

Modeling Resource Allocation in *Potamogeton pectinatus* L.

GERDA M. VAN DIJK AND J. H. JANSE¹

ABSTRACT

In the present study, a simulation model of the life cycle of *Potamogeton pectinatus* L. (sago pondweed) is presented to analyze the implications of resource allocation for long-term survival. The model is calibrated on field observations of *P. pectinatus*. The model is simple and can be used as a tool to improve understanding of the dominant mechanisms in resource allocation and long-term survival. The model is used to test the hypothesis that the resource allocation to the tubers at lower photon flux density increases and that, consequently, sloughing of the vegetation is enhanced. Simulations indicate that the increased resource allocation to the tubers under low photon flux density can explain the observed biomass development and tuber bank size adequately at various light conditions in Lake Veluwe in The Netherlands. Only at the highest shading was the calculated production much lower than the actual production. Apparently, other

mechanisms, such as an increase in photosynthesis with increased tuber formation, are involved. An increase in the resource allocation to tuber production under low photon flux density led to a lower biomass of the vegetation during the growing season, but seems an appropriate strategy in terms of reproductive output and long-term survival of the population.

Key words: simulation model, submerged macrophytes, tubers, light climate, shallow lake, sago pondweed.

INTRODUCTION

Studies on life cycles and controlling factors are of particular importance in managing submerged aquatic vegetation, for example, by revealing parts of a life cycle vulnerable to management techniques, or critical in establishment and distribution of species. The life cycle of many submerged macrophytes is characterized by the annual production of generative and vegetative propagules to survive periods unsuitable for vegetative growth. The production of propagules requires allocation of resources. Resource allocation studies are well represented in terrestrial-plant ecological literature, while such studies for submerged macrophytes have received

¹ Dutch National Institute of Public Health and Environmental Protection (RIVM), Laboratory of Water and Drinking Water Research, P.O. Box 1, 3720 BA Bilthoven, The Netherlands.

little attention so far (Madsen 1991, Titus and Hoover 1991). In terrestrial plant ecology, it is generally accepted that reproduction, growth, and maintenance interact within the individual and compete for limited resources (Bazzaz *et al.* 1987). Recent studies (Spencer and Anderson 1987, Van Dijk and Van Vierssen 1991) indicate that also in the aquatic submerged macrophyte *Potamogeton pectinatus* L., a trade-off between growth, maintenance, and reproduction occurs. The latter study revealed that at low photon flux density, the number of tubers per gram aboveground and below ground biomass produced was higher. The reproductive output at the end of the growing season was, however, lower. It was hypothesized that increased production of tubers at low photon flux density would lead to a higher demand on the carbon sink, resulting in exhaustion of resources early in the growing season.

This paper presents a simple simulation model, 'FLORA,' to simulate and test the hypothesis that increased tuber production per gram below ground biomass at lower photon flux density increases the resource allocation to the tubers and, consequently, enhances sloughing of the vegetation. Simple models are considered very useful to improving insight into the processes that may play a role under actual field conditions (Best 1991, Scheffer *et al.* 1992). The present study aims at improving the theoretical framework for understanding biomass development, reproduction and pop-

ulation dynamics of *P. pectinatus* under various light conditions through simple mathematical modeling.

EXPERIMENTAL OBSERVATIONS

In a shallow eutrophic lake (Lake Veluwe, The Netherlands, latitude 52°20'N) a long-term shading experiment was conducted (1986-1988) in an existing, homogeneous *P. pectinatus* vegetation. Stands were subjected to three different levels of shading; nets were extended above the water surface, reducing the photon flux density just above the water surface by 23, 45 and 73%, respectively. In this way four different light climate conditions in the vegetation were created: (1) a control (without shading) and (2 to 4) three shading levels (23, 45 and 73% reduction in photon flux density). More detailed information on this experiment is given by Van Dijk and Van Vierssen (1991) and Van Dijk *et al.* (1992).

