Japan. Jour. Crop Sci. 46(1): 45-52 (1977)

Studies on the Physiological Characteristics of C3 and C4 Crop Species

I. The effects of air temperature on the apparent photosynthesis, dark respiration, and nutrient absorption of some crops*

Nguyen Quoc VONG and Yoshio MURATA
(*Faculty of Agriculture, University of Tokyo, Tokyo, 113*)
Received May 4, 1976

Photosynthesis, respiration and nutrient absorption are the three basic physiological processes in the life of plants, playing an important role in their dry matter production. Thus, when growth factors and translocation processes are not limiting to the dry matter production, the quantity and quality of the dry matter produced will be determined by the level of the three physiological processes and their interrelationships.

There is clear evidence for the existence of difference between species in the rate of dry matter production, and it is becoming increasingly obvious that dry matter production of a plant is highly dependent on environmental events such as air temperature and light intensity met with during the life period. From this point, it may be quite significant to make clear what influences the air temperature will give upon photosynthesis, respiration, and nutrient absorption which have a fundamental connection with dry matter production and growth of plants.

The differential effects of temperature on the apparent photosynthesis of various species have been studied by MILLER (1960), MURATA and IYAMA (1963), MURATA et al. (1965), El-SHARKAWY and HESKETH (1964), HOFSTRA and HESKETH (1969), and others. From these results it has been concluded that the optimum temperature for leaf photosynthesis is high, 30 to 47°C, for C_4 species, while it is low, 15 to 25°C, for C_3 species (BLACK, 1973).

As for the effect of air temperature on the dark respiration of various species, MURATA and IYAMA (1963) and MURATA et al. (1965) reported that the dark respiration rate of 20 forage and grain crops increased with increasing air temperature with little specific differences. However, IMAI et al. (1973) who compared various photosynthetic properties of 9 species found that dark respiration rate was higher in C_4 species than in C_3 species.

Concerning, on the other hand, the differential effects of temperature on the nutrient uptake by root among species, little is understood, because very few works have been done on this subject.

In the present experiments described below differences were examined between several C_4 and C_3 crop species in their rates of apparent photosynthesis, dark respiration, and NH_4-N, P, and K absorption by root in relation to various air temperatures, in order to make clear what influences the air temperature would give upon the growth of plants through its effect upon the three basic physiological processes.

Materials and Methods

Plant material The C_4 species used were maize (*Zea mays* L. cv. Okuzuruwase), sorghum (*Sorghum bicolor* L. cv. Bonita), millet (*Panicum miliaceum* L. cv. Shirokibi), and barnyard millet (*Panicum crus-galli* L. cv. Hidaakabie); the C_3 species were rice (*Oryza sativa* L. subsp. *japonica* cv. Nihonbare and *O. sativa* L. subsp. *indica* cv. IR 8) and soybean (*Glycine max* L. cv. Norin 2), as summer crops, and wheat (*Triticum aestivum* L. cv. Fujimi-komugi), barley (*Hordium vulgare* L. cv. Dorirumugi), and pea (*Pisum sativum* L. cv. Sanjunichikinusaya) as winter crops. The seeds were obtained from the Central Agricultural Experiment Station, Konosu (rice and barley), Experimental Farm of University of Tokyo, Tanashi (soybean, barnyard millet), Kikyogahara Branch Office, Nagano Agricultural Experiment Station (maize), Chugoku

* Outline of this paper was reported at the 160th Meeting of the Crop Science Society.

Table 1. Species used and cultural conditions.

	Species	Plant density*	Nutrient solution	Cultured temp.**	Aeration	Photosynthesis pathway
1	Wheat	130	Kimura A	20/20	Yes	C-3
2	Barley	130	Kimura A	20/20	Yes	C-3
3	Pea	16	Kimura A	20/20	Yes	C-3
4	Soybean	16	Kimura A	30/25	Yes	C-3
5	Rice, indica	130	Kimura B	25/20	No	C-3
6	Rice, japonica	130	Kimura B	25/20	No	C-3
7	Maize	20	Kimura A	30/25	Yes	C-4
8	Sorghum	70	Kimura A	30/25	Yes	C-4
9	Millet	70	Kimura A	30/25	Yes	C-4
10	Barnyard millet	70	Kimura A	30/25	Yes	C-4

*Plant number per tray, 32×22×11 cm in size. **Day/night temperature, °C.

