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Biological Flora of the British Isles: *Phragmites australis*

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Summary

1. This account presents comprehensive information on the biology of *Phragmites australis* (Cav.) Trin. ex Steud. (*P. communis* Trin.; common reed) that is relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors and to the abiotic environment, plant structure and physiology, phenology, floral and seed characters, herbivores and diseases, as well as history including invasive spread in other regions, and conservation.

2. *Phragmites australis* is a cosmopolitan species native to the British flora and widespread in lowland habitats throughout, from the Shetland archipelago to southern England. It is widespread throughout Ireland and is native in the Channel Islands. Native populations occur naturally in temperate zones and on every continent except Antarctica. Some populations in Australia and North America have been introduced from elsewhere and have become naturalized, and in North America, some of these are known to be invasive where they compete with native local populations of *P. australis*. Typical habitats in Britain range from shallow still water along waterbody edges to marshlands, saltmarshes and drier habitat on slopes up to 470 m above sea level. Additional habitats outside Britain are springs in arid areas, riverine lowlands (−5 m above sea level) and groundwater seepage points up to 3600 m above sea level. Although it occurs on a wide range of substrates and can tolerate pH from 2·5 to 9·8, in Britain it prefers pH >4·5 and elsewhere it thrives in mildly acidic to mildly basic conditions (pH 5·5–7·5). The species plays a pivotal role in the successional transition from open water to woodland.

3. *Phragmites australis* is a tall, helophytic, wind-pollinated grass with annual shoots up to 5 m above-ground level from an extensive system of rhizomes and stolons. A single silky inflorescence develops at the end of each fertile stem and produces 500–2000 seeds. The plant is highly variable genetically and morphologically.

4. Expansion of established populations is mainly through clonal growth of the horizontal rhizome system and ground-surface stolons, while new populations can establish from rhizomes, stem fragments and seeds. Shoots generally emerge in spring, with timing determined primarily by physiology that is mediated by external conditions (e.g. local climate including frost).

5. Many populations in the British Isles have experienced some decline over the past two decades and there is concern that there might be further losses along the east coast as sea level rises. There have recently also been localized expansions, especially in highly modified habitats, where *P. australis* reedbeds have been planted as wildlife habitat, rehabilitated mineral and gravel beds, and bioremediation filter beds for industrial and transport infrastructure. Native populations outside Britain also demonstrate both types of trend: they are declining in many parts of Western Europe and North America, yet also colonize many disturbed, ruderal habitats (e.g. the edges of agricultural fields and motorways) throughout its native and non-native range and can form 'weedy' monodominant populations (e.g. in Australia and China).

Common reed. Poaceae. *Phragmites australis* (Cav.) Trin. ex Steud. (*P. communis* Trin.) is a tall, perennial helophyte with an extensive system of stout, underground rhizomes. Horizontal rhizomes to 3 cm wide, and vertical rhizomes to 1·5 cm wide, form a dense mass 20–100 cm below the surface and extend to 1·5 m below-ground. Roots 2–4 mm wide extend down to 4 m. Individual stolons can extend, along ground or water surfaces, to >10 m and support >70 stem shoots. Stems up to 3·5 m in Britain and 5·3 m elsewhere, annual, round and robust, hollow, seldom branched unless damaged or, more rarely, persisting beyond the first year. Leaves deciduous, flat apart from 0 to 3 constrictions across the blade, 20–50(60) cm long, 1–4 cm wide in Britain (smaller on sterile plants), tapering to a long point, alternately attached with smooth, loose sheaths; wing-like auricles prominent; ligule with fringe of hairs. Inflorescence a soft panicle, 15–40(60) cm long, many branches, usually dull purple to brown in Britain. Spikelets (8) 10–15 mm long, with 2–5(6) fertile florets attached to a hairy rachilla (Haslam 1972). Scattered clusters of long, white, silky hairs on smooth branches between florets. Individual florets (apart from lowest) with basal tuft of silky hairs about the same length as lemma (scales encasing the floret); lowest lemma (8) 9–13 mm, fertile lemmas as long as spikelet. Lemma and glumes (scales at base of spikelet) lanceolate; lower glume 3–4·5 mm long; 0·5–0·6 length of upper glume (Clayton *et al.* 2015b). Stamens 1–2 in lowest floret, otherwise 3. Anthers 1·3–1·8 mm. Ovary glabrous (Haslam 1972).

The genus is included in the subfamily Arundinoideae (within the ecologically and economically important group of subfamilies known as the PACMAD clade) together with *Arundo*, *Molinia* and other genera (Cotton *et al.* 2015). *Phragmites australis* is the only species in the genus present in the British Isles (Stace 2010). World-wide, the genus currently contains four species that are recognized by the World Checklist of Poaceae (Clayton *et al.* 2015a), IUCN (Lansdown 2015) and The Plant List (2013): *Phragmites australis*, *P. japonicus* Steud., *P. karka* (Retz.) Trin. ex Steud., and *P. mauritianus* Kunth. *Phragmites japonicus* is native to the eastern Russian Federation, China, and eastern Asia (Clayton *et al.* 2015b). *Phragmites karka* is native and widespread in the tropical regions of central Africa from Senegal to Ethiopia and south to Uganda; Middle East from Oman, Saudi Arabia,

the United Arab Emirates and Yemen (Cope 2007); Pakistan to China and south-eastern Asia, northern Australia and some Pacific Ocean island groups (Lambertini *et al.* 2012b; Lansdown 2013). *Phragmites mauritianus* is native to tropical Africa (Lambertini *et al.* 2012b; Roskov *et al.* 2015).

Outside Britain, and particularly in North America, *Phragmites* taxonomy has developed rapidly over the past decade, in response to a broader range of morphological variation in this continent, and five species of *Phragmites* are often recognized: *P. australis*, *P. frutescens* (H. Scholz), *P. japonicus*, *P. mauritianus* and *P. vallatoria* (L. [Veldkamp]; syn. *P. karka*) (Lambertini *et al.* 2006; Meyerson *et al.* 2012). *Phragmites frutescens* was discovered in Crete and its distinctive morphological traits distinguish it from *P. australis* and *P. mauritianus* (Scholz & Böhling 2000). Infraspecific taxa within *P. australis* are currently unresolved (Conert 1961; Clayton 1967; Lambertini 2016; Saltonstall 2016), and *P. australis* may be considered to form a species complex. Inter- and intraspecific hybridization is discussed in VIII B, and genetic variability within the species is included in V A. As the species is highly genetically variable, the lineage used in research and management needs to be ascertained and clearly recorded. Failing to do so can substantially compromise predictions of its distribution and performance, such as in North America where results from a single population, or a couple of closely located populations, have been used to generalize about *Phragmites* across North America (Meyerson, Lambert & Saltonstall 2010). We have included information on the origin of clones wherever possible and recommend caution as many of the data included here are from single or few populations within a small range and may not necessarily be representative of *P. australis* throughout its native or non-native range. As a greatly valued and exploited plant worldwide (Cope & Gray 2009), *P. australis* has been, and continues to be, introduced intentionally or accidentally into many new habitats. The complexity resulting from this multitude of introductions is discussed in XI B, including a discussion of non-native haplotypes that are overlapping the native range in North America and Australia. Taxonomic work is necessary to resolve all this uncertainty and provide clarity across the genus (Pyšek *et al.* 2013; Saltonstall 2016) and biogeographic lineages within *P. australis*.

Phragmites australis is native and widespread in both shallow, lowland freshwater habitats (along edges of lakes, ponds and rivers and in ditches, fens, marshes and swamps) and saline habitats (saltmarshes, brackish lagoons and swamps) throughout the British Isles.

I. Geographical and altitudinal distribution

Phragmites australis is native throughout Britain (Figs 1 and S1, Supporting Information; see also Section X). It is most frequent in the south-east of England, where many stands occur, whereas stands are more scattered and smaller in the north and west (Preston, Pearman & Dines 2002). There are few large reedbeds (>2 ha) in Scotland (e.g. extensive reedbeds alongside the River Tay between Perth and Dundee, M.B. Usher, personal communication; see also Bibby & Lunn 1982; Maddock 2008). It occurs throughout Ireland and is most frequent in the north.

A cosmopolitan species (Den Hartog, Květ & Sukopp 1989; Clevering, Brix & Lukavská 2001; Lambertini *et al.* 2012b), *P. australis* occurs (Lambertini *et al.* 2012a), and has been considered native, on all continents except Antarctica (but see Fig. 2 for the current status of populations world-wide), extending from Canada in the west to the far east of the Russian Federation (Lansdown 2015). It is only absent beyond the latitudinal limits of 70°N (the most northern record is from Finnmark, Norway; Dahl 1934; Hultén & Fries 1986) and 43°S (the most southern record is from Rio Chubut, Argentina; Isacch *et al.* 2006). It is one of 14 species in the British Isles classified as circumpolar wide-temperate by Preston & Hill (1997). It is thought to be the world's most widespread angiosperm (Ridley 1923; Hutchinson 1975) and belongs to the 100 most common plant species of temperate Europe (Seregin 2010). *Phragmites australis* is absent or considered non-native on most islands (Table S1), although distribution and status data are uncertain in the archipelagos of Southeast Asia.

In its native range, including Britain, the broad-scale distribution of *P. australis* is considered relatively stable (Lansdown 2015). However, at finer scales, both the loss of some native populations (e.g. The Broads wetlands, England, and in North America) and the expansion of others (e.g. in wetlands constructed for avian conservation or bioremediation) has been recorded over the past 50 years (Preston, Pearman & Dines 2002). The conservation status of native reedbeds, and the expansion of non-native populations, is dealt with in Section X.

In Britain, *P. australis* occurs from sea level to several hundred metres above sea level. Although generally a lowland species, it reaches its maximum altitude of 455 m above sea level on Llyn Gorat, Cardiganshire (Chater 2010), and has previously been recorded at 470 m on Brown Clee Hill,
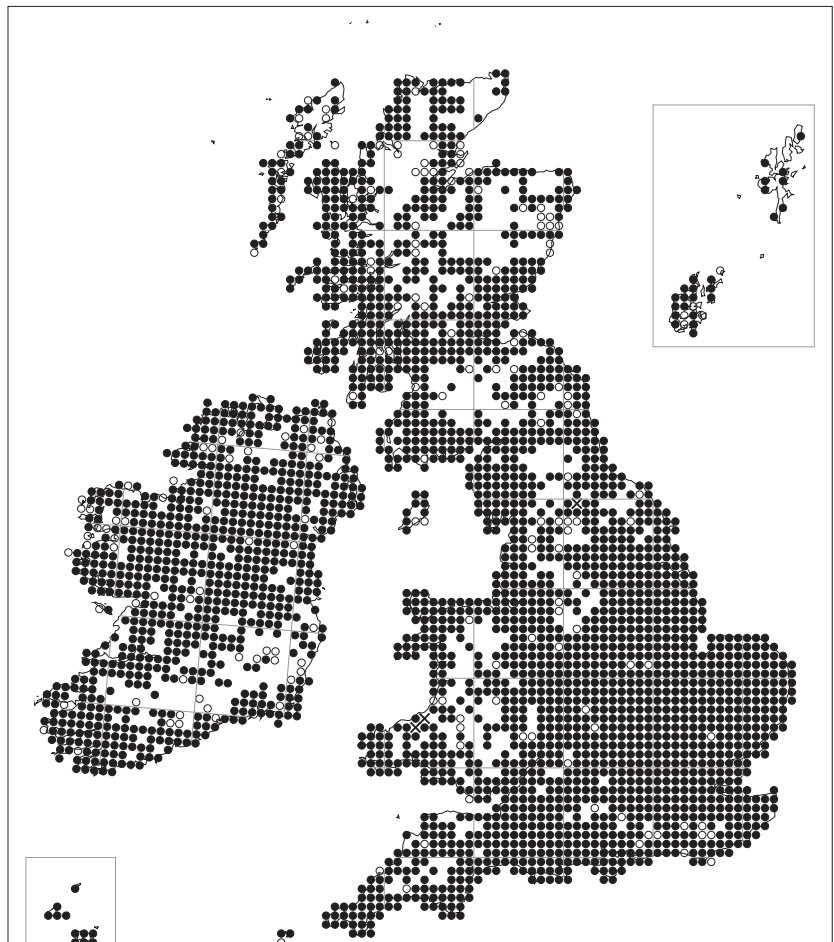

Fig. 1. The distribution of *Phragmites australis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (○) native pre 1970; (+) non-native 1970 onwards; (×) non-native pre-1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles, using Dr A. Morton's DMAP software.
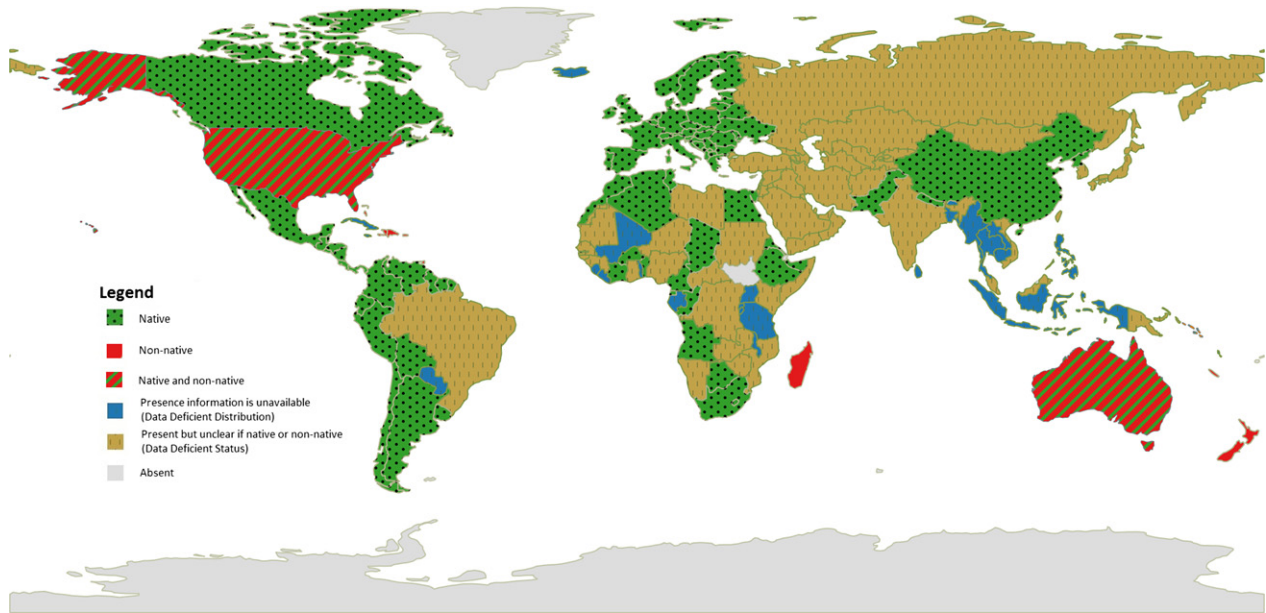
Fig. 2. Global distribution of *Phragmites australis* at a country level, with information on native or non-native status based on currently available data. See Table S1 for a compilation of distribution data and sources. [Colour figure can be viewed at wileyonlinelibrary.com]

Shropshire (Wilson 1956), 420 m in the Pennines, and c. 330 m in Scotland (Haslam 1972). The altitudinal range is greater beyond Britain, from approximately −5 m above sea level in the Manning River lowlands, Australia (Packer *et al.* 2017a), to 1910 m in the Central European Alps (Klimeš 2000) and 3600 m in Nepal (Press, Shrestha & Sutton 2016).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Phragmites australis occurs in climate zones ranging from cool (e.g. latitudinal limits of 70°N and 43°S; Dahl 1934; Haslam 1972; Isacch *et al.* 2006) to tropical (e.g. 0° at equator; Haslam 1972) and arid (e.g. oases in northern Africa and central Australia; Davies, Mackay & Whalen 2010; Pfaden-hauer & Klötzli 2014). Within Britain, it is most abundant in lowlands with a moderate climate, for example, in Maidstone in south-east England where *P. australis* has been recorded in forty-two 10-km^2 of the National Grid (Botanical Society of Britain & Ireland 2016), and the mean annual minimum temperature is 6·8 °C with 1651 sunshine hours (Met Office 2017). Stands are less abundant in lowlands with cooler climates, such as in Northern Ireland (e.g. Newcastle, where it has grown in twenty 10-km^2 in 6·2 °C and 1308 sunshine hours) and northern Scotland (e.g. Inverness, four 10-km^2, 5·6 °C and 1220 sunshine hours; see also Table 1 and Fig. 1).

Within its climatic range in Britain, *P. australis* is most commonly found in low-lying areas with shallow, still water (e.g. the edges of waterbodies, coastal tidal flats, marshes and fens). It is considered to be mostly limited by hydrology. The Ellenberg indicator value for moisture in both Britain and central Europe is 10 (i.e. shallow water to extensive periods without standing water; Ellenberg 1992; Hill, Preston & Roy 2004). Hydrology strongly influences *P. australis* growth through a range of factors including the depth, movement and stability of the water present and the nutrients within it. Large *Phragmites*-dominated reedbeds in the British Isles tend to occur in open water transition zones (e.g. lake edges in the south and west of Northern Ireland; Gibson & Crawford 2002), fen (e.g. The Broads in Norfolk; Buttery, Williams & Lambert 1965; Broads Authority 2014b), estuarine tidal flats, coastal or inland floodplains and artificial waterways (e.g. flooded clay pits and reservoirs) (Bibby & Lunn 1982; Rodwell 1998c; Cope & Gray 2009). *Phragmites australis* is consequently most abundant in these regions, although it is also more widespread as smaller pockets of these habitats occur throughout the British Isles. It can also occur on higher ground, such as in Cardiganshire (Chater 2010) and Perthshire, where there is sufficient moisture around groundwater seepage points (Spence 1964; Roberts 2000; Haslam 2010). It is usually absent where the water-table never approaches the surface.

Outside Britain, *Phragmites australis* can occur where the water-table is 2·3 m above-ground level (e.g. fringing Lake Balaton in 1996, Hungary; Engloner & Papp 2006) and has been reported to grow where the water level is c. 6 m below-ground level in Malta (Haslam 1972). The ecological amplitude of *P. australis* extends from a soil water content of 2·5–47% (Li *et al.* 2013) or a soil osmotic potential of 30–1000 kPa (Elhaak, El-Din & Sammour 1993). The optimum water level for growth of mature stems ranges from −30 to 70 cm above-ground level (Engloner & Papp 2006; Cui *et al.* 2010; Zhang *et al.* 2013). In Britain, it is most competitive in water c. 1 m below-ground level to c. 1-m above-ground level (Haslam 1971a). In the Huanghe River Delta, China, the *Phragmites australis*-dominated plant

Table 1. Frequency of *Phragmites australis* along a latitudinal and climate gradient in the lowlands of Britain. Frequency is derived from the number of tetrads (2 × 2 km) in which *P. australis* was recorded within a hectad (10 × 10 km) of the National grid (Botanical Society of Britain & Ireland 2017)

Weather station* (nearest BSBI Hectad)	Location*	Elev.* (m)	Max. temp. (°C)	Min. temp. (°C)	Air frost (days)	Sunshine (hours)	Rainfall (mm)	Number of tetrads (2-km²) of the National Grid where *Phragmites australis* was recorded as present						Total
								Pre-1930	1930–1969	1970–1986	1987–1999	2000–2009	2010 onward	
East Malling, England (TQ86)	51·283, 0·450	33	14·7	6·8	42·1	1650·8	647·8	0	1	11	18	0	12	42
Milford Haven, Wales (SM80)	51·708, −5·055	44	13·4	8·1	13·9	1625·4	1075·2	1	2	2	1	15	2	23
Murlough, Northern Ireland (J44)	54·245, −5·830	12	13·3	6·2	30·3	1307·8	983·1	1	1	3	12	3	0	20
Inverness, Scotland (NH64)	57·478, −4·223	13	12·5	5·6	42·9	1220·1	732·8	0	3	0	1	0	0	4
Baltasound, Shetland archipelago (HP60)	60·749, −0·854	15	10·2	5·4	37·7	NA	1108·1	0	1	0	1	0	0	2

*Location, elevation and climate data sourced from the Met Office (2017).

community was most diverse in −30 cm deep water, while % cover of *P. australis* was greatest in 0 cm of water (Cui *et al.* 2010). High biomass (5093 g m^{-2}) was recorded in 22 cm of water in the temperate Zhalong wetland, China (Zhang *et al.* 2013), and the tallest reported reeds (see V) grew in 10-cm-deep water in central Australia (mean water level within the stand was −4·3 cm, 95% CI 17·9–9·2; Packer *et al.* 2017a). New populations typically establish on bare, unvegetated moist soils after water levels recede as deeper water (≥5 cm) is unsuitable for seed germination and seedling establishment (Tulbure, Johnston & Auger 2007; Whyte *et al.* 2008) but supports clonal growth (Alvarez, Tron & Mauchamp 2005). *Phragmites australis* is capable of persisting for many years in sites which have ceased to be wetlands (Lansdown 2015), and rhizomes growing in floodplains can survive for approximately 10 years without flooding (Roberts 2000).

