Photosynthesis, Respiration and Growth in 1-year-old Seedlings of Pinus densiflora, Cryptomeria japonica and Chamaecyparis obtusa

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CONTENTS

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INTRODUCTION

Forest tree species differ from each other in their behavior to environmental factors, on which many informations have been accumulated, especially relating to important forest tree species. Most of these informations are based on observations of growth under various conditions. Since the growth measured in the open represents an integration of interaction among all environmental factors and plant processes extending back a certain long time, it is difficult to separate complicated effects of various factors such as light, temperature and soil moisture. Studies projecting a better understanding of the reaction of physiological processes to environmental conditions should help to explain the difference in character of species in ecological relations and to provide a good grounding for developing of silvicultural practice. Of recent years, experimental works along this line have been made extensively.

In the present paper are studied the relations of photosynthetic rate to important environmental factors. One-year-old seedlings of *Pinus densiflora* (Akamatu), *Cryptomeria japonica* (Sugi) and *Chamaecyparis obtusa* (Hinoki) which are among the most important forest tree species in Japan, are chosen as a material, and the differences in photosynthetic response are compared with the already known characters of these species.

Effects of external factors on photosynthetic rate were treated in plant physiology as the first step to explain internal processes of photosynthesis, and have been studied in plant ecology from various aspects, sometimes in relation to the plant growth under peculiar climatic conditions, and recently, in connection with the dry matter production in plants or plant communities. Thus there exists a considerable literature on various plants, but comparatively a little work has been done on the forest tree species. And these results have been useful for us to look over the growth of forest trees to a certain degree. In Japan, as to this problem, the study interesting students of silviculture has begun after World War II. Therefore, the data on photosynthesis of the important forest trees are not sufficient to characterize each of the species.

The plan of this report falls into three major parts and seven chapters. In the first four chapters, the differences between species in photosynthetic responses to light, temperature and soil moisture are studied under the comparatively controlled conditions. In succeeding Chapter V, by the use of relations in the former chapters are estimated the seasonal variations in photosynthetic rate under the nursery conditions, and the causes of seasonal change are studied in each species. In the last two chapters, after the measurement of respiration, the dry matter production of the seedling grown individually in the nursery is computed and compared with the dry weight increment determined directly. And the causes responsible for the productivity difference are discussed.

Seedlings may be sensitive to environmental factors and easy to handle as compared with older one. For this reason and to simplify the experimental conditions, an individual seedling is chosen as a material in this work. Therefore, the results obtained here may be available for the seedlings grown in nursery where they are treated as an isolated individual. But to the forest trees, the application of findings is limited, because (1) it may be questioned whether seedlings and mature trees behave in the same manner and (2) in the forest the behavior of a tree is greatly influenced by the neighboring trees. It is desirable that further studies on older trees not only at individual level but also at community level would be made in connection with recent works on dry matter production in forests.

In this work, only light, temperature and soil moisture affecting for a relatively short term are taken up as important environmental factors governing photosynthesis. Mineral nutrition and also various environmental factors acting for a longer term may be of interest in an explanation for the difference in character of species, on which would need further investigations.

I wish to express my thanks to Professor Dr. Taisitiroo SATOO, Director of Institute of Silviculture, Faculty of Agriculture, University of Tokyo, for suggesting this study as well as for constant guidance in the course of the work. Thanks are also due to Professor Emeritus Dr. Kentaro NAKAMURA and Professor Dr. Masataka OHMASA, ex-directors of the institute, for their invaluable suggestions and encouragements.

The experiment reported herein was carried out for the period 1959 to 1962 at Tokyo University Forest Experiment Station, Tanasi, Tokyo. I am indebted to Professor Masazi SENDA, Director of Research Branch, Tokyo University Forests, for permitting me to make the measurements in the station, and I take this opportunity to acknowledging the helps and encouragements received from my colleagues, particularly from Mr. Kitokuroo YAGI throughout the measuring.

CHAPTER I. DIURNAL VARIATIONS IN RATE OF PHOTOSYNTHESIS*

To obtain the daily course of photosynthesis, the rates of CO_2-uptake are measured in the field. These measurements have two objects, (1) to make clear diurnal variations under various weather conditions at different seasons, and (2) to present data available for the studies of photosynthetic response to light intensity under field conditions.

I) Material and Method

1. Material

One-year-old potgrown seedlings of *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa* had been used in the following experiments. In the fall of the previous year to the experiment, the seedlings were transplanted from a nursery to pots

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individually and had been grown outdoors until measurings. After transplanting the pots were buried to their rims in soil to avoid extreme changes in soil temperature. Water was given periodically so that soil moisture had been readily available for the seedlings over the entire growing season.

The soil in the pot was A-layer of a nursery in Tokyo University Forest Experiment Station, Tanasi, Tokyo, which was composed of silty loam of volcanic ash origin, having a field capacity of 64 percent and a permanent wilting percentage of 33.5 percent. The pots were unglazed having three different sizes, 15, 22 and 25 cm in diameter respectively. For the earlier period of experiment, the seedlings grown in smaller pot, and for the later one those in larger one were used.

2. Method of measuring CO_2-exchange

The rate of photosynthesis was estimated by measuring the rate of change in CO_2 concentration of the air before and after passing over the seedling in an open system consisting of chambers, an infrared gas analyzer with sampling units, a pump and plastic tubing.

1) Gas analyzer

Only a brief explanation of the apparatus is presented here, since the details were given in an earlier report (SATOO, NEGISI & YAMAGUCHI 1959). In figure 1, an outline of the system is presented and in figure 2 a photograph of the apparatus is shown. The air was sampled from three lines I, II and III. Line I and II were connected respectively with an assimilation chamber, in which an individual seedling was enclosed. Line III was joined to an empty chamber to determine CO_2 concentration of the outdoor air.

A part of the air flowing through the assimilation chamber (A) was used for the sample of analysis and the remainder flowed to a by-pass through a flow meter (C′). The flowing air sample was dried in a tube (B) containing silica gel. To reduce an effect of buffer action of silica gel on CO_2 (TRANQUILLINI 1952; PARKER 1953; BOSIAN 1955), a small quantity, about 20cm^3, of the agent was used here. Then the desiccated air sample reached the sampling unit, by which was controlled further flow to a sample cell (H) in the pick-up of analyzer (Beckman Liston-Becker infrared gas analyzer Model 15A). The sampling unit was composed of electric valves (E, F) and a selecter (G, Beckman automatic stream selecter Model 272).

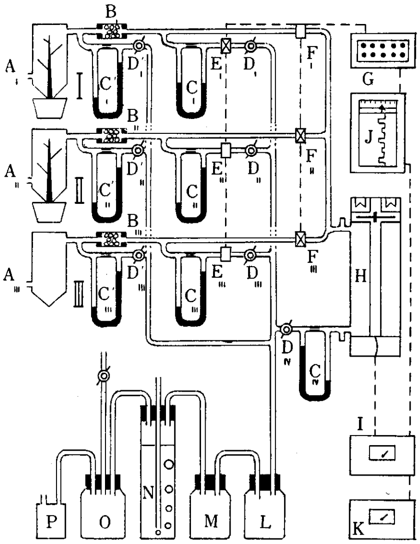

Fig. 1. Outline of the system for estimating CO_2-exchange by measuring CO_2 concentration in three open air lines alternately. For explanation of letters see text.

At intervals of 2.5 minutes, each sampling line was opened alternately to the analyzer in the following order; line I–III–II–III–I–III……

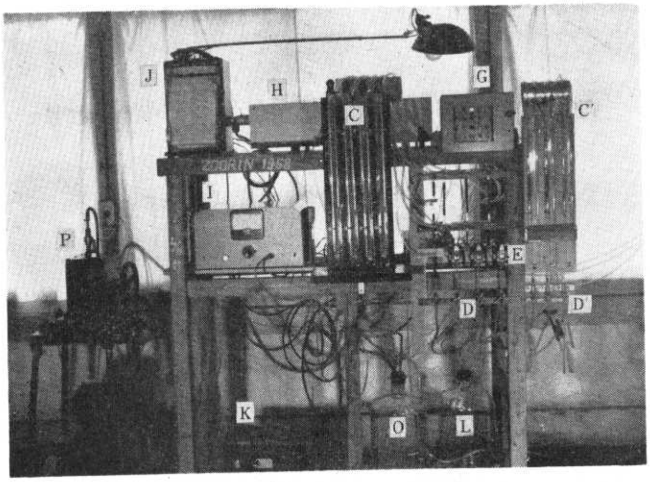

Fig. 2. Apparatus for measuring CO_2-exchange. Lettering as in figure 1.

Since the analysis of control air was made every 2.5 minutes, line I and II each was connected with the analyzer for 2.5 minutes and blocked from it for 7.5 minutes. The two electric valves, E and F in each line were coupled, when the one was opening the other was closing, and the air sample in the lines blocking from the analyzer, streamed into the by-pass to avoid CO_2 accumulation in the chamber and piping. In figure 1, line I connects with the analyzer, and crosses on the electric valves (E, F) mean shutting of them.

Velocity of air flow in each line was measured by the flow meters (C, C′) consisting of a U-tube and a capillary tube, and was adjusted by the two-way stop cocks (D, D′) in the same line. C_{IV} and D_{IV} served as controller of flow in the line connecting with the analyzer. To decrease fluctuations in the air stream, three glass bottles, a capacity of 10 litres each (L, M, O), and a water column, 120 cm high (N) were inserted in the line. Velocity of air flow in the lines conducting air sample was maintained at a constant rate of 18 litres per hour. Air flow in the entire system was made by the use of a rotary pump (P) having a capacity of 35 litres per minute.

Changes in CO_2 concentration detected in the sample cell (H) were amplified by an amplifier (I) and recorded in a recorder (J, Esterline-Angus DC 0–5 mA). Fluctuations of voltage in electric current supplied to the gas analyzer and the sampling units, were regulated by a stabilizer (K).

2) Assimilation chamber

Structure

The top of the seedling was enclosed in an assimilation chamber shown in figure 3. The structure of the chamber, which was detailed in a previous paper (NEGISI 1961), is given in figure 4.

The main part of chamber consisted of two transparent polystyrene plastic containers, the inner cylinder (A) and the outer one (B). The two cylinders were sustained by each other using a rubber packing (C) and two glass tubes, an inlet (a_1) and an outlet (a_2) of the air. To prevent the chamber from a rise of temperature, a space between the two cylinders was served as a water jacket having an inlet (b_1) and an outlet (b_2) for streaming cold water.

In using, the chamber was suspended by a string (E) and insertion of a seedling

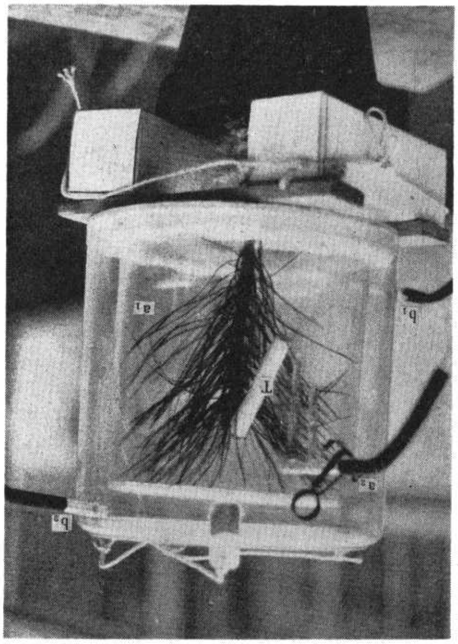

Fig. 3. Assimilation chamber enclosing 1-year-old seedling of *Pinus densiflora*. Lettering as in figure 4. **T** is a shield for radiation enveloping hot junction of the thermocouple.

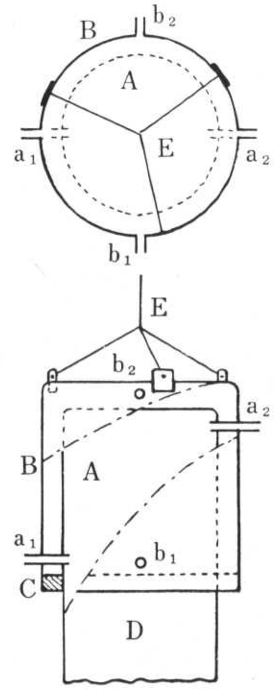

Fig. 4. Cross (upper) and longitudinal (lower) section of the assimilation chamber. For explanation of letters see text.

and a junction of thermocouple was made. By the use of thin vinyl film (D) of the lower end of the inner cylinder and a small quantity of kneaded rubber, the axis was wrapped up tightly together with the lead wires of the thermocouple.

Regulation of conditions

In the case of the measurement in the open, a question will arise as to climatic conditions in the assimilation chamber (EGLE 1960a). Owing to greenhouse effect and insufficient ventilation, temperature, humidity and CO_2 concentration in the chamber may possibly differ from those in the open, through which the photosynthetic rate will be affected.

Air temperature. It is well-known that on sunny days, a plant enclosed in the chamber without cooling is overheated and shows a remarkable depression in photosynthetic rate (PISEK & TRANQUILLINI 1954; TRANQUILLINI 1954; BOSIAN 1955; NEGISI, YAMAGUCHI, YAGI & SATOO 1961). To obtain reliable data in the field, it is necessary to protect the plant from an extreme rise of temperature. For this purpose the following means have been taken: (1) the use of a filter of optical glass (TRANQUILLINI 1954, 1955, 1957, 1959a) or water layer (NEGISI, YAMAGUCHI, YAGI & SATOO 1961) to diminish an effect of infrared radiation falling upon the chamber; (2) the use of cold water or air to make cool the chamber (BOSIAN 1955; EGLE 1960a).

The assimilation chamber used in this work was enveloped in the water jacket acting as a filter and a cooler. For the period spring to fall, tap water streaming in the jacket served for cooling. In winter, a circulation of ice water was made by the use of a small gear pump.

Cooling effect of the water jacket is evident under clear and hot weather conditions. Figure 5 is a record obtained on September 19, 1959, a sunny and hot day, and shows that it may be possible to keep the air temperature in the chamber at the same level as in the open. Daily courses of air temperature inside and outside the chamber through the four seasons are shown in figure 6, which brings out the fact that the action of water jacket appears ineffective when the outdoor temperature is relatively low as in the cases of winter or of morning in growing season. The inefficiency of water jacket in these cases may be attributed to the following causes: (1) a depression in cooling capacity by the use of relatively warm water in comparison with outdoor temperature; (2) a limited rate of air flow in the chamber in proportion to a low level of CO_2-uptake.

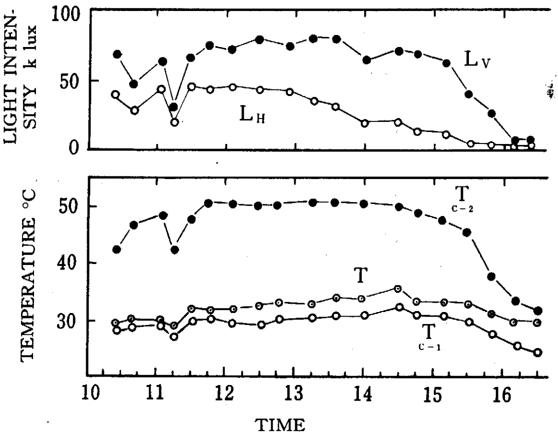

Fig. 5. Effect of a water jacket on the temperature in assimilation chamber observed on September 19, 1959. **L_V**: normal light intensity measured with a photocell placed at right angles with direct solar rays, **L_H**: horizontal light intensity measured with a photocell placed horizontally, **T_{c-1}**: air temperature in the assimilation chamber enveloped in a water jacket, **T_{c-2}**: air temperature in the assimilation chamber without a water jacket, **T**: air temperature in the open.

Air humidity. A higher air humidity in the chamber is caused by transpiration of the enclosed plant and a limited flow of the air carrying moisture. On sunny days in growing season, when the conditions are favorable for transpiration, water vapor in the chamber reaches easily to a full saturation and condenses into drops on the inside wall of the chamber.

The effects of humidity on photosynthesis have been discussed in many studies made under field conditions. BOSIAN (1960) worked on vine and *Pelargonium* with the chambers of three different conditions; uncontrolled, controlled temperature, and controlled both temperature and humidity. He pointed out experimentally that humidity has an influence on the daily course of photosynthesis. TRANQUILLINI (1963) studied the relation of moisture content in the air to photosynthetic rate of conifers, using a wind tunnel as an assimilation chamber. His work was combined with various soil moisture conditions and showed clearly that except for the spruce grown on the relatively moist soil, the photosynthetic rate decreased with increasing saturation deficit in the air at each level of soil moisture. It seems that the humidity in the chamber affects photosynthesis in the following ways: (1) the change in water conditions of the plant in

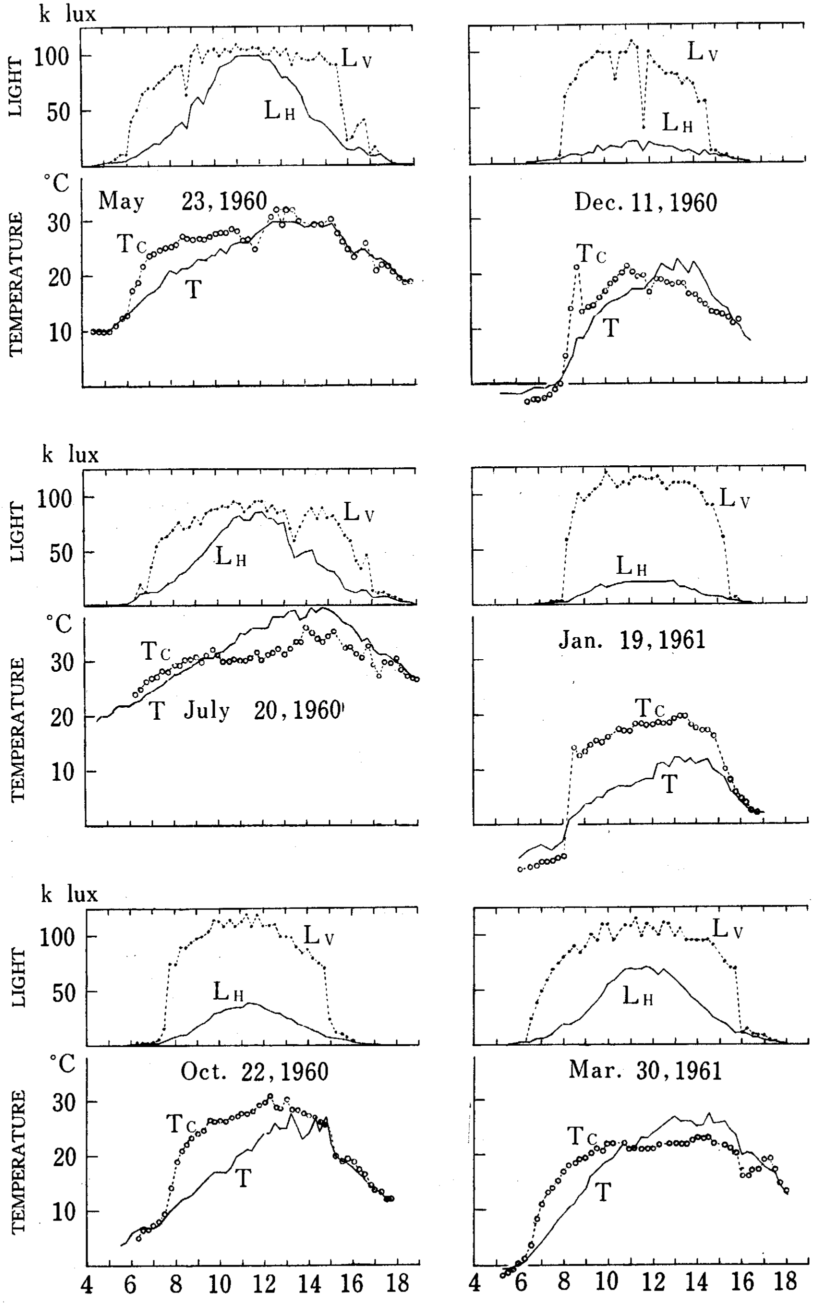

Fig. 6. Difference between the assimilation chamber and the open in daily course of air temperature at different seasons. **L_V**: normal light intensity, **L_H**: horizontal light intensity, **T_c**: air temperature in the assimilation chamber, **T**: air temperature in the open.

connection with the opening of stomata; (2) the decrease in light intensity in the chamber due to condensed water; (3) the error in estimated value caused by buffer action of the condensed water on CO_2.

Although the effect of humidity was expected, the regulation of moisture content of the air was not made in this work, because a complicated equipment was demanded for the control (Bosian 1959, 1960; Tranquillini 1963). The photosynthetic rates obtained here, therefore, may be values expected under excessive air moisture conditions and different possibly from those in the open in some degree. To prevent the chamber from a depression of light intensity, the condensed water on the inside wall was wiped away occasionally with a small rubber tube wrapping an iron rod, which was enclosed in the chamber and drived by a magnet.

CO_2 concentration. Since the photosynthetic rate is closely related with the CO_2 content of the air, an ample supply of air for the chamber is desirable. In this work, air supply to each chamber was adjusted within the range from 18 to 240 litres per hour according to the rate of CO_2-uptake, by which the depletion of CO_2 concentration caused by photosynthesis did not exceed 20 percent of the original value.

As mentioned above, the assimilation chamber used here has a weak point in regulation of climatic factors. But as a whole, this weakness is supposed to be not serious in evaluation of the results. Simple structure and low cost of this chamber are favorable for rough handlings in the field and for uses of the various dimensions fitting for the size of the seedling. Since a complicated equipment is required for a perfect air-conditioning of the chamber, it is preferable in the field work in future that the determination will be made under a higher rate of air supply by the use of a very sensitive gas analyzer such as "Super URAS" (Tranquillini 1964a, b).

3. Method of measuring climatic factors

1) Light and radiation intensity

Intensity of total day light was measured with a selenium photometer (Toshiba luxmeter Model 5). Measurings were made in the following two ways: (1) placing a photocell at right angles with direct solar rays; (2) placing a photocell horizontally. The value in the former case is "normal illumination". But that in the latter one differs from "horizontal illumination" calculated by application of the cosine law to the normal illumination, because the cosine law can not be applied to the barrier-layer type of photocell as used here. In this paper, the former values are expressed in the word "normal light intensity" and the latter ones in "horizontal light intensity".

Horizontal radiation intensity had been recorded with Robitzsh's actinograph, which was checked for accuracy with Gorczynski's pyrheliometer occasionally.

2) Air temperature

Air temperatures inside and outside the assimilation chamber were measured with a Cu-constantan thermocouple. To shield from radiation, the end of hot junction was enveloped in a cylinder of white paper, 7 cm long by 1 cm in diameter as shown in figure

3. Open air temperatures obtained with this thermocouple were close upon the values measured with Assmann's aspiration psychrometer.

For the study of the relation between temperature and photosynthesis, the temperature of the photosynthetic part (leaf temperature) is more applicable than that of the surrounding air. But, in cases in which the mean leaf temperature of the entire photosynthetic parts is measured in the field, it is difficult to protect an element of thermometer from the radiation, because the way of solar rays varies with the change of solar elevation in a day.

TRANQUILLINI devised methods for measuring mean temperature of needles with a platinum resistance thermometer, which were applied to the studies dealing with photosynthesis of *Pinus cembra* in the field (TRANQUILLINI 1954, 1955, 1957; TRANQUILLINI & TURNER 1961). We attempted to measure the temperature of needles of *Pinus densiflora* using his earlier type of thermometer (TRANQUILLINI 1955), a long platinous wire twined round the top of the seedling, and obtained a good result. But in this work, the sample seedlings were renewed in every time of determination, and it was too laborious for the measuring in a brief period to make the twining of a wire without disturbing natural leaf arrangement and without changing constant value of the wire.

4. Measurement

1) Time lag of CO_2 analysis

The air flowing in the assimilation chamber reached through the vinyl pipe to the gas analyzer in the laboratory. The distance between chamber and analyzer was about 20 m, and the time lag varying with the rate of air flow happened to the value of CO_2 analysis. Figure 7 shows that the time lag reduces with increasing velocity of air flow. In the arrangement of data were made corrections of the time lag.

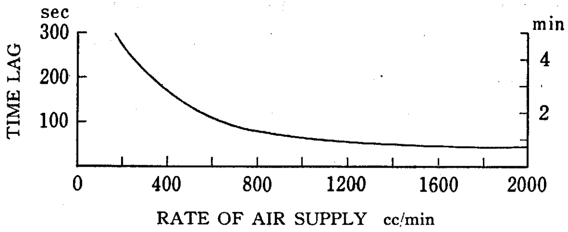

Fig. 7. Time lag in observed value of photosynthesis in relation to rate of air supply.

2) Standard procedure for determination

During the few days before the determination, an irrigation was made adequately and the level of soil moisture in the pot was held nearly at the field capacity during the measurement, by which the rate of photosynthesis may be able to reach the maximum. In the evening of a day arbitrary chosen, the top of a seedling was inserted into the chamber. A run of determination of CO_2-exchange started immediately and continued until sunset of the following day to obtain a whole daily course of photosynthesis. For the period sunrise to sunset, light intensity and air temperature had been measured at intervals of 15 minutes. The rate of air supply was adjusted occasionally.

In addition to the runs on the whole day were made the runs on a brief period. On the seedling used in the run in cloudy weather, a determination on a clear day was added to estimate the maximum rate of photosynthesis. After the completion of each run, the dry weight of the seedling was measured by oven-drying.

The determinations were made on a day arbitrary chosen from among the different days for the period April, 1960 to April, 1961. Two seedlings, one from each of the different species usually, were run simultaneously. In these determinations 37 seedlings of *Pinus densiflora,* 38 of *Cryptomeria japonica* and 32 of *Chamaecyparis obtusa* were observed, and the daily courses of photosynthesis were obtained in the following numbers; 42 in *P. densiflora,* 42 in *Cr. japonica* and 24 in *Ch. obtusa* for the period sunrise to sunset, and about 10 in each of the species for shorter periods.

II) Results and Discussion

Comparisons of the data at different seasons indicate that the relation of daily course of photosynthesis to environmental factors differs with different seasons. As will be described later in warm growing season, most of the diurnal changes in

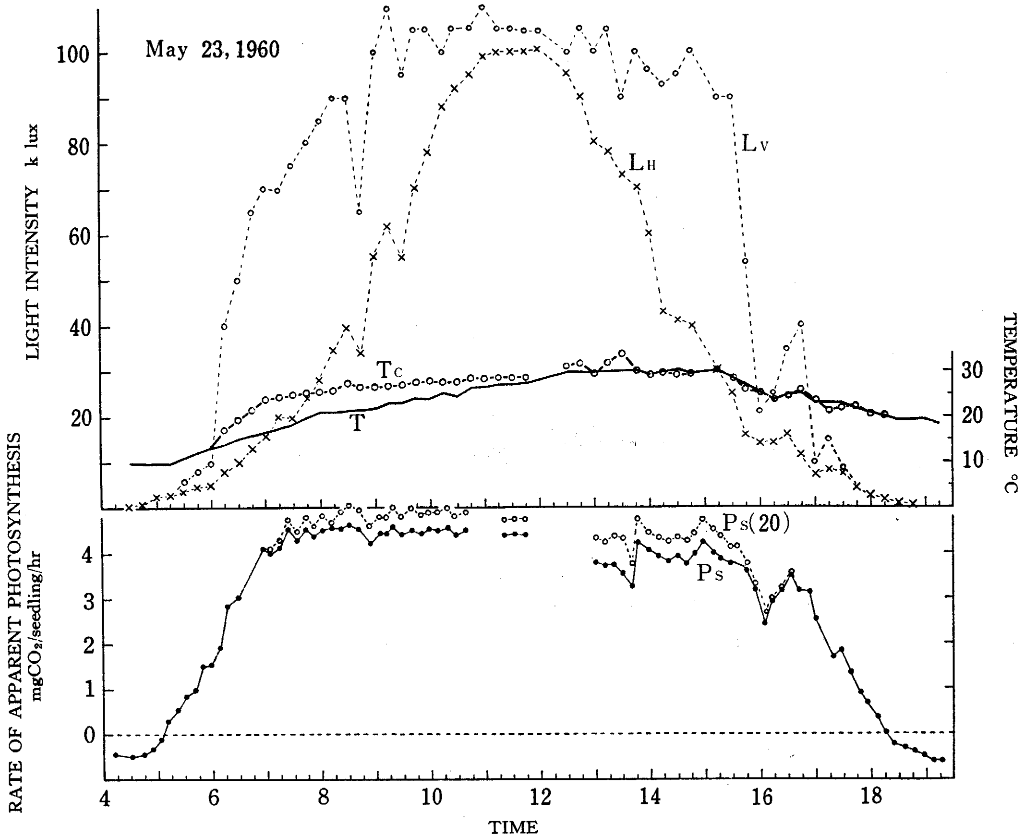

Fig. 8. Daily course of photosynthesis in *Pinus densiflora* on a clear day (May 23, 1960). **Lv**: normal light intensity, **LH**: horizontal light intensity, **Tc**: air temperature in the assimilation chamber, **T**: air temperature in the open, **Ps**: rate of apparent photosynthesis, **Ps(20)**: rate of apparent photosynthesis converted into at temperature of 20℃.

photosynthesis appear to be fairly well correlated with a few external factors. On the other hand in winter, the effects of internal factors overlap on those of external factors, through which a simple relationship in growing season may be disturbed.

1. Daily course of summer type

1) Course on a clear or a cloudy day

Abundant literature has accumulated on the diurnal variations in photosynthetic rate, in which were included papers relating *Cr. japonica* (TAKAHARA 1954; NEGISI, YAMAGUCHI, YAGI & SATOO 1961) and *Ch. obtusa* (TAKAHARA 1954). The daily courses obtained here are similar in trend to the above-mentioned literature.

For example, the daily courses of *P. densiflora* in different weathers are given in the following graphs; in figure 8 on a clear day, in figure 9 on a sunny day with a number of cloud-drifts, and in figure 10 on a cloudy day. On a bright, clear and warm day a flat-topped diurnal curve of photosynthesis is observed as shown in figure 8. The photosynthesis starts at sunrise and increases rapidly with increasing light intensity and arrives at a level near the daily maximum. Until the early evening, the rate con-

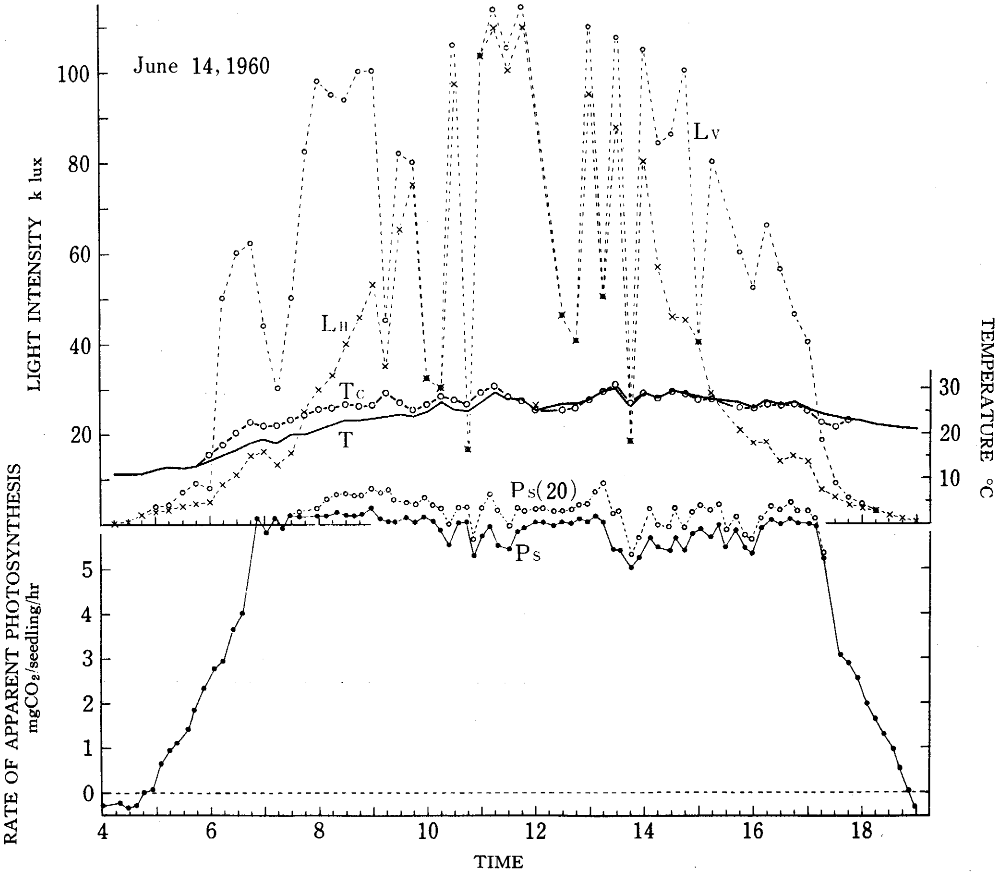

Fig. 9. Daily course of photosynthesis in *Pinus densiflora* on a sunny day with a number of cloud-drifts (June 14, 1960). Lettering as in figure 8.

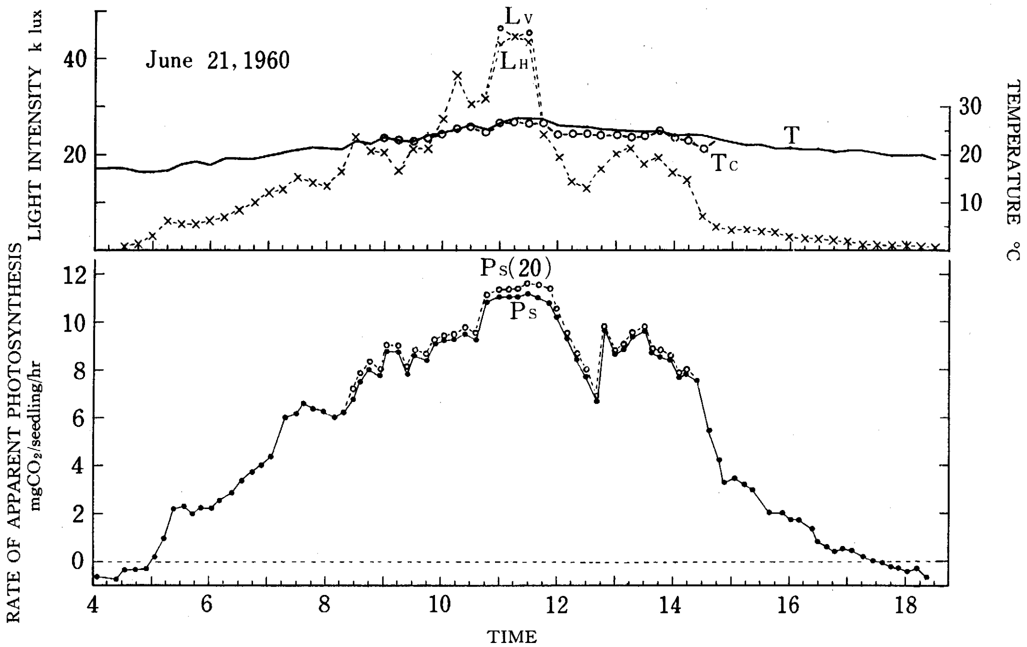

Fig. 10. Daily course of photosynthesis in *Pinus densiflora* on a cloudy day (June 21, 1960). Lettering as in figure 8.

tinues at the same level which is followed by the rapid decrease due to depression in light intensity and the cessation of photosynthesis at sunnset. On a cloudy day, the light intensity remains at a lower level below saturation, and the daily course of photosynthesis fluctuates with the change in light intensity all day long as shown in figure 10.

