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SHOOT DEVELOPMENT AND PRODUCTION STUDIES OF PHRAGMITES AUSTRALIS (CAV.) TRIN. EX STEUDEL IN SCOTTISH LOCHS

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Abstract

Studies were made on the development and production of *Phragmites australis* (Cav.) Trin. ex Steudel (= *Phragmites communis* Trin.) stands from Forfar Loch-polytrophic, Balgavies Loch-eutrophic and Loch of the Lowes-mesotrophic. Differences were detected in the shoot height, shoot dry weight, standing crop biomass, leaf area index, crop growth rate and net efficiency of solar energy conversion among the three lochs. Such differences were partly due to the different nutrient levels of the three locations. The percentage ratio of leaf to shoot weight, leaf area ratio, relative growth rate and net assimilation rate for the reed stands in the three lochs were also calculated and were compared with values from other study areas.

Introduction

The common reed, *Phragmites australis* (Cav.) Trin, ex Steudel (= *Phragmites communis* Trin.), is a cosmopolitant species and often forms an important component in the freshwater ecosystem. It commonly grows in pure or near-pure stands along the margins of lakes and reservoirs. Over the years numerous studies have been made on the productivity of the reed and the role it plays in incorporating organic matter into the freshwater ecosystem (eg. Gorham & Pearsall, 1956; Dykyjova, Ondok & Priban, 1970; Grabowski, 1973; Mason & Bryant, 1975; Andersen, 1976). These and similar studies have led to the conclusion that *Phragmites* is one of the most productive aquatic macrophytes of temperate regions (Westlake, 1963; Dykyjova, Veber & Priban, 1971). Despite its common occurrence, there have been little previous studies on the significance of reed plants in the Scottish freshwater ecosystems, although Spence (1964) reported a positive correlation between the height of *Phragmites* shoot and the mean temperature of the warmest month at sea level on the one hand, and the percentage total nitrogen and metal-ion saturation of the substrate on the other. This study recapitulates the author's investigations of the characteristics of shoot development and the productivity of *Phragmites* stands taken from Forfar Loch, Balgavies Loch and Loch of the Lowes, each of which shows a different trophic level. The results obtained were compared with those from other locations.

Materials and methods

Phragmites plants from the three lochs were investigated during 1975. Their nutrient statuses were classified as: Forfar-polytrophic, Balgavies-eutrophic, and Lowes-mesotrophic. Table 1 summarizes the physical characteristics of the three lochs. The reed grew along the loch margin forming monospecific stands in all three areas. Depending on the site, the reed within each loch grew on a variety of soil types which included gravel, sand and peat.

Shoot development study

Phragmites samples were taken monthly from March to November. Four to seven 0.25 m^2 quadrat samples were collected from each loch everytime. The number of

Table 1. Physical characteristics of the three lochs (partly adopted from Murray & Pullar, 1910).

	Forfar	Balgavies	Lowes
Length (km)	1.72	0.80	1.93
Width (km)	0.24	0.25	0.58
Area (km^2)	0.41	0.21	0.88
Mean depth (m)	3.48	2.97	6.22
Shoreline (km)	4.40	2.73	4.55
Phragmites cover* (ha)	2.03	0.89	0.84

* Estimated for the year 1975 (unpublished data).

shoots in each quadrat was noted. The shoots were harvested by clipping them at ground level and were wrapped in large plastic bags before they were transported back to the laboratory. Care was taken to avoid detachment of organs, especially leaves, from the shoot.

In the laboratory, the height of each shoot was measured by taking the distance from the clipped base to the uppermost leaf, or to the tip of the panicle if the latter was present. The number of leaves in each shoot was counted before the shoot was divided into the following portions – stem (with leaf sheath), leaf and panicle. Each portion was dried separately at 85°C for 24 hours before the dry weight was measured. Shoot dry weight was obtained by adding up the dry weights of the stem, leaf and panicle.

Production study

Monthly biomass of the standing crop in each site from each loch was measured and expressed as dry weight per m^2. Details of biomass and mineral content data in *Phragmites* plants in all the three lochs will be given in separate papers.

