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GENETIC DIVERSITY OF THE CYTOPLASM IN *TRITICUM* AND *AEGILOPS*. VII. CYTOPLASMIC EFFECTS ON RESPIRATORY AND PHOTOSYNTHETIC RATES[1]

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Since the pioneer work of Kihara (1951) on cytoplasmic effects on genome manifestations, the genetic diversity of the cytoplasms among *Triticum* and *Aegilops* species has been reported by many researchers (Fukasawa 1959; Wilson and Ross 1962; Tsunewaki and Endo 1973; Maan 1973 and others). Moreover, these data indicated that certain polyploids were cytoplasmically similar to only one of their diploid progenitors. Comparative studies of cytoplasmic similarities and differences among related species provided useful information for identification of the diploid cytoplasm and genome donor species to their related polyploids (Hori and Tsunewaki 1967; Suemoto 1968, 1973; Maan 1973, 1976, 1977; Tsunewaki 1973; Mukai and Tsunewaki 1975; Endo and Tsunewaki 1975; Panayotov and Gotsov 1975; Tsuji and Tsunewaki 1976; and Tsunewaki *et al.* 1976a, b).

Many phenotypic effects brought by interactions between the nucleus and alien cytoplasm have been reported, such as male sterility (Kihara 1951; Fukasawa 1953), pistillody (Kihara 1951), delayed heading (Fukasawa 1957), depression of plant vigor (Kihara and Tsunewaki 1962), occurrence of haploids and twins (Kihara and Tsunewaki 1962; Tsunewaki *et al.* 1968, 1976b) and variegation in leaf color (Fakasawa 1957; Mukai and Tsunewaki 1976). Since photosynthetic and respiratory rates are a manifestation of interaction between the nucleus and cytoplasmic organelles, the mitochondria and chloroplasts, the effect of an alien cytoplasm on them can be used to detect the direct nuclear-cytoplasmic interactions. The objectives of the present investigation employing cytoplasmic substitution lines of a common wheat are to examine cytoplasmic effects on photosynthetic and respiratory rates and to see cytoplasmic relationships among seven species based on these effects.

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MATERIALS AND METHODS

A cultivar of common wheat (*Triticum aestivum* L.), Chinese Spring (abbreviated to CS), and its seven cytoplasm substitution lines were used in the present investigation. Pedigrees of the cytoplasm substitution lines used are shown in Table 1. In this paper,

Table 1. Species of cytoplasm donors and the pedigrees of the cytoplasm substitution lines of a common wheat Chinese Spring (CS) used

Cytoplasm donor			Pedigree**
Species	Genome formula (n)*	Ploidy	
Ae. umbellulata	C^u	2x	*Ae. umbellulata* / CS^{15}
Ae. squarrosa	D	2x	*Ae. squarrosa* / CS^6
Ae. speltoides	S	2x	*Ae. speltoides* / EW^4 / CS^4
T. dicoccoides	AB	4x	*T. dicoccoides* / CW^4 / CS^4
Ae. cylindrica	CD	4x	*Ae. cylindrica* / CW^5 / CS^3
Ae. biuncialis	C^uM^b	4x	*Ae. biuncialis* / CW^1 / CS^4
Ae. ovata	C^uM^o	4x	*Ae. ovata* / CW^9 / CS^{11}

* After Lilienfeld (1951).

** CS, CW and EW denote Chinese Spring, other common wheat and emmer wheat, respectively.

individual cytoplasm substitution lines are indicated by the name of the cytoplasm donor (in parentheses) connected by a hyphen to that of the nucleus donor. For example, (*umbellulata*)-CS indicates that the cytoplasm donor and the nucleus donor of this cytoplasm substitution line are *Ae. umbellulata* and Chinese Spring, respectively. The normal line of CS, as the control, and its seven cytoplasm substitution lines were grown outdoors (Experiment 1) and in a greenhouse (Experiment 2). Mukai and Tsunewaki (1976) reported a large difference in chlorophyll content between the greenhouse- and outdoor-grown seedlings of the (*umbellulata*)- and (*biuncialis*)-CS. Therefore, plants were kept both outdoors and in the greenhouse to see the effect of temperature on their chlorophyll content and respiratory and photosynthetic rates. The experimental plots were arranged according to a randomized block design with four replications for each experiment. Unfortunately, data from the first replication of Experiment 2 were lost because of mechanical trouble with an infra-red gas analyser. Consequently, data were analyzed with four replications for Experiment 1 and three replications for Experiment 2. In each plot, sixty seeds were sown in the later part of January, 1976. The first completely developed leaves of fifty seedlings were used for measuring respiratory and photosynthetic rates with an infra-red gas analyser, and the two first leaves were used for an estimation of chlorophyll content. The protected LSD procedure was used for the test of mean differences.

