Gartenbauwissenschaft, **66** (4). S. 152–163, 2001, ISSN 0016–478X. © Verlag Eugen Ulmer GmbH & Co., Stuttgart

Optimisation of CO_2 and temperature control in greenhouse crops by means of growth models at different abstraction levels II. Growth models and parameter generation for lettuce crops[1)]

Optimierung der CO_2- und Temperaturführung bei Gewächshauskulturen mit Hilfe von Modellansätzen unterschiedlicher Abstraktionsebenen II. Wachstumsmodelle und Parametergeneration für Salatbestände

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Summary

To use the preferences of models at high and those at low abstraction level for optimising greenhouse climate control, in part I a concept of combining a REGRESSION model with the more mechanistic SUCROS 87 model has been developed and model parameters have been described from literature. In the investigations in this part the following parameters of the two growth models have been derived:
- REGRESSION model: Ontogenetic effects by deviding the growth period into four growth phases. For each phase the maximal value (A) and the coefficients for the effects of radiation, temperature and CO_2 concentration in multiplicative (CO_2 additive) connected terms of the regression function.
- SUCROS model: Specific Leaf Area, Photosynthetic Active Leaf Area, interception of light (reflection, transmission, absorption), photosynthesis, respiration and dry matter partitioning.

Validation with a special data set shows weak points of both approaches, but the simulated data of the REGRESSION model are closer to reality than those of the SUCROS model. The procedure of combining both models will be shown in part III.

Zusammenfassung

Um die Vorzüge von Modellen auf hoher und niedriger Abstraktionsebene für die Optimierung des Gewächshausklimas zu nutzen, wurden in Teil I ein Konzept für die Kombination eines REGRESSIONS-Modells mit dem mehr mechanistischen Model SUCROS 87 entwickelt und Modellparameter aus Literaturangaben beschrieben. In den in diesem Teil beschriebenen Untersuchungen wurden für die zwei Wachstumsmodelle folgende Parameter erarbeitet:
- REGRESSIONS-Modell: Ontogenetische Reaktionen durch Aufteilung in 4 Wachstumsphasen, für jede Phase der Höchstwert (A) und die Koeffizienten für die Wirkungen der Strahlung, der Temperatur und der CO_2 Konzentration in multiplikativ (CO_2 additiv) verknüpften Termen der Regressionsfunktion
- SUCROS-Modell: Spezifische Blattfläche, photosynthetisch wirksame Blattfläche, Lichtaufnahme (Reflexion, Transmission, Absorption), Photosynthese, Atmung und Trockensubstanzverteilung.

Die Validierung mit einem besonderen Datensatz zeigt Schwachpunkte beider Ansätze, aber die simulierten Werte des REGRESSIONS-Modells geben die Realität besser wieder als die Werte des SUCROS-Modells. Die Kombination beider Modelle wird in Teil III dargestellt.

1 Introduction

Greenhouse on-line control based on physiological and economic data can only be accomplished by modern electronic systems and adequate system theoretical approaches. Since no existing model satisfies all requirements of crops with expanding leaf areas, in part I of this contribution (ALSCHER et al., 2001) the concept of combining two models at different abstraction levels is presented and basic data for lettuce production in greenhouses are derived from literature. In this second part derivations and experiments are presented to elaborate parameters for a descriptive and for a physiological dynamic growth model for lettuce, aiming at optimising CO_2 concentration and temperature on-line control.

2 Regression model for daily growth rates

2.1 Approaches

When starting this investigation several descriptive growth models had been developed, e.g. HAMMER and LANGHANS 1976; KRUG and LIEBIG 1979a, 1979b, 1984a, 1994; ARMITAGE et al. 1981; HOPPER et al. 1985; KARLSSON and HEINS 1985. Only the regression model of KRUG and LIEBIG (1994), however, was parameterized for long term lettuce crop growth (WIEBE and LIEBIG, unpub.; MANN 1986). This model relates Mean Growth Rates (MGR) and Relative Growth Rates (RGR), respectively, to the product of theoretical maximal weight and terms for the effects of the respective growth factors, such as irradiance,

1) Based on the PhD-Thesis of ALSCHER (1993)

Table 1. Treatments and production techniques for lettuce crops (details see Alscher 1993).
Versuchsvarianten und Kulturtechniken für Salatkulturen (Näheres siehe Alscher 1993).

Year	sets	season	temp. °C set point	CO_2 concentration µLL^{-1}	Variability
1982/3	6	20.9. – 17.2.	2/2	control[7], 1000	constant[1]
			12/8	control, 600, 800, 1000, 1200	constant
1883/4	6	3.10. – 14.2.	2/2	control, 600, 800, 1000, 1200	constant
			12/8	control, 1000	constant
1984/5	6	27.9. – 6.3.	2/2	control, 800, 1200	constant
			12/8	control, 800, 1200	constant
1985/6	2	6.10. – 14.1.	12/8	control, 400, 1000	1. constant
				1000/400	2. intermittent[2]
				1000	3. $v_w < 4$ [3]
				1000	4. $v_w < 4$, $R > 40$[4]
				1000	5. $v_w < 3$, $R > 30$[4]
1986/7	2	22.10. – 28.1.	12/8	control, 1000	1. constant
				1000/400	2. intermittent[2]
				1000	3. $v_w < 3$ [3]
				1000	4. $v_w < 3$, $R > 30$[4]
1987/8	1	27.10.	12/8	control, 1000	1. constant
				1000	2. $v_w < 3$, $R > 30$[4]
1988/9	6	17.10. – 28.2.	12/8	control, 1000	1. constant
				1000, 380	2. d = 1 ,3, 9[5]
				1000, 380	3. $\bar{x}$ (d=1)[6]
1991	2	18.1. – 11.2.		on-line control according to the REGRESSION model (daily periods), according to the SUCROS model (hourly periods) and validation	