Leaf surface area (half of the total surface) of the reed stands was calculated by the product of specific leaf area (SLA) and leaf dry weight. Values for the latter were obtained from the shoot development study. Values of SLA – ratio of leaf area to leaf dry weight – were preliminarily determined by measuring the leaf surface area and leaf dry weight of foliar subsamples. Surface area of individual leaf from the subsamples was calculated by the formula A = kLB, where A is the leaf surface area, L and B are length and maximum width respectively of the leaf and k is a constant. The constant k was found to be 0.55 – a value similar to those given by Rus (1972) (0.6), Ondok (1968) (0.54) and Szajnowki (1973) (0.57) for *Phragmites* plants in their studies.

From the standing crop biomass and leaf surface area data, the following growth and production parameters were computed according to Evans (1972):

1. Leaf area index (LAI) – leaf surface area per unit ground area.
2. Leaf area ratio (LAR) – leaf surface area per unit aboveground biomass.
3. Relative growth rate (RGR) – increase in biomass per unit biomass between harvests.
4. Net assimilation rate (NAR) – increase in biomass per unit leaf surface area between harvests.
5. Crop growth rate (C) – mean rate of dry matter production per unit ground area between harvests.

The net efficiency of solar energy conversion (η) by *Phragmites* from each of the three lochs was also calculated. The conversion efficiency was expressed both in terms of total global radiation and photosynthetically active solar radiation (PhAR) by the following formulae:

$$\eta\text{global} = \frac{\text{energy content per g tissue x biomass}}{\text{total global radiation}} \times 100\%$$

$$\eta\text{PhAR} = \frac{\text{energy content per g tissue x biomass}}{\text{PhAR radiation}} \times 100\%$$

Monthly total incident global radiation data during the growing season in 1975 were obtained from the agricultural station in Invergowrie which is situated less than thirty kilometres from each of the three lochs. Photosynthetically active solar radiation was assumed to be 45% of total global radiation (Monteith, 1965). Calorific value for the *Phragmites* plant was taken as 19.46 kJ g^{-1} ash-free dry weight – an average value derived from the readings given by Kvet (1969, unpublished data quoted in Dykyjova & Pribil, 1975), Sieghardt (1973), Dykyjova & Pribil (1975), Andersen (1976) and Dykyjova & Hradecka (1976).

Results and discussion

Shoot development

Table 2 summarizes the monthly mean height, dry weight and leaf dry weight of *Phragmites* shoot growing in the three lochs. The overall pattern in the changes of shoot height was similar for all three lochs. Shoot height increase was relatively slow from March to April but rapid thereafter until August after which growth slowed down and levelled off. Maximum height was attained in September for the Balgavies plant but it was a month later for those in Forfar and Lowes (Table 2). The same pattern of changes was observed for reed plants in other areas (Haslam, 1969; Mochnacka-Lawacz, 1974a; Dykyjova & Hradecka, 1976; Szczepanska & Szczepanski, 1976). Mean height attained by *Phragmites* shoots from the three lochs were different (Table 2). It was highest in Forfar reaching 268.9 cm, and for Balgavies and Lowes they were 239.9 and 218.9 cm respectively. A considerable proportion of the Forfar shoots measured more than 300 cm tall (Fig. 1). The tallest recorded was 346 cm. Spence (1964) in his study on *Phragmites* populations in Scotland suggested the mean temperature of the warmest month determined the final height of the reed stands. However, Haslam (1971, 1972) indicated that apart from temperature, other factors including nutrient availability, competition and biotype were important. It seems very probable that in this study, the considerably greater height attained by the Forfar plants was partly due to the overall higher nutrient level of the loch. Reed plants taken from many other locations had mean shoot height between 200-300 cm (eg. Buttery & Lambert, 1965; Dykyjova, Ondok, & Priban, 1970; Mochnacka-Lawacz, 1974a & b; Komarkova & Komarek, 1975; Dykyjova & Hradecka, 1976; Szczepanska & Szczepanski, 1976) being similar to

Table 2. Monthly mean height, dry weight and leaf dry weight of *Phragmites* shoot in the three lochs during 1975. F = Forfar, B = Balgavies, L = Lowes.

