Effect of Water Economy on Plant Growth I. Influence of Water Level Lowering on the Growth of Water-cultured Tobacco Plants*

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戸塚 績**・門司正三**：タバコ水耕における水位低下と生長

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The relationship between plant growth and moisture conditions of soil has been tackled by many authors.¹⁾ However, many of them were mainly concerned with xeromorphism or with the influence of drought on transpiration and water economy, and very few have been worked on the relationship of photosynthetic and respiratory activities to water economy of plants.^{2), 3), 4)}

Water deficiency and temporary wilting of leaves are often observed in many plant species in hot and bright afternoon of midsummer, even under the mesophytic and high humid conditions in Japan. But it has scarcely been studied analytically how the growth of plants is influenced by the water deficit which has temporarily been induced by unbalanced water economy.

In the present paper, it will be discussed how the growth of tobacco plants suffers from limitation of absorbing root surface caused by lowering the water level of water culture solution. For the elucidation of this, the water deficit, mineral nutrient supply, and photosynthetic and respiratory activity of the plant will be discussed respectively, and then the growth sequence will be pursued by calculating the dry matter production in connection with the leaf water deficit.

Material and Methods

As material, *Nicotiana tabacum* L. "Bright Yellow" was selected for the reason why it is capable of normal growth even in somewhat weak illumination of 5000 lux of artificial light to keep the growth condition as possible as constant, and why it is favorable to evaluate the amount of roots active in water absorption without disturbance of tap root system, as the latter develops rather poor in this plant.

Three weeks after germination, young plants selected in equal size were water-cultured with enameled pots to provide the material for the experiment. Out of these material plants three experimental plants per pot were selected, and trans-

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planted again to Wagner's pots (18 cm. in diameter, 18 cm. in depth) on April 14, 1958, the 6th day of water culture, when the root developed about 10 cm. in length. Great care was of course taken to avoid mechanical damages especially of roots when transplanting. The Wagner's pots were located in a growth cabinet under the conditions of continuous illumination of 4500-5100 lux (ten 40 watt fluorescent tubes, Mazda, white), at $25 \pm 0.5^\circ$ (the reported optimum for tobacco plant growth was $23-29^\circ$), relative humidity of 49-62%, or 12-9 mm. Hg in saturation deficit, and CO_2 concentration of 0.539-0.562 mg./l.

The water level of culture solution was maintained with some device at constant depths, 2, 4, 6 and 8 cm. (from the top of pot), throughout the course of experiments. The experimental plants were cultured lest they should shade themselves, and for each set 2 pots were prepared. Boysen Jensen's culture solution ($\text{pH}=4.3$) was used, being dropped in the pot through a fine plastic pipe to renew the solution by ca. 1 liter a day, in order to keep constant levels of nutrient and oxygen concentrations. All the values of the latter measured in each pot by Winkler's method (at 25°) fell near 7 mg. O_2 /l.

Samplings of the material were done after 3, 7 and 11 days from the start of the constant water level treatment. At each sampling, fresh and dry weight of leaves, stems and roots, and leaf area were determined in two replications for each set.

Other two series of the same kind of experiments were carried out and have shown similar results.

Results and Discussion

1. The growth in dry weight:

The course of growth expressed in dry weight is shown in Table 1. The plants had the largest growth of 1755 mg. at the 2 cm.-set and the growth declined in parallel with the lowering of water level. The relative plant dry weights after 11 days of the experiment were 100, 87.5, 78.9 and 68.6 at the 2 cm.-, 4 cm.-, 6 cm.- and 8 cm.-sets, respectively, and this depression is severer than that in the leaf areas, where the relative values were 100, 93.2, 84.5 and 78.3.

For the sake of further analytical comparison of the growth difference, the net assimilation rate (NAR) of both extremes, the 2 cm.- and the 8 cm.-sets, was roughly calculated by the following equation (cf. e.g. Watson 1952⁹⁾).

$$\text{NAR} = \frac{\Delta W}{\bar{F}(t_2 - t_1)},$$

where ΔW indicates the increment of dry weight during the time interval of $t_2 - t_1$, and $\bar{F}$ is the leaf area at the time of t_1 . The NAR expresses the efficiency of leaves in the growth rate. The NAR calculated are:

	April 14—17	17—21	21—25
at the 2 cm.-set.....	1.59	1.21	0.92
at the 8 cm.-set.....	1.22	0.87	0.83.

The values for the 2 cm.-set always obviously exceeded those for the 8 cm.-set.