1) constant = constant set points for CO_2 concentrations at irradiances >7 Wm^{-2}
2) Enrichment with CO_2 to 1000 µLL^{-1} when the concentration has dropped to 400 µLL^{-1}
3) CO_2 enrichment only with windspeeds 4 and 3 ms^{-1}, resp.
4) CO_2 enrichment only with windspeeds 4 and 3 ms^{-1}, resp. and irradiances 40 and 30 Wm^{-2}, resp.,
5) CO_2 concentrations of 1000 and 380 µLL^{-1} alternatively in periods of 1, 3 and 9 days, resp.
6) Mean CO_2 concentration of 5) **–1 day (day before)**
7) Without CO_2 enrichment
1) Konstant = konstante Reglereinstellung für CO_2 Konzentrationen bei Bestrahlungsstärken >7 Wm^{-2}
2) CO_2 Anreicherung auf 1000 µLL^{-1} nach Konzentrationsabfall auf 400 µLL^{-1}
3) CO_2 Anreicherung nur bei Windgeschwindigkeiten <4 bzw. 3 ms^{-1}
4) CO_2 Anreicherung nur bei Windgeschwindigkeiten <4 bzw. 3 ms^{-1} und Bestrahlungsstärken >40 bzw. 30 Wm^{-2}
5) CO_2 Konzentrationen von 1000 und alternativ 380 µLL^{-1} in Perioden von 1, 3 und 9 Tagen
6) Mittlere CO_2 Konzentration von 5). **– 1. Tag (vorhergehender Tag)**
7) Ohne CO_2 Anreicherung

temperature and/or CO_2 concentration (MANN 1986). As demonstrated by BÄZLEN (1985) for radish and KRUG and LIEBIG (1995) for lettuce transplants, this approach allows to reduce the periods of growth rates to a minimum of 24 hours and consequently to simulate daily growth rates.

2.2 Parameter generation

Parameterization of the regression model is based on the experimental data of MANN (1986) from the years 1982/3 until 1984/5 as well as on own experiments from 1985/6 until 1987/8 in the same greenhouses, using the same control and measuring systems. The experimental data from 1988/89 were used for validation of the regression model. The treatments are outlined in table 1.

In the first three years only constant set points (CO_2 enrichment >7 Wm^{-2} irradiance) are used. In the following four years it was tested, in which manner fluctuating CO_2 concentrations, resulting from irradiance, wind speed or intermittent application, have to be valuated. The experiment in 1991 was established for controlling and optimising greenhouse climate due to developed models at different abstraction levels (see table 1).

In the experiments from 1982/3 to 1988/9 temperature set points were 12/8 °C and 2/2 °C day/night temperature. To vary irradiances and to consider seasonal influences the lettuce cultivar *Ravel* was planted in sets during the winter season, 16 plants per m^2. Growth was determined by successive harvesting until 150 and 200 g fresh weight, respectively, was reached and parameterized by the logistic growth function of FELDMANN (1979).

To consider ontogenetic reactions the growth of lettuce was divided into phases. Since lettuce in the period of investigation does not show distinct developmental phases, these were formally defined by weight (≤10 g; >10–50 g; >50–100 g; >100 g). In the first three phases with exponential growth RGR were calculated and daily added to ln-transformed values of the fresh

Table 2. Parameters for calculating growth rates in the 4 growth phases of lettuce (equation 5) and coefficients of determination (experiments from 1982/3 to 1987/8, n=116).
Parameter zur Berechnung der Wachstumsraten in den vier Wachstumsphasen von Kopfsalat (Gleichung 5) und Bestimmtheitsmaße (Versuche von 1982/83 bis 1987/8, n=116).

Growth phase	A (max. value)	P_1 (temperature)	P_2 (radiation)	P_3 (CO_2)	P_4 (planting weight)	R^2
1	2,753099	−0,008803	−0,001672	−0,000001	−0,286174	0,97
2	0,276997	−0,058468	−0,002562	−0,000025		0,98
3	0,168257	−0,075999	−0,002355	−0,000019		0,97
4	0,109555	−0,098964	−0,002974	−0,000011		0,95

Comment: Values were calculated using the BMDP program.
Erläuterung: Die Werte wurden per BMDP-Programm ermittelt.

weight achieved up to this day. In the fourth phase with about linear growth pseudolinear growth rate was calculated by using the RGR-function, but defining the „productive biomass" to be 100 g fresh weight for each day of this phase. These growth rates were related to the respective means of irradiance, temperature and CO_2 concentration using a multiplicative connected regression function (KRUG and LIEBIG 1984b, 1994), but in contrast to MANN (1986) due to better adaptation (see table 2) CO_2 was connected by an additive term. As incorporation of the compensation points (R_{min}, T_{min}, C_{min}) did not yield significant statistic effects, they were neglected. Within the first phase transplant weight was integrated as a fourth factor:

$$RGR = A * [1 - \exp(P_1 * T)] * [1 - \exp(P_2 * R)] * [1 - \exp(P_3 * C)] * [1 - \exp(P_4 * Pl)] \quad (5)$$

RGR = Relative Growth Rate (fresh weight, g $g^{-1}d^{-1}$); A = theoretical maximal weight (g); P = coefficients for growth factor intensities; T = temperature, R = radiation, C = CO_2 concentration, Pl = transplant weight

In the fourth phase the Absolute Growth Rate (AGR) was calculated by:

$$AGR = \exp[\log(100) + RGR] - 100 \quad (6)$$

2.3 Results

The effect of **intermittent CO_2 concentration** is demonstrated by the experiment 1988/9 (see table 1). As the controls in the autumn sets did not reach the final size, treatment 5 (set points calculated as means of the 1-day-cycle) with a variation of about ±50 µLL^{-1} is considered as a constant set point. As shown in figure 1 varying CO_2 concentrations in the range of 380–1000 µLL^{-1} in 1–9 day cycles effect the growth period according to their mean concentration. This means that treatments with intermittent and the same will be true for fluctuating concentrations can be used for deriving CO_2 effects and for validation.

For modelling lettuce growth the **parameters** of the four **growth phases**, calculated with the data sets from 1982/3 until 1987/8, excluding the variants with fluctuating CO_2 concentrations, are presented in table 2. Parameter A decreased from the first to the fourth phase. The coefficients describing the influences of temperature and irradiance increase with the ontogenetic age, but the coefficients of the CO_2 effects do not show any trend. Therefore it does not seem reasonable to describe the ontogenetic effect by special coefficients or terms. As an example in figure 2 RGR of the second growth phase is plotted over the CO_2 concentration.

