S5

Glyceria maxima swamp
Glycerietum maximae (Nowinski 1928) Hueck 1931 *emend.* Krausch 1965

Synonymy
Glycerietum aquaticae Tansley 1911; Association à *Scirpus lacustris* et *Glyceria aquatica* Allorge 1922 *p.p.*; *Scirpeto-Phragmitetum glyceriosum aquaticae* Koch 1926; *Glycerietum maximae* and *Glyceria* reedswamp Tansley 1939; *Scirpeto-Phragmitetum medioeuropaeum* (Koch 1926) R.Tx. 1941 *p.p.*; *Glyceria maxima* communities Lambert 1947*c p.p.*; *Glycerieto-Typhetum latifoliae* Neuhäusl 1959 *p.p.*; Societie van *Glyceria maxima* Westhoff & den Held 1969; *Glyceria maxima* sociation Wheeler 1975*a p.p.*

Constant species
Glyceria maxima.

Physiognomy
The *Glycerietum maximae* is always overwhelmingly dominated by *Glyceria maxima* which forms a typically dense and luxuriant cover of leafy shoots, often more than 1 m long and sometimes attaining almost 2 m. The gross appearance of the vegetation is somewhat variable: the *G. maxima* plants may be firmly anchored and the shoots largely erect forming a tall emergent swamp; in other cases, stands occur as swinging masses of marginal 'hover', loosely attached below and with the shoots showing a marked tendency to lodge. Sometimes, stretches of this kind of *Glycerietum* may become detached to form free-floating islands of vegetation. Whatever its physiognomy, the community is typically very species-poor and pure stands are common.

Growth of the leafy aerial shoots of *G. maxima* begins early in the year and stands retain their characteristic bright, fresh green colour throughout the growing season as a succession of new shoots is produced (Lambert 1947*c*, Buttery & Lambert 1965, Westlake 1966). However, the erect shoots die back rapidly around November to produce a substantial mass of compact, black and slimy litter and so, unlike some swamp communities where the dominants are largely evergreen or where there is a large amount of standing dead material, the winter appearance of the vegetation here is very different from that of the growing season (Tansley 1939, Lambert 1947*c*, Westlake 1966). Decumbent shoots may remain winter-green, perhaps because of protection from frost or wind (Lambert 1947*c*).

Sub-communities

***Glyceria maxima* sub-community:** *Glyceria aquatica* reedswamp Pallis 1911; *Glyceria maxima* floating reedswamp Lambert 1946; *Glyceria* society Spence 1964; Tall grass washlands Ratcliffe 1977 *p.p.*. This sub-community includes pure and species-poor stands in which *G. maxima* typically forms a very dense cover. Stands may be extensive and, as well as swamp or washland vegetation with erect plants, marginal and free-floating masses of 'hover' with many decumbent shoots are included here. There are no frequent associates but a variety of other species occurs occasionally and some of these can be locally abundant. *Lemna minor* and *Nymphaea alba* may be prominent on open water between the *G. maxima* shoots and there are sometimes sprawling masses of *Solanum dulcamara* or *Galium palustre*. Towards the south-east, *Berula erecta* and, especially, *Rumex hydrolapathum* can be conspicuous.

***Alisma plantago-aquatica-Sparganium erectum* sub-community:** *Glyceria aquatica* riparian reedswamp Tansley 1911 *p.p.*; *Glycerietum maximae* riparian reedswamp Butcher 1933; *Glyceria maxima* riparian zone and *Glyceria maxima* stagnant reedswamp *p.p.*. Lambert 1947*c*. Here, *G. maxima* forms an often more open cover in frequently narrow and fragmentary stands. The plants are usually tall and erect but decumbent shoots may trail out into open water. Again, the vegetation is typically species-poor but there is a little more consistent variety here than in the *Glyceria* sub-community. Especially distinctive is the frequent presence of one or more of *Alisma plantago-aquatica*, *Sparganium erectum* and *Rorippa nasturtium-aquaticum* forming a patchy understorey or fringe fronting the *G. maxima* in slightly deeper water. Other occasional species are those characteristic of riparian water margins.

Habitat

G. maxima has high mineral requirements (Lambert 1947*c*, Petersen 1949, Lang 1967) and the *Glycerietum* is very much a swamp of eutrophic water margins. It is especially characteristic of nutrient-rich, circumneutral to basic mineral substrates, such as certain alluvia, and it can maintain itself on such material even where the waters are stagnant. It also occurs on oligotrophic, neutral or fen peats provided the mineral supply is continually renewed by the movement of richer waters (Lambert 1946, 1947*c*). The typically lowland distribution of the *Glycerietum* is probably a reflection, at least in part, of these edaphic needs of the dominant rather than being a direct response to climate (Lambert 1947*c*). The community occurs, usually below 150 m, as a fringe to sluggish rivers and streams, along dykes and canals, in open-water transitions around ponds, lakes and abandoned industrial water bodies and, often more extensively, on regularly inundated flood-plain washlands and in those parts of Broadland where there is a tidally influenced movement of ponded-back fresh water.

