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Development of the husk tomato plant (Physalis ixocarpa Brot.). III. Growth analysis

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Abstract

Growth analysis of husk tomato plants cv. Rendidora was done applying classical methods. Quantities such as the Relative Growth Rate, Leaf Area Ratio, Unit Leaf Rate and others were calculated in order to describe the changes which occur in the *Physalis ixocarpa* plant during its development from emergence to death. The mentioned quantities comported differently in the four periods of the life of husk tomato, providing a good insight into the changing direction and intensity of the main physiological processes and their mutual balance. It is believed that such recognition of the properties of a plant may help breeders.

Resumen

Se realizó el analysis de desarrollo del tomate de cáscara cv. Rendidora aplicando los métodos clásicos. Los índices fisiotécnicos como Tasa Relativa de Crecimiento, Relación de Area Foliar, Tasa de Asimilación Neta y otros fueron calculados y presentados en forma de curvas para describir el desarrollo de *Physalis ixocarpa*. Los índices mencionados mostraron diferente comportamiento durante los cuatro periodos de la vida de la planta permitiendo observar los cambios en la dirección y la intensidad de los principales procesos fisiologicos y su balance momentáneo.

Key words: growth analysis, vegetative growth, reproductive development

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INTRODUCTION

The husk tomato is a widely cultivated plant in Mexico and was recently introduced into small scale cultivation in Poland. Successful trials of its cultivation were also accomplished in the USSR (Medvedev 1958). This paper is aimed at providing more information on the development of the husk tomato with the hope of helping investigators to increase its productivity. We understand the term "development" in its broader sense, as comprising growth and differentiation (Loomis 1953, Listowski 1970, Wareing and Phillips 1970, Moore 1979) and even senescence and death (Listowski 1970, Jankiewicz 1979).

Mathematical analysis of plant growth has become relatively frequent in agricultural investigations, since it allows deeper insight into crop formation at the level of a whole plant. Although the more sophisticated methods, such as measurement of photosynthesis of a single leaf, or part of it, in controlled conditions, are indispensable and supply important data, they can not fully replace the investigation of a whole plant growing under undisturbed field conditions, up to the moment of taking it for analysis (Hunt 1982).

As far as we know, growth analysis of *Physalis ixocarpa* Brot. has never been published, so the purpose of this paper was to describe the development of this plant in these terms. As a basis for calculation of the quantities employed in the growth analysis, we used the data presented in our earlier publications (Cartujano et al. 1985a, b).

MATERIAL AND METHODS

The experiment was set up in an irrigated field of the Campo Agricola Experimental, Zacatepec, Morelos in the central part of Mexico during the dry period of the year (1982.10.31–1983.02.13). The methods of cultivation, the environmental conditions and the arrangement of the experiment were described earlier (Cartujano et al. 1985a). We repeat, nevertheless, some necessary details: The field was devided into 8 plots. During the first 5 weeks after emergence (AE), four plants were taken each week from each plot for leaf area and dry matter estimation (in total $4 \times 8 = 32$ plants). During this period it was impossible to recognize the two types of plants present in the population: the erect and the prostrated ones. Later on, after 5 weeks, two prostrated and two erect plants were taken from each plot, at random, with the condition that they were healthy and had neighbours. From the 9th week AE, only one plant of each type was taken from each plot. During the period:

7th-13th week AE the samples were taken every second week. Additionally, a sample was also taken on the 14th week AE.