2) Midday drop

It is well-known that the rate of photosynthesis often reduces in varying amount during the middle of sunny day. Many reports discussed and reviewed the cause of midday inhibition of photosynthesis.

In order to see an appearance of midday depression, the data obtained on sunny days were studied. Examples of daily course of photosynthesis on a bright and sunny day, four days in each species, are shown in figure 11. Typical bimodal curves are not found, but sometimes the depressions to varying extent appear such as on June 7, July 20 and September 23 in *Ch. obtusa.* Among the species differs the midday drop in frequency of occurence and in extent of decrease; seldom and slight in *P. densiflora,* not often and moderate in *Cr. japonica,* and often and marked in *Ch. obtusa.*

Bosian (1960) worked using his perfect air-conditioning assimilation chamber and found that the midday drop of photosynthesis was attributed mainly to unnatural conditions in the chamber, i.e. overheating of the plant sample and excessive air humidity. Air temperature in the chamber used in this work fluctuated as mentioned above. To remove the effect of temperature, the course of photosynthesis observed under varying temperature was changed into a curve at a constant temperature 20℃ by the use of relation between temperature and photosynthetic rate in Chapter III.

Although the extent of the depression is decreased through the corrections of temperature as shown in figure 11, the remaining midday drops suggest an existence of influence of other factors. By the use of relation between CO_2 content and photo-

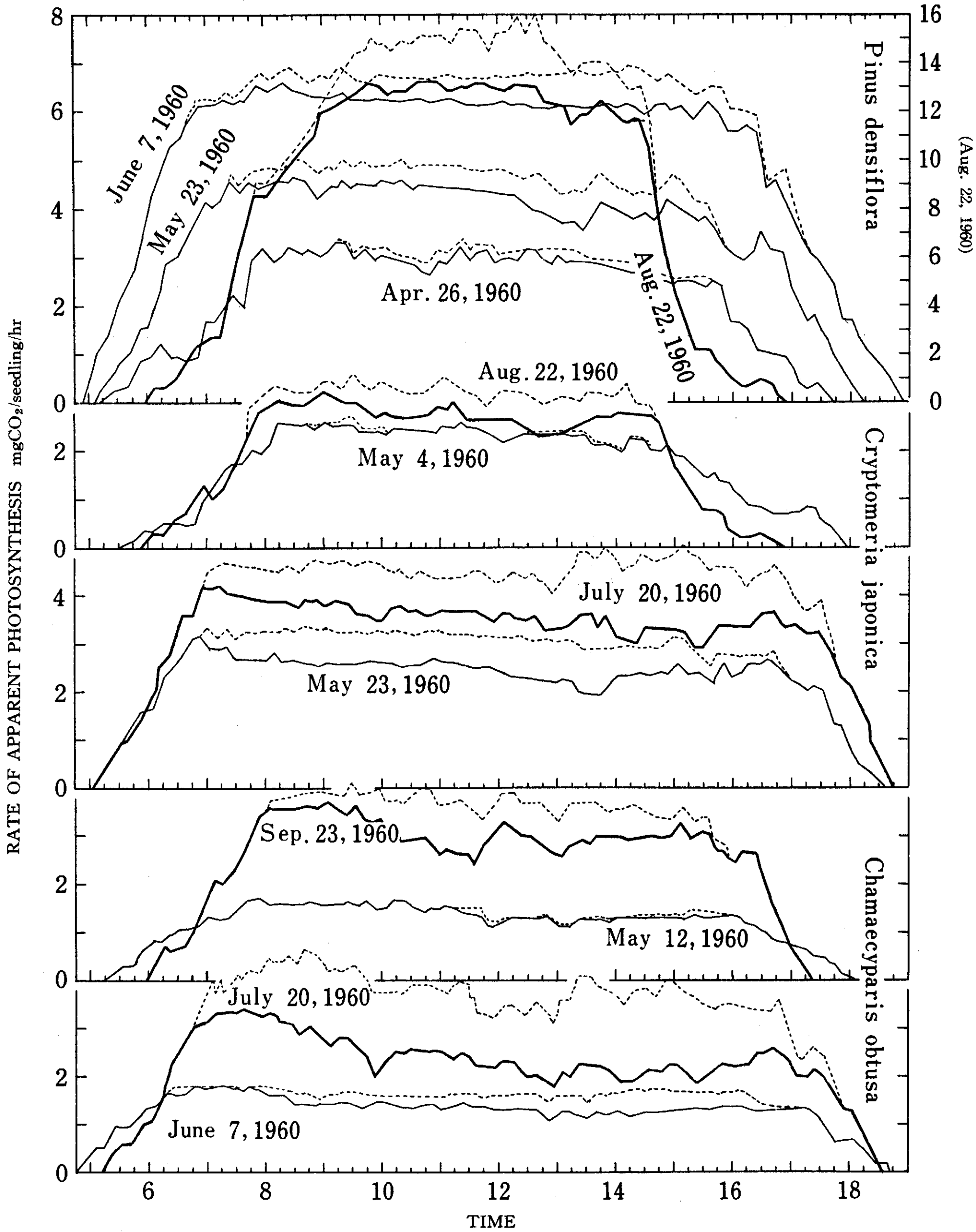

Fig. 11. Daily courses of photosynthesis on bright and sunny days drawn from observed rates (solid line) and converted ones into at 20℃ (broken line).

synthetic rate (NEGISI & SATOO 1961b), the effect of change in CO_2 concentration was studied with the same way as temperature. But the influence of CO_2 concentration was not obvious. Further discussions on other factors, e.g. water deficit, closure of stomata, accumulation of photosynthate and photo-oxidation of enzymes are not made in this paper.

2. Daily course of winter type

1) Characteristic of winter type

Examples of the daily course of photosynthetic rate of *P. densiflora* and *Cr. japonica* obtained on a bright and sunny day in winter are given in figures 12 to 15. As shown in the figures, the daily march in winter differs from that in growing season in the following two points: (1) an appearance of remarkable midday depression, e.g. on December 20, 1960 in *P. densiflora* in figure 12; (2) a relatively low photosynthetic rate in the morning. During winter months appear these characters to varying extent in each species.

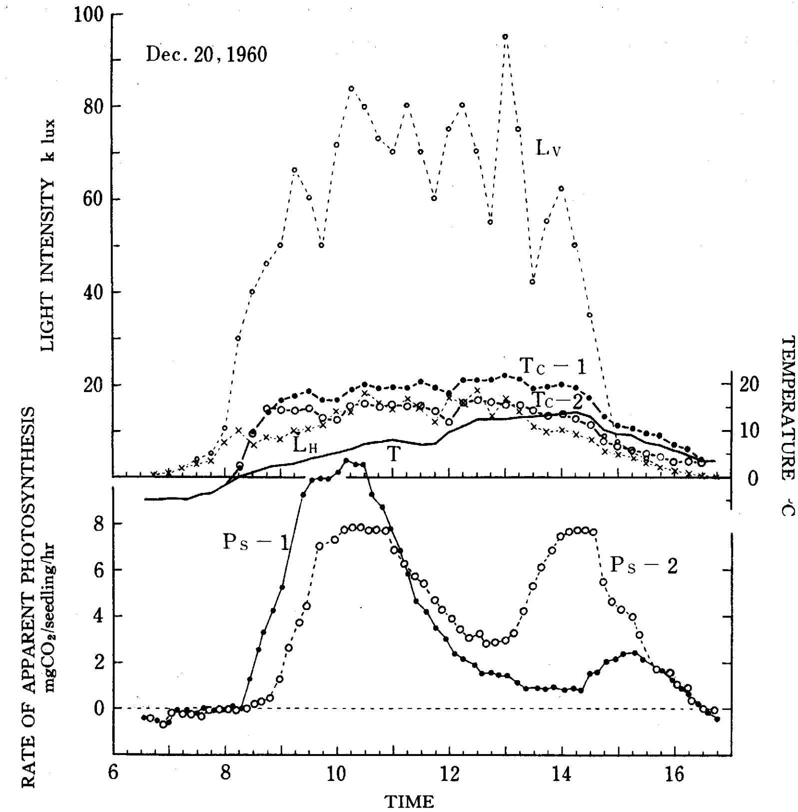

Fig. 12. Daily course of photosynthesis in *Pinus densiflora* on a clear day in winter (December 20, 1960). **L_V**: normal light intensity, **L_H**: horizontal light intensity, **$T_{c\text{-}1}$**: air temperature in the assimilation chamber cooled with flowing tap water, **$T_{c\text{-}2}$**: air temperature in the assimilation chamber cooled with circulating ice water, **T**: air temperature in the open, **$P_{s\text{-}1}$**: rate of apparent photosynthesis of the seedling in the chamber cooled with flowing tap water, **$P_{s\text{-}2}$**: rate of apparent photosynthesis of the seedling in the chamber cooled with circulating ice water.

2) Midday drop

In the above discussion on the data obtained in growing season, an excessive rising of temperature which depresses the rate of apparent photosynthesis directly through inhibiting photosynthetic process and indirectly through stimulating respiration, was mentioned as a cause of the midday decrease. The researches on evergreen trees at different seasons (Kusumoto 1957a; Nomoto, Kasanaga & Monsi 1959; Larcher 1961a) indicated that the relation between temperature and photosynthetic rate in winter differed from that in growing season. The maximum, optimum and minimum temperature of photosynthesis became lower in winter. The similar seasonal difference was observed in the three species studied here (Negisi & Satoo 1961a). Hence, it seems that a rise of temperature which will affect photosynthesis to a slight degree in growing season, possibly has a remarkable effect in winter. This possibility suggests that a rising of temperature is a cause of the midday depression represented with a typical bimodal curve in figure 12. Also the effect of temperature is guessed from the fact that the extent of depression is larger on the seedling met with a higher rise of temperature through an enclosing in the chamber cooled with tap water as may be seen in figure 12.

A distinct midday drop does not appear in midwinter. During this period as

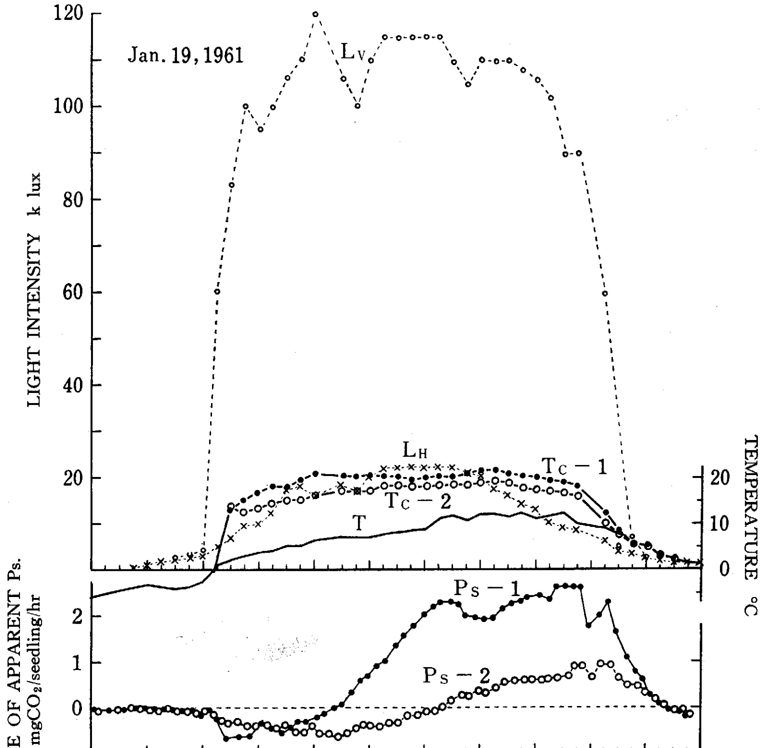

Fig. 13. Daily course of photosynthesis in *Pinus densiflora* on a clear day in winter (January 19, 1961). Lettering as in figure 12.

will be described below, the recovering from depressed photosynthetic capacity is promoted with a high temperature, through which may be diminished the possibility bringing a marked midday drop.

3) Recovery of photosynthetic capacity

Reports dealing with seasonal changes of photosynthesis of evergreen conifers indicated that a frost caused a greater decrease in photosynthetic capacity. When the plant samples were removed to warmer conditions, the gradual recoveries from depressed photosynthetic level were observed in several conifers, e.g. *Picea excelsa* (ZELLER 1951), *Picea excelsa* and *Pinus cembra* (PISEK & WINKLER 1958), *Pinus sylvestris* (BOURDEAU 1959), *Picea excelsa* (WEISE 1961), *Picea excelsa* and *Pseudotsuga taxifolia* (WEISE & POLSTER 1962). These findings support the possibility that an inactivity and a following increase in photosynthesis in the morning, as shown in figures 13 to 15, correspond to (1) the depression of photosynthetic capacity caused by frost in the previous night and (2) the gradual recovery of it due to higher temperatures after sunrise.

To determine how rapidly the photosynthetic capacity would recover under warmer conditions, 1-year-old seedlings suffering from a cold in the field were carried into the

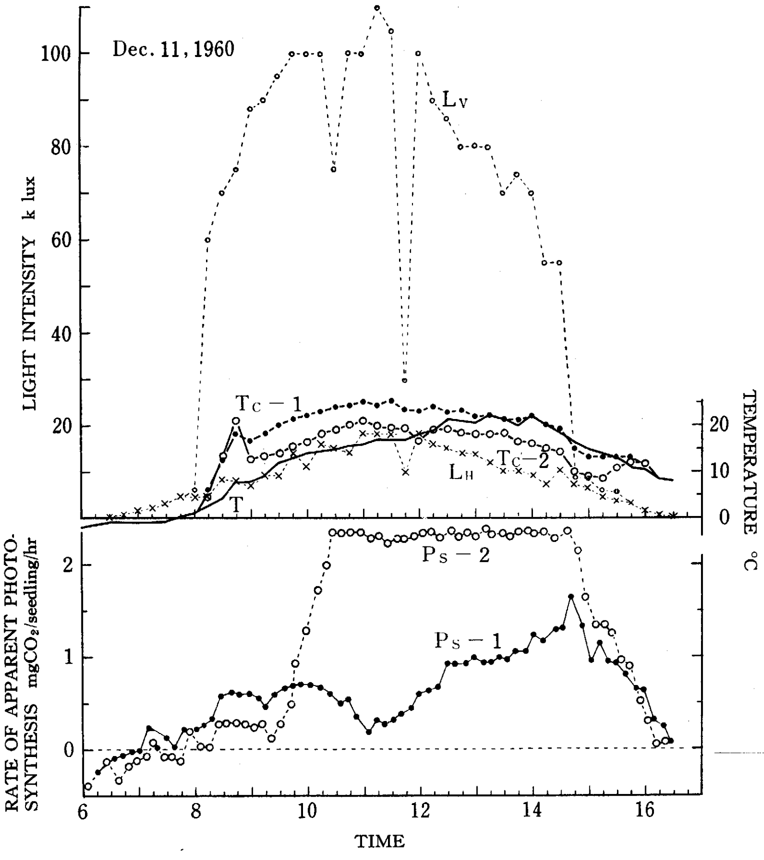

Fig. 14. Daily course of photosynthesis in *Cryptomeria japonica* on a clear day in winter (December 11, 1960). Lettering as in figure 12.

laboratory, and the changes of photosynthetic rate with the lapse of time were observed under a sufficient light intensity and at a constant temperature of 5℃ or 20℃. During January in 1961, three runs of the measurement on different days were made in the same seedling of *P. densiflora* and *Cr. japonica.*

The results are shown in figure 16. At the beginning of the measuring, the photosynthetic rate increases with elapsing time in all observations. But the rate of recovery and the further course of photosynthesis after reaching a higher level differ among different measurements. At temperature of 20℃, a progress of photosynthesis at higher rate is followed by a rapid decrease. The comparison between the result on January 9 and on January 11 indicates that a rapid recovery is expected with a higher temperature, but the same higher temperature is less effective on January 14. As a cause for this inefficiency, the effect of severe frost in the previous night is supposed in the record of daily minimum temperature in the upper graph of figure 16. The level of photosynthetic capacity in winter is lower in *Cr. japonica* than in *P. densiflora,* on which would be detailed in Chapter V.

Time courses of photosynthesis shown in figure 16 are similar in trend to those, e.g. reported by WEISE and POLSTER (1962), in which the samples suffered from the frost

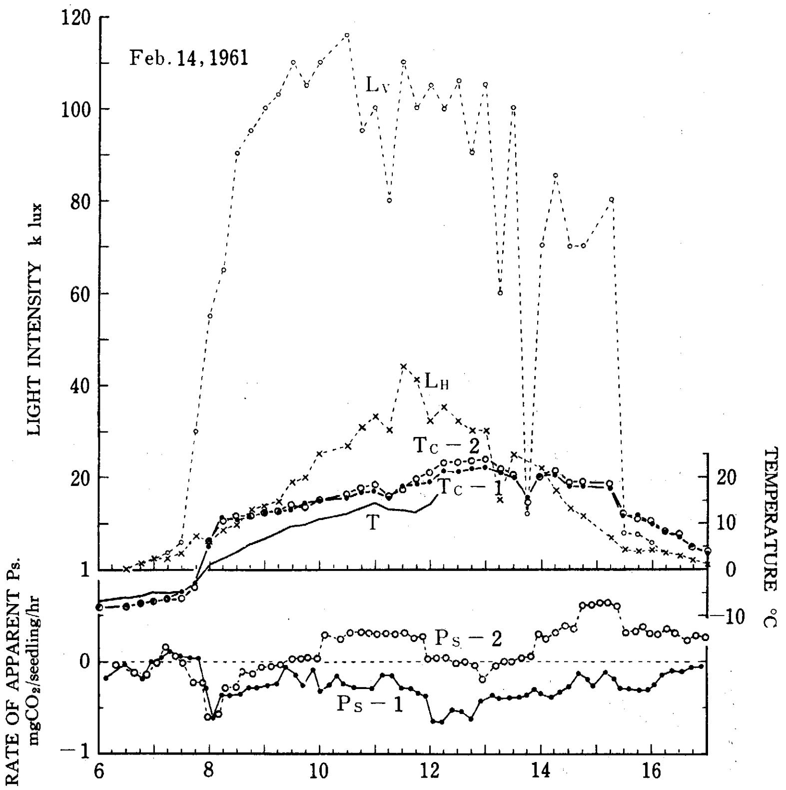

Fig. 15. Daily course of photosynthesis in *Cryptomeria japonica* on a clear day in winter (February 14, 1961). Lettering as in figure 12.

at -10℃ for three days before the measuring, and then the determinations were made under warmer conditions at a temperature between 20 and 22℃. In addition to the rate of apparent photosynthesis, they measured the rate of respiration simultaneously and found that after a certain lapse of time the rate of respiration began to increase remarkably. According to their finding, the increase of respiration is supposed as a cause for the depression of photosynthetic rate which is observed at a higher temperature

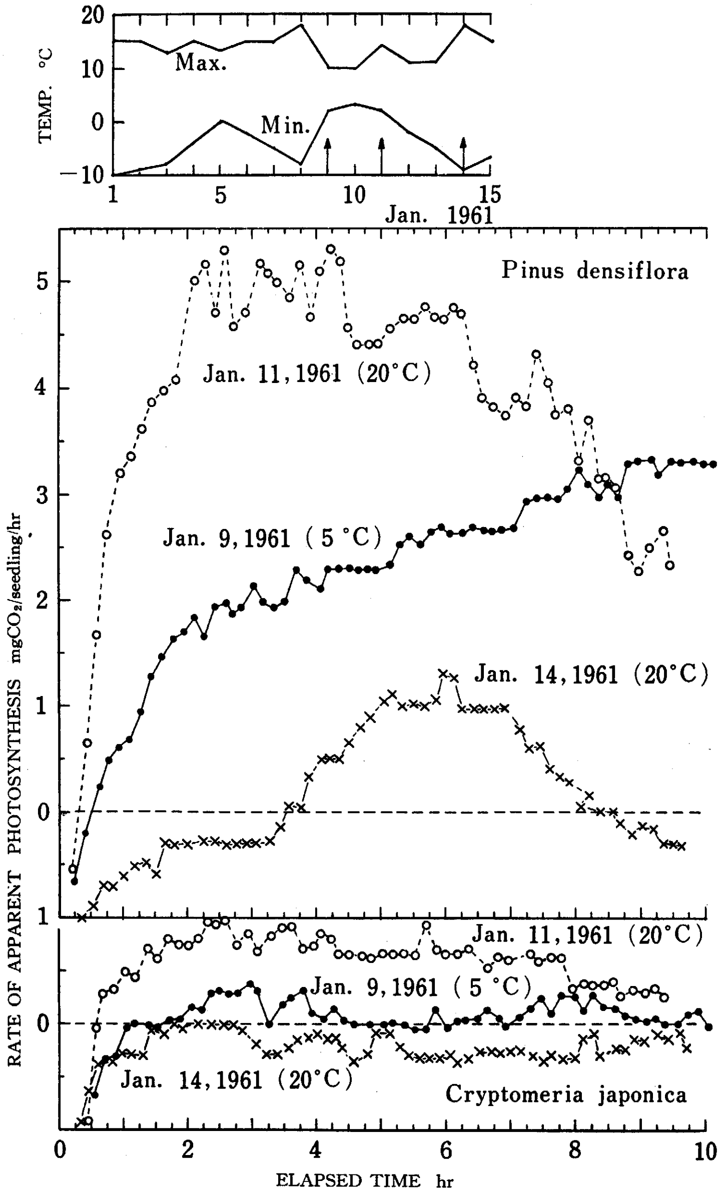

Fig. 16. Daily maximum and minimum temperature in the open (upper), and time course of photosynthetic rate of the seedlings removed to warmer conditions (lower). Arrows in the upper graph mark the measuring days.

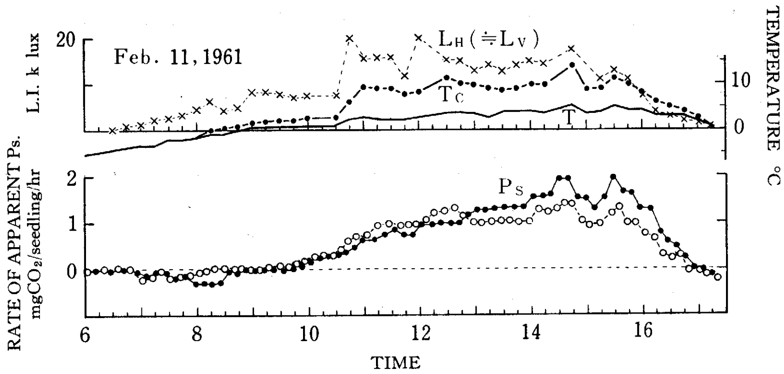

Fig. 17. Daily course of photosynthesis in *Pinus densiflora* on a cloudy day in winter (February 11, 1961). Lettering as in figure 12.

after reaching a higher level.

Since the daily variations in light intensity and temperature are not wide and the rise of temperature in the chamber does not reach to the level causing a marked midday drop on typical cloudy days in winter, the daily courses of photosynthesis in the open are probably similar to those under uniform conditions. Figure 17 represents the instances of daily course on a cloudy day in winter, in which the photosynthetic rate has continued to increase until the evening when the light intensity begins to limit photosynthesis.

When the seedlings suffered from the frost in the same degree, a rapid recovery of photosynthetic capacity is expected with a higher temperature as described above. A similar trend in effect of temperature is seen on the daily course of photosynthesis in the open. As may be seen in figures 12 to 14, the rate of recovery is higher in the seedling in the warmer chamber enveloped in tap water than that in the cooler chamber enveloped in ice water.

The daily course of photosynthetic rate in winter is very sensitive to the rise of temperature. The fact that the temperature in the chamber is higher in general than in the open on clear days in winter, suggests the possibility that the character of the winter type in diurnal variations i.e. a midday drop and a recovery of photosynthetic capacity after sunrise, appears extremely in the seedlings enclosed in the chamber.

3. Seasonal change in type of daily course

From the above description, it is clear that the levels of photosynthesis on the daily course in growing season are closely related with a few environmental factors, especially with each light intensity measured simultaneously while in winter a fairly relationship between light intensity and photosynthetic rate is disturbed by the appearance of a remarkable midday drop and the change in photosynthetic capacity. To make clear the time when the change from the summer type to the winter one or the reverse would take place, the relation between light intensity and photosynthetic rate was studied on each daily course on clear days at different seasons.

Arrangements of the data were made using the hourly mean photosynthetic rate

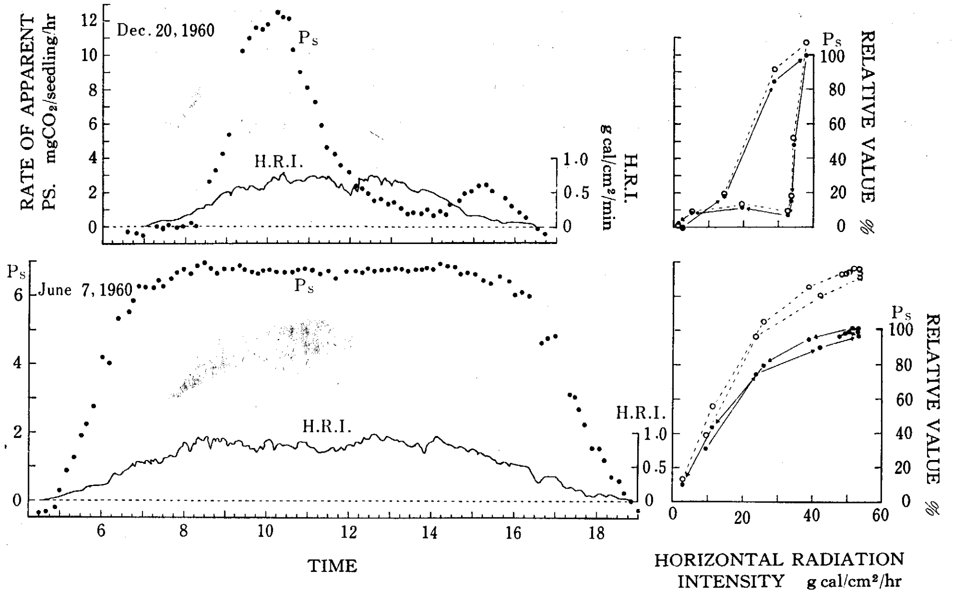

Fig. 18. Daily course of photosynthesis in *Pinus densiflora* on a clear day in winter (upper left) and in growing season (lower left), and relation between hourly horizontal radiation intensity and hourly mean photosynthetic rate in winter (upper right) and in growing season (lower right) drawn using the left figures. **H.R.I.**: horizontal radiation intensity measured with Robitzsh's actinograph, **Ps**: rate of apparent photosynthesis. Arrows in the right figures connect the values in order of elapsing time after sunrise. Further explanation in text.

and the corresponding hourly horizontal radiation intensity instead of the photosynthetic rate for 2.5 minutes of every 10 minutes and of the light intensity measured at intervals of 15 minutes, because the analysis at shorter intervals was supposed too minute for this purpose. Examples of the arrangement of data on *P. densiflora* are shown in figure 18. To remove the effect of fluctuating temperature from the daily course of photosynthesis in the left graph of the figure, the rates are converted into at 20℃, and the course is arranged in the right graph showing a relationship between horizontal radiation intensity and photosynthetic rate, in which the values are connected by the arrows in order of elapsing time after sunrise.

Since the photosynthetic rate is fairly correlated with light conditions throughout the day in growing season, the rates for the period of decreasing radiation intensity trace the same course of increasing one as seen on June 7, 1960 in lower right of figure 18. On the other hand on December 20, 1960 in upper right of figure 18, the upward course differs distinctly from the downward one owing to the appearance of marked midday drop and/or the recovery of photosynthetic capacity in the morning. Thus the relation as observed in the former case indicates the summer type in diurnal variations, while that in the latter case shows the winter one.

A part of the result in each species is shown in figures 19 to 21 respectively. Figure 19 indicates that the daily course of photosynthesis of *P. densiflora* is the summer type for the period May 2, 1960 to November 30, 1960 and the winter one from December 20, 1960 to April 5, 1961. Compared with *P. densiflora*, the winter type of *Cr. japonica* or *Ch. obtusa* appears early, in October as shown in figure 20 or 21. In the winter type, in which a midday drop happens remarkably as observed on December 20 in figure 19, the values for the period sunrise to midday trace a higher level of photosynthetic

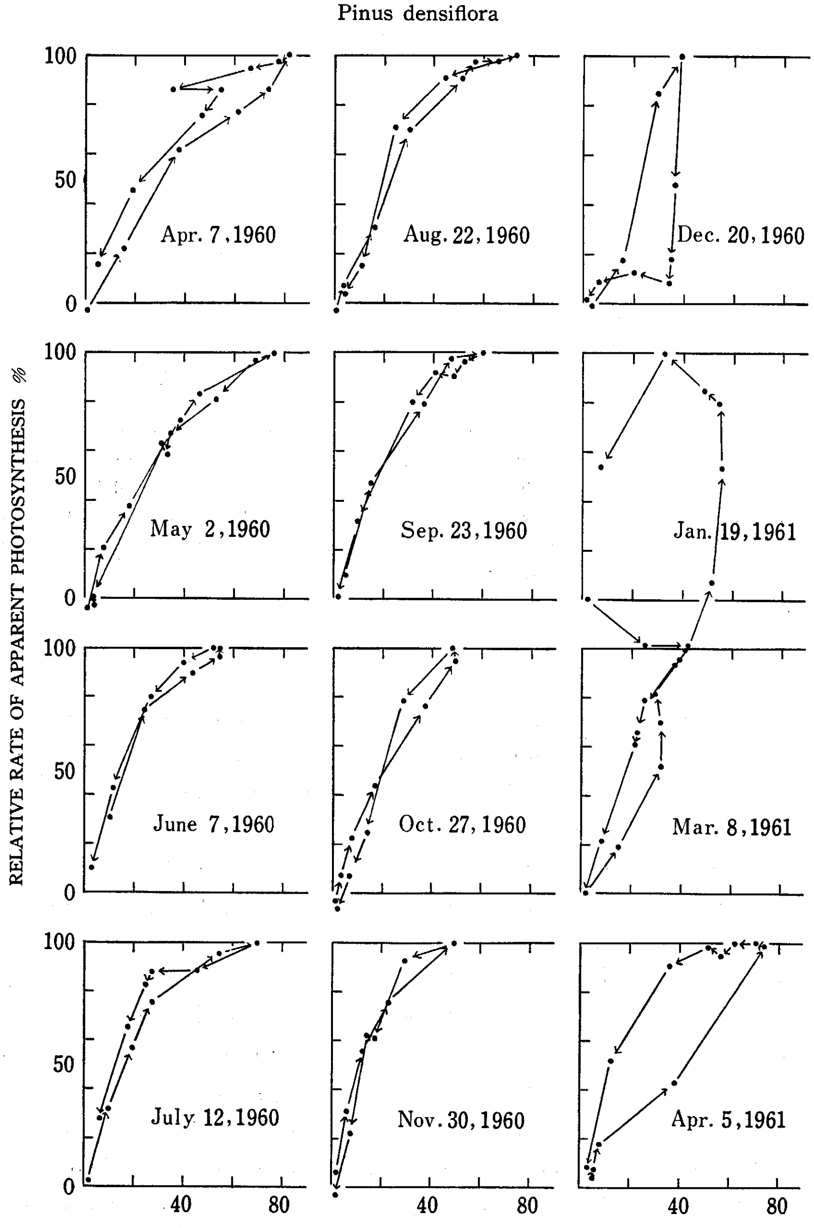

Fig. 19. Seasonal change in the relation of hourly horizontal radiation intensity to hourly mean photosynthetic rate (relative to the maximum) on clear days in *Pinus densiflora*. Arrows in the figure are the same as in figure 18.

rate than those for the period midday to sunset. In cases where an increase of photosynthetic capacity occurs markedly in the morning as observed on January 19, March 8 and April 5, 1961, the reverse takes place.

