By the same token, nature management through haymaking in the *Molinietalia* grasslands would be wrong since the natural vegetation in areas with that type of grassland would be the *Alno-Padion*.

Table 3.12 Overview of the origins of contemporary grassland communities and other open vegetation types from northwestern Europe (syntaxa after Westhoff and Den Held, 1969)

Landscape	Community	Vegetation type
Natural	*Asteretea tripolii*	Salt marshes
	Phragmitetea	Reed and sedge marshes
	Agropyro-Rumicion crispi	Riverine grassland
	Corynephoretalia	Dune grassland from acid soils
	Mesobrometum-Seslerio-Polygaletosum	Mesic calcareous grassland
	Xerobromion	Dry chalk grassland
Anthropogenic (Bronze Age origins)	*Mesobromion*	Mesic calcareous grassland
	Nardo-Calluneta	Heathland from acid soils
	Arrhenaterion elatioris	Fertilized grassland
Anthropogenic (Middle Age origins)	*Molinietalia*	Hay-meadows

Adherents of this view on nature conservation emphasize lack of natural processes and especially the lack of wild large herbivores in the present 'nature reserves'. This leads to the increased desire to reintroduce, for example, beaver and moose, to abandon red deer and wild boar hunting, and to introduce semi-wild grazers to replace the extinct aurochs with Heck cattle and the extinct wild horse with Konik horses. Within the nature conservation movement, adherents of this view have often been denounced as romanticists, implying that what they want is unattainable.

Inter alia, scientists apparently have an urge to discover very ancient remnants of particular vegetation types, remnants of a period long lost but still occurring in the countryside. One example has already been mentioned: the supposed Pleistocene origin of British chalk grasslands, for which the data are definitely too weak to prove their ancient origin. Also some 'ancient' woodlands are supposed to represent a more or less unbroken continuance of forests since the post-Pleistocene reforestation of Britain (Rackham, 1980). Again, the facts appear to be otherwise and a particular ancient woodland which was well studied proved to be 'only' 1000 years old (Day, 1993). Northwestern Europe has surely been used so long and so intensively as to preclude the occurrence of 'original' vegetation in areas that have, or had, agricultural potential. This implies that nature conservationists do not have the natural, wild examples of how northwestern Europe could, and must, look like if and when nature restoration takes place on abandoned agricultural land or even in nature reserves. This presents a major challenge, because now scientists have to find out what natural vegetation types would look like, what vertebrate species assemblages have to be reassembled, and in what densities these animals have to live in areas where nature restoration takes place. Even with the prolonged effort of palaeoecologists the past is still a very imperfect mirror – but this mirror can be used for restoring nature in northwestern Europe.

On the other hand, many conservation organizations in western Europe implicitly define nature as the occurrence of indigenous wild plant species that can maintain themselves without sowing. If at the same time the (plant) communities that have developed over centuries under management techniques from before the Industrial Revolution have to be preserved, then the term 'nature' is used to label the semi-natural landscape that can be described as pre-industrial or low-intensity farm land (Chapter 2). In that case a whole set of management techniques have to be employed to mimic the farming activities of our ancestors. These techniques include: herding sheep, grass and tree suppression, and litter removal on heaths; extensive pastoralism and tree suppression in *Mesobromion* vegetation; and haymaking, extensive grazing, tree suppression and nutrient removal in *Molinietalia* grasslands. If these techniques are to be employed, there should preferably be the same high labour input and low level of mechanization as those of our ancestors, so as to ensure the same impact on the communities. It should be remarked, too, that the costs of this type of nature management may be much higher than the type of management advocated by the 'romanticists'.

Whatever the chosen aim and its dependent set of actions, management activities must always take into account water management to maintain the proper hydrological regime, counter-action against acidification, and prevention of habitat fragmentation and input of nutrients or pollutants. This is a daunting task for which the adherents of the two (often contrasting) views definitely should form a united front against the many forces in European societies that care little for Europe's native fauna and flora or for its landscape.

ACKNOWLEDGEMENT

This chapter is dedicated to Mrs Clara Biewenga who, through her unassuming support to generations of plant ecologists, has been an important factor in the development of science in The Netherlands.

REFERENCES

Aaris-Sørensen, K. (1988) *Danmark's Forhistoriske Dyreverden: fra Istid til Vikingetid*, Gyldendal, Copenhagen.

