Japan. Jour. Crop Sci. 47(1) : 90-100 (1978)

Studies on the Physiological Characteristics of C_3 and C_4 Crop Species

II. The effects of air temperature and solar radiation on the dry matter production of some crops*

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Received July 19, 1977

The first prerequisite for a high economic yield is to increase the total dry matter production of the plants. It has already been found that dry matter yield per year of C_4 plants grown in tropical or subtropical regions is higher than that of C_3 plants grown in temperate regions[3]. Actually, under the most suitable conditions for growth, the dry matter yield of C_4 plants is generally higher than that of C_3 plants[12,29].

Dry matter production of a crop, in general, depends both on its genetic characters and on its natural and artificial environments.

In the natural environment most of edaphic and climatic factors are interrelated, so that a change in one factor is usually accompanied by changes in one or more other factors. However, when the edaphic factors such as soil structure, water and nutrient supply remain unchanged, natural environment will be characterized mainly by climatic factors. According to the recent studies of Japanese IBP, it is clear that air temperature (ambient temperature) and solar radiation are the two most influential factors which affect the dry matter production of crops in various regions of Japan[16,17,18].

In the present experiments described below, the dry matter production of nine C_3 and C_4 crop species which were cultivated under the same near natural conditions were analyzed by use of the growth analysis method[24]. As it is known that the ability for the dry matter production of a species differs according to growth conditions, the rate and pattern of dry matter production of various C_3 and C_4 species were compared in different seasons. Young plants cultivated in the natural environment for less than one month from germination were exclusively used as experimental materials from the consideration that in these plants the effect of daylength on growth may be minimum, so that it can be ignored.

Materials and Methods

Plant materials The C_3 species used were wheat (*Triticum aestivum* L. cv. Norin No. 61), barley (*Hordeum vulgare* L. cv. Kashima-mugi), and pea (*Pisum sativum* L.) as winter crops, and soybean (*Glycine max* L. cv. Norin No. 2), rice (*Oryza sativa* L. subsp. *japonica* cv. Nihonbare and *O. Sativa* L. subsp. *indica* cv. IR-8) as summer crops; the C_4 species were maize (*Zea mays* L. cv. Honkoshu), sorghum (*Sorghum bicolor* L. cv. Sudakkusu No. 11), millet (*Panicum miliaceum* L. cv. Shirokibi) and barnyard millet (*Echinochloa frumentacea* Link cv. Hida-akabie). The seeds were obtained from the Central Agricultural Experiment Station, Konosu (wheat, barley), from National Institute of Agricultural Sciences, Konosu (rice), from Experimental Farm of Faculty of Agriculture, University of Tokyo (soybean, millet, barnyard millet) and commercial stores (pea, maize and sorghum).

* Outline of this paper was reported at the 162 nd Meeting of the Crop Science Society. Part of this research was supported by the Special Research Project of Min. Education, "Systematic Development of Biological Productivity" in 1977 fiscal year.

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Table 1. Mean weekly temperature and solar radiation in various experiments.

Experiment No.	Measured period	Temperature (°C)	Solar radiation (cal cm^{-2} day^{-1})
Exp. No. 1	June 6—June 13	21.5	199.06
Exp. No. 2	June 26—July 3	24.0	218.88
Exp. No. 3	July 22—July 29	30.5	389.25
Exp. No. 4	Aug. 22—Aug. 29	28.0	257.27
Exp. No. 5	Sep. 22—Sep. 29	22.5	156.45
Exp. No. 6	Nov. 10—Nov. 17	17.0	150.95

After disinfection with 0.1% "Usprun" solution for 6 hours, the seeds were germinated in distilled water, and then transplanted into polyethylene pots (volume ca. 1 liter) each containing 1 kg soil and 2 g chemical fertilizer (N:P:K=12:18:16). The number of seedlings per pot was 6 for wheat, barley and rice, and 3 for other species. After the first harvest, the number of seedlings in the remaining pot was thinned from 6 to 4, 3 to 2 seedlings per pot, respectively.

