Ecology, conservation and management of Aspen

A Literature Review

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Cover photo: A large open grown aspen with a girth of 84 cm situated at an altitude of 453 metres on the north slopes of Morrone Birkwood, Braemar. Browsing pressure has prevented regeneration except for the adjacent suckering stems within the small enclosure

Contents

Introduction

'Studies on aspen in different parts of its range have shown it to have close associations with and play an important part in the ecology of a diverse range of flora and fauna'

As a member of the Salicaceae family, aspen shares a number of characteristics with the many species of indigenous willows. Both genera include trees or shrubs which are dioecious and produce catkins before the foliage develops. The family has an almost worldwide distribution (except Australasia) but the genus *Populus* is largely concentrated in the temperate and boreal regions of the northern hemisphere (***Figure 1***). The European aspen *Populus tremula* and the closely related Quaking aspen *P. tremuloides* of North America are two of the most common and most widely distributed broadleaved tree species in the northern circum-boreal region. *P. tremula* is found throughout Europe, Scandinavia and across north Asia to China and Japan (Worrell, 1995a). In Europe it ranges from the Mediterranean northwards to the most extreme scrub vegetation beyond the Arctic Circle (Meikle, 1984). It is rare in Iceland where there are six naturally occurring clones of *P. tremula* which were first discovered in the remote north and east between 1911 and 1993 (Sigurdsson *et al*., 1995). However, there are no records from south Greenland although poplar pollen originating from eastern Canada is regularly transported there via atmospheric air movements (Rousseau *et al*., 2005).

Aspen (*Populus tremula*) is the only poplar species that is native to Scotland. Here it has been recorded in every vice-county and occurs from sea level, on many of the outer islands, including Orkney and Shetland, to an altitude of 700 metres in the Cairngorms (MacKenzie, 2000; Preston *et al*., 2002). It has been recorded on nearly all islands of the Inner and Outer Hebrides including many that are otherwise devoid of woodland. A survey of aspen in Scotland by Worrell (1993) identified 647 sites and subsequent records collected by the Forest Commission have increased this number to 736 (Harrison, 2009). However, detailed local surveys in areas where aspen is concentrated, for example in Badenoch and Strathspey, have revealed that the number of sites may be several thousand (Parrott, 2009).

Despite its widespread occurrence in Scotland aspen exists only as small stands or solitary trees, rarely sets seed and propagates mainly by the vegetative production of suckers. It has been estimated that there are only 21 aspen dominated woods that exceed 1.5 ha in extent and that the total resource in Scotland is about 500 ha (MacGowan, 1997; Mason *et al*., 2002). The lack of colonising opportunities, aspen's palatability as a favoured browse species and its importance for biodiversity and

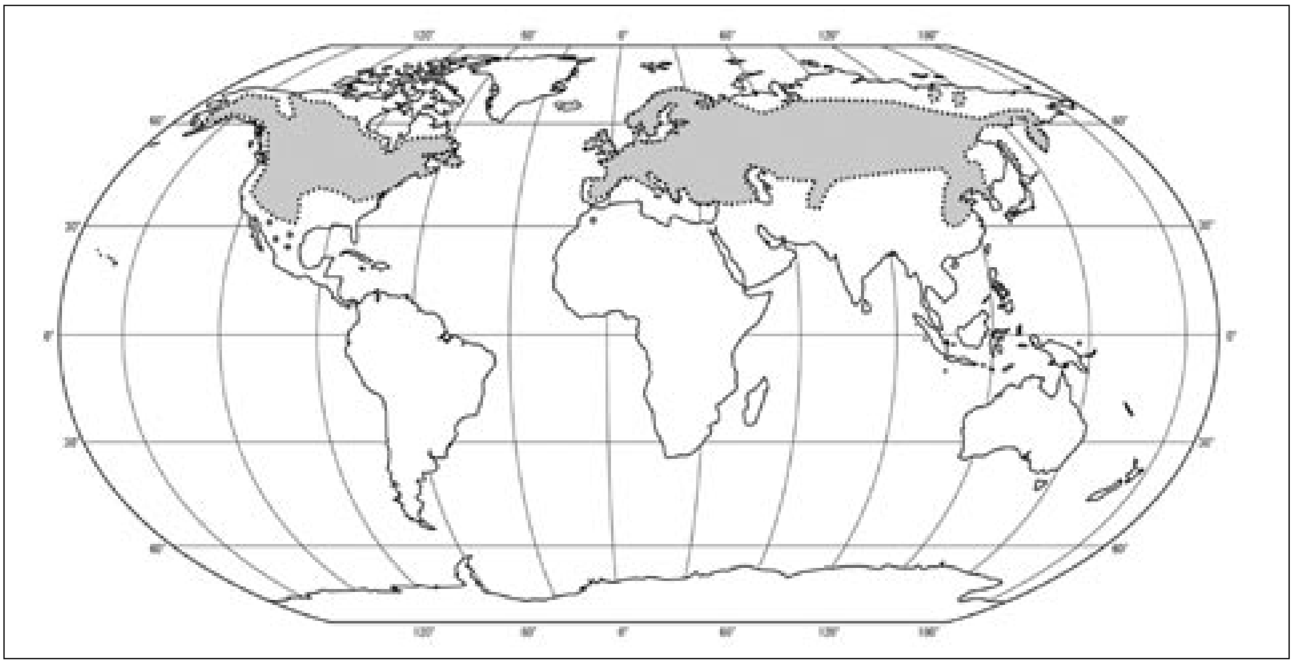

Figure 1 World distribution of naturally occurring aspen (*Populus tremula* & *P. tremuloides*).

landscape appeal has led to concerns about its genetic vulnerability and its future conservation.

Current conservation management of the tree in Scotland is afforded through the Biodiversity Action Plan (BAP) programme and its inclusion in the Upland Birchwood Habitat Action Plan (HAP) but there is no species action plan and aspens growing in communities other than birchwoods or other native woodland HAPs are outwith the scope of the BAP programme. However, there are five Species Action Plans for species dependent on aspen.

Studies on aspen in different parts of its range have shown it to have close associations with and play an important part in the ecology of a diverse range of flora and fauna. In Europe, for example, aspen has more host-specific species than any other boreal tree and is one of the most significant contributors to total epiphyte diversity in the boreal forest (Hedenas & Ericson, 2004; Kuusinen, 1994). In North America aspen is considered a keystone species and critical to the maintenance of biodiversity in western and boreal regions (Hogg *et al.*, 2005; Jones *et al.*, 2005) and there is a wealth of material published on the ecology of *P. tremuloides* (*e.g.* Shepperd *et al.*, 2006). Aspen is also an important timber tree in North America and in some Scandinavian and Baltic countries (Adams, 1990; Einspahr & Benson, 1968; Johansson, 2002) while members of the genus *Populus*, including aspen, are used as the main model for genetic, genome and physiological research on trees (Luqez *et al.*, 2008).

There have been very few studies carried out on aspects of aspen ecology or management in Britain. Worrell produced three key papers on aspen ecology (1995a & b and Worrell *et al.*, 1999), MacGowan (1997) investigated invertebrate associations, Easton (1997) studied the genetics of aspen, Cosgrove *et al.* published a review article in British Wildlife (2005), Watson and Trees for Life have reviewed aspen's place in Scotland's native woodland resource (www.treesforlife.org.uk) and there have been three papers on silviculture (Gray, 1949; Hollingsworth & Mason, 1991; Powell, 1957, in Worrell, 1995a). An important conference in Kingussie in 2001 brought together several key papers on the biodiversity of aspen (Cosgrove & Amphlett, 2002) and there is now a Highland Aspen Group that is carrying out work to extend the resource and improve its biodiversity. A second aspen conference took place in Boat of Garten in 2008 and added further information to the knowledge base (Parrott & MacKenzie, 2009). In addition there have been a small number of post-graduate studies on aspen and some specialist research papers (*e.g.* Ellis & Coppins, 2007a; Emmett & Emmett, 2001). The importance of aspen to the biodiversity of many different groups of flora and fauna in Scotland is just starting to be realized.

The purpose of this literature review is to collate current information, review recent publications and provide an up to date examination of the current knowledge of aspen. As there is very little information on the ecology and management of aspen in Britain the review has drawn heavily on published material from Europe and North America. Although the habitat associations of *P. tremuloides* in North America are different to those in Scotland the two species are morphologically and genetically very similar. Information from North American and Scandinavian studies will thus be a useful guide for future conservation work, which will help to sustain a long-term future for aspen in Scotland. ■

Taxonomy, distribution and habitat

'Together the Eurasian aspen and the Quaking aspen have the widest natural range of any tree species in the world'

Poplars only form a small part of the Salicaceae family which includes the several hundred willow species but only 40 or so poplars. The greatest variety of poplars occurs in North America and in eastern Asia and many of the planted specimens found in Britain originate from these regions. There are only a small number of poplars native or naturalised in Britain although cultivated hybrids are common in parks and gardens and improved clonal varieties have been developed for commercial forestry. Aspen is a native tree throughout Britain and Ireland while the only other native poplar is the Black poplar, *Populus nigra*, which is indigenous to riparian woodlands in the south of England. All other poplar species in the British Isles have been introduced.

There are only five poplars known by the english vernacular name of aspen. The Eurasian aspen, *Populus tremula*; the North American species *Populus tremuloides* which is commonly referred to as trembling or quaking aspen (sometimes aspen poplar), after the fluttering effect of the leaves in a breeze. In Europe *P. tremula* may also be referred to by this descriptor, for example in France where the tree is known as "le tremble". The three remaining aspens are Bigtooth Aspen of North America (*P. grandidentata*), Chinese Aspen (*P. adenopoda*) and Japanese Aspen (*P. sieboldii*). Quaking aspen, *P. tremuloides* has the widest distribution of any native tree in North America and worldwide it is only *P. tremula* and Scots pine, *Pinus sylvestris* that have a greater natural range. In the USA there are 8.2 million ha of aspen and aspen-birch forests and these are the second most common forest types in the country (Cleland *et al.*, 2001). Together, the Eurasian aspen and the Quaking aspen have the widest natural range of any tree species in the world.

The similarities between the Eurasian aspen and the North American Quaking aspen were first noted before 1803 when *P. tremuloides* was described and named by Michaux. In the 18th century *P. tremuloides* was

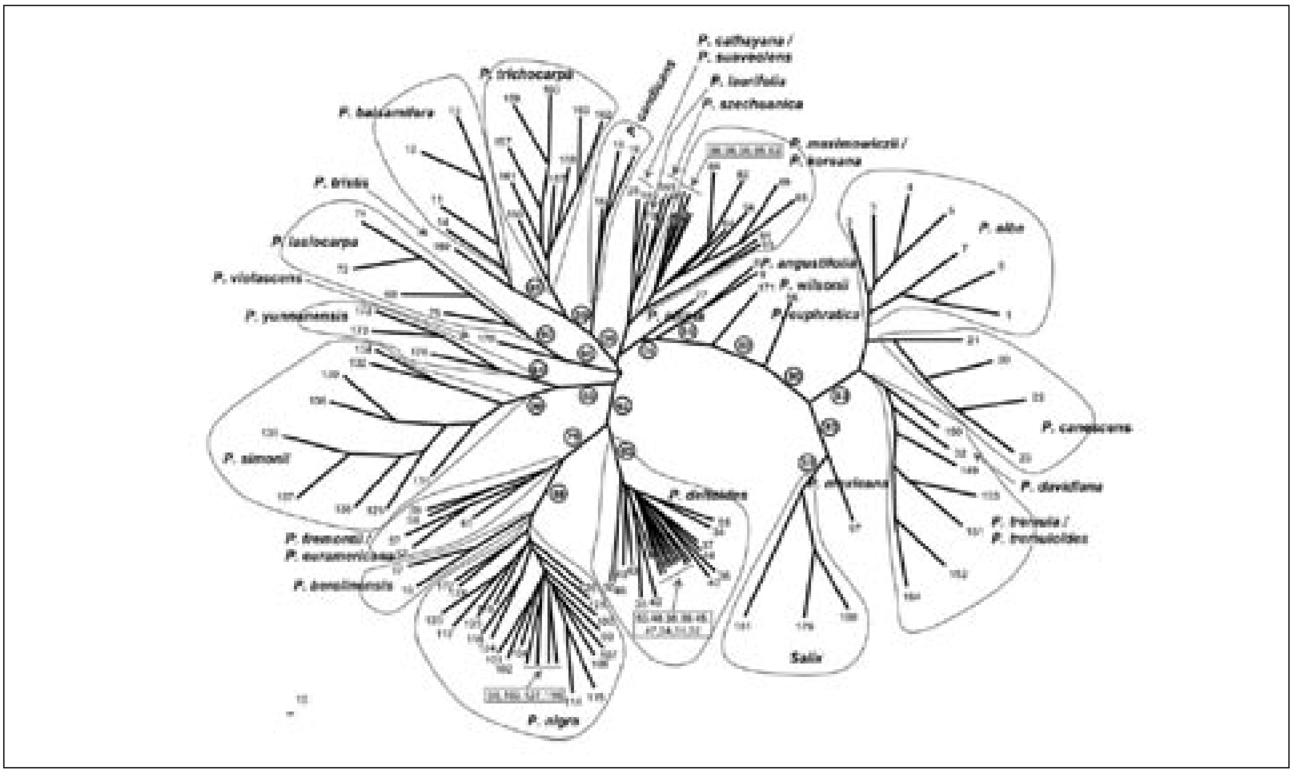

Figure 2 Dendrogram showing the phylogeny of *Populus*, constructed from genetic marker similarities. Note the close relationship of *P. tremula/tremuloides* (reprinted from Cervera *et al*., 2005 with kind permission of Springer Science & Business Media).

considered to be an American equivalent of *P. tremula* (Kimball *et al.*, 1985). Although there are no known comparative studies on the ecology of the two species, *P. tremuloides* is more closely related to *P. tremula* than to the other American aspen *P. grandidentata* (De Chantal *et al.*, 2005; Perala, 1990). Certainly, given the extent of variation throughout their respective ranges there are no distinct morphological or physiological characters that serve to differentiate the European and North American aspen species while DNA studies showed very high genetic similarities (***Figure 2***) (Cervera *et al.*, 2005). The two species also readily hybridise and produce viable seed that will grow well depending on provenance and latitude (Latva-Karjanmaa, 2006). They have been thought of as a single circum-boreal superspecies that probably originated from a common ancestor, which became separated geographically and the genetic marker data provide some support to the merging of *P. tremula*, *P. tremuloides* and *P. davidiana* (Korean poplar) into one species (***Figure 2***) (Cervera *et al.*, 2005). However, the highly variable nature of each of the species would probably make such a merger unworkable (Perala *et al.* 1999, Kimball *et al.*, 1985).

