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Methods to Estimate and Calculate Lettuce Growth

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Abstract

Because of the relatively high portion of dry matter accumulated within the leaves of the lettuce plant, the accuracy and sensitivity of a lettuce growth model may be improved by accurate and detailed morphological and physiological characteristics of each leaf growth. This work demonstrates how the required characteristics for such detailed calculations were determined according to observations in a controlled commercial greenhouse. The unfolding of each lettuce leaf was described by using a series of flap patterns, each composed of a triangle and an ellipse. This method enables an accurate presentation of the morphological changes within each leaf and tracks plant growth by sequential measurements of each leaf length, width, and distance between the leaf base and the location of the maximal leaf width. The quantification of the leaves' morphological changes can also be used for drawing information about the initiation and maturity states of each leaf life cycle. Longer observation periods than reported here are required to obtain information regarding the upper leaves of lettuce plants.

INTRODUCTION

Growth models can be used to improve greenhouse (GH) environmental control by computers, as well as to gain better understanding, designs and management of such systems. A comprehensive and mechanistic approach is not necessarily a disadvantage for such models because present computers and software can efficiently handle such model complexities. Complex models are preferred to simple models only if they are more accurate and can be used in wider ranges of environmental conditions, and only if the knowledge and complexities involved in these models can be overcome by available parameters and techniques (Albright et al., 1999).

A model able to predict microclimate effects on dry matter (DM) accumulation and the architectural development of a lettuce crop is now under development at Cornell University, and the procedures involved with its required parameters are described in this paper. The model is of a mechanistic and photosynthetic type. It considers the effects of cultivating operations on the morphological growth and development and on dry matter production and partitioning in lettuce plants. Similarly to other mechanistic models, it uses the plant's potential growth to partition assimilates among its organs (Dayan et al., 1993; Gijzen et al., 2000). However, in this model, the hypothetical estimates for plant potential growth, usually used for such purposes, are replaced by using a series of state variables which define architectural and physiological characteristics along the potential growth trajectory of each of the plant components.

Commercial Butterhead lettuce of the type grown in GHs forms loose open heads of soft leaves during its vegetative phase, initiated sequentially along short circular stems (Wien, 1997). The information required to presenting the potential morphological development and DM growth of this plant shoot includes stem and leaf dimensions, changes with time, and leaf initiation (Plastochron) rates. DM specific leaf area (SLA) and DM specific stem volume (SSV) are also required.

This paper shows how estimations of the potential sizes and growth of leaves are drawn by analyzing data measured within a commercial system where lettuce plants grow under fixed and controlled climatic conditions.

MATERIALS AND METHODS

Observations were conducted on hydroponics' lettuce (*Lactuca sativa* L., cv *Flandria*), grown in a controlled environmental agricultural facility, with integrated supplemental light control, (Both, et al., 1995; Albright et al., 2000). Data were collected from May to July 2004, while the greenhouse operated under consistent controlled air temperatures (day/night 23/19 ^{o}C, Root Zone temperature (RZT) 26^{o}C, and PPFD integral 18 mole m^{-2} day^{-1}).

On day zero seeds were sown in 3.8 cm x 3.8 cm x 3.8 cm Grodan rock wool blocks, 700 seeds m^{-2}. The trays were misted and let grow for 12 days in ebb and flow benches. Then the plants were transplanted into floating trays in a hydroponics system, 100 plants m^{-2}. On day 21 after seeding the plants were re-spaced to 39 plants m^{-2}. The plants were grown in the GH up to ±35 days after seedling (DAS). Production was continuous so that the GH contained approximately 1000 plants of each age.

One to three samples of each daily cohort were harvested. Each sample included 7-14 plants. Plants in each sample were separated into free roots, roots within the rock wool blocks, the main stem, cotyledons, and the leaves numbered serially (from the bottom). The maximal diameter and length of each stem were recorded.

The leaves, identified by their serial order along the stem, were placed on mm paper where the dimensions of each leaf - the maximum length (L), maximum width (W) and the distance from the bottom of the leaf up to the location of its maximum width (LMW) were recorded. The leaf area (LA) of each leaf group was determined using a LA meter (Licor model 3100). Leaves, stems, free roots and roots within the rock-wool blocks of each group were packed, each age group individually, dried more than 14 days at 75 $^{\circ}$C and weighed. The measured L, W and LMW of each serial leaf were presented as function of days after seedling (DAS). S-shaped curves were fitted to each data series, using the statistical curve fitting procedures in SYSTAT 2002 sections 2-59 and 11-41.