When the 5th or 7th leaf (for species of Gramineae), 3rd or 4th leaf (for soybean) and 7th or 9th leaf (for pea) elongated, 60 seedlings were harvested. Among them 15 seedlings showing uniform growth were selected and subjected to the measurement of leaf area, fresh weight and dry weight. The next measurement (the second harvest) was done 7 days later in the same way as the first measurement.

Meteorological observations were made everyday during the entire growing season on the following items: daily summation of solar radiation measured by a recording thermopile solarimeter (Noshi Denshi type, manufactured by Nakano Sokuon Kenkyusho Co., Mie, Japan) and air temperature measured by a thermocouple.

Leaf area was measured by the Automatic Leaf Area Meter (manufactured by Hayashi Denko Co., Tokyo, Japan). Dry weight was measured with materials dissected into several plant parts and dried in a forced-air drying oven at 80°C for more than 48 hours.

Growth analysis was followed by Watson's method (1952). Relative growth rate (RGR), net assimilation rate (NAR) and the other growth parameters were calculated by the following equations:

$$RGR=\frac{\log_e W_2-\log_e W_1}{t_2-t_1}, \quad \text{mg mg}^{-1}\ \text{day}^{-1}$$

$$NAR=\frac{W_2-W_1}{t_2-t_1}\times\frac{\log_e A_2-\log_e A_1}{A_2-A_1}, \quad \text{mg cm}^{-2}\ \text{day}^{-1}$$

$$LAR=\frac{1}{2}\left(\frac{A_1}{W_1}+\frac{A_2}{W_2}\right), \quad \text{cm}^2\ \text{g}^{-1}$$

where W_1, W_2 and A_1, A_2 are plant dry weight and leaf area of harvest 1 (t_1) and harvest 2 (t_2).

The experiments were carried out 6 times from May to November using plants grown in the glasshouse at the Hongo Campus of the University of Tokyo. Mean weekly temperature and solar radiation during the experimental period from harvest 1 to harvest 2 in the 6 growing seasons are shown in Table 1.

Results and Discussion

The outline of the dry weight data of the six experiments are shown in Table 2.

In order to make clear the combined effects of temperature and solar radiation on the growth parameters of crop species, 3 typical experiments with the lowest (17°C and 150.9 cal cm^{-2} day^{-1}), medium (24°C and 218.8 cal cm^{-2} day^{-1}) and the highest (30.5°C and 389.2 cal cm^{-2} day^{-1}) combinations were selected from the six experiments and various parameters were compared.

1. *Relationship of relative growth rate with temperature and solar radiation*

Comparing growth rate among various species in which they differ in plant size is an extremely difficult problem. However, we will take first the relative growth rate

Table 2. Leaf area and dry weight per plant at the first harvest and their increments in a week in various crop species.

