Estimation of Geometric Attributes and Masses of Individual Cucumber Organs Using Three-dimensional Digitizing and Allometric Relationships

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ABSTRACT. The objective of this study was to estimate geometric attributes and masses of individual cucumber (*Cucumis sativus* L.) organs in situ. Using three-dimensional (3D) digitizing techniques, geometric data were obtained that were used to establish allometric relationships between geometric organ attribute and organ mass. Moreover, the authors were looking for the effects of ontogeny and the influence of environmental factors on the allometric relationships in cucumber. If such an allometric relationship did not exist, they alternatively tested the relationship between organ dry weight and organ number counted from the top of the plant downward. Lastly, they included allometric relationships based on biomechanical approaches focused on lamina mass and petiole attributes. The digitizing method provided accurate data for the calculation of geometric plant part attributes, such as length, area, and volume. Based on these data it was possible to describe the relationships between plant part dry weight and plant part geometry by allometric functions except for internode length. Apart from this exception, two different kinds of allometric equations were used: a simple power function with two parameters and a linear function without intercept. Information about more than one dimension of the considered plant part (e.g., area or volume) led to a simple linear relationship, whereas knowledge of just one dimension, like plant part length, resulted in more complex nonlinear relationships. Ontogeny led, in general, to a reduction in the scaling exponent or in the scaling factor, whereas changes of the environment distributed these values. Considering these effects makes it possible to determine dry matter partitioning on organ scale nondestructively and investigate long-term processes on intact plants.

For many objectives in plant growth analysis and structural crop modeling, nondestructive measurement and estimation of plant organ dimensions and masses are highly desirable. One-dimensional traits such as organ length can be determined in situ with simple instruments like rulers or by electromagnetic digitizing (Sinoquet et al., 1998; Thanisawanyangkura et al., 1997). The main problem is that there is possible curvature in space, which makes the measurement of more than two points necessary (Drouet and Bonhomme, 1999). Areas, like leaf area can be estimated nondestructively through measurement of length and width (Kaitaniemi et al., 1999). This implies a constant relationship between area and the product of length and width (i.e., the maintenance of a specific shape). Often, leaf lengths and widths are highly correlated so that the determination of either dimension results in good estimations of leaf area (Williams and Martinson, 2003). Areas of leaves that do not maintain a constant shape can be estimated by a number of measurements of individual dimensions (e.g., individual ribs), which can then be used to construct triangles and calculate their areas (Sinoquet et al., 1998). Organ volume can be estimated by measuring individual dimensions like fruit diameter or circumference and multiplying the measurement with constants. This method can be successful if all other dimensions change in proportion to the measured dimension. If this does not hold, dimensions that are not proportionate have to be determined in addition, like fruit length in cucumber (Marcelis, 1992).

Masses can be determined from lengths, areas, and volumes by division through specific lengths, specific areas, and specific volumes respectively. So, leaf mass can be estimated from leaf area using the specific leaf area (SLA; measured in square centimeters per gram). In modeling, SLA is often used as a conversion factor to predict leaf area from leaf weight (Acock et al., 1979; Heuvelink, 1996). Specific leaf area is assumed to be constant or is simulated as a function of plant attributes or environmental factors (Lee and Heuvelink, 2003; Marcelis et al., 1998; Stützel, 1995). Size-related relationships like those between masses and geometric attributes are often describable by allometric functions (Niklas, 1994; Reddy et al., 1998). If the independent variable is organ mass and the dependent variable is the geometric organ attribute, the specific organ attribute can be calculated easily from the allometric relationship. But allometric relationships may be influenced by environmental conditions and there can be effects of ontogeny (Niklas, 1994; Reddy et al., 1998).

The objective of this study was to estimate geometric attributes and masses of individual cucumber organs in situ. Using three-dimensional (3D) digitizing techniques, geometric data were obtained and used to establish allometric relationships between geometric organ attribute and organ mass. Moreover, we were looking for the effects of ontogeny and the influence of environmental factors on the allometric relationships in cucumber. If such an allometric relationship did not exist, we alternatively tested the relationship between organ dry weight and organ number counted from the top of the plant downward. Lastly, we were looking for allometric

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relationships based on biomechanical approaches focused on lamina mass and petiole attributes.

