



ELSEVIER

Ecological Modelling 119 (1999) 167–176

ECOLOGICAL
MODELLING

Energy partitioning in terrestrial orchids—a model for assessing their performance

Pavel Kindlmann *, Zuzana Balounová

Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

Received 16 October 1997; accepted 28 January 1999

Abstract

A model of the within-season growth of terrestrial orchids is presented. The model predicts the size of the tubers of *Dactylorhiza majalis* and *Dactylorhiza fuchsii*. Therefore, destructive methods can be avoided when sampling these rare orchids. The correlation coefficient and the slope of the relation between two consecutive measurements of leaf area early in the season are good indicators of plant performance. The average tuber size is indicated by the correlation coefficient and the maximum photosynthetic activity of the plants by the maximum slope of this relation. Data are presented on the seasonal growth of leaves and inflorescence of *D. majalis*. This was obtained by monitoring the above ground growth of a large number of individual plants. The model predictions are compared with empirical data from the literature and new data. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Orchids; *Dactylorhiza majalis*; *Dactylorhiza fuchsii*; Seasonal energy allocation; Tuber size

1. Introduction

As the numbers of terrestrial orchids decline throughout the world, considerable concern has been expressed about their survival. Efforts are being made to halt this decline by managing areas where they still exist in a more sympathetic manner. To do this effectively, it is necessary to study

all aspects of their population ecology. This will include gathering data on their demography, as well as monitoring response of terrestrial orchids to changes in environment (Wells and Willems, 1991). However, tools are needed for measuring this response.

A good tool for this would be a simple model of the within-season energy partitioning between vegetative, reproductive and storage organs. Life history theory makes predictions about optimal energy allocation and some of the models might even be applicable to terrestrial orchids (Loehle, 1987; Pugliese, 1987; Pugliese and Kozłowski, 1990; Iwasa, 1991). Unfortunately, these models

* Corresponding author Tel.: +420-38-7775357; fax: +420-38-45985.

E-mail address: pavel@entu.cas.cz (P. Kindlmann)

mainly concentrate on theoretical predictions like the equilibrium size of the storage organ and its critical size, below which it is optimal to grow but not reproduce, etc. Predictions of the within-season patterns of energy allocation between individual parts of plants are not available and therefore a simple predictive model is needed.

Some data are available on energy allocation strategies in terrestrial orchids (Primack and Hall, 1990; Whigham, 1990; Zimmerman, 1990; Zimmerman and Whigham, 1992) and in other perennial plants (Rees, 1972; Ruiters and McKenzie, 1994, etc.). However, complete seasonal budgets of energy allocation in terrestrial orchids are rare, and have been compiled by the destructive sampling of plants (Whigham, 1984; Dixon, 1991; Leeson et al., 1991). Therefore, the budget is based on measurement made on different individuals rather than the same individual throughout a season. This method of sampling greatly limits the number of specimen measured, especially when the plants are rare.

In this paper, we present data on the seasonal growth of leaves and inflorescence of *Dactylorhiza majalis* using a non destructive sampling method, which enabled us to measure a large number of specimens and follow each of them throughout a whole season. We then present a model of within-season growth and compare its predictions with our own empirical data and that in the literature. This model predicts the size of below-ground parts and therefore, in combination with non destructive sampling might be substituted for the currently widely used destructive sampling. We verified these predictions on a limited data set that

was available on the relation between the leaf area and the below-ground parts of *D. majalis* and closely related *D. fuchsii*.

2. Material and methods

Details of the five sites, wet meadows situated in South Bohemia, are given in Table 1. No fertilisers have been applied to the sites during the period of observation. Maximum width and length of each leaf, height of the flower stalk and of the inflorescence of 30–100 plants of *D. majalis* were measured at approximately weekly intervals during the whole vegetative season in 1992 and/or 1994.