Species	Exp. No.	Harvest 1		Increment	
		LA cm²/pl	Dry wt. mg/pl	ΔA cm²/pl	ΔW mg/pl
C_3 Winter crops 1. Wheat	1	37.28	202	21.9	121
	2	38.18	185	58.1	292
	3	12.89	76	12.7	119
	4	6.26	48	6.7	76
	5	7.83	58	23.0	73
	6	52.95	261	62.7	144
2. Barley	1	27.72	150	24.2	130
	2	35.31	187	26.5	181
	3	28.33	145	14.5	215
	4	23.32	137	12.0	89
	5	21.30	139	23.0	110
	6	99.36	499	118.4	266
3. Pea	1	—	—	—	—
	2	60.56	286	45.4	244
	3	41.14	234	22.8	176
	4	32.89	188	21.1	135
	5	14.73	90	20.0	75
	6	88.89	402	59.9	139
C_3 Summer crops 4. Soybean	1	40.89	268	42.9	235
	2	90.21	441	77.2	629
	3	108.96	569	95.0	841
	4	44.87	231	68.2	380
	5	59.20	276	65.9	331
	6	36.97	222	20.8	84
5. Rice (IR-8)	1	8.60	48	16.0	85
	2	42.26	187	61.3	344
	3	25.71	122	49.3	576
	4	—	—	—	—
	5	10.69	68	15.0	92
	6	1.03	15	0.1	1
6. Rice (Nihonbare)	1	6.11	49	9.1	49
	2	18.32	110	19.0	163
	3	17.74	108	54.0	499
	4	22.26	147	18.6	245
	5	9.04	70	12.3	93
	6	1.05	16	0.1	1
C_4 Plants 7. Maize	1	115.21	524	79.7	540
	2	198.76	853	223.7	1,095
	3	215.11	967	189.7	1,573
	4	114.99	516	99.8	725
	5	93.49	460	114.0	484
	6	66.06	369	46.3	196
8. Sorghum	1	24.30	143	32.9	179
	2	69.16	323	71.0	425
	3	50.31	221	84.7	799
	4	88.93	391	64.8	552
	5	25.03	118	56.6	192
	6	10.99	69	9.0	24
9. Millet	1	22.97	86	27.3	151
	2	31.36	108	22.3	203
	3	15.03	53	82.1	377
	4	33.17	117	48.2	334
	5	33.44	128	39.4	135
	6	2.16	9	1.2	3
10 Barnyard millet	1	14.34	65	35.2	156
	2	42.70	150	77.8	466
	3	18.14	67	98.2	603
	4	53.46	233	33.5	305
	5	16.23	61	41.2	163
	6	4.03	26	7.6	20

(RGR) in order to minimize the effect of difference in plant size among crop species.

As shown in Figs. 1, 2 and 3, RGR generally increases with increasing ambient temperature and solar radiation. The pattern of these increasings, however, differs from C_3 to C_4 species except for rice. In the C_4 species, RGR increases parallel with increasing temperature and solar radiation, and reaches the highest value at the highest combination. But in the C_3 species, this tendency is not recognized. It is also observed that there is greater difference in RGR among species and groups under the combination of high temperature and strong radiation (Fig. 4a) than under the combination of low temperature and weak radiation (Fig. 4b).

In the present experiments, temperature and solar radiation changed simultaneously. Therefore, in order to compare the contribution of temperature and solar radiation to RGR separately, the whole data of the 6 experiments were subjected to multiple regression analysis. The results showed that the contribution of temperature to RGR is heavier than that of solar radiation

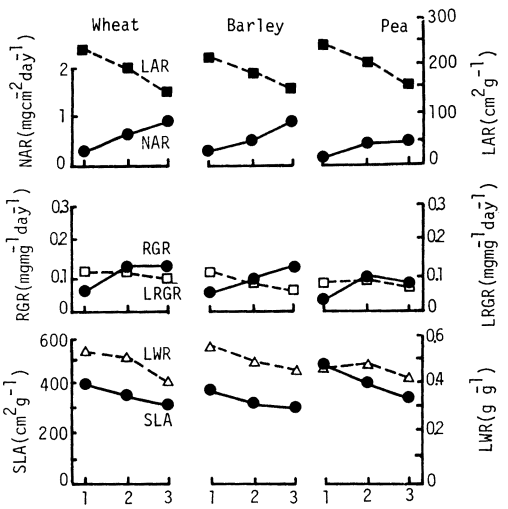

Fig. 1. Effects of temperature and solar radiation in combination on various growth parameters in C_3 winter crops.

Note: Numerals, 1, 2 and 3 on the horizontal axis correspond to Exp. No. 6, No. 2 and No. 3, respectively.