Area changes and unfolding occurring along the growth of each serial leaf were represented by series of related tongue-like and circular flaps. The area of each flap was calculated by summing the area of the ellipse representing the upper part of each flap, and a small triangle, representing the base part of each flap (EST = Ellipse + Small Triangle). The area the whole flap (triangle + ellipse) is:

$$LA = \pi \cdot a \cdot b + h \cdot \frac{b \cdot h}{h + a} = \frac{\pi \cdot (L - LMW) \cdot W}{2} + \frac{(2 \cdot LMW - L)^2 \cdot W}{2 \cdot LMW} \quad (1)$$

The auxiliary parameters are the first radius of the ellipse: ($a = L - LMW$), the second radius of the ellipse: ($b = W / 2$), the height of the small triangle ($h = L - 2a$) and half of base of the small triangle ($(b \cdot h)/(h + a)$).

The unfolding of each serial leaf was described by presenting the calculated area values vs. DAS and by fitting an S-shape curve to each leaf series. The dates of leaf initiation, maturity and maximal unfolding rates were graphically determined according to these curves (Dayan et al., 1993): logs of the derivatives of the "S" shape curves values were presented vs. DAS. The DAS value in the junction between the horizontal zero reference line (representing an unfolding rate of 1 cm^2 d^{-1}) and the linear line which connects the ascending log values was defined as the initiation date, and the junction with the logs of the descending values was defined as the maturity date. The length of each leaf cycle was calculated as the span between maturity and initiation. The maximum unfolding rates of each leaf and their timing were determined according to the maximum log values and corresponding values on the DAS axis, respectively.

The specific LA (SLA: $m^2 g_{DM}^{-1}$) for each leaf, according to its age, was determined by the ratios between the DM and the value of the measured or calculated LA of the corresponding sample.

Linear models were fitted for the changes within stem length (L') and diameter (W') values vs. DAS. The stem volume growth was described by a series of tapered pillars. The volume of each pillar was determined as a cone volume:

$$SV=\frac{\pi*(W'/2)^2*L'}{3} \quad (2)$$

The specific stem DM volume (SSV: $m^3 g_{DM}^{-1}$) for each plant age was determined according to the ratio between the calculated volumes and the measured stem DM values.

RESULTS

Examples of the dynamic changes of L, M, and LMW, which were measured on leaves of each serial number, are presented on the left part of Figure 1. The maximal values of L, W and LMW of the other leaves are presented in Table 1. The maximal W parameter of typical lower leaf (1-7) is small relatively to the L value, while the LMW is larger than the W and is 70-80% of the L value. As the serial number of the leaf ascends the W values become larger and similar to the L values, while the LMW values decrease to 50% of the L values. These changes are involved with the morphological evolution of the leaves from tongue-shaped flaps into flaps with a circular shape. On the right side of figure 1 the LA values of this leaf are presented together with the "S" shape curves fitted to these values. The logs of the unfolding rates of these leaves are presented by the asymmetric bell shaped curves adjoined to each unfolding "S" shape curve. The Maximal LA values are specified in table 1. The ratios between measured and calculated LA are presented in Figure 2, and shows a reasonable agreement (R^2= 0.95) between measured values of LA and values calculated by the EST method. The "S" shape curves, for leaves 1-18, are identified by highly significant scores (R^2 value for each curve is above 0.9). Yet, the significant score goes down as the leaf serial number increases above 18.

The upper part of Figure 3 presents the ascending log values of the leaf unfolding rates vs. DAS, while the lower part of this figure presents the descending log values. The initiation, maturity and maximal unfolding rates of each serial leaf, as well as their calculated life cycle span values, which were drawn out of Figure 3, are summarized in Table 1. In Figure 4, the initiation and maturity dates are used to show changes within the life span length values along the growing period: starting with 7 days old, plant has a constant leaf initiation rate (0.972 leaves day^{-1}). The life span length of a lower leaf is rather short (7 days). Higher leaves are growing actively for more days. Leaves above serial number 7 attain a constant maturity rate which is very similar to the initiation rate. As a result, the life cycle span of leaves 8- 18 has a constant value of 14±1.5 days. The maximum unfolding rates of these leaves are 16±2 cm^2 day^{-1}. The leaves achieve these high unfolding rates 7 days after the initiation date and continue to expand for 3 to 4 days.

