Europ.J.Hort.Sci., **70** (1). S. 7–15, 2005, ISSN 1611-4426. © Verlag Eugen Ulmer GmbH & Co. Stuttgart

Relationship between Tuber and Leaf Growth in Radish (*Raphanus sativus* L. var. *sativus*), Analysed as Result of an Optimal Process

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Summary

The relationship between the growth of the shoot and a storage organ was studied in radish (*Raphanus sativus* L. var. *sativus*). To quantify the relationship the ratio **r** of the relative growth rates of the tuber dry mass and the leaf area was used. On the basis of growth data, measured on twenty-four crops in the field and growth chamber, a system analysis was carried out to test whether the determined values of this ratio can be explained as result of an optimal process. The following hypothesis was examined: The adjustment of tuber and leaf growth occurs in such a way, that the harvest stage, defined here by a certain tuber dry mass, is attained in shortest length of time. For theoretically deriving the ratio a simple growth model and optimisation procedures were used. Inputs were the measured values of net assimilation rate and specific leaf mass. In the case of describing the growth with a mean value of ratio **r** during the growth interval from seedling stage to harvest, the calculated values were in good accordance with the measured. But, if the ratio was allowed to vary over time only the general response could be confirmed by the calculation: at first predominant leaf growth and then transition to predominant tuber growth. In order to achieve a sufficient quantitative accordance additionally several constraints (e.g. a upper limit of the relative growth rate of the tuber) were necessary. Conclusions for further investigations were drawn from the results.

Zusammenfassung

Beziehung zwischen Knollen- und Blattwachstum bei Radies (*Raphanus sativus* L. var. *sativus*), analysiert als Ergebnis eines optimalen Prozesses. Die Beziehung zwischen dem Wachstum von Spross und einem Speicherorgan wurde am Beispiel von Radies (*Raphanus sativus* L. var. *sativus*) untersucht. Als quantitative Größe für die Darstellung der Beziehung wurde der Quotient **r** aus den relativen Wachstumsraten der Knollentrockenmasse und der Blattfläche verwendet. Auf der Grundlage von Wachstumsdaten, gemessen an vierundzwanzig Kulturen im Freiland und in der Klimakammer, wurde eine Systemanalyse durchgeführt, um zu prüfen, ob die ermittelten Werte dieses Quotienten als Ergebnis eines optimalen Prozesses angesehen werden können. Geprüft wurde die Hypothese: Zwischen Knollen- und Blattwachstum stellt sich eine solche Balance ein, dass das Erntestadium, definiert durch eine bestimmte Knollentrockenmasse, in kürzester Zeit erreicht wird. Für die theoretische Bestimmung des Quotienten wurde ein einfaches Wachstumsmodell zugrunde gelegt, dessen Input die beobachteten Werte der Nettoassimilationsrate und der spezifischen Blattmasse waren. Im Falle, dass das Wachstum im Zeitintervall vom Ende des Keimblattstadiums bis zur Ernte mit einem Mittelwert des Quotienten **r** beschrieben wird, ergab sich eine gute Übereinstimmung der berechneten mit den gemessenen Werten. Im Falle zeitabhängiger Werte jedoch konnte lediglich das prinzipielle Verhalten bestätigt werden: zu Beginn vorherrschendes Blattwachstum, danach Übergang zu überwiegendem Knollenwachstum. Um eine ausreichende quantitative Übereinstimmung auch hier zu erzielen, waren zusätzlich mehrere Nebenbedingungen (z.B. eine obere Grenze der relativen Wachstumsrate der Knolle) notwendig. Aus den Ergebnissen wurden Vorschläge für die Weiterführung der Arbeiten abgeleitet.

Key words. allocation – allometry – assimilates – modelling – plant organs – relative growth rate – storage

Introduction

During plant development, the various plant parts, respectively organs, usually grow at different relative growth rates. To describe the relationship between these rates their ratio can be used as suitable quantity. If the ratio **r** of the relative growth rates of measures y_1 and y_2 of two organs is constant over time, then allometric growth is observed (PEARSALL 1927). After integration, the relation $y_1=b\ y_2^r$ is obtained, where b is an

integration constant and **r** is the well-known allometry coefficient. However, **r** cannot be generally regarded as a constant, but as a quantity, which depends on the stage of development and the environmental conditions.

The ratio **r** can be interpreted as an indirect measure for the allocation of the photosynthates between the organs, for example between shoots and roots. Therefore, it has high physiological importance, and studies on its variation during plant growth are of great relevance for explaining the allocation of assimilates between plant organs. The experimental determination of this quantity is straightforward by measuring the time course of dry masses or other amounts of the organs in certain time intervals. But it is hardly possible, to derive values for **r** from plants internal state, e.g. from biochemical or biophysical processes. An alternative may be to consider the different organ growth or allocation as process of adjustment like the gain of properties by selection during evolution or breeding and morphogenetic adaptation on changed environmental conditions. Concerning the allocation between shoots and roots, several authors have proposed models that assume such or other optimising principles for describing allocation and growth (KASTNER-MARESCH and MOONEY 1994; THORNLEY 1995; GRAY 1996; REYNOLDS and CHEN 1996; IWASA 2000).