	Temperature (°C)	Solar radiation (cal cm^{-2} day^{-1})
1 (Exp. No. 6)	17.0	150.95
2 (Exp. No. 2)	24.0	218.88
3 (Exp. No. 3)	30.5	389.25

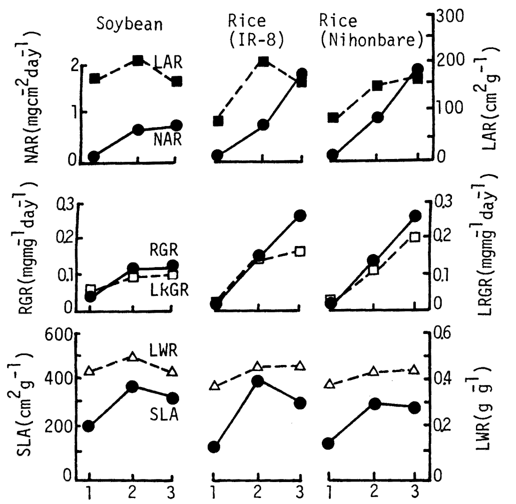

Fig. 2. Effects of temperature and solar radiation in combination on various growth parameters in C_3 summer crops.

Note: Numerals, 1, 2 and 3 on the horizontal axis are the same as in Fig. 1.

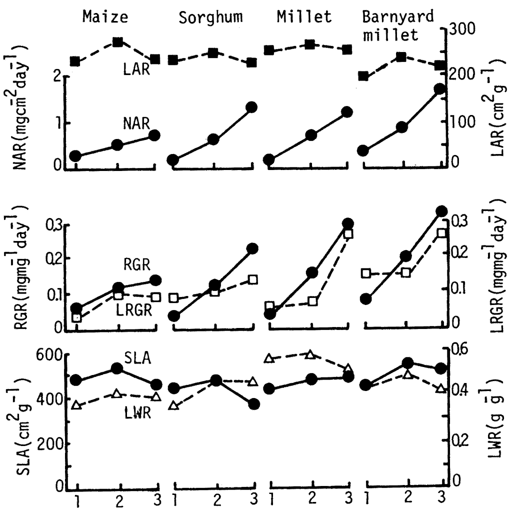

Fig. 3. Effects of temperature and solar radiation in combination on various growth parameters in C_4 plants.

Note: Numerals, 1, 2 and 3 on the horizontal axis are the same as in Fig. 1.

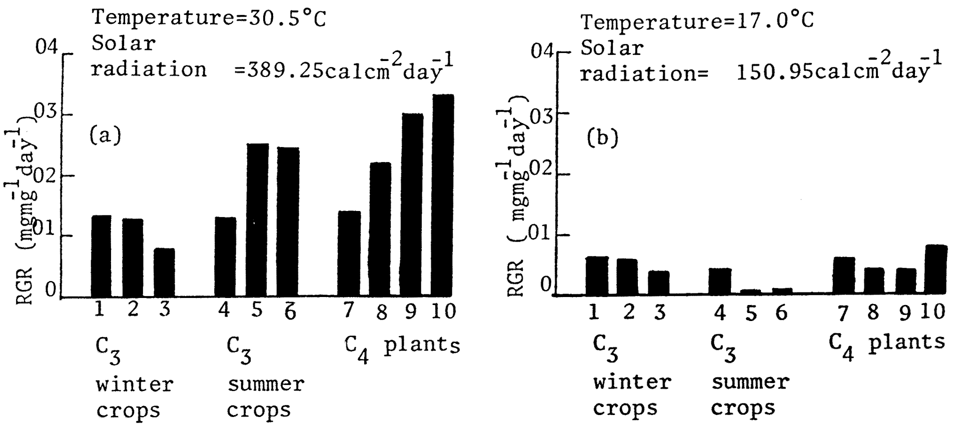

Fig. 4. Relationship of relative growth rate (RGR) with temperature and solar radiation in combination in various crop species.
Note: Numerals on the horizontal axis indicate crop name in Table 2:
1: wheat, 2: barley, 3: pea; 4: soybean, 5: rice (*indica*), 6: rice (*japonica*); 7: maize, 8: sorghum, 9: millet, 10: barnyard millet.