Figure 5 shows that the young leaves are thicker (identified by low SLA values (200±100 cm^2) than the older leaves (400± 100 cm^2 g_{DM}^{-1}). The SLA of each leaf increases within the first 7 days after initiation. The lower seven leaves have higher SLA values than the upper leaves, yet the variability of the collected data were very high.

Figure 6 shows that exponential stem volume growth occurs as a result of the stem linear elongation and thickening, measured along the plant growth cycle. For 20-35 days old plants the measured SSV are 7.5-9 cm^3 g_{DM}^{-1}. Smaller values are measured for younger plants but the variability among values is high.

Each lettuce plant accumulates, in its roots and shoots, 5 g DM during its 35 growing days. The maximum growing rate along the final stage is 0.28±5 g $plant^{-1}$ day^{-1}. Figure 7 shows that each plant component accumulated DM by exponential growth. Some 80% of the total DM accumulated in plant leaves, more than 10% in the roots (data for the final stages are assumed) and less than 10% in the stems.

DISCUSSION

The total DM quantities (5 g m^{-2}) accumulated within the plants along the 35 day growth period (Fig. 7), were not far below the high production values of different lettuce cultivars calculated and measured in GHs with similar conditions (Albright et al., 1999; Both, 1995; Wheeler, 1995). The DM accumulation rate along the final 4-5 days corresponds to 0.28 (g_{DM} $plant^{-1}$) x 73 (plants m^{-2}) ≅ 20 (g_{DM} m^{-2} day^{-1}), which is in the order of magnitude of the potential DM production of C3 plant (Keulen and Wolf, 1986). The DM accumulation curves along this period within each plant were exponential, with no symptoms of mutual competition. Exponential curves may be fitted for the DM accumulation in each plant component: stem, roots and leaves. The stem becomes a measurable sink for DM production only 7 – 10 days after seeding, yet the total DM accumulation within the stem is relatively small (Figs. 6-7). Lettuce roots accumulate 20% of the total plant DM (Fig. 7), yet detailed information about the mechanism and physiology of root growth was not obtained during this study.

The leaf initiation rate of lettuce, as was measured by the EST method, was constant (0.972 leaves $plant^{-1}$ day^{-1}). Constant leaf initiation rates of this order of magnitude [influenced by a nutrient solution temperature (RZT)] were measured for different lettuce cultivars by other methods (Bensink, 1971; Both, 1995). Other characteristics of leaf morphology and physiology change as functions of the leaf serial number and age. E.g. the lowest seven leaves of the plants were relatively thin tongue-like leaves with a relatively short life cycle span (8±1.5 days). The higher the leaves are located along the stem, their shape changes gradually into a circular shape with faster maximum unfolding rates (16±2 cm^2 day^{-1}) and a longer and constant life cycle span (Table 1:14±1.5 days). Each leaf achieves its maximal unfolding rate within 7 days. The leaf unfolds at a maximal rate for only 2-3 days. In this period of time each leaf becomes thinner (from SLA values 200± 100 to 500 ± 100 cm^2 g^{-1}). Both, who measured an average SLA of entire lettuce heads, got SLA values of the same order of magnitude (Both 1995, p. 58). Other parameters are rare in the literature. The confidence of the parameters for leaves located above serial leaf 18, is low, and some of the required information can't be retrieved (E.g. maturity date and life cycle span), as those leaves do not accomplish their life cycle within the experimental period.

CONCLUSIONS

The measured values of DM accumulation within each plant were relatively high and quite similar to the calculated or measured maximal values found by other researchers (Wheeller, 1995; Both, 1995). The maximal measured DM accumulation rates per m^2 were close to the potential and theoretical DM accumulation rates (Keulen and Wolf, 1986). The fitted total DM accumulation, as well as the shoots and roots growth curves, were exponential and showed no symptoms of mutual competition. These characterizations make a justification for using the controlled system, the specified spaces between the plants, and the measured growth curves and parameters as references for potential plant growth and DM partitioning between plants components (alternately, it shows that higher crop densities may be considered for commercial purposes) (Keulen and Wolf, 1986).

The presented observations did not yield any new detailed information about root or stem growth, by which detailed calculations can be done, yet they show that DM accumulation in both roots and shoots can be described by exponential growth curves (Fig. 7), and it seems that refinement of simple functions, by which the potential DM accumulation in roots calculated according to the potential DM accumulation in the shoot, is preferred to complete, but uncertain, modeling procedures. A similar approach was adopted in other models (Dayan et al., 1993; Gijzen et al., 2000). The DM accumulation within the plant stem is even smaller and may be calculated as a function of leaf growth.