Provided eutrophic conditions are maintained, the community seems tolerant of a wide range of water depth. Although both vegetative and reproductive development in *G. maxima* are best favoured by a water-table that is at about substrate level (Lambert 1947*c*), it can occur as an emergent rooted in up to 80 cm of water and very vigorous stands of the community can persist in stagnant waters that remain permanently above ground. Although *G. maxima* has roots which are markedly less aerenchymatous than those of *Phragmites australis* (Iverson 1949), there is little evidence to suggest that the former suffers greatly under anaerobic conditions (Buttery & Lambert 1965, Haslam 1971*b*).

The physiognomy of the community does, however, seem to be strongly influenced by the physical properties of the substrate (Lambert 1946, 1947*a*, *c*). Stands with erect shoots generally occur on firmer material. Marginal 'hover', on the other hand, develops where the *G. maxima* extends out into deeper water over loose ooze. Here, the buoyancy of the bulky but aerenchymatous aerial shoots tends to pull the roots and rhizomes free of the substrate so that they trail below a floating mass of shoots which, without substantial basal support, tend to topple over.

The ability of such marginal *Glycerietum* to rise and fall undamaged with frequent changes of water-level makes the community ideally suited to take advantage of tidally influenced water bodies such as the broads of the Yare valley in Norfolk. Here, there is a regular fluctuation in water-level of some 20–30 cm with occasional much greater variation (Lambert 1946), a movement which itself contributes to the loosening of the substrate and marginal vegetation. In such situations, *G. maxima* probably gains some competitive advantage over other swamp species which, while also being able to capitalise on the continual circulation of nutrient-laden waters, have a more rigid growth habit and/or shallow rooting system and which cannot persist as a floating mat.

Rapid lateral water movement, on the other hand, seems inimical to the development of the community. In and around Surlingham Broad on the Yare, Lambert (1946) noted that, wherever there was appreciable tidal scour, the *Glycerietum* was replaced by *P. australis* swamp. Big floods on the Yare also frequently tear away stretches of marginal *Glycerietum* which can persist for some time as free-floating islands before disintegrating or lodging in some sheltered spot (Lambert 1946, 1947*c*).

In the moving waters of streams and rivers, Butcher (1933) observed that the community was well developed only where the current velocity was less than about 0.5 km h^{-1}. In such situations, the *Glycerietum* generally occurs as the *Alisma-Sparganium* sub-community and the more fragmentary and varied nature of this vegetation is probably due in part to the continual disturbance of the habitat and the ready dispersal and germination of water-borne propagules. Here, too, substrate profiles are often steeply shelving so that zonations in relation to water depth tend to be telescoped into a narrow and rather jumbled marginal zone (Lambert 1947*c*).

G. maxima is a highly productive and palatable grass which was once much prized as a fodder and litter crop on the Fen washlands and around the Broads (Camden 1586, Curtis 1777, Lambert 1947*c*, Godwin 1978). In favourable conditions, dense stands of the *Glycerietum* can yield 0.5–1.5 kg ha^{-1} yr^{-1} dry weight (Buttery & Lambert 1965, Westlake 1966). The early start to growth and late lignification of *G. maxima* give a long possible cropping season and the ready ability of the species to tiller and production of repeated shoot generations assist in a quick recovery after mowing. In days of cheap labour, as many as three cuts were taken in a season, early crops being used for fodder and later ones for litter. Subsidary uses were for poor quality thatch, packing material and binding in brick making (Lambert 1947*c*, Godwin 1978).

Although *G. maxima* provides a good bite for cattle especially when it is young, swamp stands of the *Glycerietum* are generally inaccessible to grazing stock. Wildfowl will eat *G. maxima* where it abuts on to open water, although dense stands of the community provide an uncongenial breeding habitat for even the commonest water-birds (Fuller 1982). Although seed of many kinds is an important component of the diet of wildfowl, seed production in *G. maxima* seems to be generally low (Lambert 1947*c*). Coypu also eat *G. maxima* and the general decline of reed-swamp in the Broads (Boorman & Fuller 1981) includes some loss of *Glycerietum* by coypu grazing along the Yare.