Aaris-Sørensen, K.J. Petersen and H. Tauber (1990) *Danish Finds of Mammoth* (Mammuthus primigenius *Blumenbach*)*: stratigraphical position, dating and evidence of Late Pleistocene environment*, Danmarks Geologiske Undersøgelse, Copenhagen.

Anderson, E. (1984) Who's who in the Pleistocene: a mammalian bestiary, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 40–89, University of Arizona Press, Tucson.

Atkinson, T.C., Briffa, K.R. and Coope, G.R. (1987) Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*, **325**, 587–592.

Baudais-Lundström, K. (1978) Plant remains from a Swiss neolithic lake shore site: Brise-Lames, Auvernier. *Berichte der Deutschen Botanischen Gesellschaft*, **91**, 67-84.

Becker, B. and Kromer, B. (1991) Dendrochronology and radiocarbon calibration of the Early Holocene. in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 22–24, CBA Research Report 77, Council for British Archaeology, London.

Behre, K.E. (1967) The late glacial and early post-glacial history of vegetation and climate in northwestern Germany. *Review of Palaeobotany and Palynology*, **4**, 149–161.

Bell, F.G. (1969) The occurrence of southern, steppe and halophyte elements in Weichselian (last glacial) floras from southern Britain. *New Phytologist*, **68**, 913–922.

Bennett, K.D., Tzedakis, P.C. and Willis, K.J. (1991) Quaternary refugia of north European trees. *Journal of Biogeography*, **18**, 103–115.

Berglund, B.E., Lemdahl, G., Liedberg-Jönsson, B. and Persson, T. (1984) Biotic response to climatic changes during the time span 13,000–10,000 BP – a case study from SW Sweden, in *Climatic Changes on a Yearly to Millennial Basis*, (eds N.A. Mörner and W. Karlén), pp. 25–36, Reidel, London.

Bratlund, B. (1991) A study of hunting lesions containing flint fragments on reindeer bones at Stellmoor, Schleswig-Holstein, Germany, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 193–212, CBA Research Report 77, Council for British Archaeology, London.

Brongers, J.A. and Woltering, P.J. (1978) *De Prehistorie van Nederland: Economisch, technologisch*, Fibula-van Dishoeck, Haarlem.

Bush, M.B. (1993) An 11400 year paleoecological history of a British chalk grassland. *Journal of Vegetation Science*, **4**, 47–66.

Clason, A.T. (1980) Jager, visser, veehouder, vogellijmer, in *Voltooid Verleden Tijd?: Een hedendaagse kijk op de prehistorie*, (eds M. Chamaulan and H.T. Waterbolk), pp. 131–146, Intermediair, Amsterdam.

Clark, J.G.D. (1952) *Prehistoric Europe: the economic basis*, Methuen, London.

Coope, G.R. (1987) The response of late Quaternary insect communities to sudden climatic changes, in *Organization of Communities: Past and Present*, (eds J.H.R. Gee and P.S. Giller), pp. 421–438, Blackwell, Oxford.

Coope, G.R. (1994) The response of insect faunas to the glacial–interglacial climatic fluctuations. *Philosophical Transactions of the Royal Society, London, B*, **344**, 19–26.

Cordy, J.M. (1991) Palaeoecology of the Late Glacial and early Postglacial of Belgium and neighbouring areas, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 40–47, CBA Research Report 77, Council for British Archaeology, London.

Cronquist, A. (1968) *The Evolution and Classification of Flowering Plants*, Nelson, London.

Currant, A.P. (1991) A Late Glacial interstadial mammal fauna from Gough's Cave, Somerset, England, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 48–50, CBA Research Report 77, Council for British Archaeology, London.

Dansgaard, W., White, J.W.C. and Johnsen, S.J. (1989) The abrupt termination of the Younger Dryas event. *Nature*, **339**, 532–533.

David, A. (1991) Late glacial archaeological residues from Wales: a selection, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 141–159, CBA Research Report 77, Council for British Archaeology, London.

Day, S.P. (1993) Woodland origin and 'ancient woodland indicators': a case study from Sidlings Copse, Oxfordshire, UK. *The Holocene*, **3**, 45–53.