The procedure for measuring the respiratory and photosynthetic rates was as follows: Air was blown into a large storage bag with a fan. After the CO_2 concentration in the air bag was determined (A), the air was flowed through a thin assimilation chamber

(31×16×5 cm) containing the fifty first leaves and a water supply. At first the chamber was kept in the dark. After that, the chamber was artificially illuminated to give a light intensity of about 4,500 luxes at the leaf level. When the photosynthetic rate was saturated (B) as determined by CO_2 in the chamber, the chamber was kept in the dark again. The time to attain maximum photosynthetic rate after exposure to the light was also measured. As soon as CO_2 content of the assimilation chamber ceased to increase (C), leaf area and fresh weight were measured. The respiratory and photosynthetic rates were calculated from the difference of measured values of the CO_2 concentration between (C) and (A), and (C) and (B), respectively.

Chlorophyll was extracted from the leaves and examined spectrophotometrically. The fresh leaves weighed were ground and pestled using a chilled mortar with cold 80% acetone and $MgCO_3$. The extract was filtered through a Buchner funnel with a layer of filter paper. The residue was ground and filtered over and over again with acetone until the residue became white and no more could be extracted. Total volume of the extract was measured. The absorption spectrum of the extract was recorded by a Hitachi spectrophotometer using a 1 cm cell. The concentrations of chlorophyll a and b were calculated from the following equation, after Maclachlan and Zalik (1963):

$$Ca=\frac{(12.3\times D_{663}-0.86\times D_{645})\times V}{1{,}000\times d\times w}$$

$$Cb=\frac{(19.3\times D_{645}-3.6\times D_{663})\times V}{1{,}000\times d\times w}$$

where Ca and Cb=content of chlorophyll a and b in mg/g fresh weight, respectively.

D=optical density at the indicated wave length,

V=volume of extract in ml,

d=length of light path in cm, and

w=fresh weight of leaves in g.

The measurement for each line was repeated for each replication with different samples. The sum of content of chlorophyll a and b was used as chlorophyll content in this text.

RESULTS

I. Experiment 1 (With plants grown outdoors)

To assess characteristics of the leaf development in cytoplasm substitution lines, the fresh weight (abbreviation: fr. wt.) and chlorophyll (chl.) content were measured, as shown in Table 2. The fresh weights of all seven cytoplasm substitution lines were significantly different from that of CS. Three lines, (*umbellulata*)-, (*biuncialis*)- and (*ovata*)-CS, had significantly lower fresh weight than normal CS, while four lines, (*squarrosa*)-, (*speltoides*)-, (*dicoccoides*)- and (*cylindrica*)-CS, had significantly higher weight than normal CS. However, the chlorophyll content of the seven cytoplasm substitution lines was not significantly different from that of CS.

Respiratory rates (mg CO_2) were expressed on per 50 leaves/h and per g fr. wt./h bases, as shown in Table 2. (*Umbellulata*)- and (*biuncialis*)-CS had lower respiratory rates when expressed on per 50 leaves/h basis because of their small leaves while they

Table 2. Respiratory and photosynthetic rates of the normal line and the seven cytoplasm substitution lines of CS grown outdoors (Experiment 1)