Agricultural Experiment Station (sorghum), National Institute of Agricultural Sciences, Hiratsuka (millet), National Institute of Agricultural Sciences, Kitamoto (wheat) and Takii Shubyo commercial store (pea).

After disinfection with 0.1% Usprun solution for 6 hours, the seeds were germinated in distilled water, and then transplanted into trays (30×22×11 cm deep) containing culture solution, KIMURA's A or B solution. These trays were placed in a growth room of natural light maintained at 30/25°C, 25/20°C, or 20/20°C in the day and night temperature according to species. The culture solution was changed every 3 days. Other cultural conditions are shown in Table 1.

When the 4th or 6th leaf elongated, each species was divided into 2 groups: one for the measurement of photosynthesis and dark respiration and the other, for the determination of NH_4-N, P and K absorption.

Measurement of apparent photosynthetic and dark respiration rate One tray of seedlings was placed in an assimilation chamber. Its apparent photosynthetic rate was measured under 35 klux light intensity, 60-80% relative humidity, ca. 300 ppm CO_2 concentration of the air, and 6 levels of temperature, 12, 18, 24, 30, 36 and 42°C. It took 45 minutes to finish photosynthesis measurement at each temperature level. Dark respiration was measured 30minutes after the photosynthesis measurement at each of the 6 temperature levels. Both photosynthesis and respiration were measured by an open system using an infrared gas analyzer (Fuji Electric Co.).

Determination of nutrient absorption by root

The roots of intact seedlings were put in a plastic container (20×13×8 cm deep) which contained 1.3 liter of nutrient solution. The container was placed in a growth chamber maintained at 12, 18, 24, 30, 36 or 42°C for 3 hours under 35 klux light intensity, 60–80% relative humidity, and ca. 300 ppm CO_2 concentration of the air. Then, the seedlings were taken out, their roots were excised, blotted with tissue paper and weighed. Dry weight was measured with materials dissected into several parts and dried in a forced-air drying oven set at 80°C for more than 48 hours.

Nutrient absorption rates were calculated from the difference in NH_4-N, P and K concentration of the culture solution at the start and after 3 hours. Nutrient elements were determined by the following methods:

NH_4-N: Nessler method,
P: Vanadomolybdophosphoric yellow color method in nitric acid system (Method V of M. L. JACKSON), and
K: Flame photometer.

Nutrient absorption rates were expressed as mg element/g fresh wt. of root/3 hours. Each of the photosynthesis, respiration and nutrient absorption experiments was replicated 2 or 3 times.

Results and Discussion

1. *Effect of temperature on apparent photosynthesis*

The relationships between air temperature and apparent photosynthesis of various species are shown in Fig. 1. Although the values of apparent

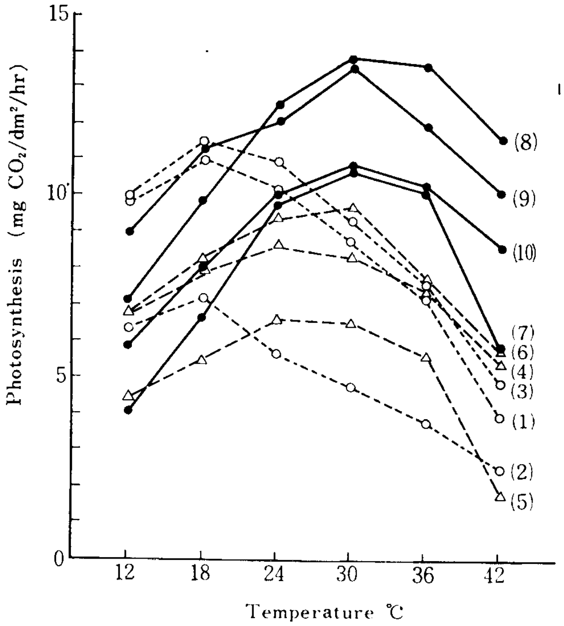

Fig. 1. Relationship between apparent photosynthesis and temperature of crops.
Note. Numerlas in the figure indicate crop name in Table 1.