Materials and Methods

PLANT CULTURE. All experiments were conducted with ‘Aramon’ cucumber in experimental greenhouses at the Institute of Biological Production Systems, Leibniz Universität, Germany (lat. 52°23’35’’N, long. 9°42’09’’E). Expt. 1 had plant density and plant distribution as factors and was laid out as a randomized, complete block design with four replications (Table 1). In isometric stands, each plant had equal distances to all neighboring plants, and row crop distances between rows were 1.86 m. Expts. 2 and 3 were laid out as split-plot designs with 1.4 plants/m² in rows 1.4 m apart. Expt. 2 consisted of ventilation temperature as the main factor and salt concentration of the nutrient solution as the subfactor. The latter was varied by the addition of table salt (NaCl). Expt. 3 included CO₂ concentration of the air as the main factor and NO₃ concentration in the nutrient solution as the subfactor. Table 2 shows the complete schedule for sowing, transplanting, and measurements of all experiments.

Plants were cultivated on rock wool slabs (Grodan, Grodania A/S, Hedehusene, Denmark), which were placed on metal gutters. The temperature for heating was set to 24 °C day/16 °C night. Ventilations opened at 24 °C during daytime, except for the high-temperature treatments in Expt. 2. The nutrient solution in Expts. 1 and 2 consisted of 0.15% Flory 2 mega (Planta GmbH, Regenstauf, Germany). In Expt. 3 we used a basic nutrient solution of 0.057% Flory 1 (Planta GmbH) and added CaNO₃·4H₂O to obtain the required concentrations of nitrate. The main stem of each plant was clipped at 220 cm. All lateral branches were removed from the main stem except for the two uppermost side shoots. Not more than one flower was allowed per axil and all flowers were removed from nodes 1 to 6. Leaves were removed when they started yellowing.

MEASUREMENTS. At each measurement date, eight plants were digitized in situ to derive geometric attributes of individual organs such as length, area, and volume. Plants were then dissected into internodes, petioles, laminae, and fruit. Each lamina area was measured with a leaf area meter (LI-3100; LI-COR, Lincoln, NE). Length and diameter of the remaining organs were measured with a ruler, except for petiole and internode diameters in Expt. 1 (these data are missing). Dry

weights of individual organs were determined after drying at 100 °C for at least 48 h.

PLANT DIGITIZING. Plants were digitized using a Fastrak 3D digitizer (Polhemus, Colchester, VT). This electromagnetic device consisted of a main unit, a transmitter, and a pointer. The transmitter produces a low-frequency electromagnetic field. When the pointer was located in this field and its button was pressed, the spatial coordinates of the pointer’s tip were recorded. Although digitizers of the same type have been used in other experiments (Sinoquet et al., 1998), it was necessary to test the methodical accuracy because of the large amount of metal in the greenhouse. Measurements were taken in the morning between 0600 and 1200 HR to minimize possible water stress.

Each plant part was digitized in a standardized sequence (Kaitaniemi et al., 1999; Rakocevic et al., 2000). For each node, one point, *N*, placed opposite the leaf axil and one point for the leaf axil, *P*, were digitized (Fig. 1A). On each lamina, 17 points were digitized (Fig. 1B). An internode was determined by two consecutive nodes, a petiole by *P* and point 1 on the lamina (Fig. 1A and B). At each fruit, the top and bottom tips and two points placed diametrically opposed at the half of its length were digitized.

DEFINITION AND QUANTIFICATION OF GEOMETRIC ORGAN ATTRIBUTES. The distance between two digitized points was defined as the Euclidian distance and it was used to define length, *S*, and diameter, *D*. Volume, *V*, was calculated according to that of cylinders with half the diameters as their radius. Lamina area is defined as the sum of 20 triangle areas as shown in Fig. 1C.

METHODOLOGICAL ACCURACY. The methodical accuracy of digitizing equals the accuracy of the recorded spatial coordinates of single points. Alternatively, we compared the internode lengths derived from digitizing with those measured by a ruler. The quality of the geometric attributes derived from digitized data was additionally analyzed for lamina area. In both cases, the precision was described by the systematic prediction error (SPE, bias), the mean squared deviation (MSD), the root mean squared deviation (RMSD), and the fraction of SPE following the approaches of Gauch et al. (2003) and Kobayashi and Salam (2000):

Bias = 1/n ∑ (x_i)² - 1/n ∑ (y_i)² [1]

Table 1. List of all treatment abbreviations (Treat) used in the three experiments to estimate geometric attributes and masses of individual cucumber organs using three-dimensional digitizing and allometric relationships.