Zonation and succession

Extensive, virtually pure stands of the *Glyceria* sub-community are quite common and sometimes completely choke small ponds, ox-bows or flat, narrow channels with standing or slow-moving water (Lambert 1947*c*, Haslam 1978). Frequently, however, the *Glycerietum* occurs as a definite zone in open-water transitions and riparian sequences, typically passing to the *Sparganietum erecti* in deeper water and, above, to the *Phalaridetum aruncinaceae*. Where banks shelve gently, the community may occur in both forms, the *Alisma-Sparganium* sub-community forming a fragmentary transition to the *Sparganietum erecti* and giving way above to a belt of the *Glyceria* sub-community. Such zonations are a very characteristic feature of pools and streams in the English lowlands.

In the rather special conditions along the Yare, the *Glyceria* sub-community often abuts directly on to the open water of the broads as marginal 'hover' or, especially where there is tidal scour, occurs behind a marginal fringe of *Phragmitetum australis*. Away from the open water, the *Glycerietum* usually gives way to some kind of fen vegetation in which both *G. maxima* and *P. australis* are important components, e.g. the *Glyceria* sub-community of the *Peucedano-Phragmitetum* or the *Epilobium hirsutum* sub-community of the *Phragmites-Urtica* fen. Although the abundance and vigour of *G. maxima* in such sequences clearly decline with increased distance from the moving broads water (Lambert 1946, Buttery & Lambert 1965), there does not seem to be a single, simple edaphic gradient related to this change.

There seems no doubt, however, that once established under favourable conditions, *G. maxima* can play a major part in successions from open water to fen. It is capable of rapid growth (Syme 1872, Lambert 1947*c*), and can readily encroach upon open water provided there is some contact between the vegetation mat and underlying sediments: at the very front of marginal 'hover' where the roots hang free in the water, there is a small reduction in growth and detached islands of *Glycerietum* quickly become chlorotic if they do not make renewed contact with the substrate (Buttery & Lambert 1965).

In sluggish streams, in dykes and in pools, *G. maxima* litter may accumulate in stagnant conditions and aid terrestrialisation. On the Yare, the *Glycerietum* often initiates succession in more sheltered but irrigated situations (Lambert 1946). Here *G. maxima* seems to have a competitive edge over *P. australis*. These species have broadly similar upper limits of growth in relation to water level and both are tolerant, though by virtue of different growth habits, of the tidal rise and fall. *G. maxima*, however, begins growth earlier from shoots which in the previous autumn have already extended up to substrate level (Lambert 1947*c*) and the expanding leafy shoots rapidly reduce light penetration below (Buttery & Lambert 1965). There is thus a dense cover of vegetation even before the shoots of *P. australis*, with its deep-seated rhizomes and perennating buds, break the surface. Where mixed stands are mown early, *G. maxima*, with its good growth of aftermath, has the additional advantage of quick recovery over *P. australis* which, though starting later, produces a single flush of shoots and attains its standing crop maximum earlier.

Where conditions begin to isolate growing *Glycerietum* on the Yare from the irrigating waters, its productivity has been shown to decline (Buttery & Lambert 1965). This isolation may happen by continued extension of the community into open water with slow peat accumulation towards the fen hinterland or within the relic arms of broads and in dykes which become blocked (Lambert 1946). It has been shown that, as *G. maxima* becomes, for some reason, unable to utilise available major nutrients, which may not themselves be externally limiting, *P. australis* can gain the ascendant because of some greater ability to tolerate conditions generally unfavourable to both species (Buttery & Lambert 1965). Like the other Broadland seres, the successions involving the *Glycerietum* are more complex than at first sight.

Alongside streams and rivers, the accumulation of substrate beneath the *Glycerietum* seems more dependent upon silting than on the build-up of litter (cf. Tansley 1939). Winter floods readily wash away the *G. maxima* remains (Lambert 1947*c*) and the repeated disturbance of the mineral material itself may continually set back any successional advance of the community which maintains itself as a permanent fringe.

Distribution

The *Glycerietum* is a lowland community, being commonest on the softer rocks of the Midlands and to the east. In Scotland, its major localities are all in kettle-hole lakes in glacio-fluvial clays (Spence 1964) and it is of very restricted occurrence in Wales (Ratcliffe & Hattey 1982).

Affinities

Species-poor *G. maxima* stands have sometimes been described as a form of the more general swamp community *Scirpeto-Phragmitetum* (e.g. Koch 1926, Tüxen 1937, LeBrun *et al.* 1949). In other schemes, a distinct *Glycerietum* has been recognised, although this has often been defined rather broadly (e.g. Hueck 1931, Jonas 1933 and, in the British descriptive literature, Tansley 1939 and Lambert 1947*c*). Such definitions have usually included more species-rich fen vegetation with prominent *G. maxima* such as that which is here placed within the *Peucedano-Phragmitetum* and the *Phragmites-Urtica* and *Phragmites-Eupatorium* communities. *G. maxima* may be locally dominant in these vegetation types though, in Britain, over a much more restricted geographical range than that occupied by the *G. maxima* swamps. Narrower interpretations of the *Glycerietum* similar to that adopted here have been pursued by Braun-Blanquet & Tüxen (1952), Jeschke (1959) and Passarge (1964). Certain workers (e.g. Westhoff & den Held 1969, Wheeler 1975, 1980*a*) have preferred to recognise a *G. maxima* society to take account of the difficulties of classifying such species-poor vegetation, though, in some cases, such communities have again included some richer stands.