To express somewhat quantitatively the difference between the summer type and the winter one, the data are arranged with the following modified way. The estimations

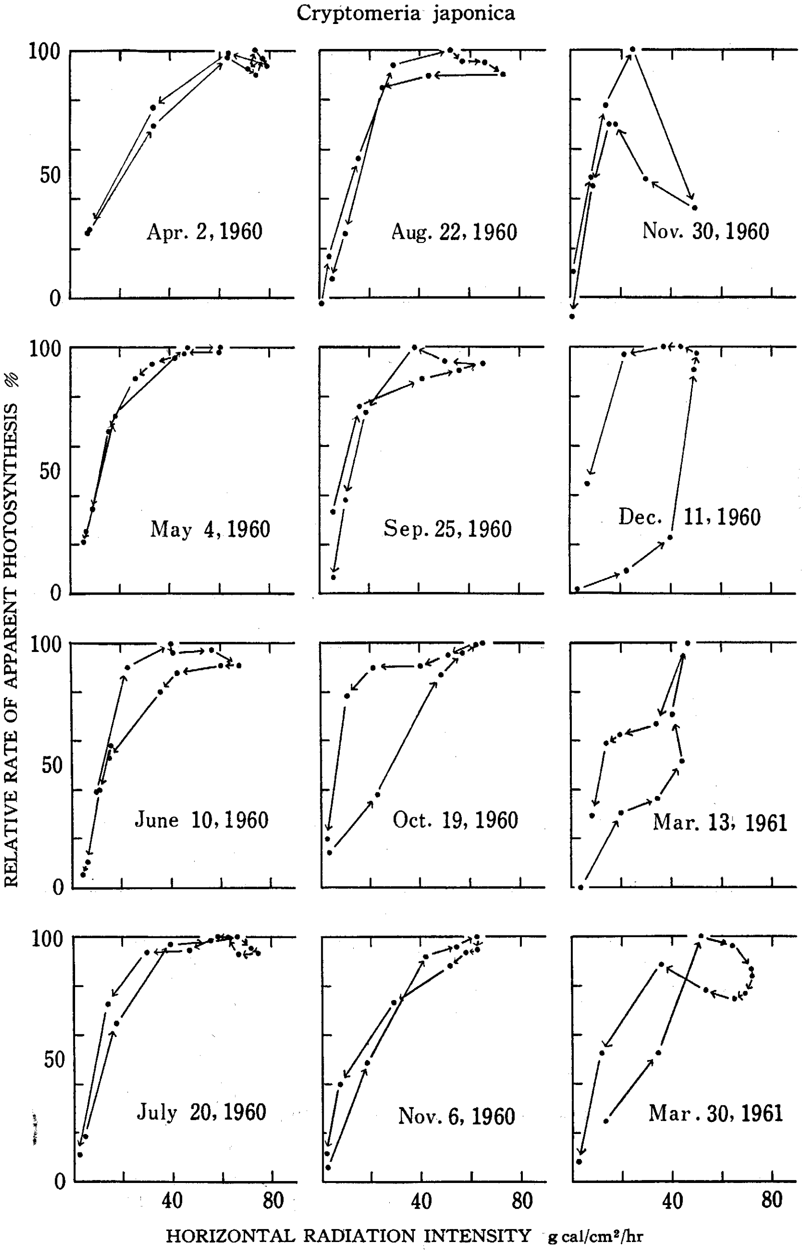

Fig. 20. Seasonal change in the relation of hourly horizontal radiation intensity to hourly mean photosynthetic rate (relative to the maximum) on clear days in *Cryptomeria japonica*. Arrows in the figure are the same as in figure 18.

of the area A and B are made on the figures such as figures 19 to 21, where A is surrounded with the abscissa, the vertical line drawn from the plotted point corresponding to the maximum radiation intensity to the abscissa and the line connecting each of the plotted points for the period sunrise to midday, and B is surrounded with the abscissa, the same vertical line as A and the line connecting plotted points for the period midday

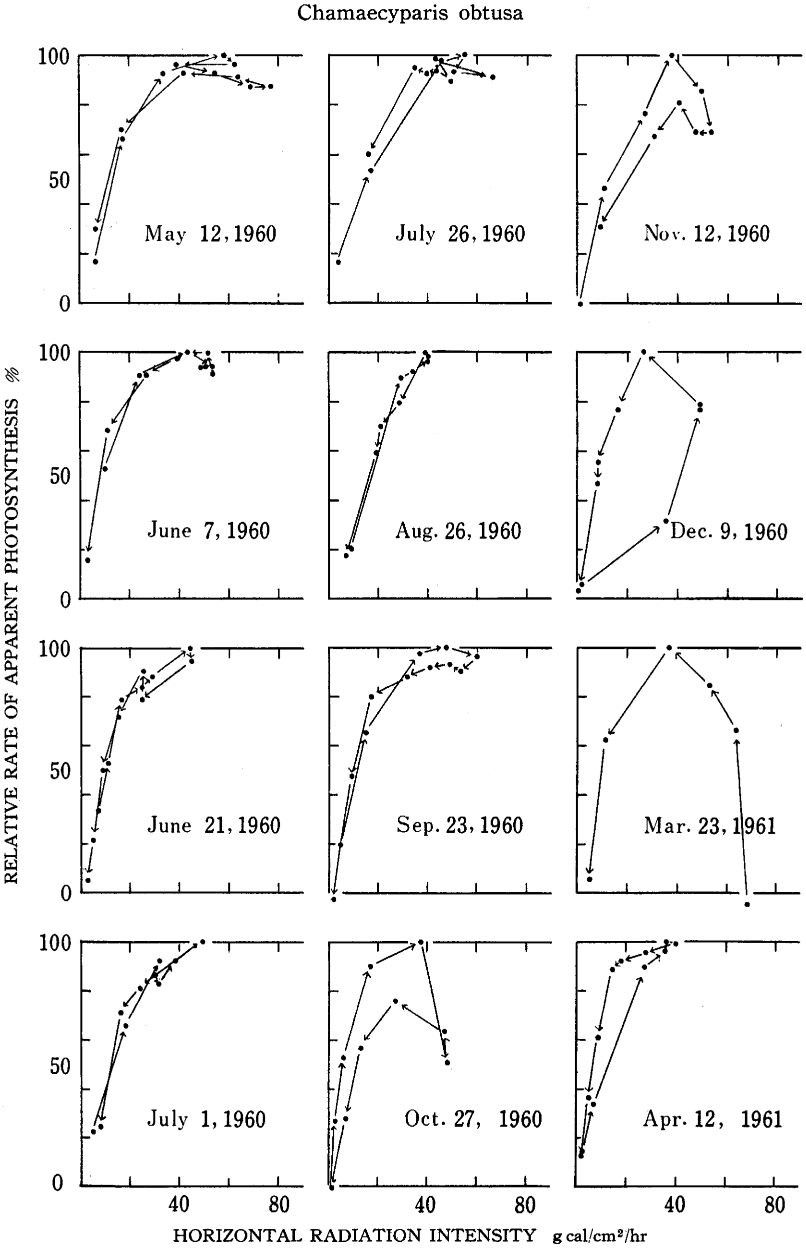

Fig. 21. Seasonal change in the relation of hourly horizontal radiation intensity to hourly mean photosynthetic rate (relative to the maximum) on clear days in *Chamaecyparis obtusa*. Arrows in the figure are the same as in figure 18.

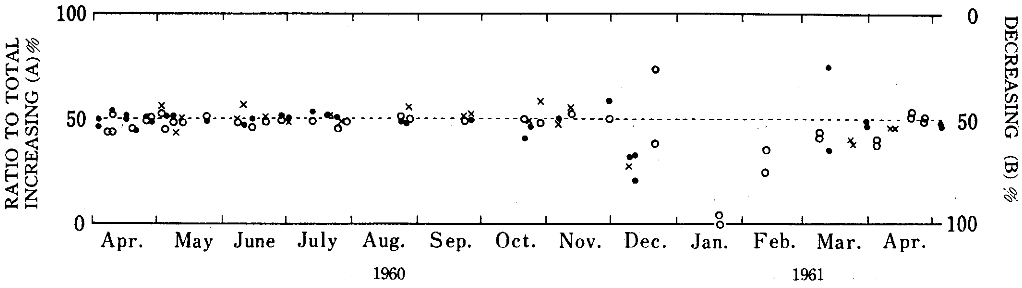

Fig. 22. Seasonal change in the relation between hourly horizontal radiation intensity and hourly mean photosynthetic rate on clear days in *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses). Further explanation in text.

to sunset. It is supposed that the difference in area between A and B indicates the following characters of each type: (1) A≒B shows the summer type; (2) A>B, the winter type with a remarkable midday drop; (3) A<B, the winter type with a marked recovery of photosynthetic capacity in the morning.

The results of the arrangement are summarized in figure 22, in which each area of A and B is expressed in percentage to the area, A plus B. The values from April to November are nearly 50 (A≒B) showing character of the summer type, while those from December to early in April become one-sided (A≠B) indicating a remarkable midday drop, or a change in photosynthetic capacity. One-sided values are observed occasionally in *Cr. japonica* and *Ch. obtusa* in October and November as discussed above. The values of *Cr. japonica* and *Ch. obtusa* in midwinter are not able to plot in figure 22, because the photosynthetic rates of the both species are very low in this season, occasionally negative all day long as shown in figure 15.

CHAPTER II. LIGHT INTENSITY IN RELATION TO RATE OF PHOTOSYNTHESIS

Because of its apparent importance to CO_2-uptake, the response of photosynthesis to light intensity has been studied extensively by many workers. The experiments were mostly made under controlled conditions using artificial light sources. But the reports based on the field data are not rare (as instances dealing with trees, CARTELLIERI 1940; POLSTER 1950, 1955; PISEK & TRANQUILLINI 1954; TRANQUILLINI 1954, 1955, 1957; POLSTER & NEUWIRTH 1958; MILLER 1959; NEGISI, YAMAGUCHI, YAGI & SATOO 1961), especially in recent years the works in this way have been made progress by means of the infrared gas analyzer.

In the open, temperature, water and other factors change together with light factor. And, in cases in which the relation between light intensity and photosynthetic rate is studied with the data in the open, it may be necessary to correct the influence of other factors. Under controlled conditions may be not required these corrections, but a question is raised how to make the light condition similar to natural one by the use of artificial light sources.

It is supposed that the artificial light differs from the natural one in the following points: (1) difference in light quality; (2) difference in distribution of light flux to each part of the sample. There is no artificial light source having perfectly the same quality as sunlight, but the first point in question may be nearly solved by the use of a light source composed of xenon-lamp and optical glass filter as reported by RÜSCH and MÜLLER (1957). The second point in question which may have smaller effect on measuring of a detached broad leaf, is able to affect remarkably the photosynthetic rate in cases, in which will be determined a sample attaching leaves in natural arrangement.

Under ordinary controlled conditions takes place a rapid decrease in light intensity with increasing distance from the light source, because the light source is equiped closely on the plant sample to obtain a high light intensity. The seedling studied here has needles in a certain range of height. And the distribution of light flux to each part of the seedling exposed to the above-mentioned light source may differ from that in the open. Therefore, even if the value of light intensity measured under controlled conditions is equivalent to that in the open, the two light intensities do not always correspond with the same level of photosynthesis respectively.

The influence of the second point in question may be relatively small on the measuring of photosynthetic organs arranged in a plane. But, an artificial arrangement of leaves as such, is not desirable probably, because a disturbance of natural arrangement may be able to change the relationship between light intensity and photosynthetic rate as shown in the researches relating to the effect of mutual shading in pine seedlings (UHL 1937; KRAMER & CLARK 1947).

These defects in artificial light conditions may be not serious, when the experiments are made in relation to factors except light one, or even if with the light factor the difference of species is mainly studied. But in this work, the relation between light intensity and photosynthetic rate is studied with the following purposes: (1) to make clear the different responses of species under various weather conditions; (2) to present light curves available for estimation of dry matter production in the field. Hence, the studies are made on the data in the open described in Chapter I.

I) Arrangement of Data

The studies based on the diurnal variations of photosynthesis were made only for the period corresponding to an appearance of the summer type. After conversion into the rate at constant temperature 20℃, the daily course was arranged in the relation between light condition and photosynthetic rate. To represent the light condition, the horizontal light intensity measured with Toshiba luxmeter Model 5 and the horizontal radiation intensity recorded with Robitzsch's actinograph were used. Because of relatively low sensitivity of Robitzsch's actinograph, the relations to radiation intensity were arranged using hourly mean values. On the data in winter were not made the studies.

II) Results and Discussion

1. Radiation intensity and photosynthetic rate

The same method of arrangement as on clear days in figures 18 to 21 was applied to the data under various weather conditions. The results in each species are summarized in figure 23 for the period May to September. In *Pinus densiflora*, as may be seen in the left graph of figure 23, the relation in May differs from that in other months, while in *Cryptomeria japonica* and *Chamaecyparis obtusa* such difference is not apparent.

To compare the relation of the species with each other, plotted points in figure 23 are collected into figure 24, from which values of *P. densiflora* in May are excluded. All the three species show a rapid increase in photosynthetic rate with radiation intensity at lower intensities. *Cr. japonica* and *Ch. obtusa* reach the maximum rate of photosynthesis at low radiation intensities in comparison with *P. densiflora*. Variations of radiation intensity affect the photosynthesis of *Cr. japonica* and *Ch. obtusa* similarly. In *Cr. japonica* and *Ch. obtusa* are observed the depressions in photosynthetic rate in higher radiation intensities, which correspond with the midday drops in daily courses of photosynthesis mentioned in Chapter I.

In *P. densiflora*, May is different from other months in photosynthetic response to radiation intensity as shown in figure 23. To give a detailed explanation of the difference, the values obtained in every measurement from late-April to May are compared with those in other times in figure 25. May 2, 4, 8 and 12 differ probably from other days in the relation, while April 27 and May 23 do not differ evidently. In early-May, the rate of photosynthesis increases slowly with increasing radiation and reaches the saturation at a higher radiation intensity.

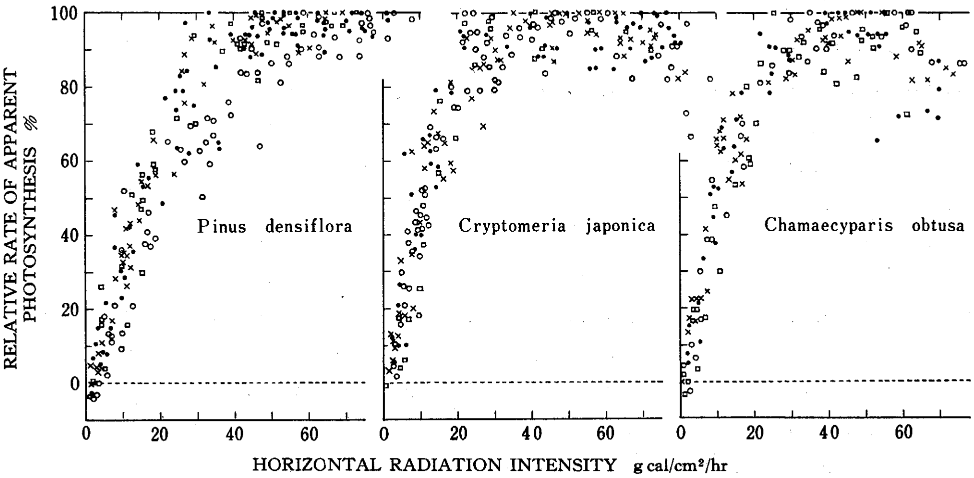

Fig. 23. Scatter diagram of the three species relating to photosynthetic response to radiation intensity observed in May (open circles), June (solid circles), July (crosses), and August and September (open squares), 1960. Rates of photosynthesis are relative to the maximum of each determination.

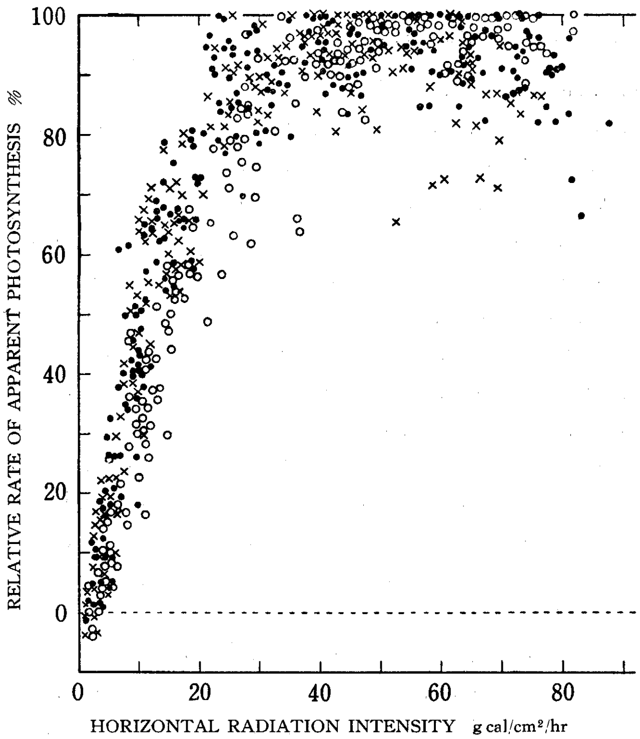

Fig. 24. Difference among *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses) in photosynthetic response to radiation intensity.

It is well-known that *P. densiflora* makes up most of the season's height-growth within a 30-day period in the beginning of growing season except that of the Lammas shoots. As will be described later, at this period, the rate of respiration increases markedly with the elongation of new shoots and needles, while the photosynthesis remains at lower levels, by which the ratio of respiratory rate to photosynthetic rate is made higher. This change in ratio may be connected directly with the difference in the relation between radiation intensity and photosynthetic rate in *P. densiflora* in May. *Cr. japonica* and *Ch. obtusa* are different from *P. densiflora* in height-growth pattern. In these two species, the height-growth and the formation of new needles have been made slowly, and no obvious change in the relation may happen.

2. Light intensity and photosynthetic rate

1) Relation of horizontal light intensity to photosynthetic rate

In this work, the normal and the horizontal light intensities were observed. The latter was not calculated values using the former but measured directly with a photocell placed horizontally as mentioned in the previous chapter. TAKEDA (1957) studied the relationship between light intensity and photosynthetic rate of rice plants using different representations of light intensity. In cases in which the sample was an isolated plant, he found that the rate of photosynthesis could be plotted against either the normal or the horizontal light intensities within much the same degree of deviation. A similar trend was observed in *Cr. japonica* (NEGISI, YAMAGUCHI, YAGI & SATOO 1961). And in this work, the studies are made mainly on the relation to horizontal light intensity, which can be measured easily in comparison with normal one.

The relation between each photosynthetic rate and corresponding horizontal light intensity was studied on the daily courses of summer type. To avoid a confusion caused by a large number of plots, only the values for the period June to September are shown in figure 26. The photosynthetic rate is clearly affected by light intensity, but a wide variation is observed in the relation. In addition to the difference among individuals, the following causes are supposed for this variation: (1) an unsteady time lag in measuring photosynthetic rate behind the corresponded light intensity owing to variable weather; (2) an insufficient time for adaptation of the seedling from one level of light intensity to another one, especially under unsettled weather conditions; (3) a difference in distribution of light flux among the parts of the seedling with changes of weather.

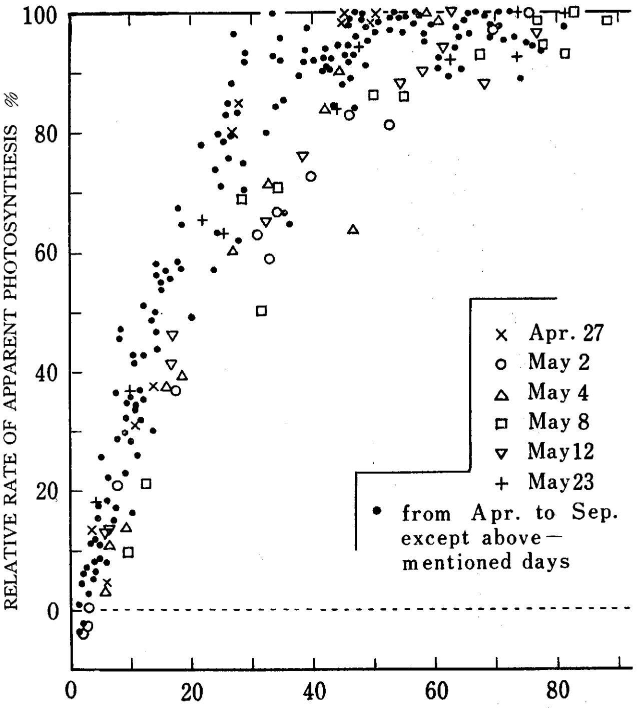

Fig. 25. Change in photosynthetic response of *Pinus densiflora* to radiation intensity during May, 1960.

2) Difference in relation to weather conditions

Comparison between clear and cloudy day

The ratio of direct sunlight or diffuse skylight to total daylight varies with the weather conditions, with which the distribution of light flux among the parts of the seedling may differ simultaneously. And, even though the light intensity measured

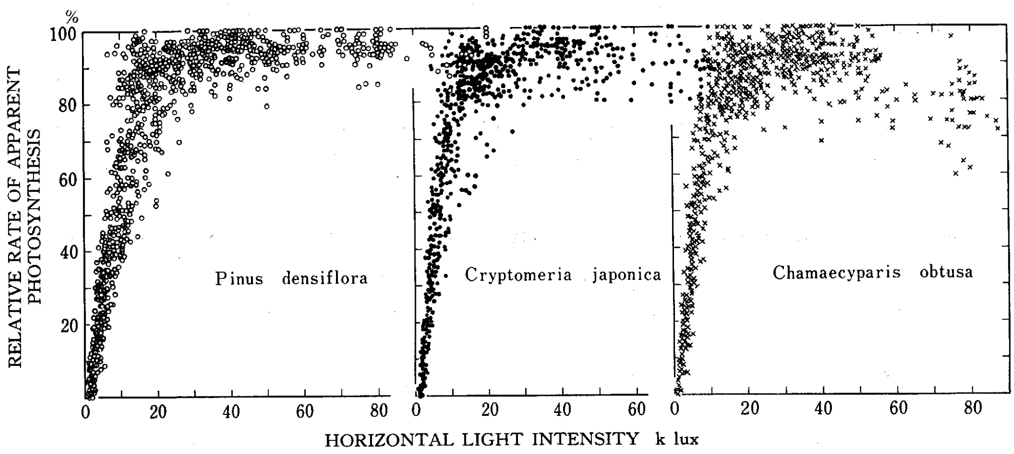

Fig. 26. Scatter diagram of the three species relating to photosynthetic response to light intensity for the period June to September. Rates of photosynthesis are relative to the maximum of each determination.

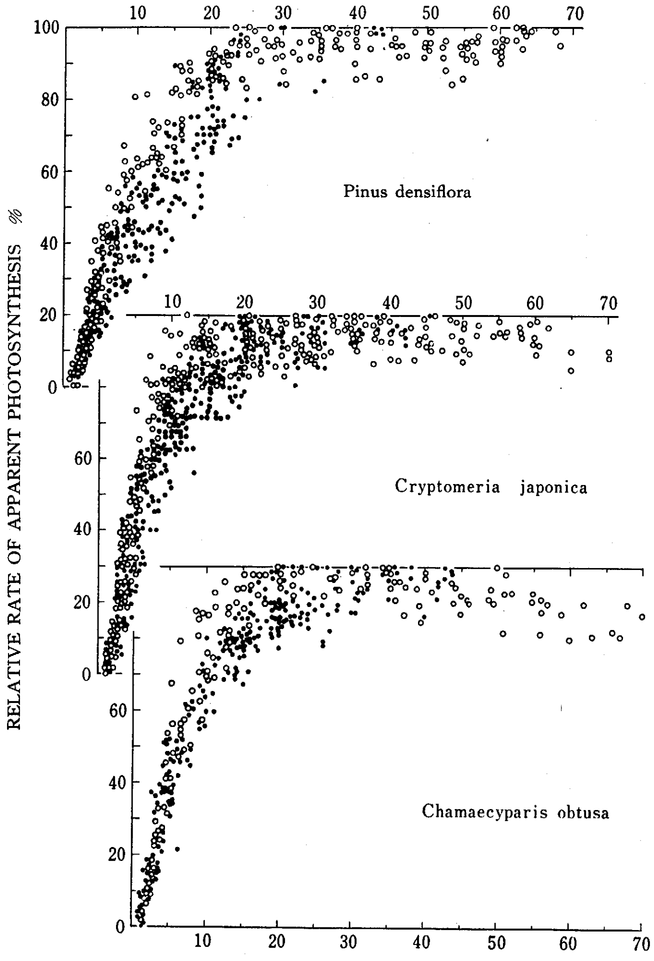

Fig. 27. Difference between typical clear (open circles) and cloudy days (solid circles) in photosynthetic response to light intensity.

with photocell on a clear day is equivalent to that on a cloudy day, it seems that the two do not always connect with the same level of photosynthesis.

To study this point, in figure 27 the relation on typical clear days is compared with that on typical cloudy days, on which incident light from all directions is nearly uniform. The relation obtained under unsettled weather conditions is excluded from this figure, because the variations caused by the above-mentioned time lag and insufficient adaptation may be marked in these conditions.

As may be seen in figure 27, the relation between horizontal light intensity and photosynthetic rate on clear days differs from that on cloudy days in each species. This difference is supposed as a cause of the scattering of values in figure 26, in which the relations under various weather conditions are plotted together. Before studying the details of difference due to weather conditions, a short explanation would be presented for a character of the luxmeter used here.

Character of the luxmeter for sensitivity to the light with various angle of incidence

Theoretically, the relation between normal light intensity (L_V) and horizontal light intensity (L_H) under direct sunlight is represented with the following formula,

$$L_H = \cos\alpha \; L_V = \sin h \; L_V$$

where α is the angle of incidence of solar ray and h is the altitude of sun. Since the photocell of the luxmeter is a barrier-type with optical glass filters and the distance of rays passing through these layers increases with increasing angle of incidence, the values obtained with the photocell placed horizontally differ from those calculated by the application of the cosine law to the normal light intensity.

In figure 28, the expected horizontal light intensities from the luxmeter plotted against the altitude of sun are compared with tha calculated values. In the whole range of solar elevation, a remarkable difference characterizing the luxmeter is observed between the both. Also, the normal and the horizontal light intensities measured practically with the luxmeter on clear days are shown in figure 28. Owing to a variation of transmission coefficient the values scatter in a certain range, but they are plotted near to the expected curves.

From these results it is clear that the measured horizontal light intensity is lower usually than the calculated one. By the application of L–H–1 in figure 28 to the result in figure 27, the relation between the horizontal light intensity and the photosynthetic rate on clear days is drawn to a broken line in figure 29. In the case of the measured horizontal light intensity, the increasing rate of photosynthesis with light intensity on clear days (L–H–2–Ps) is higher than on cloudy days, while the reverse takes place in the case of the calculated horizontal light intensity (L–H–1–Ps).

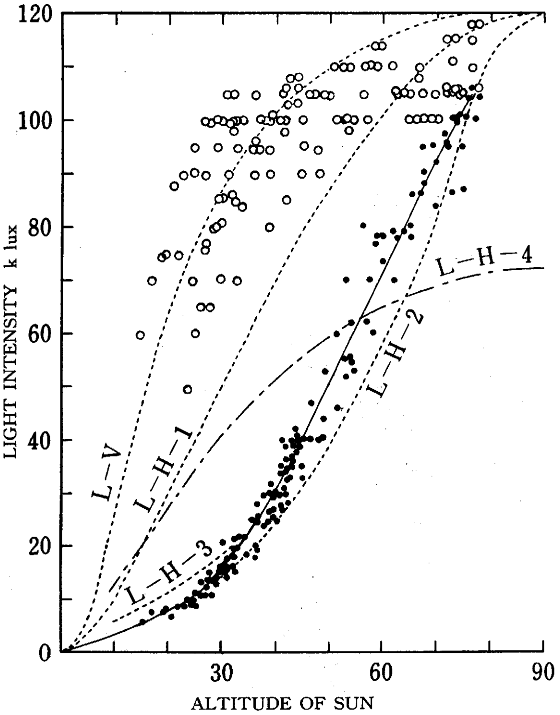

Fig. 28. Sensitivity of the luxmeter in relation to the altitude of sun. Light intensity of total daylight on a clear day with 0.7 transmission coefficient is expressed as the following values; calculated normal (L–V) and horizontal light intensity (L–H–1), expected horizontal light intensity from the photocell placed horizontally with 100 M filter (L–H–2) or with 10 M filter (L–H–3) based on the maker's data, and expected light intensity from a luxmeter having hemispherical light receiving surface (L–H–4). Light intensities measured actually on clear days are plotted with open circles (normal) and solid circles (horizontal).

Cause of the difference between clear and cloudy days

Though the difference in light quality changed with weather is supposed as a factor connecting with the different relations in figure 29, the difference in distribution of light flux among the parts of the seedling may be more important. On cloudy days, the total daylight consists of diffuse light and a difference of light intensity in all directions is smaller, and the incident light upon every photosynthetic part of the seedling is relatively uniform in intensity and corresponds closely with the value measured with the luxmeter. On the contrary on clear days, the total daylight is

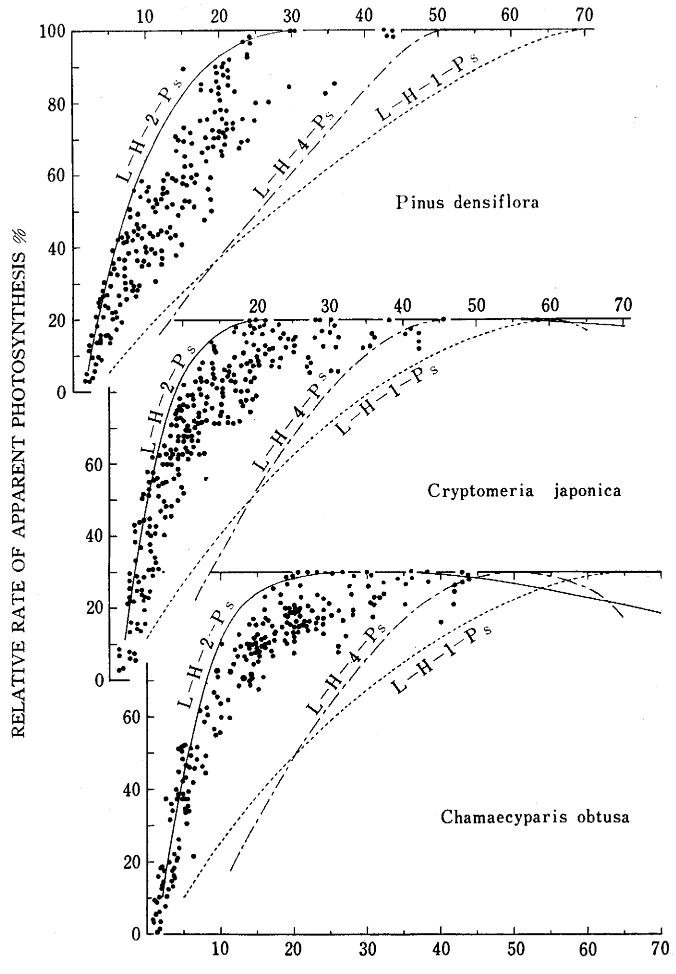

Fig. 29. Difference between typical clear (lines) and cloudy days (solid circles) in photosynthetic response to light intensity (modified figure 27). Photosynthetic rate on a clear day with 0.7 transmission coefficient is plotted against the calculated horizontal light intensity (L-H-1-Ps), the expected one from the photocell placed horizontally (L-H-2-Ps), and the expected one from a luxmeter having hemispherical light receiving surface (L-H-4-Ps).

composed of direct and diffuse light and the incident light from all directions is lacking in uniformity, and the light intensity differs considerably among different positions of the photosynthetic part, i.e. a part exposing to direct light is higher and a part receiving only diffuse light is lower in light intensity. Since the measuring of light intensity is made on the total daylight, the horizontal light intensity measured on clear days may be represented with the highest intensity among the values received by each of the photosynthetic parts. Therefore on clear days, only a part of the photosynthetic organ is equal to receiving the light intensity measured actually with the luxmeter and the remainder is under lower light intensities, and the rate of increase of photosynthesis with increasing horizontal light intensity is lower than that on cloudy days as shown in figure 29.

The difference between the light intensity measured with the luxmeter and that received by photosynthetic part may be related with the difference in shape of the surface receiving rays. When the sample is a leaf having a flat surface similar to the photocell, or if a photocell having a surface similar in shape to photosynthetic organs is able to use, the difference will become smaller.

The response of the luxmeter with a photocell of flat surface is affected by angles of incidence of the ray. To unify such character of sensitivity, improvements on the shape of receiving surface of photocell or devices for the attachment of diffusing light have been made (e.g. Wassink & Scheer 1951, Middleton 1953, Murata 1957). If we can employ the photocell having a hemispherical receiving surface and an uniform response as a luxmeter, the relation between altitude of sun and measured light intensity on clear days will be shown with a chain line (L-H-4) in figure 28. And, the relation between light intensity and photosynthetic rate may be drawn with a chain line (L-H-4-Ps) in figure 29 basing on the assumption that light intensity would be measured with such a luxmeter. As seen in figure 29, the use of such a luxmeter is not effective to diminish the difference in the relation between clear and cloudy days.

In addition to the above-mentioned character of the luxmeter, other factors having a connection with the difference in the relation between clear and cloudy days are supposed. If we can know about the light intensity, the photosynthetic rate and the light curve of each divided part of photosynthetic organ, it will be possible that the difference between clear and cloudy days is deduced from a calculation.

Since there are no data on these points, a calculation is made basing on the following assumptions: (1) A hemisphere which makes photosynthesis only on the outside surface, is assumed as a photosynthetic organ. The base of the hemisphere is put on a horizontal plane. The total daylight received by this hemisphere on a clear day is calculated using the relation between altitude of sun and light intensity of each divided part of the hemisphere; (2) Every divided part of the hemisphere is uniform in their photosynthetic capacity; (3) The same light curve as obtained on typical cloudy days is able to apply to every divided part of the hemisphere (the broken line in *P. densiflora* in figure 30).

The CO_2-uptake of the hemisphere calculated at various sun elevations is converted

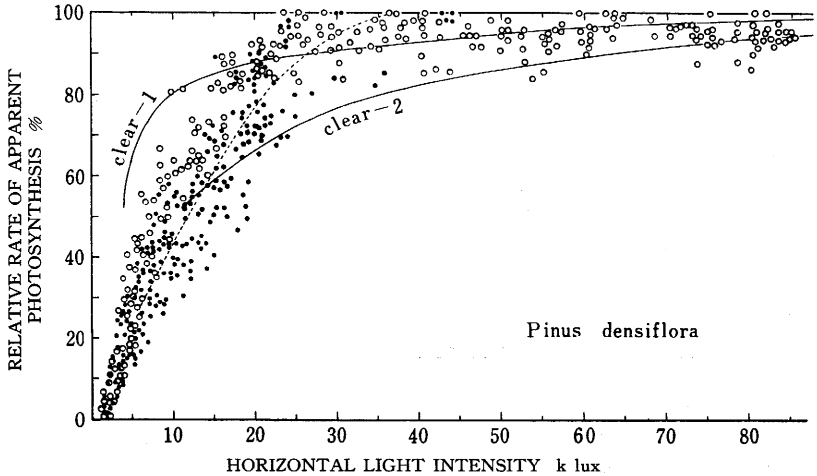

Fig. 30. Observed difference between typical clear (open circles) and cloudy days (solid circles) in photosynthetic response of *Pinus densiflora* to light intensity in comparison with the estimated response on clear days to horizontal light intensity measured with photocell placed horizontally (clear-1) or to calculated one basing on normal light intensity (clear-2). Further explanation in text.

into the rate corresponding to the horizontal light intensity. The result of calculation in *P. densiflora* is shown in figure 30. Though the difference between clear and cloudy days in the calculated relation indicates the same tendency as that in the measured one, each calculated rate differs from the observed one showing imperfections of the above assumptions. For instance, there is a question about the first assumption as shown with the curve (L-H-4-Ps) in figure 29.

Effect of weather conditions on the relation of horizontal radiation intensity to photosynthetic rate

In figure 31, the relation of horizontal radiation intensity to horizontal light intensity on clear days is compared with that on cloudy days. The difference between clear (H.R.I.-L_H-1) and cloudy day (H.R.I.-L_H-2) is partly due to the inapplicability of the cosine law to the luxmeter. The relation between horizontal radiation intensity and photosynthetic rate in *P. densiflora* on clear days and that on cloudy days were obtained using H.R.I.-L_H-1 and H.R.I.-L_H-2 in figure 31, L-H-2-Ps of *P. densiflora* in figure 29, and the broken line in figure 30. As shown in figure 31, the difference between clear (Ps-1) and cloudy days (Ps-2) is not so distinct as compared with that in horizontal light intensity. Relatively higher response to infrared ray of Robitzsh's actinograph possibly makes the difference smaller. Since the cosine law is applicable to Robitzsch's actinograph, the difference is similar in essence to the case of calculated horizontal light intensity.