The aim of this paper was the application of a similar approach for analysing the relationship between growth of the leaves and the tuber in radish (*Raphanus sativus* L. var. *sativus*). The chosen plant species may be a typical example for the distribution of assimilates between the shoot and a storage organ. The analysis was restricted to the growth interval from seedling to harvest stage. Therefore, a simple condition (objective) for the adjustment (optimising) of the plant growth could be selected: minimising the growth duration until reaching the harvest stage (HEIßNER 1998), as determined by a certain tuber dry mass. In this study two adjustments were distinguished: firstly, describing the growth with a mean (time-independent) value of ratio **r** and secondly, with a time-dependent function. This analysis based on growth data (leaf area, and tuber dry mass), obtained from radish crops grown under different environmental conditions (irradiation and temperature) (HEIßNER 1998, 2000). To demonstrate the behaviour of ratio **r** in principle (magnitude and time response), the calculations were carried out with specially chosen data sets.

Materials and Methods

List of symbols, definitions and units of the quantities in the model.

A: Leaf area (m^2); A_0: Initial value of A ($t=t_0$) (m^2); A_f: Value of A at time t_f (m^2); g_l: Relative growth rate of leaf area (d^{-1}); g_t: Relative growth rate of tuber dry mass (d^{-1}); g: $g=g_l+g_t$ (d^{-1}); J: Net assimilation rate ($g\ m^{-2}\ d^{-1}$); m_A: Specific leaf mass ($g\ m^{-2}$); m_t: Tuber dry mass (g); m_{t0}: Initial value of m_t ($t=t_0$) (g); m_{tf}: End value of m_t ($t=t_f$) (g); r_1, r_2: Model parameters for describing the different relative growth rates of leaf area and tuber dry mass (first model version) $r_1=1/(1+r)$; $r_2=r/(1+r)$; r: Ratio of the relative growth rates of tuber dry mass and leaf area (second model version) $r=g_t/g_l$; r_0: Initial value of r ($t=t_0$); t: Time (d); t_0: Time at the beginning of the growth interval (d); t_f: Time at the end of the growth interval (d); ρ_0: Ratio of leaf area and tuber dry mass at the beginning ($t=t_0$) ($m^2\ g^{-1}$).

Leaf area and tuber dry mass are related to one plant.

Table 1. Radish crops, from which the growth data were determined as basis for the analysis. Cultivars: 'Marabelle' (M), 'Rudi' (R), 'Sirri' (S) and 'Duro' (D); experimental locations: field (f) and growth chamber (g); shading treatments: non-shaded (0) and shaded (1).

Year	Sowing date	Last sample date	Crop number	Cultivar	Location	Shading treatment	Transmittance of covers	Mean daily air temperature[1)] (°C)	Mean daily irradiation (mol PAR m^{-2})
1996	15 Apr	28 May	1; 2	M	f	0; 1	0.87; 0.78	12.8	23.4
	31 May	26 June	3; 4	M	f	0; 1	0.87; 0.78	19.0	39.1
	3 Jul	31 Jul	5; 6	M	f	0; 1	0.87; 0.78	16.8	31.7
	28 Aug	2 Oct	7; 8	M	f	0; 1	0.87; 0.78	10.8	19.1
1997	17 Apr	21 May	9	M; R; S; D	f	0	0.87	not measured	37.7
	2 Dec	19 Dec	10; 11	M	g	0; 1	0.62	18.3	28.3
1998	6 Apr	18 May	12; 13	M	f	0; 1	0.62	11.9	32.6
	5 June	3 June	14; 15	M	f	0; 1	0.62	16.6	38.1
	3 Aug	28 Aug	16; 17	M	f	0; 1	0.62	16.4	35.2
1999	18 Feb	11 Mar	18	M	g	0	–	15.3	22.7
	25 May	28 June	19; 20	M	f	0; 1	0.26	15.4	37.9
	2 Aug	31 Aug	21	S	f	0	–	15.3	30.9
	9 Sept	12 Oct	22	S	f	0	–	12.5	13.9
2000	16 Feb	15 Mar	23; 24	S	g	0; 1	0.63	15.1	28.0

[1)] Only measured without cover

Primary growth data

Data from a total of twenty-four radish crops, grown in Grossbeeren (lat. 52.5 °N) at the Institute of Vegetable and Ornamental Crops, Großbeeren/Erfurt e.V., were available, partly used in earlier analyses (HEIßNER 1998; 2000) (Table 1). The data included: the dry mass of the shoot and tuber as well as the leaf area in sampling intervals from one to four days. The sampling is described in detail by HEIßNER (1998; 2000). The field grown plants were cultivated on loamy sand and the growth chamber plants on a peat substrate in seed dishes. High-pressure sodium lamps (HPS lamps) were applied in the growth chambers. Day length and temperature sets (day/night) in the growth chambers were: 1997, 16 h and 20/15 °C; 1999, 16 h and 16/14 °C; and 2000, 10 h and 18/14 °C. Planting density was about 300 m^{-2} with a row distance of about 0.1 m. Ten of the tested radish crops were imposed with an additional shading treatment (Table 1). It consisted of fleece covers or net screens to protect the plants against pests and to reduce the irradiation (PAR). The transmittance of the covers varied between 0.26 and 0.87 (Table 1). The shading treatments were defined like following: level 0, transmittance ≥0.87; level 1, transmittance <0.87.