De Boer, W.F. and Prins, H.H.T. (1990) Large herbivores that strive mightily but eat and drink as friends. *Oecologia*, **82**, 264–274.

Delcourt, H.R. and Delcourt, P.A. (1991) *Quaternary Ecology: a paleoecological perspective*, Chapman & Hall, London.

Dister, E. (1983) Zur Hochwassertoleranz von Auenwaldbäumen an lehmigen Standorten. *Verhandlungen der Gesellschaft für Ökologie*, **X**, 325–336.

Doing, H. and Doing-Huis in 't Veld, J. (1971) History of landscape and vegetation of coastal dune areas in the Province of North Holland. *Acta Botanica Neerlandica*, **20**, 183–190.

Doyle, J.A. (1978) Origin of angiosperms. *Annual Review of Ecology and Systematics*, **9**, 365–392.

Dudley, N. (1992) *Forests in Trouble: a review of the status of temperate forests worldwide*, WWF, Gland, Switzerland.

Ellenberg, H. (1978) *Vegetation Mitteleuropas mit der Alpen in ökologischer Sicht*, 2nd edn, Ulmer, Stuttgart.

Estes, R.D. (1991) *The Behavior Guide to African Mammals: including hoofed mammals, carnivores, primates*, University of California Press, Berkely.

Evans, J.G. (1972) *Land Snails in Archaeology with Special Reference to the British Isles*, Seminar, London.

Firbas, F. (1949) *Waldgeschichte Mitteleuropas*, Vol. I, Gustav Fisher Verlag, Jena.

Fritz, A. (1972) Das Spätglazial in Karnten. *Berichte der Deutschen Botanischen Gesellschaft*, **85**, 93–100.

Gerken, B. (1988) *Auen: Verborgene Lebensadren der Natur*, Rombach, Freiburg.

Gingerich, P.D. (1984) Pleistocene extinctions in the context of origination-extinction equilibria in Cenozoic mammals, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 211–222, University of Arizona Press, Tucson.

Good, R. (1964) *The Geography of the Flowering Plants*, 3rd edn, Longmans Green, London.

Godwin, H. (1975) *History of the British Flora: a factual basis for phytogeography*, 2nd edn, Cambridge University Press, Cambridge.

Graham, R.W. and Lundelius, E.L. (1984) Coevolutionary disequilibrium and Pleistocene extinctions, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 223–249, University of Arizona Press, Tucson.

Guildhay, J.E. (1984) Pleistocene extinction and environmental change: case study of the Appalachians, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 250–258, University of Arizona Press, Tucson.

Gundermann, E. and Plochmann, R. (1985) Die Waldweide as forstpolitisches Problem im Bergwald. *Forstwissenschaftliches Centralblatt*, **104**, 146–154.

Guthrie, R.D. (1990) *Frozen Fauna of the Mammoth Steppe: the story of blue babe*, University of Chicago Press, Chicago.

Handford, S.A. (transl.) (1951) *Caesar: The Conquest of Gaul*, Penguin, Harmondsworth.

Hess, H.E., Landolt, E. and Hirzel, R. (1967) *Flora der Schweiz und angrenzender Gebiete*, Vol. I, Birkhäuser, Basel.

Housley, R.A. (1991) AMS dates from the Late Glacial and early Postglacial in northwest Europe: a review, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 25–39, CBA Research Report No. 77, Council for British Archaeology, London.

Janssen, C.R. (1972) The palaeoecology of plant communities in the Dommel valley, North Brabant, The Netherlands. *Journal of Ecology*, **60**, 411–437.

Janssen, C.R. (1979) The development of palynology in relation to vegetation science, especially in the Netherlands, in *The Study of Vegetation*, (ed. M.J.A. Werger), pp. 229–246, Dr W. Junk, The Hague.

Kahlke, H.D. (1994) *Die Eiszeit*, Urania Verlag, Leipzig.

King, J.E. and Saunders, J.J. (1984) Environmental insularity and the extinction of the American mastodont, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 315–339, University of Arizona Press, Tucson.

Kinsella, T. (1969) *The Tain*, Oxford University Press, Oxford.

Klaus, W. (1972) Spätglazial-Probleme der östlichen Nordalpen Salzburgs – Inneralpines Wiener Becken. *Berichte der Deutschen Botanischen Gesellschaft*, **85**, 83–92.

