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13.—Factors affecting the Distribution and Productivity of Emergent Vegetation at Loch Leven, Kinross. By R. H. Britton*, The Nature Conservancy, Edinburgh. (With 2 text-figures and 3 tables)

Synopsis

The extent of emergent vegetation at Loch Leven has declined considerably within historical times. In 1972 only 5 per cent of the shoreline and less than 0·01 per cent of the area of the loch was occupied by emergent vegetation, the principal species being *Phragmites communis* Trin. and *Polygonum amphibium* L. The production of *Phragmites communis* was estimated from standing crop measurements and is low for a eutrophic lake. The maximum aerial shoot biomass varies from 1148 to 513 g dry wt/m^2 in the different beds. The total production of all species of emergent vegetation is insignificant when compared to other sources of primary production. Possible factors causing the low production and decline in emergent vegetation are discussed. These include water level changes, soil types, exposure to wind and wave action and grazing by wildfowl and domestic stock.

Introduction

Marginal aquatic vegetation, including both emergent and floating angiosperms, is now very scattered at Loch Leven and occupies less than 5 per cent of the total shoreline. There is, however, some evidence to suggest that this vegetation has undergone a decline within historical times and that in certain areas of the loch this decline is continuing.

Maps made prior to the lowering of the water level in 1830 show the loch surrounded by extensive marshes. A map at a scale of 1 : 63 360 surveyed in 1826–27 and engraved by John Dower shows an almost continuous band of marsh around the entire perimeter of the loch interrupted only by the mouths of the inflow burns. This marsh was at its widest along the north-east shore, where it was up to 400 m in width, narrowing to about 100 m in Kinross Bay. The floristic composition of this marshland is unknown but the fact that bitterns *Botaurus stellaris* (L.) were recorded as breeding in the eighteenth and early nineteenth centuries (Sibbald 1710) suggests that large areas of *Phragmites communis* Trin. reedswamp were present. Scott (1891) reported that the north-east shore from Pow Burn to Leven Mouth was 'very much overgrown with reeds and other aquatic plants', including tall reeds (almost certainly *Phragmites communis*) which extended considerable distances out into the water. West (1910), however, reported that there was relatively little marginal vegetation around the loch although a narrow zone of reedswamp consisting mainly of *Carex rostrata* Stokes was described extending along the south shore opposite St Serf's Island where none exists today. *Equisetum fluviatile* L. and *Eleocharis palustris* (L.) were described as relatively abundant and there were quite extensive, but sparse, beds of the former species, which does not now occur in the loch. *Phragmites* associations were described as entering the water in only a few places around the loch.

The earliest accurate large-scale maps of the loch date from the Ordnance Survey of 1854 but these do not show marginal vegetation in any detail. They do show,

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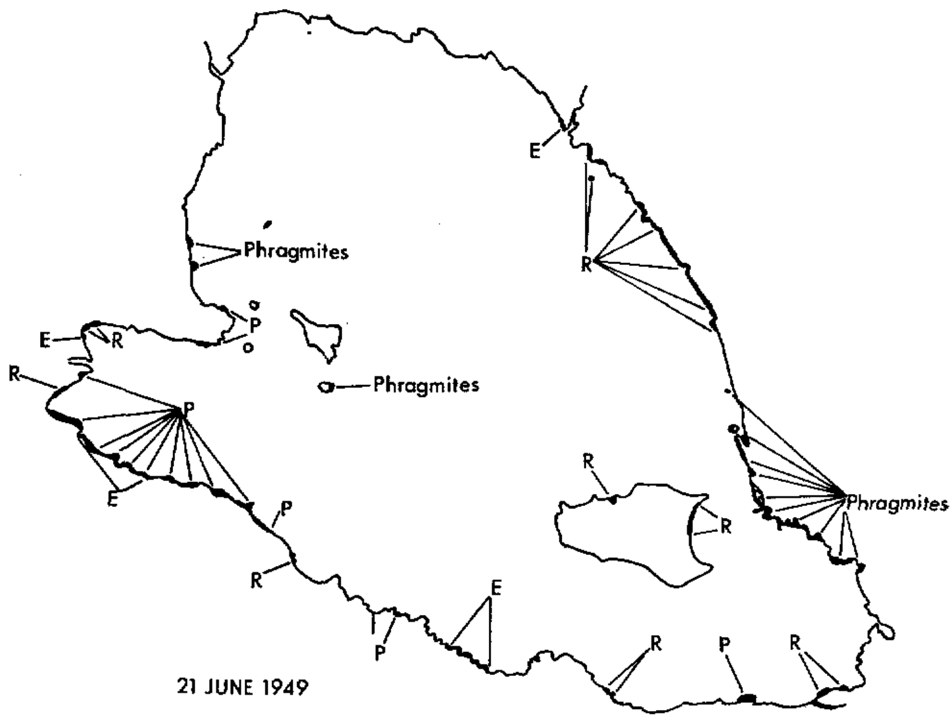
however, that there has been considerable erosion of the shoreline in many places when compared to modern maps and aerial photographs. This is particularly so of the north-east shore, where formerly there was a chain of small islands which formed a partial barrier 50 m offshore and which have now almost entirely disappeared.



