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Calibration and validation of the crop growth model LINTUL for grain amaranth (*Amaranthus* sp.)

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Summary

Grain amaranth, a C_4 plant, is a promising pseudocereal due to its valuable grain components. Knowledge of crop growth parameters is crucial for the introduction of a new crop, and the use of a crop model can help to understand yield formation and yield limiting processes. The aim of the study was to parameterise and validate the model LINTUL for grain amaranth. Basically, LINTUL estimates dry matter production from daily intercepted radiation and light use efficiency under potential growth conditions, i. e. without occurrence of any other limiting factors. A field experiment with the *A. hypochondriacus* genotypes „Neuer Typ" and „Anderer Typ" was carried out under semiarid conditions in 2004 and 2005. Field data of individual years were used for parameterisation while independent observations of the other year allowed for cross-validation, respectively. The estimated light use efficiency ranged between 2.5 and 2.8 g MJ^{-1} (total biomass per accumulated PAR). Specific leaf area estimates were lower in observations of 2004 (0.014 m^2 g^{-1}) than in observations of 2005 (0.018 m^2 g^{-1}). The light extinction coefficient of both genotypes measured before heading was 1.1. The effective sum of temperature (above a given threshold of 8°C) to anthesis was 554°C d for the genotype „Neuer Typ" and 640°C d for „Anderer Typ" in both years. The effective sum of temperature to maturity was 1127°C d in 2004, and 1249°C d in 2005 independent of the genotype. Model predictions of total biomass agreed well (RMSE: 92 to 136 g m^{-2}) with the observed biomass throughout the growing cycle including final harvest (between 749 and 1172 g m^{-2}). The estimated grain yield over time (RMSE: 47 to 112 g m^{-2}) matched the field observations including final grain yield (between 220 and 367 g m^{-2}) with less accuracy. The leaf area index was overestimated throughout the growing cycle from heading onwards to seed filling. The sharp initial increase in grain yield was underestimated suggesting that currently produced assimilates could not meet the growth capacity of the young seeds but might be complemented by internal re-translocation of biomass.

Introduction

Grain amaranth is a promising crop due to its valuable grain components. However, the low grain yield level in comparison to common cereals seems to constrict the future market opportunities of the crop. The generally low yield potential of grain amaranth is due to various reasons. Firstly, breeding work on amaranth has been marginal compared to common crops. Secondly, physiological properties of the plant might restrict the yield level. So far, little is known quantitatively about processes that limit the formation of grain yield in amaranth. The detailed analysis of crop growth parameters, the analysis of plant growth and development over time and in dependency on weather conditions may help to better understand yield formation and to reveal physiological limitations of growth and grain production.

LINTUL (Light INTerception and UtiLisation) is a generic crop growth model that follows a mechanistic approach. It was developed by simplifying the model SUCROS and was originally applied to the growth of potato (SPITTERS, 1990; SPITTERS and SCHAPENDONK, 1990). Later it was also used for different growth analysis purposes in maize (FARRÉ et al., 2000), rapeseed (HABEKOTTÉ, 1997), crambe (MATHIJSSEN and MEIJER, 1995) and grassland (SCHAPENDONK et al., 1998; RODRIGUEZ et al., 1999). LINTUL type models have the advantage that only low data input is required and model parameterisation is facilitated (BOUMAN et al., 1996). Thus, the LINTUL approach was also used for agro-ecological characterisation of potato production (VAN KEULEN and STOL, 1995), for the prediction of potential and water-limited global food production (PENNING DE PENNING DE VRIES et al., 1995) and for the simulation of wheat production under climatic change (WOLF et al., 2002). The objective of the present study was to parameterise and validate the model LINTUL for grain amaranth under potential growth conditions. The obtained parameter values shall deliver insight into limitations of growth and yield formation of grain amaranth compared to other crops. This knowledge can help to improve crop management decisions as well as breeding efforts. Furthermore, the parameterisation shall enable to include the niche crop in agro-ecological modelling approaches.

The following questions were addressed:
– Which is the range of the required physiological crop parameters for grain amaranth? Are there differences between the tested amaranth genotypes? How do parameter values differ from those of other grain crops or C_4 plants?
– Is the parameterised model able to predict leaf area, total crop biomass and biomass of individual plant compartments, especially grain yield accurately over time when compared to independent field data?

Materials and methods

Field experiments

Field experiments were conducted on the experimental farm Groß-Enzersdorf (48°15´N, 16°37´E; 153 m a. s. l.) in Eastern Austria during the growing seasons of 2004 and 2005. Mean annual precipitation at the location is 546 mm, mean annual temperature is 9.8°C. Tab. 1 shows weather data of the two vegetation periods. The soil type at the location was classified as a chernozem of alluvial origin which is rich in calcareous sediments. The texture ranges between silty loam and loamy silt. Content of humus is between 2.2 and 2.3%. Tab. 2 gives information on the field experiments. Due to the high level of soil mineral nitrogen and the high supply of P and K at the site, no fertiliser was added. Plots were irrigated twice, at the beginning of flowering and at the start of grain filling.

The experimental design was a randomised block in a split plot arrangement with two replications. Two grain amaranth genotypes were established on main plots, two crop densities on subplots. The desired crop densities of 8 and 70 plants m^{-2} were established by hand-thinning. The breeder G. Dobos, ZENO PROJEKTE, Vienna, Austria, provided the seeds of the genotypes which result from progenies of crossbreds: „Neuer Typ" (*A. hypochondriacus*) is an

early-maturing, strongly branching, semi-dwarf type reaching a plant height between 85 and 100 cm at the experimental site. „Anderer Typ" (*A. hypochondriacus*) is similar to „Neuer Typ" with respect to grain maturity, but about one week later in flowering. It is hardly branching, shows a rather compact inflorescence and reached plant heights between 115 and 130 cm under given conditions.