European aspen possesses a wide altitudinal range being found at sea level in the northern parts of its range and up to 1900 m in high mountain areas such as the Pyrenees (Powell, 1957 in Worrell, 1995a). *P. tremuloides* exhibits a similar range from sea level to 3700 m, from Alaska's Yukon River valley to Mexico, a distance of some 3000 kms, and from the Atlantic to the Pacific coasts. Both species tend to prefer the boreal climates, occurring at all elevations in the northern parts of their range but largely restricted to the cooler mountain areas in the southern latitudes *e.g.* North African Atlas mountains and Mexico's northern Sierra Madre peaks. *P. tremuloides* is able to withstand a range of climatic extremes from temperatures as low as – 57ºC below to 41ºC above, temperatures recorded for example in Montana (Madson, 1996; Perala, 1990). Although aspen's range extends into the permafrost zone of Alaska it can only survive in the warmest sites free from permafrost. Despite this wide geographical and altitudinal range aspen exhibits very little morphological variation. Worrell (1995a) reports on three geographical varieties, two from China and one from Europe, while Meikle (1984) describes some horticultural forms of *P. tremula*. However, despite the limited number of varieties or races there is a high degree of variation between different clones of the same species. There are particular differences in leaf flushing dates, autumn colouration and leaf fall as well as tree form and branching habit (Worrell, 1995a) (See ***Table 1*** on page 10). *P. tremuloides* also exists across its range as a single though highly variable species (Ellis, 1995).

Aspen was one of the first trees to colonise Britain after the end of the last Ice Age. It arrived some 9000 years ago possibly with birch *Betula* spp. and hazel *Corylus avellana* as pollen has been found in sediment cores between 9000 BP and 4000 BP (Huntley & Birks, 1983). Birks (1970) found small but consistent amounts at Abernethy in Strathspey and Davies (2003) recorded sufficient quantities of aspen pollen to include it in a diagram from west Glen Affric (***Figure 3***). Pollen diagrams from Fennoscandia and the Baltic states occasionally include *Populus* (*e.g.* ***Figure 4***) (Molinari *et al.*, 2005). Since about 4000 years BP aspen pollen appears to have disappeared from the pollen record as Holocene pollen diagrams from Scotland rarely show *Populus* after that

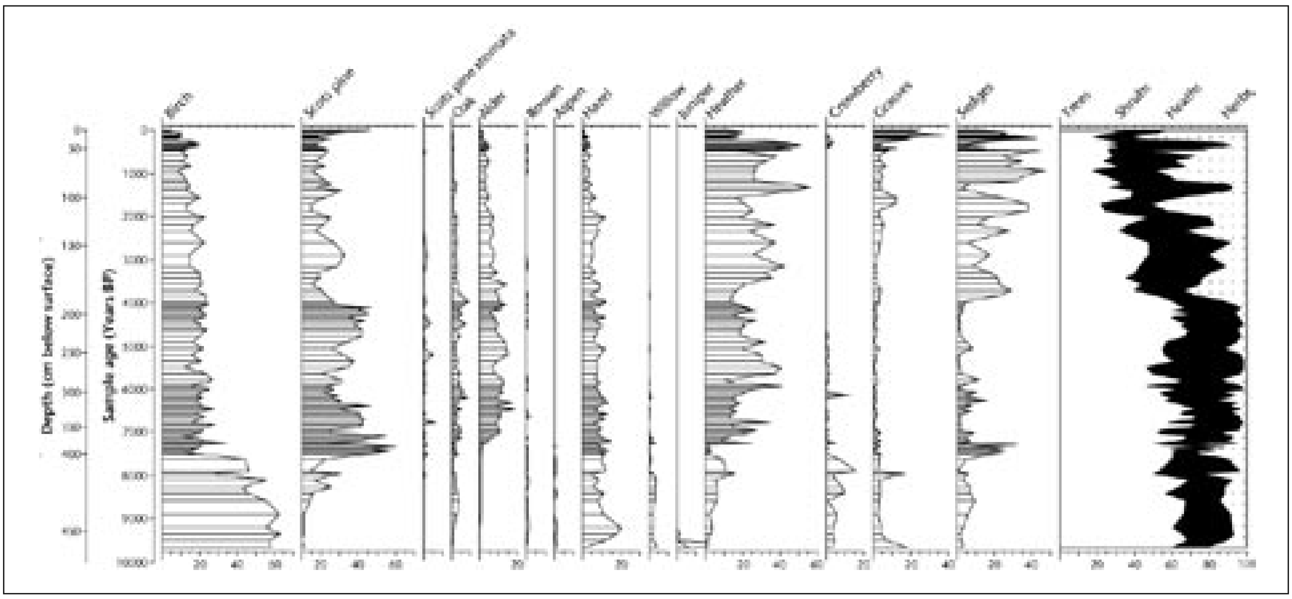

Figure 3 Selected percentage pollen data form peat-covered open ground in west Glen Affric. Note the small aspen peak from about 10000 years BP to about 7500 years BP. (From Mason *et al.*, 2004; after Davies, 2003).

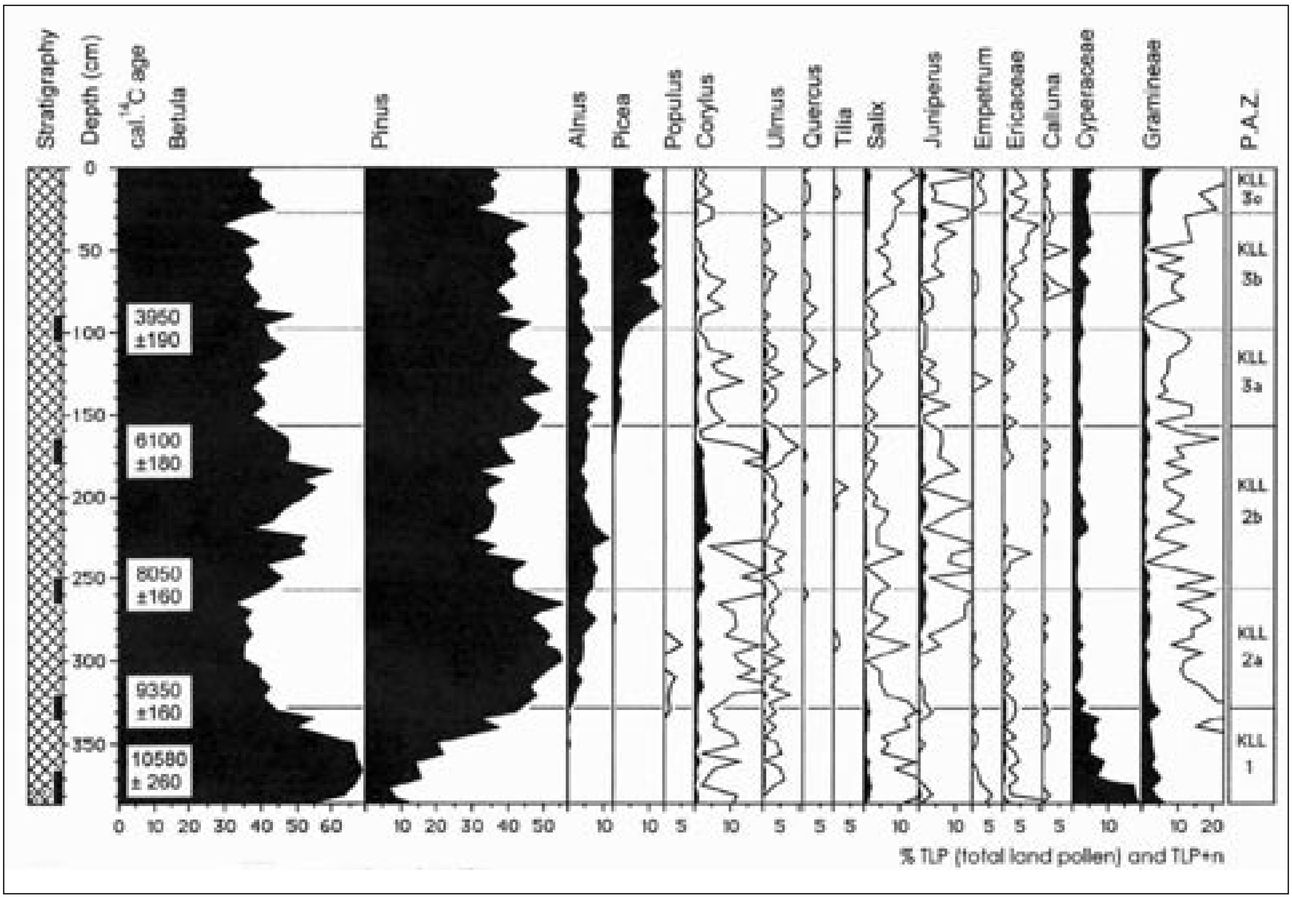

Figure 4 Pollen diagram (vascular plant taxa not shown) of Lake Kolmiloukkonen, Riisitunturi, NE Finland. The white curves are exaggerated tenfold. Note the Populus peak between 9000 and 8000 years BP. (Reprinted from Huttunen, 2007, with permission from Boreal Environmental Research).

period. It is known that aspen pollen does not survive well in the soil strata and is susceptible to microbial attack and oxidation and is not always easily identifiable, sometimes being confused with juniper pollen (R. Tipping, Univ. Stirling, pers. comm.; K. Bennett, Queens Univ., pers. comm.; Birks, 1970; Worrell, 1995a). If the species is uncommon, such as in Iceland, then aspen pollen may never be found in the sediments (Hallsdottir, 1995). It is also possible that as climate became more oceanic about 4000 years ago and conditions became cooler and wetter, the tree did not flower as frequently (Easton, 1997). Although the light demanding aspen may have been displaced by the advance of Scots pine *Pinus sylvestris* around 6500 years BP (Davies, 2003), Birks (1970) considered that aspen was likely to have remained an important component of open woodlands and woodland margins just as it is in many areas today.

Most European pollen diagrams show a *Populus* peak about 8000-10000 years ago (*e.g.* ***Figure 4***) (Wohlfarth *et al.*, 2004), which tails off to very low levels or disappears altogether, but there are occurrences of *Populus* pollen peaks recorded between about 2000 years BP and the present in northern Fennoscandia and in the Russian Karelia, possibly linked to declining *Picea* frequencies as a result of deforestation (Seppa & Birks, 2001; Vuorela *et al.*, 2001). In North America aspen was also an early coloniser at the beginning of the Holocene and was one of the dominant successional trees 8000 years ago (Fall, 1997). Pollen diagrams from the Great Lakes area and the prairie region of Canada show *Populus* peaks in the early post glacial period but the pollen persists at low levels throughout the Holocene (McAndrews, 1988). Changes in the abundance of *Populus* in North America since the late glacial may have been due directly to climatic change but may also have been caused by the effects of climate change on major competitors (Peros *et al.*, 2008). There is also the occasional small peak in the late 19th century when major disturbance events such as fire, the logging of conifers and abandoned farmland was followed by early successional colonisation by aspen or birch (***Figure 5***) (Wright *et al.*, 2004).

The current distribution of aspen in Scotland reflects the current extent and distribution of native semi-natural woodland and perhaps its potential extent. It is frequently found in coastal sites, gorges, cliffs, rock ledges and crevices near to the maximum potential treeline where no existing woodland remains. Whether it is a remnant of former woodland altered by centuries of hu-

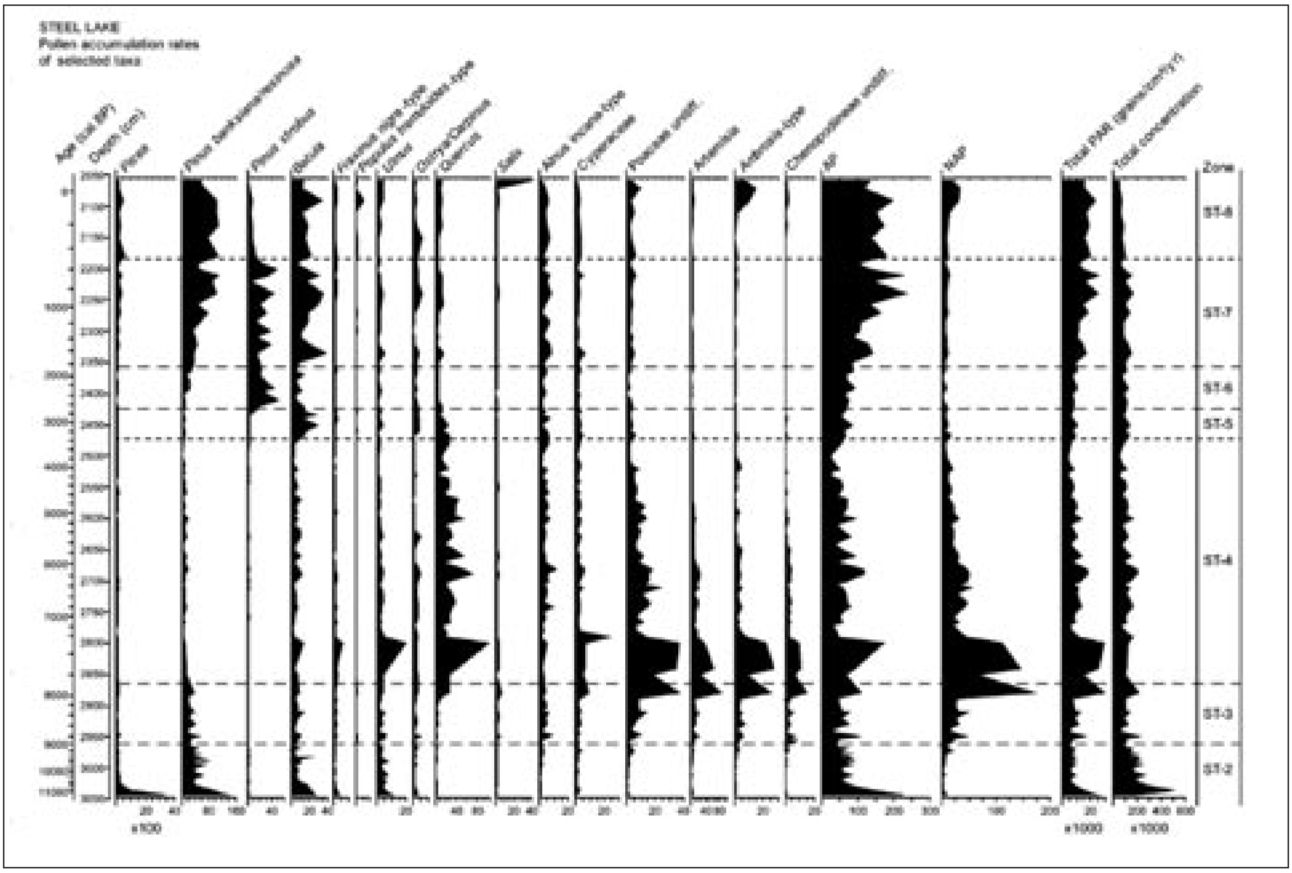

Figure 5 Pollen accumulation rates for selected taxa at Steel Lake, Minnesota, USA. The anomalous maxima between 2804 and 2873cm result from a pair of turbidites (sediments deposited by currents), which increase the rate of sediment deposition and thus the pollen accumulation rate. Note the *Populus tremuloides* peak in the 19th century. (Reprinted from Wright *et al*., 2004 with permission from Elsevier).

man intervention or whether it is a relict species from the early Ice Age colonisers is not clear. However, aspen's growth and vigour in the more fertile sites suggest that it is not a relict from the past but a key component of the woodland ecosystem and its patchy but widespread distribution may be a result of historic land use changes and past and present grazing pressures. ■

Biology

'Aspen ... has retained a high level of genetic variation despite its survival being largely dependent on vegetative reproduction'

Aspen is a deciduous tree that can grow to a height of 25 m or more. In exposed coastal cliffs and at its upper altitudinal limit where the soils are thin it has a shrubby or stunted form. However, at moderately high altitudes in Scotland aspen can achieve large sizes, for example Worrell (1995a) reports on aspen with girth diameters (dbh) of up to 40 cms at 470 m altitude and MacKenzie & Clifford (2008) recorded a mature open grown aspen of 84 cms dbh at 453 m altitude in Morrone Birkwood, Braemar (cover photo). In Strathspey Mason *et al.* (2002) recorded an aspen of 25 m height at a girth of 39 cm. In North America the Quaking aspen can grow to a height of 36 m and achieve a girth of 137 cm (Perala, 1990).