The present paper uses data on biomass and tuber bank development of *P. pectinatus* in the control for the 1986 growing season to calibrate the FLORA model (Table 1). It can be seen from Table 1 that in Lake Veluwe, *P. pectinatus* is characterized as a perennial herbaceous plant according to the definitions of Madsen (1991). It overwinters through vegetative propagules (tubers) and in spring vegetation is re-established by germination of tubers. The production of new tubers starts in June. At the end of the growing season,

TABLE 1. SUMMARY OF THE SEASONAL VARIATION IN TOTAL BIOMASS (aboveground and root/rhizome complex), ROOT:SHOOT RATIO, NUMBER OF NEWLY PRODUCED TUBERS, BIOMASS OF NEWLY PRODUCED TUBERS, AND THE NUMBER OF NEWLY PRODUCED TUBERS PER AMOUNT OF BIOMASS ROOT/RHIZOME COMPLEX IN THE CONTROL SITUATION DURING THE 1986 PERIOD.

Date	Total biomass (g AFDW m ⁻²)		Root:shoot ratio	Tubers ¹ (n m ⁻²)		Tuber biomass ¹ (g AFDW m ⁻²)		No. tubers ¹ per g AFDW root (n g ⁻¹ AFDW)	
	mean	sd	mean	mean	sd	mean	sd	mean	sd
13 May	1	1	0.36	— ³	—	—	—	—	—
26 May	9	2	0.28	—	—	—	—	—	—
9 Jun	12	1	0.36	—	—	—	—	—	—
23 Jun	27	3	0.21	18	28	0.6	0.6	3	6
7 Jul	27	11	0.18	70	45	1.6	1.5	16	8
21 Jul	46	4	0.14	85	65	2.7	1.9	15	11
4 Aug	57	9	0.09	73	6	2.3	1.2	17	2
18 Aug	59	15	0.06	155	39	5.9	1.3	44	1
12 Sep	0	0	x ²	180	65	6.9	2.9	x	x
2 Oct	0	0	x	167	56	5.0	0.8	x	x
3 Nov	0	0	x	241	98	7.9	4.0	x	x

Note: Values are calculated as grand means of three replicate experimental areas. The mean per experimental area is estimated as the mean of four to five subsamples.

¹From 23 Jun onward, the density of newly produced tubers is estimated by subtracting the number of hibernated and tubers not germinated as measured on 9 Jun from the total number of tubers measured per experimental area.

²Biomass was too low to calculate a reliable mean.

³Number of newly produced tubers was zero by definition.

the aboveground biomass and the root/rhizome complex slough away completely (Van Wijk 1988, Van Dijk and Van Vierssen 1991, Van Dijk *et al.* 1992).

MODEL

The FLORA model has been developed to simulate the seasonal cycle of vegetation biomass and tuber bank. The model consisting of three state variables was kept as simple as possible: the total vegetation biomass $DVeg$ [g AFDW m^{-2}], the biomass of the tuber bank $DProp$ [g AFDW m^{-2}], and the size of the tuber bank $NrProp$ [$n m^{-2}$] (Figure 1). The vegetation biomass includes both aboveground plant parts and the root/rhizome complex. For simplicity, the root:shoot ratio is fixed (default: 0.176). Tuber bank size and biomass were modeled separately to allow for dynamics in mean individual tuber size. The vegetation growth was modeled roughly according to the model MEGAPLANT (Scheffer *et al.* 1992), whereas aspects of the tuber development were derived from the complex model SAGA1 (Hootsmans 1991) and incorporated in FLORA in a simplified manner.

The vegetation is re-established by germination of tubers and subsequent initial growth as soon as the water temperature rises above a certain limit (10C) in spring. A certain fraction (20%) of the hibernated tubers remains dormant (Van Dijk *et al.* 1992). Further growth of the vegetation is made possible by photosynthesis. Daily irradiance and temperature follow a sine function over the year, according to average measurements in The Netherlands. The fraction of photosynthetically active irradiance (PAR) of the total global irradiance is set at 0.48; 10% of the light is reflected at the water surface (Kirk 1983). Light attenuation in the water column is modeled according to Beer's law. The extinction coefficient is the sum of the contribution of water with dissolved and particulate substances, and of the vegetation itself. The extinction coefficient of the water is fixed at $2 m^{-1}$ (Van Dijk and Achterberg 1992), the self-shading coefficient of the vegetation at $0.02 m^2 g^{-1}$ AFDW (Van der Bijl *et al.* 1989). For simplicity, the vegetation is assumed to be homogeneously distributed over depth.