	Normal line	Cytoplasm substitution line						
		(*umbel.*) -CS	(*squar.*) -CS	(*spelt.*) -CS	(*dicoc.*) -CS	(*cylin.*) -CS	(*biunc.*) -CS	(*ovata*) -CS
Fresh weight (g) /50 leaves	3.95 (100)	2.29** (58)	4.68* (118)	4.49* (114)	4.46* (113)	4.48* (113)	2.41** (61)	3.44* (87)
Chlorophyll content (mg) /g fr. wt.	1.44 (100)	1.43 (99)	1.50 (104)	1.42 (99)	1.49 (103)	1.51 (105)	1.47 (102)	1.47 (102)
Respiratory rate (mg CO_2) / 50 leaves / h	6.08 (100)	4.47* (73)	7.22 (119)	6.29 (103)	5.57 (92)	7.18 (118)	5.08 (84)	6.27 (103)
/ g fr. wt. / h	1.55 (100)	1.96* (127)	1.57 (101)	1.38 (89)	1.55 (100)	1.62 (105)	2.15** (139)	1.87 (121)
Photosynthetic rate (mg CO_2) / 50 leaves / h	17.3 (100)	12.4** (71)	18.5 (107)	17.3 (100)	17.9 (103)	18.8 (108)	12.2** (71)	16.6 (96)
/ g fr. wt. /h	4.42 (100)	5.40** (122)	4.02 (91)	3.82 (86)	3.98 (90)	4.28 (97)	5.09* (115)	4.87 (110)
/ mg chl. / h	3.11 (100)	3.83* (123)	2.70 (87)	2.71 (87)	2.69 (86)	2.80 (90)	3.48 (112)	3.37 (108)
/ 100 cm^2 / h	10.0 (100)	11.4* (114)	8.95 (8.9)	8.89 (89)	9.35 (94)	9.82 (98)	10.7 (107)	10.6 (106)
Time (min.) to attain max. photosynthetic rate under 4,500 lux.	26.8 (100)	46.3** (173)	26.0 (97)	29.3 (109)	25.5 (95)	23.8 (89)	35.5** (132)	31.8* (119)

Figures given in parentheses are percent of control.
* and **: Significantly different from the normal line at the 5% and 1% level, respectively.

had higher respiratory rates when expressed on per g fr. wt./ h basis.

Photosynthetic rates (mg CO_2) were expressed on per 50 leaves/ h, per g fr. wt./ h, per mg chl./ h and per 100 cm^2 leaf area/ h bases (Table 2). Photosynthetic rates expressed on per 50 leaves/ h were significantly lower in (*umbellulata*)- and (*biuncialis*)-CS. In contrast, these two lines had higher photosynthetic rates than normal CS when expressed on per g fr. wt./ h, per mg chl./ h and per 100 cm^2 leaf area/ h bases. Likewise, (*ovata*)-CS had high photosynthetic rates though their values were not significant.

Time in minutes required to attain maximum photosynthetic rate after the exposure to light (4,500 luxes) was measured, as shown in Table 2. Three lines, (*umbellulata*)-, (*biuncialis*)- and (*ovata*)-CS, needed much more time for the saturation than normal CS.

II. Experiment 2 (With plants grown in the greenhouse)

When plants were grown in the greenhouse, the fresh weights of (*umbellulata*)- and (*biuncialis*)-CS were significantly lower than that of normal CS (Table 3). The fresh weight of (*ovata*)-CS was lower than that of normal CS also, but the difference was not statistically significant. Those of other lines, (*squarrosa*)-, (*speltoides*)-, (*dicoc-*

Table 3. Respiratory and photosynthetic rates of the normal line and the seven cytoplasm substitution lines of CS grown in the greenhouse (Experiment 2).

	Normal line	Cytoplasm substitution line						
		(*umbel.*)-CS	(*squar.*)-CS	(*spelt.*)-CS	(*dicoc.*)-CS	(*cylin.*)-CS	(*biunc.*)-CS	(*orata*)-CS
Fresh weight (g) /50 leaves	4.72 (100)	2.93** (62)	5.65 (120)	5.19 (110)	5.35 (113)	4.86 (103)	3.20** (68)	4.59 (97)
Chlorophyll content (mg) /g fr. wt.	1.06 (100)	1.12 (105)	1.00 (94)	1.13 (106)	1.05 (99)	1.13 (106)	1.16 (110)	1.17 (110)
Respiratory rate (mg CO_2) /50 leaves /h	2.03 (100)	1.92 (95)	2.85 (141)	2.94 (145)	3.27 (161)	2.72 (134)	2.30 (114)	2.48 (123)
/g fr. wt. /h	0.46 (100)	0.66 (143)	0.51 (109)	0.58 (125)	0.60 (130)	0.58 (125)	0.74 (159)	0.54 (117)
Photosynthetic rate (mg CO_2) /50 leaves /h	12.7 (100)	12.6 (99)	14.8* (117)	15.1** (119)	15.2** (120)	13.7 (108)	12.5 (98)	14.0 (111)
/g fr. wt. /h	2.89 (100)	4.33** (150)	2.65 (92)	2.93 (102)	2.88 (100)	2.87 (99)	3.88** (135)	3.08 (107)
/mg chl. /h	2.80 (100)	3.89 (139)	2.65 (95)	2.63 (94)	2.73 (97)	2.56 (91)	3.40 (121)	2.66 (95)
/100 cm^2 /h	5.66 (100)	8.63** (152)	5.51 (87)	6.30 (111)	6.54 (115)	6.62 (117)	8.44** (149)	6.22 (110)
Time (min.) to attain max. photosynthetic rate under 4,500 lux.	24.0 (100)	31.3 (131)	22.7 (94)	23.3 (97)	23.3 (97)	20.9 (87)	25.3 (106)	23.0 (96)