Phragmites australis is intolerant of strong or irregular water movement (waves or currents). It is damaged by moderate exposure (see e.g. Hürlimann 1951; Caffrey & Beglin 1996), uncommon in fast-flowing waterways due to scouring, and absent in habitats with severe exposure to currents or tides (Haslam 1972). Sheltered areas within these exposed habitats can sometimes support small populations of *P. australis*. Regular tidal movement, such as in estuaries and saltmarshes, does not inhibit *P. australis*. In fact, estuaries and saltmarshes are habitats where populations have been expanding in Europe (e.g. Sweden; Pehrsson 1988) and North America (Chambers, Meyerson & Saltonstall 1999). In contrast, sudden, irregular changes in water level are damaging (Haslam 1970a; Ostendorp & Dienst 2009). Data and simulated hydrology from the Huanghe River Delta, China, suggest that *P. australis* can tolerate irregular fluctuations of ±0·25 m (see also V B) without compromising ecosystem function (based on environmental, ecological and productivity indicators; see Cui *et al.* 2010). After an extreme flood in Lake Constance, Germany, the fringing reedbed contracted to 23% of the original area and vitality declined (shoot density, particularly in primary shoots; Ostendorp, Dienst & Schmieder 2003).

The Ellenberg indicator values for *P. australis* for light are 7 in both Britain and central Europe (i.e. generally grows in well-lit habitats but can also occur in partial shade; Ellenberg 1992; Hill, Preston & Roy 2004). Shading decreases inflorescence density (e.g. Lambert 1946; Kassas 1952), increases flaccidity and increases leaf to stem weight ratio; all of these characteristics are reversed on transplanting to full daylight (Haslam 1972).

(B) SUBSTRATUM

Phragmites australis grows on a variety of substrata, particularly flooded soils, littoral sands, mudflats and other substrates where the water-table is present throughout the root and rhizome mass (see II A for details on the influence of water-table depth). The organic content of the substrate ranges from 1% in mineral sediments (Hürlimann 1951; Lenssen *et al.* 1999) to 97% (Misra 1938; Haslam 1972).

pH

The Ellenberg indicator value for soil reaction for *P. australis* in Britain and central Europe is 7, indicating a preference for weakly acidic to weakly basic environments (Ellenberg 1992; Hill, Preston & Roy 2004; Table 2). The pH of the soil substrate is reported to be >4·5 (Cope & Gray 2009) in Britain and from 2·5 (Bittmann 1953; Guo & Cutright 2015) to 9·8 (Gong, Li & Tiyip 2014) elsewhere, although most thriving populations occur where the pH is 5·5–7·5 (Gorham & Pearsall 1956b; Matyuk 1960). The water pH ranges from 5·7 (Šantrůčková *et al.* 2001) to 9·1 (González-Alcaraz *et al.* 2012).

Nutrients

Nutrients come from the soil (Gorham & Pearsall 1956a, b; Haslam 1965) or the water (Spence 1964). *Phragmites australis* is absent from the most oligotrophic substrates but can survive at very low-nutrient levels in some habitats (e.g. 0·05 g N kg^{-1} in reedbeds in the arid Keriya River Basin, China; Gong, Li & Tiyip 2014). Limited availability of nitrogen, phosphorus and calcium can also restrict stem height and seedling survival (Hürlimann 1951; Haslam 1971c). Seedlings are particularly influenced by nitrogen and, to a lesser extent, phosphorus levels (Haslam 1970c). Field and greenhouse experiments in Massachusetts, USA, have shown that *P. australis* can adjust the above:below-ground ratio in favour of below-ground (roots and rhizomes) in low-nutrient conditions

(Minchinton & Bertness 2003; Minchinton, Simpson & Bertness 2006).

The Ellenberg indicator value for *P. australis* for nitrogen is 6 in Britain and 7 in central Europe (Ellenberg 1992), corresponding to richly fertile places (Hill, Preston & Roy 2004). In North America, the ecological amplitude of *P. australis* covers substrates with total N concentration from 0·35 to 14·7 mg g^{-1} in experiments (Meyerson, Chambers & Vogt 1999) and up to 2·43 mg g^{-1} in field sediments (Meyerson 2000; Ruiz & Velasco 2010). Reed can grow where total N content ranges from 0·036 to 134·4 mg L^{-1} in experimental solutions (Tylová *et al.* 2013), and 1·84 mg L^{-1} in an oligotrophic fish pond in Bohemia (Čížková 1996), through to 130 mg L^{-1} in the eutrophic Mar Menor Lagoon, Spain (González-Alcaraz *et al.* 2012). Rather than total N content, its forms, especially the ratio of $NH_4^+:NO_3^-$, play a role in controlling *Phragmites* performance. A ratio <1·0 had a positive effect on growth (e.g. even at extremely high N levels, such as N-NH_4^+ of 4·4 mM and N-NO_3^- of 5·1 mM), and a ratio c. 4·0 reduced productivity and was associated with stress symptoms that resembled *P. australis* in eutrophic dieback sites (Tylová *et al.* 2013). Extensive contraction of *P. australis* reedbeds in The Broads, England, has also been linked to eutrophication, particularly elevated levels of nitrate and a corresponding increase in its ratio to potassium (Boar, Crook & Moss 1989). Replicating these eutrophic conditions in glasshouse experiments resulted in a decreased ratio of shoot to rhizome biomass and softer shoot and rhizome tissue resulting from a reduction in the proportion of sclerenchyma

Table 2. Ellenberg indicator values for *Phragmites australis*, and substratum and water conditions in which it occurs in its native range globally

	Ellenberg UK	Ellenberg EU	Substratum field	Substratum experiment	Water field	Experimental nutrient solution	Sources
pH	7	7	2·5–9·8		5·7–9·1		1; 4; 10; 14; 15
Moisture	10	10					1; 5
N	6	7	0–2·43 mg g^{-1}	0·35–14·7 mg g^{-1}	0·036–134·4 mg L^{-1}	1·84–130 mg L^{-1}	1; 3; 5; 8; 10; 11
P			0·18–6·89 mg g^{-1}	0·02–0·102 mg g^{-1}	0·0036–5·470 mg L^{-1}	0·031–31 mg L^{-1}	3; 8; 11
Fe					<89 mg L^{-1}		12
Cd			<44 mg kg^{-1}				13
As			<638 mg kg^{-1}				13
Hg			<130 μg kg^{-1}				9
Pb			<15·9 g kg^{-1}				13
Cu			<275 mg kg^{-1}				13
Cr			<218 mg kg^{-1}				16
Co			<13·8 mg kg^{-1}				16
Zn			<11 g kg^{-1}				16
Ni			<81·6 mg kg^{-1}				16
Al			<19·4 mg kg^{-1}				16
B			<8·4 mg kg^{-1}		<30 mg L^{-1}		12; 16
Ca			0·06–3·4 g kg^{-1}		7·4–54 mg L^{-1}		2; 13; 14
K			0·03–1·4 g kg^{-1}		1·16–14·9 mg L^{-1}		2; 14
Mg			<1·4 g kg^{-1}		3·6–25·6 mg L^{-1}		2; 14
Mn			0·18–0·83 g kg^{-1}		0·4–0·53 mg L^{-1}		2; 7
Salt	2	0			<65 mg L^{-1}		1; 5; 6

Sources: 1, Ellenberg (1992); 2, Čížková (1996); 3, Lenssen *et al.* (1999); 4, Šantrůčková *et al.* (2001); 5, Hill, Preston & Roy (2004); 6, Engloner (2009); 7, Morari & Giardini (2009); 8, Ruiz & Velasco (2010); 9, Anjum *et al.* (2012); 10, González-Alcaraz *et al.* (2012); 11, Tylová *et al.* (2013); 12, Allende, McCarthy & Fletcher (2014); 13, Conesa *et al.* (2014); 14, Gong, Li & Tiyip (2014); 15, Guo & Cutright (2015), 16, Morari, Dal Ferro & Cocco (2015).

cells (Boar, Crook & Moss 1989). Concentrations of sulphides reaching 500 μM in saltmarsh systems may inhibit the ability of *P. australis* to uptake N (Chambers, Mozdzer & Ambrose 1998). However, as with other nutrients, plant-available N may be affected by the salinity of the system. In New England, USA, higher concentrations of NH_4^+ in porewater of *P. australis* populations in brackish (1·5 g mg L^{-1}) relative to freshwater marshes (0·09–0·05 mg L^{-1}; Meyerson 2000; Meyerson *et al.* 2000) suggest that Na^+ in brackish systems may occupy sites on the plant's cation exchange column, making fewer sites available for NH_4^+ adsorption.

Total P in the substrate where reed occurs can range from 0·002 mg g^{-1} in exposed mineral to 0·102 mg g^{-1} in sheltered organic sediments in the littoral zone along a freshwater canal (Lenssen *et al.* 1999) and from 0·18 to 6·89 mg g^{-1} in field sediments (Ruiz & Velasco 2010). Total P content in nutrient solutions ranges from 0·031 to 31 mg L^{-1} (Tylová *et al.* 2013) and from 0·004 to 5·470 mg L^{-1} in field water (Ruiz & Velasco 2010). Phosphorus was reported to limit reed growth in the Breckland and Anglesey fens (Haslam 1965). Rather than absolute P values, the N:P ratio in the substrate seems to be important, with values below 10 resulting in increased biomass, and high ratio values above 90 resulting in changes in resource allocation, morphology, metabolic relations and lower productivity (e.g. increased shoot density and reduced shoot diameter and height, root growth and rhizome growth, Tylová *et al.* 2013).

Trace elements

Phragmites australis can perform well under rather high levels of iron and heavy metals (Table 2), such as Fe of 89 mg L^{-1} in experimental water (Allende, McCarthy & Fletcher 2014) and Cd up to 44 mg kg^{-1} in soil of saltmarshes polluted by mining wastes (Conesa *et al.* 2014), Hg 130 μg kg^{-1} in a mercury-contaminated coastal lagoon (Anjum *et al.* 2012), and Pb 15·9 g kg^{-1} and Cu 275 mg kg^{-1} in a saltmarsh polluted by mining effluent (Conesa *et al.* 2014). The tolerance of Al and B can also be high: Al up to 19·4 g kg^{-1}, B up to 8·4 mg kg^{-1} in sand (Morari, Dal Ferro & Cocco 2015), or 30 mg L^{-1} in water (Allende, McCarthy & Fletcher 2014) of constructed wetlands. *Phragmites australis* can also accumulate high concentrations of nutrients and metals in its above- and below-ground tissues, such as C (324·43 g m^{-2}), N (7·79 g m^{-2}), P (0·52 g m^{-2}), Al (0·05 g m^{-2}), K (2·90 g m^{-2}), Mn (0·07 g m^2), Mg (0·68 g m^{-2}), Ca (1·41 g m^{-2}) and Fe (0·07 g m^{-2}) recorded in plants from two Connecticut River tidal marshes (Meyerson 2000). In an Opatovický fishpond in South Bohemia, Czech Republic, the N (13·7–40·9 g m^{-2}) and P (1·4–5·3 g m^{-2}) content of *P. australis* was comparable with other littoral species: *Typha angustifolia* 24·5–46·7 and 4·5–6·5 g m^{-2}, *Typha latifolia* 50·9 and 7·7 g m^{-2}, *Sparganium erectum* 23·9–28·7 and 4–7·4 g m^{-2}, *Acorus calamus* 14·9–21·3 and 2·1–3·3 g m^{-2} (Dykyjová & Květ 1978).

Relatively high concentrations of inorganic nitrogen are taken up by *P. australis* at fairly high concentrations (González-Alcaraz *et al.* 2012). Along with *Typha* species, *Juncus effusus*, *Schoenoplectus lacustris*, *Schoenoplectus californicus* and *Phalaris arundinacea*, *P. australis* is commonly used for waste water purification in constructed wetlands (Morari & Giardini 2009; González-Alcaraz, Conesa & Álvarez-Rogel 2013) in Europe and Asia particularly (Vymazal 2013).

The performance of reed is influenced by these varying levels of trace elements, e.g. metal-ion saturation levels reduced performance in Scottish lochs (Spence 1964). Potassium and excess Ca limited growth in Switzerland (Hürlimann 1951), and in Sweden, dissolved Ca limited shoot density while soil organic content limited shoot height (Gorham & Pearsall 1956a; see also Buttery 1959; Rudescu, Niculescu & Chivu 1965; data from Björk 1967). Calcium carbonate is used in constructed wetlands for acid water depuration to achieve pH suitable for *Phragmites* growth (Allende, McCarthy & Fletcher 2014).

Biomass decomposition

Phragmites australis is characterized by lower C- and N-mineralization (decomposition) rates relative to other large wetland species, such as those of *Typha*, *Carex* and *Phalaris* (Meyerson 2000; Windham 2001; Martina *et al.* 2014). Within *P. australis* itself, the leaves are high in N relative to the rest of the plant and decompose more rapidly than other parts (Meyerson 2000). The decomposition rate is also dependent on soil moisture (Haslam 2010), and the greatest decomposition has been recorded on wet sites (Völlm & Tanneberger 2014). Decomposition rates in drier habitats can be further reduced when the litter gets trapped in the stubble of dead, broken stems and accumulates more quickly than it decomposes (Table 3; see also Haslam 2010). In the oases of Dalhousie Springs, Australia, *P. australis* litter forms a dense thatch up to 2·3 m deep among reed stubble (Packer *et al.* 2017a). The litter mat is one of the main mechanisms by which *P. australis* out-competes other species and promotes succession (Haslam 2010) and is dealt with further in IV. Very little biomass is consumed as living tissue, and most of it enters the general pool of particulate organic matter following shoot senescence and death (Gessner 2000 and the references therein). High soil organic matter accumulation rates of 0·17–0·26 kg m^{-2} $year^{-1}$ have been observed for *P. australis* (Rohani *et al.* 2014).

Salt tolerance

The Ellenberg indicator value for *P. australis* for salinity is 2 in Britain (i.e. can grow in saline soils but not predominantly) and 0 in central Europe (i.e. may occur, but not persist, in coastal areas with saline water or spray, and absent from other saline habitats; Hill, Preston & Roy 2004). The ecological amplitude of *P. australis* extends from freshwater to brackish wetlands, with 3-m-tall stems growing with pore water of 50 g Na^+ L^{-1} around Burton Island, USA, and transplanted plants flowering in 65 g Na^+ L^{-1} glasshouse

Table 3. Decomposition rates (mean ± SD, k day^{-1}) calculated as (-k) = ln (dry mass of *Phragmites australis* leaf litter remaining/dry mass of *Phragmites australis* initially)/number of days of exposure. The studies used litter bags with similar mesh sizes, as specified

Decomposition rate (k day^{-1})	Mesh size of litter bag (mm)	Site characteristics	Sources
0·0033 ± 0·00037	0·3	Near-natural fen, wet	3
0·0026 ± 0·00051	0·3	Near-natural fen, dry	3
0·0024	0·5	Oligotrophic lake	1
0·0029	0·5	Eutrophic lake	1
0·0014	0·25	Managed reedbed, seasonally flooded	2
0·0010	0·25	Managed reedbed, never flooded	2

Sources: 1, Larsen & Schierup (1981); 2, Bedford (2005); 3, Völlm & Tanneberger (2014).

conditions (M.J. Mills & J.L. Gallagher, unpublished data, cited in Hellings & Gallagher 1992).

Several studies demonstrate a negative effect of increasing salinity on growth rate (Lissner *et al.* 1999), particularly above a threshold of c. 10–12 ppt (L.A. Meyerson, unpublished data), as well as on biomass production, shoot density, height, stem diameter and amount of reserves stored in the rhizome (Tang *et al.* 2013; see also review by Engloner 2009). Haslam (1972) reported that the leaves of salt-stressed reeds are rolled and the shoots short, sparse and sterile (i.e. do not set seed or produce non-viable seed). In Rhode Island, USA, the restoration of tidal flows increased salinity to 30–32 ppt and caused severe stunting and eventual death of *P. australis* up to the marsh upland fringe (Golet *et al.* 2012). Clonal integration and spread from the upland fringe, and deep rhizomes that access freshwater, enabled growth under highly saline conditions in this marsh (Amsberry *et al.* 2000; Meyerson, Vogt & Chambers 2000). Increasing salinity is also correlated with lower values for photosynthesis (Lissner *et al.* 1999), water potential in tissues (Pagter *et al.* 2009), stomatal conductance (Zhang & Deng 2012), and higher values for water use efficiency (Pagter *et al.* 2009) and intracellular CO_2 (Zhang & Deng 2012). However, salt tolerance can be achieved due to K$^+$ uptake preventing the influx of Na$^+$ or via increased Na$^+$ exclusion by roots (Lissner *et al.* 1999; Vasquez *et al.* 2005).

III. Communities

Phragmites australis is an important component of a wide range of plant communities that span terrestrial, freshwater and brackish conditions. In the British Isles, it is monodominant to dominant in many swamp communities, dominant to common in fens and areas that have previously been disturbed, and less frequent to occasional in littoral, mire, heath and wet woodland communities (Rodwell 1998a, b, c; see also table 11.3 in Haslam 2010). In this section, we first summarize the most common community types associated with

P. australis in Britain and Ireland, and then elsewhere. A compilation of classical literature about *Phragmites*-dominated plant communities can be found in Haslam (1972, 2010) and Klötzli *et al.* (2010).

Phragmites-dominated reedbeds were historically a very important component of the water–land transition in the British Isles. Littoral communities have declined over the past 50 years due to eutrophication and disturbance (e.g. wash from boat traffic; Rodwell 1998c; Cope & Gray 2009). Despite this, *Phragmites* continues to be quite common within the water-margin community of *Typha angustifolia* (S13) and is also present in *Glycerio–Sparganion* communities (S23; Rodwell 1998c). The monodominant *P. australis* swamp and reedbed communities (S4; Rodwell 1998c) continue to be widespread throughout the British lowlands. In many cases, *Phragmites* populations are actively managed to maintain its dominance. Monodominant reedbeds (*Phragmites australis* subcommunity) tend to occur in permanently wet or regularly waterlogged habitats and are generally species-poor with no trees or shrubs, and no or few other plant species. Habitats with any of the three species most commonly associated with dense *Phragmites* reedbeds are recognized as distinct subcommunities. The *Galium palustre* subcommunity is somewhat richer in plant species than pure reedbeds, has a more open canopy, and is present throughout the British Isles but particularly around Scottish lakes. *Menyanthes trifoliata* subcommunities occur in isolated localities in Scotland and north-west England and have an open reed canopy with mixed understorey. Shorter reedbeds are frequently *Atriplex prostrata* subcommunities that are patchily restricted to coastal and inland saltmarshes. In addition to its association with *Typha* (S13), *Phragmites* is present within the communities of other tall macrophytes: *Carex* species (S1, S3, S6–S7 and S17–S18), *Cladium mariscus* (S2), *Glyceria maxima* (S5), *Schoenoplectus* species (S8, S20 and S21) and *Sparganium erectum* (S14).

Tall-herb fens, where *P. australis* is dominant within more complex, species-rich assemblages of herbs and climbers, include *Phragmites australis–Peucedanum palustre* communities (S24) confined largely to eutrophic fen peats in The Broads; scattered linear strips of *Phragmites australis–Eupatorium cannabinum* communities (S25) throughout the lowlands of England and Wales; and *Phragmites australis–Urtica dioica* communities (S26) along more eutrophic, unmown strips beside ditches, canals and ponds throughout Britain. It can also occur along the disturbed edges of anthropogenic areas such as agricultural fields and railway corridors.