Plants were sampled between emergence and maturity at six dates in 2004 and at eight dates in 2005. At each sampling date, total aboveground biomass was determined by harvesting 1.125 m^2 per plot. Ten randomly chosen plants per plot were used for the determination of the dry matter weights (48h, 100°C) of green leaves, senescent leaves on the plant, stems (including chaff), seeds and roots. Roots were sampled by digging out cuboids (40 x 40 x 28 cm^3) of the soil round the harvested plant using a spade. Subsequently, roots

were separated from earth, cleaned and dried. Total crop biomass was computed as the sum of harvested above ground biomass per area and root biomass. Root biomass resulted from aboveground biomass multiplied by the percentage of root weight of ten plants. Leaves with more than 50% yellow-coloured blade area were defined as being senescent. The green leaf area of ten plants was determined using a LI-3100 Area Meter (LICOR).

Model description and implementation

The model LINTUL was used for simulating crop growth of grain amaranth due to its comparatively low data requirements which allow for a wide-spread application. LINTUL is based on the linear relationship between produced biomass and the amount of radiation intercepted by the crop canopy which is a reasonable assumption under favourable growth conditions (MONTEITH, 1977). The applied version LINTUL 1 simulates potential crop growth under well-watered conditions, ample nutrient supply and the absence of pests, diseases and weeds (VAN ITTERSUM et al., 2003). Biomass production is based on intercepted radiation according to Lambert-Beer's law and an experimentally derived value of light use efficiency. The produced biomass is partitioned among various crop organs (leaves, stems, storage organs and roots) according to partitioning coefficients (kg organ biomass kg^{-1} total biomass) defined as a function of the development stage of the crop. The software ModelMaker (version 4, Cherwell Scientific) was used to implement the model equations and to run simulations. Model equations were obtained from the version LINTUL 1 as published by the DE WIT Graduate School for Production Ecology (1997).

Tab. 1: Mean monthly temperature, total monthly precipitation and total incident monthly photosynthetic active radiation (PAR) during the 2004 and 2005 growing seasons

	Year	May	June	July	Aug.	Sep.	Oct.
Temperature	2004	13.8	17.4	19.9	20.7	15.4	11.6
(°C)	2005	15.7	18.6	20.5	18.7	16.2	10.4
Precipitation	2004	51.0	51.0	24.8	21.8	32.4	53.6
(mm)	2005	43.4	43.4	94.6	65.4	34.8	4.0
Incident PAR	2004	232.0	280.9	299.0	220.6	154.7	67.4
(MJ m^{-2})	2005	302.3	222.2	213.5	189.0	134.2	83.8

Tab. 2: Details of the field experiments during the 2004 and 2005 growing seasons

		2004		2005	
Soil mineral N, 0–90cm		5 May, 163 kg N ha^{-1}		12 May, 166 kg N ha^{-1}	
P (CAL), 0–30cm / 30–60cm		88 / 74 mg kg^{-1}		92 / <20 mg kg^{-1}	
K (CAL), 0–30cm / 30–60cm		255 / 222 mg kg^{-1}		264 / 80 mg kg^{-1}	
Soil pH		7.7		7.5	
Sowing date		27 May		11 May	
Fertilisation		none		none	
Irrigation treatments		21 July, 20 mm		6 July, 20 mm	
		3 August, 20 mm		18 July, 20 mm	
Insecticide		15 June, Deltamethrin		30 May, Deltamethrin	
Weed control		Mechanical and hand-weeding		Mechanical and hand-weeding	
Row spacing		37.5 cm		37.5 cm	
Crop density	Neuer Typ sparse crop	9 pl. m^{-2}		8 pl. m^{-2}	
(across sampling dates)	Neuer Typ dense crop	49 pl. m^{-2}		49 pl. m^{-2}	
	Anderer Typ sparse crop	9 pl. m^{-2}		8 pl. m^{-2}	
	Anderer Typ dense crop	51 pl. m^{-2}		53 pl. m^{-2}	
Sum of temp$_{eff}$ (°C d)	Neuer Typ	554		554	
from emergence to anthesis	Anderer Typ	641		640	
	Date 1 = Emergence	7 June	0.0	25 May	0.0
	Date 2	28 June	198.1	16 June	202.4
	Date 3	8 July	305.4	30 June	392.1
Sum of temp$_{eff}$ (°C d)	Date 4	26 July	532.1	13 July	517.2
at sampling dates	Date 5	-	-	22 July	640.9
	Date 6	16 Aug.	808.6	2 Aug.	809.7
	Date 7	-	-	9 Aug.	876.8
	Date 8 = Maturity	16 Sept.	1126.5	12 Sept.	1248.9

Initial values

Average dry weights of plant organs (stems, leaves, roots) and leaf area at emergence were determined by sampling 75 seedlings per genotype grown under green house conditions to enable quick and homogeneous germination (Tab. 3). Sampling was carried out when more than 90% of the plants had emerged. A WinDIAS colour image analysis system was used for measuring initial leaf area.

Weather data

Daily global incoming radiation and average daily temperature were obtained from an automatic weather station close to the experimental plots. Photosynthetic active radiation (PAR) was calculated as 50% of global radiation. The sum of temperature was calculated by accumulating the daily values of effective temperature after emergence above a base temperature of 8°C. This threshold temperature was chosen in accordance with the base temperature for leaf appearance in *Amaranthus retroflexus* which was found to be about 8.5°C (GRAMIG and STOLTENBERG, 2007).

