EVOLUTIONARY TRENDS IN LEAF PHOTOSYNTHESIS AND RELATED LEAF CHARACTERS AMONG CULTIVATED WHEAT SPECIES AND ITS WILD RELATIVES

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Synopsis. Wild species of *Triticum* and *Aegilops* exhibited a markedly higher photosynthetic rate per leaf area (P_A) as compared to cultivated wheat species. With a lower nitrogen content per leaf area, P_A of cultivated wheats was lower than that of wild relatives, however, this low nitrogen content per leaf area was associated with the enlargement of leaf area which may bring about an increased utilization of solar radiation under a properly balanced water supply. The photosynthetic rate per unit leaf nitrogen (P_N) was rather high in the leaves with a lower nitrogen content per leaf area.

Introduction

Photosynthesis is a fundamental energy conversion process, from solar to chemical, upon which virtually all life depends. The photosynthesis of wheat plants is especially important for us as a main source of our staple food.

The photosynthetic rate, i.e. the rate of the energy conversion, has been found to depend on many environmental factors. These include leaf temperature, light intensity, the concentration of carbon dioxide in the air, air flow rate, water stress, nutrient levels, temperature preconditioning, light intensity preconditioning, soil moisture preconditioning, and physiological age.

On the other hand, there has been considerable interest in evaluating differences in photosynthetic rates between and within plant species (El-SHARKAWY *et al.*, 1965; OSADA *et al.*, 1966; WILSON *et al.*, 1967; DUNCAN *et al.*, 1968; OJIMA *et al.*, 1968; and PEARCE *et al.*, 1969, etc.). Very little information is, however, available on photosynthetic activities of different wheat species. Recently STÖY (1965) reported his results with three different cultivated spring wheat varieties that there are no remarkable photosynthetic differences within intraspecific materials. KRANZ (1966) reported net assimilation rates of different cultivated wheat species and its wild relatives in an

attempt to find out the evolutionary trends of modern hexaploid wheat, but his studies were based on the growth analysis techniques.

The research reported here was initiated to investigate the rates of photosynthesis in order to find out if differences could be detected between different wild and cultivated species of wheat and its wild relatives in *Aegilops*. It was also intended that these measurements should provide data for the establishment of a more exact picture of the evolutionary trends in wheat than available at the moment.

Materials and Methods

The materials used in these investigations, listed in Table 1, were received from the Institute of Genetics, Faculty of Agriculture, Kyoto University, Kyoto, by the kind cooperation and help of Dr. Masatake Tanaka for which the authors are highly obliged and thankful to the Institute and to Dr. Tanaka. It includes diploid, tetraploid and hexaploid species of wild and cultivated types with winter and spring habits of growth. Most of them were the plants collected at their habitats by Dr. Hitoshi Kihara and members of the plant exploration parties of Kyoto University. The last two in Table 1 (19, 20) were wheat varieties crossbred in Japan, and the strain 221-1b (14) was an allohexaploid synthesized from the strain 109 (8) and 20-2 (2) in Kyoto University.

The seeds were planted in plastic pots (9 cm diameter by 20 cm height) containing silt in the glasshouse on 20th Oct., 1967. There

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Table 1. Species and strains tested

Strain	Species	Ploidy & Genome	Wild vs. Cultivated	Winter sv. Spring
1 2-1*	<i>Aegilops speltoides</i> Tausch.	2x BB	Wild	Spring
2 20-2	<i>Ae. squarrosa</i> L. var. <i>typica</i>	" DD	"	Winter
3 20-4	" "	" "	"	Spring
4 101-1	<i>T. aegilopoides</i> Bal. var. <i>boeoticum</i> Perc.	" AA	"	Winter
5 104-1	<i>T. monococcum</i> L. var. <i>vulgare</i> Körn	" "	Cult.	"
6 106	" var. <i>hornemanni</i> Körn	" "	"	Spring
7 196-2	<i>T. araraticum</i> Jakubz. var. <i>tumaniani</i>	4x AAGG	Wild	Winter
8 109	<i>T. dicoccoides</i> Körn var. <i>spontaneo-nigrum</i> Flaksb.	" AABB	"	"
9 111	<i>T. dicoccum</i> Schübl. var. <i>liguliforme</i> Körn	" "	Cult.	Spring
10 125	<i>T. durum</i> Desf. var. <i>reichenbachii</i> Körn	" "	"	"
11 138	<i>T. persicum</i> Vav. var. <i>stramineum</i> Zhuk	" "	"	"
12 147	<i>T. turgidum</i> L. var. <i>nigro-barbatum</i> Körn	" "	"	"
13 107-1	<i>T. timopheevi</i> Zhuk. var. <i>typicum</i>	" AAGG	"	"
14 221-1b	<i>T. dicoccoides</i> <i>spontaneo-nigrum</i> (109) × <i>Ae. squarrosa</i> (20-2), Amphidiploid	6x AABDD	W × W**	Winter
15 193	<i>T. macha</i> Dek. et Men. var. <i>sub-letschumicum</i>	" "	Cult.	Winter
16 150	<i>T. compactum</i> Host var. <i>icterinum</i>	" "	"	Spring
17 157	<i>T. spelta</i> L. var. <i>duhamelianum</i> Körn	" "	"	"
18 163	<i>T. vulgare</i> Vill. var. <i>erythrospermum</i> Körn	" "	"	"
19 254	" cultivar. Akagawa-aka	" "	"	Winter
20 252	" cultivar. Konosu-25	" "	"	Spring