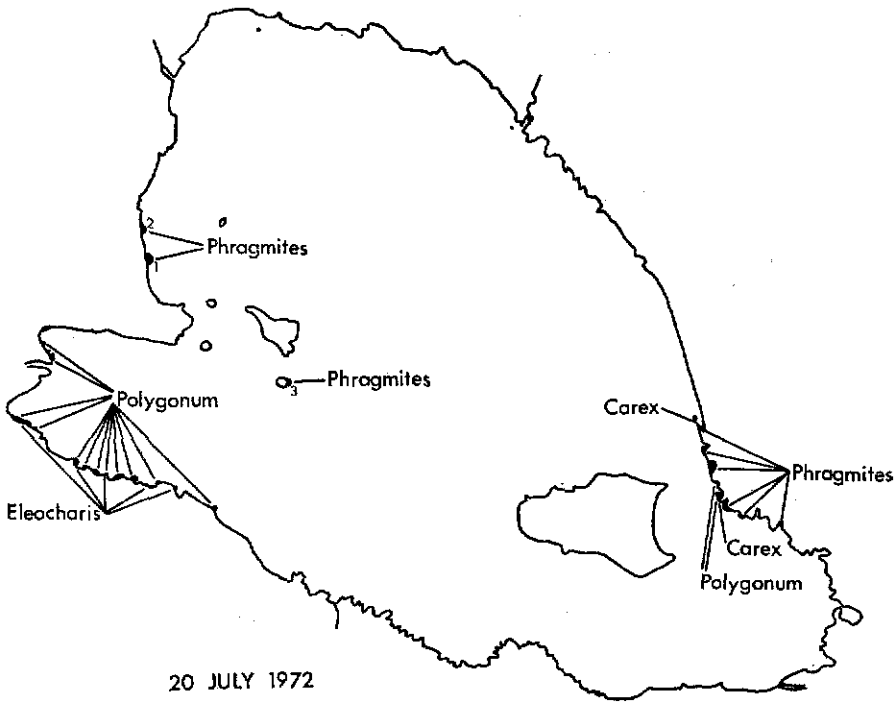
TEXT-FIG. 1.—Distribution of emergent vegetation interpreted from aerial photographs taken on 21 June 1949. E = probable *Eleocharis*, P = probable *Polygonum*, R = unidentified reed-like plants

Local farmers report that reeds were collected for thatching from along the north-east shore up until 1936, and the reported extent of these reed beds coincides with the areas where scattered remnants of *Phragmites* now occur. The earliest available aerial photographs taken in 1946–49 show areas of marginal aquatic vegetation in this region and in other parts of the loch where there is none today, but in most cases it is not possible to identify the stands to species (see text-fig. 1). The largest remaining areas of *Phragmites* on the western shores of the loch, however, occupied almost the same positions in 1946–49 as they do today.

THE PRESENT DISTRIBUTION AND PERFORMANCE OF MARGINAL VEGETATION

The distribution of the marginal vegetation has been mapped in text-fig. 2 from aerial photographs taken on 22 July 1972 at a scale of 1 : 10 000. Initial ground survey and low-level oblique aerial photography enabled each stand of vegetation to be identified to species.