Expt. 1			Expt. 2			Expt. 3		
Treat	PD (plants/m ²)	Distribution	Treat	Temp (°C)	EC (dS·m ⁻¹)	Treat	CO ₂ (μL·L ⁻¹)	NO ₃ -N (mg·L ⁻¹)
D1R1	1	Isometric	T1S1	24	1.6	C1N1	350	50
D1R2	1	Row	T1S2	24	3	C1N2	350	90
D2R1	2	Isometric	T1S3	24	5	C1N3	350	120
D2R2	2	Row	T1S4	24	7	C1N4	350	150
			T2S1	28	1.6	C2N1	800	50
			T2S2	28	3	C2N2	800	90
			T2S3	28	5	C2N3	800	120
			T2S4	28	7	C2N4	800	150

EC, electrical conductivity; PD, plant density; Treat, treatment abbreviations.

Table 2. Cultivation and measurement (M) schedule of the three experiments to estimate geometric attributes and masses of individual cucumber organs using three-dimensional digitizing and allometric relationships.

Expt.	Sowing	Transplanting	M 1 (DAT)	M 2 (DAT)	M 3 (DAT)
1	8 Apr. 2002	6 May 2002	9	23	37
2	1 Apr. 2003	29 Apr. 2003	1	15	29
3	10 June 2003	1 July 2003	7	21	35

DAT, days after transplanting; M, measurement.

$$MSD = \frac{1}{n} \sum_{i=1}^n (x_i - y_i)^2 \tag{2}$$

$$RMSD = \sqrt{\frac{1}{n} \sum_{i=1}^n (x_i - y_i)^2} \tag{3}$$

$$SPE = \frac{bias^2}{MSD} \tag{4}$$

where x_i and y_i are simulated and measured values respectively. Modifying the approach of Rakocovic et al. (2000), the accuracy was defined as 1 minus the ratio between RMSD and the mean of the conventionally measured geometric property. For this analysis we took the first measurement of Expt. 1 and the second measurement of Expts. 2 and 3 to ensure that for each experiment at least 80 organs were considered.

ALLOMETRIC RELATIONSHIPS ON AN INDIVIDUAL ORGAN LEVEL. The relationships between masses and geometric attributes such as length and area for laminae, and length and volume for petioles, internodes, and fruit were tested to be describable by allometric functions (Kaitaniemi, 2004; Reddy et al., 1998):

$$\text{Power function with two parameters: } y = a \cdot x^b \tag{5}$$

$$\text{Linear function with one parameter: } y = c \cdot x \tag{6}$$

where y is the geometric attribute of the organ and x its dry matter, a and c are called scaling coefficients, and b the scaling exponent. Dry weight was chosen as the independent variable because of its relevance to current research in the field of allometric scaling laws in biology (e.g., Enquist et al., 1999; Savage et al., 2004; West et al., 1997). In addition, specific attributes like SLA, specific petiole lengths, and so on, can be calculated easily from transformations of these allometric functions. The functions for the specific organ attributes resulting from Eqs. [5] and [6] are

$$\text{Specific organ attribute} = a \cdot W_{\text{Organ}}^{b-1} \tag{7}$$

$$\text{Specific organ attribute} = c \tag{8}$$

where W_{Organ} is the dry weight of the organ and a , b , and c are the parameters determined in Eqs. [5] and [6] respectively. For determining the scaling exponent, original variables were log transformed and an ordinary least square regression was fitted

Fig. 1. (A) Predefined positions of digitized points on the cucumber stem for a node, N , and the leaf axil, P . (B) For a cucumber lamina, 17 points were measured in this standardized sequence. Because of the symmetry of the lamina, point 1 is the pendant to point 8, point 4 to point 9, and so on. (C) The lamina area is calculated according to the presented triangulation.

to the data as recommended for predictive purposes (Kaitaniemi, 2004; Niklas, 1994). If the scaling exponent was not significantly different from one, original data were used and a linear regression without intercept was applied, or else a linear regression with intercept was fitted to the log-transformed data. F tests for parallelism were done using the SES of the scaling factor in the linear case or the SES of the scaling exponents (Rasch and Verdooren, 2004; Reddy et al., 1998). We alternatively tested the relationship between organ dry weight and organ number counted from the top of the plant downward, if such an allometric relationship did not exist. Additionally, we included allometric relationships based on biomechanical approaches focused on lamina mass and petiole attributes. The approaches were evaluated with data from Expts. 2 and 3. Statistical procedures were carried out with SAS (SAS Institute, Cary, NC).

