An Analysis of the Ecophysiological Adaptation of Tobacco Plant to a Limited Water Supply

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Mesophytes whose sound growth is promised under mesic conditions, suffer more or less the growth depression under a condition of limited water supply, although xerophytes can grow normally even under such a condition. This difference of the growth between mesophytes and xerophytes is generally ascribed to the difference in adaptability of the plants to the shortage of soil water, i. e. drought tolerance. Drought tolerance of plants is, however, a very complex character. Many workers have discussed it with various aspects¹⁾; some with reference to morphological changes of plants exposed to drought, and others from the view point of changes in physiological characters, especially concerning hydrature of leaves²⁻⁴⁾. However, there have been few analytical investigations as to how mesophytic plants can produce dry matter under a limited soil water condition.

The intensity of drought tolerance of some plants has been discussed on the basis of the water requirement⁵⁾ or transpiration efficiency, a reciprocal of the former, and of the ratio of photosynthesis to transpiration rate of a single leaf⁶⁾. In this paper an analysis of the factors affecting transpiration efficiency is made to clarify quantitatively the drought tolerance or ecophysiological adaptation of tobacco plants that were grown with limited water supply and suffered from wilting of their leaves.

1. Plant growth with a limited water supply

Nicotiana tabacum, "Bright Yellow" was used as a material. Thirty-seven-day-old plants grown under a controlled environmental condition and selected, were transplanted in enameled pots of 11 cm in diameter, 12 cm in height. The plant density was 1, 2 and 4 individuals per pot. The pots were filled with a mixture of loamy soil and vermiculite (1 : 2), 5 g synthetic fertilizers (N:P:K=15 : 15 : 10) per pot being given initially. The mixture had its field capacity of 65% and permanent wilting point of 30% on an oven-dry weight basis, and it was watered at transplanting to obtain its field capacity or more. The experiment was started 7 days after the transplanting with the soil moisture of 85%, and continued for 28 days. The plants were grown in a growth cabinet under a condition of continuous illumination of 4000 lux (ten 40-watt fluorescent tubes, Toshiba white), $29^{\circ} \pm 1^{\circ}$, relative humidity of 64% (11 mmHg in saturation deficit), and 0.035 CO₂ vol. %. The plants grew normally under the condition, and enough space between the pots avoided the mutual shading. A half number of the pots were not watered for 10 days after starting the experiment to allow the plants to wilt. The second watering on the 11th day returned the soil moisture to 85%. After that no water was supplied. The control plants were watered

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every 3 or 4 days to maintain the soil moisture to be near the field capacity throughout the experiment. The moist-control set and the dry-treated one with different densities were respectively designated as M_1 , M_2 , M_4 and D_1 , D_2 , D_4 . Samplings of the plants were made on the 10th, 20th and 28th day after starting the experiment. Fresh and dry weights of leaves, stems including petioles, and roots, and leaf area were determined with the plants of 2 pots in each set.

Dry weight growth was significantly affected by a shortage of soil moisture. Although for the first 10 days no clear difference was observed between the M and D sets in dry weight growth of individual plants (Table 1 and Fig. 1), the difference became more remarkable with progress of the time, especially in denser pots. The plant dry weight was more or less equal at the start, attained at the second sampling on the 20th day to 0.93, 0.71 and 0.59 g in the M_1 , M_2 and M_4 plots, and 0.79, 0.54 and 0.35 g in the D_1 , D_2 and D_4 plots: the latter corresponded respectively in the relative value to 0.85, 0.77 and 0.59 for former. After the second sampling the treated plants ceased their growth almost entirely, and so the dry weight of the D_1 , D_2 and D_4 plants at the final sampling on the 28th day was almost the same as that at the second sampling, i. e. 0.80, 0.55 and 0.35 g respectively, while in the M_1 , M_2 and M_4 plants the dry weight was 2.6 (+180% for the plant dry weight at the second sampling), 1.6 (+125%) and 1.1 g (+85%). Such growth difference between the M and D sets could be demonstrated with the relative growth rates (RGR, mg/mg/day) which were calculated with the data mentioned above (Fig. 2). The RGR of the dry-treated plants fell to zero in the later stage of the experiment, and this may be ascribed to the soil moisture which dropped below the wilting point, as will be discussed in the following section.

