

Seasonal Variations in Photosynthetic Capacity, Growth, Leaf Development and Productivity of Sugar Beet Plants under Optimal Nitrogen Supply*

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Abstract

Leaf development, leaf area distribution, growth and productivity (dry matter of leaves, roots, crowns; and sugar yield) of sugar beet (*Beta vulgaris* L. cv. Monoscope) plants were studied during the 1983 and 1984 growing seasons on an experimental field plantation. Photosynthetic capacity (P_c ; photosynthetic photon flux density saturated net photosynthetic rate) was measured at regular time intervals in 1984 and 1985. Using these data, the performance of a model (*SUBEMO*) simulating growth, yield and sugar accumulation was evaluated. At the end of the growing season, viz. October, about 50 leaves were developed by the sugar beet plant, yielding maximal leaf area index values of around 4 to 5. P_c changed considerably during the growing season showing significantly lower values before appearance of leaf number 20 (around mid-July), increasing later in the season and slightly decreasing near the end of the growing season (mid-October). P_c of mature leaves was significantly and positively correlated with total leaf dry matter of the sugar beet plants at the end of the growing season. Comparisons between simulated and measured dry matter production of leaves and beets (roots + crowns) confirmed the need to integrate seasonal trends in P_c in the simulation model.

Plant (dry matter) productivity is dependent upon many factors, including intrinsic CO₂ uptake rate, environmental conditions (climate, nutritional and water status of the soil), cultural management strategies, genetic variability and light intercepting leaf area. All these process and structure variables vary during the growing season, showing typical patterns in function of time or

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life span (Šesták 1985). Plant development and performance vary in function of the season (Gordon *et al.* 1982), while also changes in photosynthetic activity of leaves may take place in response to the time course of internal events, such as leaf and plant senescence (Hodáňová 1981, Šesták 1985). The integrated variations in the above mentioned dynamic processes and structural plant characteristics determine final plant yield and productivity. When modelling plant growth and/or yield seasonal patterns in plant development, seasonal changes in P_c and leaf appearance should be implemented in the model (Hodáňová 1979).

The present study aimed (1) to determine the seasonal variations and patterns in photosynthesis, plant and leaf development, and productivity, and (2) to evaluate the impact of seasonal variations in P_c on the performance of a simulation model.

MATERIAL AND METHODS

Plant materials: The data used to evaluate the performance of the model and to determine seasonal patterns in yield determining processes and characteristics were monitored during two consecutive seasons (*viz.* 1983 and 1984) on an experimental sugar beet field at Hélécine, Belgium (51°50' N, 4°50' E; 53 m above mean sea level), situated in the loamy region of the country. As usual for this region, sugar beets are grown in rotation with winter wheat and winter barley. As a consequence the experimental data for the consecutive seasons were not gathered on the same plot of the experimental plantation. However the field was evaluated as fairly uniform.

Sugar beet (*Beta vulgaris* L. cv. Monoscope) plants were grown from late April until the last week of October under normal field conditions. A 17 cm distance within rows and 45 cm distance between rows was respected. Based upon an analyses of the actual fertility level of the plough layer a basic fertilizer application (P_2O_5 , K_2O , MgO , B) was supplied. In February 1983 and 1984, the nitrogen status of 60 cm upper layer was determined. According to the N-index method (Boon 1981) a nitrogen fertilizer advice was given by the Soil Service of Belgium. Current pesticide treatments were applied to keep the crop free from weeds and diseases.

Climatological data (air temperature, relative atmospheric humidity, net short-wave radiation, daily precipitation and wind velocity) were recorded continuously and stored every 5 min with an automatic weather station (*Didcot Company*, England) controlled by an *Apple II* microcomputer. Mean daily values for air temperature, relative atmospheric humidity and wind velocity were calculated and stored together with the daily values for net short-wave radiation and precipitation on an input file for the *SUBEMO*-model (see further).