Along the banks of the Grand Canal of Dublin, Northern Ireland, the community is dominated by indigenous *Glyceria maxima*, *Schoenoplectus lacustris* and *Phragmites australis* (Caffrey & Beglin 1996). Each of these fen types is often the result of historic and/or ongoing cutting, low-intensity grazing or other intentional disturbance.

Several mire communities frequently contain *Phragmites*. It is abundant to scattered in *Schoenus nigricans–Juncus subnodulosus* mire (M13), *Juncus subnodulosus–Cirsium palustre* fen-meadow (M22), *Molinia caerulea–Cirsium dissectum*

fen-meadow (M24) and *Filipendula ulmaria-Angelica sylvestris* mire (M27), to less common in other mires (M5, M9, M21, M25-M26 and M28). The *Erica vagans–Schoenus nigricans* heath (H5) that is restricted to the Lizard peninsula, England, includes *Phragmites* as an occasional associate.

Alluvial forest communities (specifically wet woodlands of *Alnus*, *Betula* and *Salix;* W1–4, 6) and the bramble understorey community (*Rubus fruticosus–Holcus lanatus*, W24: Rodwell 1998a) are characterized by *P. australis* of various densities during different seral stages. Reed is dense in the early stages of the communities and transitions to mixed swamp and then scattered among saplings and trees in later stages. Among these wet woodlands, *Phragmites* is most commonly abundant in *Salix cinerea–Betula pubescens–Phragmites australis* wet woodlands (W2) that are scattered throughout the British lowlands (O.L. Pescott, personal communication).

Outside Britain, *P. australis* is found in many of these same community types as well as some additional ones. Over 80 plant species have been identified as commonly associated with *P. australis* in different countries world-wide (Mal & Narine 2004). As in Britain, the most vigorous populations are species-poor with none or few co-dominant species depending on environmental conditions. The most common associations throughout the native range of *P. australis* include *Typha* spp. in shallow water, *Schoenoplectus lacustris* in deep water, *Glyceria maxima* under highly eutrophic conditions or *Bolboschoenus maritimus* in salt water and nutrient-rich conditions (Klötzli *et al.* 2010). Aquatic plant communities (e.g. dominated by *Lemna* species) can occur interweaved in the water with reeds. Reeds are also sometimes common in moist habitats that have been previously modified (e.g. drainage ditches, railway sidings and roadsides) in Suffolk, England, Fojt & Harding 1995; and New Jersey, USA, Bart & Hartman 2000. *Phragmites australis* can vary from scattered to dominant in these communities.

IV. Response to biotic factors

Phragmites australis can sometimes strongly influence the structure and development of vegetation. Littoral and wetland communities are inherently under constant flux (Tyler, Smith & Burges 1998), and *P. australis* is characteristic of one stage within the hydroseral transition from open water to woodland (Tyler-Walters 2003; Haslam 2010). Reed initiates the transition by colonizing the aquatic zone (e.g. along coastline, shallow lake edges and sandy banks of streams), accumulating litter, creating substrate that can support other species and ultimately drying out the littoral zone. The different stages of successional hydroseres are found along a spatial gradient from the shore to the open water, forming a vegetation zonation from open water to littoral, marsh and ultimately alluvial forest communities (Gorham 1957; Santamaria 2002). *Phragmites–Schoenoplectus–Typha* communities often mark the transition from open brackish water to freshwater swamp (Chapman 1960). In saltmarshes in China, the transition is both spatial and temporal where salinity levels are increasing over time and the *Phragmites* community is shifting to domination by non-native *Spartina* (Haslam 2010; L.A. Meyerson, personal observation). Some emergent hydrophytes can be facilitated by *P. australis* where it is able to persist and provide protection from currents and wave action. In mire communities in Hokkaido, Japan, for example, *Lobelia dortmanna* individuals were larger and had more clonal growth and seed production within low- rather than high-density *P. australis* stands (Onimaru & Yabe 1996). Common reed can also be involved in other kinds of vegetation changes. In the same Japanese wetlands, for example, *P. australis* shifted the community away from shade-intolerant sedges (e.g. *Carex lasiocarpa* var. *occultans*) to more shade-tolerant ones (e.g. *Carex thunbergii*). In the endangered ecological community of the Tookayerta wetlands, Australia, grazing history and accumulating *P. australis* litter strongly influenced alternative states (indicated by floristic composition and abundance, soil pH, and soil nutrients) in contiguous *Phragmites*-dominated and mixed communities (Roberts 2016). Individual *P. australis* reedbeds can persist for hundreds (e.g. BP 7650–7480 cal. BP at Tregaron Bog, Wales, Hughes & Barber 2003), and potentially thousands of years (Godwin & Mitchell 1938; Godwin & Newton 1938), and therefore, the species has the potential for long-term influence on vegetation dynamics.

Phragmites australis is a strong competitor within its broad ecological niche of habitats with stable or regular hydrology and high water-table. It is most competitive in lowlands with still shallow water such as swamps, marshes and saltmarshes. Low to moderate levels of eutrophication from human activities are thought to increase the competitiveness of *P. australis* (Klötzli *et al.* 2010). Traits that contribute most to this competitive ability include stem height and density (shading out competitors, Onimaru & Yabe 1996; Meyerson, Chambers & Vogt 1999; Ailstock 2000), litter depth and density (Haslam 1972; see II B), clonal growth (Paradis *et al.* 2014), root and rhizome density (Hürlimann 1951; Klötzli *et al.* 2010; see VI A), rhizome oxygenation (through high stomatal density on the leaves and abundant aerenchyma tissue channelling air throughout the plant; Ailstock 2000; Colmer 2003), and phenotypic (Mozdzer, Brisson & Hazelton 2013), karyotypic and genotypic variation (Clevering & Lissner 1999; Koppitz 1999; Saltonstall, Lambert & Meyerson 2010). In the absence of disturbance (natural or anthropogenic) in the early stages of succession, these traits can result in monospecific stands of tall, dense reeds with limited light availability at the ground layer (Hürlimann 1951), dense litter, and top soil dominated by rhizomes and roots (see Haslam 1971a, b).

Meyerson (2000) found significantly different levels of photosynthetically active radiation (PAR) when comparing *P. australis* and *Typha* spp. populations in Connecticut, USA. At 0·25 m above the marsh surface, PAR was 0·55% and 1·08% in two *P. australis* populations, whereas it was 10·60% and 3·10% under adjacent *Typha* communities, indicating that extremely low light levels near the marsh surface in *P. australis* stands effectively eliminate competitors by hampering germination and survival of seedlings of other species.

Phragmites australis can suppress some competitors through shading (e.g. *Carex lasiocarpa* in a nutrient-rich mire in Japan), although not others (e.g. *C. thunbergii* in the same mire) (Onimaru & Yabe 1996). Establishment of non-native *Phragmites australis* in species-rich freshwater marshes of North America has resulted in some reduction of species diversity, while in brackish marshes (which are naturally less diverse), the shift towards more homogenous vegetation structure has been more apparent (Meyerson *et al.* 2000). In contrast, Güsewell & Edwards (1999) found that *P. australis* did not disproportionately reduce floristic richness within species-rich fens in Switzerland where it was present, and this appeared to be due to its growth later in the season compared with other species present. Different genotype(s) within populations are also likely to determine the strength of influence by *P. australis* on floristic richness within the community (L.A. Meyerson, personal observation). *Phragmites australis* can sometimes be suppressed by shading from competitors (e.g. alternating dominance with *Glyceria maxima* at different successional stages in fens of The Broads) (Buttery, Williams & Lambert 1965; see also Clements, Weaver & Hanson 1929).

The competitiveness of *P. australis* is reduced in drier conditions (e.g. in British reedswamps where *Typha latifolia* and *Schoenoplectus lacustris* are important competitors) and with decreasing nutrient levels. However, *Phragmites australis* can persist in habitats it cannot dominate, e.g. dry, uncultivated Breckland fens (Haslam 1972) and dwarf populations along bog edges in Fennoscandia (Gorham 1957). For example, in the wettest part of one Breckland fen, *P. australis* grew with little apical dominance, while on higher, drier ground, the stand was sparse and advancing with marked apical dominance (Haslam 1972). This fen was slowly drying, and 8 years later *P. australis* persisted but was no longer dominant (see Haslam 1970a, b). There can also be intraspecific competition. Within a stand, competition between clones can result in different clones dominating different microhabitats (Haslam 1979, 2010; Douhovnikoff & Hazelton 2014; see also review by Clevering & Lissner 1999).

Depending on their age and density, reedbeds dominated by *P. australis* support a diverse assemblage of invertebrates (see Table 4 for invertebrates associated with *Phragmites australis* in Britain, and their conservation status) and other native fauna. Invertebrates that feed on *P. australis* are described in IX A and XI, and other animals associated with reedbeds are discussed in Section X.

Human-mediated activities that directly influence *P. australis* density and dominance, and are used either to control or promote the species, include draining (Bart & Hartman 2000), burning (Haslam 2010), cutting (Güsewell 2003), grazing (Vulink, Drost & Jans 2000; Roberts 2016) and herbicides (Hazelton *et al.* 2014). These management tools are described in more detail in XI C. Other less common human influences are trampling (damages the upper rhizomes, and hence decreases bud density; Rudescu, Niculescu & Chivu 1965; Haslam 1969c; Michigan State University 2010) and salinity manipulation (Hellings & Gallagher 1992; Chambers, Mozdzer & Ambrose 1998).

V. Response to environment

(A) GREGARIOUSNESS

Phragmites australis is highly gregarious (Rodwell 1998c) and tends to occur as small to large populations in its native range. Individual populations can cover vast expanses, with the largest recorded ones covering 800 km^2 in the Liaohe Delta, China (Brix *et al.* 2014) and up to 15 000 km^2 in the Mesopotamian Marshes until the 1980s (Richardson & Hussain 2006; degradation of these marshes is dealt with in Section X A). Dominant populations in Britain typically have ≥30 live shoots per m^2 and up to c. 600 shoots per m^2 with favourable disturbance (e.g. cutting or burning; Haslam 1972). When dominant in *Phragmites australis–Peucedanum palustre* tall-herb fens (Rodwell 1998c), or fringing 2 m deep spring-fed waterholes in arid Australia, dense *Phragmites* rhizomes can sometimes form floating piers up to 1·5 m thick (Packer *et al.* 2017a). These floating reed mats are known as 'hover' in The Broads (Crook, Boar & Moss 1983; Moss 2001) and 'plav' in Romania (Pallis 1916; see also Pallis 1961 and Rudescu, Niculescu & Chivu 1965). The age of reedbeds may also influence stem density, with 29 live stems per m^2 (mean, 95% CI: 19–39) in mature (>50 years), monospecific populations (crowded with dead stems and deep litter) compared with 175 live stems (95% CI: 110–240) in young (12 years), expanding reedbeds in South Australia (Packer *et al.* 2017a; see also Haslam 1970a, 1971a).

(B) PERFORMANCE IN VARIOUS HABITATS

The range of environments where *P. australis* occurs is described in Section X, and here we summarize the main performance indicators in response to these conditions. As rhizomes persist over multiple seasons, their condition (total biomass and amount of sclerenchyma strengthening tissue) is the most reliable indicator of potential productivity (Boar 1987) in the following years. Bud density and diameter can also be a useful indicator of productivity in the next season (Haslam 1971d), and there is a strong relationship between stem height and density as indicators of productivity within a single season (Cui *et al.* 2010; Zhang *et al.* 2013).

In the favourable growing conditions of a eutrophic freshwater swamp and high solar irradiance in temperate Australia, a peak of 9890 g m^{-2} of living shoot biomass (wet weight) was measured in autumn while dry mass of below-ground biomass peaked at 21 058 g m^{-2} in winter (75% of which was rhizomes, Hocking 1989; see also Duan *et al.* 2004). Lower values are given for the northern hemisphere, where the dry mass above-ground was 1700 g m^{-2} in suitable conditions in Lake Neusiedl, Austria-Hungary (Sieghardt 1973). In a South Bohemian fishpond, Czech Republic, the mean above-ground dry mass of *P. australis* (1120 g m^{-2}) was comparable to other highly productive littoral species including *Schoenoplectus lacustris* (1100 g m^{-2}), *Typha angustifolia* (1310 g m^{-2}) and *Typha latifolia* (1230 g m^{-2}; Dykyjová & Kvĕt 1978). In North America, reported values for dry

Table 4. Invertebrates associated with *Phragmites australis* in the British Isles

Classification/species*	Conservation rating†	Sources
ARACHNIDA		
Araneae		
Clubionidae		
Clubiona juvenis Simon	Vulnerable	2
Linyphiidae		
Donacochara speciosa (Thorell)	Not listed	2
Entelecara omissa O.P.-Cambridge	Not listed	2
Gongylidiellum murcidum Simon	Not listed	2
Hypomma fulvum (Bösenberg)	Not listed	2
Salticidae		
Marpissa radiata (Grube)	Not listed	2
Tetragnathidae		
Tetragnatha striata Linnaeus Koch	Not listed	2
Trombidiformes		
Tarsonemidae		
Steneotarsonemus phragmitidis (von Schlechtendal)	Not listed	3
ENTOGNATHA		
Collembola		
Katiannidae		
Katianna australis Womersley	Not listed	
GASTROPODA		
Littorinimorpha		
Hydrobiidae		
Mercuria confusa (Frauenfeld)	Not listed	2
Succineidae		
Oxyloma (Oxyloma) sarsii (Esmark)	Not listed	2
Vertigo		
Vertigo (Vertigo) moulinsiana (Dupuy)	Nationally scarce; vulnerable	2
INSECTA		
Coleoptera		
Carabidae		
Demetrias (Risophilus) imperialis (Germar)	Nationally notable B	2
Odacantha melanura (Linnaeus)	Not listed	2
Chrysomelidae		
Anthrenocerus australis (Hope)	Not listed	10
Donacia clavipes Fabricius	Least concern	4, 5
Donacia simplex Fabricius	Least concern	4,5
Erirhinidae		
Tournotaris bimaculatus (Fabricius)	Scottish biodiversity list	5, 9
Malachiidae		
Malachius bipustulatus (Linnaeus)	Least concern	
Staphylinidae		
Alianta incana (Erichson)	Not listed	2
Aloconota (Disopora) languida Erichson	Nationally notable	2
Cypha discoidea (Erichson)	Nationally notable B	2
Dacrila fallax (Kraatz)	Nationally notable	2
Erichsonius cinerascens (Gravenhorst)	Not listed	2
Hygronoma dimidiata (Gravenhorst)	Not listed	2
Lathrobium (Lathrobium) rufipenne Gyllenhal	Vulnerable	
Manda mandibularis (Gyllenhal)	Endangered	2
Myllaena infuscata Kraatz	Not listed	2
Myllaena intermedia Erichson	Not listed	2
Myllaena minuta (Gravenhorst)	Not listed	2
Ocyusa picina (Aubé)	Not listed	2
Pachnida nigella (Erichson)	Not listed	2
Paederus riparius (Linnaeus)	Not listed	2
Rugilus angustatus (Geoffroy)	Nationally notable	2
Stenus (Metatesnus) binotatus Ljungh	Not listed	2
Stenus (Metatesnus) bifoveolatus Gyllenhal	Not listed	2
Stenus (Hypostenus) solutus Erichson	Not listed	2
Stenus (Metatesnus) butrintensis Smetana	Not listed	2

(continued)

Table 4. (continued)

Classification/species*	Conservation rating[†]	Sources
Stenus (Metatesnus) niveus Fauvel	Nationally notable B	2
Stenus (Metatesnus) pubescens Stephens	Not listed	2
Tachyporus pallidus Sharp	Not listed	2
Diptera		
Anthomyzidae		
Anagnota bicolor (Meigen)	Nationally notable	2
Cecidomyiidae		
Giraudiella inclusa (Frauenfeld)	Not listed	11
Chamaemyiidae		
*Parochthiphila spectabilis (*Loew)	Endangered	2
Chloropidae		
Cryptonevra consimilis (Collin)	Vulnerable	2
Cryptonevra nigritarsis (Duda)	Nationally notable	2
Elachiptera austriaca Duda	Nationally notable	2
Eribolus nanus (Zetterstedt)	Nationally notable	2
Eribolus slesvicensis Becker	Nationally notable	2
Lipara rufitarsis Loew	Nationally notable	2
Lipara similis Schiner	Vulnerable	2
Limoniidae		
Dicranomyia danica Kuntze	Not listed	2
Erioptera bivittata (Loew)	Vulnerable	2
Molophilus pleuralis de Meijere	Not listed	2
Thaumastoptera calceata Mik	Not listed	2
Muscidae		
Phaonia atriceps (Loew)	Nationally notable	2
Syrphidae		
Sphaerophoria loewi Zetterstedt	Near threatened	2
Tipulidae		
Tipula marginella Theowald	Scottish biodiversity list	2
Hemiptera		
Aphididae		
Hyalopterus pruni (Geoffroy)	Not listed	11
Cicadellidae		
Edwardsiana crataegi (Douglas)	Not listed	
Paralimnus phragmitis (Boheman)	Nationally notable B	2
Cixiidae		
Pentastiridius leporinus (Linnaeus)	Not listed	2
Delphacidae		
Chloriona dorsata Edwards	Nationally notable B	2
Chloriona vasconica Ribaut	Nationally notable B	2
Gerridae		
Gerris (Gerriselloides) lateralis Schummel	Not listed	2
Veliidae		
Microvelia (Microvelia) pygmaea (Dufour)	Not listed	2
Hymenoptera		
Colletidae		
Hylaeus (Prosopis) pectoralis Förster	Not listed	2
Crabronidae		
Passaloecus clypealis Faester	Rare	2
Rhopalum (Corynopus) gracile Wesmael	Vulnerable	2
Ichneumonidae		
Chorinaeus australis Thomson	Not listed	
Spilothyrateles nuptatorius (Fabricius)	Not listed	10
Melittidae		
Macropis europaea Warncke	Not listed	2
Pompilidae		
Anoplius (Anoplius) caviventris (Aurivillius)	Nationally notable B	2
Tenthredinidae		
Hemichroa australis (Serville)	Not listed	
Vespidae		
Odynerus (Spinicoxa) simillimus Morawitz, F.	England NERC S.41	2

(continued)

Table 4. (continued)

Classification/species*	Conservation rating†	Sources
Cosmopterigidae		
Lepidoptera		
Batrachedridae		
Batrachedra parvulipunctella Chrétien	Not listed	5, 7
Cosmopterix lienigiella Lienig & Zeller	Not listed	5, 7
Cosmopterix orichalcea Stainton	Not listed	5, 7
Cosmopterix scribaiella Zeller	Not listed	5, 7
Cossidae		
Phragmataecia castaneae (Hübner)	Not listed	2, 11
Crambidae		
Sclerocona acutellus (Eversmann)	Insufficiently known	5
Elachistidae		
Elachista maculicerusella (Bruand)	Not listed	5, 6
Gelechiidae		
Brachmia inornatella (Douglas)	Nationally notable B	5, 8
Hesperiidae		
Heteropterus morpheus (Pallas)	Not listed	1, 5
Noctuidae		
Aporophyla australis (Boisduval)	Not listed	10
Aporophyla australis subsp. australis (Boisduval)	Not listed	11
Chilodes maritima (Tauscher)	Not listed	5, 12
Lenisa geminipuncta (Haworth)	Not listed	11, 12
Protarchanara brevilinea (Fenn)	England NERC S.41	11
Rhizedra lutosa (Hübner)	Not listed	11
Spaelotis ravida (Denis & Schiffermüller)	Not listed	5, 12
Pieridae		
Colias alfacariensis Ribbe	Not listed	10, 11
Colias aurorina Herrich-Schäffer	Not listed	10
Colias caucasica Staudinger	Not listed	10
Colias caucasica subsp. balcanica Rebel	Not listed	10
Colias chrysotheme Esper	Not listed	10
Colias croceus (Geoffroy)	Not listed	10
Colias hyale (Linnaeus)	Not listed	10
Colias myrmidone (Esper)	Not listed	10
Colias palaeno (Linnaeus)	Not listed	10
Colias phicomone (Esper)	Not listed	10
Odonata		
Coenagrionidae		
Coenagrion armatum (Charpentier)	Regionally extinct	2
Plecoptera		
Nemouridae		
Nemoura dubitans Morton	Nationally rare; least concern	2
Trichoptera		
Limnephilidae		
Anabolia brevipennis (Curtis)	Nationally notable	2
Limnephilus binotatus Curtis	Not listed	2
Phryganeidae		
Agrypnia pagetana Curtis	Not listed	2
Trichostegia minor (Curtis)	Not listed	2
Isopoda		
Trichoniscidae		
Trichoniscoides albidus (Budde-Lund)	Not listed	2

*Taxonomy is in accordance with the National Biodiversity Network Gateway (2017) (https://data.nbn.org.uk) and Global Biodiversity Information Facility Secretariat (2017) (https://doi.org/10.15468/39omei).