We applied classical methods for the growth analysis (Briggs et al. 1920a, b. Radford 1967, Květ et al. 1971, Evans 1972, Hunt 1982). The intervals between the sampling dates were rather typical in our experiment: 1 or 2 weeks. Due to this, the mean values of the quantities in the growth analysis which we used throughout this paper were rather close to the instantaneous values and the shape of curves obtained with both types of values was quite similar. For calculation of most of the quantities used, the values of the leaf area (A) and of total dry matter of a plant (W) were used. These values were obtained from the combined curve composed, up to the 6th week AE, of the real average data, and afterwards, from the data derived from the fitted curve obtained from the equation of regression (calculated by a computer, using the minimum squares methods) (see Carujano et al. 1985a). The significance of the regression was checked at the 0.05 level. The equations were calculated separately for the prostrated (Pr) and erect (Er) plants using polinominals of higher degrees:

$$\begin{split} W_{Pr} &= 5.27360168F - 3.49405845F^2 + 0.62021093F^3 - 0.0266948F^4 \\ R^2 &= 98.1\%, \ c.v. = 27.16\% \\ W_{Er} &= 2.70274663F - 2.00668776F^2 + 0.38154421F^3 - 0.01632328F^4 \\ R^2 &= 98.0\%, \ c.v. = 28.46\% \\ A_{Pr} &= 494.906105F - 375.92989285F^2 + 86.52629043F^3 - 6.95914461F^4 \\ R^2 &= 97.8\%, \ c.v. = 29.22\% \\ A_{Er} &= 111.79575802F - 20.37816025F^2 + 4.42606288F^3 - 0.3327667F^4 \\ R^2 &= 95.0\%, \ c.v. = 40.59\% \\ Leaf \ Weight_{Pr} &= 619.2435F - 457.2584F^2 + 93.5072F^3 - 4.36587F^4 \\ R^2 &= 98.9\%, \ c.v. = 18.85\% \\ Leaf \ Weight_{Er} &= -367.4222F + 56.4141F^2 + 18.4217F^3 - 1.2698F^4 \\ R^2 &= 94.6\%, \ c.v. = 42.82\% \\ \end{split}$$

The differences between the prostrated and erect plants concerning the above quantities were not proved statistically with the method of paired plots.

The following formulas were used to calculate the indices of growth analysis:

Leaf Area Ratio (LAR):

$$\overline{LAR} = \frac{1}{2} (LAR_1 + LAR_2), \tag{1}$$

where $LAR = \frac{A}{W}$.

Leaf Weight Ratio (LWR):

$$\overline{LWR} = \frac{1}{2} (LWR_1 + LWR_2), \tag{2}$$

where LWR = $\frac{L_W}{W}$, (L_W = leaf weight).

Unit Leaf Rate (ULR):

$$\overline{ULR} = \frac{2(W_2 - W_1)}{(A_1 + A_2)(t_2 - t_1)},$$
(3)

where t = time in weeks.

This formula was used since the relation between A and W was of the type $W = c + bA^2$ (see Radford 1967), except for the data from the last two weeks (Fig. 1).

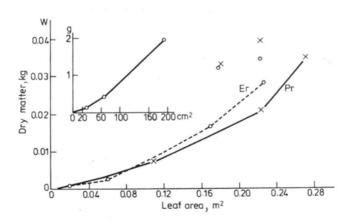


Fig. 1. Relationship between the leaf area (abscissa) and dry matter in husk tomato plants. The initial region is shown magnified on the upper left side. The points outside the curves belong to that last two dates when the plants already showed symptoms of senescence.

Pr — prostrated plants, Er — erect plants

Relative Growth Rate (RGR):

$$\overline{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}.$$
 (4)

Leaf Area Index (LAI):

$$\overline{LAI} = \frac{1}{2} (LAI_1 + LAI_2), \tag{5}$$

where LAI = $\frac{A_c}{\text{Unit Area of Land}}$, (A_c = leaf area of the plants occupying a unit area of land).

Crop Growth Rate (CGR):

$$\overline{CGR} = \frac{W_{c2} - W_{c1}}{t_2 - t_1} \times \frac{1}{P},$$
(6)

where A_c and W_c mean dry matter of plants growing on an area P. In the further text we write LAR, PGR etc. instead of \overline{LAR} , \overline{RGR} etc.

RESULTS AND DISCUSSION

This chapter is divided into two parts. In the first, the changes of each quantity of growth analysis, which took place during development are described. In the second, we depict phases of development of the plant taking advantage of the above quantities.