Results

METHODOLOGICAL ACCURACY. Digitizing overestimated internode length by 0.5 cm. The RMSD was 1.4 cm with an SPE of 14%. The accuracy of the method was 83%. If only

internodes three to the top were considered, the bias was -0.03 cm and RMSD was 0.4 cm with an SPE fraction of 0.5% and an accuracy of 95% . The mean lamina area of all leaves in Expt. 1 was 398 cm² in both cases, based on digitizing data and when measured with the leaf area meter. Removing leaves 1 and 2 from the data set increased the accuracy from 87% to 92% . The accuracies in Expts. 2 and 3 were quite similar (Table 3). There was an obvious reduction of the MSD, bias, and SPEs (except for the leaf area of Expt. 2), and improvement of accuracy when the two lowermost organs were not included. As a result of the accuracy of the digitizing and the accuracy of geometric attributes derived from digitizing, relationships between plant part dimensions determined by 3D digitizing technique and the weights of these plant parts were described for organ number three to the top, counted from bottom only.

ALLOMETRIC RELATIONSHIPS ON AN INDIVIDUAL LAMINA LEVEL. There existed general allometric relationships between lamina length and lamina dry weight in Expt. 1. The scaling coefficients were 2.949 ± 0.008 at the first measurement and 2.927 ± 0.010 at the second measurement, whereas the scaling exponents were 0.386 ± 0.010 and 0.370 ± 0.010 respectively. The coefficients of determination were 0.97 and 0.92 . At the third measurement the scaling exponent in the treatment with row distribution at low plant density (D1R2) was significantly lower than those of all other treatments. Their regression coefficients were similar to those at the second measurement, whereas the scaling exponent in case of treatment D1R2 was reduced to 0.279 ± 0.016 ($R^2 = 0.87$). Results of Expts. 2 and 3 showed similar allometric patterns. Regression coefficients of the third measurements were comparable with those at the second measurement of Expt. 1. Because of the differences, treatments at the third measurement were not considered separately, and coefficients of determination ranged between 0.75 and 0.90 . There seemed to be a strong ontogenetic drift of the scaling exponent within the first week after transplanting (Fig. 2). One explanation may be that plants in Expt. 2 had three leaves at this stage, whereas plants in Expt. 1 had five leaves. At day 9 after transplanting, the scaling exponent decreased by $0.002/d$, independent of the experiment.

A clear, linear allometric relationship between individual lamina masses and corresponding areas existed in Expt. 1 (Table 4). At the second measurement the treatment with row distribution at high plant density (D2R2) had to be considered

separately with a maintained scaling factor considerably higher than the other treatments. The third measurement revealed a further ontogenetic drift of the scaling factor. The scaling factor in the treatment with row distribution at low density (D1R2) decreased to a lower value, whereas those of all other treatments remained on their level. The evaluation with Expts. 2 and 3 is also shown in Table 4. Coefficients of determination were high and the scaling factor ranged between 193 for the treatment with high CO₂ and low nitrate (C2N1) and 352 in the case of the first measurement of Expt. 2 for all treatments.

ALLOMETRIC RELATIONSHIPS ON AN INDIVIDUAL PETIOLE LEVEL. The relationships between petiole dry weights and petiole lengths in Expt. 1 could be described sufficiently by general allometric functions with two parameters. The scaling coefficients varied between 3.242 ± 0.032 and 3.134 ± 0.019 , whereas the scaling exponents decreased with measurement date from 0.469 ± 0.016 at the first measurement to 0.447 ± 0.015 at the second for the treatment with row distribution at high plant density (D2R2), and 0.414 ± 0.024 for the other treatments. At the third measurement, all treatments could be pooled again and their scaling exponent was 0.363 ± 0.017 . The evaluation with Expts. 2 and 3 also showed allometric patterns. The scaling coefficients were similar to those in Expt. 1 and they decreased with measurement date from 0.47 to 0.41 at the second measurement and finally to 0.38 for high salt concentrations (S3 and S4) and to ≈ 0.35 for the other treatments. Thus, there existed an overall decrease of the scaling exponent of $0.006/d$ after transplanting (Fig. 3).

Petiole dry weight and petiole volume showed a clear linear allometric relationship at the first measurement of Expt. 1. The scaling factor was 23.61 ± 0.54 and the coefficient of determination was 0.89 . Unfortunately, we did not measure petiole diameters at the two latter measurement dates. In Expts. 2 and 3, the scaling factors were 24.59 ± 1.26 and 23.91 ± 0.59 at the first measurement, and 19.47 ± 0.040 and 19.85 ± 0.19 at the second measurement respectively. At the third measurement of Expt. 2, the scaling factor was 21.18 ± 0.26 , whereas at the third measurement of Expt. 3 the scaling factors were considered separately for low nitrate concentrations (C1N1 and C2N1), with a value of 19.29 ± 0.24 , and for the remaining treatments with a value of 22.88 ± 0.18 . The coefficients of determination varied between 0.89 and 0.97 .