The leaf area growth per pot indicated a parallel change with the growth of total dry weight (see also Table 1). The relative

Fig. 1. Dry weight growth of tobacco plants in the moist-control set (broken lines) and the dry-treated set (continuous lines). Abscissa is the days after starting of the experiment. In a growth cabinet, continuous illumination of 4000 lux, and 29°. Planting densities were 1 (○), 2 (◐) and 4 (●) plant(s) per pot. Arrow indicates the day of the second watering in the dry set. Soil moisture in Fig. 3.

Fig. 2. Relative growth rates (RGR) in the moist set and the dry set. Indications as in Fig. 1.

Table 1. Dry weight of leaves, stems + petioles and roots, and leaf area per pot of the tobacco plants in the moist set (M) and the dry set (D). Planting densities 1, 2 and 4 individual(s)/pot. Second watering of the dry set was made on the 11th day. In a growth cabinet, continuous illumination of 4000 lux, 29° and 64% relative humidity.

Sets	At the start					On the 10th day				
	Leaves d. w. area mg cm ²		Stems & petioles mg	Roots mg	Total mg	Leaves d. w. area mg cm ²		Stems & petioles mg	Roots mg	Total mg
M ₁	25.3	25.6	5.4	6.9	37.6	169	128.0	31	27	227
M ₂	50.6	51.2	10.8	13.8	75.2	239	168.7	40	36	315
M ₄	101.2	102.4	21.6	27.6	150.4	495	355.9	112	62	669
D ₁	25.3	25.6	5.4	6.9	37.6	143	86.7	25	24	195
D ₂	50.6	51.2	10.8	13.4	75.2	204	132.3	37	41	282
D ₄	101.2	102.4	21.6	27.6	150.4	384	270.4	82	79	544

	On the 20th day					On the 28th day				
	mg	cm ²	mg	mg	mg	g	cm ²	g	g	g
M ₁	683	434.5	155	79	927	1.72	868.5	0.51	0.36	2.59
M ₂	1019	645.5	257	138	1414	2.04	1085.0	0.68	0.41	3.13
M ₄	1668	1060.0	453	249	2369	2.78	1140.0	0.90	0.50	4.18
D ₁	571	279.5	122	94	787	0.52	268.0	0.16	0.11	0.79
D ₂	755	380.0	193	133	1081	0.72	345.5	0.19	0.16	1.07
D ₄	964	455.0	262	163	1386	0.94	429.0	0.26	0.18	1.38

values at the final sampling were, if M₁=100%, M₂ 125% and M₄ 131%, and D₁ 31%, D₂ 40% and D₄ 49%. Because of drying of fresh leaves the leaf area at the final sampling of the dry-treated plants became somewhat smaller than that at the second sampling.

2. Water consumption and transpiration efficiency

Water consumption of the pot, i.e. the total sum of the transpiration and soil surface evaporation, was determined throughout the experimental period by measuring loss in weight of the pot as a whole (Table 2). The soil-surface evaporation of the pot with the plant(s) was calculated as a difference between the total water consumption and the transpiration of the plant(s). As shown in Table 3, the soil-surface evaporation

Table 2. Mean water consumption in g/pot/day of the potted tobacco plant.

Period of measurement	Moist set			Dry set		
	M ₁	M ₂	M ₄	D ₁	D ₂	D ₄
0—10 days	63.0	68.5	69.9	53.8	56.3	61.0
10—20 days	74.4	107	147	61.6	57.5	55.9
20—28 days	253	212	264	6.0	6.1	2.8

Table 3. Soil surface evaporation (S) of the pot with plant covers in the moist set (M) and the dry set (D). Calculated as a difference between total water consumption (W) and transpiration (T). Mean values expressed as g/pot/day.