Month	Height (cm)			Shoot dry wt (g)			Leaf dry wt (g)		
	F	B	L	F	B	L	F	B	L
Mar	14.7	11.8	7.5	0.79	0.36	0.26	-	-	-
Apr	16.8	15.5	15.6	0.61	0.44	0.50	-	-	-
May	62.4	55.7	46.9	2.11	1.26	1.05	0.09	0.06	0.03
June	136.7	121.1	102.4	6.24	3.86	3.14	1.34	0.93	0.53
July	219.5	219.6	132.6	11.95	11.44	4.29	3.46	3.13	1.15
Aug	266.5	229.6	211.4	20.82	13.50	11.10	5.07	3.58	2.86
Sept	257.5	239.9	200.4	21.00	15.72	10.58	5.03	3.17	2.78
Oct	268.9	234.2	218.9	20.98	13.29	12.16	4.04	2.83	2.86
Nov	258.2	217.6	217.4	16.10	9.64	9.70	0.89	0.58	0.26

the present study. However, in some areas, the mean height of reed plants was considerably greater, reaching around 400 cm (Kvet, Svoboda & Fiala, 1969; Kvet, 1973). Such variation in shoot height was well demonstrated by Fiala (1976) who found the mean height of eight *Phragmites* stands ranging from 2 to 5 m.

The pattern of the increase in shoot dry weight was very similar to that of shoot height (Table 2). Maximum shoot dry weight was attained in September for Forfar and Balgavies plants and a month later in Lowes, with mean values measuring at 21.00, 15.72 and 12.16 g per shoot respectively. Similar to shoot height, the differences in the shoot weight were probably due to the differences in the trophic levels of the lochs. Both Gorham & Pearsall (1956) and Haslam (1971) also concluded from their studies in England that the shoot weight of *Phragmites* was commonly determined by mineral nutrition. Generally speaking, shoot weights in the present study were similar to those obtained by Mochnack-Lawacz (1974a) and Szczepanska & Szczepanski (1976) but heavier than those of Gorham & Pearsall (1956) and Mason & Bryant (1975).

Relationship between shoot height and shoot dry weight is shown in figure 1. A linear relationship between the two was found with $r = 0.894$, slightly higher than the value of $r = 0.848$ obtained by Szczepanska & Szczepanski (1976) in their study on reed plants in the Mazurian Lakeland in Poland. Similar linear relationship was apparent from the graph given by Mochnacka-Lawacz (1974a).

Leaf growth started in May, and by August, maximum leaf accumulation occurred (Table 2). The number of leaves in the shoot for all the three lochs averaged about ten in August. Hence the differences in leaf dry weight per shoot in the plants among the three lochs were due to the size of the leaves themselves rather than their number. The Forfar plants had longer and wider leaves than in the other two lochs. Most of the leaves in the shoot abscissed between October and November. Monthly changes in the ratio of leaf dry weight to shoot dry weight is shown in table 3. The ratio rose from May till July, when a maximum was reached, and then declined slowly but steadily over the next three months before it dropped drastically between October and November. Maximum leaf to shoot percentage ratios were similar for all three lochs and were between 27 and 30%. The ratio was regarded as rather 'conservative' (Kvet, Ondok, Necas & Jarvis, 1971) and did not change much. Similar values for the percentage ratio applied to *Phragmites* growing in other areas (e.g. Dykyjova, Onkok & Priban, 1970; Dykyjova & Hradecka, 1976).