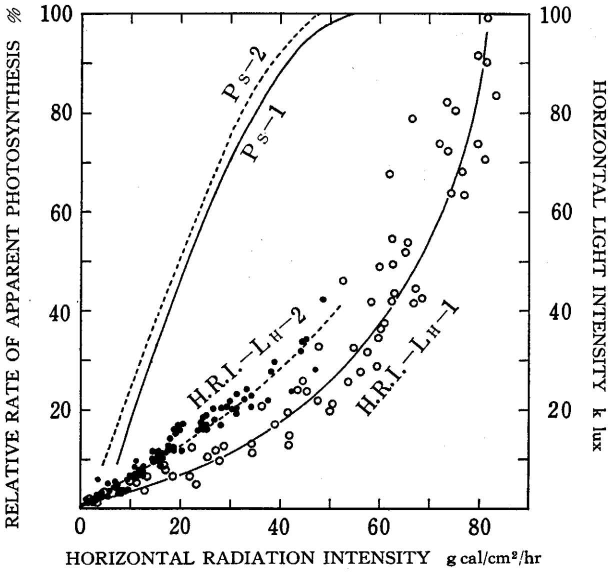

Fig. 31. Difference between the relation of horizontal radiation intensity to horizontal light intensity on clear days (open circles and H.R.I.-L_H-1) and that on cloudy days (solid circles and H.R.I.-L_H-2), and the difference between photosynthetic response of *Pinus densiflora* to horizontal radiation intensity on clear days (Ps-1) and that on cloudy days (Ps-2).

3) Difference among species

Light curve

The relation of horizontal light intensity to photosynthetic rate is similar to that of horizontal radiation intensity in difference among the three species. As shown in figure 32, the increasing rate of CO_2-uptake with light intensity in a lower range is lower in *P. densiflora* irrespective of weather conditions. On clear days is reached a light-saturated photosynthesis at about 30 k lux in *P. densiflora,* and at about 20 k lux in *Cr. japonica* and *Ch. obtusa.* The degree of depression in CO_2-uptake due to excessive light intensity, which corresponds with the midday depression, is marked in *Ch.*

obtusa, moderate in *Cr. japonica* and slight in *P. densiflora.*

Light curves of the same species were dealt with in several reports (TAKAHARA 1954; NEGISI & SATOO 1955; NEGISI, YAMAGUCHI, YAGI & SATOO 1961), in which the light curves of 1-year-old potgrown seedlings of *P. densiflora* and *Cr. japonica* under the controlled conditions (NEGISI & SATOO 1955) may be comparable to those obtained here. As seen in figure 33, the difference in light curve between the two species under the controlled conditions is similar to that under the field conditions. The difference between the two conditions may be caused by the different light conditions. Since

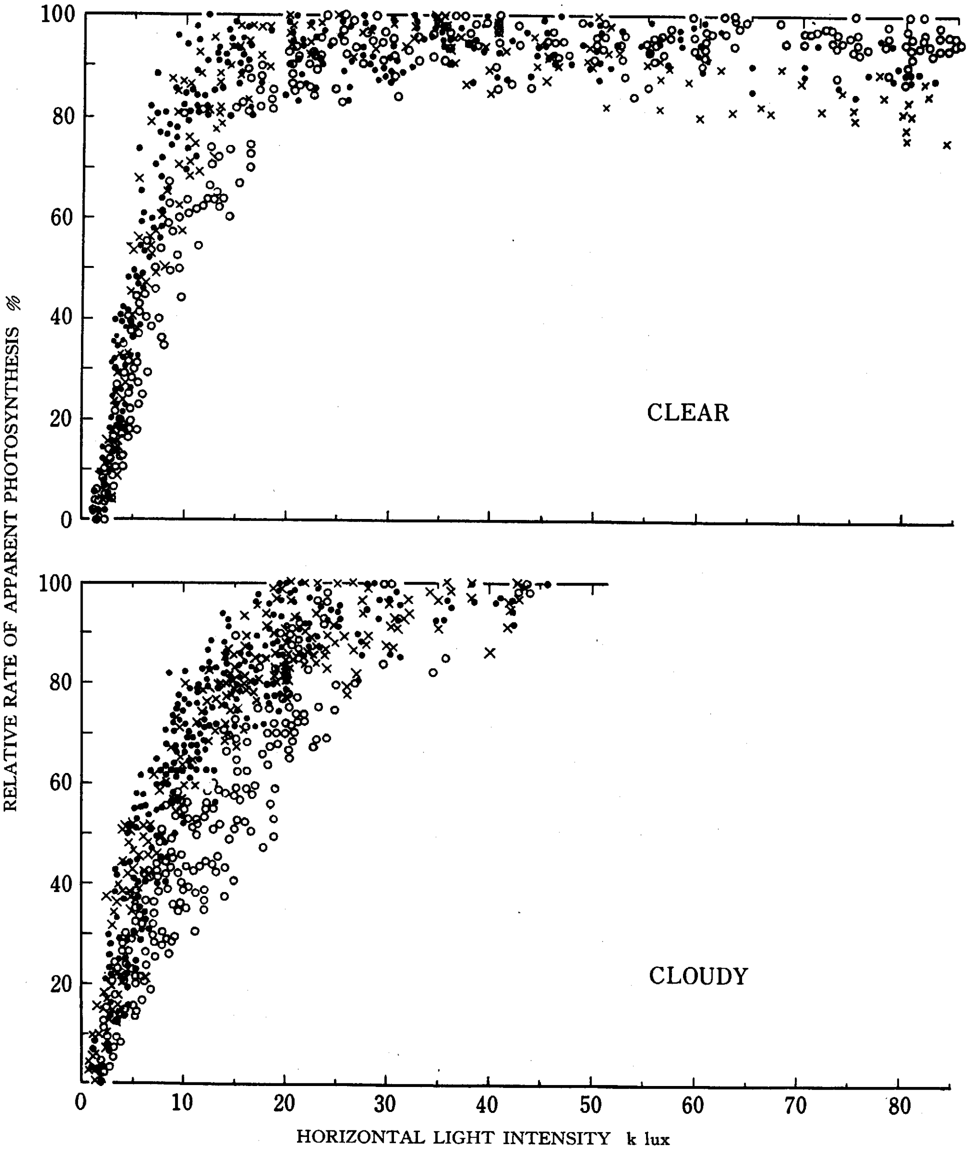

Fig. 32. Difference among *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses) in photosynthetic response to light intensity on clear and cloudy days.

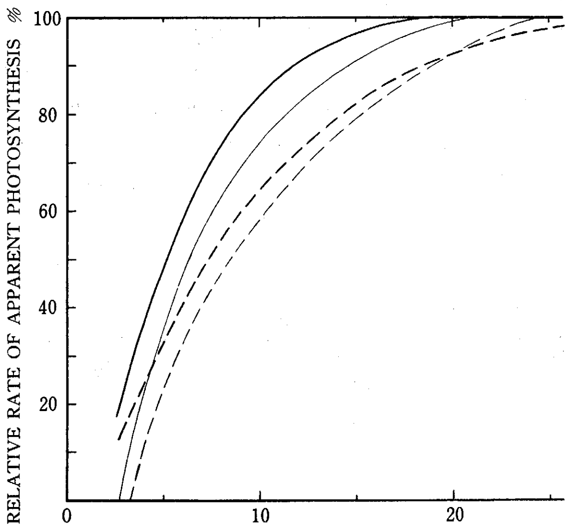

Fig. 33. Light curves of *Pinus densiflora* (thin broken line) and *Cryptomeria japonica* (thin solid line) observed under the controlled conditions as compared with those (thick lines) under the field conditions on clear days.

the measuring under the controlled conditions was made at a constant temperature 30℃, also temperature may be a factor causing the difference in light curve, especially in a lower range of light intensity.

Compensation point

In this work, the measurings only for determining the compensation point were not planned. The daily march of CO_2-exchange passes over a compensation point two times in the day usually, immediately after sunrise and before sunset at which photosynthesis is equal in rate to respiration and there is no net gas exchange. And, the horizontal light intensities at compensation point were estimated using the daily courses of summer type.

In figure 34, the compensation points are given in relation to the temperature. Two factors disturbing this relation are supposed. One is related with the time lag of the recorded photosynthetic rate behind the corresponding light intensity. In the early morning photosynthesis increases with increasing light intensity and the CO_2 concentration in the air decreases in the chamber. When the CO_2 concentration in the chamber decreases to the level in the open, the daily course of photosynthesis appears to be passing over a compensation point. But the compensation point obtained in this manner lags probably in its appearance behind the time at which CO_2-exchange of the seedling arrives actually at a compensation point, because the higher CO_2 concentration before sunrise may act as buffer in the chamber. Therefore the compensation points estimated in the early morning are possibly higher, and for the same reason those in the early evening may be lower. And, the other is that a sufficient time is not allowed for response of the seedling to a rapid changing light intensity.

To show the effect of these factors, the values in the morning are distinguished from those in the evening in figure 34. In lower temperatures, the compensation points in the morning are probably higher than those in the evening as expected above. But in higher temperatures both of them which are estimated using the daily courses in the vigorous growing season, do not differ evidently from each other. In the growing season, the effect of the above-mentioned former factor may be diminished by a higher rate of air flow connecting with vigorous CO_2-exchange of the seedling.

By the scattering of plot in figure 34 are obscured the effect of temperature and the difference among species. The compensation points of *P. densiflora* are higher from late-April to mid-May. At this period the rate of respiration increases with vigorous elongation of shoot, through which the compensation point becomes higher probably.

HIRAMATSU (1935) studied the compensation points in many trees and reported that no net CO_2-exchange was observed at 1,360 lux in *P. densiflora,* 960 lux in *Cr. japonica* and 1,030 lux in *Ch. obtusa* at temperature of 25℃. TAKAHARA (1954) showed that the compensation point of *Cr. japonica* was found at 2,500 lux and that of *Ch. obtusa* at 2,200 lux at 25℃. The result obtained here is nearer to the former than the latter. But it is well-known that the compensation point varies with difference in many factors. For instance, the seedlings grown under different light and soil moisture conditions for four months varied in level of compensation point from 490 to 3,700 lux in *Cr. japonica* and from 350 to

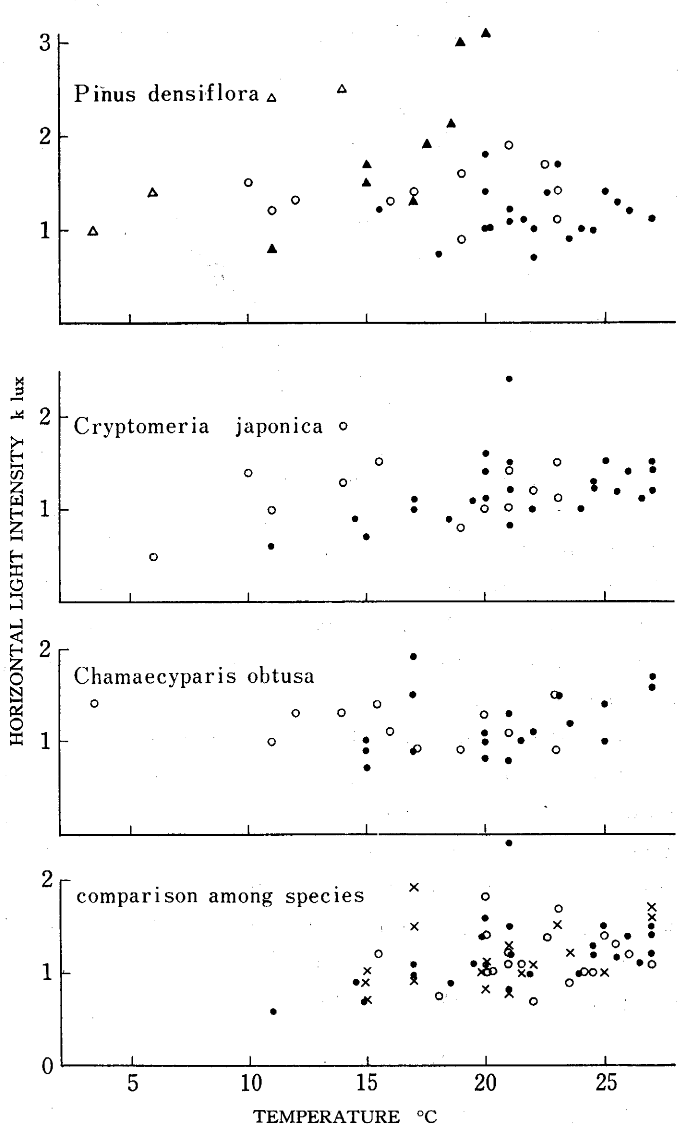

Fig. 34. Compensation point in relation to temperature. In the upper three graphs are shown compensation points of each species in the morning (open circles) and in the evening (solid circles). Triangles in *Pinus densiflora* are the values observed in the morning (open) and in the evening (solid) for the period late-April to mid-May. In the lower graph compensation points in the evening of *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses) are compared with one another.

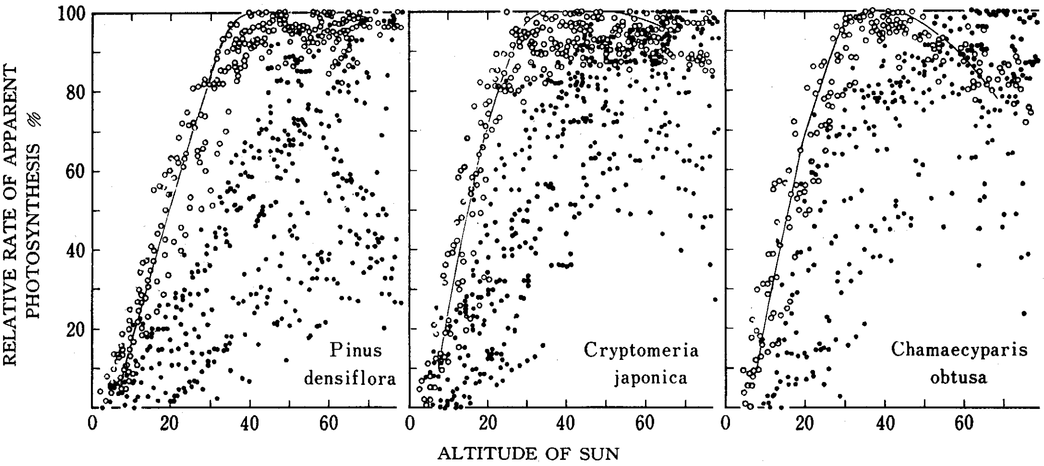

Fig. 35. Difference between clear (open circles) and cloudy days (solid circles) in photosynthetic response to altitude of sun.

940 lux in *Ch. obtusa* (TAKAHARA 1954). OGAWA (1961 a, b, c, 1962 a, b, c, d) worked on trees including the three species dealt with here and found that the daily compensation point was affected by a change in growing conditions, age of leaf, and race. Therefore, in cases in which the comparisons are made among different experiments, the consideration may be required for the difference in conditions.

3. Altitude of sun and photosynthetic rate

The horizontal light intensity increases with the altitude of sun on clear days as shown in figure 28. On cloudy days, the sky is clouded to varying extent, through which the relation differs from that on clear days. The relation of horizontal light intensity to photosynthetic rate in figure 26 was rearranged according to the altitude of sun. As shown in figure 35, the photosynthetic rate on clear days is higher than on cloudy days in each altitude of sun. The marked scattering of the rate on cloudy days is due to the fact that the clouds decrease the light intensity to varying extent.

III) Discussion Relating to Character of Species

By HONDA (1913), the tolerance ratings of forest trees in Japan were assigned to seven classes representing various degrees of ability to endure shade. According to his ratings, the decreasing order of relative tolerance of the three species is as follows: *Ch. obtusa* >*Cr. japonica*>*P. densiflora*. But many students (e.g. NAKAMURA 1937; SATOO 1952) expressed some doubt about such a fine classification, because even in the same species the ability to endure shade varies with environmental conditions to a certain extent. According to their ratings consisting of three classes, *Cr. japonica* and *Ch. obtusa* are classed as "intermediate" while *P. densiflora* is considered as "intolerant".

The light-demanding character of *P. densiflora* also was found in experiments using artificial shade in a nursery (ISIKAWA 1933; AKABAYASI 1935; GEN 1937). As summarized in figure 36, *P. densiflora* reaches its maximum photosynthesis at a light intensity higher

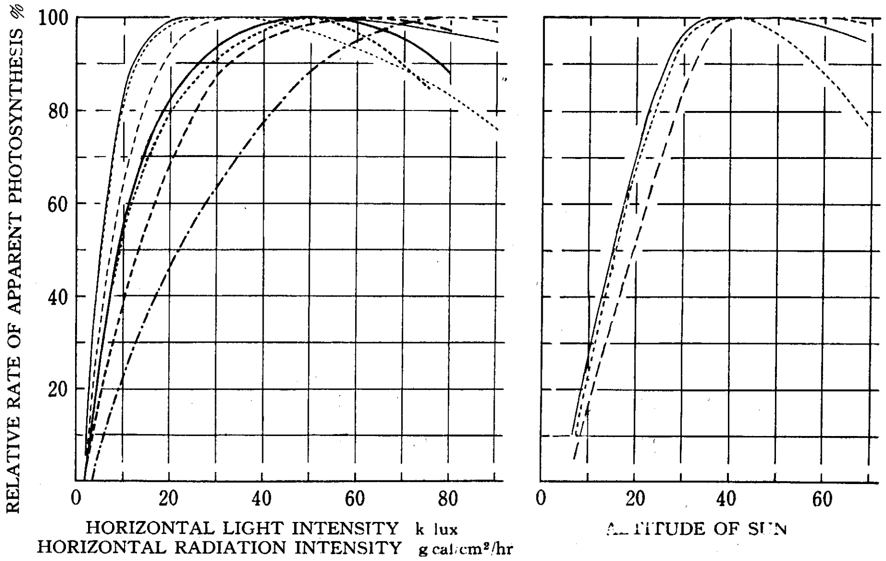

Fig. 36. Photosynthetic response of *Pinus densiflora* (broken line), *Cryptomeria japonica* (solid line) and *Chamaecyparis obtusa* (fine broken line) to horizontal light intensity (thin lines), to horizontal radiation intensity (thick lines), and to altitude of sun. Chain line shows the response of *Pinus densiflora* to horizontal radiation intensity for the period late-April to mid-May.

than two other species. This difference in saturation light intensity is well correlated with the degree of tolerance.

As mentioned above, *Cr. japonica* and *Ch. obtusa* differ from each other in degree of tolerance in the finer classification, but they belong to the same class in the rough one. The latter classification is supported by the results obtained with shading treatment (SHIRASAWA 1905; AKABAYASI 1935). This equality in degree of tolerance corresponds with the similarity of light curve between two species in lower light intensities.

But the photosynthetic response to higher light intensities differ from each other. The inhibitory effects of continuous high light intensity on photosynthesis have been reported in several tree species (DECKER 1944; BÖHNING 1949; BORMANN 1953; KOZLOWSKI 1957; RÜSCH & MÜLLER 1957; TRANQUILLINI 1963). Light inhibition was marked in shade plants as compared with in sun plants. Apparent photosynthesis of the seedlings of *P. densiflora* and *Cr. japonica* under a constant light intensity of 25 k lux remained unchanged for a period of five or six hours (NEGISI & SATOO 1955). But the responses to more higher light intensities for more longer durations have not been studied in the three species.

In this work all the light curves are based on the daily course of photosynthesis, and the decreases in photosynthetic rate at higher light intensities correspond with the midday drops. Therefore, factors other than light inhibition causing midday depression are supposed as a cause of declination of light curve at higher light intensities. But, whether the depression in photosynthetic rate is due to the strong light or to other factors, the fact that the degree of decrease is marked in *Ch. obtusa,* moderate in *Cr. japonica* and slight in *P. densiflora,* interests us in connection with the difference in degree of tolerance.

Since the ability to endure shade is dependent on many factors, the difference in light curve of photosynthesis is but one factor. And to explain only the relation between tolerance and photosynthetic response to light intensity, it is desirable that more detailed experiments, for instance, as made in the works dealing with the successional trends in Piedmont forest (KRAMER & DECKER 1944; KRAMER & CLARK 1947; KOZLOWSKI 1949, 1957; BORMANN 1953, 1956; BOURDEAU 1954) will be designed.

CHAPTER III. TEMPERATURE IN RELATION TO RATE OF PHOTOSYNTHESIS

The relation between temperature and photosynthetic rate in the same species as studied here was reported previously (NEGISI & SATOO 1961a), with which the corrections of daily course of photosynthesis were made in Chapter I and the estimations of daily photosynthetic rate will be attempted in Chapter V. Since the difference in photosynthetic response to temperature is an important factor in discussing the character of species, the point of the previous paper is presented together with a few unpublished data.

I) Material and Method

At different seasons of the year, the determinations of photosynthetic response to temperature were performed on 1-year-old potgrown seedlings of *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa.* The measurings were made under the controlled conditions using different light intensities, under which soil moisture, CO_2 concentration and other factors were not probably limiting photosynthesis.

II) Results and Discussion

1. Relation in growing season

1) At saturation light intensity

The effect of temperature on apparent photosynthesis differs with different seasons. In growing season, apparent photosynthesis of the three species increases directly with temperature to the maximum at about 20℃ when the light intensity is sufficient for a saturation of photosynthesis. As shown in figure 37, further rise of temperature causes a reduction of CO_2-uptake. *Cr. japonica* and *Ch. obtusa* are marked for their post-maximal declination of photosynthesis as compared with *P. densiflora.* Apparent photosynthesis in *P. densiflora* reaches its upper limit between 45 and 50℃, while that in two other species between 40 and 45℃.

Because of lack of the capacity for cooling, the rate at lower temperatures below 10℃ could not be measured under the controlled conditions. In the field, positive rates

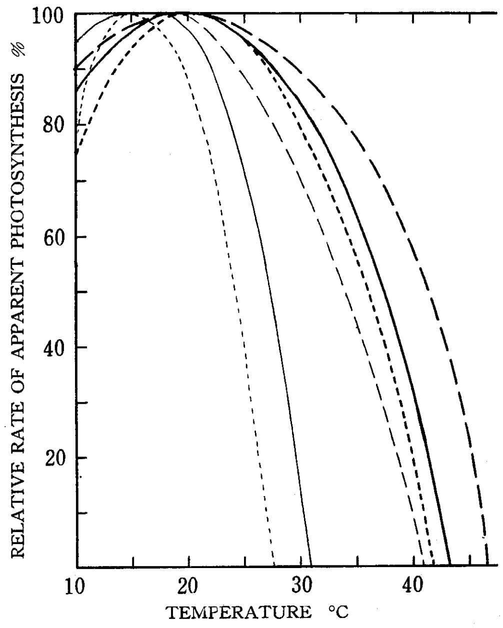

Fig. 37. Photosynthetic response of *Pinus densiflora* (broken line), *Cryptomeria japonica* (solid line) and *Chamaecyparis obtusa* (fine broken line) to temperature in growing season (thick lines) or in winter (thin lines).

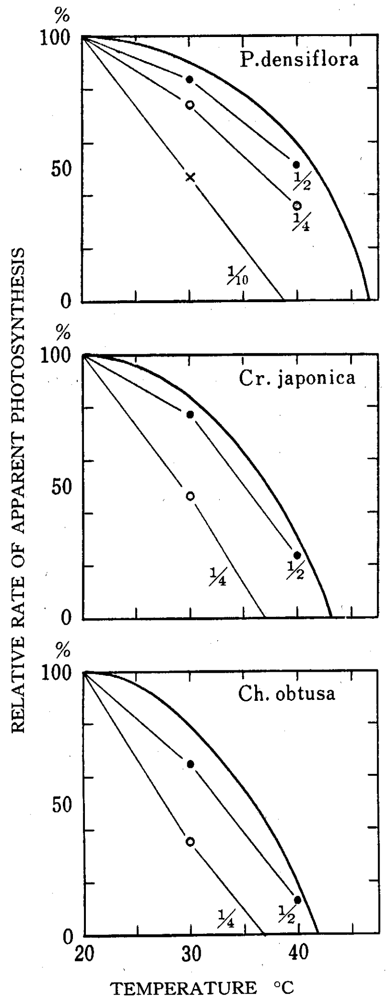

Fig. 38. Effect of light intensity on the relation of temperature to photosynthetic rate in growing season. Thick lines are the relation at saturation light intensity. Lower light intensities are represented with numerals in the graph, which express the photosynthetic rate at 20℃ relative to the rate at saturation light intensity.

of apparent photosynthesis are found down to few degrees below zero as will be detailed in Chapter V.

2) **At low light intensities**

The relations at lower light intensities below the saturation are shown in figure 38. As discussed in Chapter II, it is difficult to obtain a light intensity appropriate for the level of photosynthesis of an entire seedling under artificial light, and each light intensity in this figure is expressed by the photosynthetic rate at 20℃ relative to the rate at near-saturation light intensity. The degree of depression in photosynthetic rate at above-optimal temperatures increases with decreasing light intensity.

In Chapter I, the corrections for fluctuating temperature in daily course of photosynthesis were made using the relation at saturation light intensity. The applications of this relation to at lower light intensities below the saturation may make lower the estimated value, but the error is probably slight because the low light intensities are connected with the relatively low temperatures usually, under which a wide correction is not required.

The effect of light intensity on the relation between temperature and photosynthesis has been dealt with in many works (Stålfelt 1960a), in which reports relating evergreen conifers are included, (e.g. Nomoto, Kasanaga & Monsi 1959; Pisek & Winkler 1959; Clark 1961). According to these papers, the optimal temperature becomes low with decreasing light intensity. Though the measurement at temperatures below 20℃ was not made here, a similar trend may be expected from the result obtained at higher temperatures.

2. Relation in winter

In winter, the decrease in photosynthetic rate due to above-optimal temperature begins at a lower temperature, and the optimum and the maximum temperature in photosynthesis become low. The relation varies with degree of frost. Figure 37 shows the relation in early winter, at which the seedlings have suffered from a moderate frost.

The similar seasonal changes in photosynthetic response to temperature were observed in many evergreens (Kusumoto 1957a, 1961; Nomoto, Kasanaga & Monsi 1959; Larcher 1961a; Sakagami & Doi 1963, 1964). Since the changes of the relation in winter are related with the depression in photosynthetic capacity as discussed in the previous paper, the discussion on the time of year, at which the change takes place would be made together with the seasonal changes in photosynthetic capacity in Chapter V.

III) Discussion Relating to Character of Species

As illustrated in figure 37, *Cr. japonica* and *Ch. obtusa* are similar to each other in photosynthetic behavior to temperature, while *P. densiflora* disagrees with these two species in that it is slower in rate of depression in photosynthesis at above-optimal temperatures and higher in maximum temperature. Because of lack of data below 10℃, the difference among the species is not evident at low temperatures.

As will be detailed in Chapter V, frosts cause a decrease in photosynthetic capacity in every three species, in which *Cr. japonica* and *Ch. obtusa* are remarkable for depression as compared with *P. densiflora*. Apparent photosynthesis of the seedlings which were removed to a green house in the night to prevent from reducing photosynthetic capacity caused by frost, was found down to few degrees below zero in each species in winter. On the other hand, the seedlings left outdoors throughout winter were higher in minimum temperature of apparent photosynthesis. The extent of rise of the lower limit was small in *P. densiflora* and large in two other species. This finding may be connected with the difference of species in depression of photosynthetic capacity in winter.

P. densiflora belongs to intolerant and is able to establish under severe conditions of open land as a pioneer. It seems that these characters of the species are reflected in the ability to carry on photosynthesis over a relatively wide temperature range.

Lower, optimal and upper limits of photosynthesis in each species are related with climatic conditions in its distributing area. According to Pisek (1963), the species dealing with here are high in optimum and maximum temperature as compared with several evergreen conifers in Europe except with *Taxus baccata*. Evergreen conifers similar in optimum temperature to the three species are given in table 1. The rate of apparent photosynthesis at 40℃ was 55 percent of the maximum in *Pinus resinosa* and *Pinus taeda* (Decker 1944), and the upper limit of photosynthesis was observed at a temperature between 43 and 48℃ in *Pinus clausa* (Pharis & Woods 1960). These pines are similar to *P. densiflora* in photosynthetic response to above-optimal temperatures. Most of the evergreen broadleaved trees ranging over southern Japan (Kusumoto 1957a, b, 1961; Kusumoto & Sakimoto 1954), and several decidious trees except the species grown at a high altitude (Hiramatsu 1947) are high in optimum temperature in comparison with the three species.

Table 1. Evergreen conifers similar in optimum temperature to the three species.

Species		Opt. temp. ℃	
Pinus resinosa	U.S.A.	20～30	Decker 1944
Pinus taeda			
Pinus clausa	U.S.A.	23	Pharis & Woods 1960
Abies balsamea	Canada	22～23	Clark 1961
Picea glauca			
Abies Mariesii	Japan	20*	Kuroiwa 1960a
Abies Veitchii			

* Temperature of needles.

The only instance dealing with the same species is the report made by Sakagami and Doi (1964), in which they studied 2-year-old seedlings of *Cr. japonica*. According to their findings that the rate of apparent photosynthesis at 20℃ was lower than the rate at 30℃, the optimum temperature may be higher than that observed here. It seems that the photosynthetic response to temperature differs even in the same species with different growing conditions or different inherited qualities. In addition to these points, the difference in experimental conditions may be a cause of this discrepancy.

CHAPTER IV. SOIL MOISTURE IN RELATION TO RATE OF PHOTOSYNTHESIS

A number of experimental studies have been made on the photosynthetic response to soil moisture, from which works dealing with the following tree species are cited: (1) **orchard trees,** apple (Heinicke & Childers 1935; Schneider & Childers 1941; Childers & White 1942; Allmendinger, Kenworthy & Overholser 1943), pecan (Loustalot 1945), olive (Larcher 1963a, b); (2) **broadleaved trees,** poplars (Barner 1954, 1955; Polster & Neuwirth 1958; Neuwirth & Polster 1960; Neuwirth & Fritzsche 1964), aspen (Neuwirth & Polster 1960), oaks (Kozlowski 1949; Bourdeau 1954), sweet gum (Bormann 1953); (3) **conifers,** *Abies balsamea* (Clark 1961), *Larix leptolepis* (Doi & Sakagami 1962), *Larix decidua* (Polster & Fuchs 1960; Tranquillini 1963), *Picea excelsa* (Tranquillini 1963), *Picea glauca* (Clark 1961), *Pinus densiflora* (Negisi & Satoo 1954a, b, 1955; Doi & Sakagami 1962), *Pinus taeda* (Kozlowski 1949; Brix 1962), *Pinus cembra* (Tranquillini 1963), *Cryptomeria japonica* (Negisi & Satoo 1954b, 1955; Doi & Sakagami 1962). These reports clearly show that either an excess or a deficiency in soil moisture causes a decrease in photosynthetic rate.

The reduction of photosynthesis varies with the severity and the duration of unfavorable water conditions as well as other factors such as light intensity, temperature and air humidity. For example, some discrepancies were found among the results of the experiments made independently in *P. densiflora* under the field or controlled conditions (NEGISI & SATOO 1955; SATOO & NEGISI 1961). The effect of drying of soil seemed to be more severe under the field conditions than under the controlled conditions, which perhaps, was partly due to lower air humidity and higher leaf temperature under strong sunshine in the open. Even in the measurings under nearly similar controlled conditions, the results differed from each other. A part of this difference might be attributed to the difference in rate of drying of soil. The weather before the measuring, a slight difference in handling the seedlings, seed source and others could also have produced some differences.

These results suggest that great caution is needed in making a comparison between the findings of independent experiments. And it may be safe only to make comparison between the results of parallel experiment as made on the following trees; *Pinus taeda* and *Quercus alba* (KOZLOWSKI 1949), two species of oak (BOURDEAU 1954), poplar and aspen (NEUWIRTH & POLSTER 1960), *Picea glauca* and *Abies balsamea* (CLARK 1961), *Picea excelsa, Larix decidua* and *Pinus cembra* (TRANQUILLINI 1963), and two clones of poplar (BARNER 1955).

On the species dealing with here, the comparisons between *P. densiflora* and *Cr. japonica* under the controlled conditions were made in two successive summers (NEGISI & SATOO 1954b, 1955). The pattern of change in photosynthesis differed from each other. The rate of photosynthesis of *Cr. japonica* remained unchanged as the soil moisture decreased from a relatively wet condition just after watering to a water content below the field capacity, and with further decreasing in soil moisture a rapid reduction occured. On the other hand, the rate of photosynthesis of *P. densiflora* increased gradually with drying of soil and at a soil moisture slightly below the field capacity attained to its maximum which was immediately followed by a gradual reduction. Though the depression in photosynthetic rate of *P. densiflora* with drying of soil began at a higher soil moisture content, a positive rate was found down to a lower soil moisture content as compared with *Cr. japonica,* because the rate of reduction was less rapid.

In this work, parallel experiments are made on the three species, *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa,* in which the last was not studied in our previous works. The water deficits are regulated by limiting soil moisture supply to the plant. And to make clear the relation of photosynthesis to actual water deficits in the plant tissue itself, attentions are paid to the study on internal water balance.

I) CO_2-Exchange of Attached Seedling

1. Material and method

1) Material

One-year-old potgrown seedlings of *P. densiflora, Cr. japonica* and *Ch. obtusa* were studied. These seedlings had been grown under the same conditions as those used for the studying of daily course of photosynthetic rate in Chapter I.

The soil in the pot was A-layer of the nursery which was composed of silty loam of volcanic ash origin, having a field capacity of 64 percent and a permanent wilting percentage of 33.5 percent. To estimate soil moisture content in the pot, a gypsum block was buried in each pot, and its changes in electrical resistance were measured during the experiment.

2) Method of measuring CO_2-exchange

The measurings were made under the controlled conditions in an insulated chamber (NEGISI & SATOO 1954b) illuminated with artificial light provided by two 500-watt reflecter spot and four 300-watt reflecter flat incandescent lamps. Heat from the lamps was absorbed by a layer of water 15 cm deep. Light intensity was 45 k lux at the top of the seedling and 25 k lux at the middle, and each species was able to reach its maximum rate of photosynthesis. Air temperature in the chamber was maintained at 25℃. Although the effect of humidity was expected (TRANQUILLINI 1963), the regulation for it was not made, because a complicated equipment was required for the control. The gas analyzer and the assimilation chamber were the same as described in Chapter I.

3) Measurement of CO_2-exchange

Eight uniformly grown potted seedlings were selected in each species on July 26, 1960. After being watered sufficiently, the soil in the pots was allowed to dry in the green house. When the soil moisture was approximately at the field capacity, at which the maximum photosynthetic rate was expected in *P. densiflora* and *Cr. japonica* (NEGISI & SATOO 1954b, 1955), the measurements were made in all the seedlings. Two runs of measurement of the same seedling were made on different days within the period July 29 to August 1. The highest rate obtained in the two runs of the same seedling was regarded as its maximum photosynthetic rate.

After the determination of the maximum rate, the soil in the pots was allowed again to dry in the green house. The reduction in photosynthetic rate was measured for the period August 2 to August 12 at different intervals depending upon the decreasing rate of soil moisture. The drying of soil reached nearly the permanent wilting percentage on August 6 and about 20 percent on August 12.