Total daily production is modeled according to a Monod-type production *versus* irradiance function (a so-called P/I function), integrated over both time and depth of water. Both the maximum asymptotic value of P, P_{max} ($7.5 mg O_2 g^{-1}$ AFDW h^{-1} at 20C) and the half-saturation constant, k_m ($100 \mu E m^{-2} s^{-1}$) are dependent on temperature according to a Gaussian equation, approximating a Q_{10} of 2.0 in the observed temperature range. Maintenance respiration is modeled as a first-order process at a rate of $1.75 mg O_2 g^{-1}$ AFDW h^{-1} . Respiration in light is not modeled separately because it is already included in the production data. It is

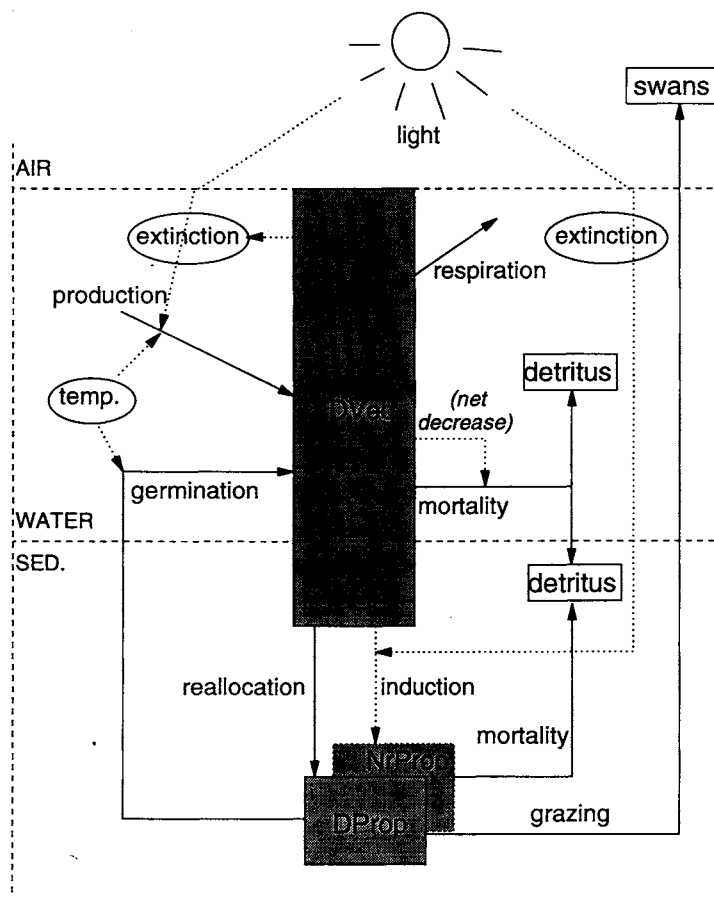


Figure 1. Conceptual diagram of the FLORA model, with the main processes determining the life cycle and resource allocation of *P. pectinatus*. State variables are: vegetation biomass (including the aboveground plant parts and the root/rhizome complex, $Dveg$), tuber bank biomass ($DProp$) and size of the tuber bank ($NrProp$).

assumed that production is not limited by nutrients. The mortality rate of the vegetation is assumed to be very low during the growing season ($0.001 d^{-1}$).

Tuber induction starts when the daily photoperiod exceeds 16 hr, a value reached in early June. The number of tubers induced per gram root/rhizome complex is defined as being dependent on the light conditions, the so-called relative photosynthetic period. This parameter has been defined as the fraction of the photoperiod during which at least $200 \mu E m^{-2} s^{-1}$ reaches the top of the vegetation (Hootsmans 1991). In the model the number of tubers per amount of roots and rhizomes is negatively linear related to the relative photoperiod: the lower the relative photoperiod, the more tubers are induced per gram root/rhizome complex (increasing from 18 under control conditions with a relative photosynthetic period of 0.8 or higher to, for example, 78 when the relative photosynthetic period drops to 0.5; unpublished data).