Tab. 3: Initial values: dry matter weight of plant organs and leaf area per seedling (means across genotypes)

	Start value (per seedling)	Standard error of mean
Stem (g pl^{-1})	0.211 x 10^{-3}	9.55 x 10^{-6}
Root (g pl^{-1})	0.219 x 10^{-3}	30.4 x 10^{-6}
Leaf (g pl^{-1})	0.380 x 10^{-3}	17.9 x 10^{-6}
Leaf area (m^2 pl^{-1})	0.0147 x 10^{-3}	0.586 x 10^{-6}

Estimation of model parameters

Light use efficiency was estimated by a linear regression of total biomass per area (including roots and senescent leaves on the plant) on cumulative intercepted radiation. The last sampling date was excluded because of unmeasured weight losses due to scattered leaves and negligible increase in biomass. This approach was already applied by FARRÉ et al. (2000) who estimated the light use efficiency of maize on the basis of measurements before anthesis only. Cumulative intercepted radiation was calculated by summarising daily intercepted radiation according to the function of Lambert-Beer. The essential daily leaf area index was derived by linear interpolation between leaf area indices of green leaves at sampling dates.

A crop-specific light extinction coefficient of 1.1 (standard error: 0.27) was determined by using a SunScan Canopy Analysis System (setting: Beer's law) at ear emergence in 2005. The instrument was not available in 2004, but a substantial year effect on this parameter is not expected. The SunScan device uses a probe of 1 m length for measurements of incident and transmitted photosynthetic active radiation. Four measurements per plot were carried out, two measurements along the rows and two measurements rectangular to the rows. One measurement consisted of one reading above the canopy followed by four readings measured in trans-sections below the canopy. No effects of genotype or crop density on the light extinction coefficient were observed.

The initial relative growth rate of leaf area was assumed to increase exponentially over thermal time as long as the temperature sum is below 330°C d and the leaf area index is below 0.75 according to SPITTERS et al. (1989). A linear regression was calculated of the natural logarithm of the increase in leaf area index, i.e. ln(LAI/LAI$_{initial}$), on the effective sum of temperature. During later development stages, it was assumed that leaf area expands in proportion to the increase in leaf dry weight, and it is calculated by multiplying the increase in leaf dry weight by the specific leaf area. Specific leaf area was determined by a linear regression of leaf area on leaf weight across all sampling dates.

Leaf senescence was assumed to be driven by ageing which starts at anthesis and by self shading which starts beyond a critical leaf area index of 4 according to SPITTERS et al. (1989). It was assumed that the death rate due to ageing depends on average daily temperature using a tabled function with linear interpolation ($\leq$10°C, 0.03; 15°C, 0.04; $\geq$30°C, 0.09). The death rate due to shading was supposed to increase linearly till a maximum of 0.03 at a leaf area index of 8. Anthesis was defined as the development stage when about 50% of the inflorescence showed anthers.

Daily produced biomass was allocated to the organs roots, green leaves, stems (including chaff) and seeds by distribution factors obtained from the plant samplings. The relative fraction shares were tabulated and linearly interpolated as a function of thermal time. The portion of biomass allocated to each plant organ was derived by dividing the increase in biomass of a plant organ by the increase in total biomass between subsequent harvest dates. The slight decrease in weight of leaves or roots at late growth stages was assumed to show that no more biomass was allocated to these plant organs. A slight increase in stems (including chaff) between the last two harvest dates was ignored, and it was assumed that the produced biomass was totally allocated to the seeds.

Model testing and statistical analysis

Calibration and validation of the model were done separately for each genotype (across both crop densities). Cross validation was carried out by using independent field data of two years (2004 and 2005). Parameter estimates based on the field experiment in 2004 were used for the simulation of growth and development under environmental conditions of 2005 and observed field data of 2005 were used for the validation of the model, and vice versa.

The parameter estimates based on regression equations were statistically evaluated by calculating the significance of the regression line and the standard error of the parameters. Comparisons were made between simulated and observed values. Root mean squared errors and mean absolute percent errors were calculated using the software IRENE (Integrated Resources for Evaluating Numerical Estimates), version 1, developed by the Research Institute for Industrial Crops, Bologna, Italy (FILA et al., 2001). Furthermore, regression analyses between simulated and observed values were carried out.

Results

Model parameterisation

Model parameters based on the data of different years and genotypes allow the characterisation of environmental and genotypic effects on crop growth. Estimated model parameters and regression statistics are given in Tab. 4. All regressions were highly significant.

The estimated light use efficiency ranged between 2.48 and 2.84. Obviously, both genotypes were more efficient in producing biomass in 2005 than in 2004. The 2005 environment was characterised by higher precipitation in July and August, but by lower radiation throughout the growing season compared to the 2004 environment. Environmental differences also affected specific leaf area and initial growth rate of leaf area. The higher specific leaf area in 2005, i.e. thinner leaves, is presumably due to higher rainfalls. However, the initial growth rate of leaf area was higher in the 2004 environment than in the 2005 environment.

Genotypic differences were obvious with regard to crop development and also with respect to the allocation of biomass to plant organs. Thermal time from emergence to full flowering was shorter with

„Neuer Typ" than with „Anderer Typ", and consequently grain yield formation started earlier with „Neuer Typ". The portion of biomass allocated to leaves of both genotypes was highest during early plant development when plant height was about 10 cm and the first leaves were formed. From the phase of stem elongation onwards (305-390°C d), a higher rate of biomass was distributed to leaves in „Anderer Typ" than in „Neuer Typ" Tab. 5.

Model testing

The time-courses of simulated and observed total biomass (including senescent leaves and root biomass), leaf area index of green leaves and grain yield of the two environments (2004 and 2005) are given in Fig. 1, 2 and 3, respectively. Fig. 4 shows regressions of simulated versus observed values throughout the growing season.

Total biomass was simulated well by the model in both environments.