* Registered number of the strain in Kyoto University.

** Wild × Wild

were six pots of each strain. Two kernels were planted in each pot, one plant was left after thinning. Pots were randomized at planting and repositioned randomly at various times during the course of the experiment. Plants were watered daily in morning and when necessary large plants were also given water at midday. Nutrient solution (47 g. ammonium sulfate, 10 g. sodium phosphate dibasic and 12 g. potassium chloride per litre) were supplied every 10-15 days interval at the rate of 10 ml. per pot. On 1st. Dec. three pots of each strain were shifted to the greenhouse to study the temperature effect on leaf photosynthesis, leaf area and leaf areal nitrogen content, etc. The day maximum and minimum temperatures in greenhouse and glasshouse were $20 \pm 5 \sim 10^\circ\text{C}$ and $15 \pm 10 \sim 3 \pm 5^\circ\text{C}$, respectively.

The full expanded individual leaves attached to the intact plants were enclosed in a glass chamber (4 mm interior thickness, 20 mm width) and exposed to a radiation flux of 55 kilolux. The light source consisted of four 500 watt reflector flat incandescent lamps mounted in front of a water filter (25 cm

thickness). In this system 1 kilolux at the surface of the chamber was equivalent to about $44 \text{ cal. dm}^{-2} \cdot \text{h}^{-1}$, most of the infrared radiation being absorbed by the filter. Air was drawn through the leaf chamber at the rate of 1 litre per minute. The temperature in the chamber was kept at $23-25^\circ\text{C}$. The CO_2 concentration of the air measured as ppm by volume at intake and exhaust was determined with the aid of the Hitachi-Horiba EIA-1A infrared CO_2 analyzer where the air temperature was kept at 20°C . The estimated photosynthetic rate at 300 ppm of CO_2 was then calculated from the following equation;

$$P = [(\Delta\text{CO}_2 \cdot F \cdot K) / LA] \times (300 / \overline{\text{CO}_2})$$

where

P = net photosynthesis as mg of CO_2 assimilated per square dm of leaf area per hour. (mg $\text{CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$)

ΔCO_2 = changes in concentration of CO_2 between intake and exhaust as ppm by volume

$\overline{\text{CO}_2}$ = mean CO_2 concentration of intake and exhaust air

F = air flow rate through the chamber (litre/hr $^{-1}$)

$K = [(0.044 \text{ mg } \text{CO}_2) / 22.4 \times (273/293)]$, the conversion factor from 10^{-6} litre of CO_2 to mg

CO₂ at 20°C.

LA=leaf area. (dm²)

After determining the photosynthetic activity, the leaves were cut from the plants, fresh weighed. The leaf areas were determined by tracing the leaves on standard bond paper, leaf drawings were cut, weighed and areas were calculated from the weight-to-area ratio of the paper. After that the leaves were placed in the electric oven at 85-90°C for four days to determine the dry weights. Nitrogen contents of individual leaves were measured by micro Kjeldahl method.

Results and Discussion

It seems to be the first time to our knowledge that wheat species of such diverse origin including diploid, tetraploid and hexaploid species of wild and cultivated types showing winter and spring habits of growth have been grown for photosynthetic comparison study. Having thus had an unique opportunity to make comparative observations we feel we should report those that might be of general interest as well as some opinions suggested by the experiments.

