Studies on the Production and Consumption of Assimilates of Trees : XI. Seasonal Changes of Photosynthesis, Respiration Rates of the Sun and Shade Leaves and Estimation of Branch Respiration by the Living Cell Area Method on the Natural Japanese Beech Forest

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https://doi.org/10.5109/23703

出版情報：九州大学大学院農学研究院紀要. 24 (2/3), pp.133-144, 1979-11. Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., 24(2·3), 133-144 (1979)

Studies on the Production and Consumption of Assimilates of Trees

XI. Seasonal Changes of Photosynthesis, Respiration Rates of the Sun and Shade Leaves and Estimation of Branch Respiration by the Living Cell Area Method on the Natural Japanese Beech Forest

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(Received July 24, 1979)

In order to obtain the fundamental information on the primary production and consumption of the Japanese beech forest at 1000 m altitude zone in Fukuoka in southern Japan, measurement of photosynthesis rate and respiration rate of the detached sun and shade leaves. and of respiration rate of the branches with various diameters had been measured monthly from October 1976 to September 1978. The photosynthesis rates of the sun and shade leaves increased from April to the end of July, then decreased at the end of October. The optimum temperature obtained by the temperature dependence curve of apparent photosynthesis was 20 to 25°C in all season. Respiration rates of the various diameters of branches were exponentially increased by increasing specific cambium and phloem area for transverse section area. We could obtain the accurate equation on the respiration rates of woody organs by the measurement of number of living cells or specific living cell area. Respiration of the branch had higher rates in the growing season than in the non-growing season. Amount of respiration of the attached bud twigs with the diameter less than 0.5 cm is very important factor to estimate the total amount of respiration of the branch.

INTRODUCTION

Japanese beech forest is distributed in northern Japan as dominant vegetation mainly in temperate zone, and highland in southern Japan. In Fukuoka in southern Japan, it is seen higher than 900 m altitude. It is well known that Japanese beech has a high growth rate in the low temperature zone at high altitude, but it has a low growth rate or will be dead when it is transplanted to the high temperature zone at low altitude. Such difference in growth might be thought to be related to the positive or negative carbon dioxide balance due to the difference of photosynthesis and respiration rate throughout the year.

In addition, the difference is caused by the genetical and ecophysiological characteristics to change its photosynthetic and respiratory acclimation in response to changes in environmental conditions such as temperature, light,

water, and other factors. In general, plants are able to adapt to within some low or high temperature range in the artificial environmental conditions (Lange et ***al.,*** 1974; Mooney ***et al., 1964,*** 1978). Even temperature acclimation of photosynthesis of leaves occurs not only after long periods of temperature treatment but also after only 24 hours of exposure to a new temperature regime (Raschke, 1970; Lange ***et al., 1974).***

Maintenance of a positive carbon dioxide balance under exceptionally high temperature ranges such as desert in summer may require that the plants possess a high photosynthetic acclimation potential (Mooney ***et al., 1978).*** There are natural fact that beech, if it is transplanted into high temperature regime, should have a positive carbon dioxide balance in order to adapt to a high temperature regime., But Han and Suzaki (1978, 1979) noted that negative carbon dioxide balance and high maintenance respiration had occured in the Japanese beech seedlings under the temperature conditions of 30 to 35°C in summer. In particular, it was found that high temperature treatment influenced profoundly on the carbon dioxide balance of Japanese beech seedlings as compared with oak (Quercus *acutissima* Carruth.) seedlings (Han and Suzaki, 1979).

For determination and analysis of the optimum and abnormal temperature conditions, it is very important to observe the carbon dioxide balance process as an ecophysiological interpretation including photosynthesis and respiration process. In general, carbon dioxide balance in plants are defined as the difference of gross photosynthesis and total respiration in a given environmental conditions. Measurement of only apparent photosynthesis of leaves actually can not represent reasonable primary productivity of forest stand which has a large non-photosynthetic organs such as stems, branches, and roots (Yoda ***et al.,*** 1965; Kira ***et al.,*** 1967; Oohata *et* ***al.,*** 1971; Larcher, 1969). At present time, we can not find any suitable analysis on the ecophysiological adaptation and primary production in the forest stand except the investigation of the carbon dioxide balance process in whole tree organs in a given environmental conditions. In addition, if estimation of long term carbon dioxide balance on the temperature effects is intended, the more detailed data of temperature dependence of leaf photosynthesis and respiration, stem, branch, and root respiration, in their developmental and seasonal trends, must be acquired (Larcher, 1969).