To standardize the conditions before the determination of photosynthesis, the seedlings scheduled to measure had been left in the dark from the evening of the preceding day to the beginning of measuring. In this work, the internal water condition of the seedling was expressed as "relative saturation deficit" as will be described below. The relation of internal water condition to soil moisture content varies with light intensity, temperature and air humidity (e.g. RUTTER & SANDS 1958; SANDS & RUTTER 1958). The standardization in the dark may be also effective to diminish an undesirable variation of the values of relative saturation deficit.

Each run of the determination was finished when the photosynthetic rate became steady. And the top of the seedling was detached from the subterranean part to measure relative saturation deficit. A small quantity of soil was sampled from the pot to obtain soil moisture content.

In the latter part of August, a similar experiment was carried out, in which 7 seedlings of *P. densiflora,* 6 of *Cr. japonica* and 5 of *Ch. obtusa* were studied. Therefore, 15 seedlings of *P. densiflora,* 14 of *Cr. japonica* and 13 of *Ch. obtusa* were measured in all.

4) **Measurement of water content**

To evaluate internal water balance of the seedling, in addition to the water content on a dry weight basis, "relative saturation deficit" (HALMA 1934; COMPTON 1936) in the top of the seedling was measured in the following way. Immediately after the ending of determination of photosynthetic rate, the top of the seedling was cut off from the subterranean part. And the detached top was weighed (original weight), and placed in water in a container. The cut surface of the stem was recut under the water to prevent from plugging of vessels by air bubble or resin. The top placed in a container was then allowed to stand in a dark chamber at relative humidity of 100 percent for 24 hours to attain its full turgidity, and was again weighed (saturated weight). Using these two weights, the relative saturation deficit was calculated as follows; relative saturation deficit $\% = (\text{saturated weight} - \text{original weight}) \times 100 / \text{saturated weight}$. There were many terms expressing the relative moisture content of plant (HEWLETT & KRAMER 1963), from which the relative water deficit was selected here by reason of the fact that it was measured easily and had been used in the works dealing with CO_2-exchange under unfavorable water conditions (PISEK & WINKLER 1956; LARCHER 1960, 1963a).

2. **Results and discussion**

1) **Soil moisture content and water condition of seedling**

The relation of soil moisture to water condition of the seedling is shown in figure 39, in which the values at higher soil moistures were observed in the seedlings which were not used for photosynthetic measurements. Because of wide individual variations in the value, the decrease in water content on a dry weight basis is becoming obvious when the drying of soil reaches nearly the permanent wilting percentage, while the individual variations are so small in relative saturation deficit that the changes are apparently found in each species over the entire range of soil moisture.

At relatively wet soil moistures, the level of relative saturation deficit of *Ch. obtusa* is lower than the other two species. With the progress of drying of soil from the field capacity to the permanent wilting percentage, the relative saturation deficit begins to decrease in all the species. The rate of reduction differs among the species, rapid in *Cr. japonica,* moderate in *Ch. obtusa* and slow in *P. densiflora.* A similar difference among the species was found in the seedlings at the first summer after their emergence by SATOO (1956).

2) **Relative saturation deficit and photosynthetic rate**

Thus the relative saturation deficit is much better than the water content on a dry weight basis in order to make clear the relation between soil moisture and water condition of the seedling. In the top left graph of figure 40, the rates of photosynthesis at different soil moisture content are plotted against the relative saturation deficit. The decrease in photosynthetic rate with increasing relative saturation deficit begins at a higher level in *P. densiflora*, at a intermediate one in *Cr. japonica* and at a lower one in *Ch. obtusa*.

3) Soil moisture content and photosynthetic rate

Using the relation in the upper graph of figure 39, the top left graph of figure 40 is modified as in the top right one of the same figure showing the relation between soil moisture content and apparent photosynthesis. The photosynthetic response to decreasing soil moisture differs with different species. The difference between *P. densiflora* and *Cr. japonica* is essentially similar to that reported in the previous paper (NEGISI & SATOO 1955).

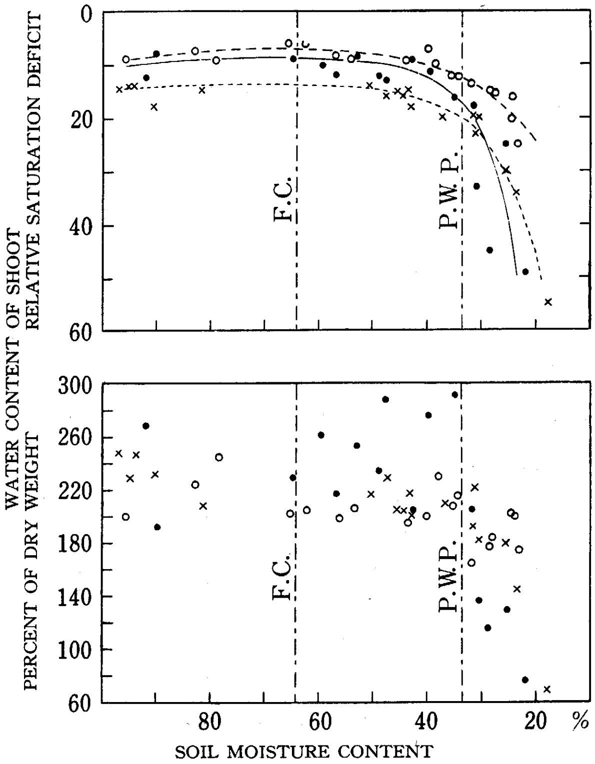

Fig. 39. Relation of soil moisture content to relative saturation deficit (upper) or to water content on a dry weight basis (lower) of the seedlings of *Pinus densiflora* (open circles and broken line), *Cryptomeria japonica* (solid circles and solid line) and *Chamaecyparis obtusa* (crosses and fine broken line). F.C.: field capacity, P.W.P.: permanent wilting percentage.

As shown in the figure, the photosynthesis of *P. densiflora* begins to decrease at a soil moisture slightly below the field capacity and continues downward gradually. On the other hand, the photosynthetic rates of *Cr. japonica* and *Ch. obtusa* remain unchanged at the earlier stage of the drying of soil, and begin to decrease rapidly at soil moisture content of about 40 percent on the dry weight basis. The apparent photosynthesis becomes negative at a soil moisture slightly below the permanent wilting percentage in *Cr. japonica,* while the positive apparent photosynthesis continues down to lower soil moistures in *P. densiflora.* From these differences in photosynthetic response, it may be clear that the sensitivity to a slight decrease of soil moisture at relatively moist stage of drying is higher in *P. densiflora* and lower in *Cr. japonica* and *Ch. obtusa,* and the resistance to an extreme depression in soil moisture content is higher in *P. densiflora,* intermediate in *Ch. obtusa* and lower in *Cr. japonica.*

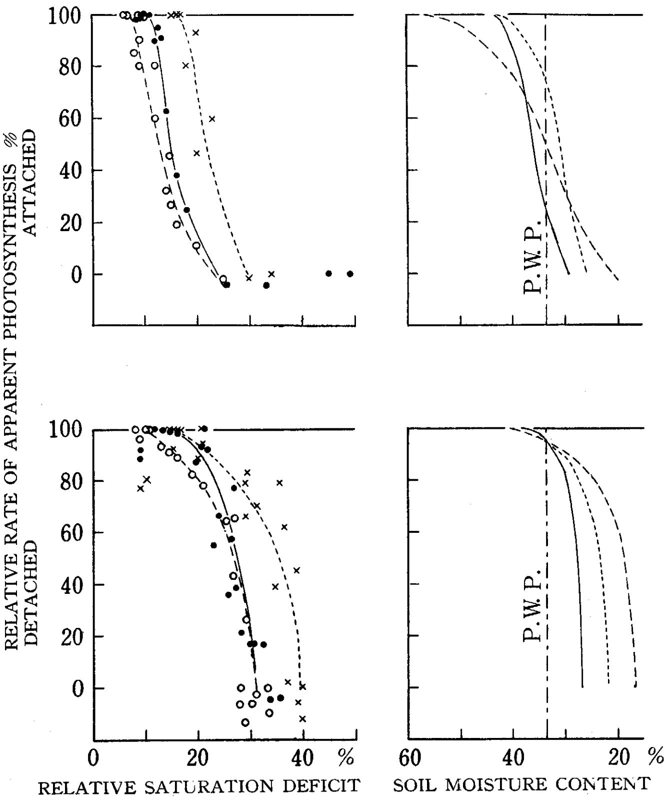

Fig. 40. Photosynthetic response of attached (upper) or detached (lower) seedlings of *Pinus densiflora* (open circles and broken lines), *Cryptomeria japonica* (solid circles and solid lines) and *Chamaecyparis obtusa* (crosses and fine broken lines) to relative saturation deficit (left) or soil moisture content (right). Lettering as in figure 39.

4) Relation of soil moisture content to CO_2-exchange observed in additional experiment

In addition to the abovementioned experiment, a measurement having the same object was made in October, 1960, using 1-year-old potgrown seedlings. Apparent photosynthesis of the seedling was measured under the controlled conditions similar to the summer experiment except that the temperature was kept at 20℃. The maximum photosynthetic rate under favorable soil moisture condition and the water content of seedling were not determined. The measurements of dark respiration at 20℃ followed close on each run of photosynthetic determination.

The results are summarized in figure 41, in which apparent photosynthesis and respiration are expressed as rate per unit dry weight. Because of the wide variation of each individual seedling, the effects of drying of soil on photosynthetic rate are not obvious in a higher soil moisture range. But at the advanced stage of drying, the same difference as described above is found between *P. densiflora* and *Cr. japonica,* i.e. a severe drying of soil is less effective for the former as compared with the latter.

As shown in figure 41, in each of the three species, a steady decrease in respiratory rate occurs with decreasing soil moisture, which agrees with the results obtained in the previous work dealing with *P. densiflora* and *Cr. japonica* (NEGISI & SATOO 1955). A similar decrease in respiration was found in *P. densiflora* and *Cr. japonica* by DOI and SAKAGAMI (1962), and in *Pinus Thunbergii* by KADOTA (1962).

On the contrary was reported in many plants, a pronounced rise in respiration in the course of decreasing water content of the soil or of the plant (STOCKER 1956; ILJIN 1957; VAADIA, RANEY & HAGAN 1961). As instances dealing with tree species, the respiratory rate of apple leaves increased to more than 60 percent (Schneider & Childers 1941), and that of *Pinus taeda* to more than 40 percent with desiccation (Brix 1962). The question whether or not this difference in response is due to only the difference of species is not answered because several students reported that the respiratory response to desiccation was affected by the speed of dehydration in the same species (Montfort & Hahn 1950; Parker 1952).

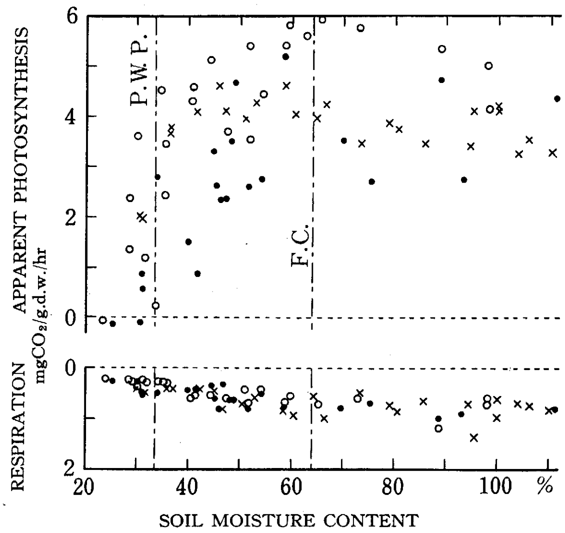

Fig. 41. Photosynthetic (upper) and respiratory response (lower) of attached seedlings of *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses) to soil moisture content. Lettering as in figure 39.

II) CO_2-Exchange of Detached Seedling

A limited water supply can produce a decreased water content in the plant which may cause a depressed rate of photosynthesis, whether through decreased protoplasmic hydration or through the influence of the water deficit on stomatal opening and thus on their diffusive capacity for CO_2.

Pisek and his co-workers (Pisek & Berger 1938; Pisek & Winkler 1953) studied the decrease in weight of water saturated excised twigs in relation to opening of stomata, and showed that the time course of decrease was useful in making a survey of stomatal movement. Further, they studied photosynthesis of detached twigs together with stomatal opening determined by the above way, and made clear the relation of stomatal movement to decrease in photosynthesis caused by dehydration (Pisek & Winkler 1956). By Larcher (1960), the study along the same line was made in the two species of oak in connection with the difference of species in resistance to drought.

To compare the response of species to desiccation with each other are observed here the changes in photosynthetic rate of detached seedlings associating with the decrease in fresh weight.

1. Material and method

One-year-old potgrown seedlings were used. After sufficient watering, the soil in the pots was allowed to dry in the green house. When the soil moisture decreased nearly to the field capacity, the seedlings were carried into the laboratory and had been left in the dark from the previous evening to the beginning of measuring. The measurements of photosynthesis were made under the conditions similar to the previous experiments, at light intensity of 25 k lux at the middle of the seedling and at temperature of 25℃.

Each run of the determination began with the measurement of potted (attached) seedling to obtain a standard rate, which was followed by the measurings of detached top of the same seedling continuing nine hours. At different intervals, were made the weighings of top to measure moisture loss due to desiccation. After the ending of the run, the detached top was placed in a water container to obtain relative saturation deficit. Four seedlings of each species were measured in August, 1961.

2. Results and discussion

1) Water condition and photosynthetic rate

In the lower left graph of figure 40, photosynthesis of the detached top is expressed as relative rate to the standard one obtained before the detachment. Photosynthetic response to desiccation differs with different species. In *P. densiflora,* the decrease begins at a slight increase in relative saturation deficit and continues downward gradually, while in *Cr. japonica,* a rapid decrease occurs when the desiccation is progressing beyond a certain high limit of relative saturation deficit. In *Ch. obtusa* the decrease in photosynthetic rate happens in a higher range of deficit as compared with two other species, which may be attributed to the difference of species in relative saturation deficit in figure 39.

To make a comparison excluding the influence of this difference of species, the results are arranged in the relation between soil moisture content and photosynthetic rate using the relation in the upper graph of figure 39. As shown in the lower right graph of figure 40, the three species differ from each other in rate of decrease and in soil moisture content at which apparent photosynthesis reaches zero, i.e. rapid and higher in *Cr. japonica,* medium and intermediate in *Ch. obtusa,* and gradual and lower in *P. densiflora.* The differences among the species are not obvious in the higher range of soil moisture, but those in the lower one agree essentially with the difference observed in the attached seedlings.

2) Effect of pace of drying

As may be seen from the comparison between upper and lower left graph of figure 40, the photosynthetic rate corresponding to a certain relative saturation deficit is higher in the detached seedling than attached one. The pace of dehydration of attached seedling is remarkably slower than detached one, i.e. in the former case a week is spent in increasing to a relative saturation deficit, at which apparent photosynthesis becomes zero, whereas in the latter one the same level of desiccation is reached in only three or four hours.

In connection with the effect of pace of drying on the change in rate of apparent photosynthesis, unpublished data observed in excised twigs (cuttings) of Sanbu-sugi, a local race of *Cr. japonica,* are presented below. Twigs, weighing an average of 5 g each, were cut off from the upper part of crown of 8-year-old trees and carried into the dark of the laboratory, in which they were placed in water in a container. A run of the determination started with the photosynthetic measurement of water-saturated twig under the controlled conditions, at light intensity of 25 k lux at the middle of the twig and at temperature of 25℃. The dehydration of twig was made in the two ways, a slow desiccation in the dark and a rapid desiccation in the light.

In the slow desiccation, a measurement of dark respiration at 25℃ followed on that of apparent photosynthesis, after which the twigs were allowed to dry in the dark until the next measuring. A run of the determination lasted ten more days, in which the measurements of CO_2-exchange and fresh weight were made at intervals of a few days. On the other hand, in the rapid desiccation the measurings of photosynthetic rate and fresh weight were made continuously. A run of the determination continued for several hours and ended when the apparent photosynthesis approached to zero. Four twigs in the slow desiccation and two in the rapid one were measured for the period May to June in 1959.

As shown in figure 42, the respiratory rate of excised twig decreases with increasing dehydration. The changes in actual photosynthesis, which is calculated by totaling the rate of apparent photosynthesis and the rate of dark respiration, indicate that CO_2-uptake is found under a remarkable dehydrated condition such as 70 percent in relative saturation deficit. The degree of decrease in photosynthetic rate with the slow desiccation is larger than that with the rapid desiccation, which agrees with the difference between attached and detached seedlings in figure 40. About the effect of pace of drying, the reverse relation was observed in *Olea europaea* by LARCHER (1963a), i.e. a rapid dehydration caused more remarkable decrease in photosynthetic rate. Since the pace of dehydration expressed as "rapid" or"slow" is relative rate and may be valid only within each of the parallel experiments, further discussions on this point are not made here.

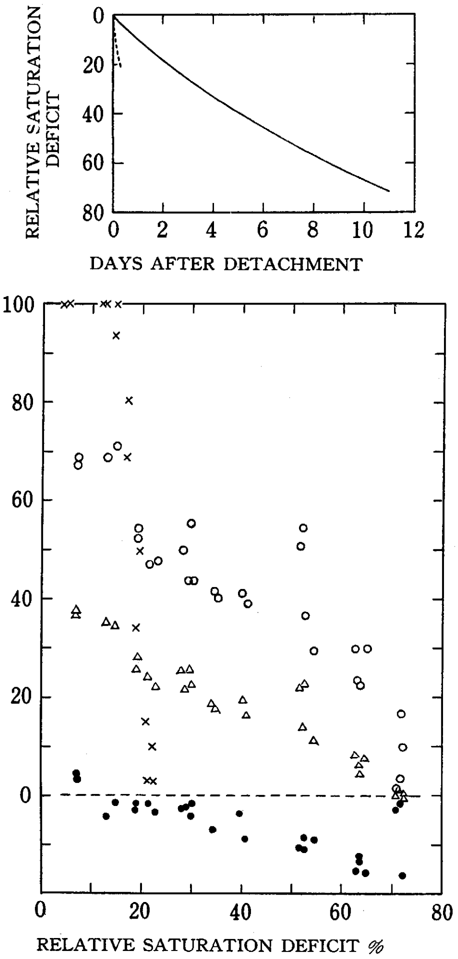

Fig. 42. Time course of change in relative saturation deficit of detached twigs of *Cryptomeria japonica* (upper) exposed to rapid (broken line) or slow desiccation (solid line), and relation of relative saturation deficit to the rates of CO_2-exchange (lower), i.e. apparent photosynthesis in rapid desiccation (crosses), and apparent photosynthesis (solid circles), actual photosynthesis (triangles) and respiration (open circles) in slow desiccation.

III) Moisture Loss of Detached Seedling

In the experiment on CO_2-exchange of detached seedlings, the measurings of fresh weight were possible only at relatively long intervals. Here, the decreases in fresh weight have been measured at short intervals to make clear the difference of species in capacity of moisture retention.

1. Material and method

One-year-old potgrown seedlings of the three species were used. The top of the seedling was cut off and saturated with water by the method previously described. The decrease in fresh weight of the water-saturated top was measured with the lapse of time. The measurement was made in a growth cabinet controlled at light intensity of 20 k lux at the middle of the sample, temperature of 20℃ and relative humidity of 75 percent. Four seedlings of each species were observed in October, 1963.

2. Results and discussion

1) Time course of transpiration

In all the species, the rate of transpiration is relatively low at the start, then increases rapidly to the maximum, after which a rapid decrease follows. The reducing pace decreases with elapsing time and the rate of transpiration becomes low and steady as shown in the lower graph of figure 43. Such a time course of transpiration or moisture loss was reported in many species. And, these changes in rate of transpiration were discussed in relation to the following stomatal movement: (1) a rapid rising of transpiration at the beginning corresponds to the opening of stomata; (2) a rapid decreasing following on the maximum is attributed to the closing of stomata due to dehydration; (3) a relatively low and steady rate at the end coincides with the cuticular transpiration after perfect closing of stomata (STÅLFELT 1929, 1932; PISEK & BERGER 1938; HYGEN 1951; PISEK & WINKLER 1953).

2) Difference among species

P. densiflora differs in decreasing pace of transpiration after attaining its maximum rate and in rate of cuticular transpiration from two other species. These differences are reflected in the decrease in fresh weight. The increase in relative saturation deficit with the lapse of time is smaller in *P. densiflora.* As compared with *Cr. japonica,* the rate of transpiration under the conditions favorable for full stomatal opening is low and the decreasing of transpiration after the maximum is slow in *Ch. obtusa*, but these differences disappear with the progress of dehydration. These differences between the two species appear also in the change of relative saturation deficit.

As has been represented in figure 39, *Ch. obtusa* differs from two other species in the relation between soil moisture content and relative saturation deficit, i.e. its relative saturation deficit at the field capacity is higher. To make clear the response of each species to drying of soil, the relation in figure 39 is modified as shown in figure 44, in which the decrease in water content of the potted seedling is expressed as relative fresh weight to that at the field capacity. The water retaining capacity under drying of soil is higher in *P. densiflora,* intermediate in *Ch. obtusa* and lower in *Cr. japonica.* These differences of species in rate of transpiration or water loss agree with those observed in 1-year-old seedlings by ITO (1950), or in seedlings at the first summer after their emergence by SATOO (1956). The fact that the difference of species is similar to that in decrease of photosynthetic rate of the detached seedling in figure 40, suggests a close relation of water content to CO_2-uptake of the seedling under deficient water conditions.

Using the time course of transpiration (PISEK & BERGER 1938; PISEK & WINKLER 1956) are estimated the stomatal movements due to dehydration as shown in table 2. The difference among the species in table 2 is partly attributed to the difference in the relation of relative saturation deficit to soil moisture content. To accord this difference, each value in table 2 is converted into that based on the fresh weight at the field capacity, at which relative saturation deficit is 7 percent in *P. densiflora,* 9 percent in *Cr. japonica* and 14 percent in *Ch. obtusa.* As shown in table 3, the response of stomatal movement to internal water deficit is highly sensitive in *P.*

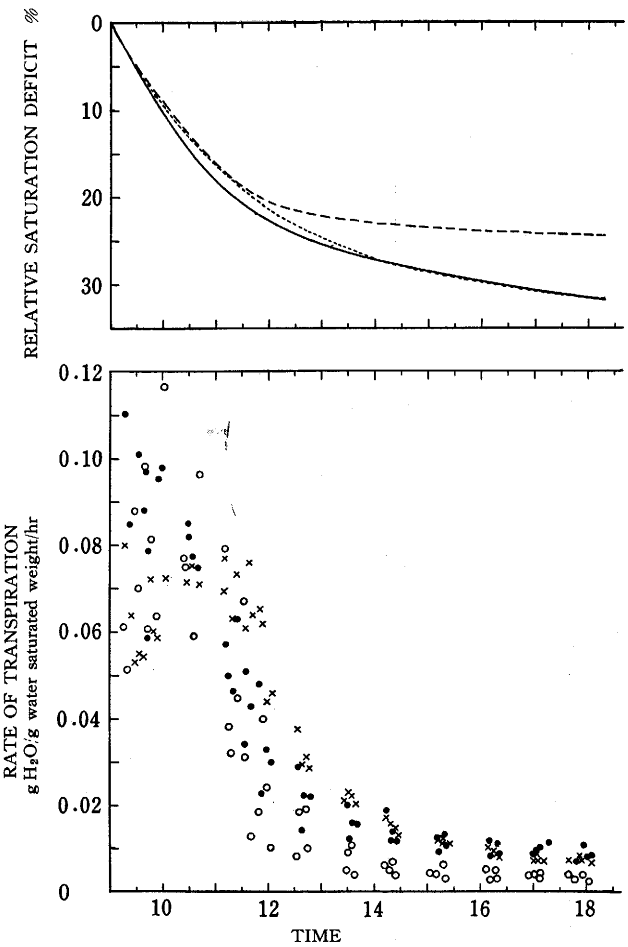

Fig. 43. Time course of change in relative saturation deficit (upper) and in rate of transpiration (lower) of water saturated detached seedlings of *Pinus densiflora* (open circles or broken line), *Cryptomeria japonica* (solid circles or solid line) and *Chamaecyparis obtusa* (crosses or fine broken line).

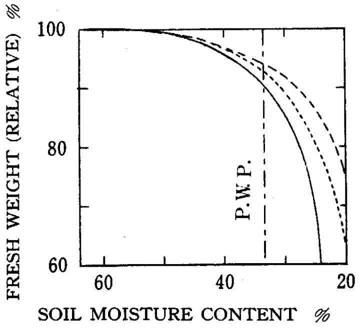

Fig. 44. Decrease in fresh weight of seedlings of *Pinus densiflora* (broken line), *Cryptomeria japonica* (solid line) and *Chamaecyparis obtusa* (fine broken line) with drying of soil.

Table 2. Relative saturation deficit (percent) at the beginning and the ending of stomatal closure.

Species	Beginning	Ending
P. densiflora	9	23
Cr. japonica	11.5	28
Ch. obtusa	18.5	30.5

Table 3. Water deficit (percent)* at the beginning and the ending of stomatal closure, based on the fresh weight at the field capacity (FW).

Species	Beginning	Ending
P. densiflora	2	17
Cr. japonica	3	21
Ch. obtusa	5	19

* (FW-actual fresh weight) ×100/FW.

densiflora. The closing of stomata of *Ch. obtusa* starts at a higher water deficit, but finishes by a lower one in comparison with *Cr. japonica.*

IV) Discussion Relating to Character of Species

The experiment on the attached seedlings shows that photosynthetic response to deficient soil moisture differs with different species. A decrease in photosynthetic rate at the initial stage of drying of soil is only apparent in *P. densiflora,* while that at the advanced stage is very marked in *Cr. japonica,* marked in *Ch. obtusa* and moderate in *P. densiflora.*

Depression in photosynthetic rate owing to deficient water supply may be attributed to a decreased protoplasmic hydration of photosynthetic organ and to a decreased diffusive capacity for CO_2 caused by closing of stomata and increasing resistance of mesophyll. To make clear the cause of the difference of species in photosynthetic response, the water content and the rate of transpiration were compared with each other. The time courses of transpiration of detached seedlings in figure 43 indicate that the closing of stomata begins at a slight decrease in water content and finishes by a higher level, and the rate of cuticular transpiration is lower in *P. densiflora* than that in two other species. Thus, *P. densiflora* is able to retain internal water at a relatively high level under deficient water condition. On the other hand, *Cr. japonica* is inferior to *P. densiflora* in capacity for regulating water balance, because in *Cr. japonica* the stomatal movement is less sensitive to dehydration and the cuticular transpiration is higher, and the water content decreases rapidly with decreasing water supply. In *Ch. obtusa,* the stomata begin to close at a lower water content but close perfectly at a higher one in comparison with *Cr. japonica,* and the pace of decrease in water content is intermediate between two other species.

A similar time course of transpiration may be expected from the potted seedlings. The differences among the species in response of stomatal movement and water content to drying of soil may be reflected in the difference in their photosynthetic behavior. For instance, in *P. densiflora,* an earlier beginning of stomatal closure at the initial stage of drying may be related with a depression in photosynthesis of the seedling retaining a relatively high water content. And, less marked decrease in photosynthetic rate of this species at the advanced stage may be partly attributed to the slower pace of water loss of photosynthetic organ resulting from a rapid closing of stomata and a lower rate of cuticular transpiration, and as given in figure 45, partly attributed to the relatively high rate of photosynthesis comparing with a decreased level of water content.

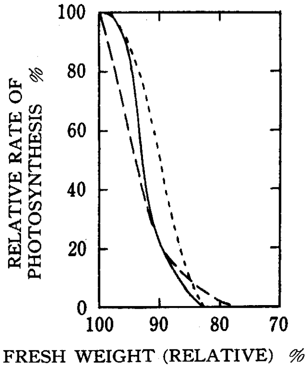

Fig. 45. Decrease in photosynthetic rate with decreasing fresh weight of seedlings of *Pinus densiflora* (broken line), *Cryptomeria japonica* (solid line) and *Chamaecyparis obtusa* (fine broken line).

It is well-known that *Cr. japonica* reaches its full growth under relatively moist conditions, while *P. densiflora* maintains a favorable water balance and indicates less decrease in growth under arid conditions, and *Ch. obtusa* seems more endurable for drought than *Cr. japonica.* In the field the response of trees to drying of soil is affected by many factors associating with water deficit, and it may be questioned whether seedlings and mature trees behave in the same manner, because the both differ from each other in extent of root growth, capacity for reserving water and adaptability to drought. Therefore, the photosynthetic response of the trees to drying of soil in the open may differ from that of the potted seedlings under the controlled conditions. But the result obtained here does not conflict with our knowledge of the ecological and silvical characters of these three species.

"Relative saturation deficit" is better than "water content on a dry weight basis" as an expression of internal water condition for studying the influence of moisture deficit on photosynthesis. But, that is not very sensitive as a quantitative measure of water deficit in the photosynthetic tissue, because most of the water in growing plants is in the vacuolated and other non-living regions.

The relation of relative saturation deficit to soil moisture varies according to species, by which the comparison among the species is complicated. Since the relation between water content and water potential differs with different species (WEATHERLEY & SLATYER 1957), a parallel measurement of diffusion pressure deficit as made by BRIX (1962) may be more useful for us to study the photosynthetic response to dehydration of protoplasm.

CHAPTER V. SEASONAL VARIATIONS IN RATE OF PHOTOSYNTHESIS*

It is sufficient to know that there are marked seasonal variations in photosynthesis, higher rate for the period spring to fall and lower one during winter (STÅLFELT 1960b;

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* An outline of Chapter V was presented at 75th Meeting of Japanese Forestry Society, Kyoto, April 1964.

Pisek 1960b). These seasonal variations may be attributed to seasonal changes in physiological condition of plants which may affect their photosynthetic capacity, and to those in external factors affecting directly photosynthesis such as light intensity, photoperiod and temperature.

Though a number of studies have been made on the seasonal variations of photosynthetic rate, most of them dealt with only photosynthetic capacity or efficiency, in which the measurements of the rate of CO_2-uptake under the uniform conditions were made at different seasons. And the reports studying the seasonal change in the open and discussing the role of external factors in it are few in number.

In the first half of this chapter, the seasonal changes in photosynthetic capacity and those in external factors are studied respectively. In the second half, the daily photosynthetic rates are estimated in 1-year-old seedlings of the three species growing under the nursery conditions and are discussed in connection with the role of each factor playing in seasonal trend of photosynthesis.

In chapters from I to IV of this paper were described the differences of species in photosynthetic response to each external factor separately. The daily photosynthetic rates estimated here show probably to what extent these differences in character of species can affect the photosynthetic production in each species under the nursery conditions.

I) Seasonal Change in Photosynthetic Capacity

1. Material and method

One-year-old seedlings of *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa* were grown in the nursery at Tanasi, in the west suburbs of Tokyo, exposing to the normal seasonal changes in light, photoperiod and temperature. Detached tops of these seedlings were used as material, instead of potted seedlings, because the potted seedlings may differ from the seedlings grown in nursery in their photosynthetic capacity even though the appearance seems to be not different. The photosynthetic capacity determined here will be used for the estimation of dry matter production of the seedlings growing under the nursery conditions. After the base of the excised top of seedling was inserted in water in a container and recut under the water, the sample was carried into the laboratory.

The rate of photosynthesis was measured under the favorable conditions. Light intensity was kept at 45 k lux at the top and 25 k lux at the middle of the detached seedling. Air temperature in the chamber was maintained at 20℃ in the spring and fall, and at 25 or 30℃ in the summer. The rates obtained at higher temperatures were converted into those at 20℃ using the relation in figure 37. The gas analyzer and the assimilation chamber were the same as described in Chapter I. For the period April to November in 1961, the photosynthetic rates of four to six individuals of each species were measured in each determination at intervals of about a month. Each run of determination was finished when the rate was leveling off.

As may be expected from figure 16, it is difficult to obtain a steady rate of photosynthesis in winter, even though the measurement is made under the constant conditions. Since the detached seedlings grown in nursery did not differ remarkably from the potted seedlings in their photosynthetic capacity in early spring and late fall, the maximum rate of the latter was served as a substitute for photosynthetic capacity of the former in winter.

2. Results and discussion

1) Seasonal trend of photosynthetic capacity

The average rates of photosynthesis per unit weight of the top of the seedling are presented in figure 46. The increase in photosynthetic capacity starts with little at February or March, and becomes rapid and marked with the lapse of time. The maximum rate of photosynthetic capacity is attained for the period midsummer to early fall, at which the rate reaches 9 mg in *P. densiflora* and 11 mg in *Cr. japonica* and *Ch. obtusa* per unit oven dry weight of the top per hour. Then the rate begins to decrease and reaches its minimum in midwinter. In *P. densiflora*, the rise in spring appears earlier and the decline in fall later, and the rate of decrease in winter is smaller than that in the other two species. Thus, the photosynthetic capacity of *P. densiflora* has been maintained at a relatively high level throughout the year.

As described above, a number of experimental studies have been made on the seasonal variations in photosynthetic capacity, in which the following evergreen conifers were dealt with: *Abies balsamea* (CLARK 1961), *Picea excelsa* (ZELLER 1951; PISEK & TRANQUILLINI 1954; PISEK & WINKLER 1958; BOURDEAU 1959), *Picea glauca* (CLARK 1961), *Picea pungens* (BOURDEAU 1959), *Tsuga canadensis* (BOURDEAU 1959), *Pinus palustris* (PARKER 1961), *Pinus rigida* (BOURDEAU & WOODWELL 1964), *Pinus taeda* (MCGREGOR & KRAMER 1963), *Pinus strobus* (MCGREGOR & KRAMER 1963; NELSON 1963), *Pinus sylvestris* (IWANOW & ORLOWA 1931; BOURDEAU 1959; PARKER 1961; POLSTER & FUCHS 1963), *Pinus cembra* (CARTELLIERI 1935; PISEK & WINKLER 1958; TRANQUILLINI 1957, 1959a), *Chamaecyparis pisifera* (NOMOTO, KASANAGA & MONSI 1959; PARKER 1961). In spite of the difference of species and the

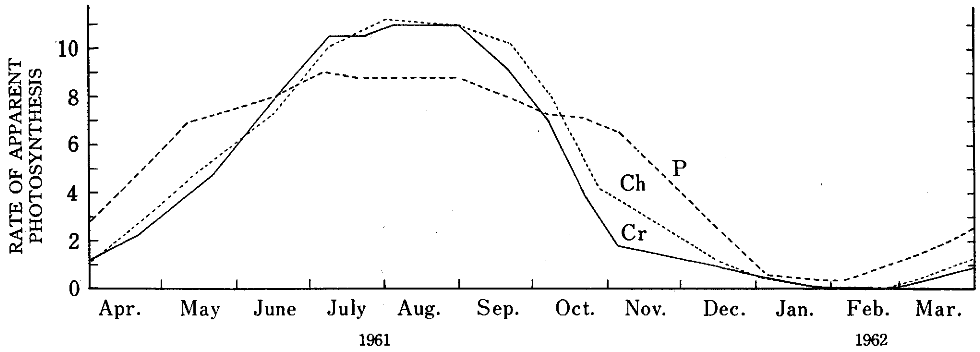

Fig. 46. Seasonal change in photosynthetic capacity (mg CO_2/g dry wt. of top of seedling/hr) measured at 20℃ and at a light intensity sufficient for leveling off the light curve in each of the three species, *Pinus densiflora* (P), *Cryptomeria japonica* (Cr) and *Chamaecyparis obtusa* (Ch).

wide variations in experimental conditions, the seasonal variations in photosynthetic capacity of the three species agree essentially with the results of those works, a higher level from spring to fall and a lower one in winter.