Maximum ages of 226 years and 321 years have been recorded in North America (Binkley, 2008; Perala, 1990). Clones however may be thousands of years old if new suckers continuously arise from the original rootstock. Such potential immortality only relates to the genome since remnant physical tissue from the original seedling would be long gone (Mitton & Grant, 1996). The age of the clone can only be inferred by indirect means although some researchers have suggested that more accurate clonal ages might be determined if DNA sequencing is used to date somatic variations (Rogers, 2007). The European aspen is thought to have an average lifespan of 60 – 100 years (Worrell, 1995a) although MacGowan (1997) has suggested that some specimens in the Scottish Highlands could be 150 years. A study of 226 aspens at 30 sites in the Highlands by Matthews in 1993 (reported in Mason *et al.*, 2002) found that the oldest specimen was 120 years and the remainder less than 100 years old.

Aspen grows best on well drained, loamy soils rich in organic matter, calcium, magnesium, potassium and nitrogen but it can survive in a variety of soils ranging from shallow sands to heavy clays. It does require annual precipitation to exceed evapotranspiration while water tables shallower than 0.6 m or deeper than 2.5 m will limit growth (Perala, 1990). Despite these requirements aspen will tolerate xeric sites such as scree habitats with thin, rocky soils (Larsen & Ripple, 2002). In riparian areas the water-holding capacity of the soils under aspen stands help to maintain the quality of the freshwater ecosystem by reducing overland flow which can lead to erosion, while nutrient-rich soils, high in organic matter, are created from the rapidly decaying annual leaf fall (Shepperd *et al.*, 2006).

The bark of some aspen trees contains chlorophyll and is capable of photosynthesis. The pigments are more abundant in the bark than in the leaves at the beginning of the growing season and this may give an early spring boost to aspen growing competitively among evergreen conifers or other shade tolerant species (Pearson & Lawrence, 1958). In summer the leaf chlorophyll takes over the photosynthetic activity while the bark loses its greenish tint and becomes white. The ability of aspen to photosynthesise at low levels through its bark during winter may help trees recover from injuries and pathogenic infestations (Shepperd *et al.*, 2006).

In Scotland aspen is most frequently associated with birchwoods and riparian woodlands. Under the National Vegetation Classification (NVC) system, these fall into the W11 and W17 (birch) communities, and in W9/W8 woodland which often occupies riparian sites. It can also be found within native pinewoods.

In a UK-wide context, Rodwell (1991) records aspen in several lowland woodland communities (W5, W6, W8, W10 and W16) but not in acid or upland birch, oak or pinewoods (W11, W17 and W18). However this is probably a reflection of the small number of samples taken from upland woodlands during the compilation of the NVC system.

Extensive stands of aspen are rare in Scotland. Few stands exceed five hectares in size (MacGowan, 1997; Parrott, 2009). The vegetative spread of aspen is often severely restricted by browsing and grazing levels although protected sites in Deeside and Strathspey may develop further in the future. More usually aspen occurs in small stands of under 0.25 ha, sometimes several clones scattered amongst larger birchwoods (Easton, 1997). Many such stands may be of a single clone, perhaps a parent tree surrounded by progeny of variable aged suckers and young trees. At other aspen sites, particularly where grazing is more intense it may be a single tree, but there is often evidence of small seedling sized suckers within the field layer nearby. In mountain areas aspen tends to survive almost exclusively as solitary individuals or in small groups on rock ledges and gorge sites inaccessible to browsing animals. Most

Season	Character	Order of usefulness (lower numbers best)
Spring	Sex of clone	1
	Date of flowering	2
	Date (and rate) of leaf flushing	3
Summer	Leaf shape, colour & size	1
	Shape of leaf blade base	2
	Leaf margin; number, size & shape of teeth	3
	Shape of leaf tip	4
	Leaf rust infection	5
Autumn	Leaf colour	1
	Date (and rate) of leaf fall	2
Any season	Bark texture	1
	Bark colour	2
	Stem form	3
	Branching habit (angle, length and internode length)	4
	Susceptibility to frost cracks	6
	Susceptibility to insects and disease injuries	7
	Self-pruning	8
	Galls	9

Table 1 The main characteristics for clone differentiation in aspen (*P. tremuloides*) (adapted from Miller, 1996; Shepperd *et al*., 2006).

stands of aspen in Europe also tend to be less than two ha and often consist of a single clone (Johansson, 2002). In North America however aspen clones can be much larger. A well-documented aspen clone in the Fishlake National Forest in Utah, known as Pando ("I spread" in Latin) extends over 40 ha (DeByle, 1990; Mitton & Grant, 1996). while some clones in the central Rockies could be much larger in area (Bartos, 2007). In the eastern Lake States, however, average clone size is 0.02-0.03 ha (Miller, 1996). It has been suggested that the difference between the east and west is due to clone size being linked to clone age since the largest clones occur in unglaciated areas of the western United States (Miller, 1996).

There is considerable variation between clones and the separate clones can be identified for example by different times of leaf flushing or leaf fall (Table 1). Such differences in clone phenology are thought to be constant as experiments by Harrison (2009) found that clones that flushed early or late did so every year. In Canada and in Scotland early June seems to be the most common peak period for leaf flushing but the timing of leaf emergence can vary by up to four weeks (Barr *et al.*, 2004; Easton, 1997). Easton's (1997) study found no geographical trends in flushing dates between north and south or between east and west Scotland. However, the variation in emergence dates would probably have obscured any underlying trends in geographical or altitudinal clines. In Europe clinal variations in leaf fall and growth cessation across a latitudinal gradient have been observed between north and south, for example in Finland (METLA, 2008) and in Sweden (Hall *et al.*, 2007).

As might be expected, climatic differences also affect leaf flushing dates. In North America Jones & DeByle (1985) found that aspen clones at the highest elevations produced leaves up to five weeks later than clones at the lower elevations.

3.1 Reproduction and growth

Aspen is a dioecious tree that produces catkins before leaf flush. It can also reproduce asexually with the production of many suckers or 'ramets' that can arise from the root system of a single parent tree. Aspen is well known for expanding out from existing trees through root suckering but occasionally regenerates successfully from seed. There are documented examples of abundant seedling regeneration in Scandinavia and North America, particularly after fire episodes (Borset, 1960; De Chantal, 2007; Kay, 1993; Romme *et al.*, 1997). Although sexual reproduction is rare, the species has a wide-ranging seed dispersal mechanism. Small single aspen seedlings found in remote and isolated locations such as seacliffs and islands could only have arrived by wind dispersed seed (Worrell, 2008) while the small size of many clones in European forests suggest that some at least are relatively young and that establishment by natural seeding could be more common than previously thought (Latva-Karjanmaa *et al.*, 2003). The ability to colonise new sites using vegetative and sexual mechanisms introduces a competitive advantage over many other tree species and may be very important to the dynamics of aspen populations. Aspen can maintain its existing populations through vegetative replacement and expansion but also colonise new areas when conditions for seed production and germination are favourable. The 1997 Easton study showed that aspen in Scotland has retained a high level of genetic variation despite its survival being largely dependent on vegetative reproduction. In Orkney Easton recorded only 12 aspen clones but these possessed the same degree of genetic variation as the mainland populations. Mason *et al.* (2002) confirm that the post-glacial "genetic structure and variability has been largely retained despite fragmentation and reduction of sexual reproduction as a consequence of vegetative persistence over long periods of time". In North America *P. tremuloides* also exhibits high genetic diversity (Hipkins & Kitzmiller, 2004) despite its dependence on asexual reproduction. The maintenance of such high levels of genetic diversity may be attributed to a) the longevity of the individual genotypes which may have retained the genetic variability associated with periods of sexual recruitment; b) clonal mutation and; c) rare periods of sexual reproduction and seedling establishment (Easton, 1997; Shepperd *et al.*, 2006).

3.1.1 Natural Regeneration – sexual

The sex ratio of aspen is generally male dominated or equal and is known to vary between environments (Wyckoff & Zasada, 2003). In Finland and Norway, a sex ratio of two males to one female have been recorded (Latva-Karjanmaa *et al.*, 2003). The male:female ratio was found to be 2.5:1 in northern mountain regions of Italy, and 1:1 in southern and central Italy (Powell, 1957 and Garamuglio, 1964 in Worrell, 1995a). In Scotland the sex ratio is reported as 3:1 in favour of male trees within Strathspey (Easton, 1997). In North America sex ratios of 2:1 male to female are found on average but with 3:1 and 1:1 ratios also observed (Burton, 2004; Perala, 1990). However, 90% of the aspen growing above 3500 m altitude are male while females are found in the low ground habitats where there is less moisture stress (Mitton & Grant, 1996). Some studies of *P. tremuloides* have found that there is a difference in the growth rate of the male and female clones, with females exhibiting a greater number and area of ramets than males although there were no significant differences in girth (Mitton & Grant, 1996; Sakai & Burris, 1985). These data are thus inconsistent with the hypothesis that investment in sexual reproduction could reduce growth rates (Sakai & Burris, 1985) although a European study of *P. tremula* found that male clones had better form and vigour (Rohmeder & Schonbach, 1959 cited by Jones & DeByle, 1985).

In Europe and North America flowering occurs only rarely although some reports suggest that a few individual trees may produce seed in most years. Wyckoff & Zasada (2003) reported that aspen (*P. tremula* and *P. tremuloides*) produce good seed crops every four – five years and males tended to flower more often than females. Flowers are wind pollinated and pollen has been recorded 320 km from the nearest possible source (Jones & DeByle, 1985) or even transported across continents (Rousseau *et al.*, 2005). Seeds are also dispersed by the wind, generally up to 500 m from the parent tree, but often for many kilometres. Water can occasionally be a dispersal mechanism (Perala, 1990). In common with most trees that use wind dispersal mechanisms aspen can produce enormous numbers of viable seed (up to 500 million seeds/ha) but successful germination and establishment can be difficult. The numbers of seed produced by individual aspen appears to rise exponentially with the age of the tree. An eight year old *P. tremula* from Estonia or Finland will on average produce 8,700 seeds while a 100 year old tree will produce 54 million seeds (Reim, 1929, in Wyckoff & Zasada, 2003). Seed viability usually exceeds 90% but the seeds are short-lived (Latva-Karjanmaa, 2003; Miller, 1996). Generally an exacting set of environmental requirements must be in place before germination can occur. These include adequate soil moisture (but not standing water or flooding), drainage, light and limited competition from other vegetation. These conditions are often met when ground has been disturbed (Worrell, 2008). Aspen seeds do not possess an endosperm, are very fragile and must be in direct contact with moisture in order to absorb water and germinate. After about five - six days the roots start to form (Perala, 1990). Seedlings are therefore vulnerable to desiccation, wash-out by heavy rain or trampling by animals following germination (De Chantal, *et al.*, 2005). The volatile compounds associated with bracken *Pteridium* spp. have been shown to inhibit the germination and growth of aspen seedlings during May and June (Dolling *et al.*, 1994). Coarse woody debris is an important medium for trapping and protecting the seeds in a stable and more favourable microclimate although other vegetation can become lush and vigorous in such circumstances and thus reduce light availability (De Chantal *et al.*, 2003). Larger dead wood aggregations can offer protection to young seedlings against browsers but smaller woody debris and individual fallen trunks are generally ineffective (De Chantal & Granstrom, 2007; Ripple & Larsen, 2001).

Fires, particularly high intensity burns, are considered to be an important mechanism for aspen regeneration from seed in North America. In Finland and in Sweden fire may also play a part although many aspen stands are found in moist depressions and seeds require high humidity levels for germination (De Chantal *et al.*, 2005). Distribution patterns and seedling requirements may not be fully understood for aspen in the European boreal regions and past forest management practices may have distorted the natural distribution of aspens.

As a result of the infrequent flowering of aspen and the difficulties of seedling establishment most regeneration occurs via root suckering from nearby 'parent' trees.

3.1.2 Natural regeneration - asexual

Vegetative or asexual reproduction in aspen also depends on a specific set of processes that trigger the production of suckers from adventitious buds on small lateral roots (0.5 – 2.5 cm diameter) that are initiated following some kind of disturbance (Edenius & Ericsson, 2007; Miller, 1996). Harvesting, fire, wind-throw, defoliation or canopy fragmentation will disrupt apical dominance and increase soil temperature and light availability all of which can independently or cumulatively stimulate sucker growth. The principal process however is dependent on the hormone balance associated with apical dominance. Auxins are produced in the aerial, photosynthesising parts of the tree and travel down to the root system where they suppress the cytokinins, the hormones that promote sucker growth. If the flow of auxins to the roots is interrupted by any kind of disturbance or damage such as felling, windthrow, wounding or severing of the roots or girdling of the stem then cytokinin production increases and suckers develop (Shepperd, 2004). Environmental factors such as a rise in soil temperature and the increased availability of light will also affect sucker production. Temperature in particular can sometimes stimulate sucker growth without any disturbance to the roots. Sucker development is optimum at soil temperatures of about 23ºC, which tend to degrade auxin and promote cytokinin. This may be the reason why aspen frequently invades adjacent open fields and grasslands (Perala, 1990). As with the requirements for seedling germination aspen suckers will not develop in waterlogged soils or during severe drought. Most suckers will develop within 20 m of the parent tree but can sometimes appear up to 30-40 m away (Latva-Karjanmaa *et al.*, 2003). The age of the 'parent' tree does not appear to impact on the number of suckers, which are supplied initially with nutrients from the 'parent' root system (Miller, 1996). Dead stems with still living root systems were also utilised by the suckers since above-ground stem decay was not necessarily transferred to the root network (Perala, 1990; Shepperd *et al.*, 2006). Aspen roots must possess aerial stems that photosynthesise in order to replace the stored carbohydrates in the root tissue. Although light is only a secondary factor involved in sucker initiation it is important to the growth of the root sucker as further development will be limited unless more or less full sunlight is available (Shepperd, 2004).
Genetic factors may affect the density of suckering ramets in some clones (Edenius & Ericsson, 2007) but the presence of a large number of vigorous sucker shoots will indicate that the aspen clone is a healthy one and will be capable of regeneration should the right conditions materialise (Shepperd *et al.*, 2006).