The total leaf area was estimated by summing q (width \times length) for all leaves of the plant. Within a species, the leaves are geometrically similar and therefore q is a constant and was in this case set equal to 0.5. Although this may not be the true value of q , it did not affect the subsequent analyses, in which the relative total leaf areas of plants are compared. For those plants that were not damaged (grazed, etc.) during the season, the total leaf area, x , as a function of time, t , was fitted by means of a logistic equation

$$dx/dt = rx(1 - x/K), \text{ with } x(0) = x_0 \quad (1)$$

to obtain the growth rate of leaves of plant i , r_i , and the asymptotic maximum leaf area of this plant, K_i . This was carried out in order to correct measuring errors and to estimate r_i . Time was used as the independent variable. The same function was used to fit the growth in the height of the

Table 1
Site details

Site name	Year	Code	Altitude	Characteristics	Dominant species	Mown
Milíkovice	1992	m92	500	Wet	<i>Serratula tinctoria</i>	Yes
	1994	m94				
Ohrazení	1994	o94	520	Less wet	<i>Betonica officinalis</i>	Yes
Vrb. Rybníky	1992	v92	400	Wet	<i>Sanguisorba officinalis</i>	No
Čakov	1994	c94	410	Partially shaded	<i>Alopecurus pratensis</i>	No
V Lísovech	1994	j94	650	Peat bog	<i>Menyanthes trifoliata</i>	No

Table 2

Correlations between the growth rate of the leaf area, r_i , maximum leaf area, K_i , maximum length of the flower stalk, S_i , and maximum length of the inflorescence, F_i , measured in different plants, i , within and between sites^a

	$\rho(r, K)$	$\rho(r, S)$	$\rho(r, F)$	$\rho(K, S)$	$\rho(K, F)$	$\rho(S, F)$	n_s	n_f
m92	−0.28	0.03	−0.19	0.46	0.34	0.55	29	40
v92	0.04	0.30	−0.42	0.95	0.72	0.66	13	4
c94	−0.99	−0.52	0.39	0.64	−0.34	0.22	38	4
j94	−0.08	−0.07	−0.02	0.61	0.66	0.66	37	52
m94	−0.74	−0.92	−0.29	0.72	−0.39	0.34	48	4
o94	−0.09	0.10	0.22	0.67	0.77	0.67	24	15
Between	−0.68	−0.78	−0.24	0.94	0.35	0.35	189	119

^a Numbers of individuals: n_s , sterile; n_f , flowering. Statistically significant values ($P < 0.05$) are lightly shaded and highly significant ones ($P < 0.01$) are heavily shaded.

flower stalk and in the length of inflorescence and to obtain their asymptotic maximum sizes for plant i , S_i and F_i , respectively. The goodness of fit was assessed by size of the “mean residuum”, calculated from the residual sum of squares, RSS as $\sqrt{\text{RSS}/n}$ where n is the number of measurements.

For verification of the model predictions of tuber size, only ten specimens of *D. majalis* and ten specimens of *D. fuchsii* were used in order to minimise the damage of the population, as this measurement is destructive. In these plants, the maximum leaf area, height of flower stalk and length of inflorescence were measured at the time of full bloom and subsequently their dry weights plus dry weights of the old and new tubers were determined. Using the relations between leaf areas and leaf weights and stalk lengths and stalk weights, the biomass of leaves and flower stalks were estimated from the biometric data.

For data fitting, the module SOLVER of EXCEL 5.0 was used.

3. Results and discussion

3.1. Empirical data

The logistic function yielded a remarkably good fit. The ‘mean residuum’ was only 5.05% of K_i on average. Therefore, there was no need to use day-degrees or other values instead of time in days as the independent variable. For leaves, the

last measurement was excluded from the regression, as the leaves began to die at their tips at the end of the season, whereas the inflorescence continued to grow for another 2 weeks.

The correlation matrix between r_i , K_i , S_i and F_i revealed highly significant positive correlations between the maximum total leaf area, K_i , maximum height of flower stalk, S_i , and maximum length of inflorescence, F_i , both between and within most sites, but not between r_i and other values (Table 2.).