†Conservation status sourced from Joint Nature Conservation Committee Designations (November 2016).

Sources: 1, Asher *et al.* (2001), 2, Buglife (2016); 3, Chater (2010); 4, Cox (2007); 5, Biological Records Centre (2017); 6, Emmet (1996); 7, Emmet & Langmaid (2002); 8, Morris (2002); 9, National Biodiversity Network Gateway (2017); 10, Tyler-Walters (2003); 11, Waring & Townsend (2017).

mass above-ground range from 980 to 2642 g m^{-2} in freshwater systems and 727–3663 g m^{-2} in brackish systems (Meyerson, Vogt & Chambers 2000). However, when grown in 90-litre pots under experimental conditions in a common garden at Průhonice near Prague, Czech Republic, plants produced on average ($n = 433$) a total dry mass of 7646 g m^{-2},

made up of 4225 g m^{-2} below (70·6% rhizomes, 29·4% roots) and 3421 g m^{-2} above ground (P. Pyšek, J. Čuda, H. Skálová, J. Doležal, O. Kauzál, K. Pyšková & L.A. Meyerson, unpublished data). Herbivores (see IX A) and season influence biomass productivity and the ratio of above to below-ground biomass. The ratio decreases steadily during summer and autumn (Hocking 1989; see also Schierup 1978), when nutrients are reallocated to rhizomes from the senescing stems and leaves, and stabilizes in winter before being reversed during the spring growing season (Sieghardt 1973; Hocking 1989). Decreasing nutrient availability and increasing salinity can also reduce above- and below-ground biomass (see review by Engloner 2009).

Temperature influences the length of the growing season, growth rate and final stem height (Haslam 1972). In Britain, where the growing season is relatively short (April to September; Haslam 1969b) and culms grow to only 3·5 m, hot summers can produce 0·5–1·0 m taller reeds than cool summers (Spence 1964; Haslam 2009). The longer growing season at lower latitudes leads to longer culms (Haslam 1972). *Phragmites australis* is highly productive in very high temperatures if sufficient water is available to cool the leaves through transpiration (Pearcy, Berry & Bartholoomew 1974; Roberts 2000; Davies, Mackay & Whalen 2010; Packer *et al.* 2017a). Tall, flowering reeds (e.g. up to 5·3 m, mean 4·1, 95% CI 3·4–4·7) occur in warm-hot climates where stable shallow water is available, such as around artesian springs in arid Australia (Packer *et al.* 2017a; see also Haslam 1972).

Although there is an increase of stem height with temperature, this relationship interacts with other factors, such as competition, nutrient status, grazing and the reed ecotype (Haslam 1972) and ploidy level (Meyerson *et al.* 2016; L.A. Meyerson, P. Pyšek, M. Lučanová, J.T. Cronin, C. Lambertini, J. Wild & J. Suda, unpublished data). In North America, Meyerson *et al.* (2000) using latitude as a proxy for temperature, reported taller *P. australis* plants for some cooler sites in New England, compared with warmer sites of lower latitude in the Mid-Atlantic region, suggesting the environment (e.g., salinity) may play a stronger role in plant height than latitude. Similarly, Cronin *et al.* (2015) found only a weak relationship between latitude and height in their surveys of >50 *P. australis* populations along the Atlantic Coasts of Europe and

Fig. 3. Typical morphology of *Phragmites australis* showing (a) panicle, (b) leaf sheath containing fringed ligule, (c) leaf blade, (d) spikelet, (e) stoma and (f) horizontal and vertical rhizomes with roots. Above-ground reed parts were collected by Bohdan Křísa in the field in the Czech Republic. Below-ground material was collected from the common garden of The Czech Academy of Sciences. Drawings by Anna Skoumalová.

North America and the Gulf Coast of the USA and found significant variability in height across both ranges.

Nutrient levels also influence productivity, particularly shoot density and allocation of biomass between above- and below-ground organs. Haslam (1965) reported that stands in comparable water regimes are tall and dense in nutrient-rich habitats and very sparse in nutrient-poor ones (see also Engloner 2009; Haslam 2010). Hydrology can modulate the effect of nutrients on growth. In southern Australia, total dry mass of 100-day old plants grown from rhizome in pot experiments ($n = 60$) increased with higher nutrient levels (0 g, 10 g or 30 g N m^{-2} $year^{-1}$) when water levels were stable, but not when the level fluctuated irregularly within the range of 31 and 105 cm deep (J.G. Packer, G.G. Ganf, C. Kueffer, J.M. Facelli & P. Pyšek, unpublished data). Shoot density ranges from low in unfavourable conditions (e.g. c. 100 stems per m^2 in a freshwater tidal zone in Holland; Mook & Van der Toorn 1982), intermediate (e.g. 105 ± 69 SD stems per m^2 in moderate 86 g m^{-2} organic content; Lenssen *et al.* 2000) and high in peat marsh (e.g. c. 200 stems per m^2; Mook & Van der Toorn 1982).

Individual shoots can grow up to 3–4 cm day^{-1} (Haslam 1972). In optimum growing conditions in Britain, seedlings grew into shoots with 10 leaves within 3 months and were adults, with the capacity to reproduce, within 2 years (Haslam 2010). A single plant can extend laterally more than 10 m in one season (Ailstock 2000) and an existing stand can expand up to 70 m in 1 year (e.g. Great Lakes, USA; Trexell-Kroll 2002).

(C) EFFECT OF FROST, DROUGHT, ETC.

Phragmites australis is very sensitive to extreme weather events (e.g. frost and flooding) and less sensitive to less rapid changes (e.g. seasonal change to winter at 3600 m in Nepal and prolonged periods of drought in Australia), suggesting that the rate of change is more influential than the type of stress. Rhizomes and buds below the water and/or soil surface can tolerate extreme disturbance (e.g. frost, flood and fire), but above-ground structures, especially leaves, are vulnerable (H. Skálová, personal observation; Haslam 1975). Severe frost (below c. −6 °C) kills many shoots in open and unflooded stands, and late-emerging shoots following frost may die from internal competition in denser stands (Haslam 1972). Shoots killed (e.g. by frost) during the emergence period are replaced, but shoots damaged later may not be (see Haslam 1969d, 1970c). Field observations over a 3-year period in Britain found that heavy spring frosts reduced density (stem and inflorescence) while warmer temperatures associated with light frosts increased density (stem and inflorescence) but reduced stem height by 10% (see table 2 in Haslam 1972). Very severe frosts (below c. −12 °C) can kill up to 100% of the shoots and these may not be replaced if heavy frosts recur (Haslam 1970c, 1971a,c, 1972). Conversely, an established stand can persist, albeit with declining density, for up to 8 years in drying conditions (e.g. fen succession in Britain, Haslam 2010). The effect of various and variable water regimes on *P. australis* is discussed in II.

VI. Structure and physiology

(A) MORPHOLOGY

Morphology depends on the genotype, climate and habitat. In typical populations, the emergence process begins in late summer with the development of a bud, forming near the base of one of the previous season's rhizomes (Fig. 3), into a horizontal rhizome (Haslam 1972). The rhizome extends for about 1 m (0·1–2·0 m) before the tip turns to become vertical and the bud remains dormant near the surface (Haslam 1972) until it emerges in spring. This cycle continues annually. Several buds may continue to develop during late summer from near the top (c. 20 cm) of the previous-year's vertical rhizome and emerge as second-year stems (shorter and thinner than the first year) or as horizontal rhizomes (Haslam 1972). Rhizomes normally live for 3–6 years or more in East Anglia and north-west Scotland (Haslam 1972).

Lateral buds can form rhizomes (horizontal or vertical) or aerial shoots depending on the level of disturbance. Buds on vertical rhizomes are more likely to develop into vertical rhizomes or aerial shoots if they are disturbed (e.g. with fire or cutting) (Haslam 1972). Vertical rhizomes may sometimes grow up through other dense vegetation (e.g. tussocks of *Carex paniculata*) and here they develop both horizontal and vertical rhizome branches (Haslam 1972). Overall, the trend is for longer rhizomes to develop into larger shoots and these are more likely to flower (Hürlimann 1951; Isambaev 1964; Haslam 1972).

Roots

Roots (2–4 mm wide) develop from many (but not all) nodes of horizontal rhizomes and grow as sparse pairs (Haslam 1972). The root mass can extend from 50 cm deep in flooded sites down to 4 m deep where the hydrology fluctuates greatly (Neubert *et al.* 2006). Although the main pairs of roots grow from below the horizontal rhizome, shorter and thinner pairs may also form from above. Vertical rhizomes also have short, narrow roots that branch after several centimetres and can form dense mats and fibrous peat (Haslam 1972). Root density tends to increase in richer, organic soils and decrease in low-nutrient habitats (Weaver & Himmel 1930; Haslam 1972).

Rhizomes

Each node bears a small, scale-like leaf and bud. Internodes are usually 5–25 cm long and are longer on horizontal rhizomes. The widest rhizomes are horizontal (e.g. up to 3 cm) rather than vertical (1–1·5 cm), and the primary rhizomes are usually wider than secondary branch rhizomes (e.g. Pallis 1916; Hürlimann 1951; Klötzli *et al.* 2010; see also Haslam 1969a). These wide, horizontal rhizomes usually terminate in vertical rhizomes and the proportion of these two types varies with hydrology, nutrients, ecotype and potentially genotype (Rudescu, Niculescu & Chivu 1965; Haslam 1972). In favourable habitat within fens in Breckland and the Netherlands, for

example, the extensive and complex rhizome system is dominated by vertical rhizomes (Haslam 1972). In Switzerland (Hürlimann 1951) and Malta, the rhizome system is less extensive and vertical rhizomes develop mostly from existing vertical rhizomes rather than terminal tips (Haslam 1972). Deep, horizontal rhizomes may be flattened, particularly in vigorous stands (Haslam 1972).

Rhizomes form a dense mass 20–100 cm below the surface and have been recorded at 1·5 m in Norfolk (Haslam 1972) and the Netherlands (Zonneveld 1959) and to 2 m in Switzerland (Hürlimann 1951; Klötzli *et al.* 2010). The depth range of horizontal rhizomes depends on soil nutrients, water-table and soil types (Haslam 1972). The average density of rhizomes has been recorded as up to c. 89·5 living per m^2 and 28·5 dead per m^2 horizontal rhizomes and c. 285 living per m^2 and 21 dead per m^2 vertical rhizomes (Krasovskii 1962; Fiala *et al.* 1968).

Aerial stems

Rhizomes develop into aerial shoots at the soil surface, even where *P. australis* is growing in open water (Haslam 1972). Aerial shoots contain sclerenchyma strengthening tissue and harden into brittle stems over summer before dying during autumn in most climates (Hürlimann 1951; Boar, Crook & Moss 1989). Larger stems can live for 2 years in more temperate climates without frost (e.g. Malta – Haslam 1972; Adelaide, Australia – J.G. Packer, personal observation; Gulf Coast, USA – J.T. Cronin, personal observation). These older stems may bear branched shoots in the second season (Haslam 1972). In northern and central Europe, by contrast, branching is usually restricted to damaged shoots (Kühl & Kohl 1993), such as those affected by moths (Pallis 1916), frost, galls (Haslam 1972) or grazing (Packer *et al.* 2017a). Fallen stems can sometimes continue to grow upwards due to pulvini thickening at the node (Arber 1934).

Shoot height increases throughout summer (May to early August in Britain; see fig. 6 in Haslam 1972; see also Haslam 1969e, 1970a), and maximum stem density is reached in early summer (June or July in Britain; Rodwell 1998c). The number of nodes on stems varies between 13 and 17 in Breckland fens, but may be as low as six (e.g. New Forest and Scotland; Haslam 1972). Stems within the stand are larger (taller and wider) and therefore more likely to form inflorescences and flower (Haslam 1972) than those along the expansion edge.

Stolons

Vertical shoots sometimes fall and may extend along the ground or water surface as stolons (or runners). Individual stolons grow to over 10 m long with more than 70 stem shoots per stolon (L.A. Meyerson, unpublished data). In wet habitats, stolons can form across water during late spring (May) in southern Europe (e.g. Malta) and mid-summer (July) in Britain (Haslam 1972). These runners can extend rapidly from the initial, fallen stems and develop shorter aerial stems with smaller leaf blades than within the main stand (Hürlimann

1951; Mueller-Stoll 1952; Haslam 1969a). Stolons live for 1–3 seasons and are more common in young populations (e.g. 2–4 years) and brackish habitats (Pallis 1961; Haslam 1972). Stolons can be the primary mechanism of expansion by existing stands (Tulbure, Johnston & Auger 2007).

Leaves

The nodes of rhizomes and shoots can develop leaves. On rhizomes, these leaves are scale-like and smooth and form a tip that bores through soil when it is young and then produces membranous layers as it ages (Haslam 1972). Aerial stems also initially form scale-like leaves that, apart from the initial transitional leaves, are replaced by fully developed leaves with blades, and sheaths that support the growing shoot. Blades of the first transitional leaves are small and triangular, while fully developed leaves are larger, longer and taper to the tip (Haslam 1972). The inside of the sheath is smooth (Arber 1934) and allows the leaf to move depending on the prevailing wind (Haslam 1972). The leaves often have one (0–3) constriction which forms in the bud and is aligned across the blade (Haslam 1972). Stomata are abundant, with up to 470–700 mm^{-2} on the upper (adaxial) and c. 670 mm^{-2} on the lower (abaxial) surface (Hürlimann 1951). Leaf blades cannot persist underwater as the chlorophyll and veins degrade (Hürlimann 1951). In most populations, the blades are shed from the sheaths by winter (Haslam 1972) unless they are growing in a temperate climate without frosts.

Inflorescences

In the British Isles, inflorescences tend to occur on the tallest stems within a population (Haslam 1972) and may only emerge on shorter stems if the conditions are favourable (Haslam 1970c). Hürlimann (1951) reported that optimal conditions are unlikely to produce sterile stems in Switzerland. The Gulf Coast lineages in North America (in the wild and under optimal conditions of common gardens) rarely produce inflorescences with seed, but it is currently unclear whether this is due to environmental conditions or lineage.

Genetic variation

Populations may differ in their date of emergence, height, straightness and colouration of stems, texture of leaves and susceptibility to environmental stressors (Haslam 1972, 2010). Rodwell (1998c) noted that variability among *P. australis* populations in Britain was presumed to be phenotypic (i.e. response of genotypes to environmental conditions, rather than genetic) Paul, Kirk & Freeland (2011) confirmed highly differentiated genetic structuring between 14 reedbeds in England, Scotland and Wales. They concluded their samples were most likely tetraploids with vegetative and sexual reproduction yet limited gene flow between reedbeds.

Notable differences exist between infraspecific taxa that are considered to form the *P. australis* species complex outside Britain (see Taxonomy section in the introductory paragraphs). In

Table 5. Arbuscular mycorrhizal fungi (AMF) taxa identified within the roots of *Phragmites australis* as operational taxonomic units (OTUs)

Closest related taxa based on OTU	Status	Organ (substrate)	Location	Source
ASCOMYCOTA				
Dothideales				
Kabatiella caulivora (Kirchn.) Karak.	Confirmed	Root (moist)	Germany	1
Hypocreales				
Cylindrocarpon sp. Wollenw.	Confirmed	Root (moist)	Germany	1
Pezizales				
Tuber maculatum Vittad.	Confirmed	Root (moist)	Germany	1
BASIDIOMYCOTA				
Agaricales				
Inocybe sp. (Fr.) Fr	Confirmed	Root (moist)	Germany	1
Laccaria pumila Fayod	Confirmed	Root (moist)	Germany	1
Lentinus tuber-regium (Fr.) Fr.	Confirmed	Root (moist)	Germany	1
GLOMEROMYCOTA				
Archaeosporales				
Ambispora gerdemannii (S.L. Rose, B.A. Daniels & Trappe) C. Walker, Vestberg & A. Schüßler	Confirmed	Root (moist)	Germany	1
Ambispora leptoticha (N.C. Schenck & G.S. Sm.) C. Walker, Vestberg & A. Schüßler	Potential	Rhizome, root (moist)	Germany	3
Archaeospora trappei (R.N. Ames & Linderman) J.B. Morton & D. Redecker	Potential	Rhizome, root (moist)	Germany	3
Geosiphon pyriformis (Kütz.) F. Wettst	Confirmed	Root (moist)	Germany	1
Diversisporales				
Acaulospora koskei Błaszk.	Confirmed	Root (moist)	Germany	1
Acaulospora laevis Gerd. & Trappe	Confirmed	Root (moist)	Germany	1
Acaulospora scrobiculata Trappe	Confirmed	Root (moist)	Germany	1
Acaulospora spinosa C. Walker & Trappe	Confirmed	Root (moist)	Germany	1
Entrophospora sp. R.N. Ames & R.W. Schneid.	Confirmed	Root (moist)	Germany	1
Gigaspora decipiens I.R. Hall & L.K. Abbott	Confirmed	Root (moist)	Germany	1
Gigaspora gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	Confirmed	Root (moist)	Germany	1
Scutellospora dipapillosa (C. Walker & Koske) C. Walker & F.E. Sanders	Confirmed	Root (moist)	Germany, Saudi Arabia	1, 2
Scutellospora dipurpurescens J.B. Morton & Koske	Confirmed	Root (moist)	Germany	1
Scutellospora pellucida (T.H. Nicolson & N.C. Schenck) C. Walker & F.E. Sanders	Confirmed	Root (moist)	Germany	1
Glomerales				
Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Claroideoglomus luteum (L.J. Kenn., J.C. Stutz & J.B. Morton) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Colletotrichum sublineola Henn. ex Sacc. & Trotter	Confirmed	Root (moist)	Germany	1
Diversispora spurca (C.M. Pfeiff., C. Walker & Bloss) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Diversispora versiformis (P. Karst.) Oehl, G.A. Silva & Sieverd.	Confirmed	Root (moist)	Germany	1
Funneliformis caledonium (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Glomus sinuosum (Gerd. & B.K. Bakshi) R.T. Almeida & N.C. Schenck	Likely	Root (moist)	Germany	3
Rhizophagus fasciculatus (Thaxt.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Rhizophagus intraradices (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1

Table 5. (continued)

Closest related taxa based on OTU	Status	Organ (substrate)	Location	Source
Rhizophagus manihotis (R.H. Howeler, Sieverd. & N.C. Schenck) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Rhizophagus prolifer (Dalpé & Declerck) C. Walker & A. Schüßler	Confirmed	Root (moist)	Germany	1
Rhizophagus vesiculifer (Thaxt.) C. Walker & A. Schüßler	Potential	Root (moist & flooded)	Germany	3
Septoglomus viscosum (T.H. Nicolson) C. Walker, D. Redecker, Stille & A. Schüßler	Confirmed	Root (moist)	Germany	1
Paraglomerales				
Paraglomus brasilianum (Spain & J. Miranda) J.B. Morton & D. Redecker	Confirmed	Root (moist)	Germany	1
Paraglomus occultum (C. Walker) J.B. Morton & D. Redecker	Confirmed	Root (moist)	Germany	1
ZYGOMYCOTA				
Mucorales				
Rhizopus sexualis (G. Sm.) Callen	Potential	Rhizome, root (moist & flooded)	Germany	3

Sources: 1, Wirsel (2004); 2, Al-Garni (2006); 3, Neubert *et al.* (2006). Fungal taxonomy is in accordance with Index Fungorum (http://www.indexfungorum.org/Index.htm).