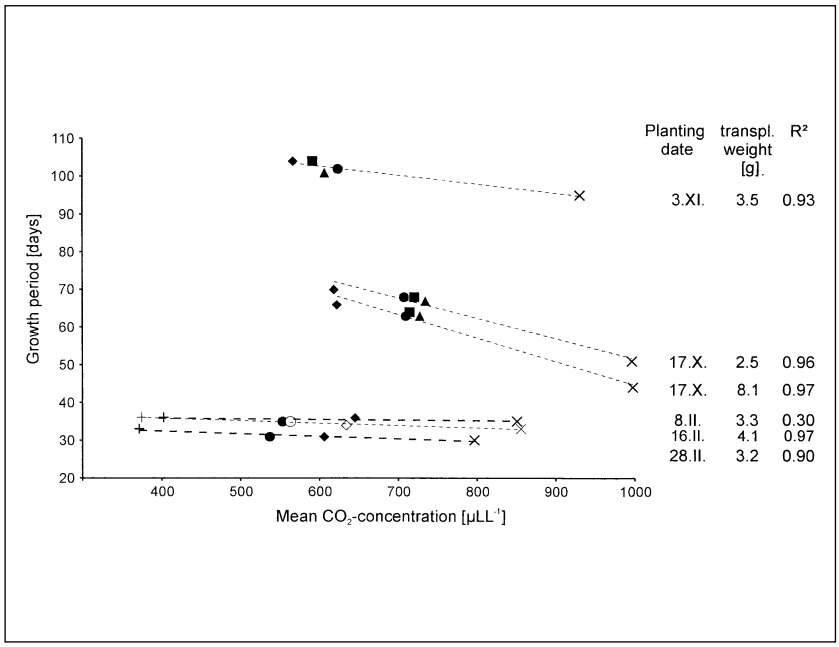


Fig. 1. Growth periods of lettuce sets (planting – 120 g fresh weight) with constant and intermittent CO_2 concentration in 1988/9 as a function of mean CO_2 concentration [1) × = const. 1000 µLL^{-1}; 2–4) cyclic changes of CO_2 set points between 380–1000 µLL^{-1} in periods of 2) ● = 1 day; 3) ▲ = 3 days; 4) ■ = 9 days; 5) ◆ = set points calculated as mean from the 1-day cycle with variation of ±50 µLL^{-1} (6) + controls in the autumn sets did not reach harvest size)].
Wachstumsdauer von Salatsätzen (Pflanzung – 120 g Frischgewicht) mit konstanter und intermittierender CO_2 Konzentration im Jahre 1988/9 als Funktion der mittleren CO_2 Konzentration. [1) × = konstant 1000 µLL^{-1}; 2–4) zyklischer Wechsel der CO_2 Reglereinstellung zwischen 380–1000 µLL^{-1} in Perioden von 2) ● = 1 Tag; 3) ▲ = 3 Tage; 4) ■ = 9 Tage; 5) ◆ = Reglereinstellungen als Mittelwerte des 1-Tageszyklus mit einer Variation von ±50 µLL^{-1} (6) + die Herbstkontrollen erreichten nicht die Erntegröße)].

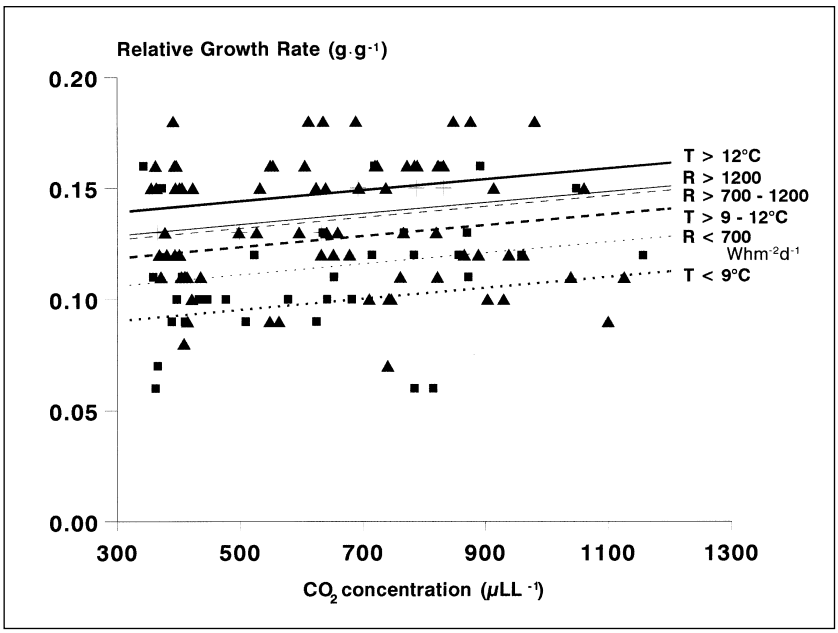


Fig. 2. Response surface for Relative Growth Rates of lettuce (10 to 50 g fresh weight) as a function of CO_2 concentration with 3 ranges of irradiances and 3 ranges of temperature (■ ≤ 9 °C, ▲ 9–12 °C, + > 12 °C). *Wirkungsflächen für Relative Wachstumsraten von Kopfsalat (10 bis 50 g Frischgewicht) als Funktion der CO_2 Konzentration für 3 Strahlungs- und 3 Temperaturklassen (■ ≤ 9 °C, ▲ 9–12 °C, + > 12 °C).*

The linear increase of RGR with the CO_2 concentration in the range of 380–1200 µLL^{-1}, but also the increase of RGR with temperature up to > 12 °C and surprisingly a distinct increase of irradiance only up to the class 700 – 1200 Whm^{-2}d^{-1} are indicated.

3 Physiological dynamic growth model for hourly growth rates

3.1 Approaches

The first mechanistic, explanatory or physiological dynamic growth model ELCROS (**el**ementary **cro**p growth **s**imulation) was developed by DE WIT and BROUWER (1968). This approach was improved and extended by numerous scientists (reviews see PENNING DE VRIES 1983; CHARLES-EDWARDS et al. 1986, THORNLEY and JOHNSON 1990). Modern versions are for example BACHROS by PENNING DE VRIES and VAN LAAR (1982) and SUCROS by SPTITTERS et al. (1989), which is used in this investigation.