2) Change associating with growth of new part

A temporary depression in photosynthetic capacity in spring was observed in some studies dealing with evergreen conifers (PISEK & WINKLER 1958; NEUWIRTH 1959; TRANQUILLINI 1959a; CLARK 1961). Since the depression is attributed to the increase of respiration associating with rapid metabolism in production of the new part, the higher the ratio of new parts to the entire sample, the more remarkable the drop in photosynthesis may be expected.

In the three species studied here, a steady gradual increase in photosynthetic capacity continues instead of a temporary decline corresponding to the growth of new part, which may be attributed to that the rising of photosynthetic capacity in old part exceeds the decrease resulting from the respiration for production of new part. For instance on May 3, 1960 were measured respectively the photosynthetic rates of the new and old part of the 1-year-old potted seedling of *P. densiflora*. This measurement was attempted together with the experiment on daily course, and was made outdoors at about 25℃ and at a light intensity sufficient for leveling off the light curve. The rate of apparent photosynthesis of entire top is 5.01 mg CO_2 per hour, while that of new part is -0.22 mg CO_2 per hour. Though the level of apparent photosynthesis is negative in the new part, its effect on the photosynthetic capacity of the entire seedling may be little. Since the rate of dark respiration is 0.42 mg CO_2 per hour in the new part, CO_2-uptake is already made by the new part on May 3.

3) Decrease caused by frost

The decline in photosynthetic capacity in fall may be partly attributed to the aging of leaves (CLARK 1961), but mainly related with the fall of temperature, on which the studies dealing with *Picea excelsa* (ZELLER 1951; PISEK & WINKLER 1958), *Pinus sylvestris* (IWANOW & ORLOWA 1931) and *Pinus cembra* (TRANQUILLINI 1957, 1959a) were reported. According to these works, the effect of frost varies with season and duration of lower temperatures. By successive warmer weather after frost, the photosynthetic capacity is revived from a lower level.

In this work the photosynthetic capacity was measured at intervals of about a month, but it is necessary to observe at shorter intervals to make clear the relation of temperature to seasonal trend of photosynthetic capacity. To answer this question indirectly, the seasonal changes in daily course of photosynthesis described in Chapter I and those in photosynthetic response to temperature in Chapter III are shown in figure 47 together with daily minimum temperature at 20 cm above the ground. The time and the temperature, at which these seasonal changes from fall to winter take place, differ with different species, later and lower in *P. densiflora*.

As observed in *P. densiflora* and *Cr. japonica* from October to November in 1960, the daily course changed to the winter type by frost is returned to the summer type for

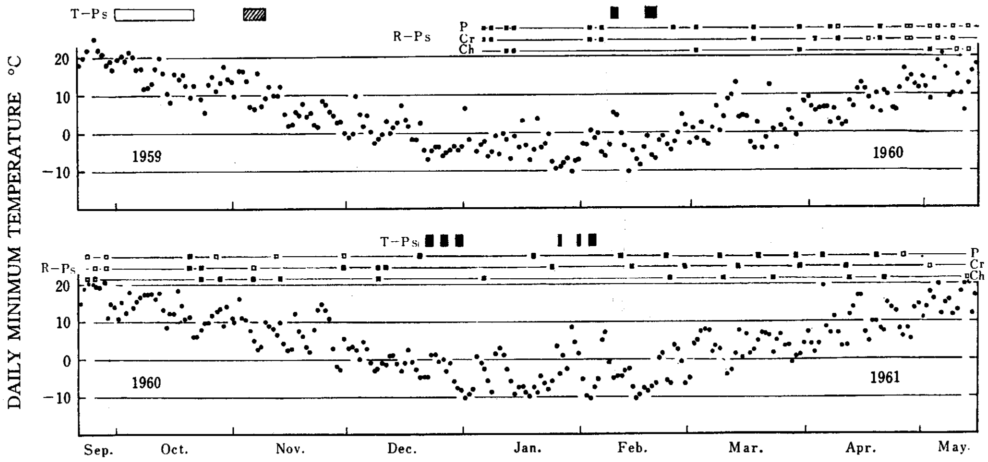

Fig. 47. Seasonal change in photosynthetic response to radiation intensity and to temperature in relation to daily minimum temperature at 20 cm above the ground. **T–Ps**: photosynthetic response to temperature; the type in growing season in all the three species (open), the type in winter only in *Cryptomeria japonica* and *Chamaecyparis obtusa* (hatched), and the type in winter in all the three species (solid), **R–Ps**: photosynthetic response to radiation intensity; the summer type (open squares), and the winter type (solid squares) in *Pinus densiflora* (P), *Cryptomeria japonica* (Cr) and *Chamaecyparis obtusa* (Ch).

a time by a continued warmer weather. Since the intervals of the measurement are too long, it is difficult to answer the question, to what degree of fall in temperature the summer relation can remain unchanged. But it seems that in *Cr. japonica* and *Ch. obtusa* the change in relation from fall to winter is associated with a succession of daily minimum temperature below 10℃, while in *P. densiflora* with a lower temperature probably near 0℃. The change from winter type to summer one takes place in spring when the daily minimum temperature above 10℃ continues.

Since the decrease of photosynthetic rate in winter is attributed to low temperature, the depression is not remarkable in a green house (PARKER 1961). To protect against the frost, the potted seedlings of the three species have been carried into the green house

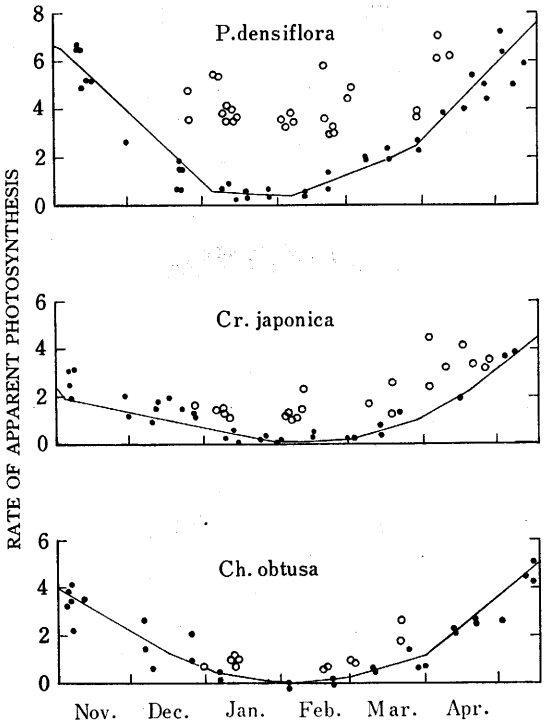

Fig. 48. Depression in photosynthetic capacity (mg CO_2/g dry wt. of top of seedling/hr) of the seedlings left outdoors throughout winter (solid circles and solid lines) and those carried into the green house only in the night (open circles).

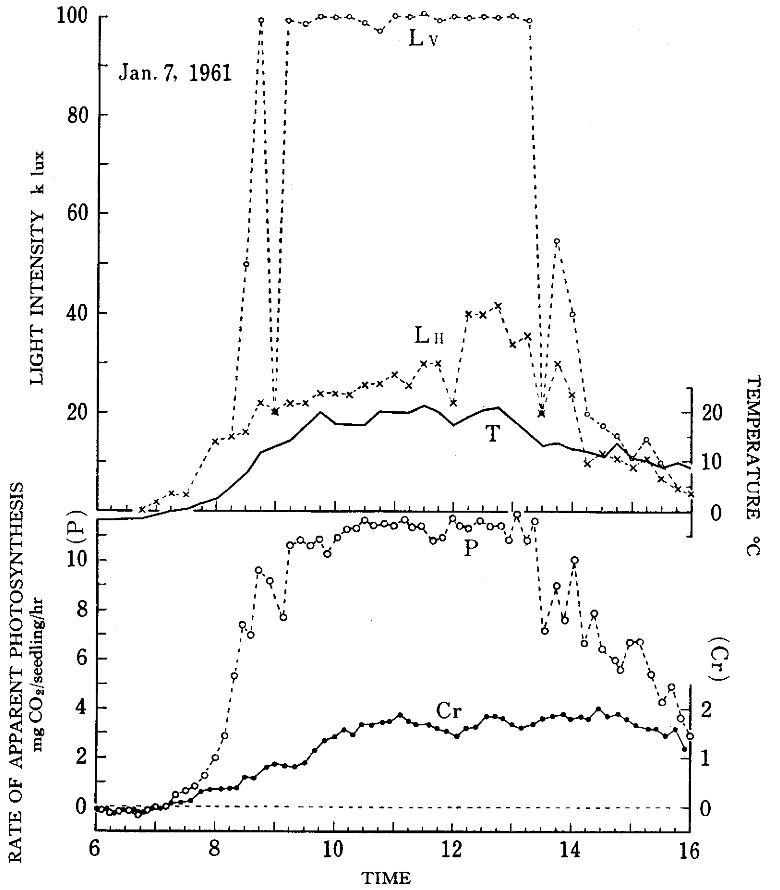

Fig. 49. Daily course of photosynthesis in *Pinus densiflora* (P) and *Cryptomeria japonica* (Cr) observed in the seedlings carried into the green house only in the night, on a clear day in winter (January 7, 1961). **Lv**: normal light intensity, **LH**: horizontal light intensity, **T**: air temperature in the open.

without heater, in which the daily minimum temperature was higher only in few degrees than in the open. The treatment was made only in the night from December to March. As may be seen in figure 48, the photosynthetic capacities of the seedlings carried into the green house are higher than those left outdoors in all the species. The effect of treatment is marked in *P. densiflora,* which may be related to less response to lower temperatures in this species.

Protection from severe frost affects also diurnal variations in photosynthetic rate as shown in figure 49. The daily course of the seedling carried into the green house differs apparently from that left in the open. The course of *P. densiflora* is similar to the summer type.

For the winter depression in photosynthetic capacity of evergreen conifers, the following causes have been discussed, the changes in content of water (PISEK & WINKLER 1958; TRANQUILLINI & HOLZER 1958; PARKER 1961), of chlorophyl (PISEK & WINKLER 1958;

NOMOTO, KASANAGA & MONSI 1959; BOURDEAU 1959; MCGREGOR & KRAMER 1963) and of sugars with hardening (PARKER 1961, 1963). Studies on these points are not made in this paper.

4) Lower limit of photosynthesis

As may be seen in figure 50, the compensation point is observed at −5℃ in *P. densiflora* and *Cr. japonica,* and at −3℃ in *Ch. obtusa.* Therefore, the three species are able to make positive photosynthesis at temperature of few degrees below zero under certain conditions.

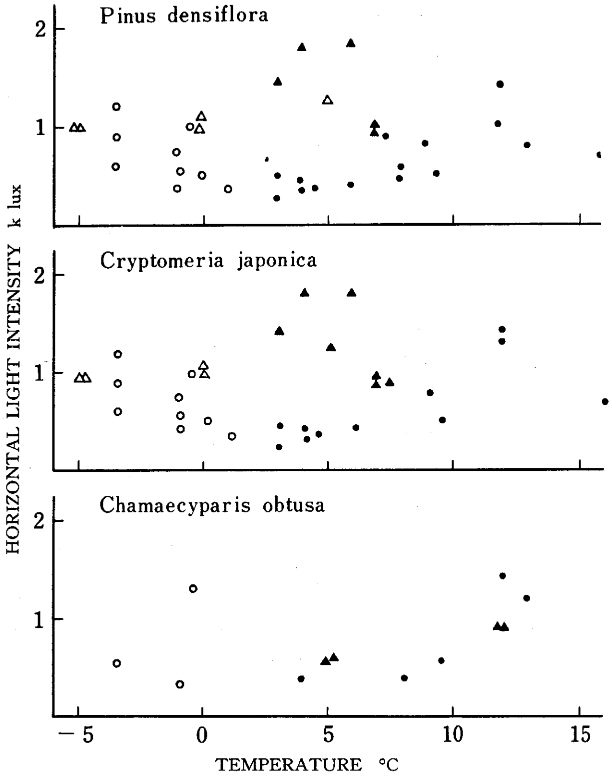

Fig. 50. Compensation point in winter in relation to temperature. Values in the morning (open triangles) or evening (solid triangles) of the seedlings left outdoors throughout winter are compared with those in the morning (open circles) or evening (solid circles) of the seedlings carried into the green house only in the night.

PAVLETIĆ and LIETH (1958) reported that the light intensity at compensation point in winter was higher than that in growing season, and became lower when the sample had been left under warmer conditions. Since the overlapped range of temperature between figure 34 and figure 50 is narrow, it is difficult to compare the winter with the growing season in the relation of compensation point to temperature. But the fact that the light intensity at compensation is lower in the seedlings carried into the green house

Table 4. Minimum temperature of positive apparent photosynthesis.

Species	Min. temp. ℃		Species	Min. temp. ℃	
Taxus baccata	−4	PISEK & REHNER 1958	*Pinus sylvestris*	−7	IWANOW & ORLOWA 1931
Picea excelsa	−2∼−3	PRINZ 1933		−2∼−3	PRINZ 1933
				−2∼−3	ÅLVIK 1939
	−2∼−3	ÅLVIK 1939		−6	FREELAND 1944
	−2∼−6	ZELLER 1951		−4	PISEK & REHNER 1958
	below 0	PARKER 1953		−3	POLSTER & FUCHS 1963
	0	PISEK & TRANQUILLINI 1954	*Pinus nigra* var. *austriaca*	−6	FREELAND 1944
	−2	PISEK & REHNER 1958	*Pinus cembra*	−4	TRANQUILLINI 1957
Picea mariana	−6	FREELAND 1944		−0.5	PISEK & REHNER 1958

than those left outdoors may indicate the seasonal changes of compensation point.

The minimum temperature of photosynthesis was studied in many works (PISEK 1960a, b). The values dealing with evergreen conifers are summarized in table 4. The lower limits of photosynthesis of the three species studied here are similar in level to those in the table.

II) Seasonal Change of Temperature and Radiation in Relation to Seasonal Trend of Photosynthesis

The effects of temperature and radiation on the seasonal trends of photosynthetic production are roughly estimated by the use of climatic data recorded in the nursery.

1. Air temperature

The method used by TRANQUILLINI and TURNER (1961) for arranging data on *Pinus cembra,* was applied here. Air temperature at 20 cm above the ground was used, because the height of 1-year-old seedlings of the three species is relatively small and the temperature at near to the ground may be closely related to their metabolism as compared with the ordinary air temperature at 150 cm high. The arrangements were made only on the values in the daytime. Hours of each hourly mean temperature arranged in every one degree were summed up monthly.

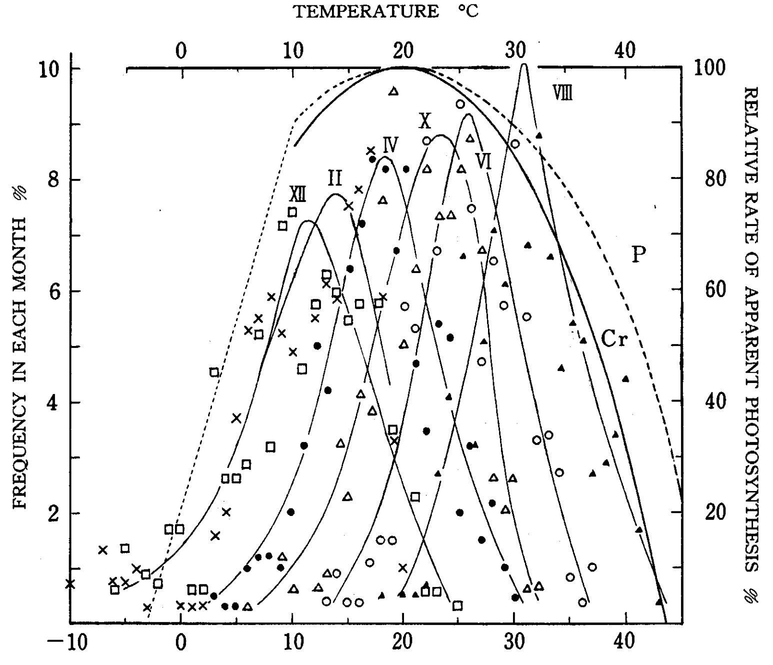

Fig. 51. Frequency curves of hourly mean air temperature at 20 cm above the ground, together with the temperature-curve of photosynthesis in *Pinus densiflora* (P, broken line) and *Cryptomeria japonica* (Cr, solid line). Frequency curves of temperature are given on April (solid circles), June (open circles), August (solid triangles), October (open triangles), December in 1960 (open squares) and February in 1961 (crosses).

The frequency curves of temperature in every month are compared with the temperature-curves of photosynthesis in figure 51, in which only the values of every other month from April, 1960 to March, 1961 are shown to avoid confusion. Temperatures suitable for photosynthesis are found in abundance in spring, April and May, and in fall, October and November as may be expected also from monthly mean temperature in the daytime shown in table I in the appendix. The summer is abundant in above-optimal temperatures, and the winter in below-optimal ones. Since the optimum temperature of photosynthesis in winter is lower than in growing season, the period of below-optimal temperature in winter may be shorter than that expected from figure 51. Because of the narrower range of temperature suitable for photosynthesis in *Cr. japonica* and *Ch. obtusa*, the effect of the seasonal changes is more remarkable in these two species than in *P. densiflora*.

2. Radiation intensity

In the studies dealing with *Pinus cembra,* the relation of seasonal changes in radiation intensity to CO_2-uptake had been studied in connection with the monthly total of radiation intensity in each of the four different ranges corresponding to different photosynthetic rate by TURNER (1961), or in connection with the seasonal changes in daily radiation intensity by TURNER and TRANQUILLINI (1961). In this work were summed up respectively hours of each range of radiation intensity devided into every 2.5 g cal/cm^2/hr. The totals per month in June and in December are compared with the light-curves of photosynthesis in figure 52. A longer photoperiod associating with higher radiation intensity in June seems to be more favorable for photosynthetic production. The months under the conditions of higher elevation of sun may have advantage in light condition over those of lower one as shown in radiation intensity of table I.

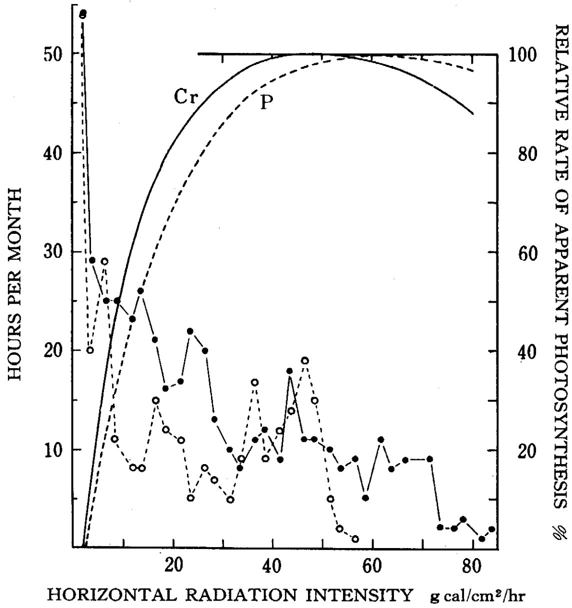

Fig. 52. Distribution of monthly radiation intensity summed up in each of the divided ranges in June (solid circles and solid line) and in December (open circles and broken line), together with the light-curve of photosynthesis in *Pinus densiflora* (P, broken line) and *Cryptomeria japonica* (Cr, solid line).

3. Duration of favorable temperature and radiation intensity

In this section, the influences of temperature and radiation intensity on seasonal changes of photosynthetic production are evaluated by another way. Durations of temperature and radiation intensity within the range in table 5, in which higher photosynthetic rates above 90

Table 5. Range of temperature and radiation intensity for attaining photosynthetic rate above 90 percent of the maximum.

Species	Temperature ℃	Radiation intensity g cal/cm^2/hr
P. densiflora	10∼29	over 33
Cr. japonica	12∼27	26 ∼78
Ch. obtusa	14∼27	29.5∼69

percent of the maximum are able to be expected in the three species, were totaled monthly. As a lower limit of the calculation, 90 percent of the maximum rate of photosynthesis was chosen considering its variations under favorable conditions, for instance, as shown in figure 24.

The results of calculation for the period April, 1960 to May, 1961 are summarized in figure 53 and in table II. The longer durations of temperature favorable for photosynthesis are found in spring and fall, and those of radiation intensity for the period spring to summer. In table 6, the durations of higher and lower temperature or radiation intensity

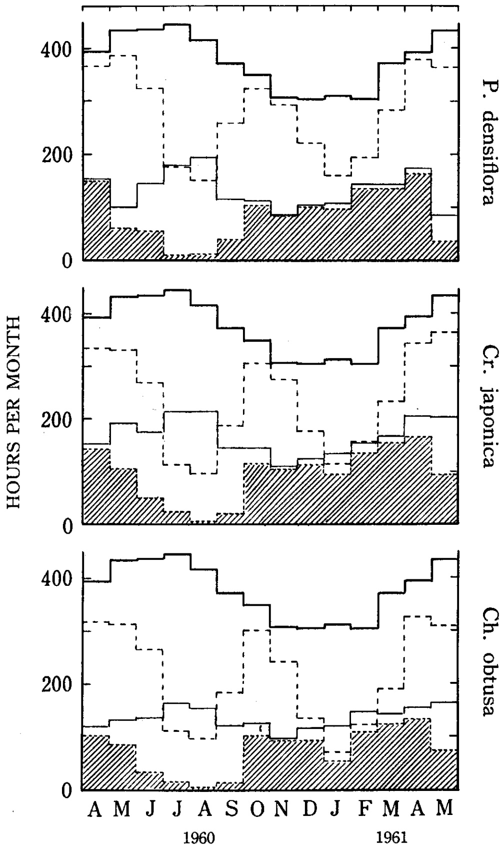

Fig. 53. Seasonal change in duration of photoperiod (thick solid line), and that of temperature (broken line), horizontal radiation intensity (thin solid line) and the both at the same time (hatched) favorable for attaining photosynthetic rate above 90 percent of the maximum.

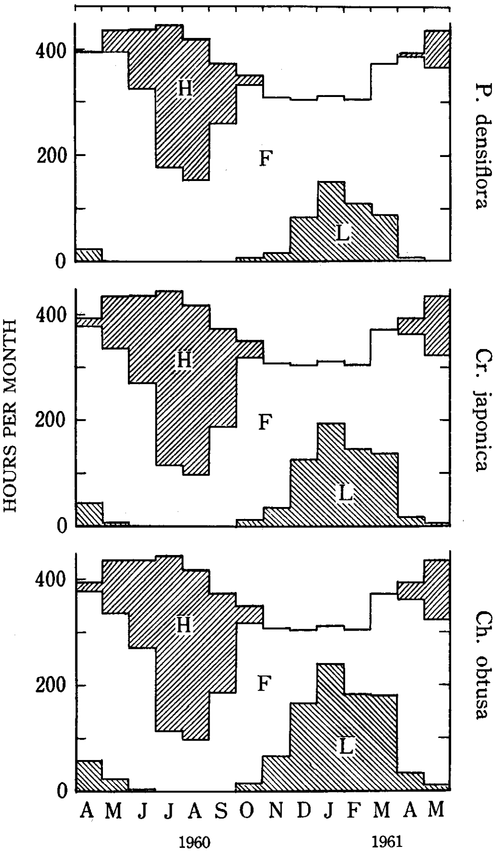

Fig. 54. Seasonal change in duration of higher (hatched, H), favorable (open, F) and lower temperature (hatched, L) for attaining photosynthetic rate above 90 percent of the maximum.

Table 6. Duration of higher (H), favorable (F) and lower (L) temperature or radiation intensity for attaining photosynthetic rate above 90 percent of the maximum. Total hours for the period April, 1960 to March, 1961 having photoperiod of 4,447 hours.

Species	Temperature			Radiation		
	L	F	H	L	F	H
P. densiflora	482	3,147	818	2,755	1.692	0
Cr. japonica	697	2,606	1,144	2,456	1,931	60
Ch. obtusa	938	2,365	1,144	2,652	1,593	202

Table 7. Duration of temperature (T), radiation intensity (R) and the both at the same time (T and R) favorable for attaining photosynthetic rate above 90 percent of the maximum in percentage to total photoperiod of 4,447 hours for the period April, 1960 to March, 1961.

Species	T	R	T and R
P. densiflora	70.8	38.1	24.5
Cr. japonica	58.6	43.4	24.5
Ch. obtusa	53.2	35.8	19.1

are compared with those of favorable one. The duration of favorable temperature in *P. densiflora* is longer than in two other species as may be expected from the difference in temperature-curves of photosynthesis. As shown in figure 54, the summer abounds with higher temperature and the winter with lower one. The difference of species in duration of higher radiation intensity, zero in *P. densiflora* and the longest in *Ch. obtusa,* is related to the difference in light-curves of photosynthesis. Most of duration of higher radiation intensity is found for the period spring to summer, when the altitude of sun is higher.

The duration in which both temperature and radiation intensity are favorable simultaneously for photosynthesis, varies with the season, shorter in summer and longer in fall, winter and spring. It is of interest to note that the shorter durations are associated with the higher photosynthetic capacity in summer, while the longer durations with the lower one.

The durations in each month in table II are summarized in table 7 for the period April, 1960 to March, 1961. The longer duration of favorable temperature in *P. densiflora* is connected with its capacity for carrying out a higher photosynthesis over a wide range of temperature, while the shorter duration of favorable radiation intensity is related with its light-demanding character reflected in the light-curve of photosynthesis. The shorter duration of favorable radiation and of both temperature and radiation in *Ch. obtusa* is mainly attributed to its decrease in photosynthetic rate at higher light intensities.

The above-mentioned results were based on the assumption that the temperature-curve of photosynthesis in growing season is available all the year round. Since the effect of temperature on apparent photosynthesis differs with different seasons, the calculation is made using the temperature-curve in winter. Though the relation between temperature and photosynthetic rate varies with degree of frost, the relation in early winter in figure 37 is applied here, in which higher rates of photosynthesis above 90 percent of the maximum are expected in the following ranges of temperature: 9～24℃

in *P. densiflora,* 9~22℃ in *Cr. japonica,* and 11~20℃ in *Ch. obtusa.* The results calculated in December, January and February are shown in table II. The durations of favorable temperature are longer than those calculated by the use of temperature-curve in growing season. The effect of this difference on the photosynthetic production will be quantitatively discussed later.

In winter as described in Chapter I, a close relationship between light intensity and photosynthetic rate is frequently disturbed by the remarkable midday drop and/or the change in photosynthetic capacity in the morning. Therefore, the application of light-curve in growing season to photosynthesis in winter may produce an error, but the rearrangement as applied to temperature is not made, because there are no data sufficient for determining the light-curve in winter.

III) Seasonal Change in Daily photosynthetic Rate in the Nursery

1. Calculation of daily photosynthetic rate

Since the determination of CO_2-exchange extending over a long term is laborious and troublesome in the open even though an advanced gas analyzer is available, the studies on seasonal change of photosynthesis *in situ* are few in number, in which works on apple (HEINICKE & CHILDERS 1937) and on *Pinus cembra* (TRANQUILLINI 1957, 1959a) are included. In this work, continuous measurements in the open are not made. But the daily rates of photosynthesis in the nursery are able to be estimated by the use of light- and temperature-curves of photosynthesis, seasonal changes in photosynthetic capacity, and records of horizontal radiation intensity and air temperature at 20 cm above the ground.

To make clear the cause of seasonal variations were made the calculations of the following four different cases from (a) to (d) respectively for the two separate periods, April, 1960 to March, 1961 and April, 1961 to March, 1962. All of these estimations were based on the assumption that the soil moisture conditions had been always maintained at an optimal level, at near the field capacity.

Calculation (**a**) was based on the assumption that photosynthesis corresponding to the maximum photosynthetic capacity continued the whole year under the conditions of radiation intensity under clear weather and of optimum temperature. The daily rates of photosynthesis were obtained by totaling hourly rates which were estimated by the use of the following data; the hourly changes in altitude of sun in Tokyo at different seasons, the relation between altitude of sun and photosynthetic rate at the optimum temperature of 20℃ in figure 36, and the maximum photosynthetic capacity in each species.

As shown in figure 36, the photosynthetic rate of each species is decreased by excessively higher light intensities and higher altitudes of sun, especially in *Ch. obtusa* and *Cr. japonica.* Therefore the rate of calculation (a) is possibly lower than that under the optimal light conditions, but it may be considered as a standard rate near the maximum. The seasonal variations in calculation (a) may be connected with the changes in photoperiod or radiation intensity caused by the seasonal change in altitude of sun.

Calculation (**b**) was based on the assumption that photosynthesis corresponding to

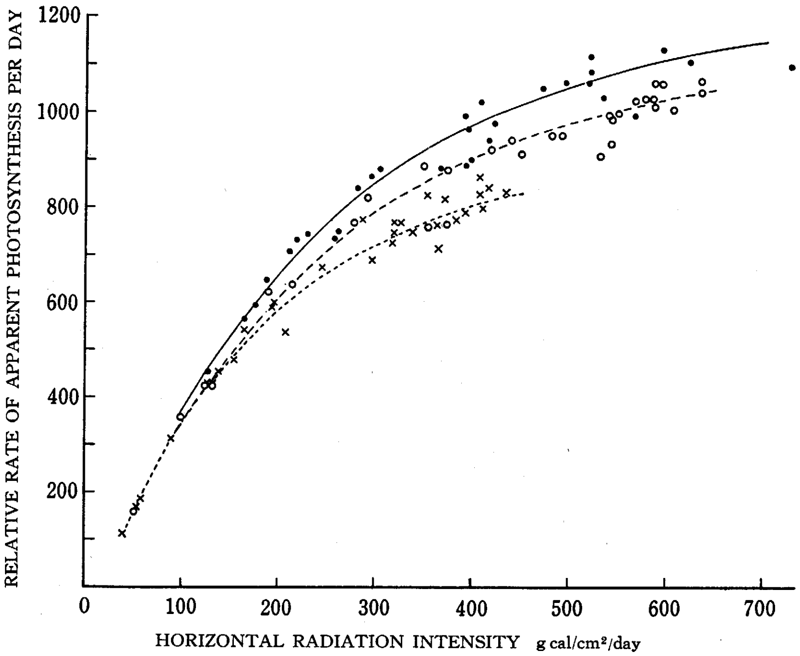

Fig. 55. Seasonal change in the relation of daily radiation intensity to daily photosynthetic rate of *Pinus densiflora* in June (solid circles and solid line), August (open circles and broken line) and October (crosses and fine broken line). Photosynthetic rate per day is obtained by totaling relative rate per hour.

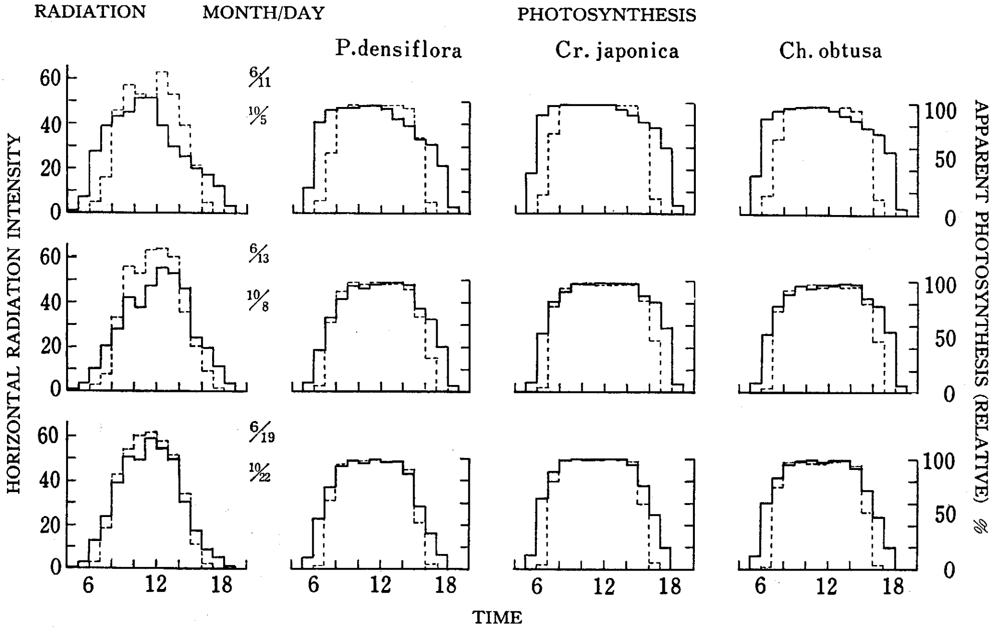

Fig. 56. Hourly distribution of radiation intensity and apparent photosynthesis of the three species on a day. Values in June (solid lines) are compared with October (broken lines) to explain the cause of seasonal change in the relation in figure 55.

the actual photosynthetic capacity in figure 46 continued under the conditions of radiation intensity under clear weather and of optimum temperature throughout the year. The difference in rate between (a) and (b) may be caused by the seasonal change in photosynthetic capacity in figure 46.

Calculation (c) was based on the assumption that photosynthesis corresponding to the actual photosynthetic capacity continued under the conditions of actual radiation intensity and of optimum temperature throughout the year. The daily rates of photosynthesis were estimated by totaling hourly rates which were calculated by the use of the hourly radiation intensity recorded with Robitzsh's actinograph and the relation between radiation intensity and photosynthetic rate at the optimum temperature of 20℃ in figure 36.

Owing to the seasonal change in distribution of daily radiation intensity among different times of day, the relation of daily radiation intensity to relative daily photosynthetic rate differs with different seasons as shown in figure 55. For instance, the days similar in radiation intensity, about 400 g cal per cm² per day are picked out in June and October, and the hourly distributions of daily radiation intensity and the daily photosynthetic rate are shown in figure 56. As may be seen in the figure, the daily photosynthetic rate at a certain daily radiation intensity in June is higher than the corresponding rate in October.

The difference between (b) and (c) may be attributed to the changes in radiation intensity caused by the daily variations in weather conditions.