North America, there are several differences between native and non-native lineages, including morphological (e.g. native genotypes generally have red, somewhat crooked stems; Swearingen & Saltonstall 2010) and phenological (e.g. non-native lineages emerge earlier in spring and persist later into autumn; Meyerson, Viola & Brown 2010; see also Section X B).

(B) MYCORRHIZA AND OTHER SYMBIOSES

Fungal

Phragmites australis is facultatively mycorrhizal (Oliveira, Dodd & Castro 2001) and is also colonized by endophytic (within plant tissue) and epiphytic (on plant tissue) fungi that are considered to be at least partly mutualistic (Harley & Harley 1987; Ernst, Mendgen & Wirsel 2003). There are no records of mycorrhizal or other fungal partners of *P. australis* in the British Isles, so here we report the mutualisms known from elsewhere in its native range.

Arbuscular mycorrhizal (AMF; Harley & Harley 1987; Neubert *et al.* 2006) and ectomycorrhizal (Neubert *et al.* 2006) fungi have been confirmed in *P. australis* (Table 5). Arbuscular fungal partners appear to be considerably more abundant and diverse than the ectomycorrhizal ones which have only recently been identified to class (Homobasidiomycetes; Neubert *et al.* 2006). The AMF community hosted by *P. australis* consists mainly of Glomeraceae (e.g. 470 spores per mL of *Glomus fasciculatum* were extracted from *P. australis* roots in Saudi Arabia; Al-Garni 2006) as well as *Acaulospora*, *Scutellospora* and, to a lesser extent, Diversisporaceae identified on the basis of operational taxonomic units (Wirsel 2004; Neubert *et al.* 2006). These symbiotic partners have been identified in association with *P. australis* across a range of habitats from oligotrophic lakes in Denmark (Sondergaard & Laegaard 1977), and acidic marshlands in the

Czech Republic (Mejstrik 1972), to eutrophic soils and sediments in Portugal (Oliveira, Dodd & Castro 2001). Mycorrhizal colonization ranges from sometimes present in flooded habitats (Mejstrik 1972; Sondergaard & Laegaard 1977; Oliveira, Dodd & Castro 2001; Wirsel 2004; Neubert *et al.* 2006; Zhang *et al.* 2014) to more abundant and diverse in drier substrates (e.g. always present on 5–100% of the root cortex in dry habitats in the Czech Republic; Mejstrik 1972; see also Oliveira, Dodd & Castro 2001; Neubert *et al.* 2006). This lack of AMF colonization in some flooded conditions suggests that reed is not reliant on AMF for survival and that other symbiotic partners (e.g. fungal endophytes) may be more important in these habitats (Wirsel 2004). The diversity and composition of AMF in *P. australis* also depend on season and the age of the individual host and population (Wirsel 2004; Neubert *et al.* 2006).

Benefits of AMF colonization in *P. australis* may include an increase in: biomass, germination and seedling growth rates in greenhouse experiments (Wu *et al.* 2014) with saline substrates (Al-Garni 2006); nutrient absorption (S, Na, K, Ca, Cr, Co, Cu, Zn, Se, Ag, Cd, Sb, Ba, La, Hg, Tl; Wu *et al.* 2014) in nutrient-poor habitats especially (Sondergaard & Laegaard 1977); and photosynthetic efficiency along with turgor potential and osmotic adjustment in saline soils (Al-Garni 2006). Colonization of *P. australis* may also have indirect influences on plant community interactions (Zhang *et al.* 2014). Different AMF partners within *P. australis* may sometimes interact and magnify any of the above benefits (Larimer, Bever & Clay 2010).

Over 150 species or isolates of endophytic fungi have been identified within *P. australis* (see, for example, table 2 in Angelini *et al.* 2012) and include taxa (Class 2 non-clavicipitaceous; Rodriguez *et al.* 2009) that can improve habitat specificity (e.g. salinity tolerance; Rodriguez *et al.* 2009) and increase productivity (e.g. increased reed biomass; Ernst, Mendgen & Wirsel 2003). The fungal communities in the

roots of healthy reed were the most diverse of 10 plant species surveyed in coastal zones of South Korea (Kim *et al.* 2014). In Italy, along lake shores where reed dieback was occurring, the diversity of endophytic communities declined along a gradient from high in healthy reeds to absent in the declining reeds (Angelini *et al.* 2012). The composition of endophytic communities changes with habitat conditions, particularly flooding depth and frequency (Van Ryckegem & Verbeken 2005; Ernst *et al.* 2011), and salinity (Van Ryckegem & Verbeken 2005). As the ecological roles of other endophytic isolates are unknown or are considered to be pathogenic (Angelini *et al.* 2012), these are dealt with IX B.

The presence of epiphytic fungi on *P. australis* has been inferred (Wirsel *et al.* 2001; Van Ryckegem & Verbeken 2005; Kowalski *et al.* 2015). Epiphytic fungi fulfil one or several ecological roles, including potentially mutualism with *P. australis* (Van Ryckegem & Verbeken 2005).

Microbial

Phragmites australis reedbeds appear to have a diverse microbial community. However, differences might often be site-rather than species-specific, as indicated by the comparison of Ravit, Ehrenfeld & Haggblom (2003) of *Spartina alterniflora* and *P. australis* microbial communities in New Jersey, USA. Borruso *et al.* (2014) found that salinity was the overriding determinant of microbial community composition in their study rather than plant species. Similarly, Song *et al.* (2015) used terminal restriction fragment length polymorphism analysis to investigate microbial diversity in *P. australis* and *Bolboschoenus* (*Scirpus*) *planiculmis* in South Korea. They concluded that it was plant diversity, rather than plant species, that determined microbial community composition. Nonetheless, very recent work by Bowen and Meyerson (unpublished data) in North America indicates highly distinct structuring of microbial communities below the species level. They compared the North American native, non-native and Gulf Coast lineages of *P. australis* using 16s rDNA/rRNA and found that North American native genotypes of *P. australis* have reduced diversity among the active bacteria compared with non-native genotypes under identical greenhouse conditions, suggesting some functional differences may occur and affect success (see IX B). They also found that in natural populations on the East, West and Gulf Coasts, species richness of active bacterial groups was much higher in the introduced lineage of *P. australis* than the native and Gulf lineages. Microbial communities within *P. australis* lineages were highly similar to one another despite spatial separation of up to 3000 km. Further research is needed to identify the nature, magnitude and direction of the ecological influence of fungal and microbial communities on *P. australis* across different ranges and habitats.

(C) PERENNATION: REPRODUCTION

Helophyte. Age at first flowering: 3–4 years in moderately good conditions after establishment by seed (Hürlimann 1951; Saltonstall, Lambert & Meyerson 2010) or 1–2 years if

established from a clonal fragment (P. Pyšek, J. Čuda, H. Skálová, J. Doležal, O. Kauzál, K. Pyšková & L.A. Meyerson, unpublished data). All shoots can potentially flower (Haslam 1972) and the percentage of stems with inflorescences varies from 25% to 90% in favourable conditions to 0% in poor (Haslam 1970b). Inflorescence and seed density increase with vigour of populations, lack of shade, warm weather, soil moisture (rainfall and/or water-table), moderate to high nutrient status, lack of grazing (Haslam 1972), and decreasing latitude and its associated warmer climate (which also increases viable seed density; McKee & Richards 1996). Flowering density varies among clones within the same marsh, and few deductions can, therefore, be made about variation with habitat unless this factor can be eliminated or accounted for (Haslam 1972). Large inflorescences are borne on the largest shoots, which are sometimes but not always fertile, while smaller shoots bear smaller (c. 1–4 cm) inflorescences and are normally sterile (Haslam 1972). The percentage of panicles with seed ranged from 0% to 100% in British reedbeds and the highest rates within this range were observed when a dry winter was followed by a hot, wet spring (McKee & Richards 1996). Up to 2000 seeds are produced per panicle (Bittmann 1953; Wijte & Gallagher 1996a). Reported seed bank densities from *Phragmites australis*-dominated wetlands are rather low; values of only 284 and 698 seeds per m^2 were counted from one study of two non-native stands in Chesapeake Bay, Maryland, USA (Baldwin, Kettenring & Whigham 2010). McKee & Richards (1996) reported that seed set and germination in stands along a latitudinal and climate gradient (34 in Britain, 5 in southern France) were predicted by overall plant height and seed mass.

Seedling establishment and the establishment of new populations from seed are rare in Britain (Haslam 1972; Rodwell 1998c; but see also Section X B on the recent colonization of newly created wetland habitats). Seedlings are common only in open (new) habitats where macrophytes are absent (i.e. dense stands of *Phragmites* limit establishment) and fallen panicles provide a seedbank (e.g. in Norfolk where establishment from dispersed seed is particularly rare; Pallis 1958; Buttery 1959). Seedlings are threatened by frost, flooding (e.g. they can only survive submersion for up to 4 weeks, Mauchamp & Mésleard 2001; see also VIII D for the influence of water depth on seedling emergence), strong heat, salt and competition in the first year of growth (e.g. in Switzerland, Hürlimann 1951; see also Haslam 1972). Hürlimann (1951) found that N was the most important element for growth, followed by P then K, in seedlings grown experimentally in Switzerland. Ter Heerdt *et al.* (2017) reported that establishment of *Phragmites australis* seedlings occurred across a gradient of soil moisture in a greenhouse experiment in the Netherlands, but emergence and survival were lowest in very dry and cold (e.g. frost) conditions.

The most favourable growing conditions for seedling development are on nutrient-rich mud, rather than sand (Hürlimann 1951), with a flow of shallow, nutrient-rich water (Haslam 1972). Spence (1964) also found increased seedling growth in more nutrient-rich conditions (silty sand) compared with peat where seedlings were stunted at 0–8 cm high after 18 months

unless they were watered with nutrient-enriched water. Similar stunting of shoots and roots occurs in the Breckland fens where seedlings grow on peat (Haslam 1972).

Once a new population of *P. australis* is established, it spreads either through vegetative reproduction from rhizome portions, stem nodes (Meyerson, Pergl & Pyšek 2014) and/or sexually by seed (Belzile *et al.* 2010; McCormick *et al.* 2010b). Seeds contribute strongly to spread of the European genotype in Quebec, Canada (Belzile *et al.* 2010). Curtis (1959) found that annual rhizome lateral spread averaged 40 cm in Wisconsin, USA, but Farnsworth & Meyerson (1999) reported that in Connecticut, USA, *P. australis* spread through the recruitment of a dense phalanx of stems behind the advancing front rather than via exploratory runners. Legehalme can also contribute to rapid population expansion (Haslam 1972; Tulbure, Johnston & Auger 2007). Rudescu, Niculescu & Chivu (1965) suggest that clones might persist for up to 1000 years. Rhizome portions are typically transported by water and are particularly associated with disturbances such as storms (Bhattarai & Cronin 2014). Humans may also introduce rhizomes to habitats inadvertently, such as through the movement of soil during restoration activities (Meyerson, Lambert & Saltonstall 2010). Rhizomes and stem nodes are viable year-round in greenhouse conditions in Europe and North America (L.A. Meyerson, unpublished data).

(D) CHROMOSOMES

Phragmites australis is an allopolyploid (Raicu *et al.* 1972; Paul, Kirk & Freeland 2011), has a base chromosome number of 12 and encompasses several ploidy levels ($4x$–$12x$) (Goldblatt & Johnson 1979; Clevering & Lissner 1999; Saltonstall, Lambert & Meyerson 2010) that together form a polyploid complex. In the British Isles, tetraploids ($4x$) have been reported from the Dublin region, Ireland (Curran 1969), and the River Sence in Leicestershire, England (Tutin 1975 in Botanical Society of Britain & Ireland 2017). World-wide it is most commonly recorded as tetraploid or octoploid ($8x$) (Clevering & Lissner 1999; Saltonstall, Lambert & Meyerson 2010), although counts of $3x$, $6x$, $7x$, $10x$, $11x$ and $12x$ have previously been recorded (Clevering & Lissner 1999).

In Europe, tetraploids and octoploids are common, but hexaploids ($6x$), decaploids ($10x$) and dodecaploids ($12x$) have also been found (Hansen *et al.* 2007). In the Danube Delta, Romania, octoploids are the most common ploidy level in freshwater habitats, while tetraploid is more predominant in saline habitats (Brix 1999). Branched stems have been noted in some hexaploid plants (Björk 1967). In North America, the native and the introduced genotypes of *P. australis* are primarily tetraploids (Saltonstall, Lambert & Meyerson 2010; but see Keller 2000). However, in the Gulf Coast of the United States, mixed cytotype populations are common ($4x$–$8x$, Lambertini *et al.* 2006). In Asia and Australia, ploidy levels range from $4x$ to $10x$ and a mixed cytotype population was reported on Lake Biwa in Japan (Nakagawa, Ohkawa & Kaneko 2013). Paul, Kirk & Freeland (2011) reported that octoploids dominate in Asia (see also Clevering & Lissner

1999; Hansen *et al.* 2007). Intraspecific genome size in *P. australis* is highly variable with monoploid genome size ranging from 0·47 to 0·57 pg (Suda *et al.* 2015; Meyerson *et al.* 2016; L.A. Meyerson, P. Pyšek, M. Lučanová, J.T. Cronin, C. Lambertini, J. Wild & J. Suda, unpublished data) and the non-native genotype has a significantly smaller genome size than native *P. australis* in North America (P. Pyšek, J. Čuda, H. Skálová, J. Doležal, O. Kauzál, K. Pyšková & L.A. Meyerson, unpublished data).

(E) PHYSIOLOGICAL DATA

Transpiration

The annual evapotranspiration of *Phragmites* stands in temperate wetlands is relatively high (c. 1000–1500 mm decrease in water level within the stand) and varies with environmental conditions (Haslam 1972). Evapotranspiration of the stands varies between years and, in the Danube Delta, increased during the vegetation season until late summer (e.g. 10–80 mm in June, 40–171 mm in July and 140–211 mm in August) before decreasing towards dormancy (e.g., 5–190 mm in September; Rudescu, Niculescu & Chivu 1965). Under extremely high temperature and intense irradiation, it reached 5·9 mm day^{-1} (Rejšková *et al.* 2012).

Transpiration occurs mostly from the upper leaf surface (Rudescu, Niculescu & Chivu 1965), reaching up to 7·8 mmol m^{-2} s^{-1} (Rejšková *et al.* 2012). Water use efficiency based on photosynthesis output and transpiration varies between 4 and 11 μmol (CO_2) m^{-2} s^{-1} mmol^{-1} (H_2O) m^{-2} s^{-1} depending on temperature and nutrient supply (Mykleby *et al.* 2015). An efficiency of 1·3 and 2·3 g of aboveground biomass kg^{-1} of water during the growing season (Headley *et al.* 2012 and Milani & Toscano 2013, respectively) is rather low compared to agricultural crops.

Photosynthesis

Photosynthesis is by the C_3 pathway (Gibson 2009). The maximum rate of photosynthesis (A_{sat}) is around 20 μmol (CO_2) m^{-2} s^{-1}, with saturation at a photosynthetic photon flux density of about 250 μmol m^{-2} s^{-1} (Eller *et al.* 2014). *Phragmites australis* is generally shade intolerant and absent beneath a dense canopy (Albert *et al.* 2013) unless nourished by an established population through clonal integration (L.A. Meyerson, personal observation). Considerably reduced relative growth rate and elongation rate were found in plants grown under low irradiance of 20 μmol m^{-2} s^{-1} if compared with plants grown under 100 and 300 μmol m^{-2} s^{-1} (Li *et al.* 2011).

Aeration

Rhizomes and roots growing in flooded populations are aerated through active pressurization of fresh air (supplying O_2) by lysigenous aerenchyma (Faußer *et al.* 2016) within the standing aerial stems (Buttery 1959), rhizomes and roots (except basal lateral ones) (Armstrong & Armstrong 1988;

Table 6. Water content, volume of expressed sap and Na, K, Mg, Ca, Fe and Cl concentration in the sap. Data from Björk (1967)

	Water content (%)	Expressed sap (mL kg^{-1} fresh mass)	Na (mM)	K (mM)	Mg (mM)	Ca (mM)	Fe (mM)	Cl (mM)
Rhizomes	80·2	594	4·9	142	5·5	2·4	0·07	92
Lower leaves	67·1	577	4·0	247	50	140	0·05	243
Upper leaves	55·0	437	2·4	141	59	85	0·04	136
Panicles	71·9	587	7·2	144	18	20	0·04	71

Table 7. Ash, water-soluble compounds (in hot water), cellulose and lignin as % of total content in individual whole stems. Data from Rudescu, Niculescu & Chivu (1965)

	Internodes	Nodes	Leaf sheaths	Shoot
Ash	2·81	3·95	11·20	7·0
Water-soluble compounds	3·22	5·44	8·42	4·2
Lignin	19·29	23·56	18·90	20·0
Cellulose	52·30	49·87	45·41	44·0

Table 8. Starch, lignin, cellulose, hydrolysable compounds (the fraction most readily decomposed) and ash as % of total content in individual whole stems during different months. Data from Rudescu, Niculescu & Chivu (1965)

	March	April	May	June	December
Starch	50·3	18·5	16·6	12·0	10·0
Lignin	8·0	8·5	12·0	16·3	20·0
Cellulose	15·5	31·9	35·4	41·3	44·0
Hydrolysable compounds	82·9	66·0	46·5	32·4	20·0
Ash	3·7	3·7	4·0	7·0	7·0

Jackson & Armstrong 1999; Faußer *et al.* 2016; see also IV for the role of oxygenation in the competitive ability of *P. australis*). Rhizome walls comprise c. 50% aerenchyma (Rudescu, Niculescu & Chivu 1965). The osmotic pressure within rhizome cells is between 1722 and 2229 kPa, depending on time of the day (morning 1722, afternoon 1945 kPa) and water conditions (1985 for plants in water, 2219 for those at wet soil and 1803 kPa for those at dry soil) (Rudescu, Niculescu & Chivu 1965). In addition, the well-developed exodermis of the roots and rhizomes reduces their radial oxygen loss (Armstrong & Armstrong 1988).

Water relations

Leaves seem to be very sensitive to water availability and their production and expansion is reduced under water deficit. Water balance is maintained through stomatal closure that results in reduced CO_2 assimilation with no effect of drought on Rubisco activity (Pagter, Bragato & Brix 2005; see also VI A for rates of stomatal density). A decrease in maximum quantum yield of photosystem II was observed under extreme drought, i.e. between the 8th and 11th day without water (Saltmarsh, Mauchamp & Rambal 2006; see V B).

(F) BIOCHEMICAL DATA

Individual plant parts differ in their water content, volume of expressible sap and concentration of elements in the sap (Table 6). The rhizomes are characterized by the highest water content and generally low concentrations of elements, while the opposite is true for the leaves (Björk 1967).

The relative content of ash and organic compounds varies between individual shoot parts and changes throughout the year (Rudescu, Niculescu & Chivu 1965) as shoots emerge, develop and die. Leaf sheaths are characterized by the highest proportion of ash and water-soluble compounds, while internodes have the highest cellulose content and nodes the highest lignin content (Table 7). The content of cellulose, lignin and ash within shoots increases during the vegetation season, while starch and hydrolysable compounds (the fraction most readily decomposed) decrease (Table 8).

VII. Phenology

Phragmites australis has the life cycle of a helophyte (primary) and geophyte (secondary; Rodwell 1998c; Preston, Pearman & Dines 2002; Hill, Preston & Roy 2004). The species overwinters with horizontal rhizomes and terminal buds near the surface (e.g. from mid-September until late March–April in Britain; see VI A for further details on the underground phenology). Shoots emerge in spring, with timing determined primarily by internal factors that are mediated by external conditions (e.g. local climate such as frost severity; Clevering, Brix & Lukavská 2001; Haslam 2010). Delays can be caused by adverse conditions such as drying and cold weather. In the northern hemisphere, spring emergence commences from late January (e.g. Malta; Haslam 2010) and is delayed at increasing latitude to late March to late April in England (Haslam 2010) and March to May in North America (L.A. Meyerson, personal observation).