The general structure of **SUCROS** is presented in figure 3. The central module **Tot**al **Ass**imilation, including the module **Assim**ilation, estimates the daily gross assimilation as a function of astronomical factors (module **Astro)** and **L**eaf **Ph**otosynthesis **Cur**ve module as a function of temperature. Respiration is considered by the modules **Resp**iration for **Mai**ntenance and **Resp**iration for **Gro**wth. Netassimilation is distributed by the module **D**ry **M**atter **Distr**ibution. The result is presented in the module **Product**ion (details see SPITTERS et al. 1989; MATITSCHKA 1995).

Since the primary module of this model is photosynthesis, which is parameterized rather precisely but dry matter distribution is difficult to parameterize, these models are primarily used to simulate growth of crops with a high Leaf Area Index (LAI) and continuous fruit production, such as cucumbers (AUGUSTIN 1984; NEDERHOFF 1994) or tomatoes (HEUVELINK

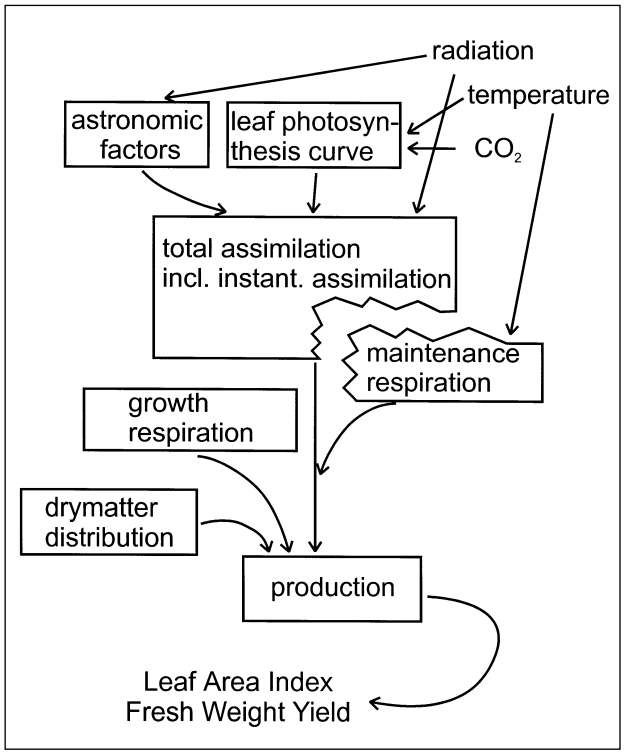


Fig. 3. Schematic diagram of the structure of SUCROS (Modules: ASTRO – astronomic factors; LPHCUR – leaf photosynthesis curve; TOTASS – total assimilation; ASSIM – instantaneous assimilation; RESP MAI – maintenance respiration; RESP GRO – growth respiration; DMDSTR – dry matter distribution; PRODCT – production, according to MATITSCHKA 1995; in der Abb. 3 sind die engl. Bezeichnungen aufgeführt).
Schematischer Aufbau von SUCROS (Module: ASTRO – astronomische Faktoren; LPHCUR – Blatt-Photosynthese-Kurve; TOTASS – totale Assimilation; ASSIM – momentane Assimilation; RESP MAI – Erhaltungsatmung; RESP GRO – Wachstumsatmung; DMDSTR – Trockensubstanzverteilung; PRODCT – Produktion, aus MATITSCHKA 1995; Erläuterung s.o.).

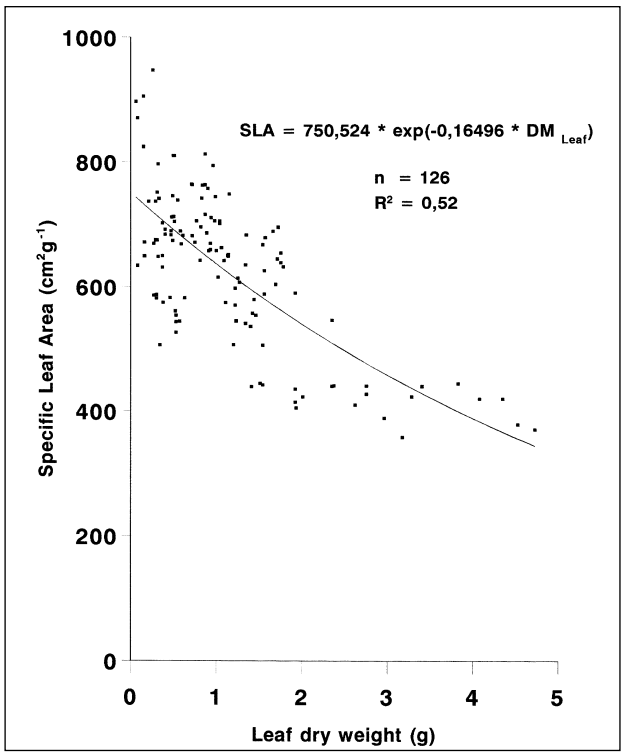


Fig 4. Relation of Specific Leaf Area to leaf dry weight of lettuce.
Beziehung zwischen Spezifischer Blattfläche und Blatttrockengewicht von Kopfsalat.

1996). For crops with expanding leaf area and developing heads, such as lettuce, the insufficiencies of the physiological approach, such as dry matter partitioning, have greater consequences and may cause errors. Therefore, explanatory models for these crops are insufficient. For lettuce, at least, no respective parameters were available. Therefore it had to be tested, if the SUCROS model, originally developed for wheat, could be parametrized to describe lettuce growth.

3.2 Parameter generation

Specific Leaf Area
In all sets and harvestings of the experiments listened in table 1 leaf dry weight and leaf area were determined and Specific Leaf Area (SLA) was calculated by dividing leaf area by leaf dry weight. For smoothing and parameterization an exponential function was used (fig. 4):

$$SLA = A * \exp(a * DM_{leaf}) \quad (7)$$

SLA = Specific leaf area ($cm^2\ g^{-1}$) ; A = theoretical maximum of SLA; a = coefficient; DM_{leaf} = leaf dry weight (g).