Table 3. Methodological accuracy of digitizing assessed by derived geometric attributes from digitized data of cucumber in Expts. 2 and 3.

	Expt. 2				Expt. 3			
	Internode length (cm)		Leaf area (cm ²)		Internode length (cm)		Leaf area (cm ²)	
	All	Top	All	Top	All	Top	All	Top
Mean ^c	7.0	6.9	514	537	7.5	7.8	580	602.0
Mean ^y	8.4	7.2	493.4	510	8.4	8.1	636	617.3
MSD	10.5	1.1	9505	9453	5.4	1.1	49047	9551
RMSD	3.2	1.1	97.5	97.2	2.3	1.1	221.5	97.7
Bias	-1.4	-0.2	20.6	26.4	-0.9	-0.3	-56.5	-15.4
SPE	17.5	4.7	4.4	7.4	15.3	9.7	6.5	2.5
Accuracy	0.54	0.85	0.81	0.82	0.69	0.86	0.62	0.84

^cMean of the geometric attribute (i.e., length or area) measured with a ruler or leaf area meter.

^yMean of the geometric attribute (i.e., length or area) derived from digitized data.

The precision is described by the systematic prediction error (bias, Eq. [1]), the mean squared deviation (MSD, Eq. [2]), the root mean squared deviation (RMSD, Eq. [3]), the fraction of systematic prediction error (SPE, Eq. [4]), and the accuracy, which is defined as 1 minus the ratio between RMSD and the mean of the conventionally measured geometric property. This analysis is applied to all internodes and all leaves (All), and to the internodes and leaves from position three to the top counted from the bottom (Top).

Fig. 2. The relationship between the scaling exponents of the allometric relationships between cucumber lamina length and lamina dry weight of all experiments and days after transplanting (DAT). Each point denotes the mean of all treatments except for Expt. 1 at 37 DAT. Here, the treatment with low plant density and row distribution (D1R2) is shown separately, and the other black point denotes the mean of the remaining treatments. The regression equation is $y = 0.410 - 0.002 \times \text{DAT}$ for $8 < \text{DAT} < 38$ ($R^2 = 0.71$), whereby the value of treatment D1R2 at DAT 37 is left out.

Table 4. Linear allometric regression analysis of lamina area in relation to leaf dry weight of cucumber.

Expt.	Measurement	Treatment ^z	$a \pm \text{SE}$	R^2
1	1	All	293.8 ± 6.3	0.93
1	2	D2R2	299.2 ± 5.5	0.93
1	2	All/(D2R2)	257.1 ± 3.8	0.90
1	3	D2R1 + D2R2	310.4 ± 4.2	0.88
1	3	D1R1	262.8 ± 3.6	0.99
1	3	D1R2	217.2 ± 4.2	0.98
2	1	All	352.1 ± 6.7	0.91
2	2	T1S4 + T2S4	203.1 ± 3.4	0.98
2	2	All/(T1S4,T2S4)	261.2 ± 3.5	0.96
2	3	All	264.4 ± 3.9	0.96
3	1	All	333.3 ± 5.9	0.98
3	2	All	235.8 ± 2.8	0.93
3	3	C2N1	193.4 ± 2.8	0.92
3	3	All/C2N1	220.9 ± 1.2	0.92

^zAll = all treatments of an experiment, D2R2 = treatment with high plant density and row distribution, All/D2R2 = all treatments of Expt. 1 without D2R2, D2R1 + D2R2 = all treatments of Expt. 1 with high plant density, D1R1 = treatment with low plant density and isometric plant distribution, D1R2 = treatment with low plant density and row distribution, T1S4 + T2S4 = treatments with the highest salt concentration in Expt. 2, All/(T1S4,T2S4) = all treatments of Expt. 2 without T1S4 and T2S4, C2N1 = treatment with high CO_2 and lowest $\text{NO}_3\text{-N}$ concentration, All/C2N1 = all treatments of Expt. 3 without C2N1.