BEHAVIOUR OF THE QUANTITIES OF GROWTH ANALYSIS (FIGS. 2-4)

As had previously been mentioned (Cartujano et al. 1985a), leaf area (A) starts to increase faster than the total dry matter (W) and all phases of leaf area development come 1–2 weeks earlier than those of dry matter (Fig. 2). This seems understandable since the leaf area which is formed needs a lapse of time to achieve its full phytosynthetic efficiency.

Leaf Area Ratio (LAR) initially augments, reaching its maximum very early — between the 2nd and 4th week AE, (Fig. 3). This augmentation is probably caused by the mentioned anticipation of dry matter production by leaf area formation. Thereafter, LAR decreases, initially more and later somewhat less. This decline reflects the fact that each unit of leaf area has to feed an increasing amount of plant organic matter. The curves of LAR for prostrated and erect plants are almost identical. They intersect between the 7th and 8th week AE but it is doubtful if this has any meaning.

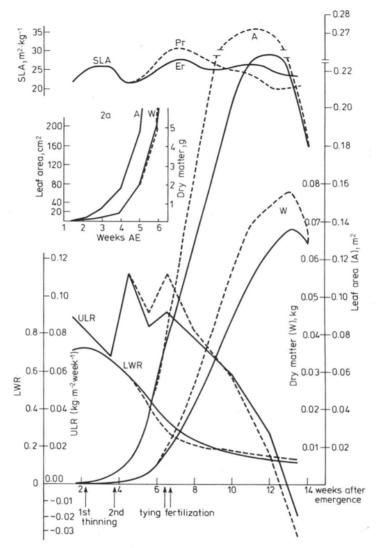


Fig. 2. Quantities of growth analysis of the aerial part of husk tomato plant: A — Leaf area, W — Total Dry Matter, LWR — Leaf Weight Ratio, ULR — Unit Leaf Rate, SLA — Specific Leaf Area in prostrated (Pr) and erect (Er) plants. During the first 5 weeks the prostrated and erect plants could not be discerned and are shown jointly. The curves of A and W are of combined type: up to the 5th week after emergence are based on the real data and for the later period on the equations of regression. The curves of the other quantities are based on mean values. In the upper-left corner (2a) magnification of the initial part of the graph for A and W

LAR, by definition, is closely related to the other two quantities: **Specific Leaf Area (SLA)** and **Leaf Weight Ratio (LWR):** LAR = $SLA \times LWR$. The same equation in more ample form is as follows:

$$LAR = \frac{Leaf Area}{Dry Matter of the Leaves} \times \frac{Dry Matter of the Leaves}{Total Dry Matter of the Plant}.$$
 (7)

The curve representing SLA (Fig. 2) ilustrates that this quantity does not change markedly during the growing season, indicating that the thickness of the leaves was rather similar during the duration of the experiment. There was only some decline between the 4th and 5th week AE, just after the second thinning of the plants, which probably reflects the appearance of several new and still thin leaves after releasing the plants from excessive competition. In several other species of plants, SLA behaves in a similar way, i.e. does not change much during the life of a plant (Evans 1972).

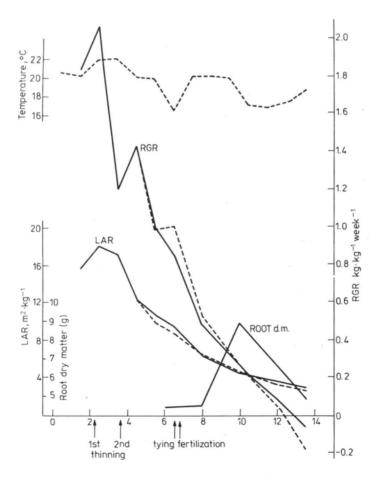


Fig. 3. Quantities of growth analysis of husk tomato plant: RGR — Relative Growth Rate, LAR — Leaf Area Ratio, Root d.m. — total root dry matter. Temperature is shown in the upper part of the graph. Other details as in Fig. 2. On the abscissa: weeks after emergence.