Figures given in parentheses are percent of control.
* and **: Significantly different from the normal line at the 5% and 1% level, respectively.

coides)- and (*cylindrica*)-CS, were higher than that of normal CS as Experiment 1 though the differences were not statistically significant. In both experiments, it was clear that the fresh weights of (*umbellulata*)-, (*biuncialis*)- and (*ovata*)-CS were lower than that of normal CS, and that those of (*squarrosa*)-, (*speltoides*)-, (*dicoccoides*)- and (*cylindrica*)-CS were higher than that of normal CS (Table 2, 3). These tendencies were more noticeable in Experiment 1 than in Experiment 2. As in Experiment 1, the chlorophyll contents of seven cytoplasm substitution lines were not significantly different from that of normal CS.

Respiratory rates were expressed on per 50 leaves/ h and per g fr. wt./ h bases (Table 3). When respiratory rates were expressed on per 50 leaves/ h basis, all cytoplasm substitution lines except (*umbellulata*)-CS had higher respiratory rates, ranging from 114 to 161 percent of normal CS. The respiratory rates of (*umbellulata*)- and (*biuncialis*)-CS were clearly distinctive. Among seven cytoplasm substitution lines, these two lines had the lowest rates when expressed on per 50 leaves/ h basis while they had the highest rates when expressed on per g fr. wt./ h basis.

Photosynthetic rates were expressed on per 50 leaves/ h, per g fr. wt./ h, per mg chl./h and per 100 cm^2 leaf area/ h bases, as shown in Table 3. In these characters,

(*umbellulata*)- and (*biuncialis*)-CS were also distinctive. These two lines showed similar rates to normal CS when expressed on per 50 leaves/ h basis. They showed higher rates when expressed on per mg chl./ h basis, though the differences were not significant. Likewise, they showed higher rates than normal CS when expressed on per 100 cm^2 leaf area/ h basis. On the other hand, the other five cytoplasm substitution lines showed higher photosynthetic rates, ranging from 108 to 120 percent of normal CS when expressed on per 50 leaves/ h basis. Their photosynthetic rates did not differ significantly from that of normal CS, however.

Time required to attain maximum photosynthetic rate after exposure to light (4,500 luxes) was measured (Table 3). Two lines, (*umbellulata*)- and (*biuncialis*)-CS, needed more time than normal CS, but the differences were not significant. In contrast to Experiment 1, (*ovata*)-CS did not need more time than normal CS. Results from the other four cytoplasm substitution lines were similar to normal CS.

III. Brief description of the effects of individual cytoplasms

(1) The *umbellulata* cytoplasm: This cytoplasm depressed the leaf development. Respiratory and photosynthetic rates per leaf were lower while the efficiency in respiration and photosynthesis was higher. The retardation in attaining maximum photosynthetic rate was observed.

(2) The *squarrosa* cytoplasm: The first leaf developed vigorously. No other consistent effect was detected.

(3) The *speltoides* cytoplasm: Similar to the *squarrosa* cytoplasm.

(4) The *dicoccoides* cytoplasm: Similar to the *squarrosa* cytoplasm.

(5) The *cylindrica* cytoplasm: Similar to the *squarrosa* cytoplasm.

(6) The *biuncialis* cytoplasm: Similar to the *umbellulata* cytoplasm.

(7) The *ovata* cytoplasm: The first leaf development was depressed in outdoor plants. No effect on respiratory and photosynthetic rates was observed. Retardation in attaining maximum photosynthetic rate was observed in Experiment 1.

Based on the above results, the seven cytoplasms can be grouped into the following three groups; (a) *umbellulata* and *biuncialis* cytoplasms, (b) *squarrosa*, *speltoides*, *dicoccoides* and *cylindrica* cytoplasms, and (c) *ovata* cytoplasm.