Tab. 4: Estimated parameters based on field experiments in 2004 and 2005 (LUE = light use efficiency, SLA = specific leaf area, IGRL = initial relative growth rate of leaf area, sum of $temp_{eff}$ = temperature sum above a base temp. of 8°C)

Year	Genotype	LUE $(g\ MJ^{-1})$	Standard error	Sign. (P)	SLA $(m^2\ g^{-1})$	Standard error	Sign. (P)	IGRL $(°C^{-1}\ d^{-1})$	Standard error	Sign. (P)	Sum of $temp_{eff}$ $(°C\ d)$ to anthesis
2004	Neuer Typ	2.58	0.103	<0.0001	0.0144	0.578×10^{-3}	<0.0001	0.0290	1.620×10^{-3}	0.0031	554
	Anderer Typ	2.48	0.056	<0.0001	0.0136	0.775×10^{-3}	<0.0001	0.0298	0.707×10^{-3}	0.0151	641
2005	Neuer Typ	2.72	0.053	<0.0001	0.0177	0.632×10^{-3}	<0.0001	0.0272	0.304×10^{-3}	0.0071	554
	Anderer Typ	2.84	0.085	<0.0001	0.0178	0.383×10^{-3}	<0.0001	0.0268	0.272×10^{-3}	0.0065	640

Tab. 5: Estimated dry matter partitioning coefficients based on field experiments in 2004 and 2005

Year	Genotype	Sampling date	Sum of $temp_{eff}$ $(°C\ d)$	Root	Stem + chaff	Leaf	Seed
2004	Neuer Typ	1	0	0.270	0.261	0.469	0.000
		2	198	0.145	0.188	0.668	0.000
		3	305	0.161	0.451	0.388	0.000
		4	532	0.082	0.816	0.102	0.000
		5			no sampling		
		6	809	0.000	0.278	0.000	0.722
		7			no sampling		
		8	1127	0.000	0.000	0.000	1.000
2004	Anderer Typ	1	0	0.270	0.261	0.469	0.000
		2	198	0.170	0.188	0.642	0.000
		3	305	0.185	0.387	0.429	0.000
		4	532	0.098	0.673	0.228	0.000
		5			no sampling		
		6	809	0.007	0.636	0.000	0.357
		7			no sampling		
		8	1127	0.000	0.000	0.000	1.000
2005	Neuer Typ	1	0	0.270	0.261	0.469	0.000
		2	202	0.107	0.180	0.713	0.000
		3	392	0.152	0.484	0.365	0.000
		4	517	0.080	0.796	0.124	0.000
		5	641	0.037	0.779	0.067	0.117
		6	810	0.012	0.249	0.000	0.740
		7	877	0.044	0.030	0.000	0.926
		8	1249	0.000	0.000	0.000	1.000
2005	Anderer Typ	1	0	0.270	0.261	0.469	0.000
		2	202	0.104	0.167	0.729	0.000
		3	392	0.176	0.380	0.445	0.000
		4	517	0.101	0.687	0.212	0.000
		5	641	0.105	0.809	0.086	0.000
		6	810	0.023	0.672	0.000	0.305
		7	877	0.037	0.324	0.000	0.640
		8	1249	0.000	0.000	0.000	1.000

With respect to crop density, the model calculates necessarily higher total biomass for the dense stands due to higher initial values. Root mean squared errors of predicted biomass figures for the 2004 and the 2005 environment were similar and amounted to values between 92 and 136 g m^{-2} (Tab. 6). Relative root mean squared errors were between 18 and 28% of the mean observed biomass.