The period of rapid emergence lasts 1–3 months, depending on conditions (e.g. within the Breckland fens, England, shoot emergence can be several weeks earlier in sheltered micro-habitats compared with exposed ones; Haslam 1972). It is prolonged by spring frosts, grazing and decreasing latitude (see fig. 5 in Haslam 1972). For example, Malta has a longer potential growing season compared with Britain (Haslam 1969c), and Spain compared with the Czech Republic (Clevering, Brix & Lukavská 2001). Most buds which emerge first are large and form tall shoots that are likely to flower in good conditions (Haslam 2010). Only a few additional shoots may continue to arise until mid-autumn in Britain, when winter frosts stop further surface growth and terminal buds await the next growing season.

Table 9. Invertebrates associated with *Phragmites australis* across different continents. Data from Tewksbury *et al.* (2002)

Order/family	Africa	Asia	Australia	Europe	North America	Total per Order
Acari				6	1	7
Pyemotidae				3		
Tarsonemidae				3	1	
Coleoptera		4		8		12
Chrysomelidae		4		6		
Curculionidae				1		
Malachiidae				1		
Diptera	7	28		51	9	95
Agromyzidae	2	5		11	4	
Anthomyzidae				2		
Asteiidae				1		
Cecidomyiidae	1	1		7	2	
Chloropidae	4	22		26	3	
Dolichopodidae				2		
Opomyzidae				1		
Scathophagidae				1		
Heteroptera		1		2		3
Lygaeidae		1				
Miridae				2		
Homoptera	4	21	2	24	5	56
Aclerdidae		3				
Aphididae	1	2	1	2	1	
Cercopidae				1		
Cicadellidae				1		
Coccidae		2		4	1	
Delphacidae				8		
Eriococcidae		1				
Pseudococcidae	3	13	1	8	3	
Hymenoptera				2	1	3
Cephidae				1		
Eurytomidae				1	1	
Lepidoptera		21		39	10	70
Cosmopterigidae		1		4		
Cossidae		1		1		
Crambidae		3		5	1	
Elachistidae		1		1	1	
Gelechiidae				2		
Hesperiidae		2		1	2	
Lasciocampidae				1		
Lymantriidae		1		1		
Noctuidae		12		22	6	
Tortricidae				1		
Thysanoptera	3	2		5	1	11
Phlaeothripidae	3	2		3	1	
Thripidae				2		
Total	14	77	2	137	27	257

Inflorescences emerge from early spring in Britain (April; Haslam 1972), with flowering and fruiting between mid-summer (late July) until autumn (mid-October; Cope & Gray 2009). Panicles start to mature around mid-August (Cope & Gray 2009). Elsewhere the inflorescence emergence depends on latitude and associated climate. When grown under the same experimental conditions in central Europe, populations originating from northern Europe (e.g. Britain and Sweden, Clevering, Brix & Lukavská 2001; see also Haslam 1972; Cope & Gray 2009) began their growth and panicle appearance earlier than populations from Mediterranean Europe (e.g. Spain, Clevering, Brix & Lukavská 2001) where the growing season is longer. A similar study found that Iranian populations grew and flowered later than European populations grown in the same conditions, and that these Iranian reeds were also taller and thicker with more stem nodes and larger panicles (Bastlová *et al.* 2006; Diyanat *et al.* 2011). Fruits ripen and set seed by late autumn and are dispersed in winter and spring (depending on local conditions) (Haslam 1972).

The lower leaf blades die and fall throughout the summer, with most blades shed by mid-summer in Britain (Haslam 1972). In dense populations, stems usually remain standing, and contribute to rhizome aeration into the next season(s), e.g., for up to two and a half seasons in the British Isles and up to 45 dead standing stems per m^2 in the following season

in Connecticut, USA (Meyerson 2000). Falling stems tend to break off at the first or second node, a few centimetres above the ground, and the remaining stumps trap litter for several years (Ailstock 2000).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

All fully developed shoots of *P. australis* have the potential to flower, although most inflorescences are produced on the largest (tallest and thickest) shoots in healthy stands (Haslam 1972, 2010). In Britain, panicles are not found on stems with <9 nodes, which is the most common number of nodes, and stems with >12 nodes always flower (Haslam 2010). In Malta, the proportion of stems with inflorescences is higher (Haslam 2010). Panicles contain hundreds of spikelets, each with 1–10 florets (Ishii & Kadono 2002; Gucker 2008). Sometimes panicles are not fully developed (e.g. empty spikelets, or with a single glume or floret) if the panicle is formed late in the growing season, or other conditions limit its emergence (Weber & Wittmann 1996; Haslam 2010). The fully formed florets are hermaphrodite (Mal & Narine 2004) with one ovule each (Ishii & Kadono 2002). Individual panicles flower for 2–3 days and each population for only about 10 days (Ishii & Kadono 2002).

Cross-pollination by wind is the main vector for sexual reproduction (Tucker 1990; Wijte & Gallagher 1996a, b). Pollen viability (88·9–99·6%) and its rate of germination on stigmas is high in Japan (98·5–100%; Ishii & Kadono 2002). Self-compatibility has also been confirmed, so self-pollination and/or agamospermy (seed production without fertilization) might occur (Ishii & Kadono 2002; Lambert & Casagrande 2007). Pollination rates in reedbeds along a river system in Japan were only 5·8% and 26·1%, respectively, while cross-pollination trials (by hand) in the laboratory achieved 64·4% to 52·4% and increased seed set, suggesting there was limitation by cross-pollination (Ishii & Kadono 2002). Meyerson, Viola & Brown (2010) also conducted hand cross-pollination trials and reported rates varying from 0% to 100%. There are no records of vivipary.

(B) HYBRIDS

There has been no reported investigation of potential interbreeding among *P. australis* lineages in Britain. Both inter- and intraspecific hybrids of *P. australis* have been widely reported in North America (Meyerson, Viola & Brown 2010; Meyerson *et al.* 2012). Introductions of a subspecies (regarded as *P. australis* subsp. *latissimus)* and *P. mauritianus* to the Gulf Coast of North America have resulted in multiple hybridization and backcrossing events (Lambertini *et al.* 2012a; Meyerson *et al.* 2012), particularly among *P. australis* and *P. mauritianus* (Lambertini *et al.* 2012a). Hybrids have also occurred in the wild between the North American native lineage and the introduced lineage from Europe (Paul *et al.* 2010; Saltonstall, Castillo & Blossey 2014; Wu, Murray &

Heffernan 2015). In South Korea, hybrids of *P. australis* and *P. japonicus* were reported (Chu *et al.* 2011). Hybrids do not appear to have morphological intermediates, but this has never been thoroughly investigated (L.A. Meyerson, personal observation), nor has heterosis in wild hybrids been reported; *P. australis* appears to be dominant world-wide.

(C) SEED PRODUCTION AND DISPERSAL

Seed production varies considerably, ranging from 500 to 2000 seeds per inflorescence (Bittmann 1953; Wijte & Gallagher 1996b). The elliptical caryopses (1·2–1·5 mm long and about half as wide; Larson 1993) and seed (0·8–1·0 mm; L.A. Meyerson, P. Pyšek, M. Lučanová, J.T. Cronin, C. Lambertini, J. Wild & J. Suda, unpublished data) are small, with an average air-dry seed mass of 0·08–0·20 mg (McKee & Richards 1996; L.A. Meyerson, P. Pyšek, M. Lučanová, J.T. Cronin, C. Lambertini, J. Wild & J. Suda, unpublished data).

The species sets seed annually but inter-annual variability in seed set rate (generally calculated as the number of mature seeds per floret) and viability has been observed (Gustafsson & Simak 1963; Meyerson, Viola & Brown 2010; Saltonstall, Lambert & Meyerson 2010). Seed set in native populations is highly variable in different seasons and regions, e.g., in Britain (0–2·6% in The Broads, apart from a single inflorescence with 83% viable seed; Chater 2010) and France (0–20%, McKee & Richards 1996; see also Chater 2010), Sweden (mean <5%, Gustafsson & Simak 1963), Switzerland (1–55% in different years; Hürlimann 1951), Canada (0–27·1%, mean 6·6%, Maheu-Giroux & de Blois 2007), and Japan (0·1–59·6%, mean 9·7%, Ishii & Kadono 2002). The strongest influences on the amount of seed produced are stand size and latitude of the population, which influences the local climate and determines the length of the growing season and timing of flowering (McKee & Richards 1996). Modelling from British and French field trials indicated that higher rates of seed set occur when low winter rainfall is followed by high spring temperatures and rainfall (McKee & Richards 1996; see also Haslam 2010). Unsuitable weather during flowering and seed setting can have a negative impact on seed set (Hürlimann 1951; Love & Love 1954; Haslam 1972). In British and French reedbeds, heavier seeds tend to come from tall reeds that produce many seeds and are more likely to germinate than lighter seeds (McKee & Richards 1996). Seeds from Europe are reported to be non-dormant at maturity but one study in the Chesapeake Bay, USA, found seeds of the non-native genotype from Europe to be dormant and have highest germination rates after cold stratification (Kettenring & Whigham 2009). Overwintering may help to increase seed viability as it allows the embryo to ripen (populations produced mostly viable seeds, compared to mostly non-viable seed previously reported from the same region in USA, Tucker 1990; Ailstock 2000).

Fungal infection, particularly by *Claviceps* species (ergot fungi), can reduce the viability of seeds substantially and is described in IX B. Genetic (Björk 1967) and habitat differences are likely to reduce the percentage of viable caryopses (Haslam 2010), and other factors which need further

investigation are meiotic disturbance, pollen lethality and self-compatibility (Gustafsson & Simak 1963; Tucker 1990; Ishii & Kadono 2002).

Wind (Wijte & Gallagher 1996a, b), and to a lesser extent water, are the main dispersers of caryopses (Gucker 2008). The mature spikelets (fruit) break at the rachilla joint and are shed with the lemma, palea and rhachilla segment (Arber 1934), and their fine, plumed hairs enable them to be carried by wind (Tucker 1990). Unshed fruits sometimes fall with the panicles and can be dispersed by water or human intervention (accidental or intentional; Marks, Lapin & Randall 1994b; Meyerson, Pergl & Pyšek 2014). Increased survival in flowing water has been confirmed in trials in Germany and the Netherlands; 90% of seeds in stagnant water survived for 10 days compared with 23 days in moving water (Broek, Diggelen & Bobbink 2005). Dispersal rates of caryopses from inflorescences also vary, e.g., 40% in 1 year compared with 1–5% in the following years in a single site (Bittmann 1953). In addition to wind and water, reed seeds are also dispersed by birds nesting and moving about in the reed, e.g. migratory Eurasian teals (*Anas crecca* L.; Brochet *et al.* 2009) and reed-nesting red-winged blackbirds (*Agelaius phoeniceus* L.; Marks, Lapin & Randall 1994b).

(D) VIABILITY OF SEEDS: GERMINATION

Seed viability is low in British plants. Germination occurs during spring and early summer (Mal & Narine 2004) and is triggered by large diurnal temperature fluctuations preceding warmer spring weather (Ekstam, Johannesson & Milberg 1999). It requires bare mud or shallow water and is threatened by flooding (Rodwell 1998c). Seeds can germinate within 2–10 days if the weather and environmental conditions are favourable, such as in Britain where tens to hundreds of new individuals emerged rapidly in an abandoned gravel pit (Haslam 2010). Germination rates under experimental conditions are higher and more consistent and have been reported as between 70% and 100% (Hürlimann 1951; Buttery 1959; Gustafsson & Simak 1963; Ekstam 1995; Saltonstall, Lambert & Meyerson 2010). Germination after 3–4 years of storage has also been recorded by Bittmann (1953) and Meyerson (unpublished data).

Germination is influenced by temperature, salinity, water depth (Marks, Lapin & Randall 1994a) and fungal infection. Temperature has a strong influence and although germination can take place over a wide range of temperatures, it is stopped by frost (e.g. Bittmann 1953) and may be slower at low temperatures (in the range of c. 10–30 °C day maximum temperature; Hürlimann 1951; Rudescu, Niculescu & Chivu 1965). Germination increases at temperatures above 30 °C day maximum temperature (Hürlimann 1951; Bittmann 1953; Rudescu, Niculescu & Chivu 1965). Salinity interacts with temperature, as high temperatures enhance germination in optimal soil conditions, while low temperatures are beneficial when the conditions are highly saline (Greenwood & MacFarlane 2006). Mildly saline conditions can increase germination, with the greatest germination of seeds collected from the Yellow River Delta, China, in 0·5% NaCl (97% ±1 SE), approximately 55%

in 2·5% NaCl and virtually non-existent in 3% NaCl (Yu *et al.* 2012; see also Wijte & Gallagher 1996a). Fungal pathogens, particularly *Claviceps* species, can prevent germination in up to 100% of the infected caryopses (Gustafsson & Simak 1963).

Increased water levels appear to reduce germination. Bittmann (1953) suggested germination is highest in substrates just below the water level, while Hürlimann (1951) records increased germination on moist substrate that is drying, a decrease with a covering of water, and none in deeper water. Although caryopses from Breckland fens germinated in 1–5 cm water (Haslam 1972), Baldwin, Kettenring & Whigham (2010) found no germination in 3·5 cm deep standing water and Spence (1964) found no germination in 5 or 15 cm water (though some, after drying the caryopses). Harris & Marshall (1960) also note increased germination from caryopses stored dry than wet. Breckland caryopses, however, germinated equally after storage at a range from 100% humidity to dry conditions in a desiccator (CaCl$_2$; Haslam 1972).

(E) SEEDLING MORPHOLOGY

The shoot (coleoptile) emerges and elongates before the root (Wijte & Gallagher 1996b). Seeds are considered to have germinated when both the shoot and root have emerged (Wijte & Gallagher 1996a). Seed reserves enable the seedlings to develop to the critical growth stage of 2–4 leaves (2–5 cm high; Fig. 4; Gustafsson & Simak 1963; Haslam 1972). They can remain at this stage for several weeks and may not develop further unless favourable conditions are present (e.g. adequate nutrients or light; Haslam 1972). The rate of growth in seedlings depends on the habitat conditions, with up to 70 shoots (c. 75 cm high) after 5 months in good conditions or only three shoots after 18 months in less favourable growing conditions (Haslam 1972; see also Bittmann 1953; Haslam 1971d).

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Invertebrates

Phragmites australis hosts more insect species than any other abundant perennial grass (Tscharntke 1999). Stands in the British Isles are associated with 108 species of invertebrates that are mainly herbivores, including 13 Coleoptera and Lepidoptera that are associated with *P. australis* as a host plant in the Database of Insects and Food Plants (Biological Records Centre 2017) and 85 other insects and snails (Table 4). Reliance on *P. australis* as a food resource varies, with many specialized, monophagous taxa. The endangered reed leopard moth (*Phragmataecia castaneae* (Hübner), Lepidoptera, Cossidae), for example, is a specialist herbivore that relies entirely on *P. australis* in the British Isles (Haslam 1972; Maddock 2008). More invertebrates have been recorded on *P. australis* throughout Europe (137 species, including 26 monophagous species; Table 9, Tscharntke 1999; Tewksbury *et al.* 2002) than within the British Isles (108 species).
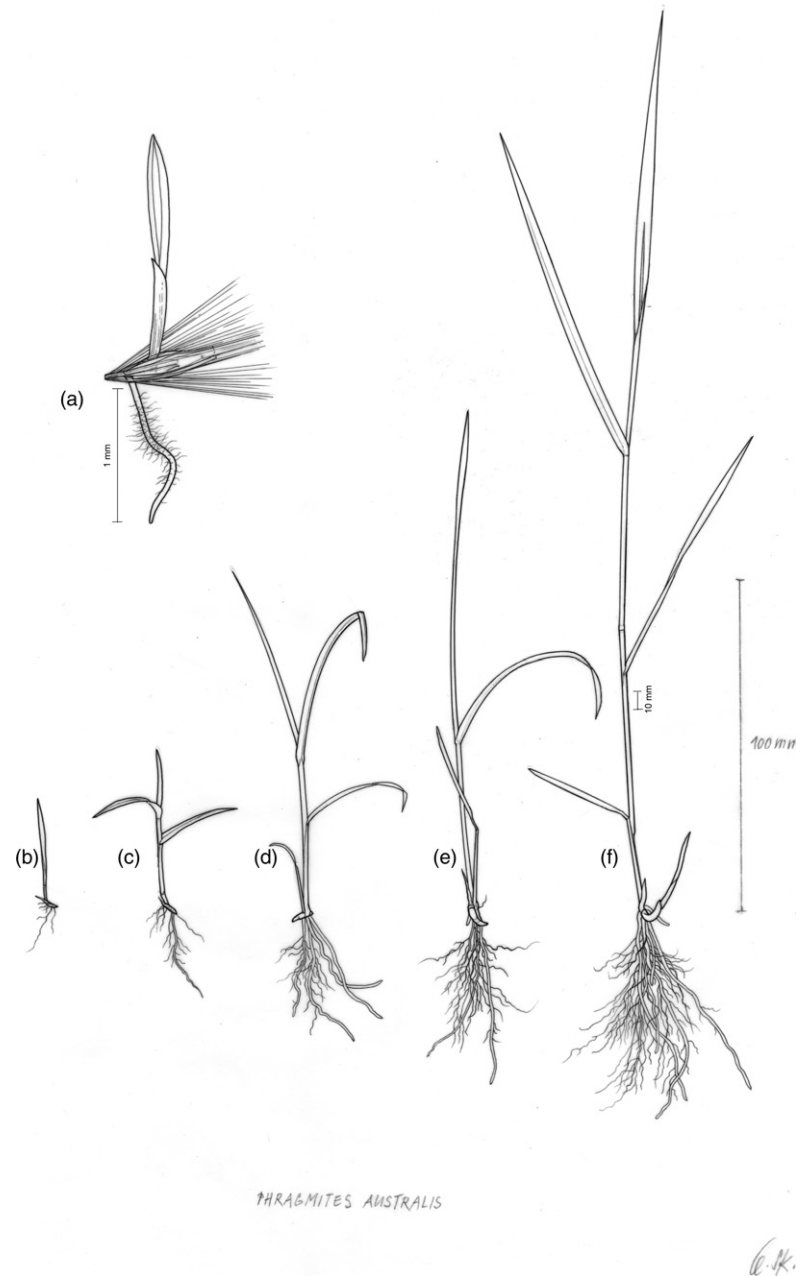
Fig. 4. The development of *Phragmites australis* from germination (a) to subsequent stages (b–e) of seedling growth until establishment (f). Material was collected from the common garden of The Czech Academy of Sciences. The seeds were dry stored for 1 year. After transfer to moist conditions in a Petri dish and 5/15 °C (night/day), the seeds germinated within about 1 week (a). They grew five leaves (f) after another 5 weeks under average temperature of 14 °C and the night/day cycle of spring in central Europe. Drawings by Anna Skoumalová.

Invertebrate herbivores can exert considerable influence on reed health, productivity (Skuhravý 1981), reproductive success (Lambert & Casagrande 2007; Cronin *et al.* 2015; Allen *et al.* 2016) and population persistence (Tscharntke 1999; Ostendorp, Dienst & Schmieder 2003). Chater (2010) reported an extensive infestation of the gall mite (*Steneotarsonemus phragmitidis* (von Schlechtendal), Araneae, Tetragnathidae) that compromised thousands of *P. australis* stems in The Broads. Herbivory impacts on *P. australis* in Europe have been reported as mostly from endophagous (within the plant body) specialists and, to a lesser extent, ectophagous (outside of the plant) feeders (Skuhravý 1981; Tscharntke 1999; Haslam 2010). The strong influence on reed performance also enables some invertebrate herbivores to influence the composition of the broader plant community (Skuhravý 1981).