However, there are few reports on the relation of photosynthetic and respiratory acclimation to the temperature and carbon dioxide balance-process in the natural forest or transplanted trees except ones from desert shrub (Mooney ***et al., 1964,*** 1978; Pearcy, 1976, 1977; Armond ***et al.,*** 1978).

We had discussed the photosynthetic and respiratory acclimation of Japanese beech seedlings under high temperature regime in the previous studies (Han and Suzaki, 1978, 1979). The present study deals with seasonal changes and temperature response of photosynthesis and respiration rate of sun and shade leaves and/or branch respiration characteristics by means of living cell area method, and this is a basic data in order to compare with the the photosynthetic and respiratory acclimation to temperature between the natural

forest and the transplanted beech at warm temperature regime.

MATERIALS AND METHODS

The measurement of photosynthesis and respiration were carried out monthly from October 1976 to September 1978 on the natural Japanese beech (*Fagus crenata* Blume) forest at Mt. Sefuri about 1000 m altitude zone, located in Fukuoka Pref. in southern Japan. Sample branches (attached and detached leaves) with various diameters of one or two meter length from a tree which was about loo-year-old, were cutted off, and they were immediately transferred to the laboratory and were maintained freshly containing with plastic basket. The sun leaves were collected from top of crown and shade leaves were collected from the part where relative illuminance was about 10 percent.

The measurement of photosynthesis and respiration rate were done by means of an open system using an infrared gas analyser (Horiba LIA-2A, Differential system). The leaves attached on cutting branches keeping in water culture were placed in a $20\times7\times3$ cm acrylglass open system assimilation chamber which had been maintained at ±0.5°C of the desired temperature adjusting with a Komatsu Yamato Coolnics Circulator. Leaf temperature of intact sample was measured by thermocouples. Air was stored in a $0.6\times1\times3$ m vinyl bag and was led into the assimilation chamber at the rate of 0.5 to 1.0 l/min. The air in the chamber was well stirred at a velocity of 1 m/sec by a fan. Illuminance was supplied with four astral lamps composed of nine incandescent lamps (24 V, 40 W).

The branch respiration rate was measured by the 10 cm diameter and 20 cm length plastic pipe chamber after the cut surfaces on both ends were sealed with Vaseline paste. Temperature in the chamber was regulated by the Toshiba Growth Cabinet TGS-13H. Air was stored in a bag and was led into the respiration chamber at a velocity of 1 to 2 l/min.

All run of measurement of photosynthesis and respiration were finished within 24 hours after the branches were cutted off from the sample tree. On the other hand, living cell area of the branch in this paper was defined as the cambium and phloem area in transverse section. Cambium and phloem area indicates the cambial zone area, differentiating xylem area, differentiating phloem area, and mature phloem area as shown in Brown's report (1971). Total cambium and phloem area of a transverse section were obtained by the full observing or summation of eight divided portion of the section as shown in Fig. 1. Measurement of the cambium and phloem area were done by following procedures: 1. Cutting the transverse section (size 0.6×0.6 cm) from bark to xylem. 2. Fixation by the FAA solution (ethyl alcohol 60 ml, acetic acid 5 ml, formalin 5 ml, and distilled water 30ml) for 24 hours. 3. Washing the sample by the tap water for 24 hours. 4. Dehydration by the 50, 70, 80, 90, 100, 100% ethyl alcohol for 24 hours, respectively. 5. Treatment by the methyl benzoate containing 1% celloidin for 12 hours. 6. Three times treatment by the chloroform solution for 1 hour. 7. Treatment by the chloroform-paraffin (m.p. 56°C) solution for 24 hours. 8. Penetration by the m.p. 56, 58,