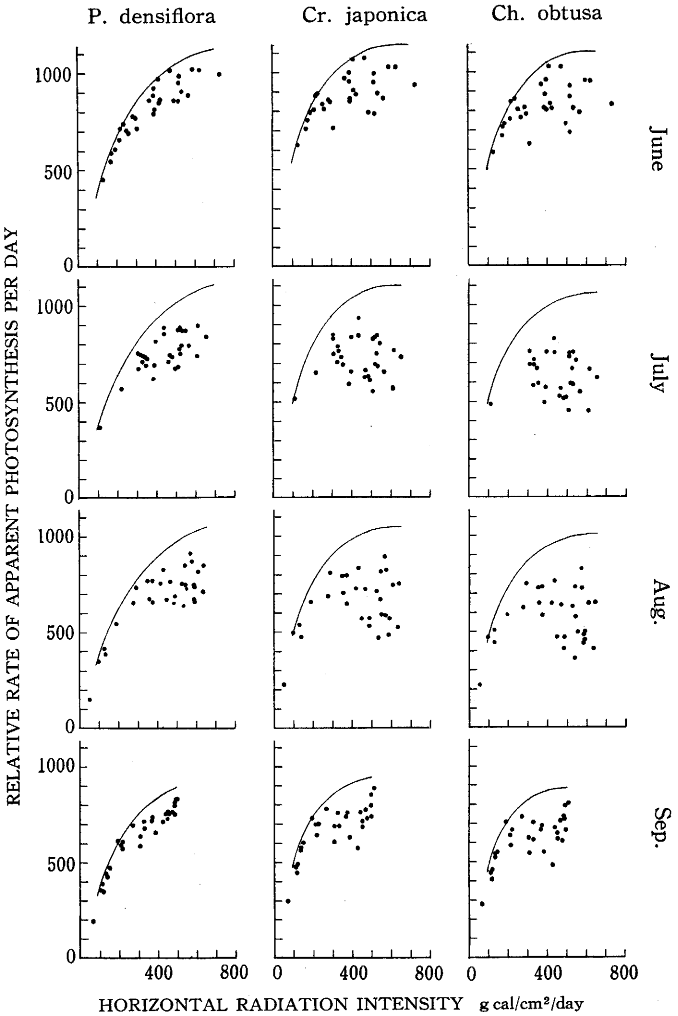

Fig. 57. Seasonal change in daily photosynthetic rate estimated by calculation (c) (solid lines) and calculation (d) (solid circles) in relation to daily radiation intensity.

Calculation (d) was the estimation of rate of photosynthesis carried out with the actual photosynthetic capacity under the conditions of actual radiation intensity and of actual temperature, which was equivalent to the rate expected in the nursery. To obtain the hourly rates of photosynthesis, the record of air temperature at 20 cm above the ground and the relation between temperature and photosynthetic rate in figure 37 were applied to the hourly rates in calculation (c). The calculation was based on the assumption that the temperature-curve of photosynthesis in growing season was available throughout the year. The error caused by application of this assumption may be not marked as will be described later. The difference between (c) and (d) may be attributed to the seasonal changes in temperature.

In figure 57 the relative daily photosynthetic rates calculated in (c) and (d) are plotted against the daily radiation intensity from June to September, 1960. The photosynthetic rates in midsummer are affected markedly by higher temperatures, and an estimation of daily photosynthetic rate paying no attention to the effect of temperature may be erroneous.

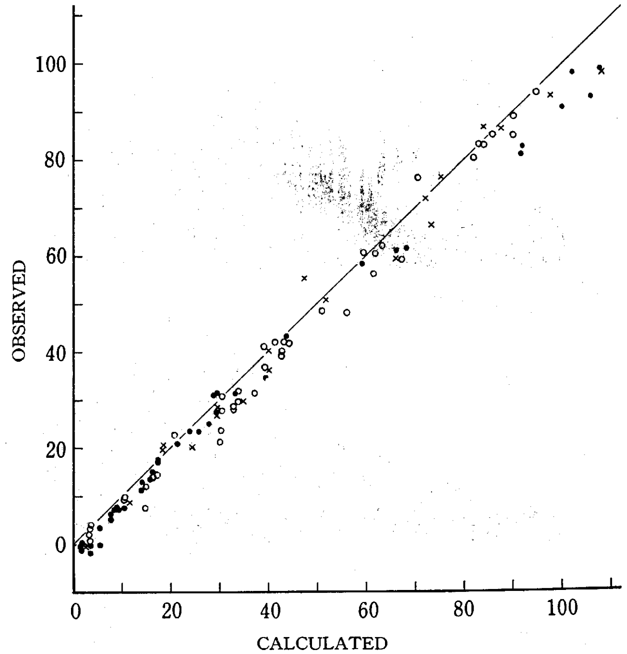

Fig. 58. Comparison between daily photosynthetic rate (mg CO_2/g dry wt. of top/day) of the potted seedling observed experimentally and that estimated by calculation (d) in *Pinus densiflora* (open circles), *Cryptomeria japonica* (solid circles) and *Chamaecyparis obtusa* (crosses). When the rate is plotted on the solid line in the graph, the both rates are equivalent to each other.

Table 8. Assumptions of calculation of daily photosynthetic rate and causes of difference in estimated value.

Calculation	Assumption of calculation			Cause of difference
	Photosynthetic capacity	Radiation intensity	Temperature	
	maximum of calculation (a)			altitude of sun** photosynthetic capacity radiation intensity*** temperature
(a)	maximum	maximum	optimum	
(b)	actual	maximum	optimum	
(c)	actual	actual	optimum	
(d)*	actual	actual	actual	

* Photosynthetic rate under the nursery conditions.

** Changes in photoperiod or radiation intensity associating with seasonal change in altitude of sun.

*** Changes in radiation intensity associating with daily variation of weather conditions.

To estimate the error of calculation, the daily photosynthetic rates of potted seedlings measured experimentally in the open are compared with those estimated by calculation (d). As shown in figure 58 the calculated rates are slightly higher than the measured ones, but the difference between them may be not serious on the whole. In winter as seen in the lower rates in figure 58, the difference becomes relatively large. This difference may be attributed to the change in pattern of daily course of photosynthesis in winter, because the calculation was based on the assumption that the daily course in growing season was applicable throughout the year. The reliability of the calculation also may be shown in the relatively small difference between the dry matter increment of the seedling measured by direct weighing and those estimated by calculation (d), on which will be detailed in Chapter VII.

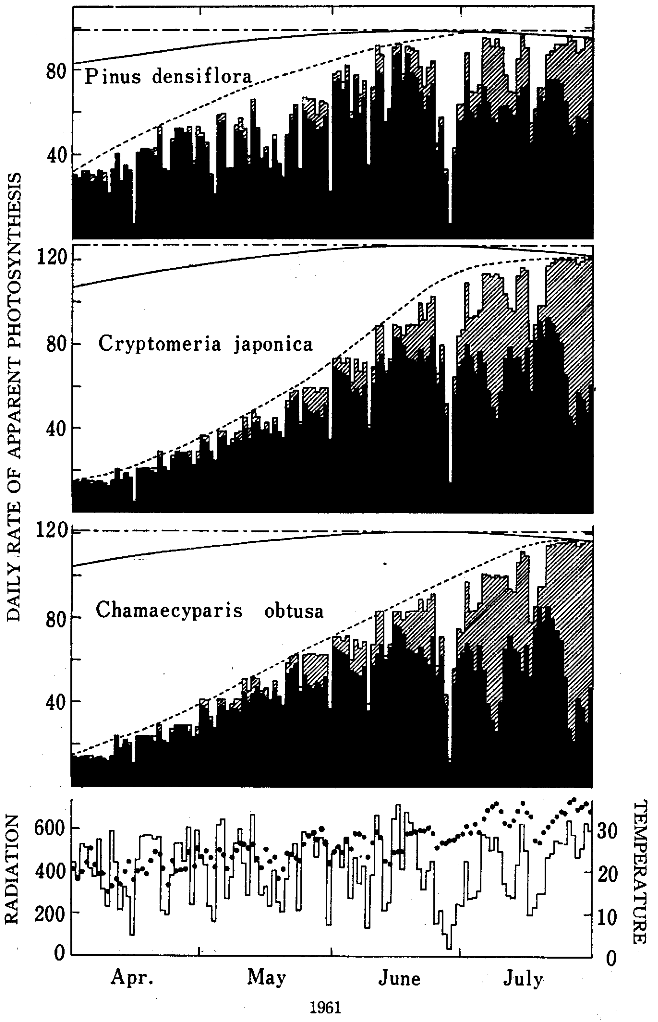

Fig. 59. Seasonal change of daily photosynthetic rate (mg CO_2/g dry wt. of top) estimated by calculation (a) (solid line), calculation (b) (broken line), calculation (c) (hatched columns), and calculation (d) corresponding to the rate in the open (solid columns), together with daily radiation intensity (solid line) and mean air temperature at 20 cm above the ground in the daytime (solid circles). Level of chain line indicates the maximum rate of calculation (a). Assumptions of each calculation and causes of difference among the calculations are summarized in table 8.

2. Seasonal variation in estimated daily photosynthetic rate

The above-mentioned assumptions of the calculations and causes of the difference in rate of different calculations are summarized in table 8. The daily photosynthetic rates obtained in these calculations are shown in figure 59 for the period April, 1960 to March, 1961. In spring, the lower level of photosynthetic capacity resulted in the lower rate of photosynthesis in the open as shown with solid columns in figure 59. The marked effect of photosynthetic capacity is expressed as a large space between broken line and solid one in the figure. The photosynthetic capacity becomes higher with the progress of time towards summer and the photosynthetic rate in the open rises, but the increase is checked by above-optimal temperatures in midsummer as shown with hatched columns in the figure. With further progress of season, the effects of higher temperatures gradually fade out, while those of reduction in photosynthetic capacity shown with a space between solid line and broken one, and the decrease in photoperiod and radiation intensity shown with a space between chain line and solid one, become conspicuous, through which the rate in the open is depressed. The decrease of photosynthesis in the open in winter is mostly due to the lower altitude of sun and the depressed photosynthetic capacity. Since the effects of daily radiation intensity and temperature are relatively small in winter, the rates in (b) and (c) are close upon those in (d), and are not plotted in the figure for the period December to March.

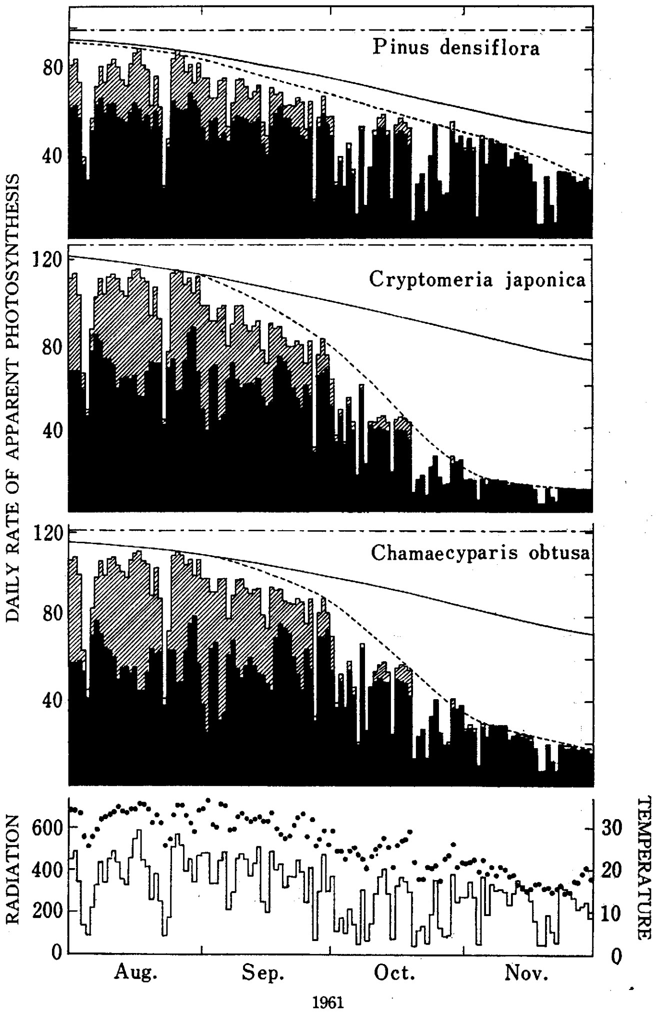

Fig. 59. (Continued).

In *P. densiflora,* the decrease in photosynthetic capacity in winter and the effect of above-optimal temperatures in summer are less remarkable as compared with two other species. For this reason the daily photosynthetic rates of *P. densiflora* have been higher in the open throughout the year.

3. Evaluation of causes of seasonal variation

The daily rates of photosynthesis calculated above were summed up monthly for the two separate periods, April, 1960 to March, 1961 and April, 1961 to March, 1962. In figure 60 and table III, the monthly rates of photosynthesis estimated by calculation (d) are shown with relative value to the maximum rate in calculation (a). The difference between them is divided into each factor causing reduction of photosynthetic rate in the open.

The influence of each factor differs in degree with different seasons. As a cause of depression in photosynthetic rate in the open, the photosynthetic capacity is remarkable for the period late fall to early spring, the altitude of sun appears evidently from fall to winter, and the temperature is conspicuous in summer and in winter, while the daily variation in radiation intensity caused by the change in weather conditions does not show an apparent seasonal trend.

The lower photosynthetic rate in the open in winter is mainly attributed to the reduction in photosynthetic capacity and the decrease in radiation intensity or photoperiod connecting with lower altitude of sun. The rate in summer is high as compared with other seasons, but it may be more higher if the effect of above-optimal temperatures is diminished. Although the radiation intensity and temperature are favorable for photosynthesis in early spring, the depressed photosynthetic capacity causes the lower rate in the open.

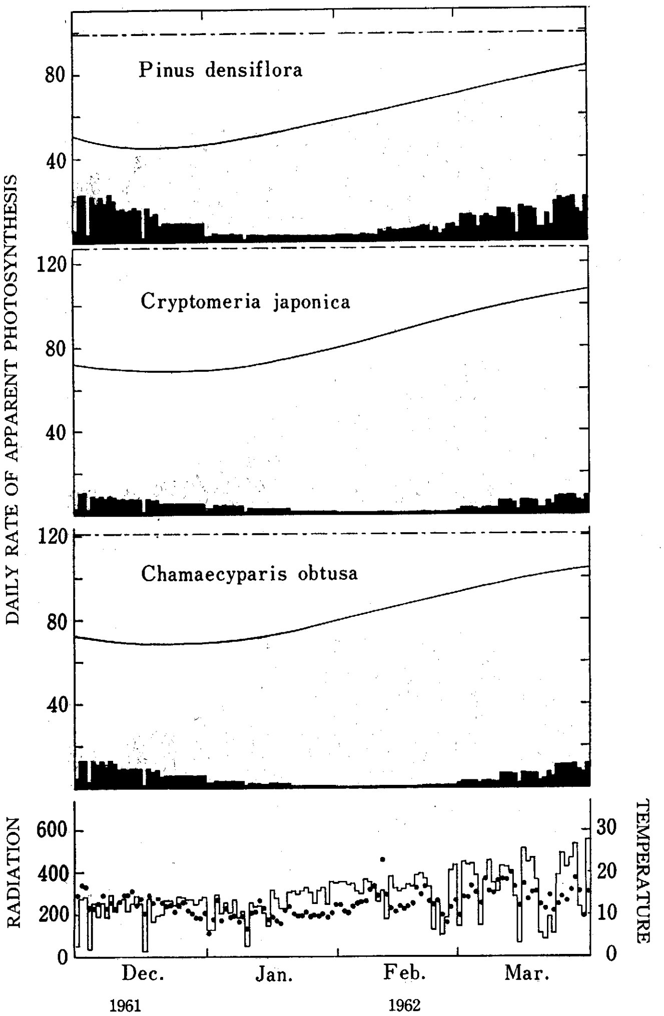

Fig. 59. (Continued).

As described above, the values in table III were based on the assumption that the temperature-curve of photosynthesis in growing season was available throughout the year. In cases in which the calculation is made for the period December, 1960 to February, 1961 using the temperature-curve in winter in figure 37, the monthly rate in midwinter increases slightly and the effect of low temperature becomes less remarkable as a cause of the depression as shown in table III D. But, the difference caused by the application of different temperature-curve seems to be not serious on the whole.

4. Difference among species

The monthly rates in

table III were totaled respectively in each of the two separate periods, April, 1960 to March, 1961 and April, 1961 to March, 1962. The results are summarized in table 9, in which each rate is given in percentage to the rate expected on the assumption that the maximum monthly rate in calculation (a) continues all the year round.

The rates in the open are remarkably low as compared with the maximum. The relatively high photosynthetic rate of *P. densiflora* in the open may be mainly attributed to its higher photosynthetic capacity extending over a long period of the year and less sensitiveness of photosynthesis to above-optimal temperatures in summer.

The weight of each cause for lowering photosynthetic rate in the open varies with different species, but the seasonal change in photosynthetic capacity is the most effective in each of the three species. The effect of radiation intensity connecting with the change in altitude of sun and in weather is remarkable in *P. densiflora,* while that of temperature is marked in *Cr. japonica* and *Ch. obtusa.* These differences show that to what extent the differences of species in the photosynthetic response to light intensity (Chapter II) and to temperature (Chapter III) appear under the nursery conditions.

IV) Problems Relating to Seasonal Variation in Photosynthesis

In early spring from March to April, the rate of photosynthesis in the open is mainly limited by photo-

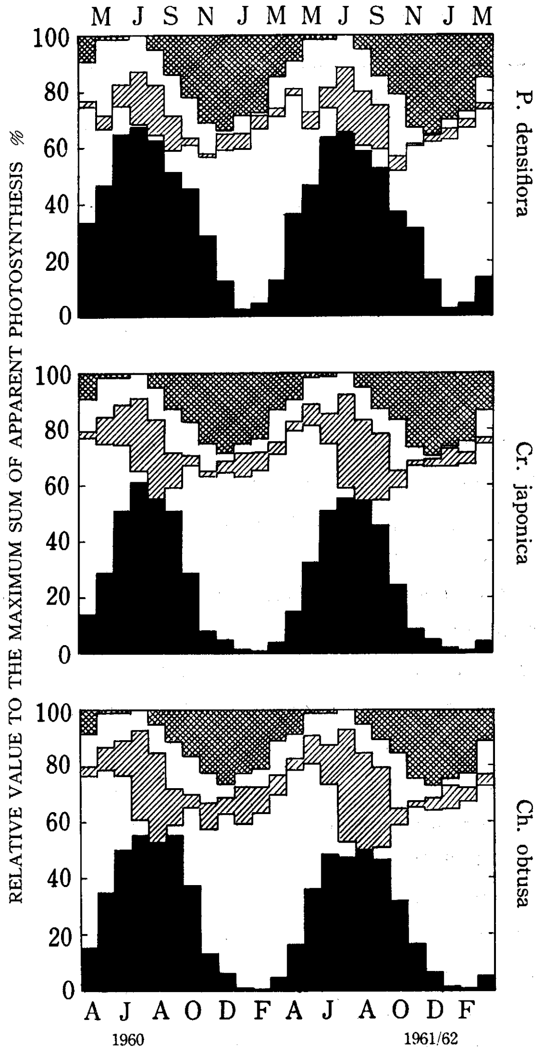

Fig. 60. Monthly rate of photosynthesis in the open estimated by calculation(d) (solid part) in percentage to the maximum obtained by calculation (a). The space between them is divided into causes lowering the rate in the open in proportion to their effect; radiation intensity or photoperiod caused by seasonal change in altitude of sun (hatched part with meshes), radiation intensity connected with daily weather conditions (open space between hatched part with meshes and that with oblique lines), temperature (hatched part with oblique lines) and photosynthetic capacity (open space between hatched part with oblique lines and solid part).

Table 9. Total sum of apparent photosynthesis per year and causes of depression of the rate in the open shown against the maximum rate. All the values are given in percentage to the maximum rate expected if the maximum monthly rate in calculation (a) will continue throughout the year.

Species	Period, April to March in the next year	Sum of apparent photosynthesis in the open	Cause of depression			
			Photo-synthetic capacity	Altitude of sun	Radiation intensity	Temperature
P. densiflora	1960/61	36.2	29.0	15.7	11.8	7.3
	1961/62	35.5	29.7	16.1	11.3	7.4
Cr. japonica	1960/61	25.7	40.8	13.5	9.7	10.3
	1961/62	24.8	42.2	13.9	8.1	11.0
Ch. obtusa	1960/61	27.3	38.0	12.3	10.2	12.2
	1961/62	25.5	39.4	12.8	9.0	13.3

synthetic capacity. In order to make better use of radiation and temperature favorable for photosynthesis in this period, it is desirable that the depression in photosynthetic capacity is prevented in midwinter and its recovery is hastened in early spring. The carrying of seedlings into the green house to protect against the severe frost is a way to attain this object. But, when an artificial increase of photosynthetic capacity is put into practice in the nursery, of course, careful attentions must be paid to the decrease in frost resistance and to the change in growth pattern in order to obtain stout seedlings.

The low temperature in winter affects directly the photosynthetic production in a small degree, but it plays a still more important role in depression of photosynthetic capacity, through which it has marked influence upon the photosynthetic production in the open indirectly. The minimum air temperature in winter becomes lower with approaching to the ground. In younger yearling growing nearer the ground, a more remarkable decrease in photosynthetic capacity may be expected, while in higher plant the decrease is less marked as observed in the twigs of *Cr. japonica* branching at 1~2 m high (NEGISI, YAMAGUCHI, YAGI & SATOO 1961).

The effect of difference in height above the ground also is expected on the role of above-optimal temperatures in summer. The nearer the height is to the ground, the higher the temperature becomes in the daytime. The effect of depressed photosynthetic rate and increased respiratory rate caused by higher temperatures may be remakable on the growth of yearlings at the first summer after their emergence as compared with that of 1-year-old seedlings.

To simplify the conditions of estimation, and to obtain the values applicable to the calculation of dry matter production of the seedlings growing under adequate soil moisture conditions in Chapter VII, all the calculations were based here on the assumption that the soil moisture had been always maintained at an optimal level, at near the field capacity. Because of irregularity in the seasonal distribution of annual precipitation, the effect of soil moisture will not show a seasonal trend as observed in radiation intensity and temperature, even though the estimation will be made considering its changes.

CHAPTER VI. RESPIRATORY RATE AND ITS SEASONAL VARIATIONS

A part of the dry matter produced by photosynthesis is consumed by respiration, and its estimation is necessary to the analysis of dry matter production. In this chapter the respiratory rates of the seedlings of the three species are determined at different seasons. The measurements are separately made on the top, aerial part, and on the root, subterranean part.

I) Respiration of Top

1. Material and method

The rate of dark respiration was estimated by measuring the rate of increase in CO_2 concentration of the air after passing over the sample. An outline of the apparatus is given in figure 61, in which CO_2 of the air before flowing into the respiration chamber is removed at the left part and the amount of CO_2 after flowing out the chamber is determined at the right part.

A part of the air flowing from a rotary pump (P) was made to be CO_2 free with passing through a column of soda lime (S) and solution of sodium hydroxide (U, V), and to be sufficiently humid in a water column (W) in order to prevent the sample from desiccating in the chamber. By means of the observation on a flow meter (X) and a simple liquid manometer (Y) and the adjustment of a two-way stop cock (R), the rate of air flow at the inlet was balanced with that at the outlet of the respiration chamber (A) under the atmospheric pressure in the open. Bottles (Q, T, Z,) were inserted in the line to decrease fluctuations in the air stream and to provide against backflow of liquids. As a respiration chamber, cylindrical glass or plastic tubes of three different dimensions, 3 cm in diameter ×30 cm in length, 4×30 cm and 5×50 cm, were used according to the size of sample.

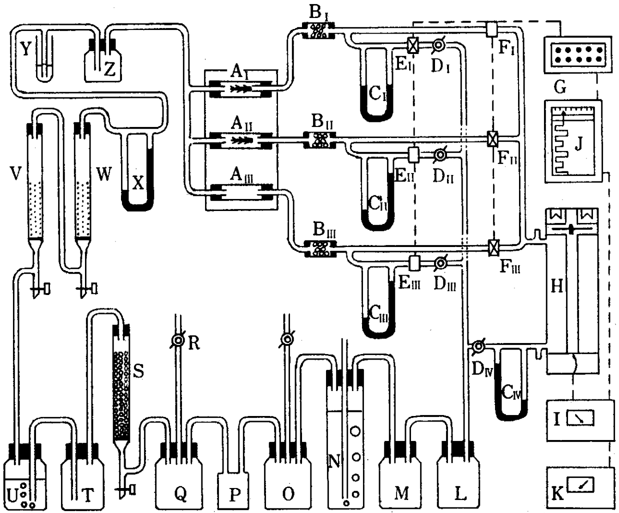

Fig. 61. Outline of the system for estimating dark respiration by measuring CO_2 concentration in three open air lines alternately. For explanation of letters see text.

The CO_2 concentration of the air stream in the three lines connecting to each of the respiration chambers was determined at the right part of figure 61, from B to P, which was detaild in the explanations of figure 1 in the text. Line I and II were connected respectively with the chamber containing a sample, while line III was joined to the empty one to reach the certainty that the supplying air was free from CO_2.

The respiratory rates of the top of 1-year-old and if necessary of 2-year-old seedlings of *Pinus densiflora, Cryptomeria japonica* and *Chamaecyparis obtusa* were measured during the period 1961 to 1962 at different intervals corresponding to the extent of seasonal change. In each measurement more than five individuals were studied in each species. Shortly after being detached from the root, the top was enclosed in the respiration chamber which was submerged in the water bath at a constant temperature 20°C from fall to spring and 25°C in summer. Each run of determination was finished when the respiratory rate was being steady.

2. Results and discussion

1) Rate of respiration per unit dry weight

As an instance, a part of the result obtained in *P. densiflora* is given in figure 62, in which the rates measured at 25°C are converted into at 20°C. The respiratory rate per unit dry weight shows a seasonal change. The rates are higher for the period late-April to mid-May, at which the elongation of the new shoots takes place. A wide variation appears in individual rate observed at the same time. But, it seems that there is no apparent correlation between the total dry weight of the top and the respiratory rate measured at each season as shown in figure 62. Similar seasonal and individual variations are observed in the other two species.

2) Seasonal variations in respiration

The mean values of respiratory rate observed at different seasons are summarized in figure 63. In all the three species, respiration increases associating with elongation of new shoot in spring. Similar rises in respiratory rate were observed in many evergreen conifers (KOZLOWSKI & GENTILE 1958; PISEK & WINKLER 1958; BOURDEAU 1959; NEUWIRTH 1959; CLARK 1961; KADOTA 1962; MCGREGOR & KRAMER 1963). Among the three species studied here, the rise is more remarkable in *P. densiflora* which makes up most of height growth within a shorter period in spring.

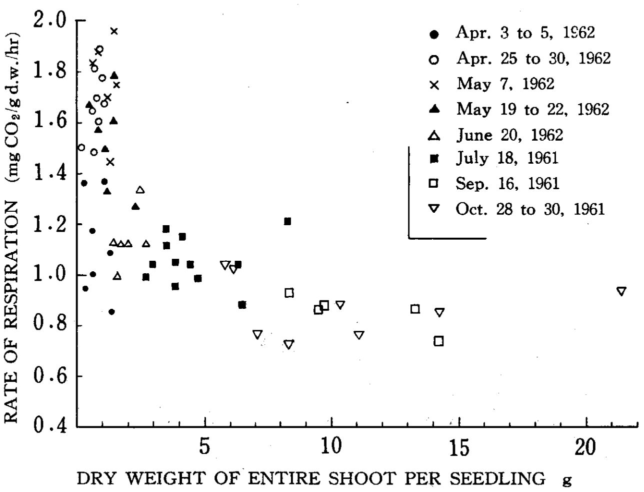

Fig. 62. Respiratory rate of the top of *Pinus densiflora* at 20°C at different seasons in relation to dry weight of the top per individual.

The respiratory rates at

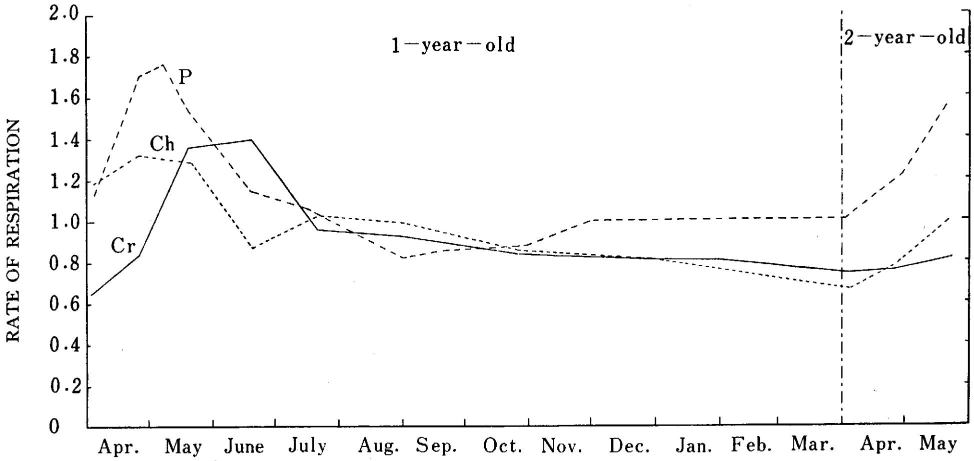

Fig. 63. Seasonal change in respiratory rate of the top at 20℃ (mg CO_2/g dry wt. of top of seedling/hr) of the three species, *Pinus densiflora* (P), *Cryptomeria japonica* (Cr) and *Chamaecyparis obtusa* (Ch).

20℃ in winter do not markedly differ from growing season, but may be somewhat higher in *P. densiflora* and somewhat lower in two other species. According to the reports relating to this subject, there is either case in change of respiratory rate in winter, lower (PISEK & WINKLER 1958; BOURDEAU 1959; PISEK & KNAPP 1959) or higher (LARCHER 1961a; MCGREGOR & KRAMER 1963). In the previous work dealt with the potted seedlings of the three species (NEGISI & SATOO 1961a), the same trend as obtained here was observed in *P. densiflora* and *Ch. obtusa* respectively, while the reverse was the case in *Cr. japonica*. Since the seasonal change of respiratory rate is affected by the difference in temperature condition of determination (PISEK & WINKLER 1958) or the difference in degree of suffered frost (LARCHER 1961a), great care may be necessary in a discussion on the difference among independent experiments even in the same species.

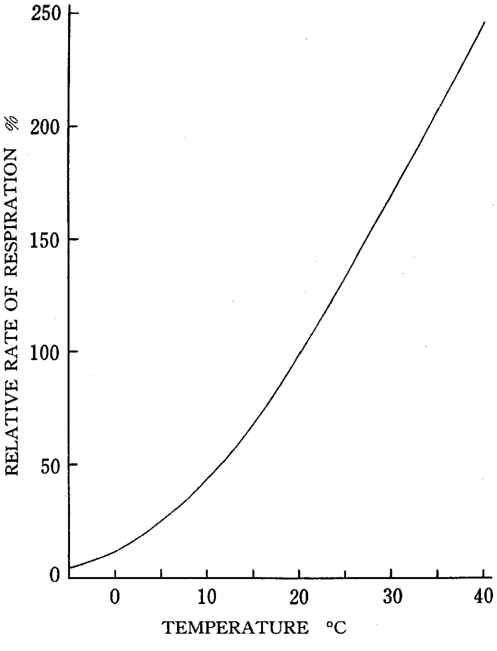

Fig. 64. Relation of temperature to respiratory rate of the top in the three species, shown in percentage to the rate at 20℃.

3) Temperature and respiratory rate

As a material for the calculation of daily respiratory rate in the open was studied the relation between temperature and respiratory rate. The measurements of respiration at a temperature between −5 and 40℃ were made at different seasons. In addition to the determinations in the same way as mentioned above, the measurings of the potted seedlings in the open were made in the night following after the measurement of the daily course of photosynthetic rate.

In respiratory response to temperature, no difference is observed among the species or seasons, and the relations are summarized in a curve in figure 64. Q_{10} of respiration is 4.4 within the range of temperature between 0 and 10℃, 2.3 between 10 and 20℃, 1.7 between 20 and 30℃, and 1.5 between 30 and 40℃.

II) Respiration of Root

The measurement of respiration of subterranean part seems to be somewhat troublesome in comparison with that of aerial part. Though the reports relating to this subject are few, the methods used in these works may be divided into the following two groups according to the conditions of the sample, (1) using samples *in situ* and (2) using samples dug out of the ground.

An instance of the former is the method devised by EIDMANN (1943), in which the pot of the potted seedling is enclosed in an air-tight container and the evolved CO_2 is determined. The respiration of microorganisms included in the total soil respiration may be a principal source of error in this method. The error due to respiration of soil microorganisms may be eliminated by the use of the materials grown with sand, gravel or water culture, but it is possible that the rate of respiration may vary with cultural condition. In this method, the size of sample is limited by the size of pot. Although the use of larger pot is desirable to avoid unnaturalness in growing conditions, the ratio of respiratory rate of microorganisms to total soil respiration may increase with increasing size of pot.

In the latter method, the subterranean part is dug out and the soil adhering to root is washed off with water. The measurement of respiration is made on the entire or if necessary on a part of the detached root system using the similar method applied to the top (as instances dealing with tree, ZIEGLER 1957; TRANQUILLINI 1959b; KUROIWA 1960a; SHIROYA *et al.* 1962). In this method, the influence of microorganisms is possibly small and the materials of various sizes are available. But unnatural conditions surrounding the sample and traumatic stimulus associating with digging and cutting of the sample may affect the rate of respiration.

Since the respiratory rate obtained here will be applied to the analysis of dry matter production of the seedling grown in the nursery, the latter method was chosen in this work after the following studies on the factors connecting with the errors.

1. Preliminary experiment on the method

1) Respiratory rate of root *in situ* and that under the measuring conditions

To avoid the error due to soil microorganisms, the root of water cultured seedling was used as a material, instead of soil cultured one. The respiration of root in the water was measured by the use of the respiration chamber devised by SASAKI (1961). This chamber consisted of an 1 litre glass bottle filled with water to about 70 percent of its entire volume, a rubber stopper having a split, an inlet and an outlet of air, and a simple liquid manometer for indicating air pressure in the space between water level and rubber stopper.

The base of the stem of water cultured seedling was put between the split, and the stopper was plugged carefully inserting the root into the bottle. After the setting of sample, the respiration chamber was placed in the same position as A in figure 61. The inlet of the air was connected with a glass filter at near the bottom of the bottle, from which CO_2 free air was bubbling into the water. The air made contact with root system in the water flowed into the gas analyzer through the outlet. By means of observation on the manometer and adjustment of the two-way stop cock connecting with the inlet of each respiration chamber, the balance of air flow between inlet and outlet was kept under the atmospheric pressure. When the rate of respiration became steady the measuring was stopped, and the root was taken out of the water in the bottle. The measurement of the same root detached from the top followed immediately after it in the same way as applied to the top.