As the decline of the NAR would be caused by the depression of net assimilation (=photosynthesis—respiration) of leaves, the increase of the ratio of non-photosynthetic organs to leaf area ($C/\bar{F}$ ratio) and the accerelation of respiration in non-photosynthetic organs (in this connection, see Iwaki 1958⁷⁾), further discussions as to each of these factors will be done in the following.

The values of the $C/\bar{F}$ ratio were 0.97, 1.18, 1.01 and 1.24 at the 2 cm.-set, and 0.97, 1.19, 1.21 and 1.11 at the 8 cm.-set, on April 14, 17, 21 and 25, respectively. Little higher values were observed in the 8 cm.-set than in the 2 cm.-set. This is because the ratio of root fresh weight to the leaf area was rather larger at the 2 cm.-set than the 8 cm.-set, while in the ratio of stem dry weight to the leaf area there was almost no difference between the two sets. At any rate, no significant difference in the $C/\bar{F}$ ratio was found out between the two sets. Accordingly it should be assumed that the difference in the NAR may be induced by the difference in photosynthesis per unit leaf area, and/or respiratory activities of non-photosynthetic organs.

Table 1. Effect of water level lowering (started April 14, 1958) on the growth in dry weight of each organ and in leaf area, and active root/leaf area ratio (fresh weight/sq. cm.).

Date	Water level lowering	Total		Leaf		Stem dry weight mg.	Root			Active root /leaf area ratio mg./sq. cm.
		dry weight mg.	rel.	dry weight mg.	Area sq. cm.		total	aerial	submerged	
Apr. 14	2 cm.	170		116	55.7	27	27.0	12	15.0	4.38
	4 cm.	163		110	52.0	26	26.8	22	4.6	1.73
	6 cm.	166		113	54.6	26	27.4	25	2.4	0.72
	8 cm.	174		119	57.6	27	28.2	28	0.2	0.26
Apr. 17	2 cm.	436	100	316	102	46	74	46	28	4.4
	4 cm.	409	93.9	295	92	44	70	38	32	4.4
	6 cm.	381	87.5	272	88	42	67	34	33	3.9
	8 cm.	383	87.9	275	91	38	70	47	23	4.3
Apr. 21	2 cm.	929	100	706	223	102	121	53	68	5.1
	4 cm.	854	91.8	640	196	92	122	41	81	6.7
	6 cm.	798	86.0	592	181	77	129	70	59	5.7
	8 cm.	700	75.5	518	151	69	113	80	33	4.7
Apr. 25	2 cm.	1755	100	1314	357	201	240	135	105	4.8
	4 cm.	1537	87.5	1165	333	221	151	61	90	4.9
	6 cm.	1386	78.9	1050	302	171	165	91	74	4.6
	8 cm.	1204	68.6	893	280	131	180	107	73	5.0

The change of the total nitrogen content of leaves was investigated by the micro-kjerdahl method in order to clarify whether or no the reduction of active root surface below the normal can affect the absorption of mineral nutrients significantly. The results shown in Table 2 were the mean values of three determina-

Table 2. Variation of total nitrogen content of the tobacco leaves
(mg. N/g. D. W.)

Water level lowering	Apr. 14	Apr. 17	Apr. 21	Apr. 25
2 cm.	45.2	32.3	37.7	31.6
4 cm.	44.8	34.1	31.5	36.0
6 cm.	46.1	32.7	31.3	27.2
8 cm.	45.5	37.9	34.9	28.7

tions. So slight difference in each set was observed, that it can hardly be suggested there was any deficiency of mineral nutrients in plant with limiting water absorption. Close relationships between photosynthetic activity and nitrogen content of leaves are well known^{(8),(9),(10)}. It does not seem, however, that the observed fluctuations in nitrogen content of the tobacco leaves may have any influence on the photosynthetic activity for 7 days after starting the experiment, when the difference clearly appeared in the growth.

2. The depression of the leaf water content :

The changes of water content of the individual organs were investigated after 24 hours from starting the water level lowering (see Table 3). All organs other

Table 3. Effect of water level lowering on the water content of leaf, stem, aerial root and submerged root (average values)
after 24 hrs. of starting the experiment.

Water level lowering	Active root/leaf area ratio mg./sq. cm.	Water content (per cent on dry weight basis)			
		Leaf	Stem	Aerial root	Submerged root
2 cm.	4.5	907	1130	1203	1327
4 cm.	4.1	883	1250	1130	1293
6 cm.	1.8	865	1227	1190	1350
8 cm.	0.9	820	1218	1053	1375

than leaf blade showed no severe depression of water content on dry weight basis.