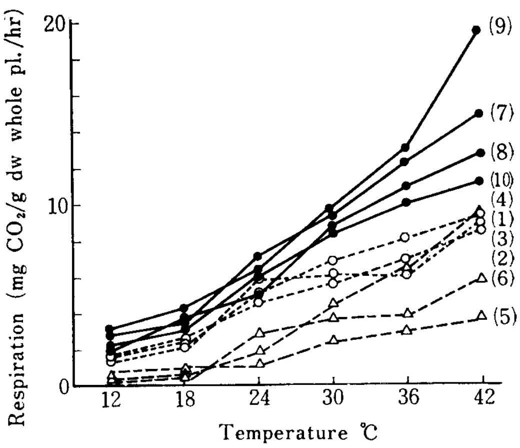

Fig. 2. Relationship between dark respiration and temperature of crops.

photosynthesis in the figure are relatively low in all the 9 species due to the low light intensity and the mutual shading of leaves within a tray, it is clearly indicated that each species has its own optimum temperature for its apparent photosynthesis: the C_4 species, sorghum, barnyard millet, maize, and millet which is firstly reported here in this respect, having higher temperatures of 30-36°C; the C_3 winter crops, barley, wheat, and pea, lower temperatures of about 18°C; and the C_3 summer crops, rice and soybean, medium temperatures of 24–30°C.

As for the optimum temperature for photosynthesis, MILLER (1960) compared creeping bentgrass and bermudagrass, MURATA and IYAMA (1963) and MURATA et al. (1965) compared 20 forage and grain crops, El-SHARKAWY and HESKETH (1964) compared sorghum, soybean, cotton, and *Thespecia populnea,* and HOFSTRA and HESKETH (1969) compared maize, sugar beet, soybean, *Atriplex hastata,* and *A. nummularia.* Besides these, optimum temperature for photosynthesis of individual species was reported in such species as dwarf pea (HELLMUTH, 1971), a desert C_4 species, *Tidestromia oblongifolia* (BJÖRKMAN et al., 1972), and others. However, it is also known that optimum temperature for photosynthesis is shifted by the growth temperature (MURATA and IYAMA, 1963; MOONEY and HARRISON, 1969; SAWADA and MIYACHI, 1974). On the other hand, it has been concluded from literature that the optimum day temperature for growth is high, 30 to 35°C, for C_4 species, while it is low, 20 to 25°C, for C_3 species (BLACK, 1973).

Taking all these results as well as the present results into consideration, it may be concluded as follows: The photosynthetic response of a species to temperature is closely associated not only with the photosynthetic pathway but also with more ecological characteristics such as the temperature or seasonal requirement for growth.

2. *Effect of temperature on dark respiration*

The effect of temperature on dark respiration is shown in Fig. 2 where dark respiration rate increases steadily and exponentially with increasing temperature in all the 9 species alike. This tendency is in good agreement with the results of MURATA and IYAMA (1963) and of MURATA et al. (1965). However, the rate of dark respiration is different from species to species: that of C_4 species, millet, maize, sorghum, and barnyard millet, is very high as compared to that of the C_3 summer crops, with the C_3 winter crops showing medium values. This is supported by the results of IMAI et al. (1973) that dark respiration rate at 30°C is higher in C_4 species than in C_3 species. Also MAENO (1969) reported that the rate of respiratory consumption of dallisgrass (C_4) was higher than that of Italian ryegrass (C_3) during their regrowth period.