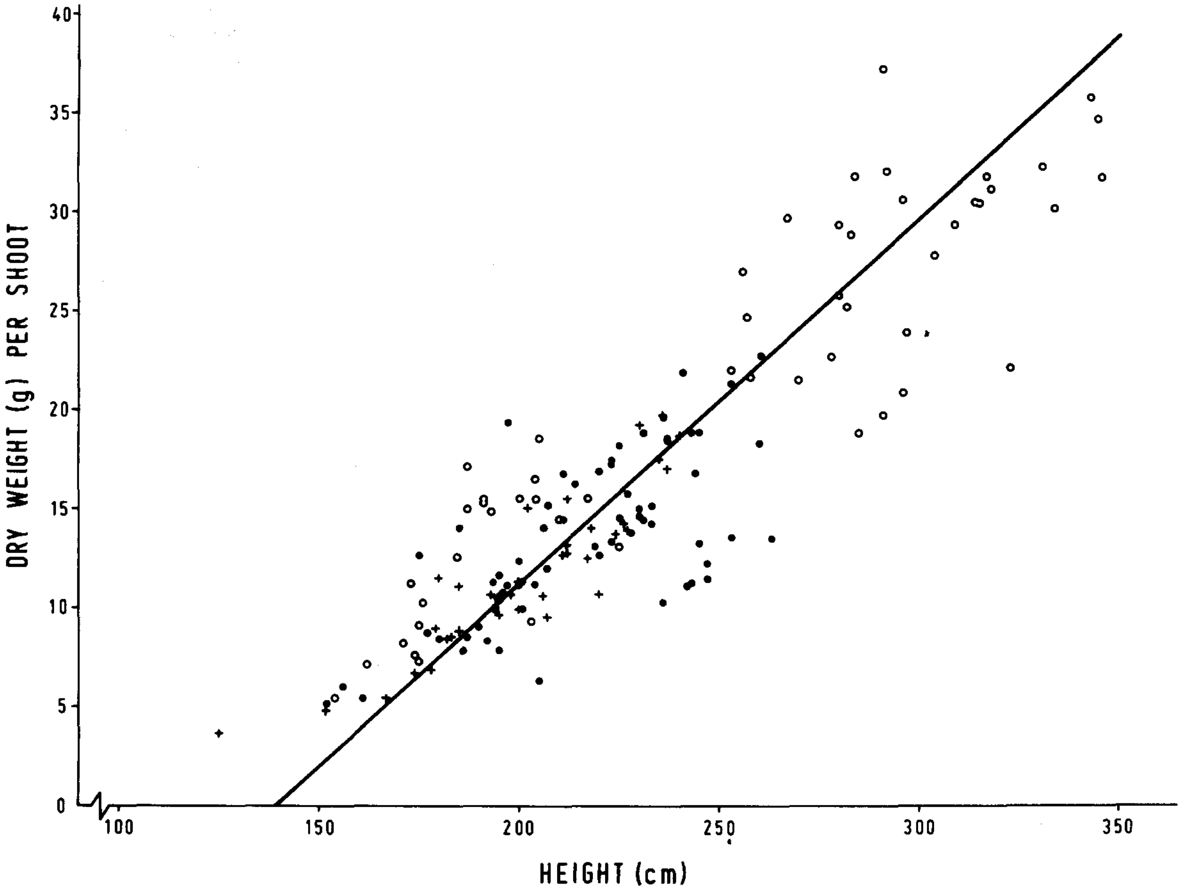

Fig. 1. Linear regression analysis between shoot dry weight and shoot height of *Phragmites* plants in the three lochs. o – Forfar, • – Balgavies, + – Lowes, $y = 139.44 + 5.42\,x$, $r = 0.894$, $P < 0.001$.

Panicle appeared prominent in August and increased to a maximum in weight for Forfar and Balgavies plants in October and for Lowes plants in November. Mean maximum panicle weight per shoot for the three lochs were 1.87, 1.23 and 1.15 g respectively. A linear relationship was found between panicle dry weight and shoot dry weight for plant samples from the three lochs, with $r = 0.7167$, significant at 0.001 level. No such relationship appeared to occur in reed plants of the Mazurian Lake region (Mochnacka-Lawacz, 1974a).

Production study

Monthly variations in biomass of reed stands in the three lochs are shown in table 4, together with data on LAI, LAR, NAR, RGR and C. Maximum biomass was reached in August for Forfar and Lowes stands, and in September for Balgavies. The 3975 g m^{-2} of biomass for

Table 3. Monthly changes in the percentage ratio of leaf dry weight to shoot dry weight of *Phragmites* during 1975.

Month	Forfar	Balgavies	Lowes
May	3.39	5.17	2.56
June	19.05	23.75	16.71
July	29.85	28.04	27.35
August	25.75	27.20	26.09
September	24.29	23.65	25.82
October	19.82	22.19	23.78
November	5.91	9.09	2.62

Table 4. Seasonal changes in biomass, leaf area index, leaf area ratio, net assimilation rate, relative growth rate and crop growth rate in *Phragmites* plants in the three lochs during 1975.