The relation between water deficit of leaf blade and water level lowering is shown in Fig. 1. Here the water deficit is calculated on the leaf area basis (29 mg. H₂O/sq. cm. in saturated conditions of leaves) and the grade of water level lowering was expressed by the ratio of submerged root (mg. fresh weight) to leaf area (sq. cm.), i. e., active root/leaf area ratio, which may also indicate the water economy of various plant types to some extent. For further discussion as to these expressions another paper will be expected in the near future.

Fig. 1. Relationship between active root/leaf area ratio (mg. fresh weight/sq. cm.) and the water deficit of leaf (per cent on the leaf area basis) obtained from various water level lowerings (○ 2 cm., ⊙ 4 cm., ⊗ 6 cm., ● 8 cm.).

Fig. 2. Variation of net assimilation (continuous line) with the leaf water deficit caused by various water level lowerings (○ 2 cm., ⊙ 4 cm., ⊗ 6 cm., ● 8 cm.) and transpiration rate (broken line, small open circles).

3. Variations of net assimilation and respiration:

The depression of photosynthesis caused by the water level lowering was detected directly by a modified Boysen Jensen's method in intact leaves of tobacco plants water-cultured under the same conditions as in the experimental series. As clearly shown in Fig. 2, the values of net assimilation (mg. $C_6H_{10}O_5$ /50 sq.cm./hr.) were decreased almost linearly until the leaf water content was decreased by 15 per cent below the normal. The respiratory activity of the leaf was hardly influenced by the leaf water deficit, its value was 0.49–0.54 mg. CO_2 /50 sq.cm./hr. in each set. Therefore, the depression of net assimilation may not be expected from high respiration with water deficiency, but from the fact that the water deficit of leaves usually induces a closure of stomata, and accordingly a depression of photosynthesis as well as of transpiration, as already suggested by Watson⁶) (see also Fig. 2). In this paper, however, the grade of stomatal opening was not especially taken into account, because the depression of plant growth caused by unbalanced water economy can be directly elucidated through the relation between net assimilation and water economy.

The reduction of water contents of roots and stems, as summarized in Table 3, was very small, so that it seems the variation of respiratory activity of these organs must be negligibly small and consequently need not to be taken into consideration regarding the depression of NAR.

From the above facts, it is evident that the decrease of the NAR at the 8 cm.-set resulted mainly from the depression of photosynthesis of leaves.

4. A theoretical calculation of the plant growth:

For the quantitative proof of the elucidation mentioned above, the causal relation of water level lowering to plant growth depression was pursued by calculating the dry matter production or the growth in connection with leaf water deficit. These calculations were carried out at the 2 cm.- and the 8 cm.-sets, for the first 7 days of the experiment before the plant recovering from the direct affection of water level lowering, and the techniques employed here were more or less the same as those used by Iwaki⁷⁾, excepting that the reduction of photosynthesis by leaf water deficit was the special concern in this paper.

The distribution ratio of the produced dry matter to the individual organs was calculated based on the data which were obtained at each sampling, provided this measure would vary linearly during sampling period. With assuming that the leaf and root grew logarithmically during each sampling interval, the variations with time of the active root/leaf area ratio were computed in Fig. 3.

The value of net assimilation of a plant under given conditions could be estimated by combining the data of Figs. 1, 2 and 3. Fig. 3 gives us the time sequence of the active root/leaf area ratio, with which the leaf water deficit can be read in Fig. 1, and with the values thus obtained the net assimilation will be easily computed from Fig. 2. At the 2 cm.-set, the active root/leaf area ratio varied so slightly that the value of net assimilation could be estimated as a constant value of 1.09 mg. $C_6H_{10}O_5$ /sq. cm./day. At the 8 cm.-set, however, the net assimilation in each day dur-

Fig. 3. Diagram showing the time trend of active root/leaf area ratio (mg./cm.²), calculated based on the growth of submerged roots in fresh weight and of leaf area.

Fig. 4. Comparison between the observed growth (continuous line) and the calculated (broken line) at the 2 cm.- and the 8 cm.-sets.

ing 7 days from starting the experiment was determined as 0.75, 0.81, 0.89, 1.09, 1.09, 1.09 and 1.09 mg. $C_6H_{10}O_5$ /sq. cm./day, respectively.