Morphological crop and plant characteristics: Every week during the growing season the total number of actual and dead leaves was determined on ten plants in four sample blocks of the experimental field. Simultaneously soil cover was also determined. For estimations of soil cover, a sheet divided in rectangles of 5 by 10 cm was placed in between the sugar beet rows. The rectangles or parts of them which were

covered by the sugar beet leaves were counted and gave a measure of soil cover. Every three to four weeks during the growing season the following measurements were made in four replications to evaluate the simulation model: fresh and dry matter of the roots, crowns and leaves, leaf area (index), sugar content of the roots and crowns on a fresh matter basis.

Response of net photosynthetic rate (P_N) on irradiance was determined in several replications for mature fully expanded leaves of intact plants at regular intervals in the field from July till October (1984 and 1985). In 1984 an open system design consisting of a portable infrared gas analyzer (*Leybold-Heraeus*, type *Binos 1*, F.R.G.) connected to a digital millivoltmeter, a twin set of pumps and a mini leaf clamp-on cuvette (inner area of 4.5 cm^2) was used, as described in detail by Ceulemans and Impens (1982). Since P_N measurements were made within 30 s, the plexi cuvette was not environment-controlled, and no significant increases in leaf temperature were observed.

During the 1985 growing season an improved version of a closed system configuration using the same infrared gas analyzer, membrane pumps and clamp-on cuvette as mentioned above was used (Ceulemans *et al.* 1986). Spot measurements of P_N were carried out within 15 s using this closed system device. Simultaneously with P_N photosynthetic photon flux density (PPFD) incident on the leaf was measured with a *Lambda* (*Licor*, Lincoln, U.S.A.) quantum sensor. P_N was expressed on a single side leaf area basis. Each set of measurements included six leaves in three replications per leaf. A rectangular hyperbola was fit through the P_N -PPFD response data (Bliss and James 1966), and photosynthetic capacity (P_c) was determined accordingly as the PPFD saturated (*i.e.* above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) P_N . When PPFD saturation had not been reached (*e.g.*, on a cloudy day) P_N was "corrected" to $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ using representative PPFD response curves (Hesketh *et al.* 1981).

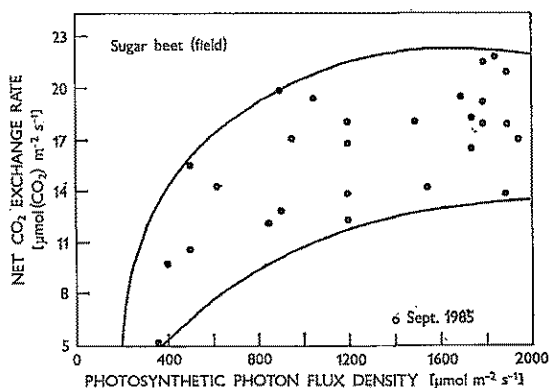


Fig. 1. Net photosynthetic rate — photosynthetic photon flux density response curve of fully developed sugar beet leaves for a typical midsummer day (6 September, 1985). Each point represents the mean value of six replications. Boundary lines were drawn by free hand.

The model *SUBEMO* (*SUGAR BEET MODEL*) was based on the original *SUBGRO* (Fick 1973) and *SUBGOL* (Hunt 1974, Ng 1980) models, both built to simulate potential sugar beet growth under California (U.S.A.) weather conditions. Using the meteorological data and the initial crop matter data as input parameters, the *SUBEMO* model has been adapted as a further refinement of the *SUBGOL* model to make it useful for specific West-European weather conditions, sugar beet cultivars and agronomic practices (Vandendriessche 1989).