Harvest date	Shoot biomass ($g\ m^{-2}$)	LAI ($m^2 m^{-2}$)	LAR ($dm^2 g^{-1}$)	RGR ($g\ g^{-1} d^{-1}$)	NAR ($g\ m^{-2} d^{-1}$)	C ($g\ m^{-2} d^{-1}$)
Forfar						
20.4	60	0	0	0.0289	-	1.2
18.5	344	0.21	0.061	0.0626	103.6	10.2
15.6	973	2.84	0.292	0.0371	12.7	22.5
15.7	1971	7.86	0.399	0.0235	5.89	33.2
13.8	3975	12.29	0.309	0.0242	7.83	69.1
24.9	3643	11.02	0.303	-0.0021	-0.69	-7.9
22.10	3295	8.00	0.243	-0.0036	-1.48	-12.4
18.11	2228	1.62	0.073	-0.0150	-20.66	-41.0
Balgavies						
21.4	42	0	0	0.0293	-	0.8
19.5	167	0.13	0.075	0.0495	65.7	4.5
16.6	304	1.01	0.333	0.0215	6.46	4.9
17.7	1307	4.76	0.364	0.0470	12.92	32.4
14.8	1314	4.40	0.335	0.0002	0.060	0.2
25.9	1351	3.84	0.284	0.0007	0.247	0.9
23.10	1083	2.93	0.270	-0.0079	-2.924	-9.6
17.11	889	1.00	0.112	-0.0082	-7.326	-8.1
Lowes						
22.4	10	0	0	0.0323	-	0.2
20.5	54	0.02	0.040	0.0608	152.0	1.6
17.6	196	0.46	0.233	0.0462	19.79	5.1
11.7	268	0.83	0.309	0.0130	4.22	3.0
15.8	669	2.22	0.332	0.0261	7.87	12.7
26.9	632	1.81	0.287	-0.0013	-0.47	-0.9
24.10	596	1.84	0.309	-0.0021	-0.68	-1.3
19.11	504	0.19	0.038	-0.0067	-17.55	-3.7

Forfar was very high and was comparable to some other regions (e.g. Dykyjova & Pribil, 1975; Lars & Lennart, 1976). Still higher biomass values were obtained in hydroponic cultures (Dykyjova, Veber & Priban, 1971). Peak biomass readings in Balgavies and Lowes were considerably lower than in Forfar (Table 4). This was due to the lower shoot weight as well as lower shoot density of the plants in the former two lochs. Mean maximum biomass in Balgavies stands measured 1351 g m^{-2} and was similar to those obtained by Gerlanczynska (1973), Mochnacka-Lawacz (1974a, b), and Fiala (1976). For Lowes, the value of 669 g m^{-2} was close to the observations by Pearsall & Gorham (1956), Buttery & Lambert (1965), Szajnowski (1973a, b), Komarkova & Komarek (1975), Mason & Bryant (1975) and Andersen (1976).

Specific leaf area was found to decrease in value as the season advanced – from 148 cm^2g^{-1} in May to 127 cm^2g^{-1} in September. The same trend was observed by Kvet, Svoboda & Fiala (1969); Dykyjova & Hradecka (1976). Such decline might be a reflection in the changes in leaf thickness and/or the relative proportions of assimilatory and conductive or mechanical tissues in leaves.

The trend in LAI was similar to that of shoot biomass for Forfar and Lowes plants, rising to a peak in August. For Balgavies, LAI peaked in July, two months ahead of the time for maximum biomass (Table 4). Maximum LAI for Balgavies and Lowes stands were 4.76 and 2.22 respectively and were in agreement with stands from other study areas (e.g. Dykyjova, Ondok & Priban, 1970-4.64; Szajnowski, 1973 – 2.27). Since LAI is a measure on the size of assimilatory surface in the stands, a high LAI value would indicate high productivity. This is shown in the very high mean LAI value of 12.29 for Forfar stands. Such high LAI of over 10 was observed by Dykyjova & Hradecka (1976). Similarly, Blackman (1962) reported on a high optimum LAI value of 13 in *Scilla hispanica.* High optimum LAI values were regarded as characteristic of grass and fodder crops (Kvet, Ondok, Necas & Jarvis, 1971). A very significant linear relationship ($r = 0.980$, $a = 2.95$, $P < 0.001$ level) was found between the maximum or near-maximum biomass of different stands and their respective LAI values as is shown in fig. 2. Szajnowski (1973a, b) detected a similar relationship in reed stands taken from the Mazurian Lakeland and from Swedish lakes (data calculated from Bjork, 1967). Correlation coefficients (r) and regression coefficients (a) for the two areas were $r = 0.85$, $a = 2.83$ and $r = 0.96$, $a = 2.75$ respectively. These values were close to the ones reported here.