Large-scale plans of each stand were then traced from the effective areas of the aerial photographs using a camera lucida attached to a low-power microscope. The area of the stands was then estimated using a planimeter to within $\pm 0{\cdot}5$ m^2, but errors in tracing and defining the limits of the stands, and errors due to distortion on the photographs, are likely to be much larger than this. Comparison of areas obtained from aerial photographs with those obtained by conventional surveying and mapping of certain vegetation stands showed differences of less than 2 per cent.



TEXT-FIG. 2.—Distribution of emergent vegetation in July 1972 from aerial photographs and ground survey. The major stands of *Phragmites* are numbered 1–3.

In the case of the largest beds of *Phragmites*, along the western shore and on Reed Bower Island, measurements of aerial shoot biomass at the time of flowering (during September) were made as estimates of the net shoot production (Milner and Hughes 1968). This was not attempted for the *Phragmites* stands on the north-eastern shore nor for the other most abundant plant species, *Polygonum amphibium* L., where heavy grazing and wave and wind damage would have made the peak biomass a bad underestimate of production. In measuring shoot biomass, quadrat samples of 0·25 m^2 were taken at 5 m intervals selected at random along transects 5 m apart running at right angles to the shore. The number and height of all shoots rooted in each quadrat was measured and the shoots were collected by shearing off at ground level and taken to the laboratory for drying at 105°C and weighing. In the case of reed bed 1, reeds were only collected for weighing from a small random sample of quadrats, the weight of the remaining shoots being calculated from the relationship between shoot height and shoot weight.

The extent of each of the four species of emergent plant as measured from the aerial photographs taken in 1972 is shown in table 1. *Phragmites* and *Polygonum* are by far the most extensive species and *Eleocharis palustris* and *Carex rostrata* only occupy very small areas of the loch margin. For both of the most abundant species the more sheltered areas of the western and south-western shores have larger areas of vegetation than the north-east shore, where the largest areas shallow enough for colonisation occur. The total extent of all emergent vegetation is however very small and accounts for less than 0·01 per cent of the total area of the loch. The three largest and most vigorous stands of *Phragmites* are numbered in text-fig. 2. These all occur on easterly facing shores where they are protected from the prevailing winds, and

TABLE 1

The extent of emergent vegetation on 22 July 1972

	North-east shore	Western shores	Total
Phragmites communis	2,950	3,757	6,707
Polygonum amphibium	1,720	4,220	5,940
Eleocharis palustris	—	—	437
Carex rostrata	—	—	195
			13,279

are all backed by wooded non-agricultural land so that they are partially shaded from the afternoon sun. All stands were rooted in the substrate and no plaur formation has been observed among the marginal vegetation. In all the beds *Phragmites* is the only higher plant present except at the very landward margin where there is sometimes a zone up to 1–2 m in width where *Phalaris arundinacea* L. and *Salix* spp. also occur.

Data on the performance of *Phragmites* in these beds are given in table 2. On most of the measured parameters *Phragmites* appears to thrive best in reed bed 1 and worst in reed bed 3 with reed bed 2 intermediate. This agrees well with observations on the expansion or decrease in area of these beds since 1949. Reed bed 1 has shown the largest increase (120·2 per cent), reed bed 2 a smaller increase (19·8 per cent), while reed bed 3, the least productive, has stayed more or less stationary (2 per cent decrease in area).

The range of water level over which *Phragmites* grows at Loch Leven is less than has been reported by many authors (e.g. Spence 1964; Haslam 1972) who report colonisation down to depths exceeding 1 m in other waters. This limited range is probably related to the relatively large annual water level fluctuations that the loch experiences (up to 1 m).

The number of shoots per unit area varies considerably both between and within the beds of *Phragmites*. Highest densities occur at the landward margins of the three large investigated beds, where locally densities of over $100/m^2$ occur. There is, however, a negative relationship between shoot density and mean shoot weight so that in beds 2 and 3 the biomass per unit area is relatively constant. In bed 1, however, the highest biomass occurs in the centre of the bed with high numbers of reeds per unit area of low mean weight towards the land and low numbers of reeds of high mean weight towards the open water.