3. *Apparent photosynthesis-dark respiration ratio*

The ratio of apparent photosynthesis to dark respiration (P/R ratio) is shown in Fig. 3 where it decreases roughly exponentially with increasing temperature in all the 9 species. In the C_4 species, the P/R ratio is lower at low temperatures, decreasing more slowly than in the C_3 species with increasing temperature. It is suggested from these that the C_4 species are inferior to the C_3 species in dry matter production in lower temperature range as far as its efficiency is concerned, disregarding long-term changes such as taking place in the productive structure and others. In addition, from Figs. 1 and 2, it is recognized that apparent photosynthesis rate of the C_4 species attains the maximum value at higher levels of respiration rate (3–4 $mgCO_2/dm^2/hr$), while the C_3 species do so at a lower levels (1 $mgCO_2/dm^2/hr$ for winter crops and 1–2 $mgCO_2/dm^2/hr$ for summer crops).

4. *Effect of temperature on nutrient absorption*

The absorption rate of NH_4-N, P and K tended to increase with increasing temperature until a maximum value is reached, and then to decrease again at still higher temperatures (Fig. 4). The optimum temperature for absorption was different among species and nutrient elements. In C_3 species the optimum temperature for the absorption of NH_4-N, P and K in rice was 36-42°C, 36°C and 42°C, respectively. In barley and wheat, that for NH_4-N was 24°C and that for both P and K was 36°C (Fig. 4-b).

In soybean and pea, that for P and K was 36–42°C and 36°C, respectively, while that for NH_4-N was not recognized at all. In all the C_4 species, the optimum temperature for NH_4-N absorption was 30°C and both for P and K was 42°C (Fig. 4-d). Interestingly, K absorption in this type of plants increased linearly with the increasing temperature attaining as high as 0.85 mg K/g fresh wt. of root/3 hours at 42°C, a value 1.2-4.7 times greater than that in comparable C_3 species. The higher rate of K absorption by the C_4 species as compared with the C_3 species was in line with the result of WORLEY et al. (1963) who found that the rate of K-uptake was higher in sudangrass, a C_4 species, than in rye, pea or soybean, C_3 species.

5. *Interrelationships between apparent photosynthesis, dark respiration, and nutrient absorption*

In contrast to the response of dark respiration rate which increased both in C_3 and C_4 species with increasing temperature up to 42°C, the rate of apparent photosynthesis reached a maximum value at various temperature levels: 18°C for C_3 winter crops, 24–30°C for C_3 summer

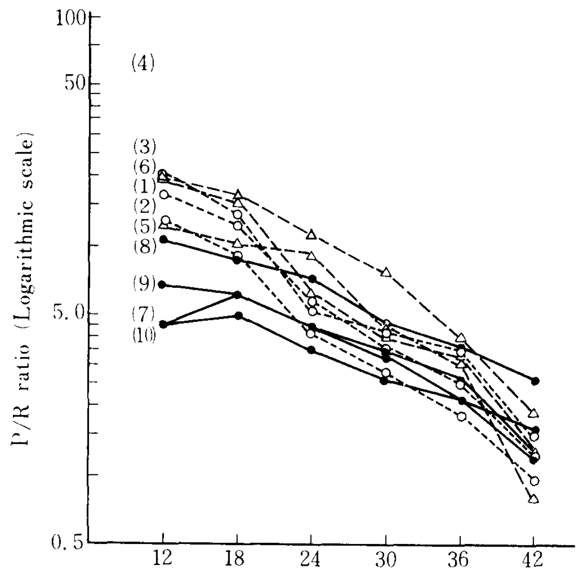

Fig. 3. Relationship beween P/R ratio and temperature in crops.

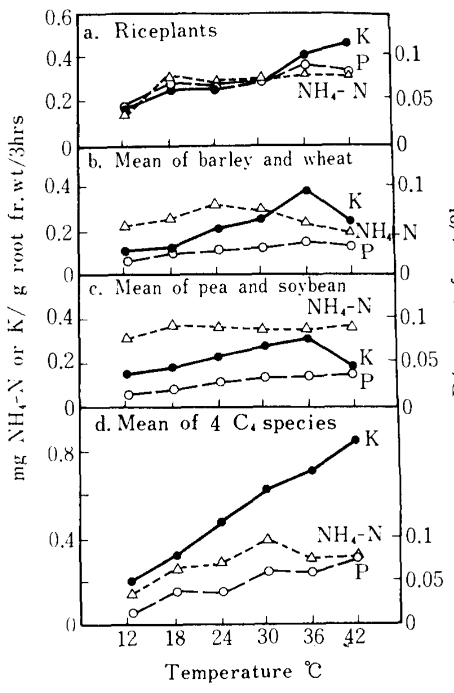

Fig. 4. Relationship between NH_4-N, P, K absorption and temperature in crops.