The leaf area index (Fig. 2) and the weight of green leaves (data not shown) were highly over-predicted by the model, especially throughout the period from heading to seed filling (sampling dates 3-6). This overestimation was most evident when simulating crop growth under environmental conditions of 2004 with parameters based on observations of 2005. While the observed leaf area index was between 1.2 and 2.3 at the most, the simulated values mounted up to values between 2.1 and 3.4 under growing conditions of 2005 and even to values between 3.9 and 5.9 under growing conditions of 2004. As a consequence, root mean squared errors were high, being 71-219% of the mean observed leaf area index. Regression of simulated versus observed leaf area index showed that the over-estimation was highest at sampling date 4 when the crops started flowering.
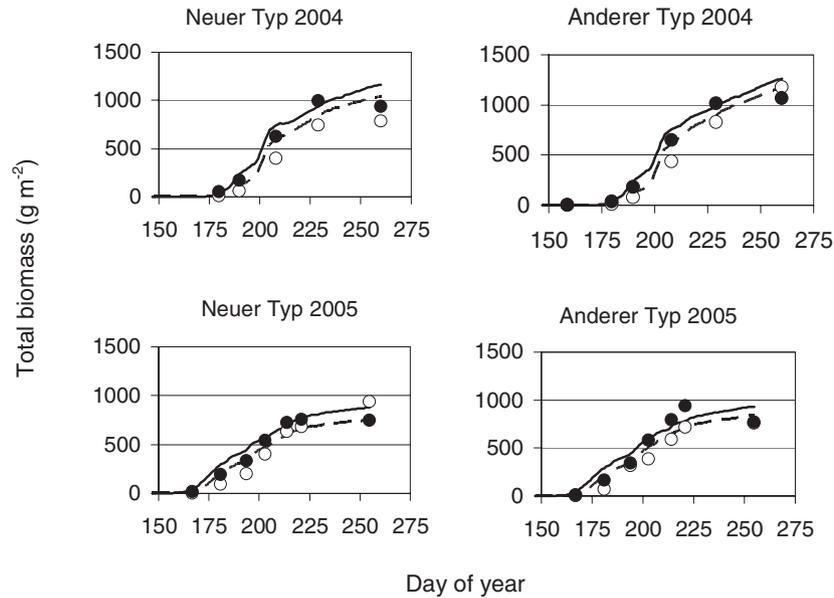
Fig. 1: Simulated and observed total biomass of two genotypes at two plant densities during crop development in 2004 and 2005
  ○ Observed (sparse crop)
  ● Observed (dense crop)
  - - - - Simulated (sparse crop)
  ─── Simulated (dense crop)
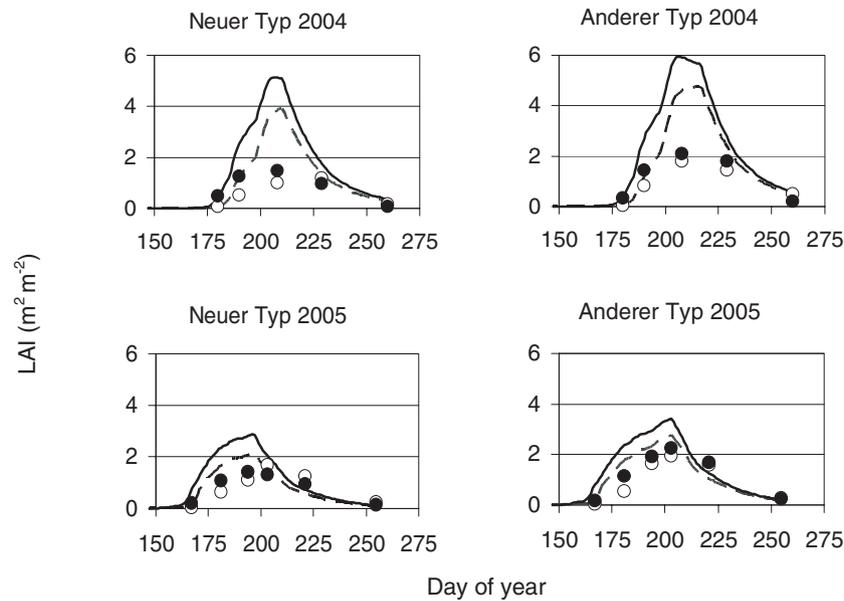
Fig. 2: Simulated and observed leaf area index of green leaves of two genotypes at two plant densities during crop development in 2004 and 2005
  ○ Observed (sparse crop)
  ● Observed (dense crop)
  - - - - Simulated (sparse crop)
  ─── Simulated (dense crop)
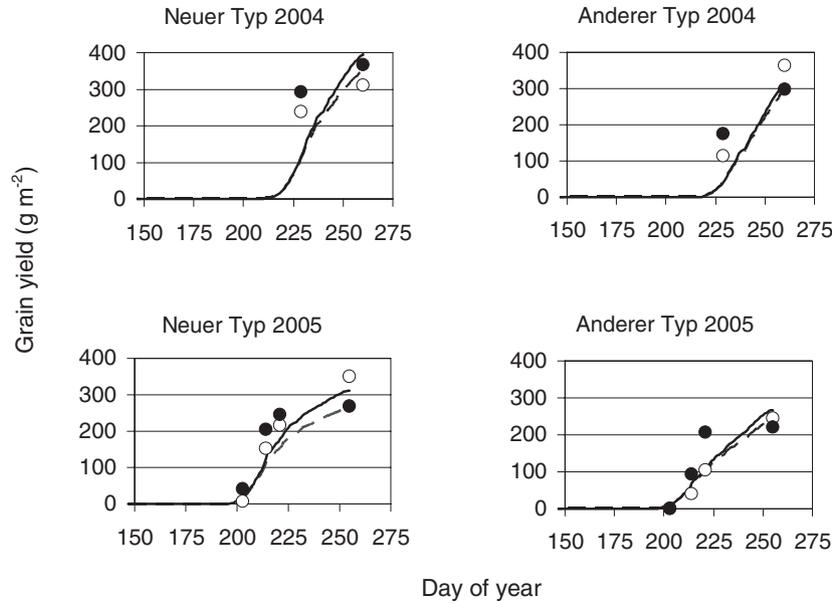
Fig. 3: Simulated and observed grain yield of two genotypes at two plant densities during crop development in 2004 and 2005

○ Observed (sparse crop)
● Observed (dense crop)
- - - - Simulated (sparse crop)
——— Simulated (dense crop)

Tab. 6: Statistical measures for observed versus simulated values (all sampling dates)

		RMSE[a] absolute (g m⁻²) (m² m⁻²)	RMSE relative (% of mean observed)	MA%E[b] (%)
Total biomass	Neuer Typ 2004	135.7	28.4	30.7
	Neuer Typ 2005	91.8	20.7	60.0
	Anderer Typ 2004	97.0	17.8	19.6
	Anderer Typ 2005	96.3	21.0	75.0
Leaf area index	Neuer Typ 2004	1.56	219.0	161.0
of green leaves	Neuer Typ 2005	0.76	90.7	113.5
	Anderer Typ 2004	1.62	155.1	82.8
	Anderer Typ 2005	0.79	71.1	125.0
Grain yield	Neuer Typ 2004	112.0	37.1	33.7
	Neuer Typ 2005	57.9	31.2	49.5
	Anderer Typ 2004	84.9	35.7	41.4
	Anderer Typ 2005	47.0	31.1	26.9

[a]RMSE: Root mean squared error calculated as $\sqrt{\dfrac{\sum_{i=1}^{n}(E_i - M_i)^2}{n}}$ where E_i is the ith estimated value, M_i is the ith measured value, and $i…n$ is the number of values.