Aspen can also produce vegetative shoots from stumps or from root collars but these are insignificant in number compared to the production of root suckers. Matthews (1991) observed that aspen did not naturally produce basal shoots but cut stumps were likely to produce shoots if suckering is physically suppressed (A. Harrison, Forest Research, pers. comm.). ■

Threats and damage

'Aspen is a highly preferred forage species for a range of herbivores'

Aspen is a highly preferred forage species for a range of herbivores and, despite its rapid height growth, browsing frequently limits successful establishment (Cosgrove *et al.*, 2005; De Chantal *et al.*, 2005, Kouki *et al.*, 2004; Shepperd *et al.*, 2006). Repeated browsing of new sucker growth can exhaust the carbohydrate reserves in the roots and prevent the sucker from carrying out its own photosynthesis although Eiberle (1975, cited in Edenius & Ericsson, 2007) found that aspen could tolerate high levels of biomass loss due to browsing. Young aspen can also be killed by the bark stripping and fraying activities of deer (Cervidae), livestock, rabbits (Leporidae) and voles (Arvicolinae). Beavers *Castor* spp. will consume young aspen and fell moderately large trees although the sucker re-growth is often avoided, perhaps because of the phenolic resins found in the bark (Jones *et al.*, 2009). Nevertheless, the felling of all the mature aspen may have damaging consequences to other aspen-dependent flora and fauna. Deer and livestock are attracted to aspen in riparian areas for example because of its association with water and the high quality of the forage that can be found under aspen trees. This can provide almost as much grazing as adjacent meadows (DeByle, 1990; Shepperd *et al.*, 2006). Aspen in areas where livestock congregate can suffer soil compaction, root damage and sucker death followed by a decline in the survival of the stand (Perala, 1990). Domestic livestock will increasingly favour aspen from summer through to autumn as their preferred grazing forage of grasses and herbs decrease in volume and nutritional quality (Shepperd *et al.*, 2006). Sheep have been reported to browse aspen more often than cattle and are also four times more destructive to aspen than cattle (DeByle, 1985; Shepperd *et al.*, 2006). Wild ungulates tend to shift from browsing to grazing of herbaceous material during summer and as animals are spread across a wider range their impact is less severe. Nevertheless, aspen leaves are a valuable source of fodder as they contain a higher fat and protein content than hay and, indeed, the leaves of most other deciduous trees (Hauge, 1988). The leaves contain an average of 17% protein in June, 13% in July and 12% in September, while fat content ranged from 7 – 10%, although there is considerable variation between clones. Studies of deer in Utah in the western United States showed that 27% of the summer diet was aspen (Mueggler, 1985). The mix of grasses, forbs and shrubs associated with aspen stands have provided grazing for livestock and wildlife in the western United States for over a century – more than 2,240 kg/ha of forage has been recorded. However, most aspen habitats in the west have been depleted by years of overgrazing. Excessive grazing by sheep in particular has altered the species composition of the ground flora by converting the rich mix of forbs and grasses into grass-dominated swards with limited diversity (Mueggler, 1985). This process has close parallels with the reduced diversity in the overgrazed grassy swards under birch and aspen woods in the Scottish Highlands (McVean & Lockie, 1969).

Aspen bark is also highly nutritious as it is low in secondary compounds and low in fibre and is thus highly digestible, providing important woody browse during winter (Hjalten & Palo, 1992; Mueggler, 1985). Some authors have described the considerable variation in feeding preferences between individual clones, which may be due to variations in the concentrations of phenolic glycosides that plants use as a defence against herbivore browsing (Environment Directorate, 2000; Whitham, 1996). The 15% or more carbohydrate content of bark tissue may also play a part in seasonal herbivory. Carbohydrates remain in aspen bark during winter, possibly because of photosynthetic activity, and in North America deer (Cervidae) and elk *Cervus canadensis* will target this resource when alternative forage is unavailable (Shepperd *et al.*, 2004). In Sweden experimental field studies on the diets of mountain hares *Lepus timidus* have found that they strongly preferred the branches of male plants, most probably because of the higher concentrations of nitrogen found in the bark of male plants (Hjalten, 1992). Sex-related foraging preferences would not explain the male-biased sex ratios described for *P. tremuloides* and *P. tremula* (see page 10) but may indicate that there may be many environmental variables that influence sex ratios in aspen.

A large number of fungi and diseases impact on aspen in European and North American forests. Most are not a threat to their host as their effects are either not permanent or they form part of the forest ecosystem and contribute to its biodiversity. The species that might be regarded as causing damage are those that have an economic impact on wood production. The fungus *Venturia tremulae* causes high mortality rates in aspen shoots and black spots on the leaves. In North America the windblown spores infect aspen's new shoots but, as the season progresses, uninfected tissue tends to become resistant (Jacobi, 2006). Pathogens such as *Neofabrea populi* and *Entoleuca mammata* have been imported into Europe and Scandinavia from North America and have the potential to cause severe infections (METLA, 2004). Bacteria, yeast and other micro-organisms can cause discolouration and decay of wood while trunk rot fungi such as *Phellinus tremula*e will damage the heartwood and causes the most widespread volume of aspen decay in North America (Perala, 1990; Parsons *et al.*, 2003). Stem cankers such as *Hypoxylon mammatum* can annually kill 1-2% of aspen east of the Rockies (Perala, 1990). In Finland aspen is an intermediate host to the pine rust fungus *Melampsora pinitorqua* and aspen trees have been eliminated from most managed forests containing pine (Kouki *et al.*, 2004). The removal of all aspens within a radius of 500 m of the conifers was found to be an effective way of preventing rust infection in plantations (Butin *et al.*, 1995).

Many invertebrates are associated with aspen (in Canada a study recorded over 300 species) but very few are a serious economic threat to aspen (Perala, 1990). Outbreaks of defoliators such as the tent caterpillars (*Malacasoma* spp.) and the aspen tortrix (*Choristoneura* spp.) can cause severe growth loss that can take three - four years for total recovery (Perala, 1990).

Aspen trees are easily killed by fire or suffer scars that allow the entry of pathogenic fungi. Fire however is part of the vegetation dynamics and succession of aspen stands in North America and parts of Europe and could be seen as beneficial unless the fires are so intense that they damage roots and reduce sucker regeneration (Perala, 1990). Conifer succession which shades out the aspen and restricts suckering has contributed to aspen decline while the suppression of wildfires has eliminated one natural disturbance regime that would have rejuvenated many North American aspen stands. Drought is another factor that can lead to a reduction in growth of aspen as trees can suffer stress and become prone to secondary diseases.

In North America in recent years there have been a number of cases of unexplained sudden aspen decline (SAD) where extensive stands of mature aspen have experienced high mortality, including that of the lateral root system, and with an absence of subsequent regeneration. The affected forests appear to be expanding exponentially in some locations, for example surveys in Colorado show an increase from 12,000 ha in 2005 to 137,000 ha in 2007 (Rogers, 2008). Severe cases have been reported throughout western North America including Alberta, Colorado, Wyoming, Utah, Nevada and Arizona but as yet no specific causal factors have been identified. Worrall *et al.* (2008) have suggested that climatic influences, particularly acute drought associated with high temperatures were primary factors and that a suite of biotic agents, often in different combinations, such as cankers and wood-boring beetles, were the contributory agents of mortality.

European aspen can readily hybridise and produce viable offspring with the North American aspen, *P. tremuloides*. There is thus a risk of gene flow between native aspen and hybrid aspen (Latva-Karjanmaa, 2006). Since pollen is wind-dispersed and has the potential to travel great distances, the impact on native aspen could be considerable, particularly if climate change triggers an increase in flowering. Hybrid aspen (*P. tremula x tremuloides*), which has faster growth and stem straightness than the native aspen, has been planted in Britain but not on a commercial scale because of its vulnerability to bacterial canker (Jobling, 1990). If disease-resistant strains were to be developed then this situation could alter. ■

Vegetation dynamics of aspen in Europe and North America

'There is a complex set of factors necessary for aspen regeneration'

Aspen is thought to be declining in a number of European countries and in many parts of North America (Brown *et al.*, 2006; Kouki *et al.*, 2004; Rogers, 2002; Smith & Smith, 2005). One study in California documented a 24% decline in the area of aspen between 1946 and 1994 while stands had also become smaller and more numerous, indicating increasing fragmentation (Di Orio *et al.*, 2005). Conifer encroachment, suppression of natural fire regimes and elk (*Cervus canadensis*), moose (*Alces alces*), deer (Cervidae) or other herbivore browsing are all associated with decreased aspen recruitment in Europe and in North America (Cosgrove *et al.*, 2005; Jones *et al.*, 2005; Kaye *et al.*, 2005). Some North American studies do report aspen regeneration at the landscape scale, although not in areas with a high elk population (Suzuki *et al.*, 1999). There are also reports from Western Canada in the 1990s of aspen dieback and reduced growth that may be linked to variations in the climate moisture index in combination with insect defoliation while a major collapse in aspen productivity between 2001 and 2003 was probably due to a severe drought (Hogg *et al.*, 2005). Sudden aspen decline in North America may have a particular impact on aspen stands that exceed 100 years of age and could result in local extinctions if regeneration subsequently fails to materialise (Rogers, 2008). These observations have led to concerns about the potential impact of climate change on the aspen forests of North America. However, some extreme climatic events can be beneficial to aspen. In the Northern Great Plains the damage to aspen stands by the impacts of an unusual but intense hailstorm led to a dramatically increased recruitment of aspen suckers that subsequently invaded adjacent grassland (Peltzer & Wilson, 2006).

In Lithuania a study by Ozolincius *et al.* (2005) of tree mortality showed that aspen more than 80 or 90 years old, along with birch and Norway spruce, had higher mortality rates than longer-lived trees such as Scots pine and oak *Quercus* spp. Stem insects and root diseases were identified as the causes of death in about 20% of cases and 60% of trees had symptoms of wind damage. Tree mortality increased by up to a factor of 10 times in extreme weather conditions and insect invasions – which may be a cause for concern in the management of aspen stands where recruitment is rare.

Studies of the spatial distribution and stand structure of aspen in Scandinavia and North America have resulted in a number of interesting conclusions and theories on how aspen has been influenced by mammalian herbivores. Aspen is a highly preferred browse species. In northern Sweden it is found in discrete patches, similar to its state in Scotland. A study by Edenius *et al.* (2002) however, found that moose, *Alces alces*, did not actively select these aspen patches but browsed on aspen at both randomly located sites (where availability of aspen was lower) and aspen stands equally in terms of overall forage level. By selecting the aspen at sites where it is rare the moose may be helping to maintain the patchy aggregated distribution of the aspen stands. In Finland aspen regeneration is very poor as a result of high browsing pressure, particularly by moose, which has increased in recent years. Old growth aspen and the many threatened species that are associated with it may disappear in a few decades as there are no new replacement aspen cohorts available (Kouki *et al.*, 2004).

In North America *P. tremuloides* stand structure is also strongly influenced by large mammalian herbivores such as elk (Kaye *et al.*, 2005) while the extirpation of the bison (*Bison bison*) from the plains of western Canada may have triggered the expansion of aspen prior to colonisation by homesteaders and subsequent fire suppression in the late 1800s (Campbell *et al.*, 1994). There have been a number of studies documenting a decrease in the cover of aspen forests, for example in Colorado, where most aspen were between 80 and 120 years old and there were few suckers < 20 years (Smith & Smith, 2005). Hessl (2002) suggested that, in addition to the browsing impact of the increasing elk population, the cessation of controlled fires in the 20^{th} century may have assisted in the decline of aspen by preventing the regeneration advantage of suckers, which can quickly re-grow after fire. Ripple & Larsen (2000) suggested that the decline of aspen in Yellowstone National Park was due to the absence of wolves (*Canis lupus*). Since most aspen were over 70 years old, there had been no new established regeneration since the 1920s and the wolf was exterminated in 1926, they postulated that wolves could have influenced the growth of aspen via the trophic cascade effect. Wolves would have predated elk and kept the population stable and on the move thereby encouraging aspen regeneration. The increase in the elk population not only led to the decline in broadleaved trees such as aspen but also resulted in the disappearance of beavers (*Castor canadensis*) (Robbins, 1998). In 1995 wolves were re-introduced to Yellowstone and by 2003 there were about 170 wolves in 16 packs. Each pack is thought to kill an average of one elk per day, which has caused a drop in the elk population from 20,000 to 10,000 (Robbins, 2004). Recent studies have shown that willows, cottonwoods and aspen are returning to riparian areas (Beschta & Ripple, 2007). Ripple and Beschta (2007) reported on the first significant aspen regeneration in northern Yellowstone for over half a century. In addition some beavers have returned to streams where the vegetation has returned to its former lushness, and there are improvements to trout habitat. The management of an ecosystem clearly benefits hugely, in this case at least, from the presence of predators in the food chain.

Fire seems to play a significant role in the rejuvenation of aspen stands in North America. In 1988 wildfires destroyed vast areas of forest in the Yellowstone area but aspen, previously unable to compete with the conifers, were able to thrive as the suckering root systems took advantage of the newly opened up forest. The same fire episode also triggered a rare occurrence of aspen regeneration by seed (Stevens *et al.*, 1999). Great numbers became established, including in areas where aspen was absent prior to the fire, as a result of the combination of high seed year, favourable weather and suitable ground conditions (Romme *et al.*, 1997). Kay (1993) reports on particularly high concentrations on riparian areas that had been burned down to the mineral soil with the highest average density of seedlings being 142,645/ha. The US Forest Service is now conducting controlled burns in order to mimic wildfires and restore vegetation succession and perhaps avoid catastrophic fires like the one in 1988 (Ellis, 1995). Despite the surge in aspen regeneration, post 1988 browsing by ungulates was still sufficiently intense to impact on most accessible aspen and it is possible that few seedlings will grow on to become mature trees. Delving into the history of the aspen at Yellowstone Romme *et al.* (1997) discovered that aspen establishment was episodic even prior to the creation of the park in 1872. It was a combination of events during the period 1870 to 1890 that triggered the establishment of much of the present day aspen. These unique events, which included low elk numbers, relatively wet climate, recent and extensive fires and the presence of wolves have not recurred since that time. At Yellowstone there is a complex set of factors necessary for aspen regeneration and, although the management of just one or two of these factors (elk and fire) may not be enough to stimulate regeneration, it would help to create the conditions for a time when weather and seed/sucker production are optimal.

A Canadian study has predicted that the potential temperature rise in combination with increased fire occurrence in Ontario will result in the shrinkage of boreal forest types and that pyrophilic species such as aspen will become more common (Thompson *et al.*, 1998). Studies of fire history in Alberta over an 840 year period indicated that the average fire interval was 69 years and that there were long term changes in the relative abundance of tree species. For example, the dominant spruce *Picea* cf. *glauca* was terminated by a fire in the 12th century and replaced by *Populus* with the *Picea* gradually increasing again over the next 800 years (Larsen & MacDonald, 1998).

There is much less information on the part played by fire in European forest habitats where aspen occurs. During pre-historic times about 10% of the boreal forest in Sweden may have been dominated by birch and aspen as a result of fire dynamics. Pyrophilic species such as aspen despite being readily burned by fire are able to quickly re-colonise the burned area and thereby alter the age structure and species composition of the forest. Natural fires remove the conifers periodically and the aspen cycle is renewed. A newly burnt area is a unique habitat and there are a number of pyrophilic insects and fungi that are specialised to living in this habitat (Wikars, 1992). A fire history study in northern Sweden showed that, between the late 1600s to late 1800s, the average fire interval was 34 to 65 years but there had been no fires since 1888, probably due to fire suppression in the wider landscape (Linder *et al.*, 1997). Over the past 100 years conifers (Norway spruce) had increased at the expense of pioneer species such as aspen, browsing was suppressing broadleaved regeneration and the volume of dead trees was as high as 30% of the total stem volume. The authors proposed that fire disturbance along with other management practices should be re-introduced in order to increase species diversity. However, Kouki (2009) is more cautious about introducing fire as a management tool to regenerate the depleted aspen resource in Finland. The fragmented nature of the stands may mean that many aspen-dependent species would be lost unless the area of aspen is very large.

