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VERIFICATION OF A MATHEMATICAL GROWTH MODEL OF *PHRAGMITES AUSTRALIS* USING FIELD DATA FROM TWO SCOTTISH LOCHS

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Abstract: A growth model of *Phragmites australis* was verified using two independent sets of published field data. The model simulates the growth pattern of a well-established, monospecific stand of *P. australis* in the absence of genetic diversity and environmental stresses of mainly nutrient and water deficiency. The model formulated using first order differential equations was combined with plant phenology and comprises five subroutines in which photosynthetically active radiation, shoot, root, rhizome and new rhizome biomass are calculated. Using the model, experimental results were reproduced within reasonable limits having concordance correlation coefficients of more than 0.75 for 70% of the output parameters, which was the main objective of the study. The modelled efficiencies of PAR were 7.15% and 3.09%, as opposed to 7.7% and 2.53% in experimental estimations, for Loch of Forfar and Loch of Balgavies, respectively. Production and seasonal fluxes of dry matter of *P. australis* in Scottish lochs were estimated using the modelled quantities for the 1975 growing season in g m^{-2}. They showed that 31% and 37% of total net photosynthate translocated to rhizomes before shoot senescence began in Loch of Forfar and Loch of Balgavies, respectively. Also in both lochs approximately 45% of total downward translocation came from accumulated shoot dry matter during senescence, while the rest came from photosynthesis before the shoots started to senesce.

INTRODUCTION

The common reed, *Phragmites australis* (CAV.) TRIN. ex STEUD., forms large masses of vegetation at the edges of ponds, lakes and watercourses where the current is slow. It is a spectacularly tall emergent macrophyte found on almost all continents, except Antarctica; it is used in many ways in many areas of the world and is economically important and valuable. Emergent macrophytes play a dominant role, acting as a buffer zone in aquatic environments. A more recently understood aspect of *P. australis* is its role in bioremediation, i.e., cleaning water containing waste material, including heavy metals and sewage.

During the past few decades considerable work has been done on the productivity, growth and other related aspects of *P. australis*. Many experimental analyses have been made, such as by DYKYJOVÁ (1971), DYKYJOVÁ et al. (1971, 1972), KVĚT (1971), HO (1979, 1981) and ČÍŽKOVÁ & BAUER (1998), and also by ARMSTRONG & BECKETT (1987), HARA et al. (1993) and ALLIRAND & GOSSE (1995), who analyzed various aspects of *P. australis* using various modelling techniques. The model developed by ARMSTRONG & BECKETT (1987) simulates aeration in submerged roots and allows for axial gas-phase diffusion in the cortex and radial liquid-phase diffusion elsewhere. This led them to analyze the important process of pressurized aeration in wetland macrophytes. HARA et al. (1993) investigated the growth dynamics and size structure of *P. australis* during one growing season at the level of the individual shoot. The model was based on a diffusion model for three shoot populations (based on age and sparsity) in which a stochastic approach was used. ALLIRAND & GOSSE (1995) developed an aboveground biomass production model for *P. australis* using the classic method used for crop plants, namely, the determination of stand phenology, and the establishment of relationships governing leaf area production, light energy absorption by the leaves, and conversion efficiency of absorbed energy into biomass. However, both the growth models by HARA et al. (1993) and ALLIRAND & GOSSE (1995) were limited to investigations of the production and growth dynamics of aboveground parts only.

We used a different approach and formulated a mathematical model to simulate the growth production (both aboveground and belowground) of a well-established, monospecific stand of *P. australis* by considering the photosynthesis, respiration, mortality and translocation of material between plant organs using first order differential equations.

This paper outlines two applications made using the model. A very brief description of the model, the functions allocated to each of its subroutines, and input and output data are also described. A detailed explanation of the model formulation is given in a separate paper (ASAEDA & KARUNARATNE 2000). An appendix lists the main equations used in the model and gives a brief explanation of them.

MATERIAL AND METHODS

Outline of the *P. australis* growth model

Five state variables (for five major plant organs) were selected depending on their importance and effectiveness to illustrate the growth of *P. australis*. Hence, the biomass of *P. australis* per square meter was divided into five major plant organs: shoots (including leaves and stems), panicles, rhizomes, roots and new rhizomes, and were evaluated in grams per square meter by ash free dry weight. The growth of each plant organ was described using five main mathematical relationships. These equations were formulated to incorporate the net growth of the plant stand as a function of photosynthesis, respiration, mortality, and to assimilate translocation between shoots and belowground organs and plant phenology. The phenological cycle of reed has an important role in growth models. Although phenological cycles are usually uneven, one-batch cycles were assumed and physical and biological factors that may affect the plant phenology were not considered explicitly. The plant phenology was interpreted in terms of simple mathematical relationships by regression analysis of published experimental data and these equations were incorporated in the growth equations to trigger the phenological cycle in the growth model. The possible clonal diversity within and among the *P. australis* stands was not considered because including such aspects in this kind of model was very difficult. We assumed that possible environmental stresses (deficiencies), such as nutrient and water do not affect the plant growth.