Tscharntke (1999) distinguished between primary and secondary invertebrate attacks on *P. australis* in Europe. Primary attackers cause direct damage and include caterpillars (e.g. *Arenostola phragmitidis* Hübner; Lepidoptera, Noctuidae; Skuhravý 1981), freshwater apple snail (*Pomacea canaliculata* (Lamarck); Architaenioglossa, Ampullariidae; Wong *et al.* 2010), *Lipara* gall flies (Diptera, Chloropidae; adults lay eggs within the stems and larvae feed on the internal tissue) (Tscharntke 1999; Mal & Narine 2004), and the reed beetle (*Donacia clavipes* F.; Coleoptera, Chrysomelidae; Tscharntke 1990, 1999). This beetle has been one of the major causal factors in dieback of European reed populations over the past 20 years (Ostendorp, Dienst & Schmieder 2003). The beetle larvae attack the rhizomes and open up their internodes, making them vulnerable to any later damage

from flooding (Ostendorp, Dienst & Schmieder 2003; Schmieder *et al.* 2004). Secondary attackers further compromise damaged or compensatory growth and are often Dipteran. These include Chloropidae fruit flies in the top of damaged shoots (Tscharntke 1999) and gall midges (e.g. *Giraudiella inclusa* (Frauenfeld), Diptera, Cecidomyiidae, and *Lasioptera arundinis* Schiner, Diptera, Cecidomyiidae) which reduce stem height by shortening the stem internodes and tips (Dykyjová, Hejný & Květ 1973; Tscharntke 1988). The latter is mutualistic with a fungus that penetrates the stem and acts as a food resource for the larvae (Rohfritsch 2008). *Archanara geminipuncta* Haworth (Lepidoptera, Noctuidae; stem-boring moth) is less common than the infamous reed beetle (*Donacia clavipes*), but has an even greater negative impact on reed populations as it causes the development of secondary shoots (Mook & Van der Toorn 1985; Tscharntke 1990, 1999) which are much less likely to produce viable seed.

Far fewer invertebrates (26 species) feed on *P. australis* in North America compared with Europe (Tewksbury *et al.* 2002), and the non-native lineages of reed suffer less herbivory than the native lineage on that continent. Most of these invertebrates appear to be introduced, including *Lipara* gall flies (Diptera, Chloropidae) (Lambert & Casagrande 2007; Allen *et al.* 2016) and the mealy plum aphid (*Hyalopterus pruni* (Geoffroy), Hemiptera, Aphididae) which causes extensive damage on native genotypes in North America (Cronin *et al.* 2015, 2016). Mealy plum aphids are widespread on *P. australis* throughout Europe and North America, often reach densities of >1000 individuals per stem, and outbreaks can kill all above-ground vegetation in some populations (Lambert & Casagrande 2007; Cronin *et al.* 2015). In contrast, Pintera (1971) found that heavily infested reedbeds in Europe did not sustain substantial damage. *Phragmites australis* is a secondary host of the aphids (the primary host is *Prunus* spp.), and aphids were more abundant on the edges compared with the interior of *P. australis* populations along the Elbe River in Germany (Tscharntke 1989).

Invertebrate damage on *P. australis* can vary with latitude and habitat. In North America, both the native and introduced *P. australis* exhibited genetically based latitudinal gradients in aphid colony size and decreasing growth rate with increasing latitude, suggesting that latitudinal gradients evolved in both genotypes in response to herbivore damage (Bhattarai *et al.* 2017). Cronin *et al.* (2015) identified non-parallel clines in herbivory in Europe and North America and a large biogeographic difference within North America. However, apart from the investigation of herbivory along latitudinal gradients in Europe and North America (Cronin *et al.* 2015; Allen *et al.* 2016; Bhattarai *et al.* 2017), no other broad geographical scale work has been published on *P. australis* herbivores. At a habitat scale within Germany, reed growing in wet conditions showed up to 96% damage by *Archanara geminipuncta* Haworth (Lepidoptera, Noctuidae; stem-boring moth), while thinner shoots in dry habitats were relatively undamaged (Tscharntke 1990). Reduced stem stiffness and increased palatability with eutrophication resulted in increased herbivore infestations across a gradient of increasing nitrogen

levels and reed dieback in Germany (Fuchs 1993; Kohl *et al.* 1995; Čížková, Strand & Lukavská 1996).

Consistent with the enemy release hypothesis, North American reedbeds of non-native haplotypes suffer less herbivory damage than the native genotype, although they are attacked by at least five herbivores that are native to North America and at least 18 that are known to be non-native (Mal & Narine 2004). In contrast, the extensive and ancient stands of *P. australis* in Europe harbour the highest species richness of native insect herbivores of all grasses in Germany (Tscharntke 1999; Tewksbury *et al.* 2002).

Vertebrates

The main native vertebrates known to feed on *P. australis* in the British Isles are water vole (*Arvicola amphibius* (L.); see Haslam 2010) and greylag goose (*Anser anser* (L.), van den Wyngaert *et al.* 2003). Grazing by greylag goose can reduce the productivity of reedbeds in two ways: (i) by increasing the density of short shoots that are less likely to flower and (ii) by increasing eutrophication in shallow lakes and marshes (van den Wyngaert *et al.* 2003). Introduced coypu (*Myocastor coypus* (Molina)) can cause considerable damage by browsing rhizomes, and young shoots (e.g. formerly in The Broads swamps, Rodwell 1998c). Fallow deer (*Dama dama* (L.)) are also introduced in Britain and graze young shoots (Haslam 1972). The use of domestic grazing animals to manage reedbeds is described in XI.

Introduced muskrat (*Ondatra zibethicus* (L.)) are considered to exert the greatest vertebrate impact in mainland Europe (Skuhravý 1981; Kiviat 2013). In Finland, for example, muskrat have been associated with reed decline (Merilainen & Toivonen 1979). In North America, rabbits (*Sylvilagus floridanus* (J.A. Allen) and *Sylvilagus* sec. *audubonii* Gray) eat leafy shoots, several small birds (e.g. *Dolichonyx oryzivorus* (L.) feed on seeds, Canada geese (*Branta canadensis* (L.)) on the leaf blades and snow geese (*Chen caerulescens* (L.) on the rhizomes (Kiviat 2013) of native and non-native haplotypes of *P. australis*. In Australia, kangaroos and wallabies forage on the young shoots and leaves of *P. australis* (Hocking, Finlayson & Chick 1998; Mal & Narine 2004).

(B) & (C) PARASITES AND DISEASES

Dodder (*Cuscuta* sp.) is the only plant parasite that has been recorded on *P. australis* within its native range, and only in North America (Kiviat 2013).

Sources of disease in native *P. australis* include fungi (Haslam 1972; Ban, Viranyi & Obadovics 1998; Mazurkiewicz-Zapalowicz 2010), oomycetes (Nechwatal, Wielgoss & Mendgen 2008a; Nelson & Karp 2013), bacteria (Starink *et al.* 1996) and viruses (Ivanovic 1992). Fungal-related disease causes the highest rate of infection, particularly *Claviceps purpurea* Fr. (Tul.) in wet summers (Haslam 1972). The rate of *Claviceps* infection varies between populations and in different weather conditions, with 0–20% of florets ($n = 5400$) infected and the caryopses aborted in four

Swedish reedbeds (Gustafsson & Simak 1963). Hürlimann (1951) also reported *Claviceps* infection of up to 20% in Switzerland and Chater (2010) found the rate varied in The Broads from 0% to 23%, but it could be as high as 50% in Breckland fens in wet summers (Haslam 1972). Flowers that fail to produce viable caryopses due to *Claviceps* infection have sclerotia (elongated, dark, hard masses of fungal hyphae) that are often more than four times longer than wide (see figs 3–4 and 6–7 in Gustafsson & Simak 1963). *Ustilago grandis* Fr. can affect over 1 ha of reedbeds in The Broads, England (Chater 2010). *Puccinia invenusta* Syd & P. Syd., fungal rust parasite, infects *P. australis* in Europe, Africa and Asia (and has no other hosts), *P. magnusiana* Körn is associated with the genus world-wide, and *P. trabutii* Roum. & Sacc. infects *P. australis* in northern Africa and southern Asia (Tucker 1990).

Fungal pathogens that are associated with different parts of the reed are reported in Haslam (1972), and although the ecological significance of these is largely unknown, they are likely to compromise the normal development of reed (Ban, Viranyi & Obadovics 1998). Damaged or exposed rhizomes (e.g. from trampling or transplanting) appear to be susceptible to fungal infection in wet conditions (Newbold, Honnor & Buckley 1989). Damaged rhizomes may be the cause of reduced post-transplant survival in some habitats (e.g. 12·8%, $n = 30$, in the Grand Canal, Northern Ireland; Caffrey & Beglin 1996). Endophytic fungi, including pathogenic taxa, have been found in roots (Wirsel *et al.* 2001; Ernst, Mendgen & Wirsel 2003; Kim *et al.* 2014), rhizomes (Ernst, Mendgen & Wirsel 2003), stems (Wirsel *et al.* 2001; Ernst, Mendgen & Wirsel 2003; Van Ryckegem & Verbeken 2005; Fischer & Rodriguez 2013), leaves/culms (Wirsel *et al.* 2001; Ernst, Mendgen & Wirsel 2003; Van Ryckegem & Verbeken 2005; Angelini *et al.* 2012) and seeds (Ernst, Mendgen & Wirsel 2003).

Nechwatal, Wielgoss & Mendgen (2005) found a new, highly aggressive oomycete, *Pythium phragmitis* Nechw. in *P. australis* leaves within declining populations at Lake Constance, Germany (see also Nechwatal, Wielgoss & Mendgen 2008b). In North America, soils from native and non-native (European) *P. australis* were dominated by *Pythium* species, with differences in composition and diversity (Nechwatal, Wielgoss & Mendgen 2008b; Nelson & Karp 2013). A follow-up study by Crocker, Karp & Nelson (2015) found that many of the *Pythium* taxa they detected in *Phragmites* in the North American Great Lakes region are also found in the native range of *P. australis* in Europe. One species, *Pythium angustatum* Sparrow had a more negative effect on seedling survival in the native lineage in the Great Lakes, compared with the introduced, but they also noted that microbial diversity in natural systems is little explored and the effects may be site specific.

Bacterial activity associated with reedbeds has been reported for Europe. In littoral lakes in the Netherlands, bacterial density increased with the seasonal increase in biomass of *P. australis*, compared with minor fluctuations in a paired survey in open water (Starink *et al.* 1996). The only viral infection reported within the native range of *P. australis* was in former Yugoslavia, where common reed was a primary source host for dwarf mosaic virus which is problematic for maize crops (Ivanovic 1992).

X. History

(A) HISTORY OF NATURAL SPREAD

The age of the Arundinoideae clade (to which *Phragmites* belongs) is estimated to be (7·3) 17·3–22·6 (34·3) million years (Cotton *et al.* 2015). Palaeoecological records of *Phragmites* reeds from c. 13 million years ago are known from Germany (Storch, Welsch & Wink 2013). In Britain, *Phragmites australis* has been abundant from the latest ice age (late Zone IV post-glacial period) onwards (Oldfield 1960; Seagrief & Godwin 1960; Pigott & Pigott 1963; Godwin 1975; Ingrouille 1995). In North America, *P. australis* remains were found in 3000-year-old peat cores from tidal marshes (Niering, Warren & Weymouth 1977) and in fossilized sloth dung in southwest USA, suggesting it may have been widespread during the Pleistocene (Hansen 1978). The remains of *P. australis*, and the peat it sometimes forms, can often be found beneath *Sphagnum* and *Eriophorum vaginatum* peat in former and current saltmarsh (Godwin & Newton 1938), and acidic bogs or mosses in the British Isles in southern England (Seagrief 1960), Wales and western England (Godwin & Mitchell 1938; Hardy 1939; Davies 1945) and northern Britain (Gorham 1957). These *Phragmites*-peat layers can be deep where mineral-rich water has been continuously present, e.g., The Broads (Jennings & Lambert 1951) and the Breckland fens (Jennings 1955). However, identifying *Phragmites* in fossil deposits using pollen grain size criteria may be difficult within assemblages with other grasses (Hall 1991). The species was known to the early herbalists and the first British botanical record appears in William Turner's *A new Herball* (Turner 1551) as a kind of reed called phragmitis which was 'well knowen of all men' and 'groweth much in England' (Clarke 1900).

In Europe and China, natural populations of *P. australis* continue to be broadly distributed across wetland and arid systems (An *et al.* 2012). More recently, it has become abundant on the edges of agricultural systems and in other disturbed areas throughout much of its native and non-native distribution. The vast Mesopotamian Marshes (see V A) dominated by *P. australis* were systematically diked and ditched by the regime of Saddam Hussein. By 2000, only 10% of these marshes remained but restoration is underway (Richardson & Hussain 2006).

Uses

The name *Phragmites* refers to the hedge-like growth habit and is derived from the Greek *phragma* for hedge, fence or screen, and Latin *phragmites* for a kind of reed growing in a hedge (Quattrocchi 2006). In Europe, humans have used *P. australis* since the last ice age in the north and along the Baltic Sea (Schaatke 1992; Ostendorp & Krumscheid-Plankert 1993), and in ancient Scandinavia, it was used by the Vikings (Price 2015). *Phragmites australis* remains have also been

found as artefacts from sites of the Anasazi indigenous peoples in southwestern Colorado, USA (Breternitz, Robinson & Gross 1986; Kane, Gross & Breternitz 1986). In Africa, *Phragmites* has been used for centuries to make mats and roofing materials and the ongoing harvesting contributes to the degradation of some wetlands (Traynor, Kotze & McKean 2010 and references therein).

Contemporary use of *P. australis* as a crop species is predominantly for roof thatching and, increasingly, manufacturing and biofuels. In Britain, it is used mainly for thatching. The crop is cut commercially from December/January until March/April in Britain, starting when the leaf blades are shed, and the cane-like stems rattle when handled. Reedbeds are increasingly being extended or recreated from seed and rhizome to restore vegetation communities (e.g. reconstructed Kingfisher Bridge fenland, Cambridgeshire; Tomkins 1998), to create wildlife habitat, and to act as filter beds for infrastructure such as roadside runoff (e.g. Kildare–Portlaoise motorway near Dublin, Northern Ireland; Gill *et al.* 2014) and sewage systems (e.g. in Dihewyd, Cardiganshire; Chater 2010).

Outside Britain, reedbeds are or were formerly exploited commercially in the Danube Delta (Rudescu, Niculescu & Chivu 1965), elsewhere in Eastern Europe (Rodewald-Rudescu 1974) and the Netherlands (Bittmann 1953). Scandinavia has begun importing *P. australis* from China for thatching (H. Brix, personal communication). Living plants are used for stabilizing river and canal banks (Bittmann 1953) and for draining and drying out new polders in the Netherlands. Aerial stems and rhizomes are used as a coffee substitute and as the basis of an alcoholic drink (Bittmann 1953; Rudescu, Niculescu & Chivu 1965). Fruits and associated silky hairs are used for stuffing (Bittmann 1953); both roots and leaves are ground and used as a starch or flour, and stems and leaves boiled to extract sugar (Plants For A Future 2015). It is also used for fencing to give frost and wind protection in horticulture (Köbbing, Thevs & Zerbe 2013), as fodder and for litter (e.g. cultivated in Argentina; Haslam 1972), and as a cellulose source for cardboard and paper and various construction materials (Haslam 1972; Kiviat 2013; Köbbing, Thevs & Zerbe 2013; Brix *et al.* 2014). In Rhode Island, USA, *P. australis* is packed with mud and used for shellfish bakes in coastal areas (L.A. Meyerson, personal observation). In China *P. australis* is used for paper-making and reed mats (An *et al.* 2012).

More recently, *P. australis* has been used as a resource and for producing ecosystem services, including phytoremediation in constructed wetlands (Hocking, Finlayson & Chick 1983; Brix 1994) and for nitrogen retention to reduce eutrophication due to the absorption rates outlined in II B (Hershner & Havens 2008). Biomass production and N absorption are reported to increase with the addition of lime ($CaCO_3$) and the resulting increase in pH from 6·3–7·2 to 6·9–8·2 (González-Alcaraz, Conesa & Álvarez-Rogel 2013). High removal efficiency for Al (96%), Cu (91%), Pb (88%) and Zn (85%), and considerable removal efficiencies for Fe (44%), Co (31%) and B (40%) were observed in constructed wetlands (Morari, Dal Ferro & Cocco 2015). Biofuel and carbon sequestration are also gaining in popularity as commercially viable uses of wild and plantation reedbeds, particularly where they are abundant and invasive (Kiviat 2013). Trials of dried reed stem pyrolysis identified the optimal heating rate of 0·42 °C s^{-1} and combustion at 550 °C to create an energy feedstock (condensed, transportable resource) that is rich in carbon, low in sulphur (Sutcu 2008) and more thermally stable than alternative grasses such as *Miscanthus* spp. and *Pennisetum* spp. (Xufeng *et al.* 2009). The reed biofuel is commercially attractive for domestic energy and viable for combined heat and power generation or co-combustion in the existing coal plants of northern China (Köbbing *et al.* 2014).

(B) MODERN INTRODUCTIONS AND INVASIONS

Local mixing, global introductions and invasive spread

Phragmites australis is used for many commercial purposes world-wide and, as described in X A, has been actively managed by humans since the last ice age. Many *P. australis* plants have been moved at different scales from the local (intentionally to stabilize canal banks (Bittmann 1953), or accidentally (Marks, Lapin & Randall 1994b; Meyerson, Pergl & Pyšek 2014) to the continental, e.g., from Europe to North America (Saltonstall 2002). The result has been a complex global web of *P. australis* population movements (Fig. 2; Saltonstall 2002; Lambertini *et al.* 2012a, b). While a few of these introductions have been identified (e.g. North America; Meyerson & Cronin 2013), others have been inferred from the non-native status of *P. australis* at regional (e.g. Brazil; Clayton *et al.* 2015a) or national levels (e.g. Australia; Saltonstall 2002). Many others are emerging and need to be investigated (e.g. Uganda; Haslam 1972) before the current and evolving biogeographic structure of *P. australis* can be understood globally.

In the British Isles, the potential presence of non-native haplotypes and/or multiple movements of *P. australis* in or out of the region does not appear to have been investigated. The genetic status of *P. australis* in Britain is discussed in VI A. There is some likelihood that evolution may have been fostered through decades of commercial, and more recently conservation, management of reedbeds, e.g., by selecting or moving ecotypes with desirable characteristics for wildlife habitat.

Emerging new insights into the presence of non-native genotypes in well-researched areas, particularly North America (Saltonstall 2002; Lambertini *et al.* 2012a, b), suggest their distribution is a much more widespread phenomenon. Multiple introductions of *P. australis* to North America have occurred (Lambertini *et al.* 2006; Meyerson *et al.* 2012; Meyerson & Cronin 2013). European haplotype M was the first lineage to be recorded as non-native and first appeared in the herbarium record in North America c. 150 years ago (Saltonstall 2002) before rapidly spreading throughout the continent (Chambers, Mozdzer & Ambrose 1998; Saltonstall 2002). Non-native lineages of *P. australis*, including haplotypes M and Delta, are expanding in North America and sometimes form monodominant populations. There is growing concern that some of the expanding populations in other parts of the world might also be cryptic, non-native lineages within the

native range of the species, e.g. the European haplotype M has been recorded in Asia and Australia (Saltonstall 2002; Hurry, James & Thompson 2013). In South America, *P. australis* is most closely related to the Land-type found in the Gulf Coast by Lambertini *et al.* (2012a), but its introduction status remains uncertain (C. Lambertini and K. Saltonstall, personal communication). In China, *P. australis* has continued to expand its distribution and haplotype M, in particular, has been distributed across the country for restoration because of its robust clonal reproduction (An *et al.* 2012). *P. australis* was introduced and is now naturalized on islands in the Pacific (New Zealand, New Caledonia, Cook Islands and Hawaii; Lansdown 2015) and the Caribbean Sea (Bahamas, Dominican Republic, Haiti, Leeward Islands, Puerto Rico, Trinidad-Tobago and Windward Islands; Clayton *et al.* 2015a). It is unknown, however, whether the species was introduced to these islands intentionally or accidentally. Whether non-native genotypes of *P. australis* have been introduced to other places such as South Africa or South America is an unresolved question.

Ecological differences between native and introduced ranges

Phragmites australis grows widely throughout its native ranges in Europe, North America, Asia and Australia. While it is an important component of wildlife habitat (Kiviat 2013), *P. australis* can also be 'weedy' and colonize the disturbed edges of agricultural fields, roadsides and edgelands, in its native range much as it does in North America where non-native genotypes are invasive (Hocking, Finlayson & Chick 1983). Genetic evidence suggests differences and, to a lesser extent, overlap in the ecological and biogeographic niches among haplotypes (Lambertini *et al.* 2006; An *et al.* 2012; Lambertini *et al.* 2012a; Guo *et al.* 2014; Cronin *et al.* 2015). *Phragmites australis* is considered to be a useful model species for understanding differences between the performance of different genotypes in native and non-native biogeographic ranges (Kueffer, Pyšek & Richardson 2013; Meyerson, Cronin & Pyšek 2016; Packer *et al.* 2017b). For example, in western China, haplotype M is found mainly in arid habitats such as deserts and dry river beds, while haplotypes O and P are more frequently found in the wetlands of eastern China (An *et al.* 2012). In North America, native *P. australis* often grows in small populations with low to moderate density but populations can also be extensive, particularly in the Mid-Atlantic coastal states reaching from New York to Virginia (Cronin *et al.* 2015). Plant species richness is lower in stands of non-native compared with native populations, particularly in freshwater systems (L.A. Meyerson, unpublished data).