In Scotland aspen is more closely associated with broadleaved woodland and fire may never have played a significant role in the dynamics of succession but there is very limited information on the role of fire as a possible disturbance mechanism in Scottish deciduous woodland. Windthrow, natural mortality and decay associated with small scale gaps in the forest may be the main causal factors involved in aspen succession in the temperate forests of Scotland. However, its present widespread distribution but limited individual stand area is largely due to historic land use practices and current levels of herbivore browsing. ■

Biodiversity

'Aspen groves are regarded as "hotspots" of biological diversity'

There are a substantial number of species associated with and dependent on aspen in Europe, including Scotland, and in North America. The biological diversity of aspen stands is disproportionate to its extent and this makes its contribution to the ecology of Scotland's native woodlands very important.

6.1 Invertebrates

Throughout Scandinavia aspen is an important species for saproxylic beetle biodiversity. In Norway for example there is a high number of rare and red-listed species associated with dead or damaged aspen, particularly on aspen snags (Sverdrup-Thygeson & Ims, 2002). In Sweden a four-year study of a single decaying aspen left on a clear-cut site recorded 193 species of saproxylic insects, including 31 on the Swedish red list (Ahnlund, 1996). In commercial forests in Finland retention of large aspen stems maintained the richness of the saproxylic beetle fauna (Kolstrom & Lumatjarvi, 2000). In a study of dead aspen (*P. tremuloides*) in Alberta saproxylic beetle diversity was higher in stumps and logs rather than in snags although the snags tended to have higher abundance levels (Hammond *et al.*, 2001). The Canadian study also found that species diversity was higher in the old growth aspen stands (over 100 years old) and that beetle diversity increased in the second year of the study, suggesting that the early wood–boring beetles "preconditioned" the wood and made it suitable for a new suite of taxa.

Studies of saproxylic beetles in Scandinavia have shown that intensive forest management has decreased the amount of dead wood and consequently decreased the population of insects that survive on dead wood. In order to combat this problem high stumps of birch and aspen (4 m height) were retained by the harvesting machines and these were found to be valuable habitats for the beetles. Jonsell *et al.* (2004) recorded 116 saproxylic species on the birch and aspen stumps, including 21 red-listed species. Many species were more associated with the man-made stumps than with natural stumps although in total more species were found in the natural stumps.

In Scotland there are a moderately large number of insects associated with aspen, including moths, butterflies, beetles and a number of Dipteran groups, particularly saproxylic insects. However, the rare saproxylic beetle fauna found on aspen in Scandinavia is absent in Scotland (MacGowan, 2009). Aspen, as one of the original pioneer tree species to colonise Britain and Scotland after the last Ice Age, has a strong association with ancient woodland sites. Its ancient connections may partly account for the number of specialist ecological associations that have survived in spite of aspen's poor representation in many woodlands.

One of the most extensive invertebrate studies on aspen was MacGowan's 1991 (reviewed 1997) study of saproxylic insects. He recorded 27 species including several Red Data Book (RDB) species that were associated with aspen. Additional work by Rotheray (2002) found 39 species of insect associated with aspen, including 14 RDB species and three endangered Dipteran species (RDB Category 1), which is more than for any other tree species in Scotland (Rotheray *et al.* 2001). One of the rare saproxylic insects is the aspen hoverfly *Hammerschmidtia ferruginea,* a UK Biodiversity Action Plan (BAP) Priority species. The larvae of this fly are entirely dependent on the decaying sap under the bark of dead aspen branches or fallen trunks that are greater than 15 cms girth (Rotheray, 2009). Thus, in order to have a continuous supply of deadwood for breeding it is only the larger stands of aspen with a range of life stages that can support viable populations of the hoverfly. Consequently *Hammerschmidtia* and many of the other saproxylic Diptera associated with aspen have been recorded in just 14 sites, all above 4.5 ha in extent, and all located in NE Scotland (Rotheray, 2002).

Of the beetles associated with aspen, one species, the large poplar longhorn beetle (*Saperda carcharius*), may have the ability to aid in the thinning of aspen stands and thereby encourage the growth of larger trees and creating deadwood for the benefit of other species. Its larvae burrow into the trunks of medium sized trees, particularly on the edge of dense stands of aspen suckers, and this activity will tend to weaken the host tree by allowing the entry of pathogenic fungi and making it susceptible to wind blow (Begg & MacGowan, 2002). Other rare beetles dependent on aspen, such as the leaf rolling weevil *Byctiscus populi*, which has been recorded in England and is a UK BAP Priority species, may also occur in Scotland but has not yet been located (Mellings & Compton, 2002). The beetle feeds and lays eggs on the leaves of young aspen suckers in sunny open locations – a life stage and habitat that can be found at many aspen sites in Scotland.

There are a number of characteristic Lepidopteran species associated with aspen in Scotland. Prescott & Stubbs (2009) record 43 moth species found on aspen of which 17 are aspen specialists. As aspen is part of the Saliceae family many of the moth larvae (*e.g.* Poplar Hawk (*Laothoe populi*) and Pale Prominent (*Pterostoma palpina*)) can also feed on the leaves of willow as well as poplars. However, a few, such as the larva of the rare Dark-bordered Beauty moth (*Epione vespertaria*) in the Scottish Highlands depend exclusively on the leaves of young suckering aspen shoots under 1 m in height. Such specialisation requires a constant supply of new shoots, which may be dependent on seasonal grazing or regular expansion of the aspen stand. Other moths that feed exclusively on aspen include the Lead coloured Drab (*Orthosia populeti*), Seraphim (*Lobophora halterata*) and Chocolate Tip (*Clostera curtula*). Young (2002) also indicates the possibility of two other rare or potentially extinct moth species that used to be present in Scotland and may yet be relocated. It is worth noting that many of the larvae feeding on aspen create folded or spun leaves as a possible protection against loss of attachment when the leaves "tremble" in the wind (Young, 2002). In Europe the larva of some Lepidopteran species may be regarded as pests of aspen, for example *Phyllonorycter apparella* with an infestation level as high as 90% of the leaves on some trees in Turkey (Tozlu *et al.*, 2002). In a landscape scale study investigating butterfly diversity in Colorado, North America butterfly species richness was found to be highest in groves of *P. tremuloides* and in wet meadows, despite these habitats only occupying a small proportion of the study area (Simonson *et al.*, 2001). Aspen groves are regarded as "hotspots" of biological diversity in the montane landscape of North America.

The importance of aspen to invertebrate species is perhaps only beginning to be understood. Research in other European countries is also revealing aspen to be a keystone species for a number of important groups. In Finland *Picea abies*, Scots pine and aspen harbour the greatest number of red listed species but the proportion of critically endangered species is highest in aspen (Tikkanen *et al.*, 2006). Also in Finland dead aspen has been found to harbour 23 species of thrips, including four species previously unknown in Finland (Kettunen *et al.*, 2005). In Poland galls found on aspen leaves were caused by ten species of mite (Skrzypczynska, 2004). Interesting ecological interactions involving galls on *P. tremuloides* have been identified in North America. Intense browsing by elk reduced the incidence of sawfly galls on the leaves of aspen and caused arthropod diversity to diminish which in turn affected the foraging patterns of insectivorous birds (Bailey & Whitham, 2003). There are many types of galls associated with aspen and the causes of the galls are not always understood. In Scotland the gall mite, *Aceria populi* is the cause of a 10 mm warty growth commonly found on the buds and twigs of aspen and a larger gall of about 20 mm may be the home of the larvae of the beetle, *Saperda populnea*. Gall-like growths on the leaves of aspen can be caused by another mite, *Phyllocoptes populi*, and many other leaf galls are the result of midges of the genus *Hermandiola*.

P. tremuloides has been found to exhibit significant phenotypic variation in secondary compounds in leaves (*e.g.* phenolic glycosides) which may play a role in interactions with phytophagous insects such as Gypsy moths and Forest tent caterpillars (Hwang & Lindroth, 1997).

In northern Sweden several terrestrial gastropod species have been linked to aspen leaf litter which is better for gastropods than the litter of any other deciduous tree species (Suominen *et al.*, 2003) and it is now known that aspen stands in managed boreal forests are important for gastropods. Suominen *et al.* also found that there is a positive species–area relationship between numbers of species and the area and connectivity of aspen stands. They recommended stands should be at least 0.05 ha and, ideally be linked to other stands. A study by Kolvula *et al.* (1999) in Finland found that deciduous leaf litter, especially that of aspen, is favoured by carabid beetles. The litter is thought to influence humidity, temperature, niche structure and food supply.

6.2 Other fauna

Aspen trees, particularly old stems, are important roost sites for bats. Natural cavities in the tree can host maternity colonies and *Phellinus tremulae* has been identified as one of the main factors in the creation of heart rot and an eventual cavity (Parsons *et al.*, 2003). Crampton & Barclay (1998) found that bats preferred tall, dying or newly dying aspen with heart rot and low leaf cover while Kalcounis & Brigham (1998) showed that bats roosted exclusively in aspen cavities despite the availability of cavities in conifer snags. One reason for this preference may be that aspen cavities were found to be 5° C cooler than the cavities of conifers.

Cavities in aspen trees can also be excavated by woodpeckers such as the yellow-bellied sapsucker *Sphyrapicus varius* of North America (Kalcounis & Brigham, 1998). In Finland the flying squirrel *Pteromys volans* uses old woodpecker cavities as dreys. It is found in deciduous boreal forest; alder *Alnus* spp. and aspen are its preferred habitat (Hanski, 1998).

In the Canadian forests of British Colombia Oaten and Larsen (2008) found that aspen stands were small mammal hotspots with significantly higher mammal densities than in mixed or pure conifer stands. They also found that the aspen stands contained a higher proportion of juveniles and reproductive-age females providing a higher biotic diversity compared to other forest types as a consequence of their contribution to the food web.

In North America aspen stands enrich local bird communities as these areas contain a higher diversity and abundance of breeding birds than pine despite the small patch size and isolation of the aspen (Griffis-Kyle & Beier, 2003). Old growth aspen stands tended to have the greatest bird diversity but young and mature stands were also important (Schleck *et al.*, 1995). A key benefit to all birds that breed in aspen stands is the abundance and diversity of invertebrate food (Richardson, 2004). In the boreal forest landscape of Scandinavia Rolstad *et al.* (2000) found that most of the nest holes of the black woodpecker *Dryocopus martius* were in live aspen trees and in Norway white-backed woodpeckers *Dendrocopos leucotos* preferred to nest in aspen forests older than 80 years (Hogstad & Stenberg, 1994). Dead trees, though rare, were the most strongly selected but fledging rate tended to be lower than in live aspen. In the mixed deciduous forests of Sweden Carlson *et al.* (1998) found that oak and aspen were the two tree species richest in cavities and that woodpecker-excavated holes dominated in the aspen, probably due to its thin bark and its susceptibility to decay, perhaps making cavity excavation easier (Shepperd *et al.*, 2006). The study also showed that only 5-10% of the available cavities were used by breeding birds. North American woodpecker holes in turn provided nest sites for tree swallows *Tachycineta bicolor*, starlings *Sturnus vulgaris*, wrens (Troglodytidae) and mountain bluebirds *Sialia currucoides* (Dobkin *et al.*, 1995). Studies of nest site selection by six woodpecker species in Norway showed that aspen comprised 95% of all nest trees (Stenberg, 1996). Capercaillie *Tetrao urogallus*, particularly males in early summer, are known to utilise aspen for food (Rolstad, 1988).

Aspen is an important food source for beavers both in North America and in Europe. Quaking aspen in North America is the primary food of the beaver, *Castor canadensis*, and as the majority of foraging takes place within 20 m or so of streamsides there can be severe impacts on aspen stands, sometimes leading to localised extinction (Shepperd *et al.*, 2006). In Norway the European beaver, *Castor fiber*, has been known to exploit aspen trees 200 metres or more from water. When food stocks run low beavers normally abandon sites but in some areas rejuvenation of the aspen is prevented by encroaching conifers, which are less suitable as beaver habitat (Barnes & Mallik, 2001). Reintroduced European beavers in the Netherlands positively selected aspen despite the species being uncommon (Nolet *et al.*, 1994). Aspen stems that are felled by beavers can produce defensive chemicals in the bark of the new shoots which may help to limit subsequent tree selection by beavers (Basey *et al.*, 1990). The re-introduction of beavers to Scotland could assist in the biodiversity of aspen and the other species that are dependent on it by helping to restructure aspen stands. However, this would depend on the quality of the existing aspen habitat and the cumulative browsing impact by beavers and other herbivores.

Aspen is one of a number of preferred forage trees utilised by large herbivores, both wild and domestic. All species of deer as well as rabbits (Leporidae), hares *Lepus* spp., sheep, goats, horses and cattle will browse on accessible aspen suckers and seedlings. In a study of diet choice of Moose, *Alces alces* in Sweden Shipley *et al*. (1998) found them to have a browsing preference for rowan *Sorbus aucuparia*, willow *Salix* spp. and aspen in winter and tended to select species with fewer, larger stems rather than those with many smaller stems.

6.3 Lichens and fungi

Aspen has recently been found to be a key habitat for nationally important lichen flora as well as being important for lichen species that are rare elsewhere in Europe, but relatively common in Scotland (Cosgrove *et al.*, 2005). Street & Street (2002) recorded 130 species of lichen on aspen in Scotland while Ellis (2009) more recently estimated the number of lichens at 300 species. Aspen bark has been found to have a higher, but frequently variable, pH than birch and Scots pine and perhaps also a more nutrient-rich bark and is therefore a more attractive substrate for lichens and other epiphytes. It is recognised that the best diversity of lichens occurs on the longest established stands and, with the large number of specialist and RDB epiphytic lichens present, this is further confirmation of an ancient ecological relationship. There could also be differences in the lichen communities between different aspen clones, possibly due to the variations in bark compounds. An ongoing study by Davies (2009) may provide further information on this subject. However, recent research has indicated that the diversity of lichens on aspen in Scotland may be declining as a consequence of the loss and fragmentation of native woodland since the 19^{th} century (Ellis & Coppins, 2007b).

In other European countries, some epiphytic lichens are used as indicators to identify forests with a high conservation value. In Sweden Uliczka & Angelstam (1999) found that indicator macrolichens had a preference for old trees or aspen. In Finland where aspen and rowan are the most important hosts for indicator lichens (Pykala *et al.*, 2006), selective logging is decreasing the persistence of these lichens, which appear not to be adequately protected by Forest Acts designed to conserve such biodiversity. The best indicator species found in Sweden were *Lobaria pulmonaria*, *Nephroma* spp., *Pannaria pezizoides* and *Parmeliella triptophylla*, which are most frequently found on old growth aspen stands and are a simple indicator of the continuity of the forest (Kuusinen, 1996). In Estonia aspen has been shown to have the highest number of lichen species on basal trunks and twigs and also the highest number of host-specific species; it makes a significant contribution to the diverse lichen flora of the boreo-nemoral forest (Juriado *et al.*, 2003). Research work on the impact on lichen species of certain types of forest logging showed that selective cutting had minimal damage to lichens on the more sunlit aspen stands but significant impact to lichens growing on shady stands (Hedenas & Ericson, 2003). There is also a possible relationship between soil properties and bark chemistry which might affect the epiphytic vegetation on aspen (Gustafsson & Eriksson, 1995). This could have implications for the types of management needed to conserve lichens as well as their use as indicators of air pollution. Hedenas *et al.* (2006) have studied the impact of a parasitic fungus, *Abrothallus suecicus*, on a lichen, *Ramalina sinensis*, specific to aspen. The parasite invades lichen on young aspen but its impact was most severe on the older aspen stands which highlights the need to maintain a succession of young aspen in order to conserve both aspen and lichen species and to take account of the impact of parasites and disease. All studies thus point to the need to promote aspen trees, old and young, for the conservation of biodiversity in boreal forests.