For each measurement, treatments are pooled if they do not show any significant differences in the slopes ($\alpha = 0.05$). The presented regression parameters are related to the clustered data. Pooled treatments, parameters with SE , and the coefficients of determination of the equation $A_L = a \cdot W_L$ are shown, where A_L is lamina area and W_L is leaf dry weight.

ALLOMETRIC RELATIONSHIPS ON AN INDIVIDUAL INTERNODE LEVEL. There existed no allometric relationship between internode dry weight and internode length, which comprised all internodes at any measurement in Expt. 1 (data not shown).

Fig. 3. The relationship between the scaling exponents of the allometric relationships between cucumber petiole length and petiole dry weight of all experiments and days after transplanting (DAT). Each point denotes the mean of all treatments except for Expt. 1 at 23 DAT, where the treatment for high plant density and row distribution (D2R2) is shown separately, and the other black point denotes the mean of the remaining treatments; and except for Expt. 2 at 35 DAT, where the points denote the means of the high (S3 and S4) and low (S1 and S2) salt concentrations. The overall regression equation is $y = 0.553 - 0.006 \times \text{DAT}$ ($R^2 = 0.85$).

However, there existed a linear relationship between internode dry weight and corresponding internode number counted from top in the range from one and nine (Table 5). The intercept was significantly different from zero, the slope was 0.063 ± 0.006 , and the coefficient of determination was 0.73. For older internodes, we did not find a relationship when we considered geometric attributes or corresponding internode number only, but older internodes reached specific internode lengths (SILs) of $\approx 10 \text{ cm} \cdot \text{g}^{-1}$ (Fig. 4). The evaluation in Expts. 2 and 3 showed similar patterns (Table 5).

Similar to petioles, there existed a linear allometric relationship between internode dry weight and internode volume at the first measurement of Expt. 1. The scaling factor was 16.63 ± 0.42 and the coefficient of determination was 0.81. High coefficients of determination affirm linear allometric relationships in the evaluation experiments. The scaling factors were ≈ 17.8 at the first measurements and ≈ 11.2 at the second measurements. When nitrate levels were increased, the scaling factors increased from 9.69 ± 0.20 up to 12.45 ± 0.24 at the third measurement of Expt. 3, whereas in Expt. 2 the relationships were independent of the applied treatments and the scaling factor was 11.37 ± 0.13 .

ALLOMETRIC RELATIONSHIPS ON AN INDIVIDUAL FRUIT LEVEL. The relationship between fruit dry weight and fruit length in Expt.1 could be clearly described by a general allometric function ($R^2 = 0.99$ and $R^2 = 0.98$). In Expts. 2 and 3, there were no influences of the different treatments on the regression parameters. Pooling the data of all measurements and experiments resulted in a high coefficient of determination of 0.99, a scaling coefficient of 2.439 ± 0.020 , and a scaling exponent of 0.357 ± 0.004 .

In all experiments, fruit dry weight was perfectly related to fruit volume in a linear manner. Pooling all data resulted in a high coefficient of determination of 0.96 and a slope of 27.27 ± 0.32 . This indicates that, irrespective of treatment, one set of

Table 5. Linear regression analysis of internode dry weight (W_1) in relation to internode position p (1–9 from top downward) of cucumber.

Expt.	Measurement	Treatment ^z	$a \pm \text{SE}$	$b \pm \text{SE}$	R^2
1	1	All	0.0565 ± 0.0218	0.0623 ± 0.0056	0.73
1	2	D2R1	0.0907 ± 0.0295	0.0876 ± 0.0050	0.95
1	2	All/D2R1	0.0691 ± 0.0174	0.0705 ± 0.0026	0.92
2	1	All	-0.0337 ± 0.0085	0.0572 ± 0.0031	0.92
2	2	T1S4	0.0537 ± 0.0221	0.0727 ± 0.0049	0.98
2	2	All/T1S4	0.1615 ± 0.0238	0.0640 ± 0.0053	0.75
2	3	T2S4	0.0027 ± 0.0309^y	0.0501 ± 0.0046	0.93
2	3	All/T2S4	0.0133 ± 0.0171^y	0.0598 ± 0.0021	0.89
3	1	All	0.0516 ± 0.0150	0.0344 ± 0.0034	0.66
3	2	All	-0.0421 ± 0.0150	0.0898 ± 0.0027	0.94
3	3	C1N1	0.0575 ± 0.0109	0.0357 ± 0.0019	0.98
3	3	All/C1N1	0.1024 ± 0.0166	0.0486 ± 0.0029	0.82

^zAll = all treatments of an experiment, D2R1 = treatment with high plant density and isometric plant distribution, All/D2R1 = all treatments of Expt. 1 without D2R1, T1S4 = treatment with low ventilation temperature and highest salt concentration, All/T1S4 = all treatments of Expt. 2 without T1S4, T2S4 = treatment with high ventilation temperature and highest salt concentration, All/T2S4 = all treatments of Expt. 2 without T2S4, C1N1 = treatment with low CO₂ and lowest NO₃-N concentration, All/C1N1 = all treatments of Expt. 3 without C1N1.