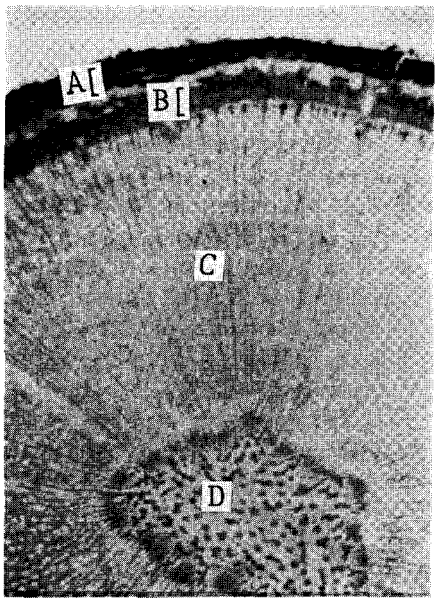

Fig. 1. Transverse section of a beech branch (2-year-old) showing arrangement of tissues. Sample was cutted at February. In this experiment, total cambium and phloem area of a transverse section was calculated by the measuring cambial and phloem zone width. A, bark; B, cambial and phloem zone; C, xylem; D, pith

62°C paraffin solution for 4 hours, respectively. 9. Making the paraffin cake (size 1 xl xl cm) by the m.p. 62°C paraffin solution. 10. Cutting the paraffin cake about 10 to 30 μm by a microtome. 11. Deparaffin by the treatment in xylol for 24 hours. 12. Double staining the safranine solution (safranine 1 g, ethyl alcohol 50 ml, and distilled water 50ml and fast green FCF solution (fast green FCF 0.5 g and absolute ethyl alcohol 100 ml). 13. Making the preparation. 14. Measuring the green color area which is only composed of living cells by the 100× microscope.

RESULTS AND DISCUSSION

I. Photosynthesis of Japanese beech leaves

The relationship between the apparent photosynthesis of sun and shade leaves and the light intensity is shown in Fig. 2. The apparent photosynthesis per unit surface area of sun and shade leaves have a tendency to increase from April to July, then to decrease toward the end of October. Seasonal change of apparent photosynthesis rate in same temperature is considered to be mainly caused by different photosynthetic activities by the leaf age, temperature sensitivities according to stomata1 and mesophyll resistance (Neilson et *al.*, 1972), and other enzyme factors (Pearcy, 1977). The general pattern of

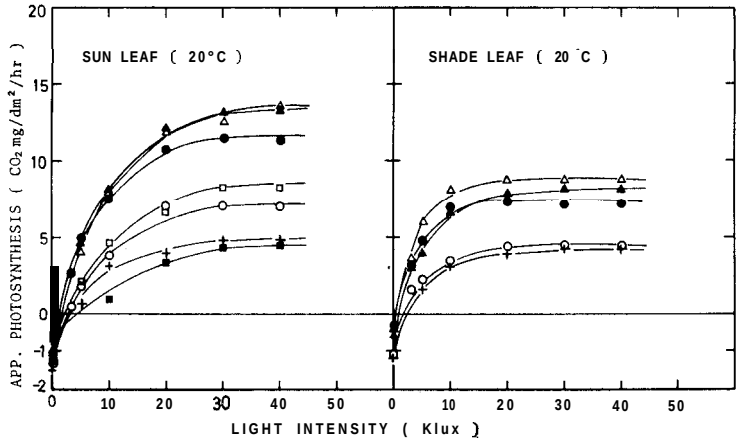

Fig. 2. Seasonal changes of photosynthesis and respiration rates of sun and shade leaves (1977). ■ , Apr. ; □, May; ▲, Jun. ; ▽, Jul.; ●, Aug.; ○, sept.; +, Oct.

photosynthesis curves in response to different season was a similar result as compared with other paper for Japanese beech forest grown at high altitude zone (Maruyama and Yamada, 1968).