Deriving growth parameters

From the measured growth data the following parameters were determined as necessary inputs for determining ratio **r** via optimisation: (1.) the net assimilation rate J, (2.) the specific leaf mass m_A, (3) the initial values of **r**, leaf area and tuber dry mass: r_0, A_0 and m_{t0} as well as (4.) the target value (end value) m_{tf} of tuber dry mass. The units of these quantities and further relations are given in the list of symbols. For their calculation the so-called "functional approach" was applied (HUNT 1982), i.e. the time courses of the measured quantities were described using empirical functions, which allows to calculate the parameters by algebraic manipulation and derivation with respect to time. For A_0, the leaf area at the beginning of the growth interval, a standard value of 0.0005 m^2 (with exception of crops in 1997, Table 1), corresponding to the measured average, was chosen. As end values of tuber dry mass the following were used: 0.3 g for the varieties 'Marabelle', 'Rudi' and 'Sirri', the round types, and 1.2 g for 'Duro', the examined oblong type. These end values are in good accordance with harvest tuber dry mass obtained in practice.

The uncertainty of ratio **r** was calculated from the standard errors of the polynomial coefficients in the fit of ln m_t against ln A by the law of error propagation. These calculations, here not given in detail, resulted in errors between 0.1 and 0.2.

*Theoretically deriving ratio **r***

To determine ratio **r** due to an adjustment (optimising) procedure, the radish growth was described by the absolute growth rates of the leaf area and the tuber dry mass using the following two model versions:

first version,

$$dA/dt = r_1 g A \quad [1]$$

$$dm_t/dt = r_2 g m_t \quad [2]$$

$$JA = g(r_1 m_A A + r_2 m_t) \quad [3]$$

second version,

$$dA/dt = g_l A \quad [4]$$

$$dm_t/dt = r g_l m_t \quad [5]$$

$$JA = g_l(m_A A + r m_t) \quad [6]$$

The first version was used in the case of unconstrained, the second of constrained ratio **r**. Both versions are equivalent: The first and second equations (eq. [1], [2] and [4], [5]) are the growth rates of the leaf area A and the tuber dry mass m_t, the third equation (eq. [3] and [6]) the balances of the dry masses. The growth rates of the state variables A and m_t are given as product of the relative growth rates (r_1 g and r_2 g or g_l and r g_l, respectively) and the state variables. The dry matter balance results from the equality of dry matter production (J A) and the sum of the growth of the two compartments (m_A g_l A+r g_l m_t; m_A: specific leaf mass). The quantities $\mathbf{r_1}$ and $\mathbf{r_2}$ are normalised by the equation: $\mathbf{r_1}+\mathbf{r_2}=1$. The relationship between **r** on the one hand and $\mathbf{r_1}$ and $\mathbf{r_2}$ on the other is given in the list of symbols. The quantity **r** is allowed to vary between zero and infinite, the coefficients $\mathbf{r_1}$ and $\mathbf{r_2}$ between zero and one.

For time-independent quantities **r**, J and m_A the above system of two differential equations has an analytical solution (HEIßNER 1998). This allows the calculation of **r**, which minimises the time interval, to reach a given value of tuber dry mass at harvest, using simply the method of determining an extremum of a function.

But in the case of time-dependent model parameters the solution is a problem of optimal control theory (KIRK 1970): Find the time-course of ratio **r** that minimises the duration for reaching a given final dry mass of the tuber. For solving the problem, numerical calculation procedures were used: the software system Hqp (FRANKE and ARNOLD 1996) for the calculation of optimal control in time discretised systems and the Fortran library TOMP (KRAFT 1994). A time discretisation of twenty equidistant intervals of the growth interval was generally sufficient for determining the time-course of ratio **r**. These intervals correspond to a length of about one day. For carrying out the procedure, additional inputs were necessary, namely constraints on ratio **r** and the relative growth rate of the tuber dry mass. Values of these quantities are given together with the results.

Results

Experimentally derived values of the growth parameters

Results are presented in Table 2 for six data sets (A, B, C, D, E and F). The mean for all measurements without crop number 9 are summarised under A, the mean for the non-shaded and shaded treatment under B and C, respectively. Whereas the results for crops with the

Table 2. Growth parameters, determined from measurements on radish-crops in the experiments from 1996 to2000 (without crop number 9). J: net assimilation rate; m_A: specific leaf mass; ρ_0: ratio of the leaf area and tuber dry mass at the beginning of the growth interval; r_0: ratio **r** at the beginning of the growth interval. Values in parentheses: standard deviation and number of measurements.