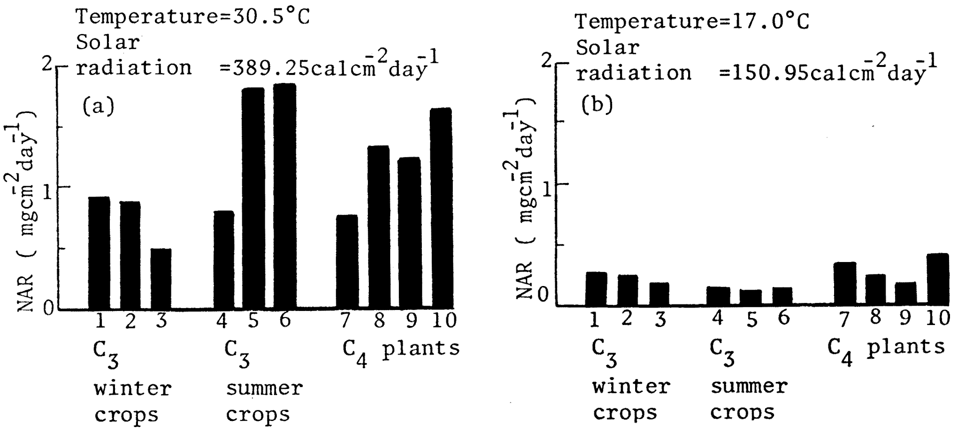

Fig. 5. Relationship of net assimilation rate (NAR) with temperature and solar radiation in combination in various crop species.
Note: Numerals on the horizontal axis are the same as in Fig. 4.

in most of the crop species. For example, in C_4 species the average contribution of temperature and solar radiation was 85% and 15%, respectively.

The above results are supported by the results on dallisgrass[9,12], bahiagrass[9,12], maize, sunflower[20,21,22,23], bean, cotton[20,21] and others. Kamiyama and Horie (1975) studied the relationship of RGR and NAR with various climatic factors in rice, maize and soybean. According to their results, RGR generally showed a parallel change with that of temperature and solar radiation and it was concluded from multiple regression analysis that temperature was most heavily responsible, with solar radiation as the second influential factor. On the other hand, the present study showed that there were distinct differences in RGR observed among species and groups under the combination of high temperature and strong solar radiation, with unclear differences under the combination of low temperature and weak radiation.

2. *Relationship of net assimilation rate with temperature and solar radiation*

Because RGR is a product of NAR and LAR, leaf area ratio, it would be expected that the variation of RGR should have some relationship with the variation of either NAR or LAR. In consequence, the pattern of response of RGR to variations in solar radiation and temperature will be an intermingling of the corresponding changes in NAR and LAR.

It is shown in the first row of Figs. 1, 2 and 3 that the change of NAR is quite similar to that of RGR shown in the second row, changing in parallel with that of temperature and solar radiation. The increasing pattern differs from C_3 to C_4 species. Thus, there is a clear difference in NAR among species and groups under high temperature and strong solar radiation (Fig. 5a). Under the combination of low temperature and weak solar radiation, however, this difference is not clear (Fig. 5b).

According to the results of many works[1,5,7,16,17,18,20,21,22,23], it has been established that NAR is in close correlation with climatic factors, and that the main climatic factors affecting NAR are solar radiation and temperature, the influence of the former being generally heavier than that of the latter. In this study, the contribution of solar radiation and temperature to NAR calculated from the standard multiple regression coefficients was very high in all the 9 crop species, 96% for C_4 species, 86% for C_3 species in which summer crops having 89% and winter crops having 84%, respectively.

Since NAR represents the net production of individual plants expressed in terms of unit leaf area, the first plant factor related to NAR is photosynthetic activity on unit leaf area. It is therefore not surprising to observe that NAR is climatic dependent, especially on solar radiation. According to the results of Murata (1975c), and Kamiyama and Horie (1975) who analyzed the extensive data of "Maximal growth rate experiment" of IBP on rice, maize, soybean and sugar beet, the change of NAR depends most heavily on the two climatic factors, solar radiation and temperature, the influence of the former being generally heavier than that of the latter. This principle has been confirmed in this study.