In consequence of the varying climatic conditions variation is rather large, but it is obvious that SLA decreases with leaf weight due to thicker leaves and hence due to ontogenetic age.

Photosynthetic active leaf area
SUCROS is based on the presumption of spherical distributed leaves. Species developing heads, such as lettuce, fulfil this requirement only during the preheading phase. With heading leaf buds are formed and inner leaves contain less or no chlorophyll. To determine photosynthetic active leaf area it has been assumed that photosynthesis is closely correlated to the chlorophyll content. Therefore, the lettuce heads were divided into three leaf layers according to 3 ranges of colour. In each layer the chlorophyll content was analysed and related to that of the exterior layer. The photosynthetic active leaf area index (LAI_{act}) was destined by multiplying Leaf Area Index (LAI) of the layers with their relative chlorophyll contents:

$$LAI_{act} = CHL_1 * LAI_1 + CHL_2 * LAI_2 + CHL_3 * LAI_3$$
(Data see Alscher 1993). (8)

The photosynthetic active leaf area index as a function of LAI was calculated by an exponential function:

$$LAI_{act} = A * [1 - \exp(a * LAI)] \quad (9)$$

LAI_{act} = photosynthetic active Leaf Area Index (m^2m^{-2}); LAI = Leaf Area Index (m^2m^{-2}); CHL = relative chlorophyll content in the respective layer; A = theoretical maximum of LAI_{act}; a = coefficient

As shown in figure 5, the decline of LAI_{act} with increasing LAI can be calculated rather precisely and begins to deviate remarkable with LAI >3.

Interception of light
Light interception properties depend on scattering, reflection, transmission and absorption. Since leaf area distribution and therewith light interception properties of lettuce differ considerably from those of wheat with more spherical distributed leaves (GOUDRIAAN 1977), respective parameters had to be determined. This was performed by tube solarimeters (1 m length) at the top of the canopy, between the rows and beneath the leaves. Incomming global irradiances (R_{flux} in Wm^{-2}) was measured by a radiometer (Kipp & Zonen). Radiant fluxes are calculated according to GOUDRIAAN (1977):

Fraction of global radiation reflected by the leaves (Re_{flux} in %):

$$Re_{flux} = A * [1 - \exp(a_1 * LAI_{act})] \quad (10)$$

A = theoretical maximal value; a = coefficient; LAI_{act} = photosynthetic active Leaf Area Index

Figure 6 shows reflection, increasing with LAI_{act} as a saturation function, approaching a value of about 0,25.

Fraction of global radiation transmitted (T_{flux}) through the leaves (%):

$$T_{flux} = \exp(-E * LAI_{act}) \quad (11)$$

E = extinction coefficient for diffuse light

Figure 7 illustrates the asymptotically decreasing transmission as a function of LAI_{act} approaching zero. The transmission measurements resulted in an extinction coefficient of 0,29.

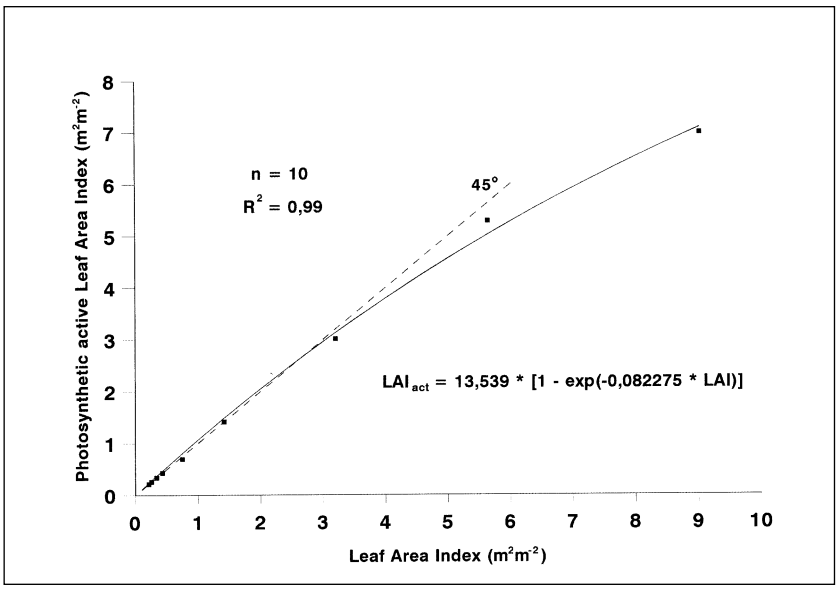


Fig. 5. Relation between photosynthetic active Leaf Area Index estimated by function (9) and Leaf Area Index calculated by dividing leaf area by leaf weight.
Beziehung zwischen dem mit Funktion (9) geschätzten photosynthetisch aktiven Blattflächenindex und dem aus dem Quotienten Blattfläche und Blatttrockengewicht errechneten Blattflächenindex.

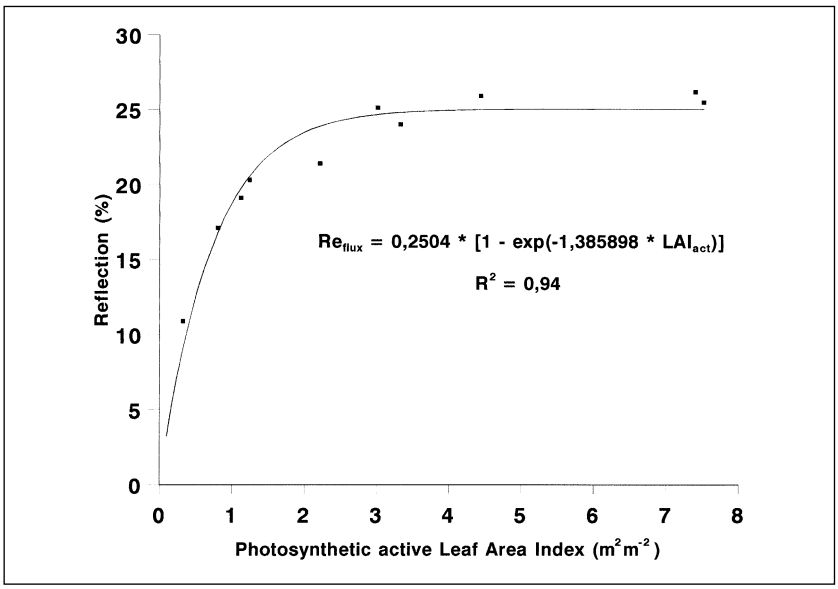


Fig. 6. Relation between radiation flux reflected by lettuce leaves and photosynthetic active Leaf Area Index.
Beziehung zwischen dem von Salatblättern reflektierten Strahlungsflux und dem photosynthetisch aktiven Blattflächenindex.