Data set	Crop number	J ($g\ m^{-2}\ d^{-1}$)	m_A ($g\ m^{-2}$)	ρ_0 ($m^2\ g^{-1}$)	r_0
A	1 to 8 and 10 to 24	8.7 (3.0; 188)	32.3 (5.5; 188)	0.13 (0.03; 23)	0.44
B	1; 3; 5; 7; 10; 12; 14; 16; 18; 19; 21; 22 and 23 (non-shaded)	9.9 (3.1; 102)	34.3 (4.7; 102)	0.13 (0.02; 13)	0.50
C	2; 4; 6; 8; 11; 13; 15; 17; 20 and 24 (shaded)	7.4 (2.4; 86)	29.9 (5.3; 86)	0.13 (0.04; 10)	0.38
D	12 (non-shaded)	9.4 (2.0; 8)	35.2 (2.8; 8)	0.13	0.44
E	20 (shaded)	4.6 (1.2; 11)	24.3 (1.9; 11)	0.11	0.14
F	19 (non-shaded)	9.9 (1.6; 8)	32.9 (4.3; 8)	0.10	0.30

Table 3. Growth parameters, determined from measurements on crops in 1997 with four varieties (crop number 9). J: net assimilation rate; m_A: specific leaf mass; m_{t0}: initial value of tuber dry mass; ρ_0: initial value of the ratio of leaf area and tuber dry mass; **r**: ratio of the relative growth rates of tuber dry mass and leaf area. Values in parentheses: standard deviation.

Cultivar/type of tuber	J ($g\ m^{-2}\ d^{-1}$)	m_A ($g\ m^{-2}$)	m_{t0} (g)	ρ_0 ($m^2\ g^{-1}$)	r Measured	r Calculated
'Marabelle'/round	9.90 (0.53)	31.1 (1.2)	0.0052 (0.0008)	0.21 (0.02)	1.76 (0.11)	1.69
'Rudi'/round	9.76 (0.91)	31.9 (0.9)	0.0082 (0.0007)	0.19 (0.01)	1.70 (0.08)	1.90
'Sirri'/round	10.19 (0.99)	31.6 (0.8)	0.0058 (0.0007)	0.21 (0.02)	1.78 (0.06)	1.76
'Duro'/oblong	10.71 (1.28)	36.1 (0.8)	0.0049 (0.0010)	0.31 (0.02)	1.53 (0.05)	1.55

lowest and largest leaf area in relation to the actually reached tuber dry mass are given under D and E. Under F the results of the non-shaded treatment corresponding to the data set under E are summarised. The influence of the shading treatment on net assimilation rate and specific leaf mass was obvious. Also the initial values r_0 of ratio **r** differed markedly dependent on the treatment, whereas ρ_0, the ratio of leaf area and tuber dry mass at the beginning of the growth interval, showed only small variations. Values of ratio **r**, derived from data set A (Table 2), are presented in Fig. 1. They showed a distinct increase during leaf growth: At the beginning, leaf growth dominated ($\mathbf{r}<0.5$), and at the end tuber growth ($\mathbf{r}>2$). Moreover, the graph shows a small, but marked influence of the shading treatment on ratio **r**: lower values under the condition of shading compared to non-shaded crops. Averaged values of ratio **r** for the six data sets were: 1.48 (A); 1.55 (B, non-shaded); 1.38 (C, shaded); 1.87 (D, non-shaded); 1.10 (E, shaded) and 1.24 (F, non-shaded). These values also reflect the observed shading effect on the relation between the relative growth rates of tuber dry mass and leaf area.

*Theoretically derived values of ratio **r***

If using the approach of describing the growth with a mean (time-independent) value during the growth interval, then the theoretically derived values of ratio **r**, obtained from the six data sets (Table 2), were: 1.28 (A); 1.31 (B, non-shaded); 1.24 (C, shaded); 1.32 (D, non-shaded); 1.09 (E, shaded) and 1.20 (F, non-shaded). Consequently, the differences between the observed and calculated values were: 0.20 (A); 0.24 (B); 0.14 (C); 0.55 (D); 0.01 (E) and 0.04 (F). Like the experimental result, the values in the non-shaded treatment were higher than that of the shaded. This is the consequence of the different values of specific leaf mass in the data sets (Table 2): The theoretically derived values of ratio **r** increase with increasing specific leaf mass (HEIßNER 1998). Furthermore, the theoretically attained values were on average lower than the measured values in these data sets. Whereas in experiment, carried out in 1997 with different varieties (crop number 9, Table 1; here growth parameters were solely determined at the beginning and end of the growth interval), experimentally and theoretically derived values of **r** agreed well (Table 3). The experimentally derived values ranged from 1.53 to 1.78, the theoretically from 1.55 to 1.90.

To demonstrate the calculation procedure for deriving time-dependent values of ratio **r**, $\mathbf{r_1}$ and $\mathbf{r_2}$, respectively, without constraints, the growth parameter of data set F were chosen. The growth of this radish crop in spring 1999 was characterised by both a relative high net assimilation rate and a high specific leaf mass (Table 2). The theoretically derived time courses of leaf area, tuber dry mass, parameter $\mathbf{r_2}$ and the relative growth rate of the tuber dry mass (Fig. 2) showed, that in the beginning leaf growth must dominate and tuber growth has to start relatively late in order, to minimise the duration for tuber growth. The main contradiction to observations however was, that the theoretically derived values of parameter $\mathbf{r_2}$ were either zero or one. This jump-like increase of $\mathbf{r_2}$ was related to a discontinuous behaviour and very large values of the relative growth rate g_t of tuber dry mass (up to about 6 d^{-1}), which were not observed in the experiments.