RESULTS AND DISCUSSION

Seasonal trend in P_c : In the P_N -PPFD response curve for a typical day (*e.g.*, 06 Sept. 1985) PPFD saturation was observed in most cases above $1 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Fig. 1) similar to values reported by Hodáňová (1979). The mean seasonal trends in P_c of mature, fully expanded leaves (Fig. 2) for the 1984 and 1985 growing seasons were

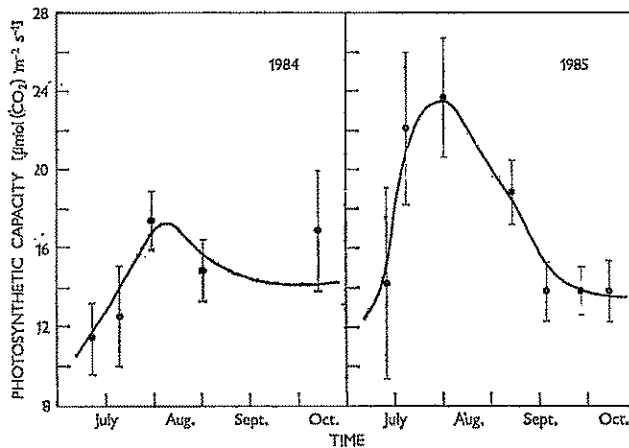


Fig. 2. Seasonal course of net photosynthetic capacity of fully developed leaves of sugar beet plants measured at Hélécine experimental field. Means \pm S.D.

in the range of values reported in literature for sugar beet (Terry and Ulrich 1973, Milford and Pearman 1975, Hodáňová 1981) although Gordon *et al.* (1982) observed significantly higher values in soybean [up to maximum $44 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$]. The sugar beet leaves measured showed a characteristic pattern of P_c over the growing season which can be more or less divided into three phases (see Gordon *et al.* 1982) *viz.* a low P_c early in the season (until beginning of July) followed by an increase during July and first half of August, and subsequently a decline in P_c as the crop senesces (after mid-August until mid-October). Although the absolute values of P_c were much higher in 1985 than in the 1984 growing season, the general pattern was the same. It is unlikely that these P_N values (mainly of young sugar beet leaves) are

controlled by the sucrose concentrations in the leaves (Milford and Pearman 1975).

In 1985 a P_c value of *ca.* $12-14 \mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ was noticed in spring, increasing to $\pm 24 \mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ in July and August, and declining slowly to $14-16 \mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ near the end of the growing season. Similar patterns have already been reported in literature for soybean (Hesketh *et al.* 1981, Larson *et al.* 1981, Gordon *et al.* 1982), sugar beet (Hodáňová 1981), *Mercurialis* (Masarovičová and Eliáš 1985) and several other species. Masarovičová and Eliáš (1985) showed that not only P_c but also the P_N -PPFD response curve significantly change during the season, but these changes could not be quantified in the present study. Moreover, the changes in the P_N response curve reported by these authors (Masarovičová and Eliáš 1985) are very pronounced because of the shade-adapted behaviour of the *Mercurialis perennis* plants they studied.

As P_c or P_N showed a typical pattern during the season, this characteristic trend should be incorporated in any growth or yield simulation model.

Plant and leaf morphology: The total number of leaves produced by sugar beet, the number of leaves actually present (expanding plus fully developed leaves) and the number of dead leaves at different times of the growing season are presented in Fig. 3 for the 1983 and 1984 growing seasons. During the 1983 growing period the plants had produced an average of 37 leaves on September 16 and an average of 48 leaves on October 20. In 1984 this figure was 38 leaves on September 28. These num-