^yNot significantly different from zero.

For each measurement, treatments are pooled if they do not show any significant differences in the slopes ($\alpha = 0.05$). The presented regression parameters are related to the clustered data. Pooled treatments, parameters with SEs, and the coefficients of determination of the equation $W_1 = a + b \cdot p$ are shown, where W_1 is internode dry weight and p is internode position.

parameters is sufficient to determine fruit dry weight from fruit length or fruit volume.

ALLOMETRIC RELATIONSHIPS BETWEEN LAMINA AND PETIOLE. Petiole dry weight was also related to lamina dry weight. Therefore, if lamina dry weight is known, petiole dry weight can easily be estimated. Pooling the data of all measurements and experiments resulted in a high coefficient of determination:

$$W_P = 0.1574 \cdot W_L^{1.3531} \quad [9]$$

with $R^2 = 0.96$ and where W_P is the petiole dry weight and W_L is the lamina dry weight.

Fig. 4. Relationship between specific internode length (SIL) and internode position counted from the top in cucumber for all measurements of Expt. 1. This experiment had the factors plant density and plant distribution. There were no significant differences between the treatments. Vertical bars represent SDs of the means ($n = 8$).

There existed also a general relationship between the specific petiole length (SPL; measured in centimeters per gram) and lamina dry weight:

$$\text{SPL} = 68.01 \cdot W_L^{-0.7349} \quad [10]$$

with $R^2 = 0.90$.

Discussion

PLANT DIGITIZING. Use of the 3D digitizing technique allows the measurement of plant dimensions in space nondestructively and with minimal interference. The outcome of plant digitizing is dependent on the standardized sequences selected for digitizing different plant components. For long, straight objects such as internodes or uncurved petioles, it is sufficient to digitize just two points to determine the length. However, the selected standardized sequence for the lamina is more complex.

The accuracy of the digitizing method is mainly influenced by the error in measuring spatial coordinates with the digitizing device in relation to the human operator and the interference of metal with the measurement sphere. The gutters in which the rock wool slabs were placed consisted of metal, but the interference of the metal with the electromagnetic measurement sphere was confined to the close vicinity of the gutters. Furthermore, the error in measuring spatial coordinates for the length calculation with the Fastrak device was reported to be ≈ 1 cm in the field (Thanisawanyangkura et al., 1997) and 0.15 cm in the laboratory (Rakocevic et al., 2000). In the greenhouse, the RMSD for internode length could have been expected to lie between these values. However, the accuracies for the first measurements of all experiments were higher than the corresponding accuracy reported by Rakocevic et al. (2000).

Leaf area computed from digitized coordinates was unbiased in all leaves. Low accuracy was related to the lowermost leaves. Moreover, the accuracy of determining the leaf area using a leaf

area meter is 95% to 99% (LI-COR, n.d.). Therefore, an accuracy of 92% (81% and 84% for Expts. 2 and 3 respectively) for leaf area calculated using the digitized data has turned out to be quite satisfactory.

ALLOMETRIC RELATIONSHIPS. Describing the relationships between plant part dry weight and plant part geometry by allometric functions turned out to be possible except for internode dry weight in relation to internode length. Apart from this exception, two different kinds of allometric equations were used, a simple power function with two parameters (Eq. [6]) and a linear function without intercept (Eq. [5]). The nonlinear regression approach based on the power function had to be used if the geometric organ attribute was length. In the case of lamina area or organ volume, the scaling exponents were not significantly different from one, thus linear regression analyses without an intercept were applied. This means that information about more than one dimension of the considered plant part (e.g., area or volume) led to a simple linear relationship, whereas knowledge of just one dimension, like plant part length, resulted in more complex nonlinear relationships.