Leaf area ratio of stands from all the three lochs in-

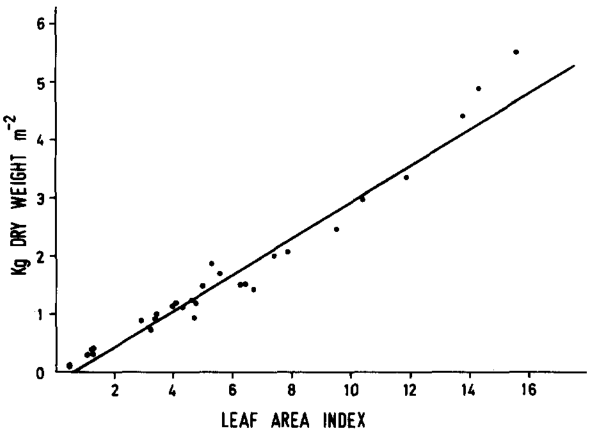

Fig. 2. Relationship between maximum biomass and leaf area index in *Phragmites* stands in the three lochs. $y = 0.853 + 2.946x$, $r = 0.980$, $P < 0.001$.

creased to a maximum in July (Forfar & Balgavies) and August (Lowes) and then decreased gradually till October followed by a considerable drop due to leaf fall (Table 4). Mean LAR (May to October) for Forfar, Balgavies and Lowes were 0.268, 0.277 and 0.252 dm^2 g^{-1} respectively and were lower than those obtained in other locations (Kvet, 1969; Dykyjova, Ondok & Priban, 1970; Dykyjova & Hradecka, 1976). Both RGR and NAR were at their maximum in May and declined over the rest of the season (Table 4). Similar trends were detected in other reed stands (Dykyjova, Ondok & Priban, 1970; Dykyjova & Hradecka, 1976; Fiala, 1976). One of the reasons for such decline in RGR and NAR was that at the start of the season, a significant proportion of the dry weight accumulation in the reed stand was translocated from the underground organs and was material incorporated from the previous season. A reverse in the direction of translocation took place later on thus leading to the possibility of underestimating the RGR and NAR values towards the end of the season. The decline in the RGR and NAR was also due to the increase with time in the proportion of non-assimilatory tissues. Crop growth rate increased to a maximum in July or August (Table 4). Maximum C for Forfar was nearly 70 g m^{-2} – indicative of the very high productivity of the stands (Dykyjova, Veber & Priban, 1971). Mean C over the growing season for the three lochs were: Forfar – 26.3, Balgavies – 8.7 and Lowes – 4.5 g m^{-2} day^{-1}.

Mean net efficiency of solar energy conversion for reed stands in the three lochs are summarized in table 5. Values are calculated as percentage of global (η global) and

Table 5. Mean net efficiency of solar energy conversion (η) for *Phragmites* in the three lochs during 1975.

Site	Harvest intervals	Days	Calorific values ($kJm^{-2}day^{-1}$)	Radiation ($kJm^{-2}day^{-1}$) Global	PhAR	η% Global	PhAR
Forfar	24.3-13.8	142	508.6	14680	6606	3.46	7.70
Balgavies	25.3-14.8	142	167.4	14718	6622	1.14	2.53
Lowes	26.3-15.8	142	87.1	14760	6643	0.59	1.31

photosynthetically active radion (η PhAR). The η PhAR pf 7.70% for Forfar was high and was comparable to those obtained by Dykyjova & Pribil (1975) (6.5 and 7.01%) and Dykyjova & Hradecka (1976) (8.27%). Lower efficiency was reported by Dykyjova, Ondok & Priban (1970) (5%) and Dykyjova, Veber & Priban (1971) (5.75%). However a very high conversion reading of 12.42% was obtained in hydroponic cultures by Dykyjova, Veber & Priban (1971). Sieghardt (1973) and Dykyjova & Pribil (1975) obtained η PhAR values similar to that of Balgavies.

Summary

In a study of the shoot development and production ecology of *Phragmites australis* stands in Scottish lochs, the following were observed:

1. Maximum shoot height and shoot dry weight of reed stands for the lochs were: Forfar (268.9 cm, 21.00 g), Balgavies (239.9, 15.72) and Lowes (218.9, 12.16).

2. Maximum values for the percentage ratio of leaf to shoot dry weight were similar for all three lochs.

3. Maximum shoot biomass and leaf area index obtained were: Forfar – 3975 g m^{-2}, 12.29 m^2m^{-2}, Balgavies – 1351, 4.76 and Lowes – 669, 2.22.

4. Significant linear relationships were found between shoot dry weight and shoot height (r = 0.894) as well as between maximum shoot biomass and leaf area index (r = 0.980).

5. Mean net efficiency of solar energy conversion (η PhAR) was 7.70% for Forfar, 2.53% for Balgavies and 1.31% for Lowes.

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