As shown in Fig. 2, sun leaves had higher CO, uptake and release rates per unit leaf surface area at all season than shade leaves. In contrast, CO, uptake and release per unit dry weight of leaf are vice versa in Fig. 3. Those results are observed in other beech species (Shulze *et al.*, 1970). The temperature dependence of apparent photosynthesis in sun and shade leaves showed in various ways for each season throughout the year. Temperature dependence curve of apparent photosynthesis rate by a quadratic equation had been slightly changed from April to September, and also temperature re-

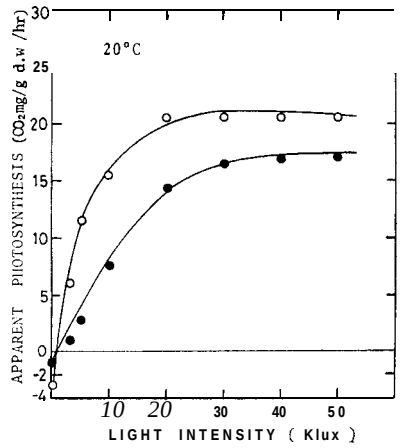

Fig. 3. Relation between apparent photosynthesis of the sun (●) and shade (○) leaves and light intensity. Jun., 1978.

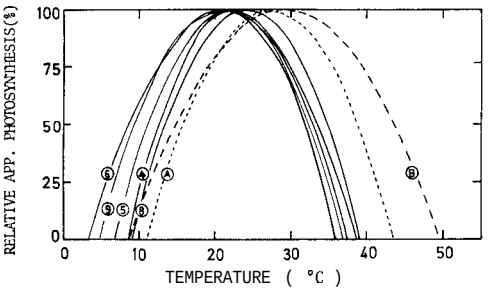

Fig. 4. Relation between the relative apparent photosynthesis rate and the temperature. ④, Apr.; ⑤, May; ⑥, Jun.; ⑧, Aug.; ⑨, Sept.; Ⓐ, Aug. (*Fagus crenata* Blume grown at low altitude and warm temperate zone, Han and Suzaki, 1979); Ⓑ, Aug. (Quercus ***acutissima*** Carruth. grown at low altitude and warm temperate zone, Han and Suzaki, 1979).

gimes of maximum relative photosynthesis indicated about 20 to 25°C in Fig. 4. The negative carbon dioxide balance of beech leaves grown at high altitude zone, estimated by a quadratic equation, was appeared in lower temperature regimes of about 35 to 40°C than that of *Fagus crenata* Blume and *Quercus acutissima* Carruth. seedlings grown at low altitude and warm temperate zone in Fig. 4 (Han and Suzaki, 1979).

The difference in photosynthetic response for temperature is an important factor in discussing the character in plants (Armond *et al., 1978;* Larcher, 1969; Mooney *et al.,* 1978; Negisi, 1966; Raschke, 1970). In Fig. 4, the differences of temperature dependence curves on the point of view of relative apparent photosynthesis and negative carbon dioxide balance are able to explain as the differences of photosynthetic and respiratory acclimation in response to past environmental conditions, i.e. effects of temperature on leaf stomata1 and mesophyll resistance (Neilson *et al.,* 1972) and enzyme activities in relation to temperature response (Pearcy, 1977).

II. Respiration of woody organs in various diameters of branches

The respiration activity of non-photosynthetic organs depends not only on the living cells but on the width of annual rings, size of stem, branch, and root diameter (Goodwin and Goddard, 1940; Löhr, 1969; Oohata *et al.,* 1971, 1972; Yoda et al., 1965). The most of carbon dioxide gas released from the bark of tree is produced by the living cells in the cambium, phloem, and other tissues, and a part of them accumulates in vessels and tracheids. Respiration of the cambium and phloem was highest and it reached to 90 to 95% of total respiration in red maple and black ash (Goodwin and Goddard, 1940). On the other hand, in the inner sap wood the living ray and longitudinal parenchyma cells have high rates of respiration, but the number is so small that total respiration is very low. The carbon dioxide gas released from heartwood is very small, and it is probably released from oxidation of organic compounds in dead cells.

The study on the respiration of woody organs proposed here is based on essentially the living cell area or the number of living cells. Although living

cell area in this paper is only defined as cambium and phloem area, the estimation of woody organs is almost accurate because the respiration from other tissues is neglisible as mentioned above.

