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Influence of air temperature and humidity during the vegetative growth on some structural characteristics of the leaf of Capsicum annuum L.[1/]

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ABSTRACT

The growth of leaves is presented with an analysis of the epidermic cells divisions and expansion of the limb. The influence of the air temperature and humidity on the growth of the leaf is also exposed.

A particularly attention is accorded to the number of stomata of the growth-leaf as also the percentage of stomata in relation with the cells in different climatic conditions.

INTRODUCTION

The size of a leaf is determined both by the size and the number of its cells. According to plant species cell division and cell growth occur simultaneously or during two successive stages. For Lupinus albus and Helianthus annus, for example, cell division does not stop until the leaf has the half ot its maximal size (SUNDERLAND, 1960). On the contrary with several varieties of Lactuca sativa (BENSINK, 1958) shows with evidence a succession of two periods, a primordial stage during occur only cell divisions, and another stage of cell expansion. Stomatal initiation occurs just before the mitosis stop, by a dissymetrical cell division (BUNKING, 1956). Actually it seems likely that the respective length not only amongst plant species, but also amongst the leaves of the same plant.

The speed of cell divisions is strongly influenced by climatic conditions. It appears (BENSINK, 1958; DALE & MURRAY, 1968) that the number of cells in a leaf generally increases when conditions favourable to photosynthesis by the leaf are realized. The primordial stage is very important since the potential expansion of a leaf is determinated by the number of its cells.

Most of the results cited were obtained with epidermic cells. It is obvious that the evolution of different tissues in a leaf is not always

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similar. In tobacco leaf primordia, for example, (AVERY, 1933) the mid-rib is differentiated first. Cell divisions stops first in epiderm, then in mesophyll, and at last in the palisade tissue. On the contrary, epidermic cells are still elongating when mesophyll cells have stopped. Furthermore, cell divisions stop first at leaf tip, then in the other lobes.

Optimal climatic conditions for these transformations are not very well known, especially as these studies are often done without an exact knowledge of the level of water supply. WAGENMANN 91961) alone points that the leaf area increases with soil moisture, either by the number of cells, or by their size, or by both of them.

It appears therefore interesting to study the influence of different transpiration conditions (caused principally by differences in relative humidity of the air) on cell divisions and cell expansion in the leaves of pepper (Capsicum annuum) seedlings. We have also studied the influence of a constant temperature during day and night compared with alternated temperatures. This problem, is very important indeed for mid season green-house crops in Southern France, and for tropical areas under trade winds, when night temperatures are high during the rainy season. This circumstance perhaps explains the low yields obtained with vegetable crops during this period.

MATERIALS AND METHODS

Growing substrate for the plants

Pepper seeds (C.V. YOLO WONDER) are germinated on wet blotting-paper during 4-5 days at 20°C, then placed in square seed pans (31 x 31 x 7 cm) filled with commercial enriched peat substrate (TKS2). The mineral nutrition of the plants can be considered at the same in the various treatments. The plant-stand at the beginning is of 50 by seed-pan, i.e., approximately 520 plants m^2. The systematic samplings during the experiments are done in a way as uniform as possible in order to decrease this density approximatively in the same way for each seed-pan. The plants are watered once a day in order to compensate evapotranspiration. Four experiments were realized in the following climatic conditions:

Climatic conditions

During the whole experimental period, the plants are kept in air conditioned rooms. Climatic conditions similar for the 4 treatments are summarized in table 1.

Artificial illumination during the day is obtained with fluorescent lamps (Power groove), the radiation of which is very strong in the spectral bed 550 - 700 nm, especially active for photosynthesis. A glass ceiling, between the lamps and the airconditioned room reduces considerably the transmission of infrared radiations. For this reason, although the liminous radiation above the plants is about 20,000 lux, energetic

Table 1.--Climatic condition similar for the 4 treatments

Conditions	Length	Total radiation: air:temperature above the plants		
		Luminous	Energetic	
Day	14 hours	20.000 lux	58 W. m^{-2}	25,5°C
Night	10 hours	0	0	Varies with the treatments.

radiation is no more than 58 $W.m^{-2}$. The distance between the lamps and the plants is progressively reduced as the lamps become older, but it is always more than 1,5m. The mass of air of the air conditioned room and of its regulating annexes (25 m^3) passes approximately 200 times during one hour through a potent air flower, so that the linear speed of the air is about 1 m. sec^{-1} in the room. Air from outside is introduced, so that air in the room is changed about 3 times during one hour. Since carbon dioxide is consumed by photosynthesis at a rate of 16 mg. $dm^{-2}.h^{-1}$, for a leaf area index equal to 1, the need for air renewal would be of one third/one hour. We can therefore consider that in the air conditioned room the carbon dioxide amount in the air remains constant and normal (0,03%).