DISCUSSION

Mukai and Tsunewaki (1976) observed a large difference in chlorophyll content between the greenhouse- and outdoor-grown seedlings of (*umbellulata*)- and (*biuncialis*)-CS. Plants were kept outdoors and in the greenhouse to see the effect of temperature on their chlorophyll content and respiratory and photosynthetic rates. In the present results, however, the difference in chlorophyll content was not observed between the greenhouse- and outdoor-grown seedlings. We had an unusually warm winter in 1975-1976, which may be the reason why the present results did not agree with Mukai and Tsunewaki's results on the chlorophyll content. Although the primary purpose in doing two experiments was not attained, the fact that the results of the two experiments were very similar to each other certified the cytoplasmic effects on characters measured.

As far as we know, this is the first report of a cytoplasmic effect on respiratory and photosynthetic rates in higher plants. The (*umbellulata*)- and (*biuncialis*)-CS had different respiratory and photosynthetic rates than normal CS. The difference can be attributed to nucleus-cytoplasm interactions. These are not unexpected results if we consider that chloroplasts and mitochondria perform the very important functions, photosynthesis and respiration, respectively. These organelles have cytoplasmic genes, but they can not self-replicate or function without cooperation from the nuclear genes.

Fraction 1 protein is a very good example which clearly shows the importance of interaction between the nucleus and cytoplasmic genes. According to Wildman and his coworkers (Chan and Wildman 1972; Kawashima and Wildman 1972; Kung 1976), this protein is found in all organisms that contain chlorophyll and is identical to ribulose-1, 5-diphosphate (RuDP) carboxylase-oxygenase, which catalyzes the crucial reactions of both photosynthesis and photorespiration. The protein consists of eight large and eight small subunits. From the studies with *Nicotiana* and cell free systems it has been shown that chloroplast and nuclear genes code for the large and small subunit, respectively. Thus, the synthesis and function of this physiologically important protein requires the close cooperation of chloroplast and nuclear genomes.

The higher photosynthetic rates per unit chlorophyll of (*umbellulata*)- and (*biuncialis*)-CS were unexpected. There are some reports showing that mutant strains had higher photosynthetic rates on a chlorophyll basis than normal strains: Highkin *et al.* (1967) have shown that the photosynthetic rate of a pea mutant on a chlorophyll basis is higher than the wild type. Such mutants have been reported in cotton by Benedict *et al.* (1972), in soybean by Keck *et al.* (1970), and in rice by Saka and Matsunaka (1975). Though these mutants had higher photosynthetic rates expressed on a chlorophyll basis than normal plants, their chlorophyll content was much less than normal plants. Therefore, their photosynthetic rates per unit leaf area were not higher than normal plants. There is no agreement on the reasons for the high photosynthetic rates of these mutants on a chlorophyll basis. The two cytoplasm substitution lines, (*umbellulata*)- and (*biuncialis*)-CS, had higher photosynthetic rates than normal CS when expressed on a chlorophyll basis, and their chlorophyll contents were comparable to normal CS. Therefore, they showed higher photosynthetic rates expressed on fresh weight and leaf area basis than normal CS. One of the possible reasons for the higher photosynthetic activity in (*umbellulata*)- and (*biuncialis*)-CS than in normal CS is smaller mesophyll cell size and relatively larger cell number per unit leaf area. According to Cooper (1978) the cell of smaller size possesses higher photosynthetic activity than larger one, and also the number of cells is another important factor for the photosynthetic rate per unit leaf area.

Their photosynthetic rates expressed on a leaf basis, however, were less than normal CS, because their leaves were small. According to Mukai and Tsunewaki (1975), the cytoplasms of *Ae. umbellulata* and *Ae. biuncialis* caused a marked overall growth retardation in CS. The dry matter weights of (*umbellulata*)- and (*biuncialis*)-CS at their maturity were significantly less than normal CS. The physiological reason is not known why (*umbellulata*)- and (*biuncialis*)-CS had reduced plant vigor in spite of higher photosynthetic rates. It can be speculated that total productivities of these lines were

less than normal CS due to their smaller leaves caused by nuclear-cytoplasmic interaction.