3. *Relationship of leaf area ratio with temperature and solar radiation*

Relationships of the second factor, LAR, with the combination of temperature and solar radiation in various crop species are shown in the first row of Figs. 1, 2 and 3. In the C_3 winter crops, LAR decreases with increasing temperature and solar radiation (Fig. 1). In contrast to this, in the C_3 summer crops, LAR increases gradually to a peak with increasing temperature and solar radiation, and then decreases (Fig. 2). This tendency in the change of LAR has been also observed in the C_4 crop species. However, in this group there is no great difference between the lowest and the highest LAR values (Fig. 3).

It would be expected that the variation of LAR should have some relationship with the variation of either SLA or LWR or both, because it can be broken down as follows:

$$\mathrm{LAR}=\frac{\mathrm{LA}}{\mathrm{W}}=\frac{\mathrm{LA}}{\mathrm{LW}}\times\frac{\mathrm{LW}}{\mathrm{W}}=\mathrm{SLA}\times\mathrm{LWR}$$

where LA is leaf area, W is dry weight of whole plant, LW is dry weight of leaves, SLA (specific leaf area) is ratio of leaf area to its dry weight, and LWR (leaf weight ratio) is ratio in the dry weight of the whole leaves to the total plant.

The relationships of SLA and LWR with temperature and solar radiation are shown in the third row of Figs. 1, 2 and 3. In these figures, the response of SLA and LWR to variations in temperature and solar radiation in the 3 groups of crops are similar to the response of LAR discussed above.

It was shown in rape, sunflower and maize[22,23], in two grasses (Ruzi grass and green panic) and two legumes (Capolo and Siratro)[14,15], in sunflower, bean, and clover[1,2], in French bean[4], and in Marquis wheat[7], that LAR increased with increasing temperature. Besides, Rajan et al. (1971, 1973) also found that LAR was inversely related to light intensity but positively linked with temperature in sunflower, bean,

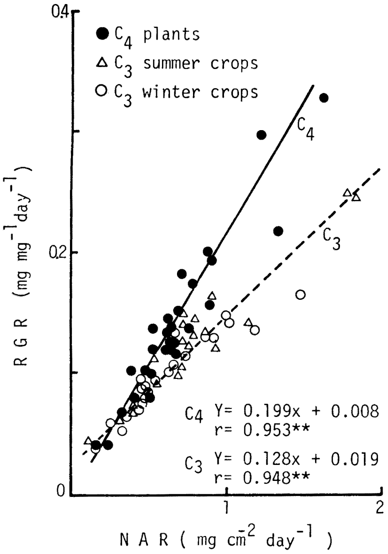

Fig. 6. Relationship between NAR and RGR in various crop species.

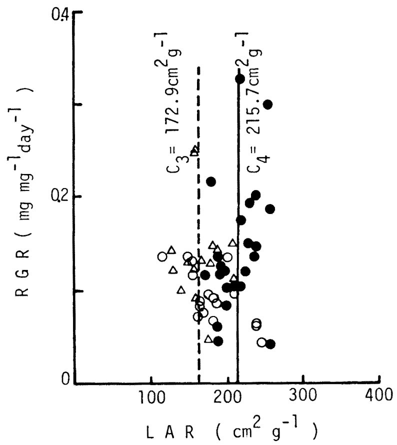

Fig. 7. Relationship between LAR and RGR in various crop species.
● C_4 plants, △ C_3 summer crops
○ C_3 winter crops.

maize, and cotton.

The same may be said with the results of Japanese IBP Experiments on rice, soybean and maize conducted for 4 years at various stations in Japan: Kamiyama and Horie (1975) showed that LAR was negatively correlated with radiation at most temperature levels except for the lowest and highest ones. Also Kumura (1975) showed clearly that the response of LWR and SLA to temperature was positive, and that to solar radiation was negative.