TABLE 2

Data on phragmites in the three most extensive stands at Loch Leven. Figures following the mean value are the 95 per cent confidence limits of the mean unless otherwise stated

Reed bed number	Height of water table above soil surface (cm)	No. of shoots/m²	Mean height of shoots (cm)	Mean no. of nodes/shoot	Percentage of shoots flowering	Mean wt/ shoot (g dry wt)	Mean shoot biomass (g dry wt/m²)	Area of bed (m²)	Total shoot biomass of bed (kg)	Net shoot* production (joules/yr)
1										
0–5 m from shore	—	77·0 ±68·5	—	—	—	5·43 ±2·81	418·1	265	110·8 (S.D. 420·7)	$1{\cdot}224 \times 10^8$
5–30 m from shore	—	64·5 ±6·3	—	—	—	17·69 ±1·28	1141·8	1400	1598·5 (S.D. 539·5)	$1{\cdot}767 \times 10^9$
> 30 m from shore	—	29·8 ±14·0	—	—	—	15·83 ±7·76	472·0	220	103·8 (S.D. 739·1)	$1{\cdot}147 \times 10^8$
Total	−10 to 59	—	274·5 ±11·6	16·7 ±0·55	—	—	—	1885	1813·2	$2{\cdot}003 \times 10^9$
2	−5 to 50	55·5 ±8·9	264·6 ±5·24	17·13 ±0·28	29·5	15·345 ±0·727	857·1 ±136·7	997·5	855·0 ±136·3	$9{\cdot}445 \times 10^8$
3	−30 to 45	84·6 ±17·4	162·4 ±3·07	13·9 ±0·41	2·3	6·01 ±0·27	512·8 ±115·8	875	448·7 ±101·3	$4{\cdot}958 \times 10^8$
Total	—	—	—	—	—	—	—	3757·5	3116·9	$3{\cdot}443 \times 10^9$

*Assuming 10 per cent loss prior to harvesting and a calorific value of 4·2 kcals/g dry wt (Westlake 1965; Straskraba 1968).

The shoot production of *Phragmites* per unit area in Loch Leven is relatively low when compared to data from other eutrophic lakes in Scandinavia (Bjork 1967) and Britain (Gorham and Pearsall 1956) but is similar to that in the Polish, Lake Mikolajskie (Kowalczewski and Wasilewski 1966). The production is similar to that of many oligotrophic waters. Shoot densities in Loch Leven are of the same order as in many of these eutrophic waters, but average shoot heights and weights are much lower and it is these that cause the low biomass figures. The percentage of shoots flowering is also relatively low when compared to other eutrophic waters and in 1972 occurred very late in the season (full panicle development did not take place till October), so that it is doubtful if fertile seed was set. In part the low production and percentage of flowering may have been caused by the exceptionally cold growing season in 1972.

The estimated total net aerial shoot production of *Phragmites* in the three major beds is $3{\cdot}443 \times 10^9$ joules/year but unfortunately there are no biomass data for the remaining stands upon which a reliable estimate of their net production can be based. These stands are however visibly less productive than those investigated, with shoot densities as low as $1/m^2$ in places and shoot heights generally of the order of 1·5 m except in very limited areas where they approach the mean height of reed bed 1. A maximum estimate of the total net *Phragmites* shoot production of $4{\cdot}975 \times 10^9$ joules/year for the whole loch can therefore be made by assuming that these beds are as productive on an area basis as reed bed 3. No data are available on the standing crops of the other species of emergent plant, but those of *Polygonum amphibium* and *Eleocharis palustris* are likely to be considerably less than for *Phragmites* so that a maximum biomass of 500 g/m^2 is reasonable (Westlake 1963). Using this figure and the same assumptions as used in calculating the production of *Phragmites*, the total net shoot production for all species of emergent plant over the whole loch is certainly less than $8{\cdot}51 \times 10^9$ joules/year. If the production of submerged organs were included this figure might be increased by up to 100 per cent (Fiala *et al.* 1968; Westlake 1968; Burian 1973), but when compared to the net production of phytoplankton (approximately $2{\cdot}256 \times 10^{14}$ joules/year (Bindloss 1974)) and submerged macrophytes (approximately $2{\cdot}6 \times 10^{12}$ joules/year (Jupp, Spence and Britton 1974)) the contribution of energy from emergent plants to the ecosystems is seen to be negligible, and is almost certainly less than that deriving from allochthonous sources.