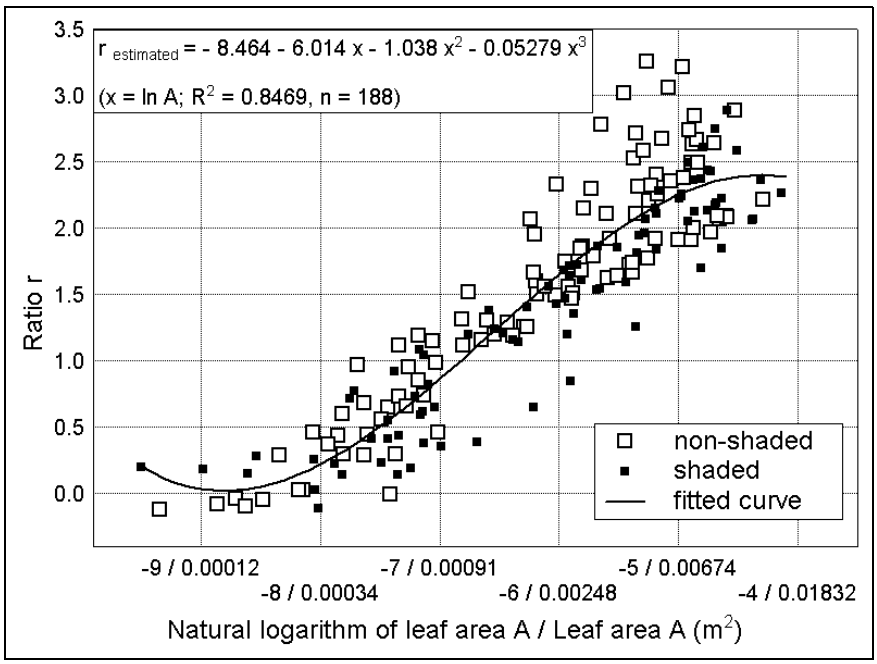


Fig. 1. Ratio **r**, derived from growth measurements on crops in the years from 1996 to 2000 (data set A, Table 2), depending on leaf area.

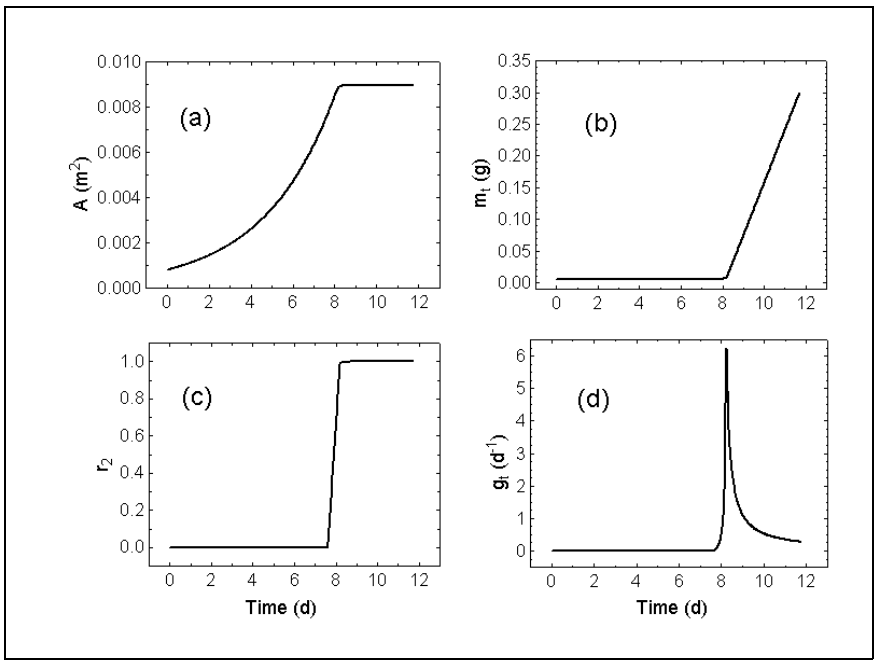


Fig. 2. Time courses of leaf area A (a), tuber dry mass m_t (b), parameter $\mathbf{r_2}$ (c) and relative growth rate g_t of tuber dry mass (d), determined by unconstrained optimisation on data set F (Table 2).

To avoid such unrealistic growth simulations, the relative growth rate of tubers was constrained to a maximum of 0.5 d^{-1}, a value, which corresponded nearly to the observed maximum. For exemplary calculations input data were chosen with time-dependent growth parameters (net assimilation rate and specific leaf mass), estimated from growth measurements in spring, early and late summer 1998 (crop number: 12 to 17, Table 1). Now the parameter $\mathbf{r_2}$ increased to values between 0.6 and 0.7, when a certain leaf area was reached (Fig. 3). Then the values remained nearly constant and just before the end of the interval a further increase until 1.0 occurred. The transition from zero to larger values of $\mathbf{r_2}$ was partly dependent on the shading treatment: In the spring and late summer crops the transition occurred later, when the plants were shaded. Not consistent with the observed growth response in these calculations were the values of the derived parameter $\mathbf{r_2}$ at the beginning and at the end of the growth interval. From the experiments followed, that $\mathbf{r_2}$ was mostly larger than zero at the beginning and always smaller than one at the end.