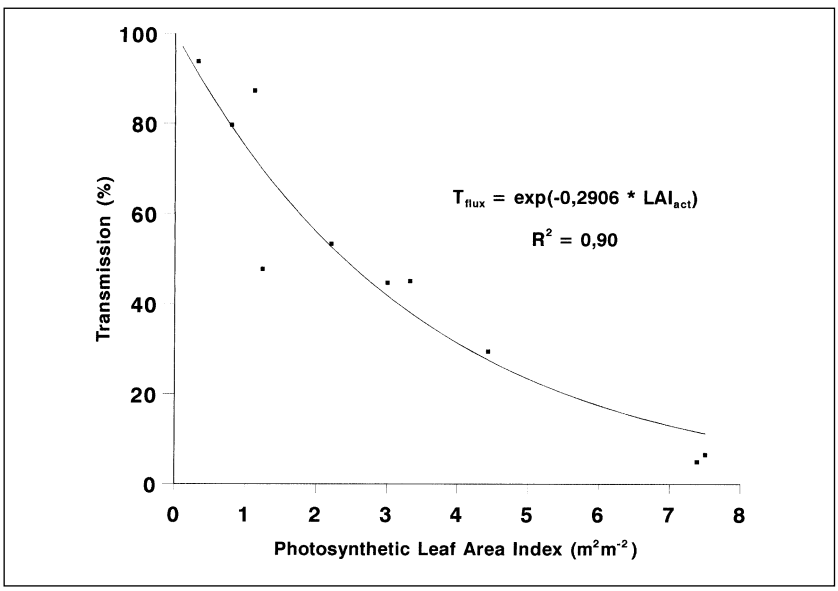


Fig. 7. Relation between radiation flux transmitted by lettuce leaves and the photosynthetic active Leaf Area Index.
Beziehung zwischen der transmittierten Globalstrahlung von Salatblättern und dem photosynthetisch aktiven Blattflächenindex.

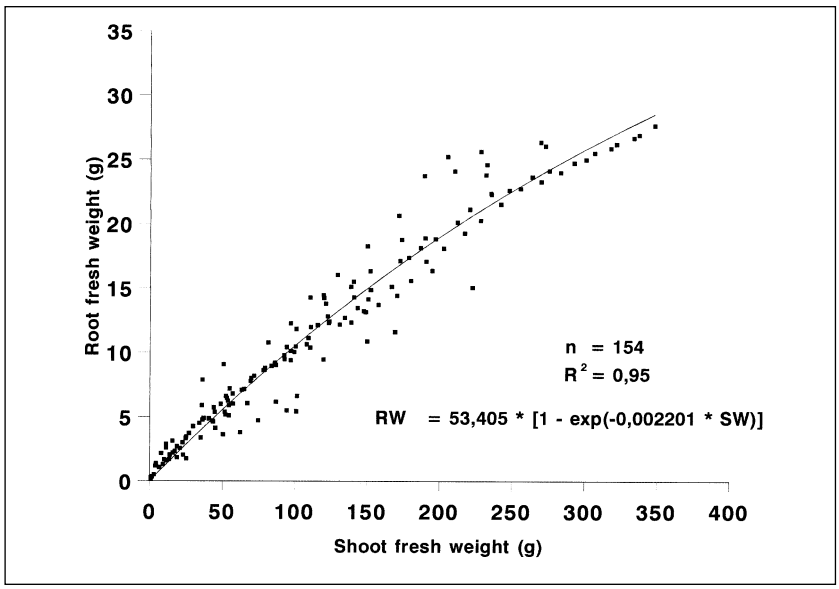


Fig 8. Relation between root and shoot fresh weight of lettuce (data of plants grown in nutrient solution in growth chambers (gained by BRUMM 1992).
Beziehung zwischen dem Wurzel- und Sproßfrischgewicht von Kopfsalat (Daten von Pflanzen in Nährlösungen und aus Klimmakammerversuchen von BRUMM 1992).

Absorbed global radiation by the leaves (A_{flux}, Wm^{-2}):

$$A_{flux} = R_{flux} - (1 - Re_{flux}) * R_{flux} * \exp(-E * LAI_{act}) \quad (12)$$

R_{flux} = global radiation at the surface of the crop

The scattering coefficient (SCA) was calculated by:

$$SCA = -(1-HVAR) * (1+HVAR)^{-1} * (1-HVAR) * (1+HVAR)^{-1} + 1 \quad (13)$$

$$HVAR = REFS * (1+1{,}6\ SINS) * 2^{-1} \quad (14)$$

HVAR = Auxiliary variable; REFS = reflection coefficient of spherical distributed leaves; SINS = sinus of angle of incoming direct radiation (Data see Alscher 1993).

Photosynthesis and respiration
To adapt **photosynthesis** of lettuce to the table function developed for wheat (GOUDRIAAN 1977), the values of temperature dependent mesophyll conductivity and for maximal photosynthesis of lettuce were shifted according to LORENZ and WIEBE (1980, irradiance 18 and 37 W m^{-2} for 10 h d^{-1}) to a maximum of 5 °C.

SUCROS parameters for **maintenance respiration**, based on the experiments of PENNING DE VRIES and VAN LAAR (1982), are considered to be of universal validity with cold adapted species and accepted. **Growth respiration** of shoot and root were calculated according to CROSPY (1963, data see Alscher 1993).