Aspen has declined throughout the boreal forests of Europe and Scandinavia, in particular the immature stands, due to the lack of regeneration (Hedenas & Ericson, 2004). In Sweden aspen regeneration is often restricted to abandoned agricultural land but Hedenas & Ericson (2004) have found that the quality of this habitat is not sufficient to conserve cyanolichens that are dependent on aspen as the best diversity of epiphytic lichens occurred in the forested landscape where conifers and aspen older than 50 years were present. In a previous paper the same authors had discovered that among aspen specialists early colonisers are sexually dispersed and late colonisers are asexually dispersed and that cyanolichens are confined to older aspen stands and did not occur in adjacent young growth (Hedenas & Ericson, 2000). Lichens with a cyanobacterial photobiont tend to be sensitive where there are high light levels and low humidity, such as on aspen growing along the forest edge or on agricultural land (Blomberg, 2002). In contrast, macrolichens with green-algae photobionts are more tolerant of exposed aspen stands. In order to conserve such lichens old growth aspen and regenerating aspen in forests need to be protected and conifers introduced onto the former agricultural habitats. Similarly in Finland there is a reduced incidence of the lichen *Lobaria pulmonaria* on aspens in intensively managed forest areas where old growth stands are fragmented; it is therefore important to ensure better habitat continuity for local colonisation and succession (Gu *et al.*, 2001).

P. tremuloides in Canada has been shown to be as important as its European counterpart for richness of epiphytic lichens (Boudreault *et al.*, 2002). Old aspen mixed wood stands and dead wood in variable states of decay in particular are important for the maintenance of lichen, bryophyte and fungi assemblages. However, time as well as a range of age and structure classes are necessary to ensure the continuity of such non-vascular assemblages and the diversity would be altered if old aspen stands were lost (Crites & Dale, 1998).

There are a number of fungal groups that are associated with aspen. Saprophytes are particularly common but are dependent on dead or decaying aspen logs. Some are generalist species and others are specific to aspen but all play an important part in the decomposition of leaves, twigs and logs. In a Norwegian study 155 species of wood decaying fungi were found on aspen. In Britain 100 species of fungi have been recorded on aspen (Emmett & Emmett, 2002). There are also a number of symbiotic mycorrhizal species such as *Leccinum aurantiacum,* which assist the growth of aspen by providing nutrients. One of the main fungal parasites of live aspen and the most common cause of the tree's death is *Phellinus tremulae*, a bracket fungus that is associated with aspen throughout Europe and North America but has only recently been recorded in Britain (Emmett & Emmett, 2001). Another parasite, *Taphrina johanssonii*, occurs on the flowers of aspen but is rarely seen in Scotland because of the infrequency of aspen flowering episodes. Aspen is a host for several species of pathogenic rusts belonging to the *Melampsora* genus, which attack the leaves and can result in defoliation.

6.4 Bryophytes

The epiphytic bryophyte flora of aspen in Scotland includes six liverworts and 29 mosses, including some rare species such as the bristle moss *Orthotrichum gymnostomum*. This UK BAP species was thought to have become extinct and has only recently been rediscovered in Strathspey and Deeside. It has now been recorded on 45 aspen trees at three different sites (Cosgrove *et al.*, 2005; Rothero, 2009). Two other rare pin cushion mosses, *O. speciosum* and *O. obtusifolium*, the latter a UK BAP Priority species, have also been recorded at several aspen sites in the Grampian Highlands (Rothero, 2002). The distribution of bryophytes on aspen is patchy with epiphytic mosses (and some lichens) being present on some aspens but absent from nearby aspens, despite both having a similar light and soil regime (Rothero, 2002). The reasons for this remain unclear but may relate to differences in bark chemistry between different aspen clones. In the Nordic countries aspen is an important substrate for epiphytic bryophytes and lichens because of its nutrient rich bark with a relatively high pH value, and in Sweden 20% of the red-listed epiphytic bryophytes are found on aspen (Hazell *et al.*, 1998). ■

Cultural context and past use

'Aspen is a tree that has great aesthetic and landscape appeal'

Aspen, along with many other plant species, has had a long history of herbal use. The bark in particular has a number of medicinal properties; it was one of the original sources of the proprietary drug aspirin, which is derived from salicylates in the bark. In North America the First Nation people valued it for its antiseptic and analgesic properties and used it in the treatment of wounds, infections and skin complaints, just as it is used in modern herbalism (Moerman, 1998). The bark appears to be the most valuable part of the tree because of its many associated properties including acting as an anodyne, anti-inflammatory, antiseptic, astringent, diaphoretic, diuretic, febrifuge, nervine and stimulant. Consequently it can be used internally in the treatment of rheumatism, arthritis, gout, lower back pain, coughs, urinary complaints, digestive and liver disorders, debility, anorexia, and also to reduce fevers and relieve the pain of menstrual cramps (see Bown, 1995). An infusion or tea made from the inner bark was the most common method of administrating the internal remedies but for external use a poultice of root or bark material could be applied. A white powder was made from aspen trees that possess photosynthesizing bark and used by First Nation peoples as a sunscreen (Moerman, 1998).

The inner bark is edible and was formerly dried, ground to a powder and mixed with other flours for making bread or used as a soup thickener (USDA, 2003). The leaves and bark can also be used in the manufacture of dyes. In Norway aspen trees were usually pollarded, as the foliage was an important fodder crop (Austad, 1988). The ground or boiled bark was also used as a livestock feed, or even for occasional human consumption during winter food shortages (Worrell, 1995b).

The timber is especially light in weight, buoyant and ideal for carving. In North America canoe paddles and tipi poles were fashioned from the wood. In Scandinavia aspen wood has been identified from the excavated remains of dugout canoes and larger sewn boats from the 16th century and earlier times (Westerdahl, 1985; Forssell, 1985). The Irish for aspen, *Ebadh*, means the 'most buoyant of wood' (Paterson, 2002). On Kizhi Island in Russia the 22 silvery cupolas on the cathedral built in 1714 are made from some 30,000 curved aspen shingles (Brumfield, 1997). Aspen has also been used to make arrows, charcoal for gunpowder and matches – the latter becoming an important industry in many parts of the world. The Celts may have used the wood of aspen for making shields believing it to have magical and protective properties because it shields the bearer on spiritual levels from the all consuming darkness associated with fear. The Bach flower remedies recommend aspen for the alleviation of fears, nightmares and other apprehensions (Elliot, 2002; Paterson, 2002).

Three thousand years ago in Mesopotamia golden crowns made from aspen leaves were placed in burial mounds, perhaps to allow the spirits of the dead to be reborn (Paterson, 2002). In ancient Ireland the measuring rod used by coffin makers on corpses was made of aspen, perhaps "as a reminder to the souls of the dead that this was not the end" (Graves, 1948). There are few customs and beliefs associated with aspen in Scotland compared to most other native trees. It has a Gaelic name, *crithean*, but there are scant place names derived from it, for example Blarcreen and Crianlarich in Argyll and *Sron a crithean* in Ardgower (Fife, undated). Aspen along with other native trees of Scotland is used to represent the letters of the gaelic alphabet – aspen being the letter 'E'. There has been an early Christian belief that the crucifixion cross was made from aspen wood and, although there is no truth in this, the association may have stifled common usage of the wood in the past. Certainly, there appears to have been a Highland superstition that discouraged the use of aspen wood in fishing or farming practices (Carmichael, 1928), although Anderson (1967) quotes an early 19th century report of aspen wood being made into "red herring casks".

Aspen is a tree that has great aesthetic and landscape appeal particularly in spring with its fluttering leaves in the breeze and in autumn when the leaves turn golden yellow and, occasionally, red.

Contemporary uses and values

'The light coloured white wood of aspen makes it ideal for quality printing'

Throughout the 20th century aspen has had a number of important uses in Europe and North America although demand has fluctuated. In Scotland aspen is important for its landscape and amenity value and more recently has been recognized for its key contribution to conservation and biodiversity in native woodlands (Cosgrove *et al.*, 2005). Perhaps owing to the scarcity of the resource in Scotland there has been no history of timber use (and very little information on growth or volume production) (Worrell, 1995b) and, in the past, foresters treated it as a weed (Nisbet, 1905) although recently the wood has been used for occasional craft products.

Despite the decline of aspen in North America and in Scandinavia over the last 100 years or so aspen has become a valued source of timber in the past few decades (Balatinecz & Kretschmann, 2001; Bartos, 2001; Sankey, 2007; Worrell, 1995b). After being considered a weed species and a competitor of conifers for many years in North America and in Europe (Cheyne, 1990; Karacic, 2005), by the 1950s aspen plywood began to be used in the construction industry and the demand for veneer quality aspen increased (Miller, 1996). Two decades later aspen timber was in demand for the manufacture of oriented strand board (OSB), used in load-bearing applications such as flooring and roofing (Karaim *et al.*, 1989). Aspen became very popular in North America for OSB and waferboard because of its abundance, white wood and light weight (Maas *et al.*, 1990). In some states waferboard is made exclusively from aspen and demand for the timber has soared since the 1960s (Youngquist & Spelter, 1990). In the prairie provinces of Canada annual aspen roundwood production has increased from 794,000 m^3 in 1970 to 8,045,000 m^3 in 1995 (Brandt *et al.*, 2003). Aspen wood is easy to sand, finish and machine, provided tools are sharp, and has good screw-holding, stapling and glueing properties (Karaim *et al.*, 1990). It does however possess low nail withdrawal resistance but its reluctance to split when nailed partly compensates for this (Wengert *et al.*, 1985). Aspen is now used in a wide diversity of products ranging from furniture parts, childrens' furniture, panels, mouldings, pallets and utility lumber (Maas *et al.*, 1990). Shingles made from aspen have been used on farm buildings and rural housing in Canada for over 20 years (Karaim *et al.*, 1990).

In the Lake States of Michigan, Wisconsin and Minnesota 50% of all pulpwood consists of aspen and it is used in 85% of the pulp mills (Adams, 1990). Commercial use also takes place in Canada, particularly in the prairie provinces and in Quebec and Ontario, where aspen is seen as being more productive than birch or any of the softwoods (Brandt *et al.*, 2003; Weingartner & Doucet, 1990). The particular value of aspen for pulp is in its short fibre of narrow diameter and thin walls and its low lignin content, which is ideal for the production of high density paper with a smooth surface (Adams, 1990). The light coloured white wood of aspen makes it ideal for quality printing and reduces the need to use environmentally harmful bleaches (Stenval, 2006). Brightness and cleanliness are critical for print quality pulp and aspen is superior to any softwood for these qualities (Cheyne, 1990).

Aspen has become very popular in North America for OSB, waferboard and paper pulp

One of the most important impacts on the quality of aspen wood for printing pulp is that of trunk rot caused by pathogenic fungi such as *Fomes* spp. or *Phellinus tremula*e (Cheyne, 1990; Miller, 1996). Staining of the wood by rot can increase costs, particularly that of bleach as a larger compensatory quantity of bleach is required to treat stained wood. The tendency for aspen to develop stem decay at a relatively early age compared to other tree species has limited its utilization in some areas (Miller, 1996). However, the advantages of aspen's bright, clear fibres compared to other species outweigh the limitations and additional costs in dealing with stain damage (Cheyne, 1990). Aspen's low resistance to decay means that untreated wood in contact with soil may only last for two years (Wengert, 1985). Although it is easily treated with preservative (Worrell, 1995b), the low permeability of the wood makes a uniform distribution of preservative difficult to achieve (Wengert, 1985).

The Nordic and Baltic countries have realized the value of aspen pulp fibre and have established large-scale plantations of aspen and hybrid aspen (*P. tremula* x *tremuloides*) (Kasanen, 2000). However, it is still of minor importance in the forest industry. In Sweden the standing volume of aspen is about 42 million m^3 or 1.5% of the total standing volume (Karacic, 2005) and in Estonia about 37 million m^3 or 7% of the total volume of forest (EBRD, 2004). In Estonia the European Union funded a new state of the art mill that processes 400,000 m^3 of aspen per year in the production of pulp for high quality paper and tissue (EBRD, 2004). The annual aspen wood production in southern Finland is about 10,000 – 15,000 m^3 logs and 150,000 – 200,000 m^3 pulpwood (Karki, 2004). In Finland aspen has been used in the manufacture of matches since the 1850s and there was a short boom in its cultivation for this product during the middle of the last century but markets declined in the 1970s and there were very few other markets for the timber (Latva-Karjanmaa 2003). However, the situation changed in the 1990s as aspen has become valuable again as a timber tree and hybrid aspen (*P. tremula* x *tremuloides*), in particular is being planted to supply pulp for the paper industry. Hybrid aspen was found to have faster growth and on the best sites could produce almost twice as much wood as native aspen. While native aspen has similar properties in terms of fibre morphology, the quality of the wood was variable (Beuker *et al.*, 2000). Studies of aspen timber strength in southern Sweden have established that the timber has greater elasticity and a higher bending strength than Norway or Sitka spruce and if visually graded can be used as a structural timber (Harald *et al.*, 2007; Worrell, 1995b).

There remain a number of technical limitations and obstacles associated with the processing of aspen timber. Aspen structural timber has huge potential if a straight and stable product can be manufactured and there are techniques available that can ensure this (Maeglin, 1990). One of the limitations is the presence of 'wetwood' (caused by a bacterial infection), which is common in aspen heartwood. In addition to the staining effect, this also makes the wood difficult to dry or the drying is not uniform. Sorting and removing the wetwood logs is therefore important for structural material. Warping of the timber can be another limiting factor as aspen has a tendency to twist and bow during drying because of longitudinal shrinkage, which is higher in aspen compared to other species (Wengert *et al.*, 1990). Correct drying and stacking of the timber is thus imperative. A reduction in moisture content from 46% to 6% takes at least 6 months (Karaim *et al.*, 1990).

Research has been carried out on the value of aspen for biofuel production in Europe and in North America. Whole trees, including tops and branches, could be utilized as part of a thinning operation or as a short rotation (10–20 year) clear fell. The mean total standing dry weight of aspen has been calculated as 148 tonnes/ha (range 28–501 tonnes/ha) (Johansson, 2002). However, some authors (*e.g.* Stone, 2001) have questioned the sustainability of total tree harvesting as the loss of nutrients, organic matter and water-holding capacity may not be worth the additional biomass from lop and top.