Period of measurement	6th—9th day			11th—12th day			18th day		
Sets	W	T	S	W	T	S	W	T	S
M ₁	21.4	10.2	11.2	24.5	18.0	6.5	65.2	58.3	6.9
M ₂	33.7	15.5	18.2	35.7	28.0	7.7	66.9	60.9	6.0
M ₄	41.5	31.3	10.2	44.8	41.5	3.3	99.8	86.5	13.3
D ₁	21.1	7.8	13.3	23.5	14.0	9.5	26.5	15.4	11.1
D ₂	20.3	9.3	11.0	26.2	16.0	10.2	24.4	11.1	13.3
D ₄	—	—	—	37.0	27.0	10.0	18.0	12.0	6.0

was somewhat larger in the early stage of the experiment in any density plot, decreasing slightly with increase of leaf area, though some exceptions were seen. There could not be observed any distinct effect of planting density and of the drying treatment of the soil on the soil-surface evaporation. The comparison between Tables 2 and 3 may reveal that the soil water was consumed mainly by the transpiration of the plant(s), as discussed before⁷.

In the moist-control set the water consumption from the pot increased remarkably in parallel with the plant growth. However, in the treated set the consumption maintained an almost constant value for 20 days after the starting of the experiment, irrespective of the planting density, and afterwards it decreased strikingly to a very low value.

Soil moisture content was determined with soil samples from the center of the pot, since its vertical change was slight. Fig. 3 illustrated the obtained results. The soil moisture content in the D set decreased for the first 10 days almost linearly with the lapse of time, and with slight difference of the value among the pots with different plant densities. In the dry-treated plants, temporary wilting developed with the depression of soil moisture. The second watering on the 11th day returned the soil moisture to ca. 85%, and the plants recovered turgescence in 2 hours. The soil moisture again decreased linearly to attain near wilting point of 30% in 10 days in the D₄ pot, and in 12 days in the D₁ pot.

Relationships between dry-matter production and drought tolerance were investigated with data obtained for 20 days of the experiment or under the condition where the soil moisture remained above the wilting point. The transpiration efficiency, mg dry-matter increment per g water consumed by

Fig. 3. Variations with time of the soil moisture content. Arrow indicates the day of the second watering in the dry set. Upper and lower thin broken lines indicate respectively level of the field capacity (65%) and the permanent wilting point (30%).

plants which was proposed after Maximov⁸⁾, indicated for the first 10 days almost the same value between the M and the D set, as shown in Table 4. The large value in

Table 4. Transpiration efficiency in mg d.w./g water of the potted tobacco plant.
Calculated by the data of Tables 1 and 2.

Period of measurement	Moist set			Dry set		
	M ₁	M ₂	M ₄	D ₁	D ₂	D ₄
0—10 days	0.33	0.35	0.74	0.29	0.37	0.65
10—20 days	0.91	1.03	1.16	0.96	1.39	1.52
20—28 days	0.65	0.77	1.02	0.65	0.88	1.06

the M₄ and D₄ pots may suggest an effect of planting density on total transpiration. For the second 10 days, however, the dry-treated plants showed higher transpiration efficiency than the moist-control plants, and the difference was large in the denser pots. These facts demonstrate that the plants which were suffering from the shortage of soil moisture could utilize more effectively the soil moisture to produce dry matter than the moist plants⁹⁻¹²⁾, and that the dry plants became more tolerant of drought than the moist plants. Analytical discussions will be made in the following section for the sake of clarification of the increase of transpiration efficiency of tobacco plants by a limited water supply. This may give some quantitative elucidation of adaptability of plants to drought conditions.

3. Analytical discussions of the transpiration efficiency

Transpiration efficiency of a plant is a ratio of dry-matter increment to water consumption in a given period⁸⁾. The dry-matter increment of the plant (ΔW) is the balance between the total photosynthate and total respiration loss¹³⁾. Total water consumption (T) is the sum total of transpiration and soil-surface evaporation. Therefore, the transpiration efficiency (E) is given by the following equation, which is similar to that already proposed by Totsuka⁷⁾:

$$E = \frac{\Delta W}{T} = \frac{q \cdot \bar{F} - r \cdot C}{T_F \cdot \bar{F} + T_C \cdot C_H + V} = \frac{q - r \cdot C / \bar{F}}{T_F + T_C \cdot C_H / \bar{F} + V / \bar{F}}$$

where $\bar{F}$ is leaf area; q , net photosynthesis per unit leaf area; r , respiration rate of non-photosynthetic system; C , weight of non-photosynthetic systems (stems, petioles, and roots); T_F , leaf transpiration rate; T_C , transpiration rate of stems+petioles; C_H , weight of stems + petioles; V , soil-surface evaporation from the ground area occupied by the plant(s). Some of the components of this equation, $C/\bar{F}$, $C_H/\bar{F}$ and T_F , will be discussed in the following.