The respiration of stem was excluded from the calculation of growth, because it is very considerable that the stem bearing chlorophyll, as known in stems of raddish and pea,^{11),12)} can compensate its respiration with its own photosynthate in an illumination of 5000 lux. The respiration rate of the aerial and the submerged roots without water deficit was determined to be 0.096 and 0.146 mg. $C_6H_{10}O_5$ /mg. dry weight/day, respectively, and there was no change in the water content, and consequently in respiration, with water level lowering, as already mentioned.

A fairly good coincidence between the observed and the calculated growth at the 2 cm.- and the 8 cm.-set is illustrated in Fig. 4, though the calculated is slightly lessened than the observed at any set—especially, at the 8 cm.-set, there are some deviations in the calculated, probably because of the fluctuation of sampling on April 17 and 21, and for the lower calculated value at the 2 cm.-set an underestimation of net assimilation under normal leaf water condition may be responsible. At any rate, from the fact that there is no extreme discrepancy between the observed and the calculated, it can be presumed that the data and methods which were employed for the calculation of the growth did not contain any fundamental errors.

In conclusion, the growth depression induced by the water level lowering or temporary unbalance of water economy results from the depression of photosynthesis caused by water deficiency in the plant, especially in leaves, during the period when the active root/leaf area ratio was recovering from serious decline after treatment up to its normal value, or the same value of the control.

Summary

1. The effect of water economy on the plant growth was investigated in young tobacco plants with water level lowering of culture solutions. The 2 cm.-, 4 cm.-, 6 cm.- and 8 cm.-sets were prepared.

2. The plant growth in dry weight was decreased in proportion to the water level lowering, i. e., the relative values of 100:87.5:78.9:68.6 were observed at the 2 cm.-, 4 cm.-, 6 cm.- and 8 cm.-sets, respectively. Also the lowest net assimilation rate (NAR) was obtained at the 8 cm.-set.

3. The ratio of the dry weight of non-photosynthetic organs to the leaf area indicated no difference among the sets.

4. With lowering the water level, heavy water deficit was induced in leaves, but no deficit was observed in stems and roots. A clear relationship was discovered between the leaf water deficit and the ratio of submerged roots to leaf area (active root/leaf area ratio), which was used here as an indicator of the grade of water level lowering.

5. The net assimilation decreased almost linearly with progress of the leaf

water deficit, while no change was observed in respiratory activity of leaves as to water deficit and no special depression of nitrogen content in leaves was detected during the experimental period.

6. The growth in dry weight at the 2 cm.- and 8 cm.-sets was calculated theoretically with the net assimilation, which was affected by the leaf water deficit caused by water level lowering. The agreement between the calculated and the observed proves that the primary cause of the growth depression with water level lowering is the suppressed photosynthesis of leaves.

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摘 要

水分経済と物質生産の両面から、植物の一時的しおれがその後の生長にどのような影響を与えるかを追及するために、タバコ幼植物を水耕し、その水位を 2, 4, 6, 8 cm. の四段階に低下させ、約 5000 lux の連続照射、温度 25°, 湿度 49~62%, CO₂ 濃度約 0.55 mg./l. の条件のもとで栽培した。水位の低下につれて生長は減退した。すなわち実験開始 11 日後の乾物生長量の割合は 2, 4, 6, 8 cm. 区においてそれぞれ 100, 87.5, 78.9, 68.6 となり、最初の 3 日間の平均一日当りの純同化率 NAR は水位の低下の順に減少した。NAR を支配する各因子の変化は次のようであつた。a) 非同化器官と葉面積との割合は各区において大差なかつた。b) 水位低下により葉に水分欠乏が生じた。c) 葉の水分欠乏と、水位低下の度合を表わす根の生長に対する葉面積の割合 (active root/leaf area ratio) との間には密接な関係があつた。d) 葉の窒素含量には顕著な変化はみられなかつた。e) 葉の水分欠乏が進行するにつれて同化量はほぼ直線的に減少したが、呼吸量はほとんど変らなかつた。f) 茎、根の含水量変化は認められなかつた。従つて茎、根の呼吸率の変化は起らなかつたと考えられる。

以上の諸事実にもとづいて生長の低下の原因をさらに確かめるために、葉の水分欠乏と物質生産を結びつけて 2 cm. 区と 8 cm. 区の生長を計算した結果、実測値とほとんど一致した。それ故、水位低下によつて生じた生長量の減少は主として葉の水分欠乏による同化量の減少の結果といえる。