Re-allocation of biomass from the vegetation to the induced propagules is modeled as a first-order propagule

growth (with a maximum rate of 0.05 d^{-1}) with a fixed efficiency, until all tubers have reached the pre-defined maximum biomass per tuber (0.03 g AFDW). The re-allocation is also made dependent on the vegetation biomass available.

The decline of the vegetation at the end of the growing season is modeled as a sharp increase in the mortality rate as soon as the production is no longer sufficient to sustain both maintenance respiration and re-allocation to the tubers.

In the model's definition, tubers can get lost due to natural mortality (taken as 0.001 d^{-1}) or as a result of grazing by Bewick's swans (*Cygnus bewickii*) in winter (set at 15 October to 15 March). This is estimated as 250 g AFDW per animal per day assuming a swan density of 0.4 ha^{-1} vegetated lake (Hootsmans and Vermaat 1991b).

Simulations have investigated the hypothesis that the increase in the amount of tubers formed per unit plant biomass with lower photosynthetic period affects the biomass development and reproductive output. The model is calibrated on the basis of control conditions and is applied according to data

of the *P. pectinatus* biomass development at the three shading levels (2 to 4).

RESULTS AND DISCUSSION

After calibration, the calculated biomass development of the vegetation and the tuber bank size agreed well with actual data in the control situation (Figure 2) ignoring that the simulated vegetation biomass started to slough later in the season and thus reached a higher maximum value than the actual vegetation. In such large water bodies as Lake Veluwe, sloughing of the vegetation at the end of the growing season is largely enhanced by autumn storms (Van Wijk 1988). To ensure no masking of any possible resource allocation effects at the end of the growing season, a tentative storm factor was not included in the model. The results of the simulations of the vegetation biomass at the shading levels 2 and 3 (25 and 50%) fitted the actual data adequately, whereas at level 4 the simulation underestimated the actual data considerably during