a) $C/\bar{F}$ and $C_H/\bar{F}$: Table 5 shows the fresh weight of each organ in non-photosynthetic system of the plants at each sampling. Total fresh weight of non-photosynthetic system of the moist plants increased 20 days after starting the experiment to almost double of that of the dry plants of corresponding densities. However, $C/\bar{F}$ value of both sets was almost the same, though the high density pots indicated somewhat higher $C/\bar{F}$ values. The values of $C_H/\bar{F}$ were smaller in the D set than in the M set, because the limited water supply suppressed the growth of stems and petioles more

Table 5. Stems+petioles and roots (tap and lateral) in fresh weight g/pot, $C/\bar{F}$ (g fresh weight of non-photosynthetic systems per cm^2 leaf area), and $C_H/\bar{F}$ (g fresh weight of stems+petioles per cm^2 leaf area) in the moist set (M) and the dry set (D).

Sets	At the start					On the 10th day					On the 20th day				
	Stems + petioles	Roots		$C/\bar{F}$	$C_H/\bar{F}$	Stems + petioles	Roots		$C/\bar{F}$	$C_H/\bar{F}$	Stems + petioles	Roots		$C/\bar{F}$	$C_H/\bar{F}$
		tap	lateral				tap	lateral				tap	lateral		
M ₁	0.12	0	0.05	6.7	4.7	0.69	0.05	0.34	8.5	5.4	2.82	0.20	0.96	9.2	6.5
M ₂	0.24	0	0.10	"	"	0.82	0.02	0.45	7.6	4.9	4.36	0.27	1.53	9.5	6.8
M ₄	0.48	0	0.20	"	"	2.31	0.09	0.90	9.3	6.5	7.30	0.46	2.82	10.0	6.9
D ₁	0.12	0	0.05	"	"	0.39	0.02	0.34	8.6	4.5	1.53	0.13	1.09	9.8	5.5
D ₂	0.24	0	0.10	"	"	0.54	0.04	0.54	8.6	4.1	2.32	0.25	1.35	10.3	6.1
D ₄	0.48	0	0.20	"	"	1.18	0.05	0.90	7.9	4.4	2.90	0.27	1.65	10.6	6.4

heavily than the growth of roots and leaves. As seen in the above-mentioned equation, the decrease of $C/\bar{F}$ and $C_H/\bar{F}$ values can induce the increase of transpiration efficiency. Therefore, the increase of the transpiration efficiency in the D plants should result from the decrease of the $C_H/\bar{F}$ value, since the $C/\bar{F}$ decrease of these plants was not brought about by the limitation of water supply.

Figs. 4 (left) and 5 (right). Total transpiration per pot (left) and transpiration rate of a leaf (right) in the moist and the dry sets. Arrow indicates the day of the second watering in the dry set. Indications as in Fig. 1.

b) T_F : Changes of the total transpiration from the pot were pursued, as shown in Fig. 4, by measuring the weight loss of the pot covered its soil surface with vinyl film. In the M set, the daily transpiration per pot was increased generally in parallel with the increase of the leaf area. In the D set, the transpiration amount was slightly less on the 10th day of the experiment than on the 4th day, but it increased rapidly after the second watering. The increased transpiration, however, was again depressed with the decrease of soil moisture that reached nearly the wilting point on the 20th day.