Factors Limiting the Production and Distribution of the Vegetation

In the preceding sections it has been shown that emergent vegetation is now very limited in distribution at Loch Leven and that within the surviving stands of *Phragmites* productivity is low for eutrophic sites. Work is now in progress to investigate the factors which limit the growth of this vegetation. Among the possible factors are water depth and water level fluctuations, soil type, exposure to wind and wave action, grazing by domesticated stock, and grazing by wildfowl.

Water Depth. Phragmites grows to a depth of 1·1 m in Scottish waters and *Polygonum amphibium* to a depth of 2 m (Spence 1964). 17·5 per cent of the loch area is less than 1 m deep and 25 per cent less than 2 m so that water depth on its own is not a factor generally limiting the growth of these species at Loch Leven. The outer edge of reed bed 3 which grows on a relatively steeply shelving shoreline may however be limited by depth.

Water level fluctuations are artificially controlled at Loch Leven and highest water levels generally occur in winter and spring with low water in early autumn. High water levels in the spring are disadvantageous to the emerging shoots of aquatic plants as they are then more exposed to wave action and require more growth supplied from energy stores in the rhizome before photosynthetic activity can begin. A change in water level regime occurred in the year 1949; prior to that date spring and summer water levels were generally at least 10 cm lower than they have been since. This may have been a contributory factor in the decline of emergent vegetation which dates from some time after 1936.

Soil Type. Throughout almost the entire littoral zone the soil consists largely of inorganic particles from silt through to boulders. Gyttja and other organic sediments are restricted to a very few sheltered lagoons protected from wave action. The predominant soil type is a coarse sand with less than 1 per cent of organic matter, but locally areas of gravel, stones and clay occur in the zone occupied by marginal vegetation.

TABLE 3

Mean soil particle size (mm) in top 20 cm within beds of emergent vegetation

Reed bed 1	0·382	S.D.	0·149
Reed bed 2	0·557	S.D.	0·436
Unvegetated area between beds 1 and 2	1·274	S.D.	0·300
Reed bed 3	12·066	S.D.	13·964
Reeds on N.E. shore	0·388	S.D.	0·285

The particle size distribution of 20 cm deep cores of soil taken on a random basis throughout each of the major beds of emergent vegetation was determined by sieving the dried samples and weighing each fraction. The mean particle size for all samples within each bed are shown in table 3.

For the three major beds of *Phragmites* there is an inverse relationship between the mean soil particle size of the bed and the mean biomass of *Phragmites* per unit area with the lowest biomass in the very stony reed bed 3. Many authors (e.g. Gorham and Pearsall 1956; Bjork 1967) report that *Phragmites* grows best on a fine-grained sediment, and therefore it is reasonable to assume that the low biomass figures found, especially in reed bed 3, are largely a result of the unfavourable nature of the soil. There is, however, no significant difference in particle size distribution between the soil in the most prolific reed bed 1 and the very sparse stands on the north-east shore and some other factor must be limiting the productivity of these stands.

The nature of the soil may also limit the distribution of *Phragmites*. The unvegetated area of shoreline between reed beds 1 and 2 has a significantly greater mean particle size than the areas within the bed, and reed bed 1 itself is surrounded by an area of stones and dense clay which must be very impenetrable to advancing *Phragmites* rhizomes. This may explain why these two beds have advanced relatively little over the past 25 years.

Exposure to Wind and Wave Action. Loch Leven is a large and relatively exposed lake, the prevailing wind being from the south-west. Most of the stands of emergent vegetation sustain some wind or wave damage during the growing season, and the dead stems of *Phragmites* are usually broken in the winter by the combined action of waves, wind and ice.

The present distribution of emergent vegetation is clearly related to exposure to wind. All the most vigorous stands of vegetation remaining are located on westerly and south-westerly shores where they are protected from prevailing winds, and those stands on the north-easterly shores are restricted to the southern part which is somewhat protected from extreme exposure by St Serf's Island. On the more exposed parts of this shore where regression of *Phragmites* has been noted in recent years rhizomes of extinct stands are exposed by wave action at times of low water level, and this process of rhizome erosion is continuing in some areas.