Dry matter partitioning
Shoot and root growth relationships are a function of the species and the environmental conditions (BROUWER 1967). Due to the enormous expenditure and methodical difficulties respective data are scanty. For lettuce only data of crops grown in nutrient solution and in growth chambers were available (BRUMM 1992; STEINGROBE 1992). As demonstrated in figure 8 these data can be parameterized by an allometric function and were used to calculate root fresh weight (RW in g):

$$RW = A * [1 - \exp(a * SW)] \quad (15)$$

SW = shoot fresh weight (g); A = theoretical maximum of root weight; a = coefficient

4 Comparison of the response surfaces of the REGRESSION and the SUCROS MODEL

To compare the parameters derived by the REGRESSION model and the SUCROS model the data of the experiment 1991, which were not included to calculate the response surfaces of the regression k-model, were used to calculate the RGR from planting to 60 g fresh weight and related to the intensities of radiation, temperature and CO_2 concentration. In figure 9 it is obvious that the response surfaces of the two models differ considerably. In an average the RGR of the SUCROS model are higher than those of the regression model, but fitting to the measured data is inferior.

This can be explained by the fact that the SUCROS model parameters describe potential growth, which in periods with suboptimal environmental conditions must be superior to real growth.

Concerning the slopes of the curves the measured data are to concentrated to allow for any judgement. Remarkable, however, are:
- higher RGR of the Regression model with irradiances up to about 800 $Whm^{-2}d^{-1}$, due to a stronger increase with very low irradiances
- the steep increase of RGR of the SUCROS model up to a temperature of 5 °C, which is in contrast to the results of LORENZ and WIEBE (1980) and has to be verified
- concerning CO_2 concentration ≥ 600 μLL^{-1}, the slopes of the two curves are comparable.

In conclusion the parameters of the two models differ and – in the range tested – those of the REGRESSION model are closer to reality than those derived for the SUCROS model.

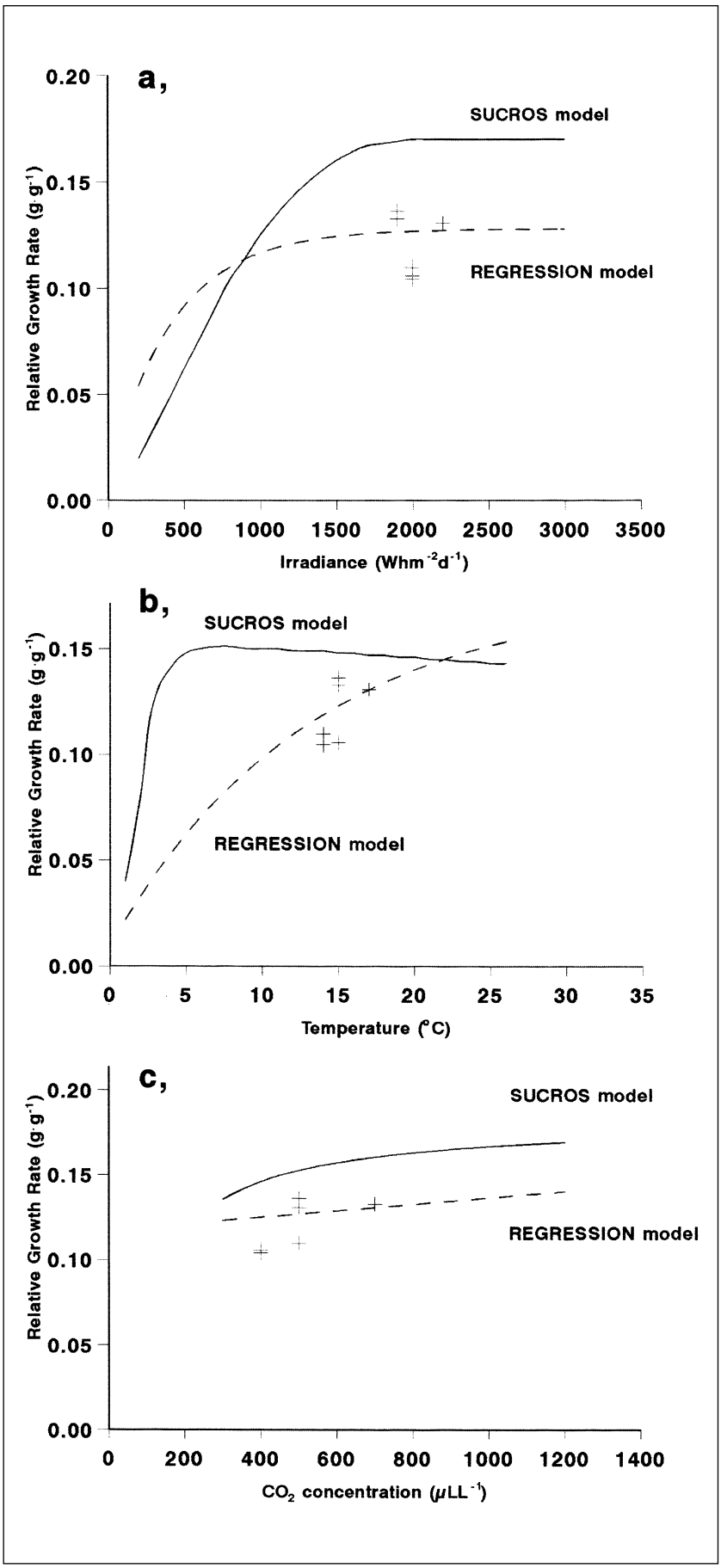


Fig. 9. Comparison of RELATIVE GROWTH RATES (60 g fw.), estimated by the REGRESSION MODEL and by the SUCROS MODEL as a function of:
a. irradiance (temperature 16 °C, CO_2 concentration 500 µLL^{-1})
b. temperature (irradiance 2100 Whm^{-2}d^{-1}, CO_2 concentration 500 µLL^{-1})
c. CO_2 concentration (irradiance 2100 Whm^{-2}d^{-1}, temperature 16 °C).
Vergleich der RELATIVEN WACHSTUMSRATEN (60g FG.), geschätzt mittels des REGRESSIONS- und des SUCROS-Modells als Funktion der:
a. *Bestrahlungsstärke (Temperatur 16 °C, CO_2 Konzentration 500 µLL^{-1})*
b. Temperatur (Bestrahlungsstärke 2100 Whm^{-2} d^{-1}, CO_2-Konzentraton 500 µLL^{-1})
c. CO_2 Konzentration (Bestrahlungsstärke 2100 Whm^{-2}d^{-1}, Temperatur 16 °C).