The differences in plant performance due to mowing are shown in Fig. 1. On mown sites, the average total leaf area, K_i , was small, but the reproductive effort, measured as S_i/K_i , was large. Thus, mowing results in plants investing more in reproduction.

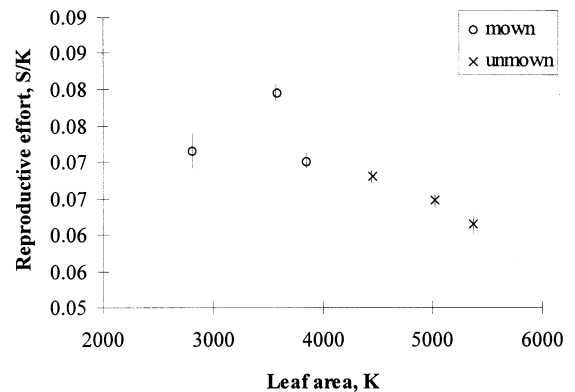


Fig. 1. Reproductive effort, measured as the ratio of maximum length of the flower stalk, S , to the maximum leaf area, K , against K . Bars indicate standard errors.

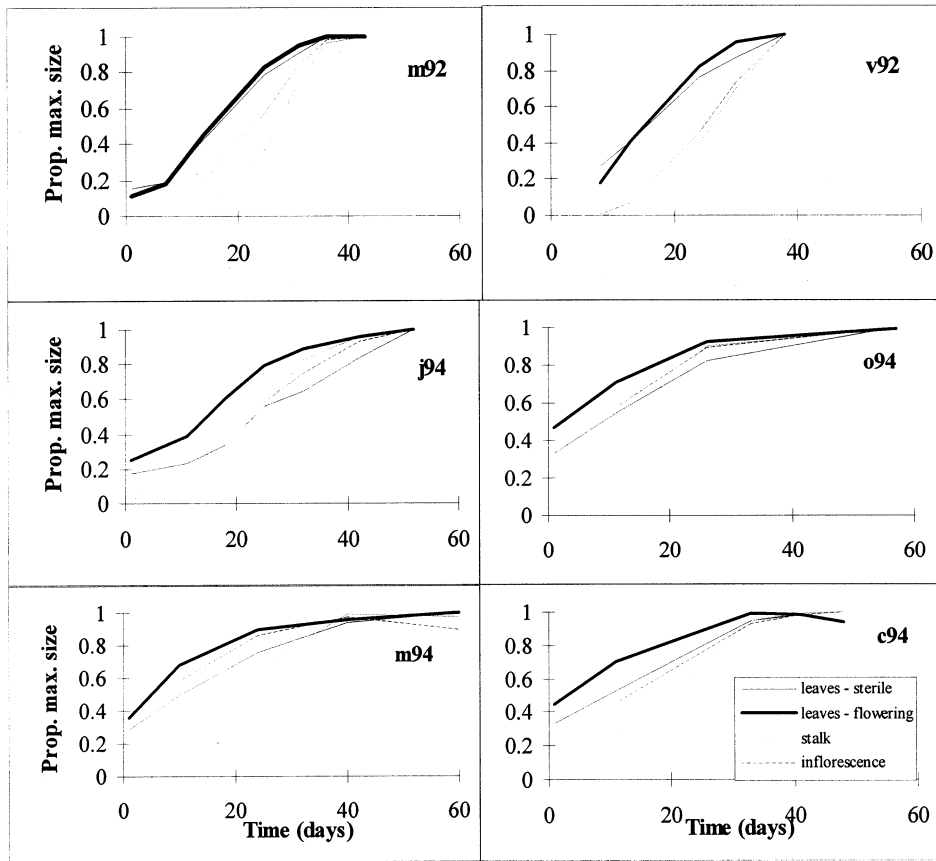


Fig. 2. Proportion of the maximum size reached by individual parts of the plants against time. Site codes (Table 1.) indicated in the first column, numbers of individuals are the same as in Table 2.