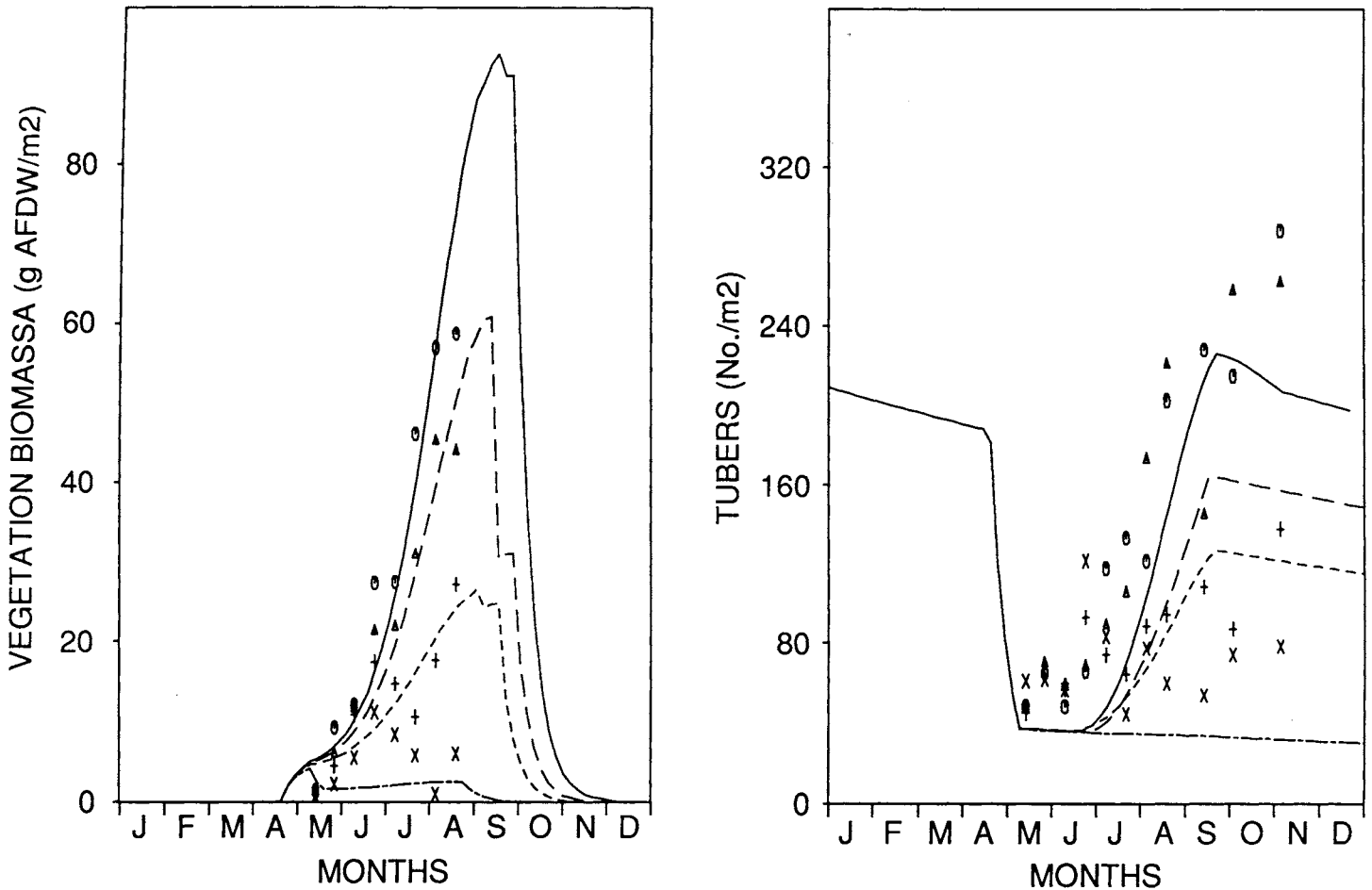


Figure 2. Results of the simulations (lines) of the vegetation biomass (left) and size of the tuber bank (right) with the FLORA model, as well as actual data of the 1986 growing season (symbols) for the control situation on the basis of which the model is calibrated (—, 0), and the three shading levels (level 2: ---, Δ; level 3: ···, +; level 4: — · —, x).

almost the entire growing season. The simulation derived that with increasing shading the maximum biomass was reached earlier in the season. This agrees with the field observations and supports the idea that with increasing allocation of resources to the tubers, sloughing of the vegetation is enhanced.

The calculated tuber density at the lowest photon flux density, level 4, was much lower than the observed density (Figure 2). Obviously, the model is not able to simulate the biomass development at low photon flux densities. The calculated production at level 4 was too low to represent the actual production adequately, as both the calculated vegetation biomass and tuber density were lower than the actual data. Apparently, other mechanisms, which are not modeled are involved at these light conditions. The observed difference in calculated and real production at level 4 may result from the assumption that the biomass was equally distributed over depth. It is well accepted that *P. pectinatus* may allocate most of its biomass just below the water surface (Van Wijk 1988). However, even when most of the biomass was allocated just below the water surface, the main shading factor (the nets) remained. So far studies have not shown a response of *P. pectinatus* to low light photon flux densities by acclimation of its photosynthetic tissue (Van der Bijl *et al.* 1989, Hootsmans and Vermaat 1991a). However, in these studies no clear distinction was made between tuber-producing and non-tuber-producing plants under various light conditions. The discrepancy between the calculated and real production at level 4 may be explained by an increase in photosynthesis with tuber formation which has not been modeled. In terrestrial plant ecology, increase of photosynthesis during the production of reproductive propagules is a common phenomenon (*e.g.* Ng and Loomis 1984). The effect of reproduction on leaf photosynthesis can probably be attributed to an increase in reproductive sinks (Reekie and Bazzaz 1987). Evidence exists that an increase in photosynthesis with tuber formation occurs in *P. pectinatus* as well (Hootsmans and Vermaat 1991a).