Because of the relatively high portion of DM, accumulated within the leaves of the plant (Fig. 7), the accuracy and sensitivity of a lettuce growth model can be improved

by knowing accurate and detailed morphological and physiological characteristics of each leaf as it grows. The required information changes due to plant age and leaf serial number (Figs. 1, 3, 5, Table -1). Describing lettuce leaves by using series of flap patterns, each composed of a small triangle and an ellipse, is an example of the special methods required for attaining this information. This study demonstrates that the EST method enables an accurate presentation of the morphological changes along leaf growth by measuring L, W, and LMW. It was shown that the measured morphological information can be used for drawing details about the initiation and maturity state of each leaf life cycle span too. Longer observation periods than those reported here are required in order to obtain more reliable information especially on the upper leaves.

ACKNOWLEDGEMENTS

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Nomenclature

DAS: Days After Seedling (days).
DM: Dry Matter
EST: Ellipse + Small Triangle.
g_{DM}: gram Dry Matter.
L: Leaf length (cm).
LA: Leaf Area (cm).
LAI: Leaf Area Index
LMW: Distance from bottom up to the horizontal maximal width line.
SLA: Specific LA ($cm^2 g_{DM}^{-1}$)
SSV: Specific stem volume ($cm^3 g_{DM}^{-1}$)
SV: Stem volume(cm^3).
W: Leaf maximum width (cm)

Tables

Table 1. Additional morphological and physiological characterizations of distinct serial leaves along the lettuce stem, as drawn from basic morphological measurements.

Leaf Serial Num.	Max dimension			Life Cycle			Max Unfolding		
	L cm	W cm	LMW cm	Initiation DAS	Maturity DAS	span Days	rate cm^2/day	Timing DAS	Leaf age Days
1	4.6	2.4	3.6	7.2	10.5	3.3	1.73	9	1.8
2	7.5	4	5	8.2	14.4	6.2	3.04	11	2.8
3	9.5	5.2	6.8	9.9	18	8.1	5.13	14.1	4.2
4	11.2	6.5	8.3	10.9	20.8	9.9	6.64	16	5.1
5	12	7.9	8.3	11.8	24	12.2	7.66	18	6.2
6	12.7	8.8	8.2	13.9	24.8	10.9	13.56	19	5.1
7	14	10.9	9.8	15	25	10	21.79	21	6
8	14.5	11.5	9.8	15	29	14	14.63	22	7
9	14	12	9	16	29.5	13.5	17.19	23	7
10	14.5	13.5	9.6	16	32.9	16.9	15.68	25	9
11	16.4	14	12	18.6	34	15.4	16.15	27	8.4
12	16.1	14.2	13	20.8	34	13.2	18.22	28	7.2
13	15.8	13.8	12.4	22	34.2	12.2	20.18	28	6
14	15.9	13	13	22.7	35.2	12.5	17.16	29	6.3
15	14.3	13.8	12	23.2	36.5	13.3	16.33	30	6.8
16				23.2	37.2	14	16.12	31	7.8
17				24.8	38.2	13.4	13.11	32	7.2
18				25	39	14	12.18	32	7