Differences in photosynthetic rate per unit leaf area (P_A) in relation to wild vs. cultivated types, winter vs. spring habits, and ploidy levels.

From the results shown in Fig. 1 (a, b) and Fig. 2, it can be pointed out that *Triticum aegilopoides* var. boeoticum⁽⁴⁾ showed the highest photosynthetic rate per unit leaf area (P_A) among the diploid plants observed, *T. araraticum* var. tumaniani⁽⁷⁾, which was followed by *T. dicoccoides* var. spontaneonigrum⁽⁸⁾ among the tetraploid plants, and an artificial allohexaploid⁽¹⁴⁾ synthesized from the cross between *T. dicoccoides*⁽⁸⁾ and *Aegilops squarrosa*⁽²⁾ showed the highest P_A among the hexaploid plants. These materials which showed high P_A values were, without exception, wild plants with a winter growth habit or an induced allopolyploid whose parents were of wild and winter types.

On the contrary, cultivated, spring types

	Wild Winter	Wild Spring	Cultivated Winter	Cultivated Spring
diploid	○	○	—○—	—○—
tetraploid	□			—□—
hexaploid	○		—○—	—○—

Fig. 1. (a). *January*. The relationship between Photosynthetic rate per unit leaf area and Nitrogen content per leaf area observed among different species and strains grown in green-house (White) and in glass-house (Black).

Fig. 1. (b). *February*.

Fig. 2. The relationship between Photosynthetic rate per unit leaf area and Nitrogen content per leaf area observed among different species and strains. (Average of January and February under green-house and glass-house conditions).

of different levels of ploidy generally showed a lower photosynthetic rate per unit leaf area (P_A) as in the case of *T. monococcum* var. *hornemanni*⁽⁶⁾ in diploids, *T. turgidum* var. *nigro-barbatum*⁽¹²⁾, *T. dicoccum* var. *liguliforme*⁽⁹⁾ and *T. durum* var. *reichenbachii*⁽¹⁰⁾ in tetraploids as well as *T. vulgare* var. *erythrosperrum*⁽¹⁸⁾ and *T. spelta* var. *duhamelianum*⁽¹⁷⁾ in hexaploids.

On the whole, wild plants of *Triticum* and *Aegilops* exhibited a markedly higher photosynthetic rate per unit leaf area (P_A) as compared to cultivated wheat species. In case of *Brassica* and its allied genera in the family Cruciferae the same tendency has been observed, and taking into consideration the conditions of their habitats it was stated that

wild *xerophytes* tended to show a higher P_A than cultivated *mesophytes* (TSUNODA *et al.* 1967). It might be assumed that the situations are the same in the case of wild and cultivated plants of *Triticum* and *Aegilops*. In this case the authors have had no opportunity to visit their actual habitats, however, we have heard from the members of the University of Kyoto who collected these materials on their habitats that many wild plants were growing on very dry land.

The difference in P_A between winter and spring types was not so clear partly because of the limitation of the number of the former types observed. However, it seems that the photosynthetic rate per unit leaf area (P_A) tended to be higher in winter types as compared to spring types. This tendency was more marked among materials grown in glasshouse than grown in greenhouse.

Fig. 1 (a,b) and Fig. 2 clearly showed that the diploid species observed exhibited on an average a higher photosynthetic rate per unit leaf area (P_A) as compared to the tetra- and hexaploid species. However, it seems to be questionable whether there exists a direct relation between the ploidy level and the P_A . It may be said that wild diploid species showed a higher

P_A as compared to cultivated tetra- and hexaploid species. However, it was not clear that diploid plants generally showed a higher P_A as compared to tetra- and hexaploid plants. As seen from Fig. 1 (a, b) and Fig. 2, the wild tetraploid species^(7,8) and the hexaploid plant synthesized from wild species⁽¹⁴⁾ showed rather a higher mean P_A than the cultivated diploid species observed^(5,6).

Anyway, it seems to be worthy of attention that out of 20 strains observed a wild plant of diploid AA genome, *T. aegilopoides*⁽⁴⁾ exhibited the highest P_A , and a strain of cultivated hexaploid AABBDD genome bread wheats, *T. vulgare*⁽¹⁸⁾ the lowest mean P_A .

Relationship between photosynthetic rate per unit leaf area (P_A) and nitrogen content per leaf area.