The FLORA model enables us to simulate well the biomass development of *P. pectinatus* under various light conditions, despite its simple structure and generalizations. The present analysis revealed that the hypothesis of an increased tuber production at lower photon flux density enhancing the sloughing of the vegetation seems valuable. It is likely that photosynthesis is positively correlated with tuber formation.

Considering its relatively simple structure the FLORA model is applicable to a variety of aquatic ecosystems although calibration is a prerequisite. In its present form it is calibrated for the typical Lake Veluwe conditions with *P. pectinatus* exhibiting a wide phenotypic plasticity. Under field conditions both an annual and a perennial life cycle have

been observed (Van Wijk 1988). Furthermore, allocation to reproduction varies greatly with extremes in environmental conditions ranging, for example, from 5 to 42% of the total biomass for *P. pectinatus*, depending on whether it is found in sheltered or partially exposed habitats (Kautsky 1987). Under typical environmental conditions, biomass allocation to propagation is quite consistent at about 30% of total biomass for annual and perennial submerged macrophytes (Madsen 1991, Table 3) and terrestrial plants (Fitter 1986). Compared to these observations, relatively little biomass was allocated to the tubers in Lake Veluwe. Including the non-germinated hibernated tubers, however, results in a tuber contribution of 24% (Van Dijk and Van Vierssen 1991). Van Wijk *et al.* (1988) found enhanced tuber production under reduced light conditions in a greenhouse culturing experiment (long-day conditions of 16 hr) with tubers originating from Lake Veluwe. Tuber mass (AFDW) was 26% of total biomass while this was only 7% in the control culture in Lake Veluwe tubers. As it is not always clear whether the non-germinated hibernated tubers are included in the tuber biomass, data such as given by Madsen (1991) should be interpreted with caution.

The number of tubers produced per gram AFDW root/rhizome complex may be highly variable under different conditions. Spencer and Anderson (1987) found a maximum of about 550 tubers per gram AFDW root/rhizome complex (assuming an AFDW:DW ratio of 0.60 as in Van Wijk (1988)) for plants grown under a 10-hr photoperiod. This is about seven times higher than the highest value observed in Lake Veluwe. Such short-day conditions occurred, however, in Lake Veluwe only at the very end of the growing season when most of the vegetation had already died off.

The question on what the ecological implications of an increased resource allocation at lower photon flux densities are in terms of long-term survival of the population may arise. Running the simulation for several years (Figure 3, left) revealed that in the control situation, the vegetation biomass development was stable, with a maximum biomass of about 90 g AFDW m⁻². At shading levels 2 and 3 the average biomass steadily decreased with the years until very low values at level 3 after five years. The highest shading was not included as the model simulations were not reliable at that level. A lower vegetation biomass thus entails the risk of too low a tuber production and, finally, extinction of the population. This extinction may be enhanced or retarded by relatively bad or good meteorological conditions, respectively. The simulation showed that although the vegetation was able to photosynthesize at shading level 3, too few tubers were formed to sustain survival in the long term. This conclusion agrees with field observations (Van Dijk *et al.* 1992).

Increased resource allocation to reproductive propagules with lower photon flux density has a negative impact on the

maximum vegetation biomass on a short term, but it seems an adequate strategy in terms of survival on a long term (Figure 3, right). Without an increased resource allocation the vegetation will become extinct more rapidly.

Many studies have been focusing on the photosynthetic production, the reproductive output of submerged macrophytes and the effects of various conditions on that. The results of the present study strongly indicate that also total resource allocation to reproduction, with its effect on vegetative growth, is a prerequisite to consider in explaining the population dynamics of submerged macrophytes under various environmental conditions.