It may be concluded from the results of this study as well as the literatures cited above that in the C_3 winter crop species the change of LAR is mainly dependent on the variation of solar radiation. This is in good agreement with the results of Warren Wilson (1967) and Ludlow et al. (1971b). In the C_3 summer crop species and C_4 species, however, temperature response is maximal at low light intensities and minimal at high light intensities. That is, under the condition where light intensity ranges from 151 to 219 cal cm^{-2} day^{-1}, the effect of temperature on LAR is heavier than that of solar radiation, but under the combinated condition of strong solar radiation and high temperature, LAR seems to be affected simultaneously by these two climatic factors, the effect being a little greater in the former than in the latter.

It will be recalled that LAR may be analyzed from two factors, SLA and LWR. As mentioned above[13] the response of SLA and LWR to temperature was positive and that to solar radiation was negative. In the present experiments, the relationships of SLA and LWR with solar radiation and temperature, as seen in Figs. 1, 2 and 3, show that the contribution of solar radiation is generally heavy in the C_3 winter crop species, while in the C_3 summer crop species and C_4 crop species. i.e., in the tropical origin plants, SLA and LWR tend to be more strongly affected by temperature under the condition of weak solar radiation, with minimal temperature response under strong solar radiation. This tendency is in good agreement with observations of Rajan et al. (1973).

Thus, in the C_3 winter crop species, LAR tends to be negatively affected, as a net result, by the two climatic factors while in the C_4 species, LAR appears to be little affected by the climatic factors. In the C_3 summer crops, on the other hand, LAR is unevenly affected by the two climatic factors. Further it is recognized that a part of the change in LAR is due to the variation of specific leaf area and leaf weight ratio among

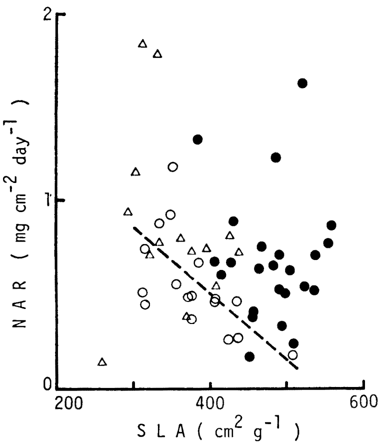

Fig. 8. Relationship between SLA and NAR in various crop species.
● C_4 plants r = −0.027
△ C_3 summer crops r = −0.137
○ C_3 winter crops r = −0.763**

species.

4. *Relationships among various growth parameters*

As shown in Fig. 6, there is close positive correlation observed between NAR and RGR in all the 9 species included. The regression lines, however, differ from C_3 to C_4 species. This is due to the difference in LAR, the other factor which composes RGR. As shown in Fig. 7 LAR is higher for the C_4 species, mean 215.7 cm^{-2} g^{-1}, than for the C_3 species, mean 172.9 cm^{-2} g^{-1}. From multiple regression analysis, it has been shown that the contribution of NAR to RGR is more than 78% in both the types.

Hayashi (1968) reported with 18 rice varieties that there was a close negetive correlation between NAR and specific leaf area. In the present experiment, as shown in Fig. 8, a close negative correlation between SLA and NAR was observed only among the C_3 winter species (r = −0.763**). From this result, it may be inferred that, in the C_3 winter species, the leaf thickness is directly related to the rate of leaf photosynthesis, consequently, causing the variation of NAR. This is quite in good agreement with many literature results[6,10,19,25,26,27,28].

From these results, it may be concluded

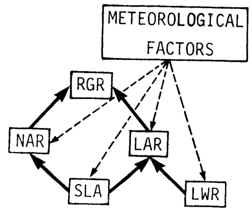

Fig. 9. Components of relative growth rate and their relationships with meteorological factors. Solid arrows indicate direct relationships, broken arrows, indirect ones.

that the influence of climatic factors on the relative growth rate of plants has been exerted mainly through the effect of temperature and solar radiation on NAR which is closely related with photosynthetic activity on unit leaf area and to a smaller extent on LAR which is related to the other two growth factors, specific leaf area and leaf weight ratio. These relationships are depicted in Fig. 9.