As shown in Fig. 5, specific cambium and phloem area (camblum and phloem area per transverse section area) was decreased with the increasing transverse section area. When diameter of the branch is X, cambium and phloem area or number of living cells in the cambium and phloem is CPA, and transverse section area is T [$T=\pi(X/2)^2$], specific cambium and phloem area is S=CPA/T, and the relation between S and T are expressed as hyperbolic equation (1),

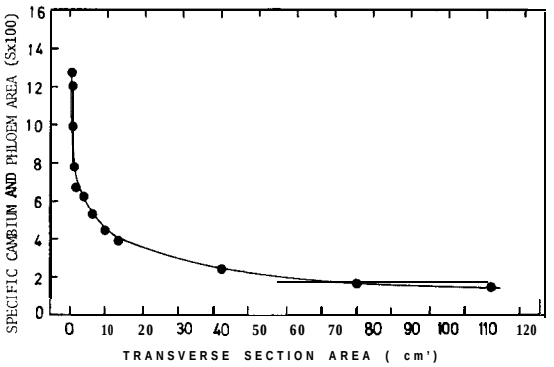

Fig. 5. Relation between the specific cambium and phloem area (S) and the transverse section area (T). Samples were collected from a branch at February.

$$S=\frac{1}{a\sqrt{T}+b} \qquad (1)$$

where a and b are constants, and they are determined by species and season. Rewriting equation (1) as a diameter (X) function, we are able to obtain the equation (2) from equation (1).

$$S=\frac{4}{a\pi X^2+4b} \qquad (2)$$

In Fig. 5, the value of S is very well fitted in equation (1) (R=O. 93, 1 % level) within 0.3 to 12 cm diameter of branches. On the other hand, size of S is directly related with diameter of branch and other woody organs, and it exists a certain minimum and maximum value. In this study, minimum value of S is 1 % in the 12cm diameter of branches. The respiration rate per dry weight of branch was increased by the increasing S in Fig. 6, because S value has a same meaning as most of living cell area per transverse section area. The respiration rates, however, are higher in growing season (April to September) than in non-growing season (October to March) in Fig. 6. As shown in Fig. 6, relation between the respiration rate and the S is well fitted by the exponential curve as following equation (3) ,

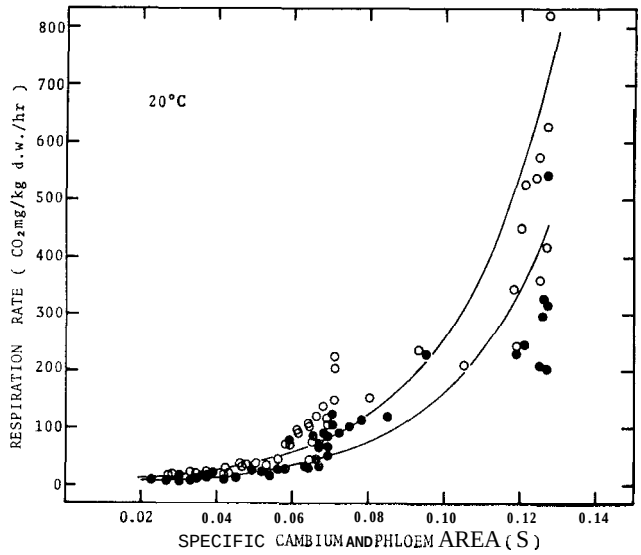

Fig. 6. Relation between the respiration rate of branch and the specific cambium and phloem area. ●, Oct., 1976 to Mar., 1977 and Oct., 1977 to Mar., 1978; ○, Apr. to Sept., 1977 and Apr. to Sept., 1978.

$$R = me^{nS} \tag{3}$$

where m and n are constants, and they are determined by the species and season. In Fig. 6, the differences of respiration rates in growing and non-growing season are considered to be mainly related to the differences of respiratory activities by age of living cells, nutrient concentration of woody organs, activity of cambial zone response of season, translocation of assimilate, and other enzyme factors.

Relation between the respiration rate per unit dry weight of branches and the square diameter is shown in Fig. 7. In it, respiration rate per unit dry weight of woody organs is hyperbolically decreased with increasing square diameter. It is considered to be related to the specific living cell area that is hyperbolically decreased with increasing diameter of branches as above shown in Fig. 2.