As could be expected, Leaf Weight Ratio (LWR) show a behaviour very similar to that of LAR (Figs. 2 and 3), since SLA is relatively stable. The form of the curve of LWR indicated that the participation of dry matter of leaves in the total dry matter of a plant diminishes during the major part of plant life as a consequence of increasing dry matter of stems, fruits etc. This constitutes an element of a well-known phenomenon of ontogenetic drift. The decrease of LAR and LWR with ontogenetic drift has been reported by several authors (Evans 1972, Solorzano 1980, Nilwik 1981a, Hunt 1982).

Unit Leaf Rate (ULR) starts with high values (Fig. 2) and then drops between the 3rd and 4th week AE, probably due to the strong competition among the plants which occurred at that time. After thinning

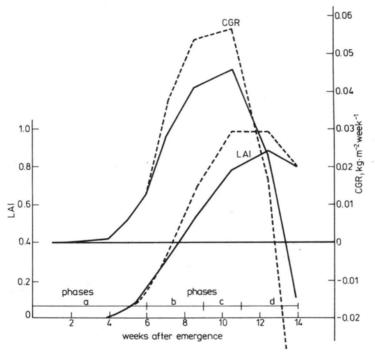


Fig. 4. Quantities of growth analysis of husk tomato plant: CGR — Crop Growth Rate, LAI — Leaf Area Index. Other details as in Fig. 2. Phases of husk tomato development marked at the bottom

the plants on the 25th day AE, the ULR rose rapidly and then dropped again to show a new peak between the 6th and 7th week. This new peak, especially pronounced in the prostrated plants, could result from improved light conditions after tying the plants to strings. At that time also fertilization with nitrogen for the second time was done. Two other factors which could contribute to this peak were: temporary lowering

of temperature (Fig. 3) which could reduce respiration, and a known phenomenon of stimulation of photosynthetic efficiency by massive formation of generative organs, which in *Physalis*, began at that time (see Cartujano et al. 1985b). After the 7th week AE the ULR decreased rapidly to below zero at the end of the experiment. The decrease was more rapid in the prostrated plants — this coincides well with their earlier senescence (Cartujano et al. 1985a).

In the works of different authors, ULR shows various performances. A decrease of ULR with age, similar to that in the second part of *Physalis* life, was shown in dicotyledoneous plants by Sivakumar and Shaw (1978), Watson (1971), Solorzano (1980) and Nilwik (1981a, b). In other plants like maize and sorgo, ULR increases to a certain value which is relatively stable for a long period and then drops toward the end of plant life (Nichiporovich 1956, Zavala 1982, see also Hunt 1982). In pine seedlings, Drew (1982) found cyclic fluctuations of ULR, parallel to those of RGR and opposite to the fluctuations of root growth. This phenomenon probably reflects strong competition between root and shoot growth in this species.

One of the reasons for the decrease of ULR with ontogenetic drift is that each unit of leaf area has to feed larger and larger masses of scarcely photosynthesizing or non-photosynthesizing parts of a plant like stems and fruits, which utilize leaf photosynthates for their respiration (compare decreasing LAR). This agrees with the opinion that ULR depicts the general balance between the assimilation and dissimilation of a plant (Evans 1972, Żelawski and Sztencel 1981, Pietkiewicz 1985a, b). In connection with this, it may be mentioned that Fukai and Salisbury (1977) have found that dark respiration is proportional to the dry matter during a large period of plant life. Therefore, one may suppose that when the dry matter of a plant increases, total respiration rises (see Nilwik 1981b).

The other cause of decreasing ULR values as the plant ages, may be the internal shading within the plant (Zavala 1982). This factor probably is not of great importance in the husk tomato due to its low LAI values (see further text). Still another cause of ULR decline may be the diminishing photosynthetic activity of older leaves. This factor certainly has some significance in husk tomato plants, since their lower leaves are of a relatively short duration, at least in cv. Rendidora.