Klein, R.G. (1974) Ice-Age hunters of the Ukraine. *Scientific American*, **230**, 96–105.

Klein, R.G. (1984) Mammalian extinctions and Stone Age people in Africa, in *Quaternary Extinctions: a prehistoric revolution*, (eds P.S. Martin and R.G. Klein), pp. 553–573, University of Arizona Press, Tucson.

Knapp, H.D. (1979/1980) Geobotanische Studien an Waldgrenzstandorten des Hercynischen Florengebietes. Vol. I, *Flora*, **168**, 276–319. Vol. II, *Flora*, **168**, 468–510. Vol. III, *Flora*, **169**, 177–215.

Knörzer, K.H. (1971) Urgeschichtler Unkräuter im Rheinland: ein Beitrage zur Entsehungsgeschichte der Segetalgesellschaften. *Vegetatio*, **23**, 89–11.

Knörzer, K.H. (1975) Entstehung und Entwicklung der Grülandvegetation im Rheinland. *Decheniana*, **127**, 195–214.

Kolstrup, E. (1991) Palaeoenvironmental developments during the Late Glacial of the Weichselien, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 91–96, CBA Research Report No. 77, Council for British Archaeology, London.

Kooistra, L.I. (1994) Landbouw in een onbedijkt rivierengebied, in *Romeinen, Friezen en Franken in het Hart van Nederland: Van Traiectum tot Dorestad 50 v.C.–900 n.C.*, (eds W.A. Van Es and W.A.M. Hessing), pp. 126–129, Rijksdienst voor het Oudheidkundig Bodemonderzoek, Amersfoort.

Kosina, R. (1978) The cultivated and wild plants from the XIth century granaries on the cathedral-island in Wroclaw. *Berichte der Deutschen Botanischen Gesellschaft*, **91**, 121–128.

Kral, F. (1972) Zur Vegetationsgeschichte der Hohenstufen im Dachsteingebiet. *Berichte der Deutschen Botanischen Gesellschaft*, **85**, 137–152.

Kurtén, B. (1972) *The Ice Age*, Rupert Hart-Davis, London.

Lange, E. (1976) Zur Entwicklung der natürlichen und anthropgenen Vegetation in frügeschichtliger Zeit. *Feddes Repertorium*, **87**, 5–30.

Larsson, L. (1991) The Late Palaeolithic in southern Sweden: investigations in a marginal region, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 122–127, CBA Research Report 77, Council for British Archaeology, London.

Lewis, J. (1991) A Late Glacial and early Postglacial site at Three Ways Wharf, Uxbridge, England: interim report, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 246–255, CBA Research Report 77, Council for British Archaeology, London.

Lister, A.M. (1991) Late Glacial mammoths in Britain, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 51–59, CBA Research Report 77, Council for British Archaeology, London.

Loth, P.E. and Prins, H.H.T. (1986) Spatial patterns of the landscape and vegetation of Lake Manyara National Park. *ITC Journal*, **1986-2**, 115–130.

Louwe Kooijmans, L.P. (1980) De lage landen toen: Prehistorische bewoning van onze kuststreken, in *Voltooid Verleden Tijd?: Een hedendaagse kijk op de prehistorie*, (eds M. Chamaulan and H.T. Waterbolk), pp. 21–46, Intermediair, Amsterdam.

Mai, D.H. (1965) Der Florenwechsel im jüngeren Tertiär Mitteleuropas. *Feddes Repertorium*, **70**, 157–169.

Marks, P.L. (1983) On the origin of the field plants of the northeastern United States. *American Naturalist*, **122**, 210–228.

Moe, D. and Rackham, O. (1992) Pollarding as a possible explanation of the Neolithic elmfall. *Vegetation History and Archaeobotany*, **1**, 63–68.

Mol, D. and van Essen, H. (1992) *De Mammoet: Sporen uit de IJstijd*, BZZTôH, The Hague.

Moore, P.D. (1987) Chalk grasslands in the ice age. *Nature*, **329**, 388–389.

Oldfield, F. (1967) The paleoecology of an early neolithic waterlogged site in northwestern England. *Review of Palaeobotany and Palynology*, **4**, 67–70.