On the other hand, we are theoretically able to get a hyperbolic equation (4) from above mentioned equation (2) and (3).

$$R = \exp_e\left[\frac{4n}{a\pi X^2 + 4b} + \ln m\right] \tag{4}$$

So far as two patterns of respiration rate each for growing and non-growing season are distinguished, this equation (4) is well fitted experimental data as related with respiration rates per size of square diameter. According to Yoda et al. (1965, 1968), CO_2 released from the bark of diameter of stem and branch was hyperbolically decreased with increasing diameter and square diameter. Thus we might be able to obtain the more accurate respiration rate in the

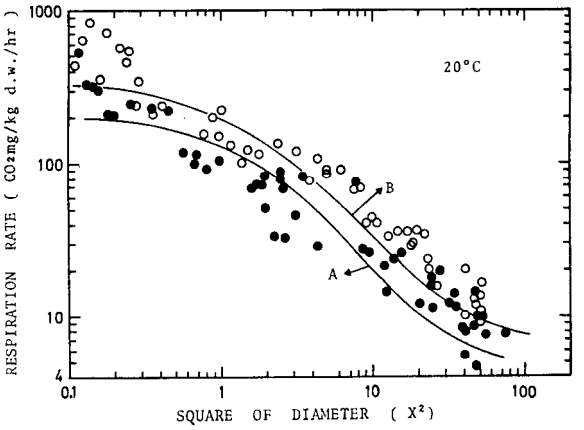

Fig. 7. Relation between respiration rate of branch and square of diameter (X^2). ●, Oct., 1976 to Mar., 1977, Oct., 1977 to Mar., 1978; ○, Apr. to Sept., 1977, Apr. to Sept., 1978. A and B curves are estimated by equation (4).

cutted woody organs such as stems, branches, and roots by the living cell area method. Recently according to Negisi (1978), bark respiration, CO_2 release from the bark of a standing young *Pinus densiflora* tree, showed occasional fluctuation independent of temperature, i.e. an apparent daytime depression or a level lower than expected from the bark temperature. The daytime depression is supposed to be related to the suppressed rate of lateral CO, flux in woody tissues due to the loss by transpiration flow and/or the inhibition of respiration by water deficit.

Respiration process in the big size of woody organs of standing trees may be required to examine the other technical method on the various diameters.

III. Respiration of bud and seasonal change of branch respiration rate

Respiration rate of twigs with bud was the highest in the woody organs of branches. The effects of temperature on the respiration rate of them were shown in Fig. 8. In particular, those effects in non-growing season were different in each season, and it increased considerably in March and April. It is considered that the increase is caused by the movement of nutrient according to emergence of leaf and new shoot and/or activity of bud itself. Respiration rate of bud on the twigs with diameter less than 0.5 cm reached to a half or more of total twigs respiration as shown in Fig. 8.

On the other hand, in spite of distribution of dry weight in single branch composed of a tapering form, the total respiration in the various diameters of single branch distributed in a non-tapering form as shown in Fig. 9. When branches are divided with those diameters in each group in Fig. 9, the tendency may be thought due to the almost same amount of living cells although diameters are quite different. However, estimation of potential respiration released from a great deal of branches in the forest stand can be calculated to use the mean respiration rate of middle diameter of single branch.

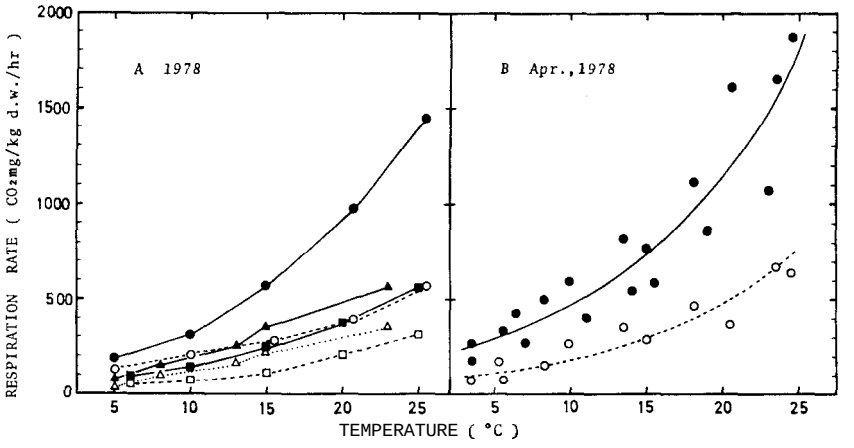

Fig. 8. Effect of temperature on the respiration rate of the attached bud twigs and detached bud twigs less than 0.5cm diameter, respectively. A : ●, Mar.; ▲, Jan.; ❑ , Feb. are attached bud twigs. ○, Mar.; △, Jan.: □, Feb. are detached bud twigs. B: ●, Apr. (attached bud twigs). ○, Apr. (detached bud twigs).