Fig. 2 shows the average proportion of maximum size reached by individual parts of the plants at particular instants of the season at each site. Flowering plants developed their leaves more quickly than sterile plants. The flower stalks and inflorescences started to develop after the leaves, and continued to grow even when the leaves had already started to wither. The latter observation is seen in the averages in c94 (Fig. 2), and individual plants at other sites (not shown). Fig. 2 also suggests that each of the plant parts increased in size sigmoidally.

A strong linear relationship was obtained when measurements of leaf areas of a set of plants one week were compared with those of the next week (Table 3). For each plant, we had two numbers: leaf area in one week and leaf area in the next.

We were interested in how these values were correlated: will a plant that was large one week also be large the following week? This question is not as trivial as it seems to be: early in the season, the increments in leaf areas are largely dependent on the size of the storage organ, and therefore the answer may be NO. Later in the season, the increments are mainly dependent on the leaf area itself, as the increment is due to assimilation, therefore one would expect the correlation coefficient to be large. This was confirmed by our data. During the course of the season, the correlation between leaf areas of plants one week and those the next week increased, even if the number of plants measured (the number of degrees of freedom) has never decreased, therefore, the correlation becomes more significant in the course of the

season. This means that late in the season, the largest plants in the cohort measured one week were the largest in the same cohort also the next week, which was not the case, however, early in the season. The correlation coefficients were almost consistently larger for sterile than for flowering plants at the same time and site. At mown sites, the correlation coefficients were smaller than at unmown sites, when measured at the same instant early in the season (Table 3, days 7–8 in 1992, days 10–11 in 1994). One exception, c94, may be due to an extremely small number of specimens.

The slopes of the above linear relationships

declined with time and approached 1 late in the season, consistently with the logistic growth. However, their initial values were large for the orchids growing in the mown wet meadows (m92, m94, o94) and in the peat-bog (j94) and small for those growing in the unmown wet meadows (v92, c94). There was a large variation and therefore no clear trend in the intercepts of these relationships.

3.2. The within-season growth model

Components (variables)—functions of time, t :

v Vegetative organs (leaves, roots)

Table 3

Correlation coefficients, ρ , slopes, q and intercepts, k for the linear relationships between total leaf area in two consecutive measurements, the first at time t , for sterile and flowering plants at different sites^a

Site	Time t	Sterile			Flowering		
		ρ	k	q	ρ	k	q
m92	1				0.34	408	0.63
	7	0.87	199	1.95	0.75	230	1.97
	14	0.93	-4	1.82	0.93	275	1.61
	25	0.99	66	1.11	0.96	-48	1.17
	31	0.99	82	1.04	0.98	8	1.06
v92	8	0.96	142	1.22	0.86	867	0.86
	13	0.94	-110	1.98	0.96	1049	1.28
	24	0.99	-135	1.28	0.96	693	0.91
	30	0.99	-19	1.14			
c94	1	0.48	879	0.75	0.94	262	1.40
	11	0.76	804	1.04	0.90	1200	0.98
	33	0.92	-169	1.09			
j94	1	0.98	-54	1.45	0.89	165	1.40
	11	0.96	-85	1.63	0.91	678	1.22
	18	0.90	389	1.39	0.95	586	1.13
	25	0.99	268	1.04	0.97	219	1.07
	32	0.97	773	0.97	0.99	282	1.02
	42	0.98	636	0.98	0.99	92	1.02
m94	1	0.88	189	1.61	0.83	-339	2.19
	10	0.95	222	1.35	0.97	-1962	2.13
	24	0.94	94	1.19	0.99	-20	1.07
	40	0.99	65	1.03	0.99	-101	1.08
o94	1	0.82	412	1.39	0.81	347	1.46
	11	0.92	176	1.39	0.95	-147	1.37
	26	0.98	-181	1.29	0.96	428	0.97

^a Mown sites are in boldface, year 1992 is shaded. Numbers of individuals are the same as in Table 2.