Opravil, E. (1978) Synanthrope Pflanzengesellschaften aus der Burgwallzeit (8.–10. Jh.) in der Tschechoslowakei. *Berichte der Deutschen Botanischen Gesellschaft*, **91**, 97–106.

Pastor, J., Dewey, B., Naiman, R.J. *et al.* (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, 74, 467–480.

Peglar, S.M. (1993) The mid-Holocene *Ulmus* decline at Diss Mere, Norfolk, UK: a year-by-year pollen stratigraphy from annual laminations. *The Holocene*, 3, 1–13.

Peglar, S.M. and Birks, H.J.B. (1993) The mid-Holocene *Ulmus* fall at Diss Mere, South-East England – disease and human impact? *Vegetation History and Archaeobotany*, 2, 61–68.

Pennington, W. (1969) *The History of the British Vegetation*, English University Press, London.

Perry, I. and Moore, P.D. (1987) Dutch elm disease as an analogue of Neolithic elm decline. *Nature (Lond.)*, 326, 72–73.

Perschke, P. (1972) Die Vegetationsentwicklung im Waldviertel Niederösterreichs. *Berichte der Deutschen Botanischen Gesellschaft*, 85, 129–136.

Pignatti, E. and Pignatti, S. (1975) Syntaxonomy of the *Sesleria varia* grasslands of the calcareous Alps. *Vegetatio*, 30, 5–14.

Pounds, N.J.G. (1974) *An Economic History of Medieval Europe*, Longman, London.

Prins, H.H.T. (1996) *Ecology and Behaviour of the African Buffalo: social inequality and decision making*, Chapman & Hall, London.

Prins, H.H.T. and Van der Jeugd, H.P. (1993) Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, 81, 305–314.

Prins, H.H.T. and Reitsma, J.R. (1989) Mammalian biomass in an African equatorial rain forest. *Journal of Animal Ecology*, 58, 851–861.

Rackham, O. (1980) *Ancient Woodland: its history, vegetation and uses in England*, Edward Arnold, London.

Ralska-Jasiewiczowa, M. (1972) Remarks on the Late-glacial and Holocene history of vegetation in the eastern part of the Polish Carpathians. *Berichte der Deutschen Botanischen Gesellschaft*, 85, 101–112.

Reid, C. and Chandler, E.M. (1915) The Pliocene floras of the Dutch–Prussian border. *Mededelingen Rijksopsporingsdienst van Delfstoffen*, 6.

Reid, C. and Chandler, E.M. (1933) *The London Clay Flora*, British Museum, London.

Reuter, M. (1920) Die Waldweide. *Allgemeine Forst- und Jagdzeitung*, 96, 40–49.

Roebroeks, W. (1990) *Oermensen in Nederland: De archaeologie van de Oude Steentijd*, Meulenhoff, Amsterdam.

Schmeidl, H. (1972) Zur spät- und postglazialen Vegetationsgeschichte am Nordrand der bayerischen Voralpen. *Berichte der Deutschen Botanischen Gesellschaft*, 85, 79–82.

Schmidt, G. (1969) *Vegetationgeographie auf ökologisch-soziologischer Grundlage*, Teubner Verlag, Leipzig.

Sercelj, A. (1972) Verschiebung und Inversion der postglazialen Waldphasen am südostlichen Rand der Alpen. *Berichte der Deutschen Botanischen Gesellschaft*, 85, 123–128.

Shepherd, W.G. (transl.) (1983) *Horace: The complete Odes and Epodes with the Centennial Hymne*, Penguin, Harmondsworth.

Shimwell, D.W. (1971) Festuco-Brometea Br. Bl. and R. TX, 1943 in the British Isles: the phytogeography and phytosociology of limestone grasslands. *Vegetatio*, 23, 1–28.

Simmons, I.G. (1981) Culture and environment, in *The Environment in British Prehistory*, (eds I.G. Simmons and M.J. Tooley), pp. 282–291, Duckworth, London.

Simmons, I.G., Dimbley, G.W. and Grigson, C. (1981) The Mesolithic, in *The Environment in British Prehistory*, (eds I.G. Simmons and M.J. Tooley), pp. 82–124, Duckworth, London.

Slicher van Bath, B.H. (1976) *Agrarische Geschiedenis van West-Europa, 500–1850*, Spectrum, Utrecht.