Therefore, in addition to the constraint on the relative growth rate of the tuber dry mass the permissible range of ratio **r** was limited by an initial value $r_0>0$ and a maximal r_{max}. The calculation of ratio **r** using the parameter means from data set A (Table 2) resulted in a time course, which corresponded to the observed (Fig. 4), if the following constraints for ratio **r** were chosen:

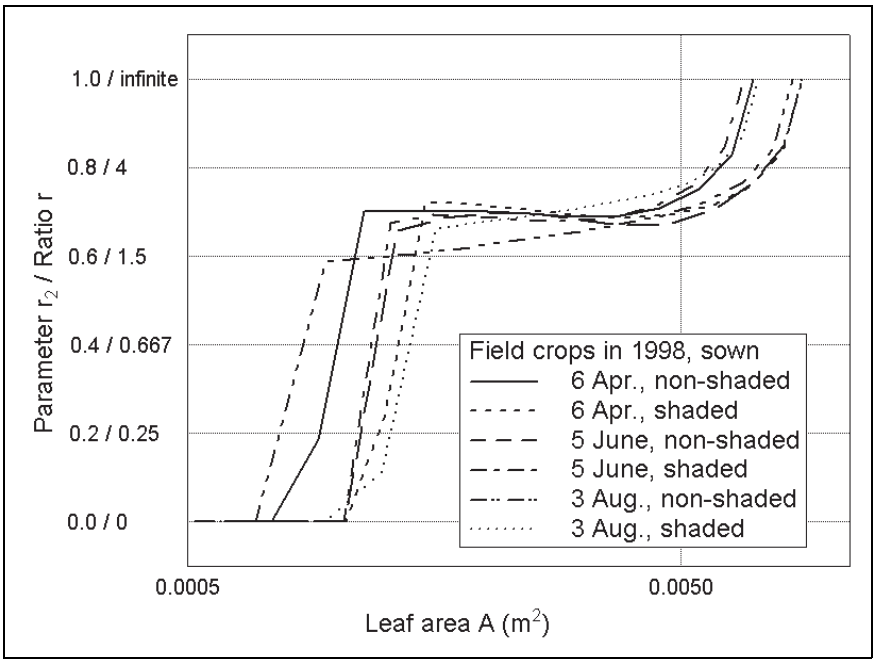


Fig. 3. Parameter $\mathbf{r_2}$, determined by constrained optimisation (g_{tmax}=0.5 d^{-1}), using the growth measurements in 1998 (Table 1), depending on leaf area. Input were time-dependent values of net assimilation rate and specific leaf mass.

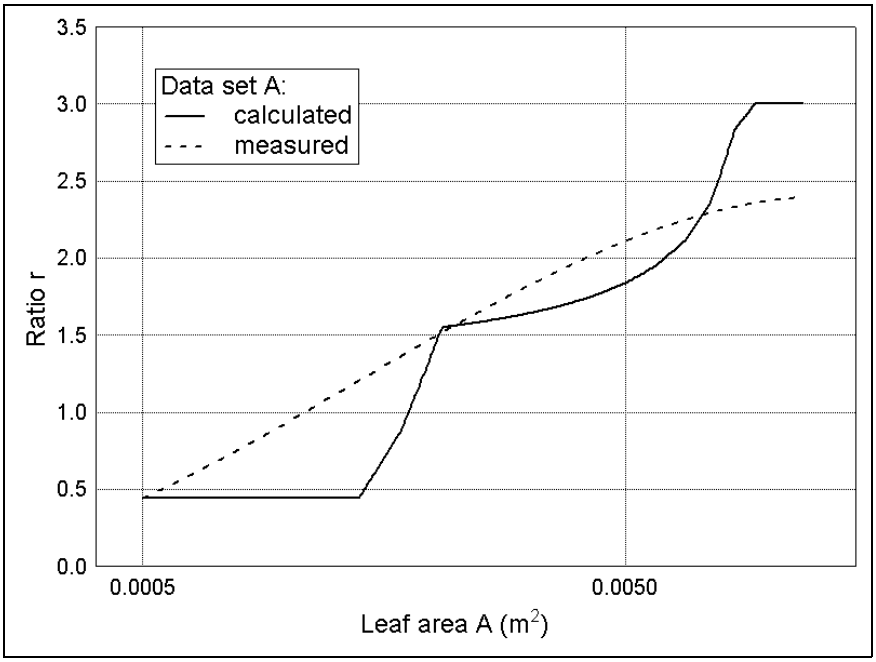


Fig. 4. Ratio **r**, derived from growth measurements and calculated by constrained optimisation (g_{tmax}=0.35 d^{-1}, r_{max}=3.0), using data set A (Table 2), depending on leaf area.

r_0=0.44; r_{max}=3.0. Moreover, the relative growth rate of the tuber dry mass was limited: g_{tmax}=0.35 d^{-1}.

To complement the above result and considering the dependency of ratio **r** on the shading treatment (Fig. 3), the data sets D and E with the observed minimal and maximal ratio of tuber dry mass and leaf area at the end of the growth interval were used for the calculations. These were carried out using the following constraints and target values : r_0=0.44 and 0.14; r_{max}=3.5 and 2.5; g_{tmax}=0.35 d^{-1}; m_{tf}=0.2 and 0.4 g for D and E, respectively . Both measurements and calculations showed, that under non-shaded conditions ratio **r** increased more strongly with leaf area than under shaded conditions (Fig. 5).