Summary

In order to make clear the effects of temperature and solar radiation on relative growth rate, RGR, net assimilation rate, NAR, leaf area ratio, LAR, and other growth parameters as well as on differences in the pattern of dry matter production among species, 6 experiments were carried out, using the seedlings of 9 species including C_3 winter crops, C_3 summer crops and C_4 crop species. Main results obtained are as follows:

1) There was clear difference in RGR exhibited among species and groups under the condition of high temperature and strong solar radiation. In the case of low temperature and weak solar radiation, however, difference was not so clear.

2) As a result of examination regarding the cause for the difference in RGR carried out by dividing it into two components, NAR and LAR, it has been revealed out that there is a clear difference among species and groups in NAR under the condition of high temperature and strong solar radiation, but that under the condition of low temperature and weak solar radiation,

difference in NAR among species and groups is not clear.

From multiple regression analysis, evidence has been obtained that contribution of temperature and solar radiation to NAR is very high, more than 86%, in all the 3 groups.

3) Further, it has been made clear that LAR, one of the factors composing RGR, tends to be negatively affected, as a net result by the two climatic factors in the C_3 winter crops, while there is no such effect recognizable in the C_4 species, with intermediate response in the C_3 summer crops. Besides these, by the examination on SLA and LWR which compose LAR, it has been concluded that the change in LAR was affected through both SLA and LWR.

4) Net assimilation rate is closely related with RGR in all the 9 crop species. The regression line, however, differs from C_3 to C_4 species. This difference is due mainly to the difference in LAR of the two groups.

5) There is an evidence for the existence of a close relationship in the C_3 winter species between SLA and NAR, suggesting that in this group the climatic response and species difference in RGR may be exerted through the effect of SLA on NAR.

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〔和 文 摘 要〕

C_3 型および C_4 型作物の生理的特性に関する研究

第2報 各種作物の乾物生産に及ぼす温度および日射量の影響

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温度，日射量に対する各種の作物の生長パラメーターの変化とそれらの相互関係を調査する目的で C_3 型の夏作物2種，冬作物3種および C_4 型作物4種を用いて試験を行なった．

土壌によって網室で幼植物を栽培し，その葉面積，各部乾物重を調査し，WATSON (1952) の式によって相対生長率 (RGR)，純同化率 (NAR) などを計算した．試験は5月～11月に6回行なった．結果の概要は次の通りであった．

1. 高温・強光（日射）の場合に RGR のグループ間差異が明らかであったが，低温・弱光の場合は RGR の値はいずれも非常に小さく，グループ間あるいは種間の差異も縮少した (Fig. 4).

2. RGR の差を NAR と葉面積比率 (LAR) の2つに分けて検討したところ，高温・強光の場合は NAR のグループ間の差が著しいが低温・弱光の場合は NAR の値が非常に小さく，グループ間あるいは種間の差異も著しく縮少した (Fig. 5). この NAR の変動の原因については，標準偏回帰係数を計算したところ，温度と日射量だけで NAR の変動の，C_4 型作物では 96%，C_3 型作物では 86% をそれぞれ説明できることがわかった．

3. 次に，RGR を構成する残りの1因子 LAR に対する温度と日射量の総合的影響を調べたところ，C_3 型の冬作物ではマイナス方向にかなり大きく働くのに対し，C_4 型作物ではほとんど影響なく，C_3 型の夏作物では両者の中間にあることが明らかになった．

また，LAR の変化を比葉面積 (SLA) と葉重比 (LWR) に分けてみると，その変化は両者を通じて現われていると結論することができる (Fig. 9).

4. RGR と NAR との間には非常に高い正の相関々係があるが回帰直線は C_3 型と C_4 型作物とではかなり異なる (Fig. 6). このちがいは両グループ間の LAR のちがいによることがわかった (Fig. 7).

5. 比葉面積 (SLA) は一般に LAR と密接な相関を示すが，C_3 型の冬作物の場合には NAR とも密接な相関を示したことから (Fig. 8)，このグループでは RGR の種間差および気象条件の影響に対して，SLA が LAR, NAR の両者を通じて関与するものと推定された．