[b]MA%E: Mean absolute percent error calculated as $100 \cdot \sum_{i=1}^{n} \dfrac{|E_i - M_i|}{|M_i|} \cdot \dfrac{1}{n}$

The time-course of grain yield formation (Fig. 3) was simulated with less accuracy than the production of total biomass. Especially the sharp rise in grain weight at the beginning of grain formation was underestimated by the model. Root mean squared errors were between 47 and 112 g m⁻², i. e. 31-37% of the mean observed grain yield. Grain yield levels at maturity were predicted quite satisfactorily, but some deviations from observed yield levels had to be noticed.

Discussion

Experimental conditions

The experimental site provided appropriate conditions for potential growth. The high level of soil mineral nitrogen and the high level of available phosphor and potassium ensured ample supply of nutrients. The typical growth limiting factor at the site is the low precipitation. Therefore, plots were irrigated twice during the growing cycle. Grain yield in irrigated plots was higher than in neighbouring not irrigated plots reported in a different field study (GIMPLINGER et al., 2008). This effect was especially obvious in the 2004 environment with lower precipitation. Higher yield in irrigated plots suggests that the irrigation treatments met the water demands of the crop. Diseases did not occur. Flea beetles (*Phyllotreta* spp.) and the sugar-beet weevil (*Bothynoderes* sp.) which infested plants at emergence were controlled by an insecticide. Mechanical and hand-weeding provided a weed-free environment.

The attained level of grain yield was similar to the level of yield found in field experiments under favourable conditions elsewhere (JAMRIŠKA, 1996; AUFHAMMER and KÜBLER, 1998). Mean observed grain yields at harvest of „Neuer Typ" were 338 and 309 g m⁻², observed grain yields of „Anderer Typ" were 331 and 232 g m² in the 2004 and 2005 environment, respectively.

Due to the small data base, crop density effects were not taken into account. Yet, it is known that rising plant density affects the allocation patterns of biomass, e. g. slightly decreases the harvest index (GIMPLINGER et al., 2008). As parameterisation was based on genotypes (averaged across densities), crop density differences calculated by the model merely reflect the differences in start values depending on the defined number of seedlings per area.

Model parameterisation

Model predictions are highly dependent on model parameters. Therefore, parameters should be defined precisely and deserve closer attention. FARRÉ et al. (2000) analysed the sensitivity of the model LINTUL to changes in input parameters in growth simulations of

(a)

y = 66.17 + 0.98x
R² = 0.94

(b)

y = 0.08 + 1.67x
R² = 0.62

(c)

y = -22.06 + 0.92x
R² = 0.70
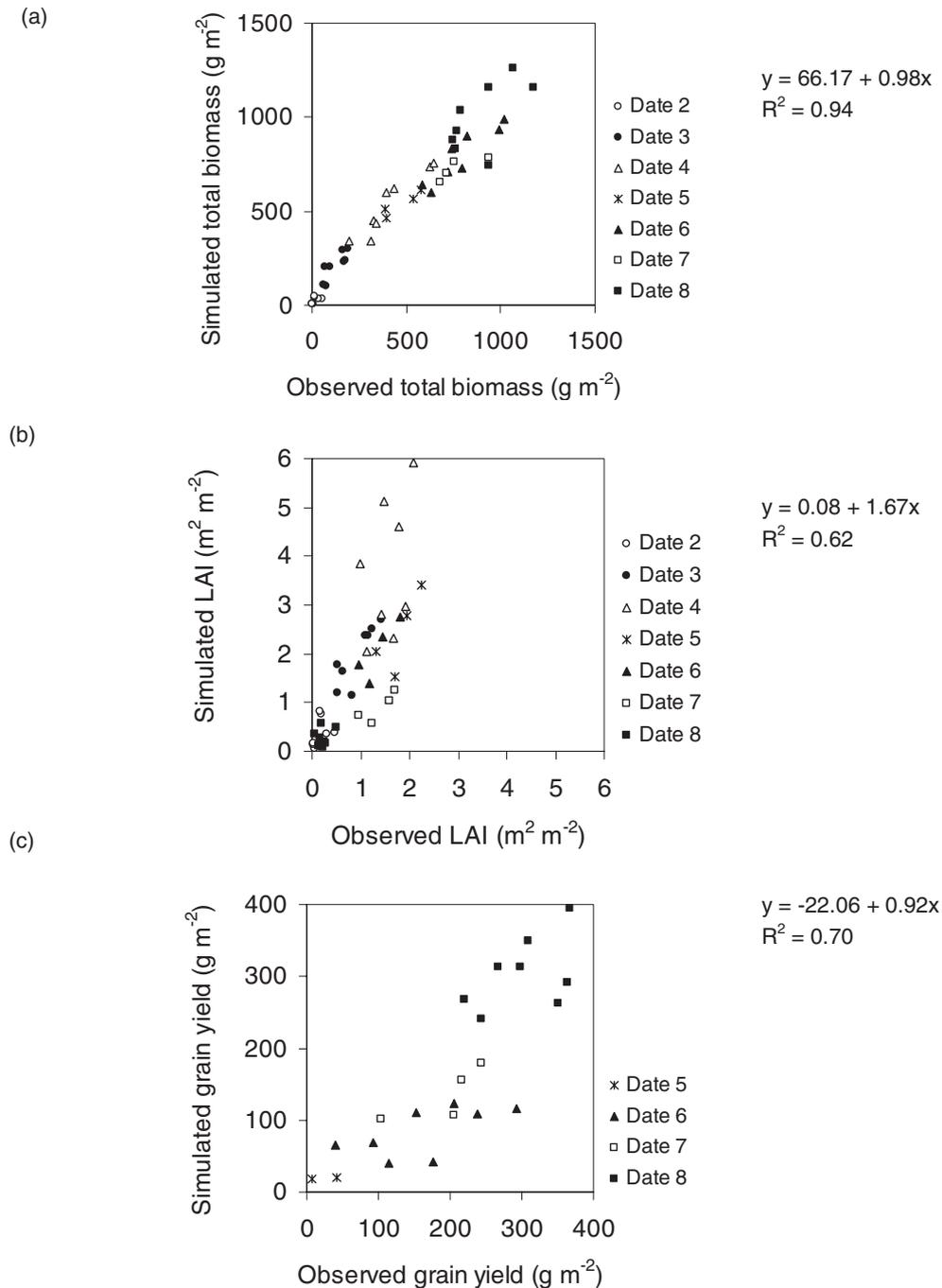
Fig. 4: Simulated versus observed values of total biomass (a), leaf area index (LAI) of green leaves (b) and grain yield (c)