In the different treatments, relative humidity and night temperature are not the same (Table 2) with the same of air renewal, and increase of relative humidity leads to a decrease of transpiration by the plants. A slight difference in leaf temperature is therefore measured with several thermocouples pricked in the secondary veins of the leaves. Measuring the water loss of some pots (evaporation by the soil is avoided by covering it with an aluminum foil), and the corresponding leaf areas (for one side of the leaf only) allows to compute leaf transpiration for periods of several days.

Table 2.--Differences in climatic conditions between the treatments

Treatments	Night temperature	Relative humidity ±5%	Leaf temperature during the day	Leaf transpiration $mg.cm^{-2}.mn^{-1}$
1	19.0 °C	40%	25.0 °C	0.13
2	19.0 °C	72%	25.3 °C	0.05
3	25.5 °C	40%	25.0 °C	0.13
4	25.5 °C	72%	25.3 °C	0.05

Measured realized

Sampling. Three leaves (3rd, 5th and 7th leaves following the cotyledons) chosen for their uniform repartition along, the main stem are regularly taken from 20 plants. These three leaves are characteristic of the juvenile stage of the pepper plant. Samplings are done go from the apparition of the 3rd leaf, till the complete differentiation of the 7th leaf. Each figurative point on the graphs is the mean of 20 samples.

Leaf area. The limb of a very young leaf is folded on its mid-rib, the predominant part of such a leaf. It is therefore very difficult to estimate a leaf area reduced to this mid-rib. For leaves smaller than 3 cm^2, it is possible to measure the leaf area with a graphic planimeter with an approximate of 0,1 cm^2. For leaves larger than 3 cm^3 the leaf area can be measured more quickly.

RESULTS

Leaf growth

The general shape of the curves expressing the growth in leaf area (for the 3 leaves sampled, 3rd, 5th and 7th) in terms of time is in good agreement with generally accepted results, especially for plants growing alone, some leaves of which go on growing during the whole time of the experiments. The maximal growth-speed increases with the leaf-rank. As a consequence at the same physiologic age, (during the vegetative stage) a leaf of the rank n is larger than a leaf of the rank (n - 1).

The climatic conditions of treatment 1 and 3 differ from those of the treatments 2 and 4 only by the relative humidity of the air. The decrease of air saturation deficit reduces appreciably transpiration, and induces only a slight increase of leaf temperature. The difference in temperature cannot explain the differences observed for growth. Leaf area is greater under high humidity and this increase is yet greater when the rank of the leaf higher.

The effect of air saturation deficit is especially important when the night temperature is high (treatment 3 compared to 4). As a result the influence of air moisture on leaf development will be especially determinant in tropical areas, where air temperatures during the night remain high. On the 60th day after sowing, the increase in leaf area is very important (140%) and the plants are approximately five days earlier with strong relative humidity.

Climatic conditions in treatments 1 and 2, compared to 3 and 4 differ only by night temperature (19,0 or 25,5°C). Low night temperatures are clearly favorable to leaf growth, which is 100% superior in dry atmosphere, 25% in wet atmosphere.

Table 3.--Leaf areas on the 60th day after sowing (cm^2)

Treatments	3rd leaf	5th leaf	7th leaf	Total area of the 3 leaves
1 (40%,25/19)	55	90	95	240
2 (72%,25/19)	95	120	150	365
3 (40%,25/25)	30	40	50	120
4 (72%,25/25)	60	105	125	290

Growth in area of the epidermic cells of the leaf

The mean area of the cells does not reach a distinct maximal value during the life of a leaf in our experimental conditions. The mean area of the cells decreases with the leaf-rank. For the same treatment these curves cannot be inferred from each other by a translation of the time-scale (fig. 5).

In the same way that for macroscopic leaf growth, the growth in area of epidermic cells is accelerated under wet conditions (fig. 6, 7, 8). Low night temperatures favour cell expansion, especially in dry conditions.

Table 4.--Mean areas (in pm^2) of epidermic cells on the 60th day after sowing (precision $\pm$ 50 pm^2)

Treatments	3rd leaf	5th leaf	7th leaf
1 (40%, 25/19)	3900	3300	2800
2 (72%, 25/19)	4600	4000	3500
3 (40%, 25/25)	9800	2300	2100
4 (72%, 25/25)	4200	3500	3100

Number of cells in the leaf epidermis

The number of cells in the epidermis of a leaf (in Pepper plants during the juvenile stage) increases with leaf rank (table 5). In constant climatic experimental conditions the area of leaves of an higher rank is always greater since the cells are more numerous, although they are smaller. With an approximation of $\mp$ 2 days for the length of the primordial stage we can state that it does not change with air relative humidity or with night temperature. On the contrary, the cell division intensity is accelerated in wet conditions. High night temperature increases also leaf earliness: the end of cell division occurs 3 days earlier in dry conditions, 8 days earlier in wet conditions. Low night temperature (or large differences in temperatures between night and day) favor cell divisions intensity, especially in dry conditions. This increase is more important in high-rank leaves.