Figures

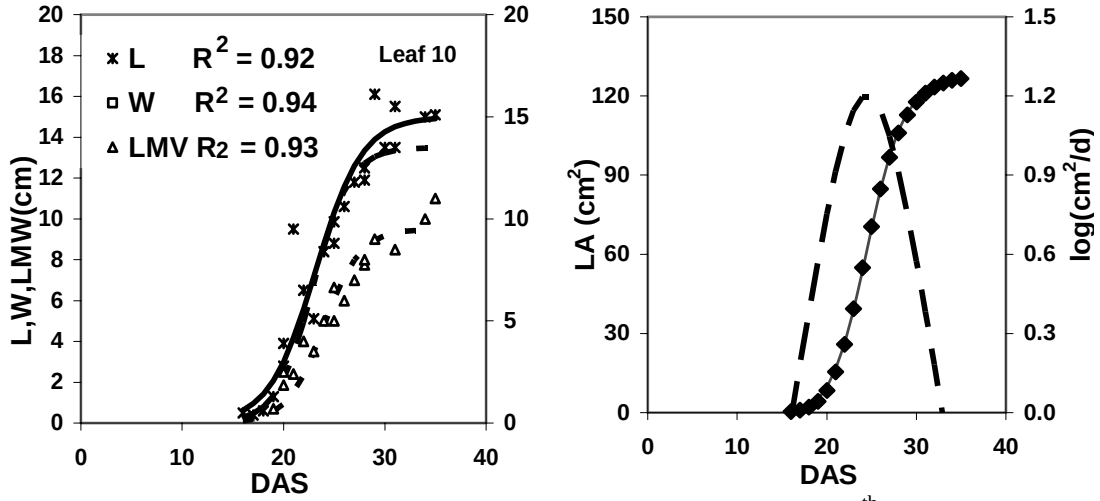

Fig. 1. **On the left side**: Changes within L, M, and LMW of the 10th serial leaf along a growth period of the plant, and "S" shape curves which were fitted to the measured data. **On the right side**: Symbols represent leaf unfolding rates, calculated by EST, according to the "S" shaped curves adopted to the L,W and LMW; Logs of the unfolding rates are presented by asymmetric bell shape curves.

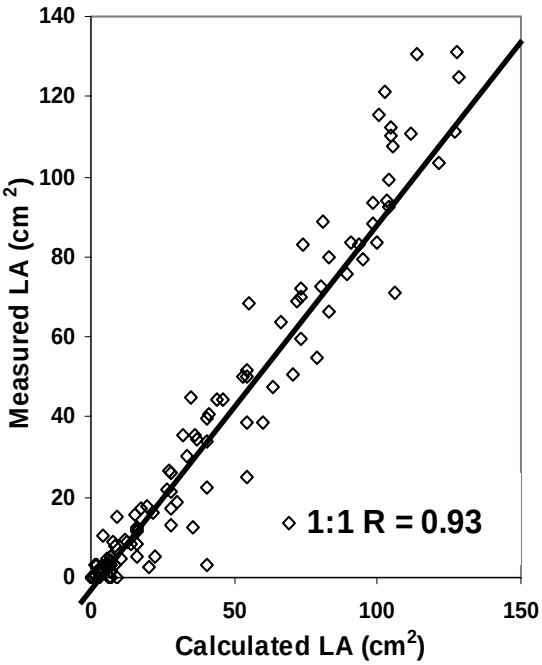

Fig. 2. Measured LA of leaves sample vs. calculated areas of an ellipse + small triangle of the same leaf .

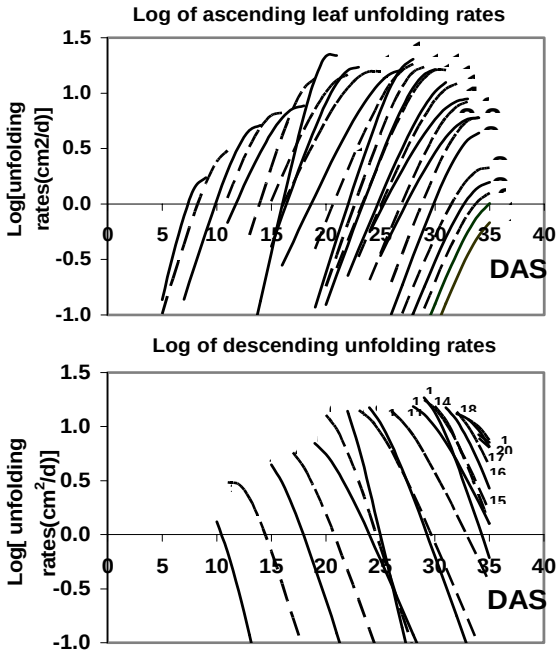

Fig. 3. Upper fig: lines assigned to the ascending logs of the leaf unfolding rates vs. DAS. Lower fig: the descending logs.