- g* Generative organs (inflorescence stalk, inflorescence and seeds)
- s* Old (parent) tuber-storage organ
- z* New (replacement) tuber-storage organ

Assumptions made about the energy flow between the components of the model:

A1. Energy supplied by tuber to vegetative organs is positively correlated with the size of both components. Here, the simplest (linear) relationships are assumed.

A2. Energy E gained by vegetative organs via assimilation is an allometric function of their size: $E = av^\alpha$, where $\alpha = 1$.

A3. Growth of both the reproductive (g) and new storage (z) organs is initially exponential.

The activity (both input and output of energy) of the vegetative organs sigmoidally declines in the course of the season. This is due to both their senescence and competition with other plants later in the season. Here e^{-t^d} is used, where d is a parameter determining the rate of senescence.

The above assumptions lead to a growth model of the form:

$$\begin{aligned} ds/dt &= -bsv & s(0) &= s_0, \\ dv/dt &= bsv & v(0) &= v_0, \\ & + e^{-t^d}(av^\alpha - R_g g - R_z z), \\ dg/dt &= e^{-t^d} R_g g, & g(0) &= g_0, \\ dz/dt &= e^{-t^d} R_z z, & z(0) &= z_0, \end{aligned}$$

where a , α , b , d , R_g and R_z are parameters. As for mathematical reasons, the initial values $g(0)$ and $z(0)$ are positive (g and/or z as a solution of Eq. (1) would be constant and equal to zero for any positive t otherwise), the model as stated does not apply prior to the initiation of generative and replacement storage organs.

3.3. Discussion of model assumptions

Roots are not an independent component, as: (1) they are likely to reflect the size of the leaves; and (2) their total biomass is relatively small (Dixon, 1991). The sub-components of the reproductive organs are not treated separately,

as (1) they all serve reproduction; and (2) their sizes are closely correlated even during the season (Fig. 2). It is unlikely that the number of components in the model will have to be increased, unless very specific questions are posed, e.g. if the effect of pollinators were studied and if the pollination success were low, then the energy otherwise devoted to seed production would probably be stored instead.

It is assumed that a large tuber can supply leaves more energy per unit time and that the flow of energy from the tuber to the leaves is restricted by the size of the leaves—small leaves are not able to use as much energy as large leaves (A1). It is not clear whether these relationships are linear, but our results indicate linearity.

Allometric dependence of energy production on the size of vegetative organs of the form assumed in (A2) is a common assumption in most energy partitioning models. Here, $\alpha = 1$ was used, as leaves are flat and therefore assimilation is assumed to depend linearly on leaf area. However, our unpublished simulations indicate that the model output is not sensitive to changes of α .

Energy partitioning models predict a ‘bang-bang’ strategy, which is first to invest everything into growth and at an appropriate instant to suddenly switch to pure reproduction without further investments into vegetative organs, if the growth rate of g and/or z is not constrained (or if the constraint does not have to be taken into account, as there is not enough energy produced by the vegetative organs to support the growth of reproductive or storage organs at this maximum rate anyway). If the constraint on their growth rate, here denoted by R_g and R_z , has to be taken into account, the prediction is (Kozłowski and Ziolkó, 1988; Kindlmann and Dixon, 1989) a simultaneous growth with g and/or z growing at a maximum speed (i.e. exponentially with the growth rate equal to the constraint). Therefore, it is reasonable to assume exponential growth of reproductive (g) and new storage (z) organs (A3), if the growth of vegetative (v) and g and/or z is simultaneous. For