Smith, A.G., Grigson, C., Hillman, G. and Tooley, M.J. (1981) The Neolithic, in *The Environment in British Prehistory*, (eds I.G. Simmons and M.J. Tooley), pp. 125–209, Duckworth, London.

Smith, R.E.F. (1959) *The Origin of Farming in Russia*, Mouton, Paris.

Späth, V. (1988) Zur Hochwassertoleranz von Auewaldbäumen. *Natur und Landschaft*, 63, 312–315.

Stott, P.A. (1971) A Mesobrometum referable to the subassociation *Mesobrometum-seslerio–Polygaletosum* Tx. described for the Somme-valley. *Vegetatio*, 23, 61–70.

Street, M. (1991) Bedburg-Königshoven: a Pre-Boreal Mesolithic site in the Lower Rhineland, Germany, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 256–270, CBA Research Report 77, Council for British Archaeology, London.

Stuart, A.J. (1991) Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. *Biological Review*, 66, 453–562.

Stuart, A.J. and Gibbard, P.L. (1986) Pleistocene occurrence of hippopotamus in Britain. With appendix: Pollen analysis from hippopotamus bones from the Cromer Forest Bed series. *Quartärpaläontologie*, 6, 209–218.

Ten Cate, C.L. (1972) *Wann God Mast gibt: Bilder aus der Geschichte der Schweinenzucht im Walde*, Centre for Agricultural Publishing and Documentation, Wageningen.

Ter Kuile, E.H. (1976) *De Tijd van Rome's laatste Keizers: Veertien brieven van Appollinaris Sidonius uit de jaren 455–475*, De Walburg Pers, Zutphen.

Tinsley, H.M. and Grigson, C. (1981) The Bronze Age, in *The Environment in British Prehistory*, (eds I.G. Simmons and M.J. Tooley), pp. 210–249, Duckworth, London.

Tipping, R. (1991) Climatic change in Scotland during the Devensian Late Glacial: the palynological record, in *The Late Glacial in North-west Europe: human adaptation and environmental change at the end of the Pleistocene*, (eds N. Barton, A.J. Roberts and D.A. Roe), pp. 7–21, CBA Research Report 77, Council for British Archaeology, London.

Turner, C. (1975) Der Einfluss grosser Mammalier auf die interglaziale Vegetation. *Quartärpaläontologie*, 1, 13–19.

Turner, J. (1981) The Iron Age, in *The Environment in British Prehistory*, (eds I.G. Simmons and M.J. Tooley), pp. 250–281, Duckworth, London.

Tüxen, R. (1974) Synchronologie einzelner Vegetationseinheiten in Europa, in *Vegetation Dynamics*, (ed. R. Knapp), Handbooks of Vegetation Science, Vol. VIII, pp. 267–292, Dr W. Junk, The Hague.

Van den Hoek Ostende (1990) *Tegelen, ons Land 2 Miljoen Jaar geleden*, Teylers Museum, Haarlem.

Van Es, W.A. (1972) *De Romeinen in Nederland*, 2nd edn, Fibula-van Dishoeck, Bussum.

Van Es, W.A. (1994) De Romeinse Vrede, in *Romeinen, Friezen en Franken in het Hart van Nederland: Van Traiectum tot Dorestad 50 v.C.–900 n.C.*, (eds W.A. Van Es and W.A.M. Hessing), pp. 48–63, Rijksdienst voor het Oudheidkundig Bodemonderzoek, Amersfoort.

Van Wieren, S.E. (1995) The potential role of large herbivores in nature conservation and extensive land use in Europe. *Biological Journal of the Linnean Society*, 56 Suppl. A, 11–23.

Van Zeist, W. (1959) Studies on the Post-Boreal vegetational history of south-eastern Drenthe (Netherlands). *Acta Botanica Neerlandica*, 8, 156–185.

Van Zeist, W. (1974) Palaeobotanical studies of settlement sites in the coastal area of The Netherlands. *Palaeohistoria*, **14**, 223–371.

Van Zeist, W. (1980) Prehistorische cultuurplanten, onstaan, verspreiding, verbouw, in *Voltooid Verleden Tijd?: Een hedendaagse kijk op de prehistorie*, (eds M. Chamaulan and H.T. Waterbolk), pp. 147–165, Intermediair, Amsterdam.