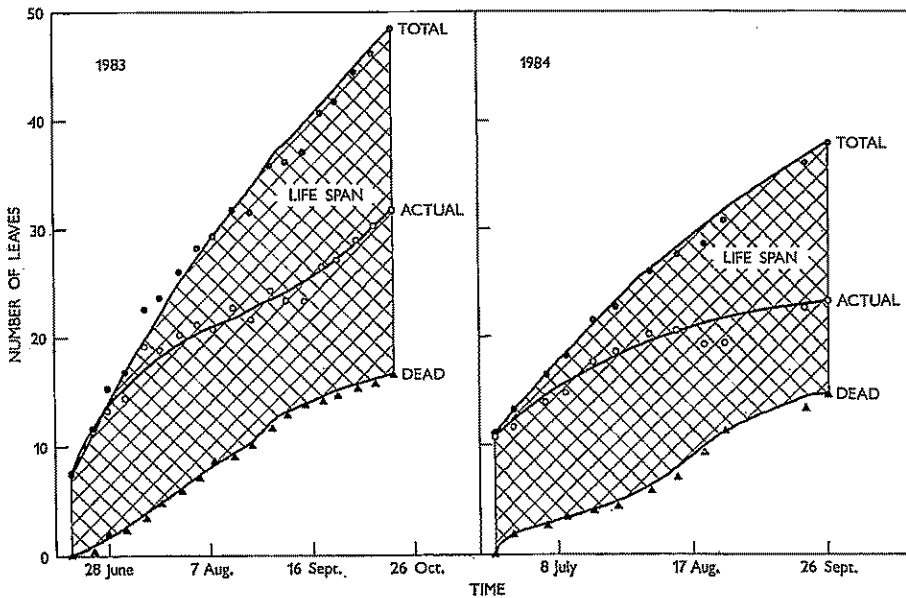


Fig. 3. Seasonal course of leaf numbers and life span for sugar beet plants grown at the Hélécine experimental field site. Each point represents the mean value of 40 plants.

bers of leaves produced by sugar beet cv. Monoscope are significantly lower than the values reported for cv. Dobrovická A grown in an experimental field near Prague (Hodáňová 1981).

As soon as 7 – 11 leaves were produced, the first developed leaves started to die. Thereafter and until the beginning of August, the new leaves appeared more or less at the same rate as the old leaves died. After mid-August, a nearly constant number of 20 – 25 leaves was maintained on the plants. Leaf growth characteristics were more pronounced to change during the first half of the vegetation period than P_c (Hodáňová 1981).

Dry matter production: Dry matter production of leaves, roots (including crowns), and of the total plant (leaves, roots and fibrous roots) were plot against time (Fig. 4). The simulated dry matter production is shown as a continuous line while observed

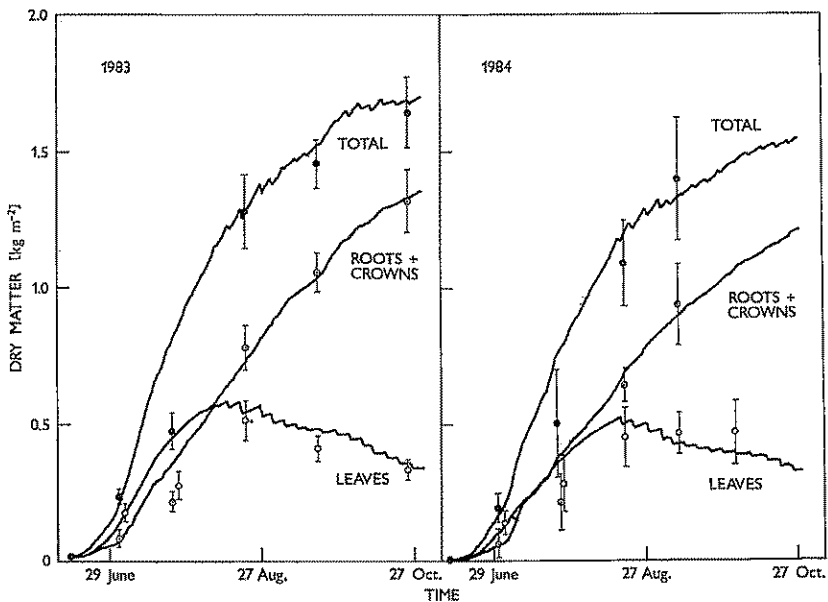


Fig. 4. Simulated (full lines) and observed (points) dry matter production of leaves, roots (including crowns) and total plants during two consecutive growing seasons. Simulation results are from the SUBEMO model; observed dry matters are mean values (\pm S.D.) of four replications. — simulation results; \circ — (measured) total plant d.m.; \odot — (measured) roots + crowns d.m.; \bullet — (measured) leaves d.m.

field measurements are presented by their means and standard deviations at regular time intervals. Comparison of the dry matter production for the total plants, the roots and crowns, and the leaves showed very good agreement between measured and simulated results. Most of the time the simulation results were situated between the standard deviation of the measurements.