The transpiration rate per unit leaf area, T_F , was calculated from the data in Table 1 and Fig. 4, and its difference between the M and the D set was illustrated in Fig. 5. The first depression of transpiration rate not only in the D set but also in the M set might be mainly caused by some effects of the enlargement of each transpiring area and of the plant density. The transpiration rate in the M set showed rather in general stable values. In the D set, a recovery of the transpiration rate was observed after the second watering. Afterwards, however, the successive drying of the soils induced a rapid reduction of the leaf transpiration rate. It may be conclusive that this reduction of the transpiration rate has, as generally suggested, a major effect on the increase of transpiration efficiency of a plant exposed to drought.

c) *Factors affecting photosynthetic rate*: In order to clarify the effect of soil moisture deficiency on the photosynthetic activity, net assimilation rate (NAR, mg d. w./dm²/day) was calculated by a method reported in a previous paper¹⁴. The obtained values were as follows;

	Control			Treated		
	M ₁	M ₂	M ₄	D ₁	D ₂	D ₄
For the first 10 days	0.74	0.47	0.51	0.62	0.40	0.38
For the second 10 days	0.55	0.65	0.48	0.68	0.60	0.31

Although the NARs of the D₄ plants were smaller than those of the corresponding M₄ plants, no clear difference between the NARs of both sets was observed. In other words, the treated plants could maintain a certain high value of NAR, suffering from heavy depression of soil moisture content. The observed fact that the soil water shortage had only a slight effect on the NARs may accord with the report of some workers¹⁵⁻¹⁷.

Fig. 6. Leaf water deficit in % of a saturated water content. Indications as in Fig. 1.

It is generally believed that the leaf water deficit could cause the decrease of photosynthetic rate of leaves^{14, 18-25}. In the leaves of tobacco plants which were limited in water supply, marked wilting was observed during the experimental period. The leaf water deficit²⁶ increased successively in the dry-treated plants, especially of the dense pot, while no serious deficit was observed in the moist-control ones (Fig. 6). The NARs of the treated plants, as mentioned above, slightly differed from those of the control, and this indicated that the photosynthetic rate per unit leaf area might be to some extent

irrespective of the shortage of soil moisture. Simonis²²⁾ has already reported that the photosynthetic rate and the leaf dry weight per unit area were somewhat larger in *Trifolium* grown on dry soils than in that grown on moist soils.

The leaf water deficit can mainly be determined, as already discussed in a previous paper²⁶⁾, by the active root/leaf area ratio ($C_w/\bar{F}$ ratio) and the transpiration rate of a leaf. With special reference to these values, factors which relate the increase of the leaf water deficit were investigated. Fig. 7 shows the changes of the $C_w/\bar{F}$ ratio calculated by the data of lateral roots (Table 4) and leaf area (Table 1). The $C_w/\bar{F}$ ratio in the dry-treated plants increased remarkably for the first 10 days, though that in the moist-control changed in a narrow range. The high $C_w/\bar{F}$ ratio of the treated plants must lower the leaf water deficit, provided that the transpiration rate and the ability of water absorption of roots are unchanged.

Even in the case of the same $C_w/\bar{F}$ ratio, the root surface per unit fresh weight of roots can increase with decrease of the diameter of roots²⁶⁾. Diameters of about 400 fine roots were measured on the 10th day. The mean diameters were in the M₁, M₂ and M₄ plants 0.28, 0.30 and 0.29 mm, respectively. The relative value of the root diameter in the D₁, D₂ and D₄ plants was respectively 1.01, 0.88 and 0.94 of that of the control plants. Such a slight decrease, in general, of root diameter of the treated plants may act favorably for the water economy of the plants through the increase of water absorbing surface of the roots.

The leaf dry matter index, i. e. dry matter in mg per leaf area in cm², being an index for leaf thickness, is also a factor influencing the photosynthetic rate^{22, 27)}. This index increased in parallel with the leaf water deficit (see Fig. 8), and was larger in the treated plants than in the control ones. This suggests that the leaf water deficit may suppress the leaf growth in area, and that the thickness of leaves may diminish the decrease of photosynthetic rate of leaves caused by with increasing leaf water deficit. The facts reported by Simonis²²⁾ demonstrate the above-mentioned suggestions.

Respiration rate of non-photosynthetic systems and transpiration rate of stems and petioles should take part in the changes of transpiration efficiency, as seen in the equation. As to the effect of the changes of water content of stems and petioles on the transpiration rates and respiratory activities of these organs no observations were

Fig. 7. Ratio of fresh weight of lateral root to leaf area ($C_w/\bar{F}$ ratio). Indications as in Fig. 1.

Fig. 8. Leaf dry matter index which shows the thickness of leaves. Indications as in Fig. 1.

made. These problems remain for further investigations.