As shown in Fig. 1 (a, b) and Fig. 2, there existed a positive correlation between P_A and nitrogen content per leaf area among materials grown in greenhouse as well as in glasshouse. A higher P_A of wild plants tended to be associated with a higher nitrogen content per leaf area, and a lower P_A of cultivated types with a lower leaf areal nitrogen content.

Besides, Fig. 1 (a, b) showed that the nitrogen content per leaf area was remarkably reduced in the materials grown in greenhouse as compared to the materials grown in glasshouse, and further that P_A was rather high in the former despite of their low leaf areal nitrogen content. Here it can be seen that there exists a sort of temperature preconditioning effect to leaf photosynthesis, and that the increase of P_A due to this effect tended to be greater in spring types as compared to winter types.

Relationship between photosynthetic rate per unit leaf nitrogen (P_N) and nitrogen content per leaf area.

As mentioned above, the nitrogen content per leaf area was positively correlated with the photosynthetic rate per unit leaf area (P_A). While, as shown in Fig. 3 (a, b) the photosynthetic rate per unit leaf nitrogen (P_N) was negatively correlated with the leaf areal nitrogen content. Thus, cultivated types having a lower nitrogen content per leaf area tended to show a lower P_A . However, the P_N was not necessarily lower in cultivated types.

Fig. 3 (a, b) also showed that P_N was remarkably high in the materials grown in greenhouse as compared to the materials grown in glasshouse, and that this high P_N was associated with the reduction in leaf areal nitrogen content.

Variation in leaf area and nitrogen content.

The relationship between leaf area and nitrogen content per leaf area is given in Fig. 4 (a, b). It shows a negative correlation. Fig. 4 (a, b) indicates two groups. One is the group composed of all the diploid species

Fig. 3. (a). *January*. The relationship between Photosynthetic rate per unit leaf nitrogen and Nitrogen content per leaf area observed among different species and strains grown in green-house (White) and glass-house (Black).

Fig. 3. (b). *February*.

observed (1~6) and in addition one tetraploid species, *T. araraticum* var. *tumaniani*⁽⁷⁾; the other is the group of the remaining tetraploid and hexaploid species. The smallness of leaf area of the former group as a whole shown in Fig. 4 seems to be not only due to their relatively high nitrogen content per leaf area but also due to the smallness of their seed size which brought about the smallness of the

Fig. 4. (a). *January*. The relationship between Leaf area and Nitrogen content per leaf area observed among different species and strains grown in green-house (White) and in glass-house (Black).

Fig. 4. (b). *February*.

plants and single leaves.

Thus, from the results shown in Fig. 4 and the observations on seed sizes, it can be pointed out that at least two factors seem to have a bearing on the variation in single leaf area; one is the seed size and the other is the leaf nitrogen content. The smaller the seed size, the smaller the single leaf area. The higher the leaf areal nitrogen content, the smaller

the leaf area.

As for the latter factor, the nitrogen content per leaf area, wild plants generally showed a higher content as already mentioned and this characteristic was associated with the smallness of the leaves. Whereas cultivated types tended to enlarge the leaf area with a lower nitrogen content per leaf area, as shown in Fig. 4 (a, b). If we may use here the term "thick" meaning a higher nitrogen content per leaf area and "thin" a lower content, it can be said that wild types tended to have "thick" small leaves and cultivated types "thin" large leaves. This trend just coincides with that observed between wild *xerophytes* and cultivated *mesophytes* in *Brassica* and its allied genera (TSUNODA et al. 1967), and it may be allowed to assume that the "thick" small leaf of the wild plants

is an expression of their xerophytic nature, and that the "thin" large leaf of the cultivated wheats is an adaptable form to an improved environmental condition of water supply and water balance.

With "thin" leaves or with a lower nitrogen content per leaf area, the photosynthetic rate per leaf area (P_A) of cultivated wheats is rather lower than that of wild relatives. However, this low nitrogen content per leaf area is associated with the enlargement of leaf area which may bring about an increased utilization of solar radiation under conditions of well balanced moisture supply. The photosynthetic rate per unit leaf nitrogen (P_N) was rather high in the case of leaves with a lower nitrogen content per leaf area (Fig. 3). This means that decrease of P_A due to a lower nitrogen content per leaf area (Figs. 1, 2) was compensated by the increase of the leaf area.