maize. They found that the simulated grain yield was particularly sensitive to changes in light use efficiency, but also to changes in the light extinction coefficient and in the rate of leaf senescence whereas changes in specific leaf area or in the partitioning coefficients to root and shoot hardly affected crop yield. In LINTUL, the effective sum of temperature controls plant development. However, no data were available to examine the base temperature of the used grain amaranth species carefully. Therefore the estimated base temperature might also be a potential source of inaccurate model predictions.
The estimated model parameters of the tested amaranth genotypes resulted in reasonable values compared to earlier findings in amaranth and other crops. Hardly any differences between genotypes could be noted except for the dry matter portions partitioned to each plant

organ. Yet, differences between years were obvious for several parameter estimates.

Light use efficiency
Several studies revealed that light use efficiency is not constant throughout the development of a crop, e.g. throughout the growth of maize (SINCLAIR and MUCHOW, 1999), wheat (CALDERINI et al., 1997) and rapeseed (HABEKOTTÉ, 1997). In the presented study, the linear regression of biomass of amaranth against the accumulated PAR (based on a constant light extinction coefficient) did not suggest any variability in light use efficiency throughout the growing period. Only shortly before grain maturation light use efficiency decreased

probably due to senescent leaves scattered to the ground. However, the data of this period were excluded from the calculation of light use efficiency. Light use efficiency estimates might have been more accurate if the periodic measurements of biomass and leaf area were accompanied by periodic measurements of radiation intercepted by the canopy.

Light use efficiency also includes root growth, but it is often expressed with reference to shoot biomass per accumulated PAR only. For comparisons with other findings, the recalculated light use efficiency for our data based on shoot biomass ranges between 2.26 and 2.57 g MJ^{-1}. These values found under semiarid conditions are slightly lower than the light use efficiency between 2.44 and 2.83 g MJ^{-1} reported earlier by KAUL et al. (2000) and values from 2.54 to 3.02 g MJ^{-1} found by KRUSE (1996) under moister conditions in Southwest Germany. Higher light use efficiency values in the 2005 environment might also be due to the higher precipitation in this year, indicating slight drought stress despite irrigation in 2004.

The calculated light use efficiency of amaranth is similar to values of sorghum, but it is lower than most findings from other C_4 plants and lower than that of C_3 cereals (SINCLAIR and MUCHOW, 1999). The low light use efficiency of amaranth compared to maize and sugarcane can be attributed to the comparably high protein and fat content of amaranth grains. It is well known that differences in the energy content of the biochemical constituents strongly contribute to variations in light use efficiency (SINCLAIR and MUCHOW, 1999). The lower light use efficiency might also be due to the subtype of C_4 photosynthesis. Leakage of CO_2 out of the bundle sheath and energy costs for refixing CO_2 are greater in plants following the NAD-ME subpathway, as found in *Amaranthus*, than in plants using the NADP-ME subpathway, and greater in C_4 dicotyledons than in mono-cotyledons (PEARCY and EHLERINGER, 1984; KUBASEK et al., 2007) because C_4 dicotyledones lack the suberised lamella in the walls separating the mesophyll and the bundle sheath cells in the leaves (KIGEL, 1994).

Light extinction coefficient

LINTUL is based on a constant light extinction coefficient. Yet, it is known to be variable throughout the life cycle of most crops (VAN HEEMST, 1998) and it can be reduced by drought (FARRÉ et al., 2000). KRUSE (1996) also reported that the extinction coefficient of amaranth is variable during the season amounting to 1 during heading and decreasing to 0.8 towards harvest. In our experiment, the single value was based on measurements taken before heading in 2005 only and amounted to 1.1 for both genotypes. Yet, own measurements in a field study without irrigation treatments in 2006 led to the same value (data not shown) and suggest little variability of this parameter at the site. In comparison to other crops, the light extinction of amaranth canopies is high which is typical for a dicotyledonous species showing horizontally oriented leaves.

Specific leaf area

It is known that specific leaf area is not constant throughout the growing season and can be affected by environmental conditions (VAN DELDEN et al., 2000). For example, water stress during ageing of a crop may reduce specific leaf area (LUDLOW, 1975). Apart from the growth phase after emergence, our linear regression plots used for parameter estimation did not suggest reductions of the specific leaf area (of green leaves) during ageing. However, differences of specific leaf area between years were noted, and the lower specific leaf area found in 2004 might be explained again by some water stress occurring although plots were irrigated. This is in accordance with LIU and STÜTZEL (2004) who found that water stress significant-ly reduced specific leaf area of young vegetable amaranth plants

(*Amaranthus* spp.) grown in pots.