Input data

The meteorological conditions of the location during the growing season and the rhizome and root biomass just before the spring growth of shoots were required to start the simulation. Daily mean air temperature and daily total global radiation (throughout the growing season) are in ^{o}C and mol photons m^{-2} d^{-1}, respectively, while rhizome and root biomass are in g m^{-2}.

The date of shoot emergence was considered as a forcing function and hence it was estimated using observed data. One-day time steps were used in the computation.

Meteorology subroutine

This subroutine calculates the photosynthetically active radiation using the total global radiation, which was given as input data.

Rhizome subroutine

This subroutine calculates the daily change in rhizome biomass that includes such processes as remobilization of stored matter from rhizomes to shoots at the beginning of the growing season and translocation of photosynthesized material and shoot dry matter to rhizomes towards the end of the growing season.

Shoot subroutine

This subroutine deals with the daily change in total aboveground biomass. The aboveground part of the *P. australis* stand was stratified into 1 cm-thick horizontal layers in which the dry matter budget and elongation were calculated separately. For each layer, growth equations were solved simultaneously using the forth-order Runge-Kutta method. The time scale was in Julian days. From the observed data of KVĚT et al. (1969), HO (1979) and HOCKING (1989), a leaf/stem ratio was formed and the shoot biomass was divided accordingly, into leaf and stem (with leaf sheaths) biomass. Plant elongation was considered in the following way. The biomass increment for each time step of each layer was calculated and if the growth was positive, a portion of the increased biomass was allocated for elongation, while the rest was allocated for the growth of the same layer.

Panicle biomass was also calculated in this subroutine. The shoot photosynthesis and dry matter translocation were considered as the major sources of panicle production.

Root subroutine

The daily change in root biomass including the interactions with rhizomes and shoots was computed. Initially, root growth was stimulated by rhizome reserves similar to shoots and later the shoots also contributed to the growth of roots.

New rhizome subroutine

The biomass of the rhizome, which grows in the current growing season, was calculated in this subroutine. The main source supporting its growth was considered as shoot translocations.

Output data

The model can simulate the seasonal variation of the above-ground biomass, i.e., shoot, leaf, stem and panicle biomass, as well as leaf area index (LAI). It can also calculate the vertical distribution of shoot biomass, LAI, seasonal variation of shoot height and the below-ground biomass, i.e., rhizomes, new rhizomes and roots for a given growing season.

Experimental study

HO (1979, 1981) investigated the development and production of *P. australis* stands from three lochs (Loch of Forfar, Loch of Balgavies and Loch of Lowes) in Scotland. He classified

Forfar as polytrophic, Balgavies as eutrophic and Lowes as mesotrophic. For physical characteristics and location details of the three lochs see Ho (1979, 1981). The reed grew along the loch margin forming monospecific stands in all three locations. The model was constructed assuming no nutrient stresses throughout the growing season. Therefore Loch of Forfar and Loch of Balgavies were selected for simulations considering their nutrient status (we assumed that nutrients are abundant and no restriction on growth exists due to lack of nutrients in them).

P. australis samples were taken monthly from March to November 1975. On each sampling day, four to seven 0.25 m^2 quadrant samples were collected from each loch. The number of shoots in each quadrant was noted and they were harvested by clipping at ground level. In the laboratory, the height of each shoot was measured from the clipped base to the uppermost leaf or to the tip of the panicle if a panicle was present. Shoots were divided into stems with leaf sheaths, leaves and panicles and each portion was dried separately at 85 °C for 24 hours before the dry weight was measured. The monthly biomass of the standing crop at each site at each loch was measured and was expressed as dry weight per square meter (Ho 1981).

The meteorological data required for our simulation were obtained from The Meteorological Office, UK. The daily totals of global radiation were obtained from Mylnefield, which is the nearest meteorological station that recorded solar radiation for the year 1975. The mean air temperatures for Loch of Forfar and Loch of Balgavies were obtained from Mylnefield and Arbroath, respectively.

In the experimental study belowground biomass was not measured. Rhizome biomass just before the spring growth of shoots was required as input data for the model. As measurements for the seasonal course of aboveground biomass were available, we investigated the possibility of estimating the initial rhizome biomass from these aerial parts, i.e., using a root/shoot ratio. The common definition of root/shoot ratio used in production analysis refers to a quantity measured at a particular growth stage; e.g., root/shoot ratio in June, August and October. This ratio may change according to latitude, trophic level, history, water level, hydrology in general and chance. DYKYJOVÁ et al. (1972) in their study of winter hydroponic cultures concluded that the root/shoot ratio may be a relatively constant quantity of the species characteristic, but only for a given growth phase. They further stated that if the root/shoot ratio is calculated when the photosynthetic parts are at maximum development, the underground biomass is underestimated and vice versa. DYKYJOVÁ et al. (1971) in their experiments of outdoor hydroponic cultures showed that the root/shoot ratio varied between 0.46 to 2.61, depending on the age of plants and on what day the plants were planted and harvested. However, these ratios were determined only at the end of the cultivation period (after 5 to 6 months from the start of growth). Furthermore FIALA (1973), in his study of growth and production of underground organs of *P. australis* in fish ponds in the Czech Republic, found that the values of the root/shoot ratio at different growth phases varied with a relatively wide amplitude, approximately from 1.5 to 5.5. Considering this evidence we concluded that the underground biomass of *P. australis* at an intermediate stage of growth cannot be estimated by using the common root/shoot ratio. We could see, however, that a relationship exists between the maximum aboveground biomass and the belowground biomass including both rhizome and root just before the spring growth of shoots of the same season (referred to as the initial belowground/maximum shoot ratio hereafter). We calculated this ratio for three different stands of *P. australis* in the Mirrool Creek, New South Wales, Australia, in the Opatovický fishpond, the Czech Republic and in North Jutland, Denmark.