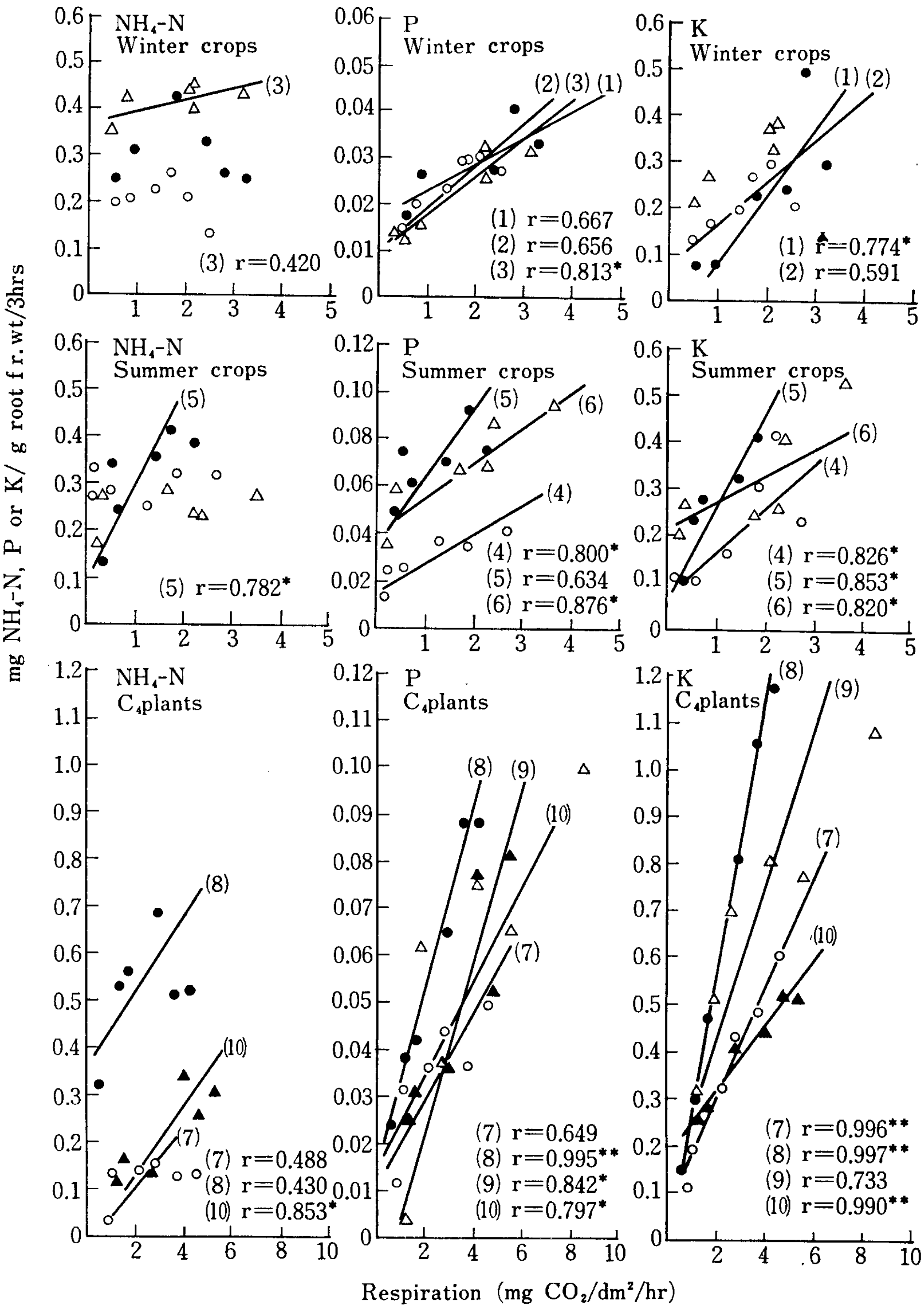

Fig. 5. Relationship between NH_4-N, P, K and respiration of crops.
Note. Numerals in parenthesis indicate crop name in Table 1.

crops, and 30–36°C for C_4 crop species. Thus, no consistent relationship could be found between variations in photosynthesis and those in respiration in the present experiment. However, nutrient absorption was found to be correlated very closely with dark respiration rate in both C_4 and C_3 species (Fig. 5) and with apparent photosynthesis in some cases (Fig. 6).