Estimates of specific leaf area between 0.014 and 0.018 m^2 g^{-1} are low compared to the range found in C_3 cereals like wheat, barley and rice (0.020) or C_3 dicots like oilseed rape (0.019-0.022) or sunflower (0.025-0.035) (BOONS-PRINS et al., 1993). However, the specific leaf area of amaranth is similar to values of C_4 monocots like maize (0.016, BOONS-PRINS et al., 1993) and sorghum (0.019, VAN HEEMST, 1988), and it is higher than the specific leaf area of sugarcane (0.08-0.012, VAN HEEMST, 1988). Measurements of the thin and tiny cotyledons at emergence resulted in high specific leaf area which was similar to cotyledons of maize and sorghum (BOONS-PRINS et al., 1993; VAN HEEMST, 1988).

Growth rate of leaf area

The original version of LINTUL calculates leaf area expansion as an exponential function of temperature from emergence onwards till a leaf area index of 0.75 or a temperature sum of 330°C d is reached. Thereafter, leaf area is assumed to expand in proportion to the increase in leaf dry weight. The analysis of leaf area expansion versus thermal time up to a leaf area index of 1.0 showed that the relative leaf area growth rates of potato, winter and spring wheat were 0.018, 0.007 and 0.011°C^{-1} d^{-1}, respectively (VAN DELDEN et al., 2000). Compared to these crops, the initial relative growth rate of the tiny amaranth leaves between 0.027 and 0.030°C^{-1} d^{-1}, as estimated from our data, is remarkably high which could be connected with the comparatively high base temperature of 8°C for amaranth.

It is critical to define the right switching point from temperature- to radiation-driven leaf expansion, and differences between crops arise. VAN DELDEN et al. (2001) found that model performances were best when using a threshold leaf area index of 1.0 in potato and of 1.5 in wheat. Presumably a crop-specific switching point determined for grain amaranth might improve model performance. Changing model parameters towards a later switching point resulted in a reduced initial growth rate and subsequently more accurate model predictions especially with respect to leaf area (data not shown).

Biomass allocation patterns

When comparing allocation patterns of grain amaranth with those determined for maize (FARRÉ et al., 2000), clear differences become obvious. The dry matter fraction allocated to roots in amaranth was only half of the fraction found in maize. To some extent, our com-paratively rough method of root sampling might account for this effect. Outstanding in grain amaranth is the high fraction of biomass partitioned to leaves at emergence and the even higher fraction allocated to leaves up to the sampling date where plants have up to 15 leaves and reach a plant height of about 10 cm, i. e. at about 200 °C d.

Model testing

The time course of total biomass production of grain amaranth was simulated quite well by LINTUL for both genotypes in both tested environments. Total biomass at harvest also was predicted quite satisfactorily.

The determined maximum leaf area index of the tested amaranth genotypes between 1.2 and 2.3 is rather low compared to values reported by others. KRUSE (1996) for example recorded a leaf area index of more than 4 in amaranth stands sown at a row distance of 30 cm. Outstanding is the severe overestimation of leaf area by the model, especially in the simulations of crop growth in 2004 due to the parameter estimates based on field data of 2005. The high specific leaf area and the high light use efficiency found under field conditions in 2005 promoted these overestimates of the leaf area as well as the

high allocation of biomass to leaves in early growth stages.

When analysing the growth of maize by using the model LINTUL 2 (including water limitations), FARRÉ et al. (2000) also found that the leaf area index was overestimated. Yet, this was only obvious in sub-optimal irrigation treatments due to underestimated leaf senescence. When calibrating the closely related model WOFOST for several crops in different environments, BOONS-PRINS et al. (1993) stressed that it was often necessary to adopt dry matter partitioning especially when too much leaf area was calculated while at the same time the produced storage organs were underestimated. However, in our study the properly simulated grain yields and the highly overestimated leaf weights conflict with a simple shift of dry matter from leaves to storage organs.

The agreement between observed and simulated grain yield was not as accurate as the prediction of total biomass. The model underestimated the steep dry matter increase at the beginning of grain formation. This fact might indicate that not only current assimilates are used for grain filling, but also mobilised assimilates from other plant organs. In LINTUL it is assumed that grain filling is exclusively based on current photosynthesis. As already stressed by SPITTERS (1990), this assumption does not hold for a number of crops, e.g. cereals. It is well known that reserve assimilates stored in other plant organs (e.g. in stems) may contribute to the growth of storage organs. To include these translocation processes it would be necessary to add an algorithm to the original LINTUL model. HABEKOTTÉ (1997) included an additional state variable for reserve assimilates in the model LINTUL-BRASNAP for rape. When current assimilation cannot not meet the growth capacity of the seeds, additional assimilates are supplied from this reserve pool. It may be assumed that similar adaptations of LINTUL for amaranth would result in more accurate predictions of grain yield formation.

Conclusions

The parameterisation of LINTUL for amaranth yielded reasonable and significant values. Parameters were affected by environmental conditions. Differences between years could be noted especially for light use efficiency and specific leaf area. Obviously, accurate model predictions require model parameterisation under adequate environmental conditions. The estimated light use efficiency was slightly lower than found earlier in amaranth and low compared to other C_4 crops like sugarcane or maize, but similar to sorghum. It was also lower than the light use efficiency of cereals. The determined light extinction coefficient was rather high compared to other dicotyledonous plants. Specific leaf area was slightly lower than values found in cereals or oilseed rape.

LINTUL properly simulated the production of total biomass of grain amaranth under potential growth conditions. Total biomass at harvest and also the time course of biomass formation were predicted accurately. Grain yield levels at harvest were simulated less well, yet satisfactorily. Model simulations revealed that leaf weight and leaf area throughout the period from heading to seed setting were overestimated while the sharp rise in grain yield at the beginning of yield formation was underestimated. Presumably reserve assimilates from leaves or other plant organs contribute to the production of grain yield. In summary, the simple model LINTUL can simulate the progress of growth and yield formation of amaranth rather exactly. However, model predictions of grain yield are hardly precise enough for using the model as a crop management tool on individual fields.

Acknowledgements

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