Mirrool Creek, New South Wales, Australia

HOCKING (1989) studied the growth production of a *P. australis* stand in Mirrool Creek, New South Wales, Australia. Mirrool Creek is a natural water course, that receives drainage water from irrigated farmland in the Murrumbidgee Irrigation Area (MIA). The climate of the region is warm, dry continental. In the MIA, Mirrool Creek was fringed by extensive stands of *P. australis*. The water table was usually 5–10 cm deep, but sometimes flooded more deeply (up to 50 cm). The water in Mirrool Creek was turbid, slightly saline and was enriched by fertilizer run-off that leached from irrigated farmland (HOCKING 1989). The plant stand was investigated in the 1979/1980 growing season and an initial belowground/maximum shoot ratio of 2.10 was found. Initial root biomass amounted to 16% of the total initial belowground biomass.

Opatovický fishpond, the Czech Republic

The *P. australis* stand in the Opatovický fishpond was studied by DYKYJOVÁ & HRADECKÁ (1976). The site was a limosal ecotype and was waterlogged, but was never actually flooded with fishpond water. The habitat was sheltered by tall stands *of Picea abies* (L.) H. KARST. and *Quercus robur* L. and by shrubs of *Populus tremula* L., *Alnus glutinosa* (L.) P. GAERTN. and *Salix cinerea* L. A waste-water channel from a nearby farm crossed the reed stand. The waste-water irrigated the whole area in spring or autumn when the water level rose in the fishpond (DYKYJOVÁ & HRADECKÁ 1976). In this stand, belowground parts were sampled in May at the earliest. Hence the ratio between the belowground biomass in May and the maximum shoot biomass was calculated and a value of 1.35 was found. For *P. australis* stands in this region rhizome biomass reached a near minimum value in May. Hence we presumed (by comparing the other rhizome and shoot biomass values) that the initial belowground/maximum shoot ratio for this stand can be in the range of 1.7–2.2. However, in this study, root biomass was not calculated separately.

North Jutland, Denmark

The investigation was carried-out by SCHIERUP (1978) in the Vejlerne Nature Reserve, a wetland area in the province of Thy in North Jutland, Denmark. The Vejlerne wetland area is a system of shallow fiords or broads reclaimed from Lim Fiord during the latter part of the 19th century. The sampling area was situated in the western part of the smallest broad, Han Vejle. To ensure a genetically and morphologically uniform plant material, the sampling area was selected from within a clone of *P. australis* covering about 700 m^2 in Han Vejle. The *P. australis* stand, being at least 25 years old, appeared to be in dynamic equilibrium, equilibrium being supposed to be reached after some 10 years. The water level was +20 cm relative to the detritus surface from October to April, decreasing to -20 cm in July (SCHIERUP 1978). Both aboveground biomass and belowground biomass were investigated throughout the growth season and an initial belowground/maximum shoot ratio of 1.98 was found. Initial root biomass amounted to 11% of the total initial belowground biomass.

It was evident that the initial belowground/maximum shoot ratio followed a similar trend in the three study sites. These comparisons showed that a mean value of 2.04 could be apportioned to the initial belowground/maximum shoot ratio. Further, they showed that the initial root biomass comprised, 13.5% (mean value) of total initial belowground biomass. Hence in this analysis, these values were used to estimate the initial rhizome and root biomass of both Loch of Forfar and Loch of Balgavies.

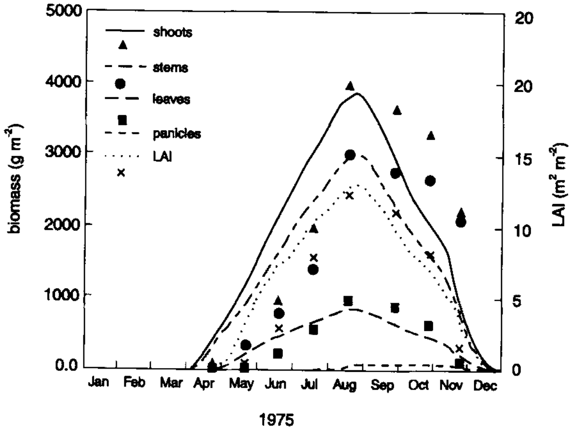

Fig. 1. Seasonal variation in aboveground biomass of *P. australis* (1975 growing season – Loch of Forfar, Scotland). Model simulations are represented by lines. Observed data (represented by symbols) from Ho (1979). LAI: leaf area index.