In conclusion, seasonal variations in P_c growth, leaf development and productivity of sugar beet plants under optimal nitrogen supply were demonstrated. Moreover, good agreement between productivity simulated by the *SUBEMO*-model and observed productivity data was observed, and confirmed the need to integrate seasonal trends in P_c in the simulation model.

REFERENCES

- Bliss, C. I., James, A. T.: Fitting the rectangular hyperbola. — *Biometrics* 22: 573—602, 1966.
- Boon, R.: [Nitrogen application based on soil profile analysis for winter wheat and sugar beet on deep loam and sand-loam soils.] — *Pedologie* 31 (3): 347—363, 1981.
- Ceulemans, R., Impens, I.: L'étude des échanges photosynthétiques de CO_2 comme mesure de la croissance et de la production de différentes plantes agricoles, ornementales et horticoles. — *Rev. agr.* 35: 2631—2653, 1982.
- Ceulemans, R., Kockelbergh, F., Impens, I.: A fast, low cost and low power requiring device for improving closed loop CO_2 measuring systems. — *J. exp. Bot.* 37: 1234—1244, 1986.
- Fick, G. W.: Analysis and Simulation of the Growth of Sugar Beet (*Beta vulgaris* L.). — Ph. D. Thesis. University of California, Davis 1973.
- Gordon, A. J., Hesketh, J. D., Peters, D. B.: Soybean leaf photosynthesis in relation to maturity classification and stage of growth. — *Photosynth. Res.* 3: 81—93, 1982.
- Hesketh, J. D., Ogren, W. L., Hageman, M. E., Peters, D. B.: Correlations among leaf CO_2 exchange rates, areas and enzyme activities among soybean cultivars. — *Photosynth. Res.* 2: 21—30, 1981.
- Hodáňová, D.: Sugar beet canopy photosynthesis as limited by leaf age and irradiance. Estimation by models. — *Photosynthetica* 13: 376—385, 1979.
- Hodáňová, D.: Photosynthetic capacity, irradiance and sequential senescence of sugar beet leaves. — *Biol. Plant.* 23: 58—67, 1981.
- Hunt, W. F.: Respiratory Control and its Prediction by a Dynamic Model of Sugar Beet Growth. — Ph. D. Thesis. University of California, Davis 1974.
- Larson, E. M., Hesketh, J. D., Woolley, J. T., Peters, D. B.: Seasonal variations in apparent photosynthesis among plant stands of different soybean cultivars. — *Photosynth. Res.* 2: 3—20, 1981.
- Masarovičová, E., Eliáš, P.: Seasonal changes in the photosynthetic response of *Mercurialis perennis* plants from different light regime conditions. — *Biol. Plant.* 27: 41—50, 1985.
- Milford, G. F. J., Pearman, I.: The relationship between photosynthesis and the concentrations of carbohydrates in the leaves of sugar beet. — *Photosynthetica* 9: 78—83, 1975.
- Ng, E.: Morphogenesis, Leaf Development and Senescence in Sugar Beet (*Beta vulgaris* L.). — Ph. D. Thesis. University of California, Davis 1980.
- Šesták, Z. (ed.): Photosynthesis During Leaf Development. — Academia, Praha; Dr. W. Junk Publ., Dordrecht — Boston — Lancaster 1985.
- Terry, N., Ulrich, A.: Effects of potassium deficiency on the photosynthesis and respiration of leaves of sugar beet. — *Plant Physiol.* 51: 783—786, 1973.
- Vandendriessche, H.: Gebruik en validatie van SUBEMO. [Use and evaluation of SUBEMO.] — In: Simulatie als Hulpmiddel bij het Stikstofbestedingsadvies voor de Teelten Winterarwe en Suikerbieten. Pp. 83—105. Comité voor Toegepaste Bodemkunde, I.W.O.N.L., Leuven—Herlee 1989.