Relationships between nutrient absorption and dark respiration are shown in Fig. 5. In this figure, although the correlation of dark respiration rate with NH_4-N absorption is not so close, that with P and K absorption is very close in all the species. This may be taken as a proof to show that nutrient absorption of plant root is heavily dependent on the respiratory activity of the whole plant. In addition, the relationships in the C_4 species gave higher regression coefficient than in the C_3 species. This may indicate the higher efficiency of respiratory

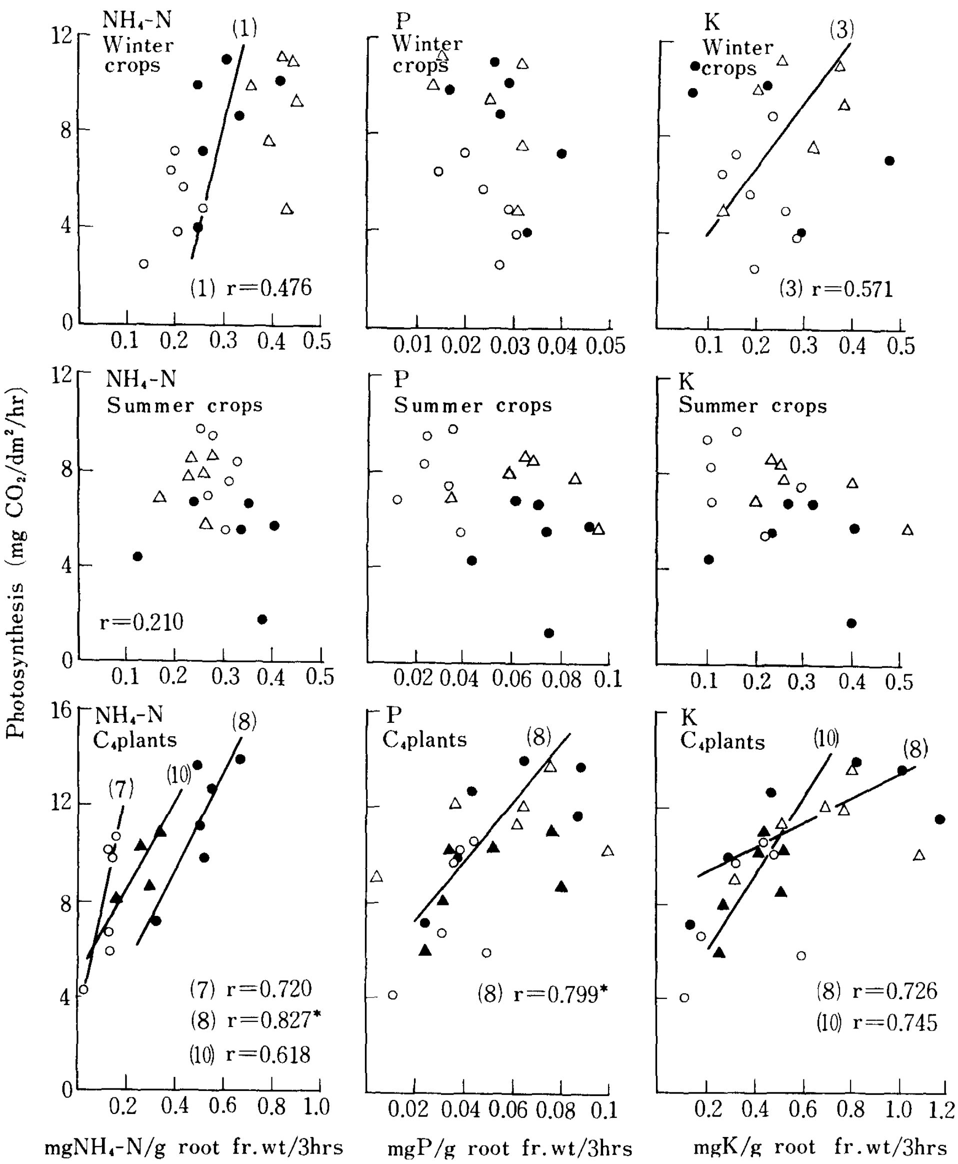

Fig. 6. Relationship between photosynthesis and NH_4-N, P, K absorption of crops.

process in the C_4 species in absorbing nutrients, especially K, than in the C_3 species.

Relationships between apparent photosynthesis and nutrient absorption are shown in Fig. 6. There is no relationships observed between apparent photosynthesis and P and K absorption in the C_3 species, but close relationships are recognized in the C_4 species. This is in line with the generally observed facts that photosynthetic activity depends heavily on nitrogen content of the leaf (MURATA, 1969). It may be suggested from these data that in the C_4 species the effect of varying temperature from 12 to 42°C on photosynthetic activity is basically exerted through the metabolism of chloroplast proteins which are, in turn, limited by nitrogen absorption.

Summary