Most forest tree species return between 50% and 80% of their annual nutrient uptake to the soil but aspen retains over half of its uptake and is particularly efficient at retaining calcium, sulphur and zinc, thereby limiting loss by leaching and improving soil fertility. The ability to absorb zinc and other trace elements allows aspen and hybrid aspen to survive on the spoil heaps of mining operations and assist in the reclamation of post-mining landscapes, for example lignite mines in Germany, opencast oil shale quarries in Estonia and many sites laid bare by coal spoil, heavy metal and smelter pollution in North America (Cripps, 2003; Pastor, 1990; Tullus *et al.*, 2008). In North America aspen has been found to naturally colonise large areas of polluted industrial sites and to tolerate soils with low pH, low fertility and heavy metal content. The ability to sucker is also an advantage for rapidly extending across new areas of bare ground. Some aspen forests have developed diverse habitats and thrived for over 70 years on mine tailings near smelter sites. Aspen has a mutualistic relationship with a small group of mycorrhizal fungi from the genera *Laccaria, Inocybe, Paxillus* and *Scleroderma* which help to increase phosphorus uptake and ameliorate soil conditions and may be essential for aspen to establish in contaminated soils (Cripps, 2003). Beneficial mycorrihiza such as *Laccaria laccata* have been recorded with aspen and other *Populus* species on uranium tailings and the spoil heaps of old arsenic mines in England (Benson *et al.*, 1980).

A previous section mentioned the value of aspen communities as a source of forage for livestock and wildlife.

Aspen bark is 50% digestible and the wood is 35% digestible and both can be ground up and manufactured into pellets for cattle. Steamed aspen pellets can contribute up to 30% of the dry matter diet of beef cattle without adversely affecting weight gain or quality. A similar proportion can be used as a roughage substitute for mature sheep (Mueggler, 1985).

Aspen has been used indirectly as a nurse crop for shade tolerant species, mainly conifers (DeByle, 1990). Other reports have considered the species to have serious disadvantages as a nurse crop because it can hinder the development of other species and even when cut out will frequently return as vigorous sucker growth (Nisbet, 1905; Worrell, 1995b). However, Borset (in Worrell, 1995b) considers that the advantages of the aspen presence in terms of soil improvement for example may outweigh any disadvantages.

Forested ecosystems have a high potential for carbon sequestration as they can store substantial amounts of carbon in the soil and in the vegetation. The extensive aspen forests in North America are a significant carbon sink and can be utilised to mitigate the rise in atmospheric CO_2 and the anticipated global warming. However, the effectiveness of any strategy will depend on the types of management and the rotation length. Aspen stands on a 40 year rotation will store more carbon than those on a 15 year rotation (typical for biofuels) and also more carbon than old growth forests (Alban & Perala, 1992; Chen *et al.*, 1998). After 60-80 years total ecosystem carbon in the aspen forests will have reached its maximum and there will be losses due to decomposition although dead wood can sequester carbon for long periods of time, provided it is not burned (Chambers *et al.*, 2000).

Aspen has very particular aesthetic and visual qualities and in the Rocky Mountains of North America is associated with recreation and scenic beauty. Here it has a more multi-purpose function and is managed for landscape, watershed protection, soil conservation, wildlife and small-scale timber use (Wengert *et al.*, 1990).

Aspen in Scotland plays a similar role in terms of nature conservation and amenity value but, as stand areas are small, it does not yet possess the appeal of an extensive aspen landscape. There is very little aspen timber production in Scotland at the present time although there may be future opportunities available from new planting schemes involving aspen (Worrell, 1995b). There may also be future developments that could utilize aspen, because it has a higher wood density than poplar, in biomass production (Harrison, 2009). ■

Propagation

'Aspen from seed is by far the most productive, the fastest and the most economical means of propagation'

In order to introduce or re-introduce aspen into areas where none currently exists the planting of aspen trees is the only feasible option. In Scotland aspen has only been planted in small amounts for amenity and conservation purposes and until recently most of the planting stock has originated from imported sources (Ennos *et al.* 2000; Hollingsworth & Mason, 1991). Native origin sources are now the preferred option but, as local-origin aspen seed is only rarely available in Scotland, planting stock is generally propagated by vegetative means (Worrell, 1999).

In Europe and in North America there have been five different methods used to produce aspen for planting schemes.

9.1 Root cuttings

This is a relatively simple procedure that can produce up to 200 plants from one 2-year old stock plant per year although the success rate can be lower than 50% and there is considerable variation among different clones (Stenvall, 2006). It is important to use cuttings that are under 2 cm diameter and plants can be produced without the need of misting equipment (Jobling, 1990).

9.2 Stem cuttings

This method has a better success rate but requires laboratory or heated greenhouse conditions, is laborious and costly and only produces a few plants from each stock plant per year (Hall *et al.*, 1990; Stenval, 2006). However, a great many small stem cuttings can be produced at the same time in order to bulk up the quantities. Hardwood cuttings tend to have a poor success rate but new softwood stem cuttings can be more readily induced to grow (Perala, 1990). Tissue culture using micro-propagation techniques has also been attempted with considerable success but again laboratory procedures are required (Hall *et al.* 1989).

9.3 Transplanted cuttings

This involves the removal of young root suckers (stem plus a section of root) from existing trees and transplanting, usually into nursery rows for a year until the root system has developed, and then planting out (Jobling, 1990). The process has a moderate success rate but is slow and only feasible if a small number of aspen plants are required. Using hardwood cuttings from the second year of growth is another method but is also slow, requires a rooting compound and may have poor establishment success.

9.4 Root sucker cuttings

This has been the most successful of the vegetative propagation techniques and was first tried with *P. tremula*. Sections of root are collected from parent trees during the dormant season, kept in a suitable medium and when suckers develop these are severed from the root and grown on under humid greenhouse conditions, usually in a misting unit. The root suckers can continue to produce additional sucker shoots and these in turn can be grown on to act as stock for future cuttings. The timing for the collection of the root sections may be crucial to the ability of the root cuttings to produce the maximum number of new shoots. The level of carbohydrates, which are necessary for regeneration, are highest during dormancy but then start to diminish in spring as the carbohydrates are transported back to the aerial buds (Stenvall, 2006). Root sucker cutting is now the standard procedure used in the vegetative production of aspen in Europe and North America (USDA, 1985) and the method of collection and production have been described by Hollingsworth & Mason (1991), Trees for Life (www.treesforlife.org) and Schier *et al.*, (1985). Rooting success is generally very high at between 90-100% when propagating the shoots under mist in greenhouse conditions (Mason *et al.*, 2002) but there is considerable clonal variation (Hollingsworth & Mason, 1993). The entire propagation process is labour intensive for a production output of hundreds of shoots and, unless there is a large-scale commercial operation, can only supply plants for conservation and amenity.

9.5 Seed

Aspen from seed is by far the most productive, the fastest and the most economical means of propagation (Schier *et al.*, 1985). The production of seedlings requires less equipment, labour and space compared to any of the vegetative procedures and has the potential to produce seedlings in the tens of thousands rather than the hundreds. In Europe aspen is frequently grown from seed (Jobling, 1990), and although it is carried out only occa-

Vegetative propagation from root sucker cuttings is widely used to produce small quantities of planting material

sionally in Scotland (Worrell, 1995b), there are several publications that describe the collection, germination and development process (Gray, 1949; Jobling, 1990; Worrell, 1995b & 1999). There are also other advantages to using seed. Seed stock can take full account of any adaptive variation in the gene pool, will introduce natural selection pressures and will be better able to take advantage of change in the environment, particularly if that change differs from anything that aspen populations have experienced throughout the Holocene. In order to cope with future climate change aspen must be able to maintain genetic diversity; the only way to do this is through sexual reproduction (Romme *et al.*, 2001; Miller, 1996).

Seed can be collected from natural stands or from a seed orchard – the latter having the advantages of controlled production (Vanhala & Hubert, 2009). Seed or sucker cuttings for a seed orchard could be collected from superior clones with desirable characteristics and treated for maximum seed production. Seed orchards would ideally be isolated from any potential external pollen contamination, sited in an area with soils and climate best suited to seed production and managed to maximize flowering and seed production, for example inside a polytunnel.

Wild seed would normally be collected from trees that are most likely to bear viable seed such as areas where aspen is abundant and thus probably near to a synchronized pollen source or from edge trees and isolated trees which can flower more often than those in dense stands (Schier *et al.*, 1985; Worrell, 1995b). Aspen can also be induced to flower by girdling the stem, either by stripping a ring of bark or by drawing a wire underlain by a metal strip around the stem (Jensen, 1942 in Schier *et al.*, 1985). The girdling would not be deep enough to kill the aspen as the damaged area would in time cicatrise and become overgrown (Nisbet, 1905). Small amounts of seed can be collected from cut and trimmed branches which are then left standing in water until seed matures. It may also be possible to carry out the same procedure with male and female branches and artificially pollinate the female catkins (Worrell, 1995b). Aspen seed can be stored for future use by drying the seed down to 5% moisture content and keeping it in a sealed vacuum at a low temperature. Viability of the seed is reported to be good for at least three years (Jobling, 1990). ■

Management

'The traditional approach to aspen managed for timber has been to clearfell, allow suckers to regenerate without the need for any thinning and then clear again when the stand reaches maturity'

10.1 Growth and yield

There are no specific growth models for aspen in Scotland and the nearest equivalent, suggested by Mason *et al.* (2002) would be the yield class table for sycamore/ash/birch which gives maximum Mean Annual Increment (MAI) range from 4–12 m^3/ha/yr based on a 40–55 year rotation (Hamilton & Christie, 1971). Worrell (1995b) quotes Scandinavian values of 4–10 m^3/ha/year for a similar rotation age. A study of growth and biomass of aspen in Sweden reported MAI values for total dry weight ranging from 1.23–7 tonnes/ha/yr (mean 3.16 ± 0.25 tonnes/ha/yr), which is close to the range of other studies of European aspen (4–14.2 tonnes/ha/yr) and of North American *Populus tremuloides* (0.8 – 11.5 tonnes/ha/yr) (Johansson, 2002). Other North American reports give a production of 10.2m^3/ha/yr for a managed aspen stand but occasional exceptional growth of 14.6m^3/ha/yr has been recorded in Minnesota (Perala, 1990). In Sweden mean annual production of aspen on fertile ground was 7 – 10 m^3/ha (Karacic, 2005). In contrast trials of the faster growing hybrid aspen (*P. tremula* x *tremuloides*) produced yields above 20m^3/ha/yr over a 20-25 year managed rotation (Karacic, 2005).

Basal areas exceeding 25m^2/ha are considered necessary for economic production but undisturbed and unmanaged aspen stands in Scandinavia rarely achieve this figure (Johansson, 2002). In the North American Lake States basal areas of 32.9m^2/ha have been reported (USDA, 2008).

In terms of height growth the best sites for aspen in North America produce trees that on average exceed 21 metres. Mean heights below 16.7 m are regarded as having a poor site index (Martin & Lorimer, 1997). Worrell (1995a) quotes Norwegian yield model heights of 20-29 m at age 70 years with occasional top heights from other countries in western Europe and Scandinavia averaging 25-30 m. Mason *et al.* (2002) reported on heights in Scotland ranging from 6 – 18 m with the taller trees found on the sheltered and more fertile sites, although aspen up to 25 m have also been recorded.

The rate of early height growth can be variable. Sucker growth for *P. tremuloides* in the first year can range from 0.3 m to 2.5 m with decreased growth in the second year and averaging 3–5 m total height by 5 years old (Miller, 1996). This is faster than the 1.5–3 m average height growth after 6 years recorded by Mason *et al.* (2002) but very comparable with the 3.5–5 m height growth recorded for a superior aspen clone in the same study. In Norway Worrell (1995a) describes four-year old suckers up to 6.7 m in height, with a girth diameter of 4.2 cm and with the longest annual shoot extending to 2.2 m.

10.2 Management for timber

There is a considerable body of published information on the management of aspen in North America, Europe and Scandinavia but despite some early guides (Weigle & Frothingham, 1911; Zehngraff, 1949) aspen was an under-utilised resource until the early 1970s (USDA, 2008). In Europe and Scandinavia there is also considerable management information on aspen, particularly on hybrid aspen (Beuker *et al.*, 2000; Karacic, 2005; Johansson, 2002). In the past few decades as commercial interest in aspen began to flourish in North America there have been a series of symposia and guides focusing on aspen ecology, use and management (DeByle & Winokur, 1985, Adams, 1990, USDA, 2001; USDA, 2008).

In Scotland there have only been some very preliminary reviews relating to aspen management (Mason *et al.*, 2002; Worrell, 1995b).

10.3 Silviculture

10.3.1 Regeneration and establishment

The traditional approach to aspen managed for timber in North America has been to clearfell, allow suckers to regenerate the site without the need for any thinning and then clear again when the stand reaches maturity (Cleland *et al.*, 2001). Similar practices occur in Sweden where despite the high initial density of suckers the self-thinning ability of aspen means that there is little requirement to thin prior to harvesting (Karacic, 2005). A complete clearfell has been shown to promote extensive and vigorous sucker regeneration on good sites while typical silvicultural techniques such as thinning, seed tree retention and pruning have had variable success in the improvement of growth and yield (Bokalo *et al.*, 2007). Regeneration from seed is too unpredictable to be a reliable form of crop replacement. Early management guidance had already established that the retention of some aspen trees after felling produced less prolific and less vigorous sucker regeneration (Zehngraff, 1949). It is the felled stumps that propagate the next crop not the aspen that might be retained (Miller, 1996). This is because aspen responds best to disturbance-driven change such as fire, windthrow or man-made disturbance such as clear fell logging. This releases the aspen clones from apical dominance and increases available light (Shepperd, 2001). Mean sucker densities of 80,000 stems/ha have been recorded in the year following a clearfell although extensive self-thinning takes place where sucker densities are high (Murray & Kenkel, 2001). Between 25 and 50 aspen trees relatively evenly distributed across a hectare can, after felling, produce over 10,000 suckers (Miller, 1996); this is more than enough to replenish the stand. Worrell (1995b) refers to claims by some authors (*e.g.* Gray, 1949) that regeneration of aspen by suckers produces slower growth rates and leads to an increase in decay but there is no firm evidence or research to support this view.

The timing of harvesting operations can affect sucker regeneration. Heavy machinery in early spring for example can cause compaction of the soil, increased wetness and damage to shallow rooted aspen roots. All of these factors can result in reduced or patchy regeneration (Bates *et al.*, 1990; Navratil *et al.*, 1990). Nevertheless, sucker densities after a summer felling can be very high due to the increased soil temperature as a result of clearing and disturbance (Miller, 1996). Some studies have reported that excessive amounts of coarse woody debris can decrease soil temperature and inhibit root sucker development (Miller, 1996) while others have suggested that genetic variation is the main factor controlling sucker density following disturbance (Murray & Kenkel, 2001). Winter harvesting is generally recommended as the best time, at least in North America, for maximum sucker regeneration as mechanical damage is reduced and there are greater carbohydrate stores in the roots, which give a boost to future growth (Murray & Kenkel, 2001). Borset (in Worrell, 1995b) reports that most suckers are produced after a winter felling and least following a late summer cut. However, sucker regeneration will probably be more than adequate for regeneration purposes whatever time of year the trees are felled.