Table 5.--Mean number of cells in the upper epidermis of a pepper leaf (millions of ceils)

Treatments	3rd leaf	5th leaf	7th leaf
(40%, ^{1} 25/19)	1,5	3,3	4,2
(72%, ^{2} 25/19)	1,6	3,5	5,2
(40%, ^{3} 25/25)	1,4	2,1	2,5
(72%, ^{4} 25/25)	1,6	3,0	3,3

Variations in stomatal density

Owing to cell growth, stomatal density for 1 mm^2 of leaf is not constant, it increases very quickly at the end of cell division, then decreases to a limiting value which could be reached if the cell decreases to a limiting value which could be reached if the cell expansion would stop. On the contrary, the percentage of stomata to the total number of cells, in given climatic conditions, does not vary any more with time after stomatal differentiation.

The percentage of stomata to the total number of cells is therefore increased of more than 60% in wet atmosphere, with low night temperatures (comparison of 1 and 2) of more than 20% with high night temperatures (3 and 4). Stomatal differentiation seem to be less influenced by a

Table 6.--Percentage of stomata to the total number of cells (upper epidermis of the leaf; with an approximation of ± 0,5%)

Treatments	3rd leaf	5th leaf	7th leaf	Mean
1 (40%, 25/19)	7,1%	5,6%	6,5%	6,4%
2 (72%, 25/19)	11,0%	10,6%	9,4%	10,3%
3 (40%, 25/25)	6,3%	6,8%	7,7%	6,9%
4 (72%, 25/25)	6,6%	9,5%	9,1%	8,4%

variation of night temperature. However, in wet conditions the percentage of stomata is slightly higher under low night temperatures.

Owing to the difference in leaf growth in the two conditions, the stomatal density for 1 mm^2 reaches more rapidly its limiting value under high night temperatures (fig. 9 and 10).

DISCUSSION

Leaf growth dynamics

In the experimental conditions of our air-conditioned rooms, the experiments did not last a time long enough to reach a complete stop of leaf growth. Other observations allow us to think that a stop in leaf growth in natural conditions for a plant population is amongst other causes a consequence of a shortage of light. On the contrary in our experiments the plants could be considered as alone. Further more the leaves are radially disposed without overlapping (In trials realized now in Guadeloupe the experiments are kept a longer time to reach a final stop in growth).

The growth of a pepper leaf proceeds therefore in two distinct successive steps: the primordial stage during which cell divisions occur and the cell expansion stage, the expansion potential of a leaf being strongly linked with rate of cell division during the first stage.

It will be interesting to verify if the systematic decrease of cell area is always linked with leaf-rank, and that in any instance these curves will not be deductible from each other by a translation of the time-scale.

It is generally accepted that each plant species has a characteristic stomatal density. It is true in given climatic conditions, when the leaf has reached its mature stage, when cell expansion stops. We have demonstrated again that this density varies with leaf-age, a maximal density being reached when the cell divisions stop.

Influence of air moisture on the structural characteristics of a leaf

Although numerous authors (SUNDERLAND, 1960; DALE, 1964; MILTHORDE, 1959; NEWTON, 1963; MILTHORPE & NEWTON, 1963) have studied the growth of leaves under various environmental conditions one of them was concerned with sweet peppers, nor with influenced of the relative humidity of the air. From our studies it appears that pepper is very susceptible to water and transpiration conditions, since in spite of the supply low transpiration rates reached in our experiments, we can observe that a variation in relative humidity from 40% to 72% has a strong influence on global growth and stomatal differentiation. The stomatal density varies during leaf differentiation, but also with climatic conditions.

Influence of night temperature on the structural characteristics of a leaf

The night temperature effects are numerous. We know that respiration during the night decreases with temperature. If night temperature is kept the same as day temperature, consequently plant respiration increases, and of course losses in dry matter. Furthermore, for the same photosynthetic rate, the leaf, root ratio can be different. A compensation phenomenon can also occur between leaf thickness and leaf area.

As stated above, leaf area depends also on night temperature which, when high, restrains leaf expansion. Finally we have noted general times and interaction between moisture and night temperature effects on leaf development. Probably a similar interaction occurs with other climatic factors.

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