Relative Growth Rate (Fig. 3). The curve begins with high values but drops abruptly between the 3rd and 4th week AE. This decrease is probably caused by strong competition for light and nutrients among the plants, probably occurring at that time. After thinning them, the RGR rises immediately but only for a short time. From the 5th week AE on,

the RGR shows a steep decrease to values below zero at the end of the experiment. This decline was temporarily handicaped in prostrated plants at the 6-7th week AE, probably due to tying the plants to strings, and to the 2nd fertilization with nitrogen. Tying the plants obviously influenced the prostrated plants more by placing them in better light conditions.

The abrupt decrease of RGR after the 7th week AE is conceivable when one takes into account the following cardinal relationship: RGR = ULR × LAR (Briggs et al. 1920a, b, Hunt 1982). Since both quantities on the right: ULR and LAR decrease rather parallely towards the end of plant life, the same must occur with RGR. This decrease was somewhat faster in prostrated plants due to their evident faster senescence (Cartujano et al. 1985a, b).

Many other authors show similar comportment of RGR (Sivakumar and Shaw 1978, Nilwik 1981a, see also Evans 1972 and Hunt 1982). In broad beans, high values of RGR lasted up to the midlife of a plant (Solorzano 1980). In cassava, the RGR curve (similarly like that of ULR) showed two peaks: one during the early development and the other during tuberization (San José and Mayobre 1982).

According to Żelawski and Sztencel (1981) and Pietkiewicz (1985a, b). the weight of the root system should be included in the calculation of RGR. Nevertheless, there are very many authors who abandon this due to the difficulty of root investigation. In our case, we have investigated the root system of 4 plants on each of the following dates (6th, 8th, 10th, 12th and 14th week AE) and the detailed results are published elswhere (Mulato et al. 1986). The characteristic feature of the root system development was that its dry matter was close in its magnitude to that of the aerial part at the 6th week AE and then this proportion changed (Fig. 3) so that at the 10th week AE the dry matter of the aerial part was 5-6 times as large as that of the root system. This comportment is understandable when one takes into account, that in Mexico where Physalis ixocarpa originates, the rain falls very irregularly at the beginning of the rainy period, so the young plant needs a strong root system to survive. Thereafter, during the full rainy period, the size of the root system is probably of less importance and even plants with relatively scarce roots may survive.

Leaf Area Index (LAI), (Fig. 4). The curves of LAI reach a maximum from the 9th to 13th weeks AE for the prostrated plants, and between the 11th to 13th week AE for the erect ones. This difference confirms the mentioned observation that the prostrated plants have a shorter life cycle. The values of LAI for prostrated plants tend to be higher (compare the data for leaf area in Fig. 2). Generally, the values of LAI

for husk tomato are exceptionally low in comparison with those for other species, for instance sugar-beet (Watson 1971, Hunt 1982).

Crop Growth Rate (CGR) curves (Fig. 4) for both types of plants are of a similar type. Initially the joint curve increases steeply up to the 6-7th week AE, i.e. up to the time when a great number of reproductive organs are formed. From this time on, the increase of CGR slows down up to the 10th week AE. This probably reflects the increasing proportion in the plant body of the parts which are mainly consumers of photosynthates (fruits, stems etc.). After reaching a maximum at about the 10th week AE, the CGR values sharply drop to values below zero at the 13-14th week AE. Several factors may contribute to the final decrease of CGR: some leaves abscise, and some of the leaves which are still present show lowered photosynthetic activity, which is reflected by low ULR of individual plants (a high percentage of the leaves yellow and wilt at the end of plant life). The respiratory needs of the plant increase too (see earlier discussion). The number of fruits of all sizes, after reaching a maximum between 11th and 13th week AE, decreased (see Cartujano 1985a, b), probably in connection to the decreasing ULR and massive abscission of flower buds, flowers and young fruits (Mulato et al. 1985, Jankiewicz and Borkowski - in preparation).