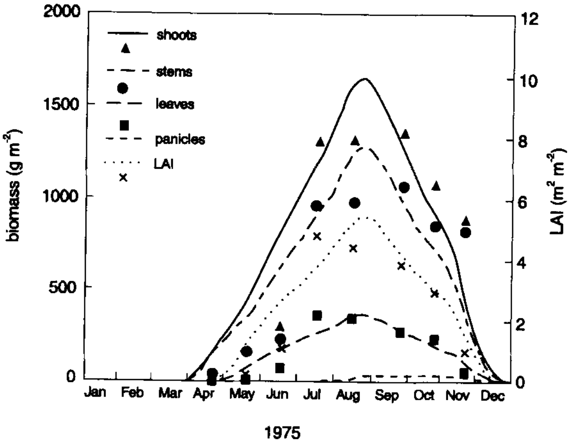

Fig. 2. Seasonal variation in aboveground biomass of *P. australis* (1975 growing season – Loch of Balgavies, Scotland). Model simulations are represented by lines. Observed data (represented by symbols) from Ho (1979). LAI: leaf area index.

RESULTS

The capability of the model to predict the seasonal variation of shoot biomass and shoot height of *P. australis* was verified using published data from two different populations of *P. australis* growing in Loch of Forfar and Loch of Balgavies in Scotland during the 1975 growing season.

The seasonal variation in the aboveground biomass, i.e., total shoot, stem and leaf biomass, and the leaf area index, of *P. australis* was simulated and was compared with field measurements (Figs. 1, 2). Even though no field data for comparison existed, figures also show the panicle biomass of *P. australis*. Figs. 3 and 4 show the seasonal variation in shoot height of *P. australis* for Loch of Forfar and Loch of Balgavies, respectively. Higher values were recorded in measured, as well as simulated results, of shoot biomass of Loch of Forfar, which had the higher nutrient status. A comparison of Figs. 1 and 2 shows a large discrepancy (the Forfar value is almost double the value of Balgavies) between the maximum shoot biomass attained by the two stands whereas only a slight increase in shoot height exists. Hence, the larger increase in shoot biomass in Loch of Forfar cannot be attributed to the slight increase in shoot height only. Even though Ho (1979) gave no evidence, presuming that the shoot density and/or shoot diameter of Forfar shoots are much larger than that of Balgavies seems fair. Also, in this case, the fact that the considerably greater shoot biomass attained by Forfar plants was partly due to the overall higher nutrient level of the loch seems probable (Ho 1979). A higher belowground biomass in turn gives rise to a higher shoot biomass. Therefore, the model simulates a higher shoot biomass for Forfar plants, even though it does not consider the effect of nutrient status on growth.

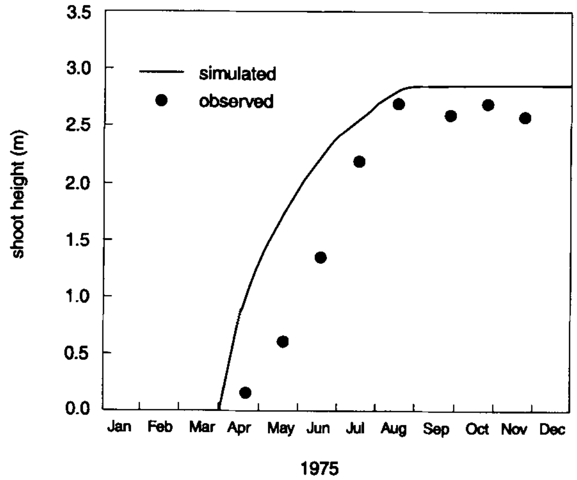

Fig. 3. Seasonal variation in shoot height of *P. australis* (1975 growing season – Loch of Forfar, Scotland). Observed data (represented by symbols) from Ho (1979).

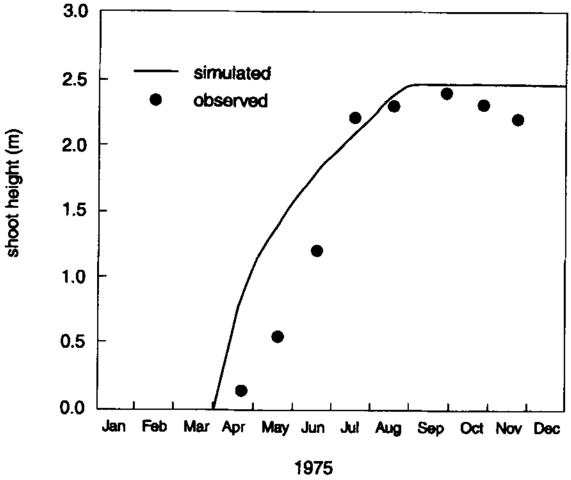

Fig. 4. Seasonal variation in shoot height of *P. australis* (1975 growing season – Loch of Balgavies, Scotland). Observed data (represented by symbols) from Ho (1979).