Finally, calculations were carried out to test the possibility of estimating the model parameters: J, m_A, m_{tf}, g_{tmax} and r_{max}, using the optimisation procedure for ratio **r** in hand with observation on leaf area and tuber dry mass. The data sets D and E were exemplary chosen for these calculations, because these were representative for very different tuber dry mass: leaf area ratios (Table 2). The test with these data sets was successful (Table 4). Estimating the parameters by iterated calculations resulted in a fit, which could explain more than 95 % of the variance in measured data. Particularly, the estimated values (Table 4) of the net assimilation rate and the specific leaf mass were in good accordance with observations given in Table 2.

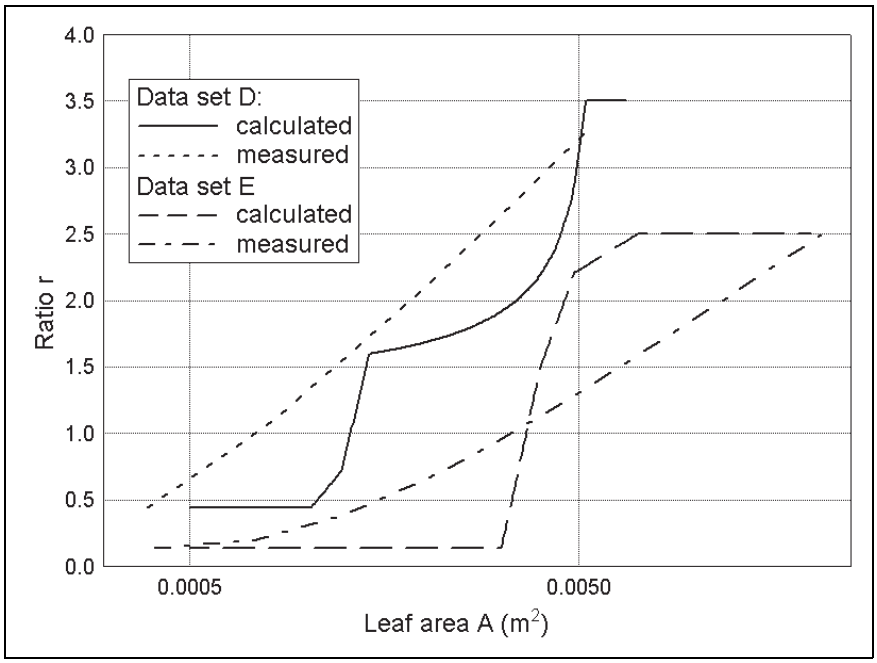


Fig. 5. Ratio **r**, derived from growth measurements and calculated by constrained optimisation (g_{tmax}=0.35 d^{-1}, r_{max}=3.5 and 2.5), using data set D and E (Table 2), depending on leaf area.

Discussion

The analysis, carried out with growth data on radish crops from seedling to harvest stage, demonstrated a possible way to explain the different growth of leaves and tuber. The tested hypothesis was: The relationship between the relative growth rates of the organs is the result of an optimal process, in which the time interval for reaching a certain dry mass of the tuber is minimal. To describe the relationship quantitatively, the ratio of the relative growth rates of the tuber dry mass and the leaf area – ratio **r** – was chosen. Important inputs for the calculations were: the net assimilation rate and the specific leaf mass, derived from growth measurements in the various crops. The tests covered two cases: firstly, describing the growth with a mean (time-independent) value of the ratio and secondly, with a time-dependent function.

In the case of a time-independent ratio, the accordance between the values, derived experimentally and theoretically was sufficient: the maximal difference between the observed and calculated **r**-values was 0.6, the least <0.1 and in average about 0.1, therefore, less than 10 % of the estimated mean **r**-values. The deviations (bias) could be caused by incorrect inputs, partly dependent on their measuring error (see standard deviations, Table 2 and 3). These inputs were: the specific leaf mass, the initial value of the leaf area, the ratio of leaf area and tuber dry mass at the beginning and the tuber dry mass at the end of the investigated interval. Variations of these quantities have a marked effect on the calculated values (HEIßNER 1998). For example, with leaf areas smaller than about 0.001 m^2 the calculated values of ratio **r** increased with increasing ρ_0, the ratio of leaf area and tuber dry mass at the beginning. This fact contributed mainly for the differences between the measured and calculated values of ratio **r** in data sets A to F: Here the initial values were very small (A_0=0.0005 m^2 and $\rho_0 \approx 0.1$ $m^2\ g^{-1}$). This resulted in smaller calculated than measured values. In case of data set F, for example, accordance can be obtained, if the following initial values are chosen: A_0=0.001 m^2 and ρ_0=0.16 $m^2\ g^{-1}$. This stage conforms approximately with the beginning of the true leaf growth. Furthermore, the error of the experimentally derived value of ratio **r** must be considered, which was in average 10 % to 20 %. For that reason, it is allowed to confirm the hypothesis for a time-independent value of ratio **r** during the considered growth interval.