Concerning CGR, Loomis and Williams (1969) mention that there are 2 groups of plants—in one, CGR reaches its maximum value and then drops, whereas in the other, "a plateau response has been found with CGR remaining constant as LAI increased... The breaking point of such a curve occurs at a LAI level sufficient to provide full cover" (see Donald 1961). Husk tomato may be ranked among the first of these groups.

PHASES OF DEVELOPMENT OF THE HUSK TOMATO

When describing the development of this plant we considered it convenient to split its life cycle into 4 phases according to its leaf area development (Cartujano et al. 1985a).

In phase "a" (0-6th week AE), leaf area and dry matter of the plant show nearly exponential growth (Fig. 1) (Cartujano et al. 1985a). During this period the values of RGR are high (Fig. 3). The behaviour of these 3 quantities show that photosynthates produced in this period are mainly used to generate new photosynthetic apparatus which results in nearly exponential growth of the leaf area and of the whole plant dry matter: the leaves formed during this period are very large and probably are efficient. This in turn contributes to high values of RGR. The plant body is mainly composed of leaves, which is reflected by high

values of LAR and LWR. Toward the end of this period the production of flower buds, flowers and the first fruits begins. This is probably the cause that the growth of the leaf area changes its character from nearly exponential to rectilinear at the end of this phase (see Żelawski and Sztencel 1981).

During phase "b" (6-9th week AE), leaf area and dry matter of the plant increase at a very high rate, but this increase is rectilinear. The fast increase of these two quantities indicates that the plant takes advantage of the great photosynthetic apparatus formed during the previous phase and continues to add to it. This last fact is reflected by the steep increase of LAI. The photosynthetic efficiency of the plant to produce dry matter (ULR) is still high at the beginning of this phase but decrease drastically during its second part. This last phenomenon is related to the increased proportion of stems and reproductive parts (which are mainly consumers of assimilates) in the total dry matter of the plant. This is well visualized by the gradual decline of LWR and LAR. Thus, the photosynthates produced by the leaves are used in larger and larger proportion to support the respiration of stems, reproductive parts and roots, so that the percentage of assimilates remaining available for the production of new dry matter of a plant declines more and more. On the other hand, the formation and thickening of the stems in this phase may be considered as preparation of a framework to support the fruits and other parts of the plant body which increase in weight. As shown by Cartujano et al. (1985b) the number of flower buds and flowers reaches its maximum at the end of this phase. The number of young fruits is also increasing fast. However, CGR already starts to slow down.

Phase "c" (9-11th week AE). Leaf area shows lessening increments, and reaches its maximum at the end of this phase (11th week AE). LAI and CGR attain their maximum at the same time. The total dry matter grows rectilinearly and its maximum comes in the next phase. LAR and LWR decrease continuously for the same reason as in the previous phase. The decrease of these two quantities is obviously followed by a decrease of RGR. The other reason for RGR decrease is the progressive diminution of ULR (explanation as in phase "b"). The dry matter of the stems as well as the level of their ramification and the dry matter of apices increase greatly (Cartujano et al. 1985a). This last fact means that the production of the reproductive parts rises, because in husk tomatoes, each node bears a reproductive unit. A rapid increase of the number of reproductive parts induces increasing competition for photosynthates and water and mineral elements among these parts, but, on the other hand, diminishing ULR and LAR reflect that the availability of photosynthates goes down. Also the number of root apices seems to decrease at the 10th week AE, although the root dry matter shows its maximum at the same time. The decrease of the number of root apices may be understood as a result of strong competition between the aerial and subterranean parts of a plant (Mulato et al. 1986). Similar competition was frequently observed in fruit trees during the reproductive phase (see Jankiewicz 1979). The coincidence of all these factors at least partly explains the drastic decrease of the number of flower buds and flowers which occurs during phase "c", no doubt due to increased abscission. Meanwhile, the fruits become probably the greatest sink for photosynthates (Cartujano et al. 1985b). The total number of fruits reaches its maximum at the end of this phase. Nevertheless, limited supply of nutrients probably causes a large proportion of a youngest fruits to be shed before reaching a diameter of 2 cm (Mulato et al. 1985). During this phase, the major harvest starts. The fresh matter of harvested fruits nearly reaches its maximum in prostrated plants at the 11th week AE. In erect plants this maximum comes later (Cartujano et al. 1985a, b).