Experimental barriers of sandbags 5 m long and extending to the water surface were constructed in 1972 on a very exposed part of the north-east shore. *Phragmites* rhizomes taken from reed bed 1 and Duddingston Loch, Midlothian, were planted in the shelter of these barriers and in exposed plots during March–April to determine the effects of exposure. Unfortunately, all emerging shoots were heavily grazed by wildfowl so that no plant reached more than a few centimetres above the water surface and the majority were killed. The results, such as they are, indicate that over one growing season there was no difference in the numbers of plants surviving and in the number and height of shoots produced between sheltered and exposed plots. The Loch Leven clone of *Phragmites* did, however, produce significantly more shoots than those plants obtained from Duddingston Loch, suggesting that it is better adapted to the environmental conditions in Loch Leven than the Duddingston clone which was obtained from a sheltered situation on a soft gyttja soil. Any differences in performance between sheltered and unsheltered plots and between clones may be very different in the second season of growth after the effects of winter storms have been felt.

A separate sandbag barrier was also constructed in the spring of 1972 enclosing half of a small bay of approximately 0·4 ha extent, the remaining half being exposed to the prevailing wind. In 1971 this bay had been occupied by scattered wave-damaged *Polygonum amphibium*, but in 1972 a vigorous growth of this species covering 1327 m^2 occurred in the enclosed section compared to only scattered growths covering less than 200 m^2 in the exposed half. In the winter of 1972–73 the exposed part of the bay was severely eroded by storm damage while the protected area remained intact.

Grazing by Domesticated Stock. Over half of the shoreline at Loch Leven has in recent years been grazed to some extent by sheep, cattle or horses, but all the remaining beds of emergent vegetation occur in areas which have remained almost free from any grazing pressure. Prior to about 1936 there was little grazing on most of the north-east shore of the loch where reed beds once flourished, but after that date cattle were put on this land and grazing pressure was relatively heavy until the last few years, since when it has ceased. The shore here is very gently shelving and the bottom of firm sand so that cattle can wade considerable distances into the loch to graze. Cattle feed readily on *Phragmites* and heavy grazing or trampling will eradicate this species (Haslam 1968, 1972), so that grazing pressure was almost certainly a major factor in bringing about a decline in the reedswamp. Grazing may be now preventing the establishment of reedswamp in certain areas, but the pressure from domestic stock on established beds of vegetation is negligible.

Grazing by Wildfowl. All the stands of emergent vegetation at Loch Leven show some signs of damage by grazing wildfowl. The effect is least in the case of the three large beds of *Phragmites* on the eastern shores, where grazing by wildfowl is restricted to shoots at the outer margin of the bed which are often severely grazed down to water level. This may be limiting the expansion of these beds but cannot account for their low biomass per unit area.

The stands of *Phragmites* on the north-east shores are more severely affected, possibly because the low density of shoots found in these stands does not form a barrier to wildfowl (Kvet and Hudec 1971), and most isolated shoots are stunted and branched due to the formation of lateral replacement shoots. Rather scattered experimental plantings along this shore were grazed almost to extinction by wildfowl. The birds responsible were mainly mute swans, *Cygnus olor* (Gmelin), and coot, *Fulica atra* L., which may have turned more to feeding on marginal vegetation since the recent decline of the submerged vegetation. This grazing pressure has probably been responsible for some of the decline in emergent vegetation, but since wildfowl do not seem to enter dense reed growth to feed, some other factor must have caused the depletion of the reed beds in the first instance.

The limited areas of *Carex rostrata* are heavily grazed by geese in the winter months and *Polygonum amphibium* is grazed by coot and other wildfowl in the summer, but it is not known how grazing affects the distribution and productivity of these species.

Attempts to rehabilitate the emergent vegetation at Loch Leven will require the exclusion of grazing wildfowl and domesticated stock. Protection from wave erosion in the form of offshore barriers may be required in the more exposed areas. A wider range of species than is now present could be planted experimentally. These could include species which are little grazed by wildfowl (e.g. *Typha angustifolia* L.) and species resistant to wave action (e.g. *Schoenoplectus lacustris* L. and *Scirpus maritimus* L.).

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