In the experimental study, the shoot height increase in the initial stage of growth was relatively slow, but was rapid thereafter until August when growth slowed down and levelled off. In the simulated results, however, the slow initial shoot height increase was masked by the constant elongation rate assumed in the model.

The LAI is an important index to explain the production of any plant stand. Also, it is a measure of the size of assimilatory surface in the stands; a high LAI value indicates high productivity (Ho 1979). This is well illustrated by the higher LAI found at Loch of Forfar, where a higher shoot biomass was measured as well. The capability of the model to simulate different LAI values corresponding to varying production levels was well illustrated by the positive linear correlation of LAI to shoot dry weight (per square meter in kilograms) ($r = 0.996$, $P < 0.0001$) (Fig. 5). In Fig. 5, all simulated data for both the lochs were pooled and were plotted on the same graph. It also reproduces the linear relationship between maximum or near maximum biomass of different stands in Scottish lochs and their respective leaf area index values formed by Ho (1979) ($r = 0.98$, $P < 0.001$). SZAJNOWSKI (1973a,b) found a similar relationship in reed stands in the Mazurian Lakeland.

The estimation of production and seasonal fluxes of dry matter using only experimental results or field measurements may prove to be a difficult or sometimes an impossible task for a marsh plant like *P. australis*. Such an extensive study in field conditions is frequently not possible throughout the whole growing season. At such times, mathematical or stochastic models which can describe plant behaviour in close proximity become convenient tools. Sometimes it is surprising to see the large quantities of energy that has been burnt by shoot or rhizome respiration during a single growing season. We estimated the production and seasonal fluxes of dry matter of *P. australis* in Scottish lochs using the modelled quantities (Fig. 6). All values

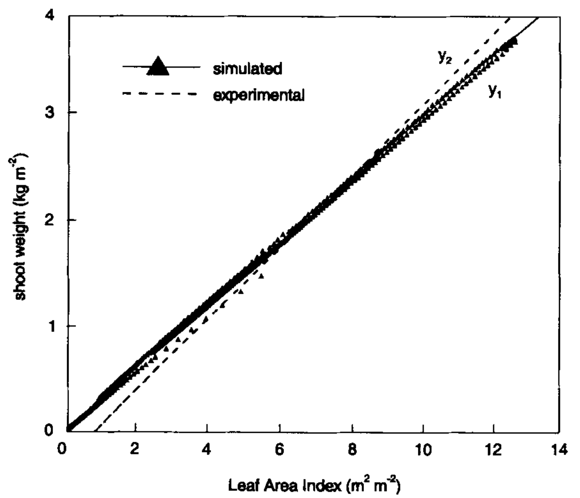

Fig. 5. Relationship between shoot dry weight and leaf area index of *P. australis* (y_1: (shoot dry weight) = 0.012 + 0.2974 . (LAI), $r = 0.996$, $P < 0.0001$), from modelled values of both Loch of Forfar and Loch of Balgavies, and y_2: (shoot dry weight) = -0.290 + 0.3394 . (LAI), $r = 0.980$, $P < 0.001$), reproduced from Ho (1979).

given in the figure were calculated for the 1975 growing season, in g m^{-2}. This figure shows that in the Loch of Forfar 31% and in the Loch of Balgavies 37% of total net photosynthate translocated to belowground organs before shoot senescence began. HOCKING (1989) and LYTLE & HULL (1980) found similar values of 22% and 30% for *P. australis* and *Spartina alterniflora* LOISEL., respectively. We found that for both lochs approximately 45% of total downward translocation came from accumulated shoot dry matter during senescence, while the rest came from photosynthesis before the shoots started to senesce.

In total, we can say that the simulated results describe the experimental results within reasonable limits. 70% of the output parameters show a concordance correlation coefficient of more than 0.75 (Tab. 1). Hence, we can conclude that the validation of the *P. australis* growth model is successful and it can be used to predict the seasonal variation of aboveground biomass of a well-established, monospecific stand of *P. australis* in the absence of genetic diversity and environmental stresses. However, further validation is necessary to confirm the ability of the model to predict the seasonal course of belowground biomass.

DISCUSSION

The objective of the study was to verify a mathematical model developed to simulate the growth pattern of a well-established, monospecific stand of *P. australis* in the absence of genetic diversity and environmental stresses such as nutrient deficiency and/or water deficiency. This was its first verification on two independent sets of published field data. The difficulty in finding good quality, suitable data sets (which present the seasonal growth pattern of both aboveground and belowground biomass of the same population of *P. australis*) poses a considerable setback in such verifications.

A special feature of the model presented in this paper is its ability to predict the growth pattern of monospecific stands of *P. australis* from varying locations (ASAEDA & KARUNARATNE 2000). The application of the aboveground biomass production model of *P. australis*, produced by ALLIRAND & GOSSE (1995) is limited to a specific location and hence restricts its value as a prediction model. Predicting the growth and production of reed is indispensable in aquatic and wetland management and making such tools commercially available for such purposes is long overdue.