In the case of a time-dependent function of ratio **r** the basic response could be confirmed: At first predominant leaf growth and then transition to predominant tuber growth was observed both in measured, and simulated data. An increase of relative tuber growth rate in comparison to that of the leaves during the vegetation was also established by BAZLEN (1985). Growth experiments with carrots also showed, that throughout growth the storage organ has an increasing relative growth rate compared with that of the shoot (BARNES 1979; CURRAH and BARNES 1979; HOLE 1996).

To avoid an unrealistic growth behaviour as result of the optimisation procedure – such as hard discontinuous time courses and very large values of ratio **r** – additionally a limitation for the relative growth rate of the tuber dry mass had to be used. This requirement can be interpreted as a biophysical and biochemical limitation of the velocity of assimilate transport, as well as by a limited rate of cell division and expansion. Not expected was, that – after attaining a certain leaf area – ratio **r** increased very strong. This response like a step-function could not be confirmed from the measurements. Possibly, the intervals between the samplings were too long and the sample sizes too small, to prove such a time pattern experimentally correct. A further inconsistency between the experimentally and theoretically derived values of ratio **r** was the fact, that at the end of the growth interval the calculated values of ratio **r** approached infinite, whereas the measured amounted to

Table 4. Model parameters, estimated from data sets E and D (Table 2) by iteratively optimising. J: net assimilation rate; m_A: specific leaf mass; m_{tf}: end (target) value of tuber dry mass; g_{tmax}: upper limit of the relative growth rate of tuber dry mass; r_{max}: upper limit of ratio **r**; R^2: coefficient of determination.

Data set	Sowing date	Treatment	J ($g\ m^{-2}\ d^{-1}$)	m_A ($g\ m^{-2}$)	m_{tf} (g)	g_{tmax} (g)	r_{max}	R^2	
								Leaf area	Tuber dry mass
D	6 Apr 1998	non-shaded	9.6	37.2	0.15	0.35	3.5	0.99	0.98
E	25 May 1999	shaded	3.9	22.0	0.40	0.25	2.0	0.95	0.96

about three (Fig. 1). Therefore, also ratio **r** was constrained in the optimisation. From the necessity of several additional conditions (constraints) for calculating the time behaviour of ratio **r** follows, that the originally chosen hypothesis was not adequate with reality.

In accordance with the experiments, the calculations indicated an effect of the shading treatment on ratio **r**. Under non-shaded conditions, higher values of ratio **r** were observed than under shaded. Furthermore, the time courses of ratio **r** were different in dependency on the shading treatment: Under non-shaded conditions ratio **r** increased earlier than under shaded. But the effects were small and not clear enough, so that these must be confirmed in detail in further experiments. Possibly, this influence is caused by changes in the carbon supply, that results in modifications in the carbon allocation (LEMAIRE and MILLARD 1999). From investigations on radish crops under varied irradiation levels and plant densities MARCELIS et al. (1997) likewise concluded, that an improved carbon supply, caused by higher radiation levels and lower plant densities, favoured dry matter allocation to the tuber.

Furthermore, it was possible to fit the growth of leaf area and tuber dry mass very well (data set D and E; $R^2 \geq 0.95$) , if the growth parameters (J, m_A) including the constraints and the target value (g_{tmax}, r_{max} and m_{tf}) were estimated by iteratively optimising. All these parameters have physiological meaning and are dependent on the environmental conditions (e.g. shading).

With the analysis, carried out on growth data in radish, many points were found, which can used for interpreting the relationship between tuber and leaf growth as result of an optimal process. But further work is necessary, to complement the study, which is up to now partly qualitative. Further advance of the method for deriving ratio **r** by optimisation may be obtainable with expanded growth models and different optimisation criteria. For improving the used growth model it is desirable to substitute the parameter J, the net assimilation rate, by an expression, which reflects photosynthesis and respiration as important physiological processes. Moreover, the specific leaf mass m_A should be represented as a function of the environmental conditions. An improvement of the model should be also possible by considering the growing compartments like in the NICOLET model (SEGINER 2004). Enlarged growth intervals, e.g. from seed to seed stage, may lead to improved results, too. But such procedures presume comprehensive extended models. Perhaps, proceedings with formulation the optimisation criterion in the following manner might lead to successful solutions for combining short term objectives, that means adaptation on different external conditions (radiation, air temperature or air humidity) with long term targets for simulation the ontogenetic plant behaviour. The steps are: (1.) Extending the growth model by a rate equation for **r** (t) or similar functions: $dr/dt = f(\mathbf{r}, m_t, A, J, m_A, \mathbf{p})$ and (2.) Estimating the parameter vector **p** by using optimisation criteria, which are evaluated over several growth cycles with randomly fluctuating environments. The criterion might be some function of mean (μ) and variance (σ) of the growth duration analogue to the μ-σ criteria used in decision theory under uncertainty (SINN 1989). Such an approach would enable the inclusion of "ontogenetic drift" (COLEMAN and MCCONNAUGHAY 1995), i.e. the dependence of ratio **r** on the phenotypic state in terms of tuber mass, leaf area or other suitable variables.

Acknowledgements

We would like to thank Mrs Jutta Lenk for her careful technical assistance.

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Received September 15, 2003 / Accepted January 21, 2005

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