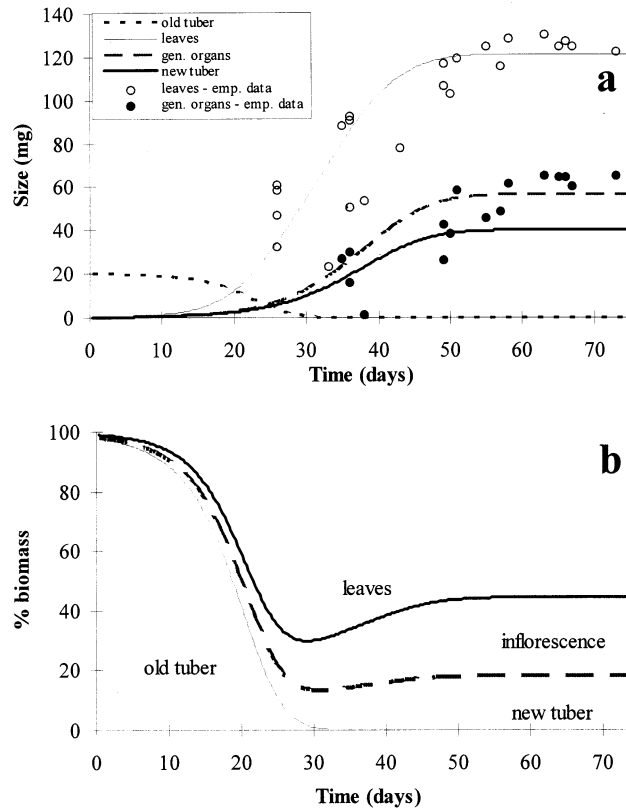


Fig. 3. Model (1) fitted to data from the site m92 (lines) and validated using data from the remaining sites. Parameters fitted: $a = 4.01$, $b = 0.205$, $R_z = 3.604$, $R_g = 3.834$, $d = 5.045$, $s_0 = 20$.

those species, where flowering and vegetative growth do not occur simultaneously, the model would have to be modified.

The parameters may depend on environmental conditions like temperature, shading or competition with neighbouring plants. This is particularly relevant for those modelling assimilation (a), or distribution of products of assimilation (R_g and R_z). Thus, one can expect a range of a values in a population, varying from plant to plant. It is impossible to guess a priori, whether either R_g or R_z is dependent on a . Therefore, in the subsequent section, this question is addressed by comparing the model's outputs with empirical data.

Sigmoidal decline in photosynthetic activity and in the output of energy from the vegetative organs in the course of a season is quite general, and the shape of this dependence (driven by the parameter d) may be species-specific.

3.4. Comparison of model's predictions with empirical data

The model was run for a broad range of parameter values: α equal to 1, 0.75 and 0.67, a from 1 to 2.5, b from 0.2 to 0.6, s_0 from 4 to 20. The aim was to find the typical trends in behaviour.

The typical prediction for constant parameters is shown in Fig. 3. Here, the model was fitted to the data from the site m92. The parameters so obtained, along with their standard errors, were: $a = 4.01 \pm 0.01$, $b = 0.205 \pm 0.001$, $R_z = 3.60 \pm 0.01$, $R_g = 3.83 \pm 0.02$, $d = 5.04 \pm 0.03$, $s_0 = 19.85 \pm 0.04$. Subsequently, the model was validated using data from the other sites. Thus the lines in this figure represent model predictions based on the data from m92, while points are data on leaf and flower stalk weights from the other

sites. Bearing in mind the geographic distances of the sites and the fact that the data were measured in different years, the model fit is very good. The size of the old tuber sigmoidally declines with the decline in the later stages close to exponential. The leaf area sigmoidally increases, followed after a delay by a sigmoidal increase in the size of the inflorescence and of the new tuber (see also Fig. 2 for comparison with our empirical data). The inflorescence and tuber continue to increase in size and approach an asymptote even after the leaves have started to wither. This pattern is supported not only by the data presented here, but closely imitates that observed in other studies on energy partitioning in various orchid species (Whigham, 1984; Dixon, 1991; Leeson et al., 1991).