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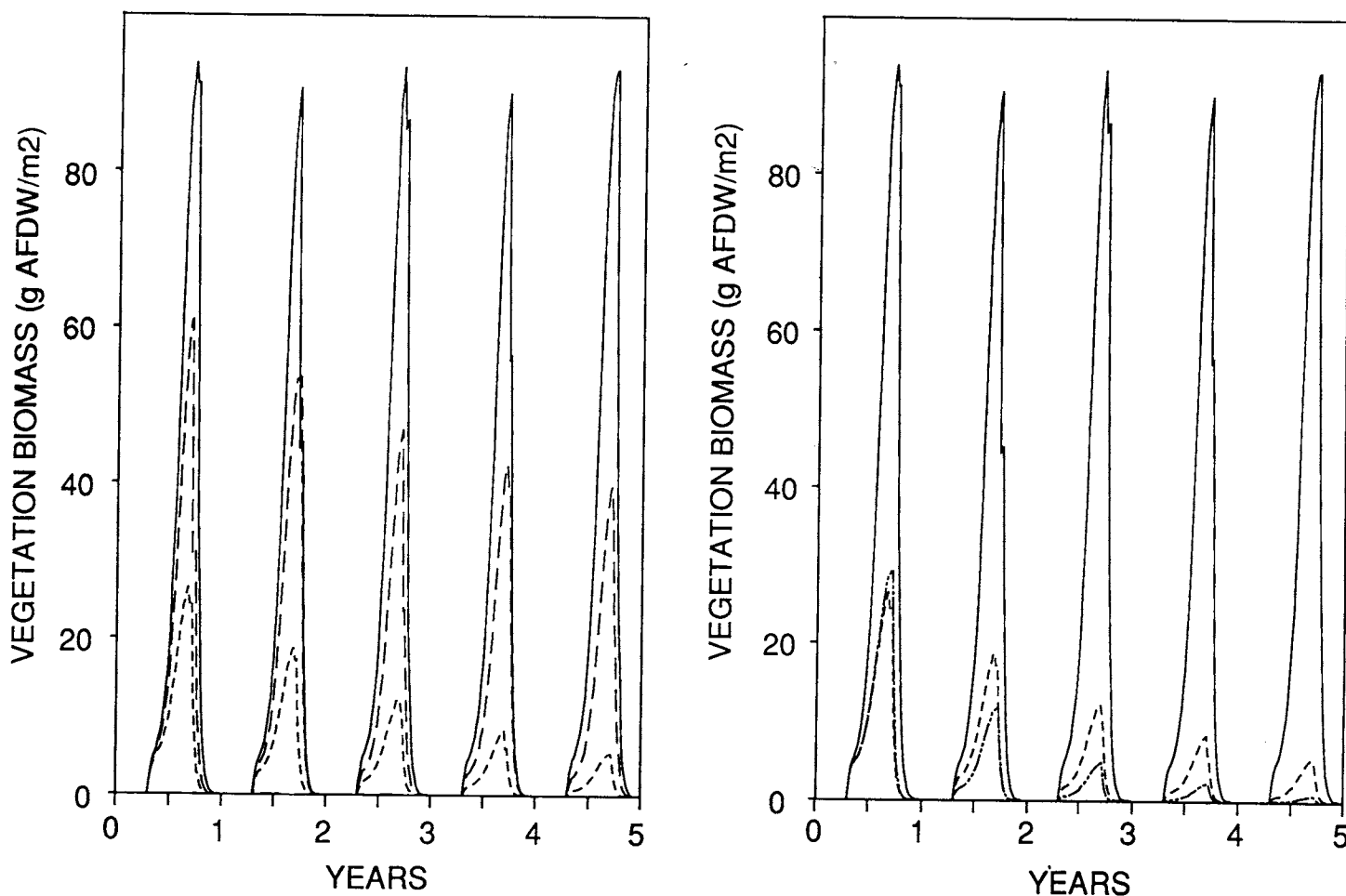


Figure 3. At the left are the results of a 5-yr simulation of the biomass of the vegetation in Lake Veluwe in the control situation: —, shading level 2; — —, and shading level 3: ····. At the right are the results of a 5-year simulation of the biomass of the vegetation in Lake Veluwe in the control situation: —, shading level 3, with an increased tuber production factor due to lower photon flux density: — ···, and shading level 3, without an increased tuber production factor: ····.

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