Phase "d" (11–14th week AE). The leaf area which reached its maximum at the end of the previous phase is decreasing in this phase.

Total dry matter reaches its maximum at the 13th week AE, i.e. 2 weeks after the leaf area attained its maximum. The reason for this delay has already been explained: the newly formed leaves need some time to reach their maximum efficiency (see also Cartujano et al. 1985a, b). The majority of quantities representing vegetative growth decrease during this phase: LAI, LAR and LWR. Especially drastically (to zero or below) decrease CGR, RGR and ULR. On the other hand, in this phase the plant reaches its maximum size and maximum degree of ramification. The plant tends to cease its growth, which is reflected among others, by the formation of very short internodes (Mulato et al. 1985). Also the leaves formed at that time are very small (as is observed in common practice). Cardenas (1981) also reports that the late fruits are smaller than the early ones. The number of flower buds present on the plant decreases with the exception of the smallest ones. This indicates that the majority of flower buds are shed when they are very small. The number of flowers is also low, with the exception of these of "class 4". This may be interpreted as the last reproductive efforts of a plant the wild plants may endeavor not only to produce fruits but also to produce more pollen to pollinate other plants). The largest fruits formed during the previous phase gradually attain commercial size and are harvested. The fresh matter of harvested fruits per week reaches its maximum at the 12th week AE for the prostrated plants and at the 13th–14th week AE for the erect ones. However, many fruits less than 2 cm in diameter continue to be shed. Probably, the effort of a plant to feed the largest fruits promotes the shedding of the smaller ones. to feed the largest fruits promotes the shedding of the smaller ones

which already do not have any chance to ripen. On the other hand, the reproductive effort of a plant probably speeds its senescence. At the end of this phase a plant gets partly yellow and looses many of its leaves. Some parts of the plants start to wilt and die.

Concluding, in our opinion, the results of this work strongly support the view that growth analysis using classical methods and rather short intervals between samplings is of great help in describing crop formation in plants. Such a description may be useful to breeders to construct reasonable ideotypes of a productive plant (Donald 1968, Evans 1975) by indicating physiological basis of high productivity. In sorgo, for example, several characteristics of plant growth, like LAI and Leaf Area Duration (LAD) show relatively high percentage of inheritance and are well correlated with the yielding capacity (Zavala 1982). The description of plant development using growth indices may also help to improve cultural practices, for instance, the decrease of CGR and ULR before the 2nd thinning in our experiment indicate that this practice should be done earlier, or fewer plants should be left during the first thinning.

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Rozwój miechunki pomidorowej (Physalis ixocarpa Brot.). III. Analiza wzrostu

Streszczenie

Wykonano analizę wzrostu miechunki odmiany "Rendidora" stosując metodę klasyczną. Na podstawie oznaczania suchej masy rośliny i pomiarów powierzchni liści co 1–2 tygodnie, obliczono takie wskaźniki, jak: Względna Szybkość Wzrostu (RGR), Wskaźnik Ulistnienia Rośliny (LAR), Jednostkowa Produktywność Liści (ULR, NAR) i inne, w celu opisania zmian jakie zachodzą w roślinie w czasie jej rozwoju. Wymienione wskaźniki zachowywały się różnie w każdym z czterech okresów życia rośliny, pozwalając na lepsze określenie zmian w intensywności głównych procesów fizjologicznych i ich wzajemnej równowagi. Uzyskane wyniki sugerują, że wskaźnikowa analiza wzrostu rośliny może być pomocna dla hodowców.