In conclusion, it can be said that the drought tolerance of plants grown under a limited water supply can be increased by the following changes of their ecophysiological characters which determine the utilization of soil moisture to dry-matter production; smallness of transpiration rate of the leaf, fresh weight of stems + petioles per unit leaf area, and suppression of the increase of leaf water deficit by increase of the fresh weight of active roots per unit leaf area and by decrease of the diameter of the roots. Thickening of leaves also compensates the decrease of photosynthetic rate.

Summary

Analytical studies of a transpiration efficiency were made to clarify the ecophysiological adaptability of potted tobacco plants to a limited water supply.

1. Dry weight growth was significantly affected by soil moisture shortage. The relative growth rate (RGR) of the dry-treated plants decreased slightly in the early stage, but remarkably in the later stage. However, there was slight difference in the net assimilation rate (NAR) between the moist-control and dry-treated plants throughout the experiment.

2. Water consumption per pot was increased in the control set with increase of the plant weight and leaf area. In the treated plants the water consumption was limited clearly with transient wilting caused by the depression of soil moisture.

3. Leaf water deficit was more distinct in the treated plants than in the control plants, but this was slightly compensated by increase of fine roots and the increase of leaf dry matter index.

4. The active root/leaf area ratio ($C_w/\bar{F}$ ratio) increased in the treated plants to about one and a half times than that of the control plants 10 days after starting the experiment. This increase is favorable for the water economy of the plant.

5. A similar transpiration efficiency was calculated for the first 10 days in the control and the treated plants, but the latter increased their transpiration efficiency for the second 10 days with depression of soil moisture. High plant density (4 plants per pot) gave also high transpiration efficiency.

6. An equation was formulated to analyze the transpiration efficiency, and the factors effective in increasing the efficiency of the dry-treated plants were discussed. The main factors were the decreased fresh weight of stems + petioles per unit leaf area ($C_H/\bar{F}$) and the lowered transpiration rate of the leaf under the drought condition.

7. Drought tolerance of the tobacco plants to a limited water supply was strengthened by (a) low development of stems and petioles in comparison with leaf area, (b) low transpiration rate of the leaf, (c) increase of water absorbing area caused by decreasing diameter of fine roots, and (d) remarkable increase of leaf thickness which may reduce the depression of photosynthetic rate with compensating the leaf water deficit.

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摘 要

戸塚 績, 門司正三: 土壌乾燥に対するタバコの適応性について

土壌含水量低下に対するタバコの生態生理学的適応性を明らかにするために蒸散効率を解析した, 発芽後37日目のタバコを栽植密度を変えて鉢植えし, 4,000 lux の連続照射, 温度29°, 湿度64%, CO₂ 濃度0.035%のもとで28日間栽培した。湿潤区(M)の鉢の土壌含水量は実験期間中ほぼ野外容水量(65%)に保った。乾燥区(D)では実験開始時と, それより10日後とに85%になるまで給水した。土壌含水量は2回目の給水より10日後にほぼ永久しおれ点(30%)に達した。土壌水分が減少するにつれてD区では葉の水分欠差が高まり, 単位葉面積あたりの葉乾重が増加した。また側根の直径がいくぶん減少した。相対生長率は実験期間中 M 区ではあまり差がみられなかったが, D 区では後期に著しく低下した。しかし純同化率は実験期間を通じて両区の間でほとんど差がみられなかった。実験開始後20日間の水消費量と乾物増加量とから求めた蒸散効率は D 区の方が M 区より大きかった。蒸散効率に関する関係式をつくり, その要因を検討した結果, 単位葉面積あたりの茎(葉柄を含む)の生量減少と葉の蒸散率の著しい低下が D 区の蒸散効率を高めた主な要因であった。

以上の結果, 水供給が制限された植物では葉の蒸散率が著しく低下し, 葉面積生長に比して地上部非同化器官の生長が低下して植物体の水消費が抑制される。一方, 単位葉面積あたりの側根の生量が増加し, 側根の直径が減少して葉の水分欠差の増加が抑制される。さらに単位葉面積あたりの葉の乾量の著しい増加が葉の水欠乏による光合成能率の低下を軽減して, 耐乾燥性が高められると推論される。(東京大学理学部植物学教室)