In this study a method was proposed to estimate the initial rhizome biomass in terms of maximum shoot biomass of the same season. Even though no direct proof exists from past

Table 1. Concordance correlation coefficients (r_C) between experimental and simulated results.

Loch	Correlation coefficient (r_C)				
	Shoots	Stems	Leaves	LAI	Shoot height
Forfar	+0.725	+0.657	+0.892	+0.905	+0.944
Balgavies	+0.792	+0.729	+0.909	+0.902	+0.961

studies, we are fully aware that this ratio may tend to change because of the sudden changes in trophic level, water level, hydrology in general and by chance. A change in this ratio may also affect the simulation results. Hence, a sensitivity analysis was performed to investigate the influence of this ratio on the simulation results. The initial belowground/maximum shoot ratio were varied from 1.2 to 2.8 in steps of 0.2 and the percentage change (with respect to the values obtained with an initial belowground/maximum shoot ratio of 2.04) in maximum shoot biomass and maximum shoot height was analyzed. The analyses showed that initial belowground/maximum shoot ratio at 1.2 produced 29.8% and 33.8% changes in maximum shoot biomass and 3.9% and 8.5% changes in maximum shoot height for Loch of Forfar and Loch of Balgavies, respectively; the same ratio at 2.8 produced corresponding changes of +18.5% and +23.3%, for maximum shoot biomass, and +10.4% and +4.1% for maximum shoot height in Loch of Forfar and Loch of Balgavies, respectively. Although the lower limit of 1.2 for the ratio is a relatively low value, the percentage values of deviation of maximum shoot biomass and maximum shoot height are relatively low. Therefore the initial belowground/maximum shoot ratio shows moderate sensitivity to the simulation results, implying that a smaller change in this ratio (e.g. 2.04 ± 0.4) may not exert a significant impact on model predictions. Changes in initial root biomass exerted only minor effects on maximum shoot biomass and maximum shoot height compared with the initial belowground/maximum shoot ratio.

KUBÍN et al. (1994) proved that reed decline is a consequence of eutrophication. In a nutrient-poor habitat less aboveground biomass and greater starch content were found in rhizomes of *P. australis* compared with a nutrient-rich habitat. Detailed studies have been made on the causes of reed decline in the Central European regions and some other parts of the world (ČÍŽKOVÁ et al. 1992, 1996, KUBÍN & MELZER 1996, REA 1996). The model as formulated now, however, is incapable of making long-term simulations to distinguish such nutrient differences. However, this model can be modified to include such fine details and the effect of water level variation, and then it can be used to predict the stability of a reed bed in the long term.

The net efficiency of solar energy conversion by *P. australis* was also computed using simulation results. This can be considered as a convenient tool to quantify the total annual production rate as a function of solar radiation. A widely-used form of the conversion efficiency in terms of the total global radiation, or photosynthetically active radiation (PAR), is given by:

$$\eta_{\text{Solar, PAR}} = \frac{(\text{Energy content per gram of tissue}) . (\text{biomass})}{(\text{Total solar radiation or PAR during the growing season})} \cdot 100\%$$

HO (1979) used the calorific value for *P. australis* as 19.46 kJ g^{-1} ash-free dry weight, an average value taken from the readings of KVĚT (1969, unpublished data quoted in DYKYJOVÁ & PŘIBIL 1975), SIEGHARDT (1973), DYKYJOVÁ & PŘIBIL (1975), ANDERSON (1976) and