Based on the effect on respiratory and photosynthetic rates, the seven cytoplasms were placed into three groups. This grouping agreed well with the classification of plasma type by Tsunewaki *et al.* (1976a). They carried out for the first time a full scale experiment to grasp genetic characteristics of the cytoplasms of *Triticum* and *Aegilops* species. They found the presence of at least eight distinctly different plasma types among those species. Based on two cluster analyses, the cytoplasms of *Ae. umbellulata* and *Ae. biuncialis* were classified into C^u plasma type. In the present results, (*umbellulata*)- and (*biuncialis*)-CS clearly showed very similar features in both Experiment 1 and 2. Thus, the present results supported the hypothesis that the cytoplasm of *Ae. biuncialis* was derived from the C^u genome donor, i. e. *Ae. umbellulata* (Mukai and Tsunewaki 1975).

The cytoplasms of the four species, *squarrosa*, *speltoides*, *dicoccoides*, and *cylindrica*, were grouped together based on their effects on respiratory and photosynthetic rates. Their effects were not different from that of the cytoplasm of common wheat. Tsunewaki *et al.* (1976a) placed these five cytoplasms into the same group based on two cluster analyses. However, this phenotypic similarity does not necessarily mean that the cytoplasms of *squarrosa*, *speltoides*, *dicoccoides*, *cylindrica* and common wheat are genetically similar to each other. Kihara (1973) demonstrated that common wheat with the *squarrosa* cytoplasm did not differ from its normal line, while emmer wheat with this cytoplasm showed severe growth depression and sterility. His results clearly indicated that the D genome present in common wheat nucleus harmoniousiy interacts with the *squarrosa* cytoplasm and conceals the otherwise deleterious effects of this cytoplasm on character expression of wheat plants. Considering the results of Kihara, Tsunewaki *et al.* (1976a) grouped the cytoplasms of *squarrosa* and *cylindrica* into D plasma type and those of *speltoides*, *dicoccoides* and common wheat into S plasma type. When common wheat is used as the tester nucleus, it is difficult to detect genetic difference between S type and D type cytoplasms. In this point, other tester nuclei, such as emmer wheat and hexaploid *Triticale*, are more preferable.

The cytoplasm of *Ae. ovata* was classified into the third group based on a couple of distinctive characters. From the genome constitution of *Ae. ovata*, either of C^u- or M-genome diploid progenitor can be the donor of the cytoplasm. Mukai and Tsunewaki (1975) reported that the cytoplasm of *Ae. ovata* was presumably derived from the M-genome donor since the cytoplasm of *Ae. ovata* was very different from that of the C^u-genome donor, i. e., *Ae. umbellulata*. The present results indicated that the cytoplasm of *Ae. ovata* was different from that of *Ae. umbellulata*, thus supported their results. Furthermore, Maan (1977) claimed that *Ae. mutica* (genome formula Mt Mt) was most likely the cytoplasm and M-genome donor to *Ae. ovata*.

SUMMARY

Respiratory and photosynthetic rates of seven cytoplasm substitution lines of a common wheat were investigated. The cytoplasm substitution lines used were (*umbellulata*)-, (*squarrosa*)-, (*speltoides*)-, (*dicoccoides*)-, (*cylindrica*)-, (*biuncialis*)-, and

(*ovata*)-CS. The investigation was conducted in four replications with each of the outdoor- and greenhouse-grown plants. In each replication, the first completely developed leaves of fifty seedlings were used for measuring respiratory and photosynthetic rates with an infra-red gas analyser. The first two leaves of other seedlings were used for an estimation of chlorophyll content. The results obtained are summarized as follows:

(1) The *umbellulata* and *biuncialis* cytoplasms depressed the leaf development; thus both respiratory and photosynthetic rates per leaf became lower, though the efficiency in respiration and photosynthesis was higher. They also caused retardation in attaining maximum photosynthetic rate.

(2) The *squarrosa*, *speltoides*, *dicoccoides* and *cylindrica* cytoplasms caused vigorous development of the first leaf. No other consistent effect was detected with them.

(3) The *ovata* cytoplasm depressed the first leaf development, and caused the retardation in attaining maximum photosynthetic rate in plants grown outdoors. No effect on both respiratory and photosynthetic rates was observed.

The results clearly showed that there is cytoplasmic control of respiration and photosynthesis. The present results also agreed with the classification of plasma types by Tsunewaki *et al.* (1976a). The phylogenetic significance of this grouping was discussed.

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