Fig. 4. shows the model's predictions of the this-to-next measurement in leaf area, when a is constant and s_0 varies. The dependence is consistently approximately linear, surprisingly even if α is different from 1, i.e. if assimilation is non-linearly dependent on leaf area. When the model is run for different values of initial tuber size, the correlation between this and next leaf area is weak early in the season. This is because the increment in leaf area initially depends more on what is supplied from the tuber than on the leaf area itself. Our data (Table 3) show a conspicuous increase in correlation coefficients in the course of the season, which confirms this prediction.

Low correlation coefficients early in the season imply a low influence of the tuber at this time, i.e.

it is small. This is also indirectly supported by our data in Table 3, as one would expect sterile plants to have small tuber, as they are likely to be juvenile, and small average tuber size in unmown sites, where the conditions are less favourable than at mown sites. Thus, the correlation coefficient between two consecutive measurements of leaf areas of a set of plants might be a good indirect estimator of the average tuber sizes, when different sites are being compared.

The slope of the dependence declines as the season proceeds, because of the decline in the assimilation rate, a , both in Fig. 4 (theoretical prediction) and in Table 3 (empirical data). The maximum slope, by definition, correlates with the maximum value of a in the model. The empirical data (Table 3) indicate that the slope is small in unmown meadows, which can be explained by lower photosynthetic activity (lower a) due to the presence of last year's dry biomass. At site c94, there is an additional component: shading by surrounding trees (Table 1).

3.5. Predictions of new tuber size

Parameters obtained in Section 3.4 were subsequently used to predict sizes of new tubers. As explained in Section 2, for direct testing of the model predictions about tuber sizes only data about final sizes of the new tubers and leaf areas for the two sets of ten individuals of experimental plants of *D. majalis* and of ten individuals of *D. fuchsii* were available. It was assumed that the differences between plants were mainly due to microhabitat differences in climate, which affect above all the assimilation and energy translocation parameters a , b , R_z and R_g . Therefore, these parameters were varied, each at the same rate, i.e. each of them was multiplied by a number k , which was chosen from the interval 0–1.2 with step 0.05 (its larger values gave predictions outside the observed range of leaf areas and tuber sizes). The line in Fig. 5 is the model prediction for different values of k taken from this interval, points are empirical data from the experimental plants of *D. majalis* and of *D. fuchsii*. Surprisingly, even the data on the closely related *D. fuchsii* also closely fit the prediction. This result may serve as

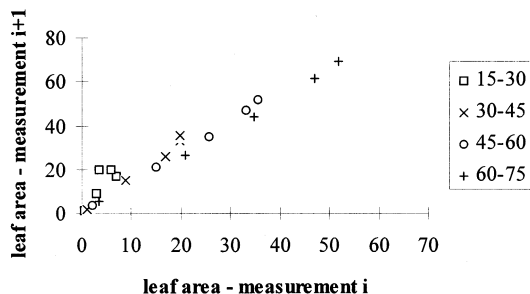


Fig. 4. Relation between two consecutive measurements of leaf area, as predicted by model (1). Parameters as in Fig. 1, but s_0 varies from 8 to 16. Dates of measurements indicated in the inset.

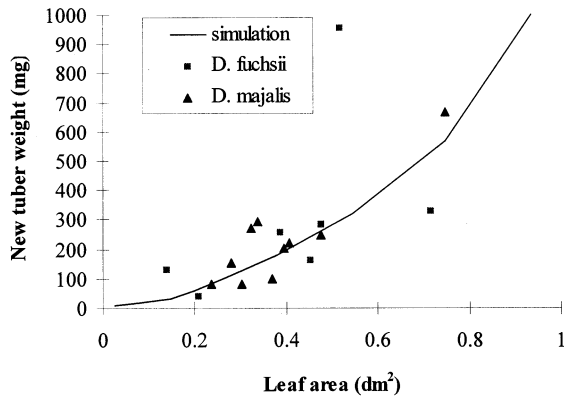


Fig. 5. Relation between leaf area and new tuber weight at the time of full bloom, as predicted by the simulation model (1) line, compared with empirical data on *D. majalis* (triangles) and *D. fuchsii* (squares).

an independent verification of the model and indicate its applicability to other closely related species. One outlier in *D. fuchsii* was a damaged plant.