In areas where aspen does not occur it can be planted using transplants from either a vegetative or a seed source. Mason *et al.* (2002) reported good growth and survival of sucker cuttings planted at five sites in Scotland after six years. Zasada *et al.* (1987) reported good growth from a planting trial of seedlings in Alaska. However Shepperd & Mata (2005) recorded poor survival rates after six years of container grown seedlings planted in a riparian area in Colorado. The use of container grown seedlings, fenced enclosures and moist riparian soils may not always guarantee success. In the latter situation competing vegetation and exposure to increased numbers of rodents protected by the fence may have played a part in the losses. Worrell (1995b) recommends well-developed transplants and suggests planting relatively deeply to avoid desiccation of the roots. Several sources (*e.g.* Worrell, 2008) suggest that plants will grow best in freely drained mineral soils (*e.g.* brown earths, podsols, iron pans, sandy, silt or light to medium clay types) and that dry sites, deep peat or heavy clay soils should be avoided if the crop is to produce timber. Waterlogged soils are also unsuitable. Transplants tolerate dry sub-optimal conditions although growth is typically slow and the trees bushy with stems of poor form. Stocking densities will normally be similar to other species (*e.g.* 2 metre spacing) but could be reduced if there is natural regeneration present already. Worrell (1995b) recommends that the presence of natural regeneration of other species is beneficial as it helps to protect the aspen from grazing impacts. If vegetatively produced suckers are transplanted for conservation objectives then it is generally recommended that a range of clones, including female and male plants, from native sources are used in order to maintain genetic diversity (Hubert & Cundall, 2006). Mason *et al.* (2002) suggest that plants be sourced from a minimum of 10 to 20 clones, depending on the size of the planting scheme. The Forest Reproductive Materials regulations (Forestry Commission, 2007) stipulate that each single tree from which root sections are taken must be registered as a separate clone in the National Register and that donor trees must be at least 110 metres apart.

It is generally recommended that the origin of trees used in planting schemes be sourced as near to the planting site as possible (Souter, 1991; Herbert *et al.*, 1999). In Scotland the statutory definition of local origin is based on the two broad regions of provenance in Scotland (east and west) as defined in the Forest Reproductive Materials Regulations (FC, 2007). These regulations apply to the marketing of aspen reproductive material and those of certain other native species. Recent evidence based on field trials has established that broadleaved seed stock, including aspen, from eastern continental Europe should not be planted in Great Britain; that transplanting seed from the north to the south within GB (of the order of hundreds of kilometres) is likely to lead to a loss of vigour compared with local material; and the northward movement of seed may result in a gain in vigour, but the long-term implications are not known, as transplants may for example be more susceptible to late spring frost (Hubert & Cundall, 2006). Quoting Norwegian guidelines, Worrell (1995b) advises that aspen stock should not be planted more than 1° latitude or 100 km north or south of the seed origin. More recently Worrell (2008) has found no evidence of maladaptation resulting from the transfer of aspen seed across large environmental gradients such as from Hungary to Scotland. The high degree of clonal variation in aspen in Scotland and the lack of any obvious geographical trends (Easton, 1997) has led to some speculation that seed origin may not be critical provided it is Scottish (Worrell, pers. comm.). Aspen growth trials in Scotland over a 14 year period have shown that the same clones grew equally well in either the east or the west of the country (Harrison, 2009). Further research from ongoing growth and provenance trials by Forest Research may provide clearer guidance on this subject.

In North America Stevens *et al.* (1999) studied the genetic variation of aspen seedlings following a rare episode of natural regeneration in Yellowstone National Park and found that there was no significant differentiation among the sampled populations at different elevations or geographic locations. However, there may well be differences associated with the movement of seed across some more distant geographical boundaries. Jones & DeByle (1985) concluded that there was a clinal pattern associated with genetic variation. Aspen seedlings from the western United States when grown in the east (Massachusetts) almost all died by age 12 while seedlings of Lake States origin survived. Similarly, Kimball *et al.* (1985) have reported that *P. tremula* from middle latitude European sources and *P. tremuloides* from the Lake States grew well in Massachusetts but Scandinavian origin *P. tremula* and western origin *P. tremuloides* did not.

Fertilising young aspen with NPK seems to be effective in some cases at increasing growth. Worrell (1995b) refers to examples in southern Norway where girth of pole sized trees with large crowns increased by 35% but small crowned trees showed little reaction. Gray (1949) found that applying cow manure or organic compost produced vigorous growth in nursery planting stock. In Alberta, Canada an experiment monitoring the effects of fertiliser and irrigation on aspen seedlings showed that stem volume increased by 78% after three growing seasons (van den Driessche & Martens, 2003). However, in the same experiment the application of fertiliser without irrigation resulted in no effect on growth, and it also decreased survival by 17%.

10.3.2 Thinning

Thinning a forest crop in order to increase productivity and to remove the least valuable timber trees is a tried and tested method common in forestry management. However, there are pros and cons in relation to the thinning of aspen. A number of studies have demonstrated that aspen responds favourably to thinning with an increase in diameter growth and a reduction in the length of pulpwood rotations (Cleland *et al.*, 2001; Zehngraff, 1949; Jones & Shepperd, 1985a). However, there are some mixed results depending on age of thinning and on site conditions. In the North American Lake States thinning new sucker growth (ages 1 to 5 years) is generally ineffective and thinning stands greater than 30 or 40 years old may only show a moderate improvement at best (Jones *et al.*, 1990; Miller, 1996). Penner *et al.* (2001, in Bokalo *et al.*, 2007) found that thinning a stand of 4000-5000 stems/ha at age 20 years produced similar results to an unthinned stand that had self-thinned to 1000-2000 stems/ha by the age of 36 years. In contrast, thinning experiments on aspen growing further north in Quebec found that there were volume improvements in both a 45-year old stand and in a 5-year old stand (Weingartner & Doucet, 1990). Other studies showed a decline in volume production with increasing thinning intensity (Navratil *et al.*, 1990). The most effective age seems to be pole stage aspen, between ages 7 and 15 years (Miller, 1996) with a spacing of about 2.5 metres or 1600 stems/ha (Zehngraff, 1949; Miller, 1996; Worrell, 1995b). The arguments against thinning aspen include increased branch size and greater risk of decay through larger branch stubs, increased risk of infestation by poplar borer beetle and increased risk of canker infection, which appears to prefer low stand densities (Cleland *et al.*, 2001; Miller, 1996). Thinning aspen stands may also initiate an increase in the understorey shrub layer which may restrict aspen regeneration after the final harvest (Navratil *et al.*, 1990). Since aspen is a very dynamic species, particularly during the first 20 years, and is able to self-thin as the stand develops, some authors have questioned the need to thin on cost grounds (DeByle, 1990). Thinning may also be damaging to certain flora and faunal groups that may be dependent on aspen. The final choice will probably depend on the site and the objectives of management. Generally if the timber is destined for pulp and fibreboard, thinning is not recommended as there is little point in growing larger trees, but if sawlogs are required then thinning could be considered (Miller, 1996).

10.3.3 Rotation period

A number of North American sources recommend that harvesting for timber production should not be beyond 80 years in order to avoid losses from decay and excessive staining (Jones & Shepperd, 1985b; Miller, 1996). On better sites a rotation age of 60 years has been suggested. A study by Pothier *et al.* (2004) showed that at 60 years there was a loss of volume and the proportion of tree mortality and decay increased substantially. Earlier guidance had recommended a 55 year rotation and suggested that if larger sized trees were required then production should be obtained through management to produce faster growth (Zehngraff, 1949). One recommended rotation period for European aspen is 60–80 years and if the output is for biofuel production then a rotation of 20–40 years is acceptable (Johansson, 2002). Other European recommendations are for a rotation age of 40–60 years (Karacic, 2005; Worrell, 1995b). In the Lake States of North America a rotation age of about 25 years is suggested if maximizing fibre production is the objective and growing conditions are good (Perala, 1973). There may however be a reduction in productivity with repeated short rotation cycles possibly because of regenerative stress that might result in the root systems failing to produce enough suckers (Miller, 1996). Pastor (1990) suggested that whole tree harvesting and short rotations (30 years or less) were a substantial drain on soil nutrient reserves, since a great deal of nutrients is stored in tree crowns.

There may not be any overall silvicultural solution for increasing productivity in the management of aspen because clones sizes are often small and clonal variation may be considerable. For example, there is evidence of clonal variation in the extent of decay although genetic influences may only account for 30% of the variation and the rest may be due to site conditions (Miller, 1996). Stain and decay in aspen timber are the most important factors that affect commercial utilization of the timber but identifying the most susceptible clones has practical difficulties when clone sizes are small and several clones are in close proximity. There are also clonal and/or site differences in the age at which decay begins while aspen decline itself may be a complex process that is thought to be linked to factors such as insect defoliation, pathogens and extreme climatic events (Pothier *et al.*, 2004).

One of the issues facing the management of aspen in North America and Europe is that it is largely natural stands that are being utilized for timber or for livestock grazing and management is not promoting replacement of the resource (USDA, 1985). The demand for OSB manufactured from aspen in North America has put a huge strain on the sustainability of the resource. Ironically, OSB had been regarded as an ecofriendly product as it used 'weed' species such as aspen, thereby safeguarding the old-growth forests (Kerasote, 2001). Kouki *et al.* (2004) report on the loss of old growth aspen as a consequence of forest management in Finland. Smith & Smith (2005) describe the change in dominance from pure aspen to conifer forests in Utah. With the increase in aspen utilization for timber the species has taken on an important economic role in Scandinavia and in North America (Karacic, 2005; Miller, 1996). However, despite this importance management that is damaging to the sustainability of the aspen resource continues to be practiced. Aspen is gradually being replaced by other hardwoods, by conifers (that shade out aspen and restrict replacement suckering), by grazing and conversion to other land uses (Cleland *et al.*, 2001; Shepperd *et al.*, 2006; Spencer *et al.*, 1990).

10.4 Management for conservation or multi-purpose objectives

There is a range of published material on the management of aspen for specific ecological purposes (Adams, 1990; DeByle & Winokur, 1985; Kouki et al., 2004; USDA, 2001; USDA, 2008).

Mason *et al.* (2002) have suggested that if an aspen stand is to sustain itself and its associated species there should be a minimum of three age classes. These should include old growth aspen of 80 – 120 years of age along with a dead wood component, immature or medium age trees 30 – 50 years old and sapling or pole stage trees less than 10 years. Timber production could still be an option for part of a site if practiced with multi-purpose objectives and included the retention of trees, particularly old growth elements and other age classes with dependent species associations (Cleland *et al.*, 2001). Limited intervention may to some degree emulate natural disturbances such as windblow thereby increasing structural complexity and biodiversity. The retention of trees in the canopy may reduce the amount of new sucker growth but mature trees left in isolation will be prone to windblow and will eventually contribute to the deadwood component (USDA, 2008). However, management for biodiversity is a complex process in the aspen ecosystem because of the wide range of flora and fauna, many of them with quite precise specializations that depend on different parts of the aspen habitat. Prescott (2009) reports on the use of seasonal stock grazing (or cutting by hand) to promote and maintain the short aspen suckers that are the main food source of the rare Dark Bordered Beauty moth. And in aspen stands where there is a shortage of dead fallen trees MacGowan (2009) describes the felling of dead aspen snags to provide the food source for the larvae of the aspen hoverfly. Some remedial management techniques are best applied only to situations where there is a risk of local extinction as the felling of live trees, to provide emergency dead wood habitat for example, could be damaging to the ecological needs of other aspen-dependent species such as lichens and bryophytes.

Restoring aspen stands that are of a fragmented nature is an important conservation management objective in Scotland where small groups of aspen are frequently isolated from each other. Isolation can prevent the colonization of new habitats and poses a threat to many aspen-dependent species that have poor dispersal ability (MacGowan, 2002). Aerial surveys using colour infra red or high definition photography has proved to be a rapid and useful means to map the fragmented aspen stands, particularly in spring when the unflushed aspen leaves stand out from the other trees (Miller, 1996; Parrott, 2006). Detailed mapping will be an essential tool in helping identify areas for the establishment of new aspen stands and in the creation of habitat networks of aspen-rich native woodland. ■

Conclusions

'Aspen has proven to be a resilient species with a great ability to adapt to a variety of environments'

Many of the aspen forests throughout the boreal region are missing key components of their life stage classes. In many cases, important natural disturbances have been curtailed or dynamic life cycle patterns have been altered. In some instances all three elements have impacted on the aspen resource. The main factors involved in the current state of the aspen resource are overbrowsing by livestock and wild herbivores, forestry management practices and the control and regulation of two important natural disturbance mechanisms – fire and flooding (Linder *et al.*, 1997; Shepperd *et al.*, 2006). Fire was probably the main disturbance system in North American and Scandinavian forests (Murray & Kenkel, 2001) but is probably less important in the temperate deciduous forests of Scotland where windblow in association with natural mortality and decay has a greater impact on woodland structure and heterogeneity. Although timber harvesting has taken over as a major disturbance factor in North America and Scandinavia the suppression of natural fires has resulted in a dramatic increase in conifers at the expense of the aspen forests. In Scotland landscape-scale dynamics of aspen as a result of disturbance factors are largely absent because of the very small size of the stands. Most areas of aspen consist of one life stage class or occasionally two. The four phases of stand development recognized by Oliver & Larsen (1996) are generally present on a few protected aspen sites where woods are either enclosed by a fence and/or browsing levels have been sufficiently reduced to allow regeneration to become established.

Published material by Worrell (1995), Mason *et al.* (2002), Cosgrove & Amphlett (2002), Cosgrove *et al.* (2005) and Parrott & MacKenzie (2009) contain substantial information on the contribution and importance of aspen in Scotland to landscape, wildlife and biodiversity and also its potential as an important timber crop in the future. The consequences of deteriorating aspen habitats, the failure of regeneration and the prevention of succession will have impacts not just on aspen but also on all its associated species. Many aspen-dependent species would be unable to colonise new areas if local aspen extinctions took place in a fragmented landscape. Management solutions to restore aspen habitat needs to consider a reduction in browsing, expansion and diversification of existing aspen stands and new planting of aspen to improve the linkages between the fragmented populations.

Climate change may have important impacts on the dynamics of aspen. A number of studies have pointed out the need to have moisture present in the soils in order to produce the best growth and quality of aspen (Weingartner & Doucet, 1990). A change in the environment may create conditions better suited to seed production and seedling establishment. Changes in rainfall patterns might mean that dry sites become more suited to quality aspen growth but it may be more difficult for aspen to survive on marginal sites. Aspen growing on ecotones perhaps at the higher altitude levels might be affected while higher temperatures and increased rainfall could facilitate rapid growth in competing species, population increases of defoliating insects and greater impact from pathogenic fungi (Shepperd *et al.*, 2006). Aspen, with its wide tolerance levels to a range of soil types and altitude gradients, its ability to reproduce asexually without significant loss of genetic variation and with the possibility of occasional sexual reproduction to produce new genetic individuals, could be well suited to take advantage of climate change. Aspen has proven to be a resilient species with a great ability to adapt to a variety of environments but, to ensure that genetic diversity is maintained during a period of impending climate change, sexual reproduction (or new planting from seed) may be essential (Romme *et al.*, 2001). This is best achieved if the existing population is in a healthy and vigorous condition, with its full complement of stand development phases from old growth to stem initiation and with larger and more extensive populations, created by natural expansion or by planting of new stands. ■

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The European aspen *Populus tremula* and the closely related Quaking aspen *Populus tremuloides* of North America have the widest natural range of any tree species in the world. Aspen was one of the first tree species to colonise the landscape after the last ice age. Its ability to produce large numbers of suckers has resulted in extensive stands of single aspen clones covering many hectares, which some regard as being the largest, and oldest, living organisms on the planet. Aspen is a keystone species for a diversity of flora and fauna throughout its range. It plays a valuable role in landscape diversity and amenity. In North America and the Baltic States, aspen is an important timber tree.

The purpose of this review is to collate information from published sources and provide an up-to-date account of current knowledge relating to aspen, with particular reference to Scotland.