Floristic table S5

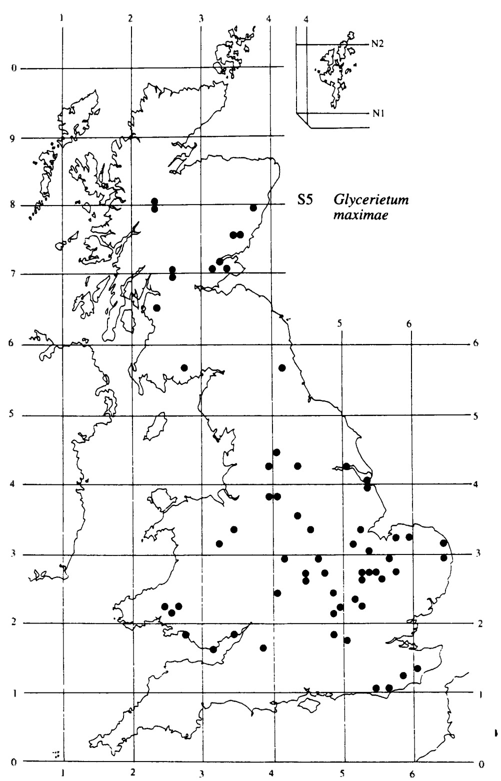
	a	b	5
Glyceria maxima	V (5–10)	V (5–10)	V (5–10)
Rumex hydrolapathum	II (2–6)	I (3)	I (2–6)
Lemna minor	II (1–9)		I (1–9)
Berula erecta	I (2–5)		I (2–5)
Solanum dulcamara	I (2–7)		I (2–7)
Nymphaea alba	I (3–4)		I (3–4)
Rumex crispus	I (2–3)		I (2–3)
Mentha aquatica	I (1–4)		I (1–4)
Galium palustre	I (1–6)		I (1–6)
Juncus effusus	I (1–6)		I (1–6)
Riccia fluitans	I (5)		I (5)
Epilobium hirsutum	I (4)		I (4)
Apium inundatum	I (5)		I (5)
Urtica dioica	I (4)		I (4)
Galium aparine	I (3)		I (3)
Filipendula ulmaria	I (4)		I (4)
Iris pseudacorus	I (1)		I (1)
Ranunculus ficaria	I (5)		I (5)
Equisetum palustre	I (1)		I (1)
Lycopus europaeus	I (3)		I (3)
Poa trivialis	I (3)		I (3)
Angelica sylvestris	I (3)		I (3)
Carex riparia	I (1)		I (1)
Alisma plantago-aquatica		III (2–4)	I (2–4)
Sparganium erectum		III (4–6)	I (4–6)
Nasturtium officinale		III (2–4)	I (2–4)
Lythrum salicaria		I (3–4)	I (3–4)
Ranunculus repens		I (1–2)	I (1–2)
Ranunculus acris		I (2–3)	I (2–3)
Carex otrubae		I (4)	I (4)
Myosotis scorpioides		I (3)	I (3)
Phalaris arundinacea		I (6)	I (6)
Cirsium arvense		I (3)	I (3)
Glechoma hederacea		I (2)	I (2)

https://doi.org/10.1017/9781107340817.035 Published online by Cambridge University Press

Floristic table S5 (*cont.*)

	a	b	5
Eupatorium cannabinum		I (4)	I (4)
Calystegia sepium		I (2)	I (2)
Cirsium palustre		I (3)	I (3)
Carex acuta		I (4)	I (4)
Equisetum fluviatile		I (2)	I (2)
Alopecurus pratensis		I (4)	I (4)
Callitriche stagnalis	I (2)	I (3)	I (2–3)
Phragmites australis	I (1)	I (3–4)	I (1–4)
Polygonum amphibium	I (2)	I (4–6)	I (2–6)
Rumex obtusifolius	I (2)	I (2–3)	I (2–3)
Number of samples	104	16	120
Number of species/sample	4 (1–11)	5 (2–8)	4 (1–11)
Vegetation height (cm)	104 (40–180)	94 (40–180)	103 (40–180)
Vegetation cover (%)	94 (60–100)	88 (55–100)	93 (55–100)

a *Glyceria maxima* sub-community
b *Alisma plantago-aquatica-Sparganium erectum* sub-community
5 *Glycerietum maximae* (total)



https://doi.org/10.1017/9781107340817.035 Published online by Cambridge University Press