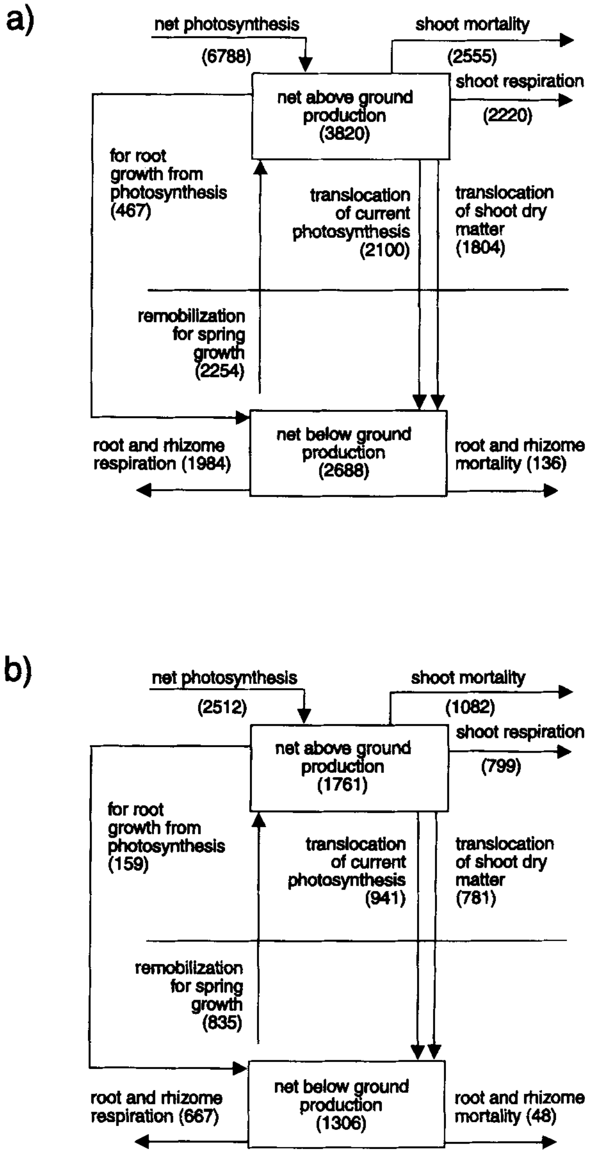

Fig. 6. Production and seasonal fluxes of dry matter in *P. australis* constructed using the modelled quantities. (a) – Loch of Forfar, Scotland; (b) – Loch of Balgavies, Scotland. Production is expressed as g m^{-2} and fluxes are expressed as g m^{-2} growing season^{-1} (Growing season – 1975 is specified from April to November).

DYKYJOVÁ & HRADECKÁ (1976). We used the same value in our calculations. Photosynthetically active radiation was assumed to be 45% of total global radiation. The values were calculated as a percentage of global (η_{solar}) and photosynthetically active radiation (η_{PAR}). Tab. 2 summarizes the comparison between the simulated and experimental mean net efficiencies of solar energy conversion for reed stands in the two lochs. The modelled efficiencies compare well with the experimental efficiencies. Loch of Forfar had the higher

Table. 2. Comparisons of mean net efficiency of solar energy conversion for *P. australis* in Scottish lochs during the 1975 growing season (from April to August).

Loch	Solar energy conversion efficiencies (%)			
	Simulated		Experimental	
	η_{Solar}	η_{PAR}	η_{Solar}	η_{PAR}
Forfar	3.22	7.15	3.46	7.70
Balgavies	1.39	3.09	1.14	2.53

solar energy conversion efficiencies where a higher production was found as well. These values can be considered as high, but comparable with the values of other studies of highly productive stands of *P. australis* (Dykyjová & Přibil 1975, Dykyjová & Hradecká 1976, Hocking 1989).

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APPENDIX

Governing equations for biomass

$$\frac{dB_{\mathrm{rhi}}}{dt} = -R_{\mathrm{rhi}} - D_{\mathrm{rhi}} - Rhif \,.\, f_{\mathrm{rhi}} + y \,.\, \sum_{i=1}^{i=i_{\max}} \varepsilon_{\mathrm{sht}} \,.\, b_{\mathrm{sht}}(i) \,.\, f_{\mathrm{sht}} + y \,.\, \sum_{i=1}^{i=i_{\max}} \varepsilon_{\mathrm{ph}} \,.\, Ph_{\mathrm{sht}}(i) \,.\, f_{\mathrm{ph}} \qquad (1)$$

$$\frac{dB_{\mathrm{rt}}}{dt} = G_{\mathrm{rt}} \,.\, f_{rt} - R_{\mathrm{rt}} - D_{\mathrm{rt}} + x \,.\, Rhif \,.\, f_{\mathrm{rhi}} \qquad (2)$$

$$\frac{dB_{\mathrm{n}}}{dt} = -R_{\mathrm{n}} - D_{\mathrm{n}} + (1-y) \,.\, \sum_{i=1}^{i=i_{\max}} \varepsilon_{\mathrm{sht}} \,.\, b_{\mathrm{sht}}(i) \,.\, f_{\mathrm{sht}} + (1-y) \,.\, \sum_{i=1}^{i=i_{\max}} \varepsilon_{\mathrm{ph}} \,.\, Ph_{\mathrm{sht}}(i) \,.\, f_{\mathrm{ph}} \qquad (3)$$

$$\begin{aligned} \frac{db_{\mathrm{sht}}(i)}{dt} &= Ph_{\mathrm{sht}}(i) - R_{\mathrm{sht}}(i) - D_{\mathrm{sht}}(i) + (1-x) \,.\, Rhif \,.\, f_{\mathrm{rhi}} \,.\, (b_{\mathrm{sht}}(i)/B_{\mathrm{sht}}) \\ &- \varepsilon_{\mathrm{sht}} \,.\, b_{\mathrm{sht}}(i) \,.\, f_{\mathrm{sht}} - \varepsilon_{\mathrm{ph}} \,.\, Ph_{\mathrm{sht}}(i) \,.\, f_{\mathrm{ph}} - (b_{\mathrm{sht}}(i) \,.\, \varepsilon_{\mathrm{p}} - Ph_{\mathrm{sht}}(i) \,.\, k) \,.\, ff \\ &- G_{\mathrm{rt}} \,.\, f_{\mathrm{rt}} \,.\, (b_{\mathrm{sht}}(i)/B_{\mathrm{sht}}) \qquad (4) \end{aligned}$$

$$\frac{db_{\mathrm{p}}(i)}{dt} = -R_{\mathrm{p}}(i) - D_{\mathrm{p}}(i) + \sum_{i=1}^{i=i_{\max}} Ph_{\mathrm{sht}}(i) \,.\, k \,.\, ff + \sum_{i=1}^{i=i_{\max}} \varepsilon_{\mathrm{p}} \,.\, b_{\mathrm{sht}}(i) \,.\, ff \qquad (5)$$