4. Conclusions

The results presented here confirm that the model could be used in combination with non-destructive measurements of leaf area and inflorescence to estimate the size of the old and new tubers, and the photosynthetic activity of the plants. The tuber size can be measured only by using destructive methods.

The correlation coefficient and the slope of the relation between two consecutive measurements of leaf area early in the season are also good candidates as estimators of the average tuber size and of the maximum size of the plants, when different sites are being compared. Before their general acceptance, however, these relationships need to be tested using empirical data that include measurements of tuber size and of photosynthetic activity.

Acknowledgements

This research was supported by grant No. 206/

95/1549 of the GA CR. The authors are indebted to A.F.G. Dixon, J. Květ, A.R. Watkinson, J. Willems for reading and commenting on the manuscript.

References

- Dixon, K., 1991. Seeder/clonal concepts in Western Australian orchids. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids, SPB Acad. Publ. bv, The Hague, The Netherlands, pp. 111–123.
- Iwasa, Y., 1991. Pessimistic plant: optimal growth schedule in stochastic environments. *Theor. Pop. Biol.* 40, 246–268.
- Kindlmann, P., Dixon, A.F.G., 1989. Developmental constraints in the evolution of reproductive strategies: telescoping of generations in parthenogenetic aphids. *Funct. Ecol.* 3, 531–537.
- Kozłowski, J., Ziolkó, M., 1988. Gradual transition from vegetative to reproductive growth is optimal when the maximum rate of reproductive growth is limited. *Theor. Pop. Biol.* 34, 118–129.
- Leeson, E., Haynes, C., Wells, T.C.E., 1991. Studies of the phenology and dry matter allocation of *Dactylorhiza fuchsii*. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids, SPB Acad. Publ. bv, The Hague, The Netherlands, pp. 125–138.
- Loehle, C., 1987. Partitioning of reproductive effort in clonal plants: a benefit-cost model. *Oikos* 49, 199–208.
- Primack, R.B., Hall, P., 1990. Costs of reproduction in the pink lady slipper orchid, a 4-year experimental study. *Am. Nat.* 136, 638–656.
- Pugliese, A., 1987. Optimal resource allocation and optimal size in perennial herbs. *J. Theor. Biol.* 126, 33–49.
- Pugliese, A., Kozłowski, J., 1990. Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts. *Evol. Ecol.* 4, 75–89.
- Rees, A.R., 1972. *The Growth of Bulbs*. Academic Press, London.
- Ruiters, C., McKenzie, B., 1994. Seasonal allocation and efficiency patterns of biomass and resources in the perennial geophyte *Sparaxis grandiflora* subspecies *fimbriata* (Iridaceae) in lowland coastal fynbos, South Africa. *Ann. Bot.* 74, 633–646.
- Wells T.C.E., Willems J.H., 1991. Preface. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids, SPB Acad. Publ. bv, The Hague, The Netherlands, pp. 7–8.
- Whigham, D.F., 1984. Biomass and nutrient allocation of *Tipularia discolor* (Orchidaceae). *Oikos* 42, 303–313.
- Whigham, D.F., 1990. The effect of experimental defoliation on the growth and reproduction of a woodland orchid, *Tipularia discolor*. *Can. J. Bot.* 68, 1812–1816.

Zimmerman, J.K., 1990. Role of pseudotubers in growth and flowering of *Catasetum viridiflavum* (Orchidaceae). *Am. J. Bot.* 77, 533–542.

Zimmerman, J.K., Whigham, D.F., 1992. Ecological functions of carbohydrates stored in corms of *Tipularia discolor* (Orchidaceae). *Funct. Ecol.* 6, 575–581.