In short, wild plants tended to have "thick" small leaves showing high P_A while cultivated wheats "thin" large leaves showing low P_A . Further, it was considered that this change from "thick" small leaves towards "thin" large leaves may have been proceeded in accordance with improved water supply. However, it should be mentioned that the cultivated types observed in this paper were mainly primitive

cultivars. In the case of some modern wheat cultivars which shall be dealt with in another paper, the change of reverse direction, i.e., from "thin" large towards "thick" small leaves seems to be going on under abundant supply of nitrogen and other nutrients like the case of rice plants which have already been stated (TSUNODA, 1959).

Several remarks should be added here on the relationships between the leaf characters and the ploidy level. Among the materials of this study it was observed that an artificial allopolyploid, 221-1b⁽¹⁴⁾ had large leaves than both the parental strains (2 and 8), and that many tetraploid and hexaploid species observed tended to have larger leaves as compared to diploid species. However, it should be mentioned that *Triticum araraticum* var. *tumaniani*⁽⁷⁾, a wild tetraploid species, was as small as diploid species in seed, plant, and leaf size.

An artificial allopolyploid, 221-1b⁽¹⁴⁾ showed a higher nitrogen content per leaf area as compared to its parental strains (2 and 8). Many cultivated tetraploid and hexaploid species, however, had rather a lower nitrogen content per unit leaf area as compared to diploid species. These might be considered to be examples of the genic modification of plant characters towards the reverse direction against the general trends caused by the increase in chromosome number.

Summary

Measurements of the rates of photosynthesis were conducted on the intact leaves of the *Triticum* and *Aegilops* species grown in greenhouse and glasshouse conditions during the winter 1967-68 in Sendai, Japan.

Out of 20 strains of different species, a wild plant of diploid AA genome, *Triticum aegilopoides* var. *boeoticum* showed the highest photosynthetic rate per unit leaf area (P_A), and a strain of cultivated hexaploid AABBDD genome bread wheat, *T. vulgare* var. *erythrospermum* the lowest mean P_A .

On the whole, wild plants of *Triticum* and *Aegilops* exhibited a markedly higher P_A as compared to cultivated wheat species. There existed a positive correlation between P_A and nitrogen content per leaf area. Further, the nitrogen content per leaf area was negatively

correlated with the leaf area. With a lower nitrogen content per leaf area, P_A of cultivated wheats was lower than that of wild relatives. However, this low nitrogen content per leaf area was associated with the enlargement of leaf area which might bring about an increased utilization of solar radiation under a properly balanced water supply. The photosynthetic rate per unit leaf nitrogen (P_N) was rather high in the leaves with a lower nitrogen content per leaf area.

The difference in P_A between winter and spring types was not so clear partly because of the limitation of the number of the former types observed. However, P_A tended to be higher in winter types as compared to spring types. This tendency was more marked among materials grown in glasshouse than grown in greenhouse.

Diploid species exhibited on an average a higher P_A as compared to tetraploid and hexaploid species. However, it seems to be questionable whether there exists a direct relation between the ploidy level and the P_A .

The wild tetraploid species and the hexaploid plant synthesized from wild species showed rather a higher mean P_A than the cultivated diploid species observed.

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葉光合成ならびに関連葉形質についての栽培小麦種と近縁野生植物の進化傾向

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野生型と栽培型、冬型と春型、2, 4, 6 倍性のものを含む小麦属, *Aegilops* 属植物を、温室ならびにガラス室で育て、着生葉について葉光合成能力を測定した。全20系統中、葉面当り光合成率 (P_A) が最高であったのは野生2倍種 *T. aegilopoides* の1系統で、最低であったのは栽培6倍パン小麦 *T. vulgare* の1系統であった。

全体として野生植物は栽培小麦に比べ高い P_A を示した。 P_A と葉面当り窒素量とは正の相関が、後者と葉面積とは負の相関がある。栽培小麦は関連野生植物よりも葉面当り窒素含量が低く P_A は低い、葉面当り窒素含

量が低いことが葉面積の増大と結びついており、水分供給が良い条件下では太陽光線をより良く利用することになるであろう。葉窒素当りの光合成率 (P_N) はむしろ葉面当り窒素含量の低い葉の方が高かった。

冬型は春型よりも P_A が高い傾向を示し、特にガラス室(低温)で育てた場合差がより明らかであった。2倍性種は平均してみると倍数性種より高い P_A を示した。しかし4, 6倍性の場合でも野生種や野生種から人工合成された植物は P_A が高く、倍数レベルと P_A に直接の関係があるかどうかは疑問である。