where, B (g m^{-2} d^{-1}) and b (g m^{-2} d^{-1}(1 cm height)$^{-1}$) are biomass and subscripts, rhi, rt, n, sht, and p represent rhizomes, roots, newly-formed rhizomes (during the year), shoots and panicles, respectively; $f_{\mathrm{rhi}}=1$ when $t_b \le t \le t_e$, otherwise 0; $f_{\mathrm{sht}}=1$ when $t_s \le t$, otherwise 0; $f_{\mathrm{ph}}=1$ when $t_p \le t \le t_s$, otherwise 0; $\varepsilon_{\mathrm{sht}}$ and $\varepsilon_{\mathrm{ph}}$ are fractions reallocated from shoots and current photosynthesis to the belowground organs, respectively, of which fraction y was allocated to the original rhizomes and the rest to new rhizomes; $f_{\mathrm{rt}}=1.0$ when $t_r \le t \le t_p$, otherwise 0; (i), represents the quantity in the i th layer; $ff=1.0$ when $t_f \le t$, otherwise 0; $i_{\max}$ is the maximum number of layers in the plant stand; t_b, t_r, t_e, t_p, t_f, and t_s are the times of growth commencement, formation of new roots, ending of mobilization of stored reserves from rhizomes to shoots and roots, commencement of translocation of current photosynthesized material to belowground organs, appearance of panicles and start of shoot senescence, respectively; k and ε_p are the fractions of contribution of current photosynthesis and accumulated shoot dry matter, respectively, to the formation of panicles; R and D are the respiration and mortality (g m^{-2} d^{-1}), respectively, which were proportional to their biomass (ASAEDA et al. 2000, ASAEDA & BON 1997, HOOTSMANS 1994) and mean daily temperature.

$$R_x = \beta_x \,.\, \theta^{(T-20)} \,.\, B_x \quad \text{and} \quad D_x = \gamma_x \,.\, \theta^{(T-20)} \,.\, B_x \qquad (6), (7)$$

where γ and β are the specific rates of mortality and respiration at 20 °C and subscript x refers to rhizome, root, new rhizome, shoot or panicle; θ is the temperature coefficient; T is the daily averaged temperature; *Rhif* is the flow of stored material from rhizomes to roots and to shoots during the initial stage of the growing season. The amount of material flow from the rhizomes was assumed to be proportional to its biomass and daily mean temperature.

$$Rhif = \alpha_{\mathrm{rhi}} \,.\, \theta^{(T\text{-}20)} \,.\, B_{\mathrm{rhi}} \tag{8}$$

where B_{rhi} is the specific transfer rate of rhizome biomass.

Supply of photosynthesized material for root growth is given by

$$G_{\mathrm{rt}} = g_{\mathrm{m}} \cdot \frac{K_{\mathrm{rt}}}{K_{\mathrm{rt}} + Age_{\mathrm{rt}}} \cdot B_{\mathrm{rt}} \tag{9}$$

where g_{m} is the specific growth rate of roots; K_{rt} is the half saturation coefficient of root age and Age_{rt} is the age of roots in days from the start of root growth.

Total shoot biomass is given by summing the shoot biomass in each layer.

$$B_{\mathrm{sht}} = \sum_{i=1}^{i=i_{\mathrm{max}}} b_{\mathrm{sht}}(i) \tag{10}$$

A constant shoot elongation rate was assumed even though it increases from the start of the growing season until the end of the rapid growth period and then declines. Shoot elongation per day in meters is given by

$$\frac{(\text{ biomass increase in the } i \text{ th layer}) \,.\, q \,.\, (\text{ thickness of the stratified layer})}{(\text{ biomass in the } i \text{ th layer}) - (\text{ biomass increase in the } i \text{ th layer}) \,.\, q} \tag{11}$$

where, q is the fraction of biomass contributed to shoot elongation from each layer.

Net plant photosynthesis (g m^{-2} d^{-1}) in i th layer is given by a form of the Michaelis-Menten equation.

$$Ph_{\mathrm{sht}}(i) = P_{\mathrm{m}} \,.\, k_{\mathrm{co}} \,.\, \theta^{(T-20)} \cdot \frac{I_{\mathrm{PAR}}(i)}{K_{\mathrm{PAR}} + I_{\mathrm{PAR}}(i)} \cdot \frac{K_{\mathrm{age}}}{K_{\mathrm{age}} + Age_{\mathrm{sht}}} \,.\, b_{\mathrm{sht}}(i) \tag{12}$$

where, P_{m} is the specific net daily photosynthesis rate of the plant top at 20 °C in the absence of light and nutrient limitations; k_{co} is the conversion constant of carbon dioxide to ash-free dry weight; I_{PAR} is the photosynthetically active radiation in i th layer; Age_{sht} is the age of shoots from the start of growth; K_{PAR} and K_{age} are the half saturation coefficients of PAR and age, respectively.