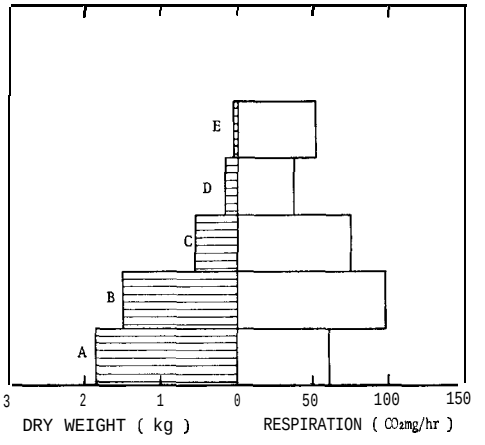

Fig. 9. Vertical distribution of dry weight and respiration in the single branch. A: $4.0cm \leq D < 6.5cm$; B: $2.5cm \leq D < 4.0cm$; C: $1.5cm \leq D < 2.5cm$; D : $0.5cm \leq D < 1.5cm$; E : $D < 0.5cm$ (twigs with bud) ; D : Diameter

As shown in Fig. 10, seasonal changes of the respiration rate did not remarkably differ in all various diameter of branch. In general, respiration rates of the various diameters of branches were higher in growing season as compared with non-growing season in the same temperature. It is clear that respiration rate of woody organs is increased by the increasing activities of living cells. On the point of above view, respiration of twigs with bud less than 0.5 cm diameter is an important factor in estimating the consumption of

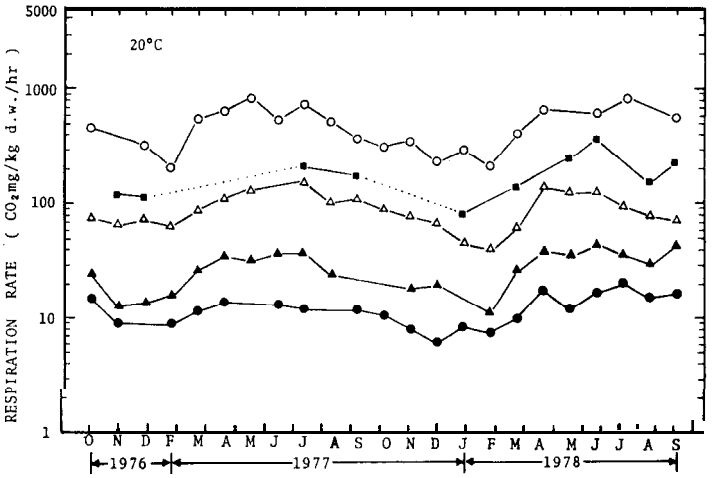

Fig. 10. Seasonal changes of the branch respiration rate (October, 1976 to September, 1978). ○, 0.2cm ≦ D < 0.5cm(detached bud); ■ , 0.5cm ≦ D < 1. Ocm; △, 1. Ocm ≦ D < 3. Ocm; ▲, 3. 0cm ≦ D < 5. Ocm; ●, 5. 0cm ≦ D < 7. Ocm; D: Diameter of branch

woody organs.

ACKNOWLEDGEMENTS

We would like to express our great appreciation to Professor Hiroshi Miyajima and the members of Silviculture Laboratory of Forestry, Faculty of Agriculture, Kyushu University, for their invaluable suggestions and helps in field works.