Van Zeist, W., Van Hoorn, T.C., Bottema, S. and Woldring, H. (1976) An agricultural experiment in the unprotected salt marsh. *Palaeohistoria*, **18**, 11–153.

Vera, F.W.M. (1997) Metaforen voor de Wildernis: Eik, hazelaar, rund en paard. Doctoral thesis, Wageningen Agricultural University, Wageningen.

Vicherek, J. (1973) *Die Pflanzengesellschaften der Halophyten- und Subhalophytenvegetation der Tschechoslowakei*, Vegetace CSSR, A5, Academia, Praha.

Von Denffer, D., Schumacher, W., Mägdefrau, K. and Ehrendorffer, F. (1976) *Strasburger's Textbook of Botany: New English edition*, Longman, London.

WallisDeVries, M.F. (1994) Foraging in a landscape mosaic: diet selection and performance of free-ranging cattle in heathland and riverine grassland. Doctoral thesis, Wageningen Agricultural University, Wageningen, The Netherlands.

Walter, H. (1927) *Einführung in die allgemeine Pflanzengeographie Deutschlands*, Gustav Fisher Verlag, Jena.

Walter, H. (1968) *Die Vegetation der Erde in öko-physiologische Betrachtung, Vol. II: Die gemäsigten und arktischen Zonen*, Gustav Fisher Verlag, Jena.

Waterbolk, H.T. (1954) *De Praehistorische Mens en zijn Milieu: Een palynologisch onderzoek naar de menselijke invloed op de plantengroei van de diluviale gronden in Nederland*, Van Gorcum, Assen.

Waterbolk, H.T. (1985) Archaeologie, in *Geschiedenis van Drenthe*, (eds J. Heringa, D.P. Blok, M.G. Buist and H.T. Waterbolk), pp. 15–90, Tjeenk Willink, Groningen.

Waterbolk, T.H. and Boersma, J.W. (1976) Bewoning in vøør- en vroeghistorische tijd, in *Historie van Groningen Stad en Land*, (eds W.J. Formsma, M.G. Buist, W.R.H. Koops *et al.*), pp. 13–74, Tjeenk Willink and Bouma's Boekhuis, Groningen.

Webb, S.D. (1977) A history of savanna vertebrates in the new world. Part I. North America. *Annual Review of Ecology and Systematics*, 8, 355–380.

Webb, S.D. (1978) A history of savanna vertebrates in the new world. Part II. South America. *Annual Review of Ecology and Systematics*, 9, 393–426.

Wegmüller, S. (1972) Neuere palynologische Ergebnisse aus den Westalpen. *Berichte der Deutschen Botanischen Gesellschaft*, **85**, 75–78.

Welten, M. (1972) Das Spätglazial im nördlichen Voralpengebiet der Schweitz: Veelauf, floristisches, chronologisches. *Berichte der Deutschen Botanischen Gesellschaft*, 85, 69–74.

Westhoff, V. and Den Held, A.J. (1969) *Plantengemeenschappen in Nederland*, W.J. Thieme, Zutphen.

Westhoff, V. and Van Leeuwen, C.G. (1966) Ökologische und systematische Beziehungen zwischen natürlichen und anthropogene Vegetation, in *Anthropogene Vegetation*, (ed. R. Tüxen), pp. 156–172, Dr W. Junk, The Hague.

Willerding, U. (1978) Paläo-ethnobotanische Befunde an mittelalterlichen Pflanzenresten aus Süd-Niedersachsen und dem östlichen Westfalen. *Berichte der Deutschen Botanischen Gesellschaft*, **91**, 129–160.

Zagwijn, W.H. (1960) Aspects of the Pliocene and early Pleistocene vegetation in The Netherlands, 2 vols. Doctoral thesis, University of Leyden, Leijden.

Zagwijn, W.H. (1971) Vegetational history of the coastal dunes in the western Netherlands. *Acta Botanica Neerlandica*, **20**, 174–182.

Zlotin, R.I. and Khodashova, K.S. (1980) *The Role of Animals in Biological Cycling of Forest-Steppe Ecosystems*, (English edn, ed. N.R. French), Dowden, Hutchinson and Ross, Stroudsburg.