5 Discussion

All models are approximations to reality, each of them with preferences and weak points, which have to be weighted according to the respective goal. The general features of the two models used are discussed by KRUG and LIEBIG (1979a, 1979b, 1984b, 1994; PENNING DE VRIES 1983) and will not be recapitulated here.

Concerning the **REGRESSION MODEL** one simplification is the use of mean intensities of the growth factors. Regarding irradiance and temperature this proved to be justified for several species [irradiance – kohlrabi (LIEBIG 1988; FINK 1991); temperature – tomato (CALVERT 1964; HUSSEY 1965), cucumber (KRUG and LIEBIG 1981), radish (KRUG 1991)], but others, such as lettuce (WIEBE and LORENZ 1977) reacted specifically to the diurnal amplitude. Since the night temperature was very low and did not differ much, this reaction was not incorporated in this investigation.

Regarding CO_2 concentration the statement of MORTENSEN (1984) of superiority of intermittent CO_2 enrichment was disproved by MORTENSEN (1986, 1987), NEDERHOFF and VAN UFFELEN (1988). Also the experiments presented here confirm that plants – here lettuce – are able to integrate varying CO_2 concentrations to a mean concentration, facilitating the statistical evaluation.

In former investigations the CO_2 effect was integrated into the regression function by a multiplicative term, considering the interaction with irradiance and temperature (MANN 1986; CHALLA 1989; KRUG and LIEBIG 1994). In this evaluation the interaction to irradiance and temperature was not significant. Therefore an additive term, resulting in the highest coefficient of determination, was preferred. This procedure, however, overestimates the CO_2 effect $< 500\,\mu L L^{-1}$ (fig. 9).

The influence of the ontogenetic age was considered by classifying into formal defined growth phases, which had proved to be most suitable during the vegetative phase of radish (BAZLEN 1985) and other crops (see KRUG and LIEBIG 1994). The reactions within these phases were parameterized by a multiplicative regression function (KRUG and LIEBIG 1984b, 1994), based on the MITSCHERLICH function (MITSCHERLICH 1919). The parameters of the MITSCHERLICH function are considered to represent physiological meanings, which would enlighten the black box and easen calculation and interpretation. According to the parameters listened in table 2 this cannot be confirmed for A (theoretical maximal weight), which differs considerably between the phases. A deviates especially from a physiological reasonable value with young plants with an exponential increase in weight. It decreases with the ontogenetic age and in further experiments it should be tested, if an A value derived from a more or less complete growth curve can be used for all ontogenetic phases.

The coefficients of temperature, radiation and CO_2 do not show reasonable relations as well, which could be interpreted physiologically. Over that the introduction of compensation points and a temperature minimum did not improve approximation, as already shown by MANN (1986). Therefore, the REGRESSION model, as it has been used here, has still to be considered as a predominantly statistical approach.

In the bulk of these data, in contrast to MANN (1986), who used part of these data and to other investigations and species (KRUG and LIEBIG 1979b, 1988, 1994), no special seasonal effects could be identified. The same was true for radish var. niger (KRUG and LIEBIG 1984a). Until now these discrepancies cannot be explained. Regarding this investigation it cannot be excluded that integration of so many experiments, run in different years, the seasonal effect was covered over by variability. Despite of these deficiencies the coefficients of determination were rather high and validation resulted in a good approximation. Despite of some deficiencies REGRESSION models proved reliable to estimate growth rates in periods ≥ 24 hours, if the boundary conditions are comparable (CHALLA 1989; KRUG and LIEBIG 1994, 1995).

Concerning the **physiological – dynamic growth model** SUCROS the structure could be accepted from Spitters et al. (1989), but the parameters for the lettuce crop had to be worked out. A main problem was the aspherical distribution of the leaves by heading with its consequences for light interception.

Regarding **reflection** the measured data could be presented rather precisely by the exponential function (fig. 5). The values with a maximum of 25 %, however, look rather high compared to the value of 5 % with wheat (GOUDRIAAN 1977). Also the measurements to determine **transmission** produced reasonable data (fig. 6), resulting in an extinction coefficient of maximal 0,29, parameterizing **absorption**. This value differs considerably from the theoretical value of 0,79 (SPITTERS et al. 1989). This difference may be explained by the specific morphology of lettuce, but uncertainties of classifying the leaves into leaflayers and in assuming a linear relationship between chlorophyll content and photosynthesis will have attributed. In this module more detailed experiments are needed.

Some uncertainties exist by accepting data from PENNING DE VRIES and VAN LAAR (1982) for **respiration** of lettuce heads, by using data from the same authors for temperature dependent mesophyll conductivity, which were adapted to temperature reaction of photosynthesis worked out by LORENZ and WIEBE (1980). In general parameterization of photosynthesis by the SUCROS model is considered to be rather reliable. If this applies to heading crops such as lettuce, has to be confirmed.

In the mechanistic models **dry matter partitioning** is parameterized by an allometric function, that means at a descriptive level and suffers by lack of data. According to BROUWER (1967) the relation between shoot and root is not constant, but it is depending on the environment. By integrating modification factors the varying influences of climate, water and nutrition status of the crop on dry matter partitioning can be taken into account (LOOMIS et al. 1979, VAN KEULEN and SELIGMANN 1987). In these experiments with lettuce in the vegetative phase and without extreme conditions the relation between shoot and root fresh weight could be parameterized by an exponential function with high coefficients for determination (fig. 8).

In general it can be concluded that the physiological dynamic growth models, beyond their explaining value, are suitable to react very quickly to changing climatic conditions, but because of lack of knowledge and of considering after-effects and error propagation they do suffer by considerable deviations from reality in long term simulations (literature see Alscher 1993).

By comparing the response surfaces of the two approaches with each other and with measured data, the validity of the two models can be tested. Figure 9 shows some weak points of both approaches. These are especially concerning the SUCROS model low temperature reaction and general overestimation by calculating growth potential, concerning the REGRESSION model high temperature reaction and overestimation of the CO_2 effect at low concentrations. This means that both approaches have to be improved by more detailed investigations.

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Eingereicht: 01. 10. 98/06. 10. 00

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