REFERENCES

Armond, P. A., U. Schreiber, and 0. Björkman 1978 Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata. Plant Physiol., 61: 411-415*

Brown, C. L. 1971 Secondary growth. In "Trees: Structure and Function," ed. by M. Zimmermann and C. L. Brown, Springer-Verlag, Berlin, pp. 67-123

Goodwin, R. H. and D. R. Goddard 1940 The oxygen consumption of isolated woody tissues. *Am. J. Bot.,* 21: 234-237

Han, S. S., and T. Suzaki 1978 Studies on the production and consumption of assimilates of trees III. Effect of dark respiration and photorespiration on gross photosynthesis of Japanese beech (*Fagus crenata* Blume) seedling. *Annual Mtg. Jap. For. Soc., 89:* 197-*200* (in Japanese)

Han, S. S. and T. Suzaki 1979 Studies on the production and consumption of assimilates of trees XII. Respiration for growth and maintenance, and CO, Balance on the Japanese beech (*Fagus crenata* Blume) and oak (*Quercus acutissima* Carruth.) seedlings. *Annual Mtg. Jap. For. Soc., 90:* in press (in Japanese)

Kira, T. and T. Shidei 1967 Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. *Jap. J. Ecol.*, 17: 70-87

Lange, 0. L., E. D. Schulze, M. Evenari, L. Kappen and N. Buschbom 1974 The temperature-related photosynthetic capacity of plants under desert conditions I. Seasonal changes of the photosynthetic response to temperature. *Oecologia*, 17 : 97-110

Larcher, W. 1969 The effects of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica*, 3: 167-198

Löhr, E. 1969 Respirationsintensität in Stämmen, Zweigen und Blättern von Laubbäumen im tropischen Regenwald und in temperierten Wäldern. *Physiol. Plant., 22: 86-93*

Maruyama, K. and M. Yamada 1968 Ecological studies on beech forest 16. Seasonal course on apparent photosynthesis and respiration rate in detached leaves of Japanese beech at different altitudes. *Bull. Niigata Univ. For., 3: 17-26* (in Japanese)

Mooney, H. A. and M. West 1964 Photosynthetic acclimation of plants of diverse origin. *Amer. J. Bot.. 51: 825-827*

Mooney, H. A., 0. Björkman, and G. J. Collatz 1978 Photosynthetic acclimation to temperature in the desert shrub, *Larrea* diuaricata. *Plant Physiol.. 61: 406-410*

Negisi, K. 1966 Photosynthesis, respiration and growth in l-year-old seedlings of *Pinus densiflora, Criptomeria japonica* and *Chamaecyparis obtusa. Bull. Tokyo Univ. For., 62* : l-115

Negisi, K. 1978 Daytime depression in bark respiration and radial shrinkage in stem of a standing young *Pinus densiflora* tree. *J. Jap. For. Soc., 60: 380-382*

Neilson, R. E., M. M. Ludlow and P. G. Jarvis 1972 Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.) II. Response to temperature. *J. Appl. Ecol., 9: 721-745*

Oohata, S. and T. Shidei 1972 Seasonal changes in respiratory rate of stems and their growth. *Bull. Kyoto Univ. For..* 43: 63-72

Oohata, S., T. Yamakura. H. Saito and T. Shidei 1971 A study on the vertical distribution of respiratory activity of a 40-year-old stand of *Chamaecyparis obtusa. Bull. Kyoto Univ. For., 42: 103-116*

Pearcy. R. W. 1976 Temperature responses of growth and photosynthetic CO_2 exchange rates *in* coastal and desert races of *Atriplex lentiformis. Oecologia, 26: 245-255*

Pearcy. R. W. 1977 Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriblex lentiformis* (Torr.) Wats. *Plant Physiol.. 59: 795-799*

Raschke, K. 1970 temperature dependence of CO, assimilation and stomata1 aperture in leaf sections of Zea mays. *Planta, 91: 336-363*

Schulze. E. D. 1970 Der CO,-Gaswechsel der Buche (*Fagus silvatica* L.) in Abhängigkeit von den Klimafaktoren im Fleiland. Flora, 159: 177-232

Yoda, K., T. Nakai and H. Sato 1968 Estimation of the total amount of respiration of forest communities. *JIBP-PT-F, 42:* 81–93 (in Japanese)

Yoda. K., K. Shinozaki and H. Ogawa 1965 Estimation of the total amount of respiration in woody organs of trees and forest communities. *J. Biol.* Osaka *City Univ.,* 16: 15-26