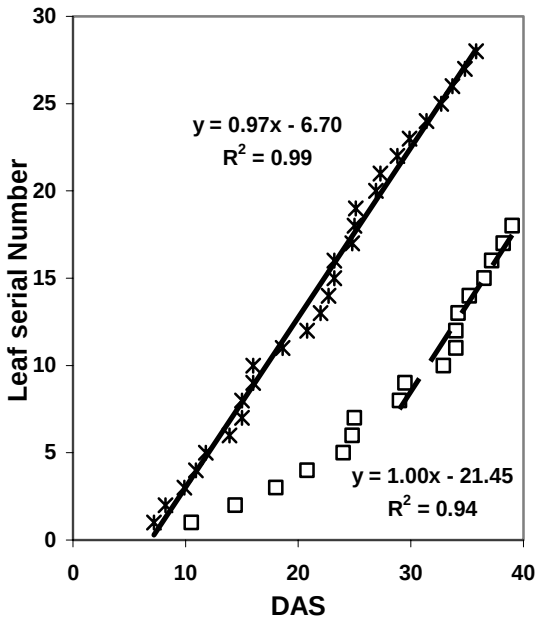

Fig. 4. Leaf initiation rates (the upper solid line), maturity rates (lower scattered line) and life cycles (horizontal spans between lines) vs. DAS.

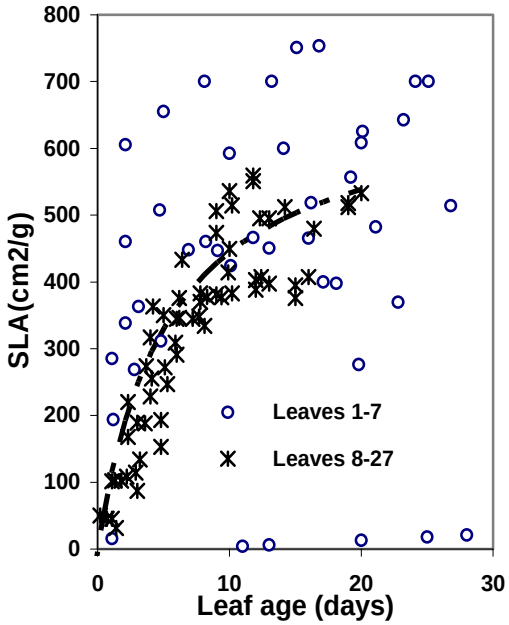

Fig. 5. Crosses and fitted curve represent the leaf age dependent specific leaf area (SLA) values of the 8th-35th leaves. Circles represent the SLA of leaves no. 1 to 7.

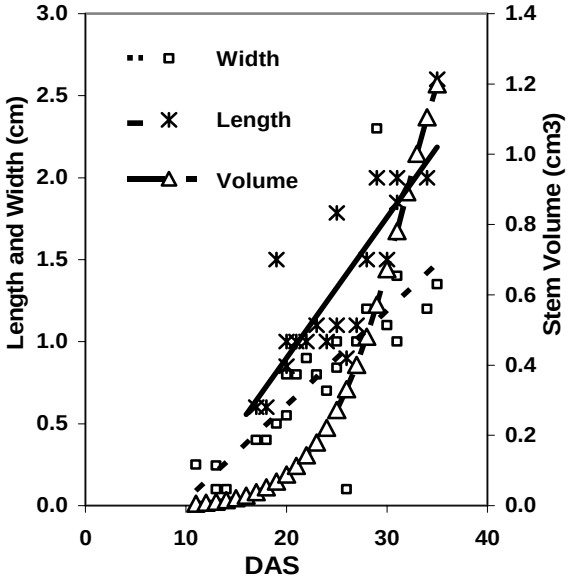

Fig. 6. The measured changes within stem length and diameter as plant growth proceeds and the calculated volumes of the conical pods representing these stems.

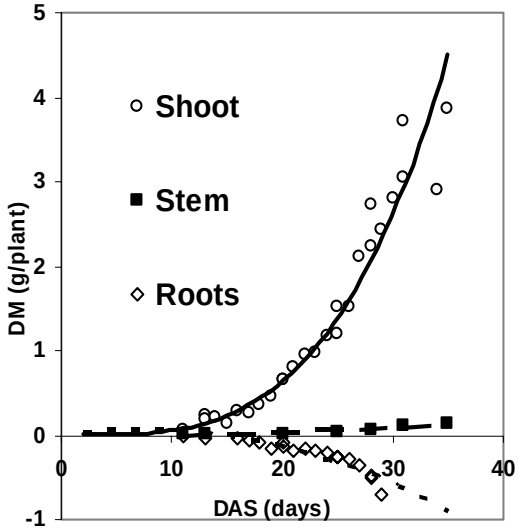

Fig. 7. DM accumulation within lettuce plant along 35 days. Circles represent DM accumulation within the shoots (leaves + stems), squares represent DM accumulation within the stems, and rhombuses, in the roots.