Short-term influence of air temperature upon the photosynthesis, dark respiration, and nutrient absorption in C_3 plants (3 winter crop species and 2 summer crop species) and C_4 plants (4 species) were investigated. Based on the data obtained, the interrelationships among nutrient absorption, dark respiration, and apparent photosynthesis were examined. The results obtained are as follows:

1) The optimum temperature for photosynthesis was high in the C_4 species: 30–36°C,

low in the C_3 winter crops: about 18°C, and medium in the C_3 summer crops: 24–30°C (Fig. 1).

2) Dark respiration rates showed a steady, exponential increase with increasing temperature in all the 9 species. In the C_4 species, dark respiration rate was higher than that in the C_3 species (Fig. 2).

3) The apparent photosynthesis-dark respiration ratio (P/R ratio) of all the 9 species showed an exponential decrease with increasing temperature. In the C_4 species this ratio was lower at low temperatures, decreasing more slowly with increasing temperature than in the C_3 species (Fig. 3).

4) The NH_4-N, P and K absorption rates differed from species to species. In general, the optimum temperature for K absorption in the C_4 species was very high and its acceleration by increasing temperature was very remarkable compared to the C_3 species.

From these data it has been suggested that in the C_4 species the effect of varying temperature from 12 to 42°C on photosynthetic activity is basically exerted through the metabolism of chloroplast protein which are, in turn, limited by nitrogen absorption. Further, NH_4-N, P and K absorption was found to be very closely correlated with respiration rate, and especially in the C_4 species, indicating higher efficiency of respiratory process to absorb nutrients in the C_4 species than in the C_3 species.