The linear relationship between leaf dry weight and leaf area was expected, because to determine leaf area from dry weight, the SLA is frequently used as a constant conversion factor on the crop level (i.e., over all leaves) (Heuvelink, 1996; Stützel, 1995). Our results, however, indicate a linear relationship even at the single-leaf level. To improve the estimation of leaf dry weight would require the incorporation of environmental factors, particularly light and temperature (Alt, 1999; Alt et al., 2000). However, this raises the question of whether allometric functions can still be used to describe the resulting relationships. Overall, there were clear ontogenetic drifts of the scaling factors, which in turn are the SLAs resulting from Eq. [8]. In general, an increase in time led to a decrease in SLA, except for the treatment with row distribution at high plant density (D2R2) in Expt. 1, which remained on a constant level of 300 cm²·g⁻¹, and the treatments with the highest salt concentrations (S4) in Expt. 2. This reduction of the SLA with ontogenesis was also observed in many other species such as rice, wheat, and radish (Bultynck et al., 2004; Dingkuhn et al., 1997; Usuda, 2004).

In the case of lamina length and petiole length, the scaling exponents decreased with time and influences of environmental factors revealed for the two last measurements. The scaling factor in case of petiole volume was equivalent to specific petiole volume (SPV; measured in cubic centimeters per gram). Specific petiole volume was reduced from measurements 1 to 3 from 24 cm³·g⁻¹ to 20 cm³·g⁻¹. At the last measurement, a decrease in nitrate led to a decrease in SPV from 23 cm³·g⁻¹ to 19 cm³·g⁻¹. Specific internode volume, the scaling factor in the case of internode volume, varied in a similar manner. This decrease of the scaling exponents with time in the case of length and volume refers to an ontogenetic drift, which can be partly related to the size of the leaf. Larger ones seem to invest a larger fraction of biomass in support structure (Poorter and Nagel, 2000).

Describing the dry weight distribution to the internodes based solely on the internode length was impossible. We used the node number counted from the top of the plant downward as a measure for internode age, but not even the node number was related to internode dry weight for node numbers more than nine. However, the dry weight of older internodes can be

calculated from their length using the constant overall threshold for specific internode length, SIL (measured in centimeters per gram), as conversion factor. Particularly for internodes, detailed information about environmental data might have improved dry weight estimation. There were no ontogenetic drifts and effects of environment on the allometric relationships between fruit dry weight and fruit length or volume. However, aborted fruit were not considered. Generative growth of older fruits seemed to be maintained at a constant level, thus genetic patterns of reproduction might be the dominant factor for fruit growth.

Lastly, we included Eqs. [9] and [10], representing general overall relationships between lamina dry weight and petiole dry weight and, conversely, relationships between lamina dry weight and specific petiole length. The high coefficients of correlation might indicate that these relationships are functionally based and not variable in relation to the applied treatments, nor did they show ontogenetic drifts. A combination of these equations leads to a regression equation between lamina dry weight (W_L) and petiole length (S_p) resulting in

$$W_L \propto S_p^{1.6} \quad [11]$$

Niklas (1994) showed a similar proportion for 193 simple and palmate leaves representing a total of 19 dicot and monocot species:

$$W_L \propto S_p^{1.74} \quad [12]$$

Cucumber leaves are simple (i.e., without leaflets), palmate veined, and shallow lobed (Robinson and Decker-Walters, 1997). This specific shape of the cucumber lamina might be responsible for the differences in the exponents of Eqs. [11] and [12].

Structural plant models focus on the shape and orientation in space of the components comprising a plant (Prusinkiewicz and Lindenmayer, 1990). Thus, there exist several structural plant models that do not consider organ dry weight at all (e.g., Kahlen, 2006; Ruiz-Ramos and Minguez, 2006; Watanabe et al., 2005). Incorporation of specific organ attributes into structural models would allow one to convert geometric organ attributes to the dry weights of organs. These weight data could be used to apply model approaches based on biomechanics (i.e., the tip deflection angle of a leaf could be modeled as a function of the mass force applied per unit length of petiole and length of the petiole) (Niklas, 1994).

Conclusion

The digitizing method provided an accurate data basis for the calculation of geometric plant part attributes, such as length, area, and volume. The relationships between mass and geometric attributes such as length and area for laminae, and length and volume for petioles, internodes, and fruit were describable by allometric functions, except for internode length. However, effects of ontogeny and influences of environment occurred. Ontogeny led, in general, to a reduction in the scaling exponent or in the scaling factor, whereas changes of the environment distributed these values. Considering these effects makes it possible to determine dry matter partitioning on an organ scale nondestructively and to investigate long-term processes on intact plants. Nevertheless, one focus of future work should be

to improve the estimation of specific organ attributes like SLA to increase the accuracy of single-organ dry matter estimation.

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