Invasion by non-native *P. australis* is a multi-stage process (*sensu* Richardson & Pyšek 2006; Guo *et al.* 2014) and is limited by poor drainage and lack of burial opportunities for seed and rhizome fragments, or salinity during the early stages. However, established non-native *P. australis* can extend into less favourable anoxic and highly saline areas (Bart & Hartman 2002). While often facilitated by disturbance (Chambers, Meyerson & Saltonstall 1999; Meyerson *et al.*

2000; Silliman *et al.* 2014), introduced non-native *P. australis* also readily colonizes undisturbed ecosystems. Among reported predictors of persistence and expansion are stand area (Kettenring *et al.* 2011) and genetic diversity (Belzile *et al.* 2010; McCormick *et al.* 2010a; Kettenring *et al.* 2011; Kirk *et al.* 2011). Genome size may also relate to competitiveness, with smaller genome plants of the non-native haplotype M outcompeting native haplotypes with larger genomes in North America (Suda *et al.* 2015; Meyerson *et al.* 2016; Pyšek, J. Čuda, H. Skálová, J. Doležal, O. Kauzál, K. Pyšková & L.A. Meyerson, unpublished data).

XI. Conservation

Conservation approaches within ecosystems dominated by *Phragmites australis* vary considerably, depending on management goals, habitat type, and genotype. The main management goals range along a continuum from reversing contraction in native populations (e.g. Britain, continental Europe, North America), increasing or decreasing the extent and density of native *P. australis* populations to balance multiple conservation targets (e.g. habitat needs of threatened birds in reedbeds vs maintenance of plant diversity in fens), to managing expansion of invasive non-native haplotypes (e.g. North America). In its core habitats, *P. australis* is sometimes considered a problematic high-performing species (Hocking, Finlayson & Chick 1983; Güsewell 1997; Ostendorp & Dienst 2009) as it forms dense monospecific populations that require active management to retain floristic richness (Fojt & Harding 1995; Güsewell, Le Nedic & Buttler 2000). It is this tendency to dominate and form extensive populations that is also particularly problematic in the non-native lineages invading North America (Hocking, Finlayson & Chick 1983; Chambers, Meyerson & Saltonstall 1999; Meyerson, Vogt & Chambers 2000; Saltonstall 2002; Meadows & Saltonstall 2007; McCormick *et al.* 2010a). Successful management of reedbeds is often complex due to the need to balance the sometimes conflicting needs of different species associated with *P. australis* and associated habitats, ideally through an adaptive-management approach (Ailstock 2000).

(A) SPECIES CONSERVATION

Phragmites australis is not currently threatened in the British Isles (JNCC 2014), nor globally (IUCN category Least Concern; Lansdown 2015). Although the species is widespread with about 5000 ha of reedbeds throughout the British Isles, these mainly small fragmented populations (less than 18% are >20 ha; Natural England and RSPB 2014) are a Priority Habitat in the UK Biodiversity Action Plan (Maddock 2008). Likewise in Europe, the major focus has been concern about the declining ecological condition of reedbeds and contraction over several decades (van der Putten 1997; Graveland 1998; Brix 1999), most recently in Italy (Fogli, Marchesini & Gerdol 2002). In contrast, the dieback at Lake Constance, Germany, has been seen more positively and considered to play an important role in promoting diversity within wetland

communities by increasing structural heterogeneity and hindering over-dominance by *P. australis* (Ostendorp & Dienst 2009). Contraction of native reedbeds has also occurred beyond Europe, including in North America where native *P. australis* is declining in Rhode Island and elsewhere but remains stable in other locations (Meyerson 2007; Saltonstall, Castillo & Blossey 2014). The causes of dieback in Europe appear to be interactions that include hydrology, herbivory by beetles and eutrophication reducing the resilience of reed to exposure from waves and erosion (Brix 1999) and limiting internal aeration such as oxygenation of rhizomes (Colmer 2003; see IX). The decline in eastern Australia occurred over a similar time frame as in Europe and is considered to be due to high levels of eutrophication (Roberts 2000). The conservation status of *P. australis* in other parts of its native range is largely unknown. Almost nothing is known about populations in South America, very little in Africa, and although knowledge is building in China (An *et al.* 2012; Li *et al.* 2013) and Japan (Nakagawa, Ohkawa & Kaneko 2013; Haraguchi 2014), very little is known of its status in Southeast Asia.

Threats to native reedbeds include habitat degradation (contraction due to hydrological regulation, drainage or conversion to other land uses), inappropriate disturbance regimes (e.g. extremes of too much or too little cutting hastening the succession to woodland), rising sea levels (e.g. east coast of England), pollution (e.g. fresh water habitats becoming increasingly eutrophic), introduction of herbivores and pathogens (e.g. North America), and climate change (e.g. increasing frequency of flooding events) (The Wildlife Trusts 2015; Buglife 2016). *Phragmites australis* has been predicted to move polewards (i.e. towards the northern and southern extent of its natural range) under future temperature and precipitation levels (Edwards, Still & Donoghue 2007). Freshwater sites dominated by *P. australis* are a naturally dynamic stage in hydroseres from open water to woodland (Tyler, Smith & Burges 1998). Hotter and drier summers may expose freshwater reedbeds to drought and promote succession, while an increase in wetter winters and extreme rainfall events could lead to waterlogging and limited access for cutting and other conservation strategies (Natural England and RSPB 2014). Altered hydrology associated with climate change may also lead to an expansion of agricultural areas, with freshwater (e.g. in Bulgaria, Czech Republic and Russia) and coastal marshes (e.g. in Estonia) at high risk in Eastern Europe (Hartig, Grozev & Rosenzweig 1997). Increased water fluctuations are predicted with climate change, and this instability combined with the increased regulation of rivers and lakes is expected to affect *Phragmites* (Ostendorp & Dienst 2009). Recommended mitigation measures include prioritizing sites with secure water supply, ensuring appropriate and flexible management to retain different stages of hydroseres as a landscape mosaic, linking isolated populations to enable gene-flow, and increasing heterogeneity (species and structural) through different aged reedbeds to create a landscape mosaic (Natural England and RSPB 2014; Buglife 2016).

(B) HABITAT CONSERVATION

Phragmites australis is sometimes considered to be a conservation priority because of the wide range of ecosystem processes and native biota supported by healthy, functioning reedbeds (Kiviat 2013). Coastline protection, water catchment filtration and mitigation of stream bed erosion are all facilitated by *P. australis* (Roberts 2000; Kiviat 2013), while species-rich reed communities can sometimes support threatened plant species. In Britain, reedbeds provide the sole habitat for some bird communities, most critically for breeding habitat of six nationally rare birds that include bittern (*Botaurus stellaris* (L.)), marsh harrier (*Circus aeruginosus* (L.)), bearded tit (*Panurus biarmicus* (L.)) (Bibby & Lunn 1982; Maddock 2008) and, in Northern Ireland particularly, the declining corn crake (*Crex crex* (L.)) (Green 1996; National Museums Northern Ireland 2011). Other threatened birds rely on it for roosting and feeding sites, such as the globally threatened aquatic warbler (*Acrocephalus paludicola* (Vieillot); The Wildlife Trusts 2015). Over 108 native invertebrates, including threatened species like the threatened Fenn's Wainscott moth (*Protarchanara brevilinea* Fenn, Lepidoptera: Noctuidae), rely on reedbeds in Britain (Table 4; see also Maddock 2008). *Phragmites australis* can have both beneficial and negative effects on native amphibians, and these conflicting needs should be taken into account in reed management. Delayed growth under high reed densities in species that normally develop rapidly (e.g. wood frog, *Lithobates sylvaticus* (LeConte)) may extend their exposure to the combined risk of predation and habitat loss, particularly later in the season when waterbodies dry out (Perez, Mazerolle & Brisson 2013). In contrast, a positive effect on native North American bullfrog (*Rana catesbeiana* (Shaw)) larval performance has been reported from non-native *P. australis* (Rogalski & Skelly 2012). Planning at multiple spatial scales (Hazelton *et al.* 2014) can promote connectivity and heterogeneity, both at the species level and structurally, resulting in a dynamic mosaic of reedbeds and other plant communities (Tyler, Smith & Burges 1998; Trnka *et al.* 2014) and with positive effects for native wildlife (Valkama, Lyytinen & Koricheva 2008).

(C) MANAGEMENT OF NATIVE *PHRAGMITES AUSTRALIS*

Within its native range in the British Isles, mainland Europe, and Australia, *P. australis* is managed as a keystone species with an often substantial effect on ecosystem composition and functioning. In North America, native *P. australis* is a minor component of most wetlands. In the British Isles, and in many other areas of the native distribution, maintaining the reedbed community requires active intervention to halt the hydroseral progression. Fens and reedbeds have been actively managed for centuries, particularly in Europe, and prioritizing a range of conservation goals is likely to be an ongoing necessity if the characteristic biodiversity that relies on reed habitat is to be retained (Bibby & Lunn 1982; Cowie *et al.* 1992; Gilbert *et al.* 2005). At the same time, there is some concern about expansion within the native range, e.g., in species-rich Swiss fens where there is

concern about the loss of rare plant species (Güsewell, Le Nedic & Buttler 2000), and in Swedish saltmarshes that provide an internationally important habitat for water birds (Pehrsson 1988). The management of native populations involves almost exclusively physical management such as changes of hydrology, cutting or grazing, while herbicide is rarely used.

Physical management

Hydrology has the greatest influence on *P. australis*, and active water management is, therefore, the most effective way to increase or decrease reed health and dominance (Bart & Hartman 2000; McCartney & De La Hera 2004). In the British Isles, water and substrate (e.g. by dredging) are actively manipulated to ensure adequate flows and diverse habitats for reedbeds and other wetland communities such as in The Broads (Kelly 2013), Wicken Fen (McCartney & De La Hera 2004) and the Kingfisher's Bridge restoration in Cambridgeshire (Tomkins 1998). Along the wetlands of the Murray River in South Australia, control measures of dominant, native *P. australis* are most effective during the dry periods of the managed hydrological cycle (Mason, Turner & Packer 2015). Overall, healthy *P. australis* is promoted by regular hydrological regimes that include a period of gentle flooding to recharge soil moisture and clear away biomass debris that limits reed and the diversity of other native plants (Lenssen 1998).

Fire has been used successfully as a reed management approach in Britain for many years (Haslam 2010). Fire, particularly in spring, can be used to promote reedbeds by removing litter buildup (to slow hydroseres), reducing competing species, supplying nutrients and increasing emergence and stem density by exposing the bed to frost (where this is light and therefore beneficial; Haslam 2009). Burns may be cool (nothing affected below c. 10 cm) through to very intense (scorched soil surface and emergence delayed by up to 2 months) (Haslam 2009). Shoots emerging after a summer fire are likely to be shorter due to a much reduced growing season (Haslam 1968). Reedbeds in the Murray-Darling basin of Australia develop a dense mass of roots and rhizomes after 5 years that prevents most other management options (Mason, Turner & Packer 2015). In North America, accidental fires can also promote non-native *P. australis* populations by increasing light and nutrient availability and are therefore an undesirable management strategy.

Cutting maintains the reed stage of the hydroseres. Cutting in summer after the main emergence (Rodwell 1998c) causes a reduction of the crop in the following year, e.g. by 40% in the Breckland fens (Haslam 1972). Cutting in autumn has less impact, and winter cutting (when the reeds are hardened and the carbohydrates are in the rhizome) has no negative effect. All cutting exposes beds to potential damage from heavy frost (Rudescu, Niculescu & Chivu 1965) and flooding. Increased cutting increases the density of reeds in mixed sedge communities, and shoot size in some communities e.g. Molinietum (Godwin 1941). In the Netherlands, cutting in spring and autumn kills *P. australis* in marshes. In Swiss fens, by contrast, cutting frequency where reed is not dominant has no long-term effect on shoot size or density (Güsewell, Le Nedic

& Buttler 2000), although adding summer cutting to the more common winter cut did slightly increase reed biomass (Güsewell 2003). Combining cutting with inundation (permanently flooded or re-flooded ≤14 days later) to cover cut stems by at least 15 cm of water appears to kill the shoots and prevent growth for up to 18 months (Hellings & Gallagher 1992; Roberts 2016).

Grazing, especially when combined with altering hydrology, can be quite effective. Reed is palatable to several domesticated animals, including cattle (*Bos taurus* L.), goat (*Capra hircus* L.), greylag goose (*Anser anser* L.), horse (*Equus ferus caballus* L.) and water buffalo (*Bubalus bubalis* L.), which are used to control the height, density and successional state of reedbeds (Vulink, van Eerden & Drent 2010; Sweers *et al.* 2013; Silliman *et al.* 2014). In one fenland system, The Broads in England, a herd of 25 Konik and Welsh ponies, are used to selectively graze grasses (incl. *P. australis*) and sedges across six sites between spring and autumn each year (Broads Authority 2014a). Although the short, and therefore, young or depauperate, shoots are preferentially grazed (Haslam 1972), goats reduced *P. australis* cover from 100% to 20% in an existing marsh reedbed in Maryland, USA, where no other food resource was available (Silliman *et al.* 2014). Grazing has a far greater effect on nutrient-poor populations as replacement buds are limited by mineral deficiency. Spence (1964) concluded that grazing accelerates the natural consequences of lowered water-table and changes the course of succession (Haslam 1972). Intensive grazing in a eutrophic wetland dominated by reed and tall herbs in the Netherlands reduced *P. australis* (Vulink, Drost & Jans 2000; see also Lambert 1948 and Bittmann 1953 who recorded reed extinction), while dominant reed increases after grazing ceases (Dahlbeck 1945; Ranwell 1961) and reed density is influenced for up to 20 years after grazing is removed (Roberts 2016).

Cutting rhizomes (hoeing, ploughing, clearing of ditches, etc.) stimulates the growth of new shoots if the water is warm enough (Haslam 1972). Digging out rhizomes entirely prevents the re-growth of reed for the longest time and is the most effective long-term strategy where expansion of dominant *P. australis* is threatening other flora (Mason, Turner & Packer 2015; S. Güsewell, personal communication). Rhizome removal can also be used to create heterogeneous microhabitats within the reedbed, such as small, moist depressions for threatened flora, although this is extremely difficult and time-consuming as any remaining rhizomes will re-colonize (Farnsworth & Meyerson 1999).

The use of herbicide to control native *P. australis* is rare and has only been reported in a single study from North America. Hunt *et al.* (2017) collated data on the management of 209 stands in Canada and USA and found that 11% of stands were treated with herbicide.

(D) MANAGEMENT OF NON-NATIVE *PHRAGMITES AUSTRALIS*

Differentiating non-native from native haplotypes, such as in North America and in Australia, is a major challenge and a

critical step to successfully managing non-native *P. australis*. An emerging new solution to this challenge is the use of genome size as a cost-effective indicator to assess the likelihood of invasiveness in *P. australis* populations where the lineage is unknown (Suda *et al.* 2015; Meyerson *et al.* 2016). In North America, the threat of non-native haplotypes requires ongoing active management to control invasions at sites where native species are negatively affected. Here, we summarize the strategies most commonly used to control non-native haplotypes of *P. australis*.

Biological management

Invertebrate herbivores have long been explored as a potential biological agent to control *P. australis* where it is non-native or a problematic cosmopolitan (Tewksbury *et al.* 2002; Häfliger, Schwarzländer & Blossey 2006). However, there is considerable debate about this approach because the North American native genotype of *P. australis* suffers significantly more damage by herbivores than the introduced genotype (Cronin *et al.* 2015, 2016; Allen *et al.* 2016; Bhattarai *et al.* 2017) raising concerns about the conservation of the native lineage (Meyerson *et al.* 2009). Emerging research that will enhance management of non-native *P. australis* may include promoting beneficial microbial communities that support its native competitors (Kowalski *et al.* 2015).

Chemical management

Herbicide is the most commonly used method of controlling non-native *P. australis* in North America (Hazelton *et al.* 2014). Isopropylamine salt of glyphosate, N-(phosphono-methyl) glycine, is often used as the active ingredient and has effectively reduced *P. australis* abundance in non-tidal wetlands on Chesapeake Bay, USA (Ailstock, Norman & Bushmann 2001). Combining herbicide with a follow-up burn can increase effectiveness, particularly where there is a diverse seed bank present (Ailstock, Norman & Bushmann 2001). However, Farnsworth & Meyerson (1999) reported that although treatment with glyphosate in one marsh initially resulted in increased plant species diversity, the failure to prevent reinvasion resulted in a near *P. australis* monoculture in just a few years. Chemical control of *P. australis* requires repeated applications annually and the effect on long-term recovery at the community or ecosystem-level is largely unknown (Hazelton *et al.* 2014).

Hydrological management

The re-introduction of tidal flow, by removing restrictions and increasing salinity, has been used effectively to manage introduced *P. australis* in coastal marshes of North America (see Roman & Burdick 2012 and references therein for reviews of this topic; Golet *et al.* 2012). Removal of *P. australis* via restoration of tidal flow resulted in the recovery of faunal communities over relatively short time periods (Dibble & Meyerson 2012; Dibble, Pooler & Meyerson 2013). Similarly,

Gratton & Denno (2006) found that removal of *P. australis* resulted in the restoration of the arthropod food web, and Dibble & Meyerson (2012) found that reduction of *P. australis* through the restoration of tidal flow restored the physiological condition of fish. Through removal of tidal restrictions in brackish and saltmarsh systems, *P. australis* can be managed without the use of chemicals, but this strategy does not work for freshwater tidal and inland marsh systems.

(E) GLOBAL CHANGE

Depending on the study region and population (including different haplotypes), *Phragmites australis* appears to be either vulnerable to global change (climatic and anthropogenic) or highly adaptable. There have been concerns in the British Isles and Europe for several decades that reedbeds are declining (Den Hartog, Kvĕt & Sukopp 1989) and contracting due to human-influenced environmental changes that increase reed's vulnerability to natural disturbances (Brix 1999). Possible future threats to reedbed communities are habitat disturbance and climate change (including sea level rise associated with this). The increasing frequency of extreme weather events (e.g. Lake Constance flood; Ostendorp, Dienst & Schmieder 2003) combined with the subsequently elevated populations of pathogens such as *Pythium phragmitis* (Nechwatal, Wielgoss & Mendgen 2008b) is likely to threaten the productivity and functional benefits of native reedbeds (Cui *et al.* 2010; see II for the threshold of flooding that reed can cope with). Regulation of rivers and lakes creates artificial high-flow events that similarly inhibit *Phragmites* performance (Ostendorp & Dienst 2009). In the British Isles, future coastal distribution along the eastern coast particularly is predicted to contract further due to sea level rise (Natural England and RSPB 2014; The Wildlife Trusts 2015). Coastal populations in other parts of the native range are likely to be at a similar risk of inundations (Grenfell *et al.* 2016).

Highly competitive haplotypes (e.g. haplotype M) are likely to continue expanding under future global change scenarios (Mazur, Kowalski & Galbraith 2014), particularly where they are non-native and less inhibited by natural herbivores and other threats. Non-native haplotypes are already increasing in North America in response to human-disturbed environments (Chambers, Meyerson & Saltonstall 1999), and the potential for similar scenarios in Australia (Saltonstall 2002; Packer *et al.* 2017a), Africa, Asia and South America is a growing concern. Further research is needed to resolve the taxonomic status at genus and species level, and to understand the influence of biogeographic lineages on native ecosystems so that management regimes, for both native and non-native *P. australis*, can be targeted more effectively to achieve conservation goals.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. The distribution and frequency of *Phragmites australis* in the British Isles, based on the number of 2×2 km tetrads it has been recorded in within each 10×10 km hectad of the National Grid.

Table S1. Compilation of distribution data for *Phragmites australis* at a country level.