References

1. BLACK, C. C. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. Ann. Rev. Plant Physiol. **24**: 253—286.
2. BJÖRKMAN, O., R. W. PEARCY, A. T. HARRISON and H. MOONEY 1972. Photosynthetic adaptation to high temperatures: A field study in Death Valley, California. Science **175**: 786—789.
3. COOPER, J. P. and N. M. TAINTON 1968. Light and temperature requirements for the growth of tropical and temperate grasses. Herbage Abstr. **38**: 167—176.
4. DECKER, J. P. 1944. Effect of temperature on photosynthesis and respiration in red and loblolly pines. Plant Physiol. **19**: 679—688.
5. EL-SHARKAWY, M. A. and J. D. HESKETH 1964. Effects of temperature and water deficit on leaf photosynthetic rates of different species. Crop Science **4**: 514—518.
6. HELLMUTH, E. O. 1971. The effect of varying air-CO_2 level, leaf temperature, and illuminance on the CO_2 exchange of the dwarf pea, *Pisum sativum* L. var. Meteor. Photosynthetica **5**: 190—194.
7. HESKETH, J. D. and D. N. BAKER 1969. Relative rates of leaf expansion in seedlings of species with differing photosynthetic rates. J. Arizona Acad. Sci. **5**: 216—221.
8. HOFSTRA, G. and J. D. HESKETH 1969. Effects of temperature on the gas exchange of leaves in the light and dark. Planta **85**: 228—237.
9. IMAI, H., M. FUKUYAMA, Y. YAMADA and T. HARADA 1973. Comparative studies on the photosynthesis of higher plants. Soil Sci. Plant Nutr. **19**: 61—71.
10. MILLER, V. J. 1960. Temperature effect on the rate of apparent photosynthesis of seaside bent and bermudagrass. Proc. Amer. Soc. Hort. Sci. **75**: 700—703.
11. MOONEY, H. A. and A. T. HARRISON 1969. The influence of conditioning temperature on subsequent temperature-related photosynthetic capacity in higher plants. In Prediction and measurement of photosynthetic productivity. Proc. IBP/PP Technical Meet. Trebon, 1969, 411—417.
12. MURATA, Y. 1969. Physiological responses to nitrogen in plants. In Physiological aspects of crop yield. ASA and CSSA, 235—259.
13. ———— and J. IYAMA 1963. Studies on the photosynthesis of forage crops. II. Influence of air temperature upon the photosynthesis of some forage and grain crops. Proc. Crop Sci. Soc. Japan **31**: 315—322.
14. ————, ———— and T. HONMA 1965. Ibid. IV. Influence of air temperature upon the photosynthesis and respiration of alfalfa and several southern type forage crops. ibid. **34**: 154—158.
15. SAWADA, S. I. and S. MIYACHI 1974. Effects of growth temperature on photosynthetic carbon metabolism in green plants. I. Photosynthetic activities of various plants acclimatized to varied temperatures. Plant and Cell Physiol. **15**: 111—120.
16. WORLEY, R. E., R. E. BLASER and G. W. THOMAS 1963. Temperature effect on potassium uptake and respiration by warm and cool season grasses and legumes. Crop Science **3**: 13—16.

〔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1報 各種作物の光合成，呼吸および養分吸収に及ぼす温度の影響

グェン・コック・ボン・村 田 吉 男
（東京大学農学部）

温度に対する各種の作物の光合成，呼吸および養分吸収を総合的に比較する目的で C_3 型の夏作物（2種）と冬作物（3種）および C_4 型の作物（4種）を用いて水耕法で3種類の試験を行なった．結果の概要は次の通りであった．

1．みかけの光合成の最適温度は C_4 型では高く 30～36°C に，C_3 型の冬作物では低く 18°C 前後に，そして C_3 型の夏作物では両者の中間の 24～30°C にみられた (Fig. 1).

2．暗呼吸と温度との関係はいずれの種においても，指数曲線で示されるが，C_4 型の作物の呼吸活性は全般的に C_3 型の作物に比べて著しく高いことが明らかになった (Fig. 2).

3．みかけの光合成と呼吸の比率 (P/R 比) はいずれの種においても温度の上昇に従って逆指数関数的に低下する．この低下は C_3 型では急で C_4 型では緩やかである (Fig. 3).

4．3要素の吸収率と温度との関係は種により多少違うが，一般にその最適温度は NH_4-N では 24～36°C，P と K では 36～42°C であった．C_4 型では C_3 型に比べ K の吸収速度が著しく大きく，温度上昇による促進も大きいことが明らかになった (Fig. 4).

以上の結果から温度に対する各種作物の光合成，呼吸および養分吸収の反応において次のような相互関係が存在することがわかった (Fig. 5 および Fig. 6). C_4 型の作物と C_3 の冬作物の一部に NH_4-N 吸収と光合成速度との間に密接な相関関係が認められた．これは従来の多くの成績と合せ考えると，窒素吸収速度が光合成能力に限定的に働いていることを示すものと判断される．他方，養分吸収と呼吸速度との間にはどの作物においても極めて明らかな相関が認められた．このことは養分吸収が呼吸活性に強く依存することを示すものと考えられる．