The measurements were made on 1-year-old water cultured seedlings of *Cr. japonica* in early November, 1961 at 20℃. The results of seven individuals are given in table 10. As shown in the table, the difference between (A) and (B) seems to be not remarkable.

In the above-mentioned measurement, the effect of detachment was combined with that of change in surroundings. To study these two effects separatory were made the measurements in April, 1962. It seems that each procedure has no apparent influence on the respiratory rate of root as shown in table 11. If the results described here can apply to the seedlings grown in the nursery, the error associating with the preparation of sample will be endurable.

Table 10. Comparison of respiratory rate (mg CO_2/entire root/hr) between attached root in the water (A) and detached root in the humid air (B), observed in 1-year-old water cultured seedlings of *Cr. japonica.*

A	B	B/A×100 (%)
5.03	5.60	111
5.00	5.42	108
3.81	3.51	92
6.13	6.11	100
4.65	5.12	110
5.80	6.16	106
4.32	4.14	96

Table 11. Comparison of respiratory rate (mg CO_2/entire root/hr) among attached root in the water (A), attached root in the humid air (A′), detached root in the water (B′), and detached root in the humid air (B), observed in 1-year-old water cultured seedlings of *Cr. japonica.*

A	A′	B′	B
1.41	1.34		
2.21	2.18		
2.18		2.13	
2.07		2.09	
2.86		2.84	
1.93			1.88
1.37			1.29

2) Time course of respiration of dug out and detached root

If the change connecting with the preparation of sample affects rapidly the respiration of root, it will be

Table 12. Time course of respiratory rate (mg CO_2/entire root/hr) of dug out and detached root of 1-year-old seedling grown in the nursery.

Species	Hours after preparation of sample						
	0.5～1.5	1.5～2.5	2.5～3.5	3.5～4.5	4.5～5.5	5.5～6.5	6.5～7.5
P. densiflora	3.44	3.49	3.43	3.36			
	4.27	4.39	4.37	4.33			
Cr. japonica	4.93	4.89	4.75	4.65	4.63	4.45	4.31
	3.27	3.34	3.32	3.26	3.18	3.10	3.05
Ch. obtusa	2.05	2.10	2.19	2.18			
	1.77	1.83	1.84	1.80			

reflected upon the time course of respiratory rate. The root of 1-year-old seedling grown in the nursery was dug out, washed and detached, and its time course of respiration was determined. The measurements were made on the three species in August and September in 1961. As may be seen in table 12, the respiratory rate remains comparatively unchanged during first few hours after the preparation of sample.

These results obtained by the preliminary experiments show that dug and detached root is available as a material for estimating respiratory rate of the seedlings grown in the nursery.

2. Material and method

The measurements of respiratory rate of root in the three species were made at different seasons during the period October, 1960 to January 1962, at various intervals corresponding to the extent of seasonal change. In each measurement more than five individuals were studied in each species. The root of 1-year-old or if necessary 2-year-old seedling grown in the nursery was carefully dug out of the ground, washed with water, wiped with filter paper and detached from the top. Immediately after these preparations, the root was enclosed in the cylindrical respiration chamber which was submerged in the water bath at a constant temperature of 20℃ from fall to spring and 25℃ in summer, and the rate of respiration was determined with the same method as applied to the top. Each run of determination was finished when the rate became steady.

3. Results and discussion

1) Rate of respiration per unit dry weight

A part of the result obtained in *P. densiflora* is given in figure 65, in which the rates at 25℃ are converted into at 20℃. The respiratory rate per unit dry weight changes with season. A wide variation is observed in individual rates in the same season, and it seems that the rate per unit dry weight decreases with increasing total dry weight of root per individual. Similar variations are observed in two other species.

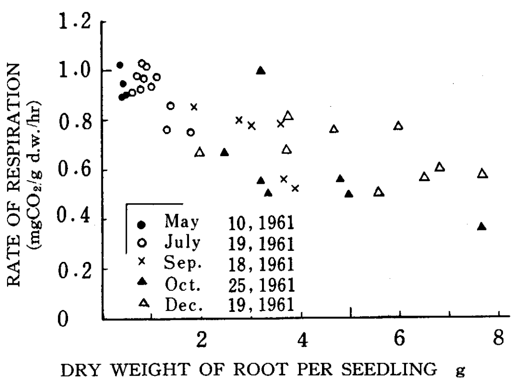

Fig. 65. Respiratory rate of the root of *Pinus densiflora* at 20℃ at different seasons in relation to dry weight of the root per individual.

2) Seasonal variations in respiration

The mean values of respiratory rate observed at different seasons are given in figure 66. The seasonal variations in root differ from those in top. The rate increases in spring in every species, in which *P. densiflora* begins to rise earlier. In *Cr. japonica* and *Ch. obtusa,* lower respiratory rates are observed in summer. The rates of all the species decrease in winter. The depression in summer was detected in the potted tree seedlings of several species by EIDMANN (1943) and also in the thinner detached root of *Cr. japonica* and *Ch. obtusa* by KARIZUMI and TERADA (1960). The fact that the rate of elongation of root hair is lower in summer than before and after that, may be connected with the depression in respiratory rate observed in *Cr. japonica* and *Ch. obtusa.*

The respiratory rate per unit dry weight of root hair or thinner root is higher than of lignified or thicker root (KARIZUMI & TERADA 1960; KADOTA 1962). It is supposed that the ratio of root hair or thinner root in dry weight may decrease with increasing dry weight of the whole subterranean part of the individual. Since the dry weight of

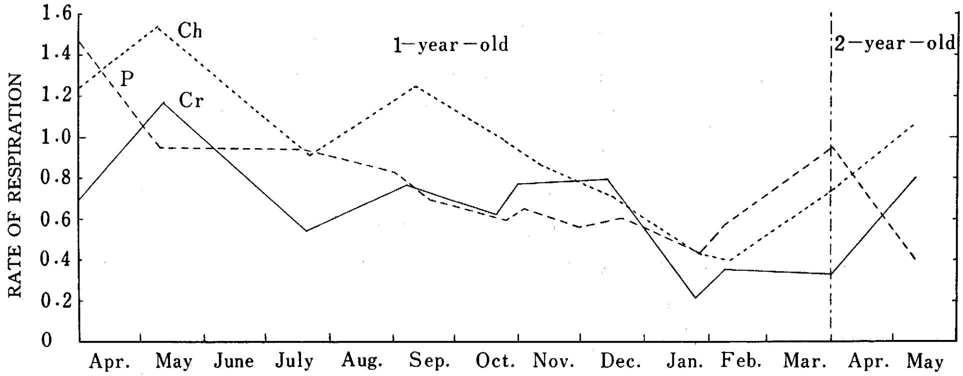

Fig. 66. Seasonal change in respiratory rate of the root at 20℃ (mg CO_2/g dry wt. of root of seedling/hr) of the three species, *Pinus densiflora* (P), *Cryptomeria japonica* (Cr) and *Chamaecyparis obtusa* (Ch).

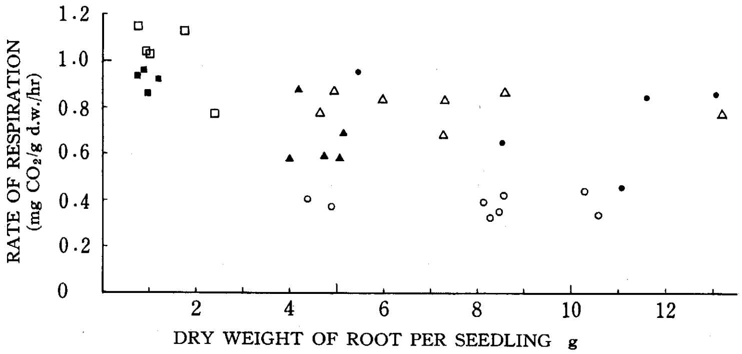

Fig. 67. Difference in respiratory rate of the root per unit dry weight between the seedlings grown in the pot (solid symbols) and those grown in the nursery (open symbols). Measurements of 2-year-old seedlings of *Pinus densiflora* (circles), *Cryptomeria japonica* (triangles) and *Chamaecyparis obtusa* (squares) were made using dug out and detached root in May, 1962 at 20℃.

subterranean part per individual increases with season, the changes in frequency distribution of thickness of root affect possibly the seasonal trend shown in figure 66.

For a similar reason, it is desirable that the comparison of different species is made among the individuals similar in dimensions. EIDMANN (1943) studied the potted tree seedlings of 15 species and found that the respiratory rate of root per unit weight varied widely with the species. In respiratory rate of root, the three species dealt with here are similar to the group having a lower level of respiration among the species studied by him. But, it is possible that the rate of seedling growing in pot may differ from that in nursery, because the ratio of thinner root to thicker one and the ratio of root to top probably change with difference in cultural conditions. As shown in figure 67, the respiratory rates of potgrown root are higher in *P. densiflora* and lower in two other species than those grown in the nursery. The rates of pine species obtained by TRANQUILLINI (1959b) and by SHIROYA *et al.* (1962) are close to the three species studied here.

III) Estimation of Respiratory Rate in the Nursery

1. Estimaion of daily rate of respiration

The daily rates of respiration per unit dry weight under the nursery conditions were estimated for the period April, 1960 to March, 1962. The rates of top were separately totaled in the daytime and in the night, using the respiratory rate per unit dry weight at different seasons in figure 63, the record of air temperature at 20 cm above the ground and the temperature-curve of respiration in figure 64. The calculation in the daytime was based on the assumption that the respiratory rate in a light is equivalent to dark respiration (EGLE 1960b). In the estimation of rate of root were used the respiratory rate in figure 66 and the record of soil temperature at 20 cm below the ground. Since the response of respiration of root to temperature was similar to that of top in all the species, the corrections to temperature were made using the temperature-curve in figure 64.

2. Seasonal variation in monthly rate of respiration

The daily rates of respiration per unit weight are summed up monthly in table IV. The level of rate in each month is mainly affected by the seasonal changes in respiratory rate per unit weight and temperature.

Owing to the increase in respiratory rate connecting with the elongation of new shoot and the higher air temperatures, the rate of top is higher in the months from late spring to early fall. The lower rates of the root in winter are caused by the decrease in respiratory rate per unit weight and the lower soil temperatures. In the annual rate of respiration of the top, the rate in the daytime is about twice as large as that in the night in each species. The higher rate in the daytime is mainly attributed to higher temperatures, especially those associated with longer photoperiods in the warm season.

CHAPTER VII. DRY MATTER PRODUCTION OF INDIVIDUAL SEEDLING

It is well-known that the dry matter produced by photosynthesis is used by the plant in various ways, i.e. respiration of living protoplasm, formation of new tissues (growth), and accumulation of reserve foods for future needs. The share of photosynthate allotted to growth and reserves corresponds with the dry weight increment of plant. By BOYSEN JENSEN (1932) was originally discussed plant growth in relation to the balance between income and outgo in dry matter production. His study has been followed by a number of students, and many informations relating to the dry matter production were accumulated. The dry matter production in a plant or a plant community is maintained only through the dry matter reproduction, on which five typical reproduction systems were presented by MONSI (1960). In order that the plant continues to exist and to grow, a part of the produced dry matter must be transformed into production system.

Income, outgo and surplus in the dry matter production are estimated in various ways. By Danish researchers (MÖLLER 1945; MÖLLER, MÜLLER & NIELSEN 1954), were obtained the incomes of forest stands by summing up the direct determined biomass and the total matter consumption. The estimation of income based on the measuring of photosynthetic rate is made in different two ways. In the one way, the income is calculated using photosynthetic rates measured in the open. In few reports was made a relatively exact estimation based on the photosynthetic rate extending over a longer term (HEINICKE & CHILDERS 1937; TRANQUILLINI 1959b, 1962a), while in many works was able to make only a rough estimation because of the lack of data (POLSTER 1950, 1955; HUBER & POLSTER 1955; POLSTER & NEUWIRTH 1958; MILLER 1959). And, the other way was used in a number of studies, in that the income is calculated using photosynthetic rates measured in connection with important external and internal conditions of a plant or a plant community (as instances dealing with tree species, NOMOTO, KASANAGA & MONSI 1959; TAZAKI 1959; KIMURA 1960; KUROIWA 1960b; KUSUMOTO 1961; LARCHER 1961b; NOMOTO 1964). Though the apparatus for measuring CO_2-uptake develops, an extensive determination extending over a long term in the open is not easy, and it seems that the latter way is effective to make the estimation under various conditions.

In this chapter, the surplus production of an individual seedling is calculated as a balance between the income estimated in Chapter V with the above-mentioned latter way and the outgo in Chapter VI. The estimations are made on the seedlings having average dimensions, and the calculated values are compared with the dry weight increment measured directly in the nursery. Differences in dry matter production are discussed among the species.

I) Seasonal Course of Growth

1. Material and method

1) Material

The studies were made on 1-year-old seedlings of the three species grown in the nursery. In the fall of the previous year, uniformly grown 1,000 seedlings of *Pinus densiflora* and *Cryptomeria japonica* each and 500 seedlings of *Chamaecyparis obtusa* were selected according to size, and transplanted with square spacing of 15 cm. Three tensionmeters were buried in the bed, and irrigations were made when the drying of soil reached 40 cm Hg in soil moisture tension so that soil moisture had been readily available for the seedlings over the entire growing season. In addition to the materials for measuring the growth, those for measuring the photosynthetic capacity in Chapter V and the respiration in Chapter VI were chosen from the same lot of the seedlings.

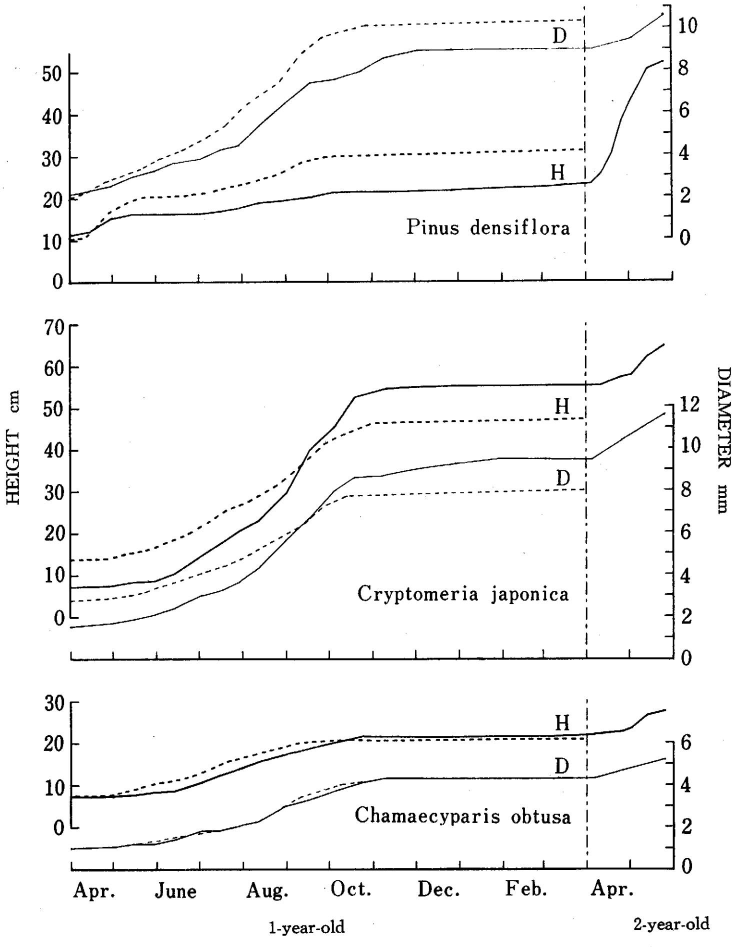

Fig. 68. Seasonal course of growth in height (H, thick lines) and diameter at base (D, thin lines) for the period spring in 1960 to spring in 1961 (solid lines) and that 1961 to 1962 (broken lines).

2) Measurement of growth

Though the selection of seedlings was made before the transplanting, the growth on the transplant bed varied widely with the individuals. To obtain a seasonal course of average dry weight increment, height and diameter at base had been periodically measured on the same plants, 14 seedlings arbitrary chosen in each of the three species, and the individuals having average values both in height and diameter were selected at regular intervals to determine dry weight.

The measurements of growth were separatory made for the two periods, April, 1960 to May, 1961 and April, 1961 to March, 1962. Height and diameter had been measured at intervals of two weeks in growing season and of a month in winter. The samplings of the seedling for determining dry weight were made at intervals of a month. In each species 3 to 4 individuals having nearly average dimension, and about 10 individuals

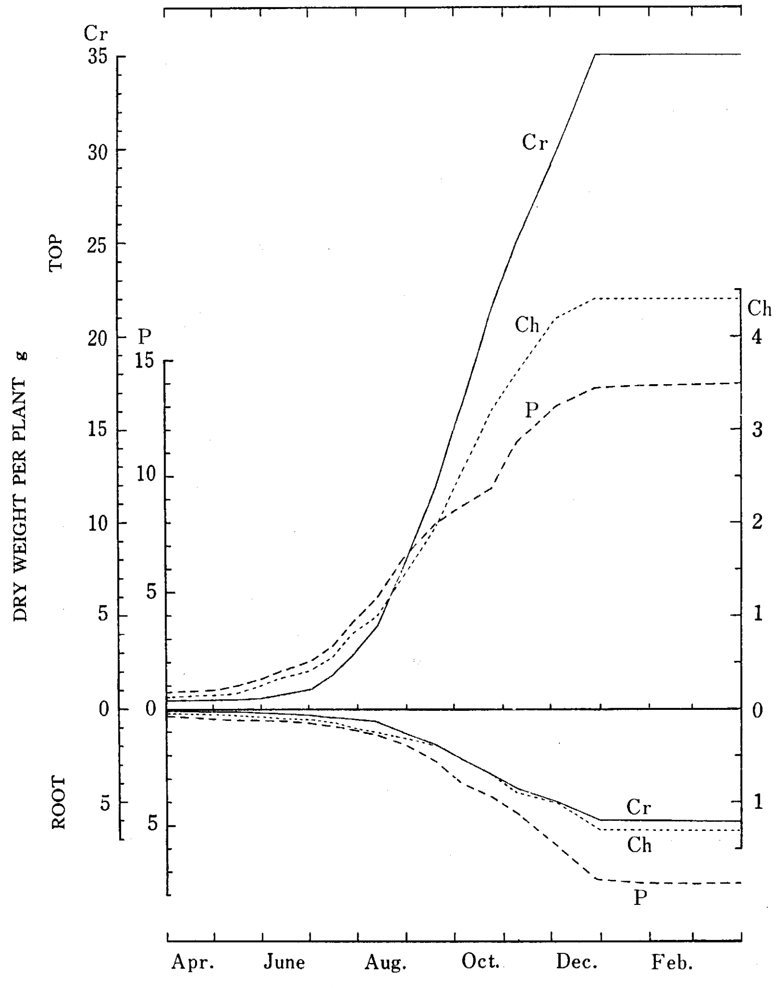

Fig. 69. Seasonal course of growth in dry weight in *Pinus densiflora* (P), *Cryptomeria japonica* (Cr) and *Chamaecyparis obtusa* (Ch).

of various dimensions were dug out at each sampling. Then, the seedlings were washed with water, divided into the top (aerial part) and the root (subterranean part), and dried in the oven at 105℃. The values of dry weight obtained on the samples of various sizes were useful to check the difference in height and diameter between the computed average value and the sampled one. Further dividing of the top into photosynthetic and aphotosynthetic part was not made, because it is not easy to distinguish needles from other parts for the seedlings of *Cr. japonica* and *Ch. obtusa*.

2. Results and discussion

1) Height and diameter

The seasonal courses of height and diameter growth are shown in figure 68. In *P. densiflora* as is known sufficiently, a great part of the season's height growth is made within a shorter period in spring, and a gradual increase from summer to early fall is due to Lammas shoot growth. The vigorous height growth of *P. densiflora* at the beginning of growing season is reflected in its relation between radiation intensity and photosynthetic rate, and in its seasonal trend of respiratory rate as have been described. On the other hand, in *Cr. japonica* and *Ch. obtusa* the height growth is made extending over whole growing season. The diameter growth continues throughout growing season in each of the three species.

2) Dry weight

The seasonal courses of growth in dry weight corresponding to the average height and diameter growth in 1960 are given in figure 69. In each of the three species the dry weight increment has been made over the entire growing season. Because of individual variations the changes of weight in winter are not obvious.

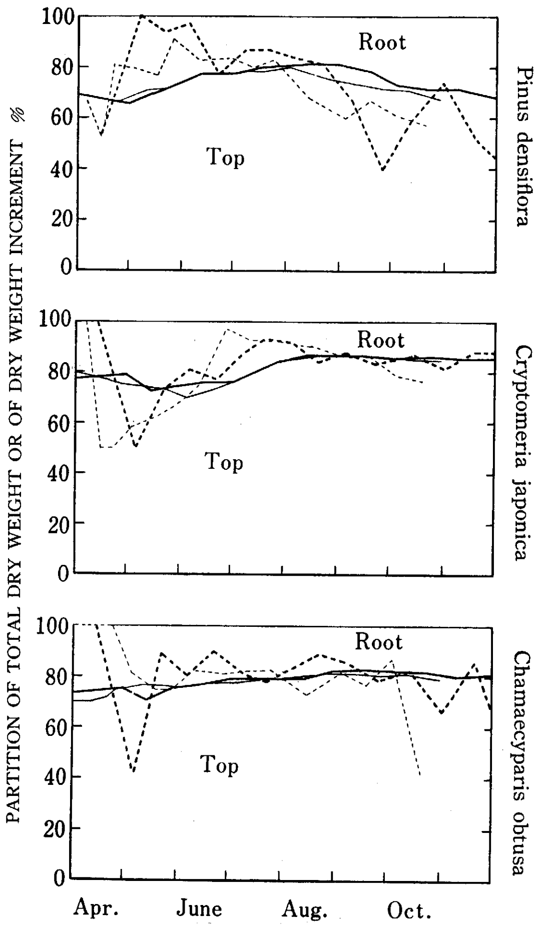

Fig. 70. Seasonal change in ratio of the top or the root to the total dry-weight in 1960 (thick solid lines) and in 1961 (thin solid lines), and that in distribution of dry matter increment in 1960 (thick broken lines) and in 1961 (thin broken lines).

A relatively vigorous growth of the pine in early spring is made mainly at the expense of reserves, which causes a decrease in dry weight of older parts, for instance, as shown in *Pinus* *sylvestris* by RUTTER (1957). In 1-year-old seedlings of *P. densiflora,* the depression is not apparent, but in 2-year-old seedlings occurs a temporary decrease in dry weight of the root in early spring.

3) Ratio between top and root in dry weight

As shown in figure 70, the ratio between top and root changes with the seasonal changes in distribution of dry matter increment between them. In *P. densiflora,* the ratio of root to top in dry weight throughout the year, and also that in increment during the great part of the growing season are higher than in two other species.

II) Carbon Content of Seedling

Carbon content in the top and the root of each seedling was respectively determined at different seasons, with which the income and the outgo expressed in mg CO_2 were converted into the values in weight of dry matter. Three individuals were sampled from the seedlings dried for measuring the growth in weight, ground thoroughly and analyzed with modified Tiurin's method (KAWADA 1955). The results of analysis are summarized in table 13. Though the value varies with the species, part and season, the content seems to be about 50 percent of the dry matter. To simplify the calculation, the following estimations of dry matter production are based on the assumption that carbon content of the seedling is always 50 percent.

Table 13. Mean value of carbon content in percentage to the weight of dry matter.

Species	Part	Date of sampling in 1960				
		Apr. 1	May 10	July 28	Oct. 4	Dec. 1
P. densiflora	Top	50.3	50.9	51.1	52.7	52.2
	Root	45.1	50.4	48.5	49.4	49.5
Cr. japonica	Top	48.3	50.1	51.9	52.3	51.6
	Root	48.2	48.7	50.1	51.1	48.8
Ch. obtusa	Top	48.3	48.9	51.5	51.8	51.1
	Root	48.6	51.1	49.4	49.3	49.0

III) Income and Outgo in Relation to Dry Weight Increment

1. Estimation of dry matter increment

On the first day in each month, the daily dry matter product of the seedling having an average dry weight as shown in figure 69 was calculated using the daily photosynthetic rate per unit dry weight in Chapter V and the above-mentioned carbon content. The respiratory losses of the top in the night and of the root throughout the day were estimated using the daily rate of respiration per unit dry weight in Chapter VI. The surplus product obtained as a balance after reduction of the respiratory loss from the photosynthetic product, was divided into the top and the root respectively in proportion to the distribution ratio in figure 70.

On the following day, the calculation was made using the dry weight of seedling, inclusive of the increment on the previous day. The calculations in the same way were repeated day by day. A run of the repeated daily calculation was started on the first day in each month and finished on the final day in the same month, which was followed by a new run in the next month starting with the average dry weight measured in the nursery instead of the calculated one.

The calculations were made for the two separate period respectively, April, 1960 to March, 1961 and April, 1961 to March, 1962. From April to November, the calculation was repeated day by day as mentioned above. But in the winter months, the calculation was made monthly basing on the assumption that the dry weight of seedling remained unchanged throughout the month, because the changes in dry weight of the seedling were not apparent in this season in the nursery. The results of calculation are summarized monthly in table V.

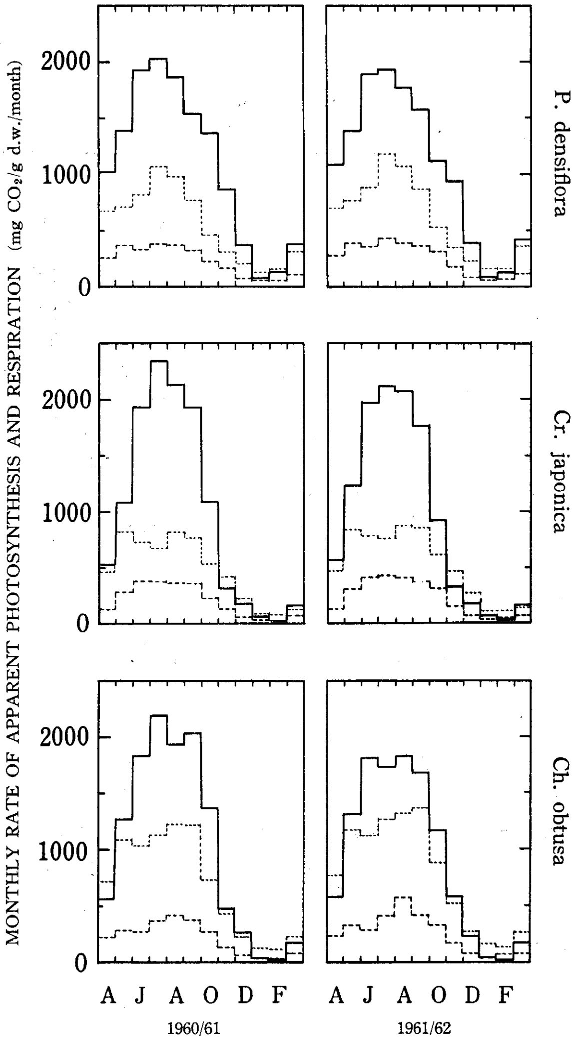

Fig. 71. Seasonal change in monthly photosynthetic rate (solid lines), respiratory rate of the top in the night (broken lines) and respiratory rate of the root throughout the day (fine broken lines) per unit dry weight.

2. Results and discussion

1) Seasonal change

Since the dry weight of an individual seedling increases with season, the seasonal variations in photosynthetic and respiratory rate per individual seedling differ from those per unit dry weight. The seasonal variations per unit weight shown in table III and IV are summarized in figure 71. Higher monthly rates of photosynthesis per unit weight are observed for the period June to September, while those per individual are found late in fall as shown in figure 72 and table V. The increasing photosynthetic system in fall has great influence on the photosynthetic rate per individual in comparison with the decreasing photosynthetic capacity and the shortening photoperiod. Also, higher respiratory rates per individual appear later than those per unit weight. The gain per individual, which was calculated as a balance after reduction of the respiratory losses of the top in the night and of the root throughout the day from the photosynthetic product, is higher in fall and lower in winter. In midwinter

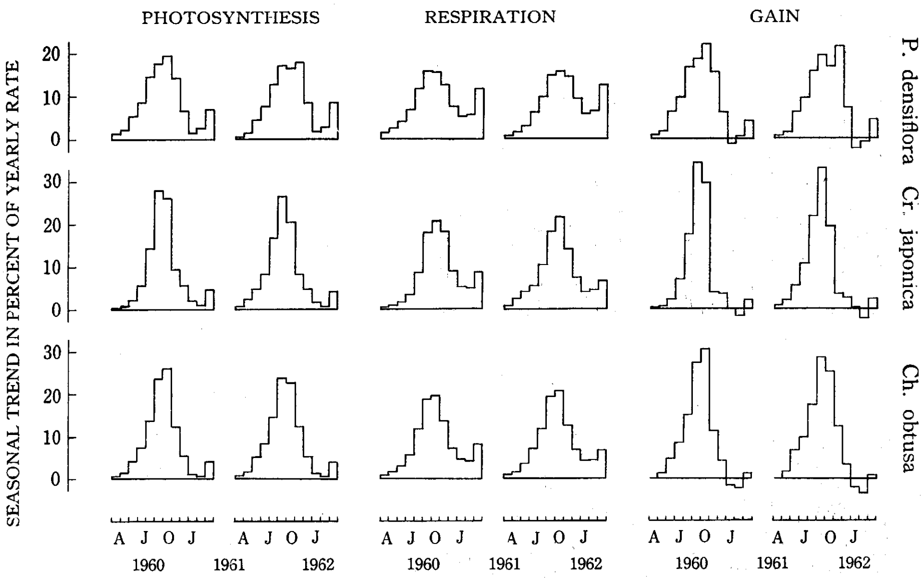

Fig. 72. Distribution of annual photosynthetic product, respiratory loss and surplus product (gain) per individual seedling among the months.

Table 14. Distribution of annual income, outgo and surplus product among the three periods in the year.

Species	Period		Distribution ratio in percentage to annual sum		
	Year	Month	Income* (P)	Outgo** (R_1+R_2)	Gain*** ($P-R_1-R_2$)
P. densiflora	1960/61	Apr. ~ July	17.1	14.9	18.5
		Aug. ~ Nov.	65.3	55.1	72.1
		Dec. ~ Mar.	17.6	30.0	9.4
	1961/62	Apr. ~ July	14.6	11.5	17.8
		Aug. ~ Nov.	63.9	54.5	73.5
		Dec. ~ Mar.	21.5	34.0	8.7
Cr. japonica	1960/61	Apr. ~ July	8.7	6.5	10.3
		Aug. ~ Nov.	77.8	65.3	85.4
		Dec. ~ Mar.	13.5	28.2	4.3
	1961/62	Apr. ~ July	16.3	13.0	18.8
		Aug. ~ Nov.	72.1	64.4	78.2
		Dec. ~ Mar.	11.6	22.6	3.0
Ch. obtusa	1960/61	Apr. ~ July	13.3	11.6	14.4
		Aug. ~ Nov.	75.7	64.1	84.2
		Dec. ~ Mar.	11.0	24.3	1.4
	1961/62	Apr. ~ July	16.0	13.4	18.4
		Aug. ~ Nov.	73.3	64.5	83.2
		Dec. ~ Mar.	10.7	22.1	−1.6

* Photosynthetic product (P).

** Respiratory loss of the top in the night (R_1) and that of the root throughout the day (R_2).

*** Surplus product ($P-R_1-R_2$).

the seedlings are not able to synthesize enough foods to compensate for the respiratory losses.

To express relative importance of each season to the annual growth of 1-year-old seedling are shown in table 14 the distributions of annual income, outgo and gain per individual among the three periods; April to July, August to November and December to March. As may be apparent in the table, the income and the outgo are higher for the period August to November, and most of the surplus product is gained in this period in each species. The similar seasonal trends of surplus product, higher from summer to fall and negative in midwinter, were also observed in the seedlings of *Pinus taeda* and *Pinus strobus* by McGregor (1958).

In figure 73, the distributions of photosynthate among the respiratory losses and the surplus (growth) are shown in each month respectively. The ratio of respiratory consumption is lower for the period summer to fall and higher in winter. As shown in figure 72, the respiratory loss indicates a seasonal trend similar to the photosynthetic product, but the degree of winter depression of the former is smaller than of the latter, and the former is not sufficiently compensated by the latter in midwinter. But the deficit throughout the winter is so small that it may be covered by photosynthetic production in a few days of growing season, as in dry matter production of *Pinus sylvestris* studied by Polster and Fuchs (1963).

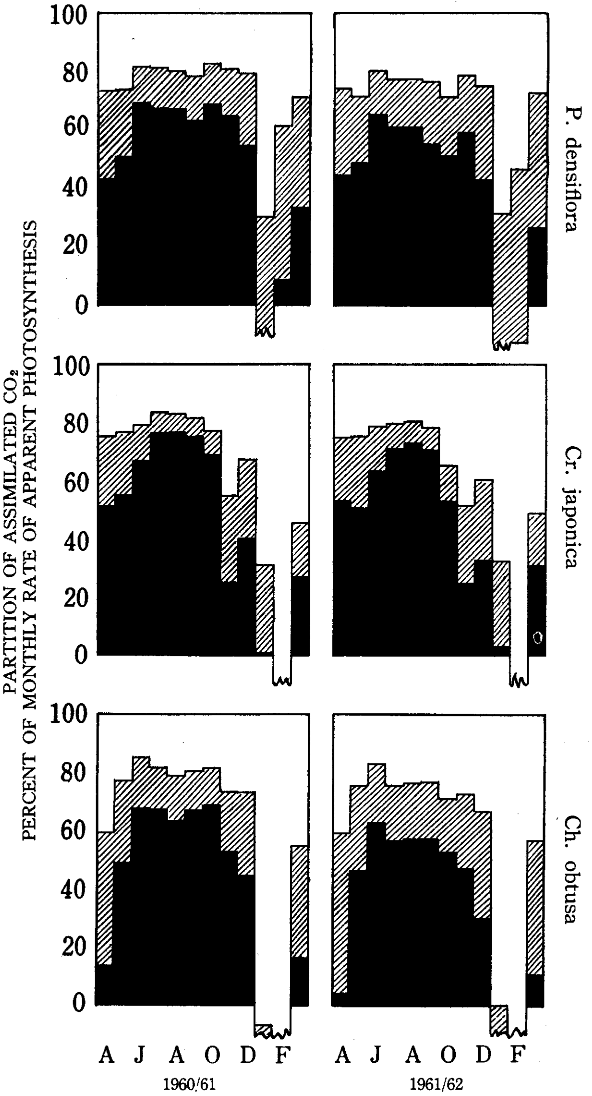

Fig. 73. Distribution of photosynthetic product among the respiratory loss of the top in the night (open parts), that of the root throughout the day (hatched parts) and the gain (solid parts) per individual seedling in each month.

In table V and figure 74, the calculated dry matter increments in each month are compared with the corresponding direct determined increments of the seedlings grown in the nursery. From the summer to the middle of fall, both values agree with each

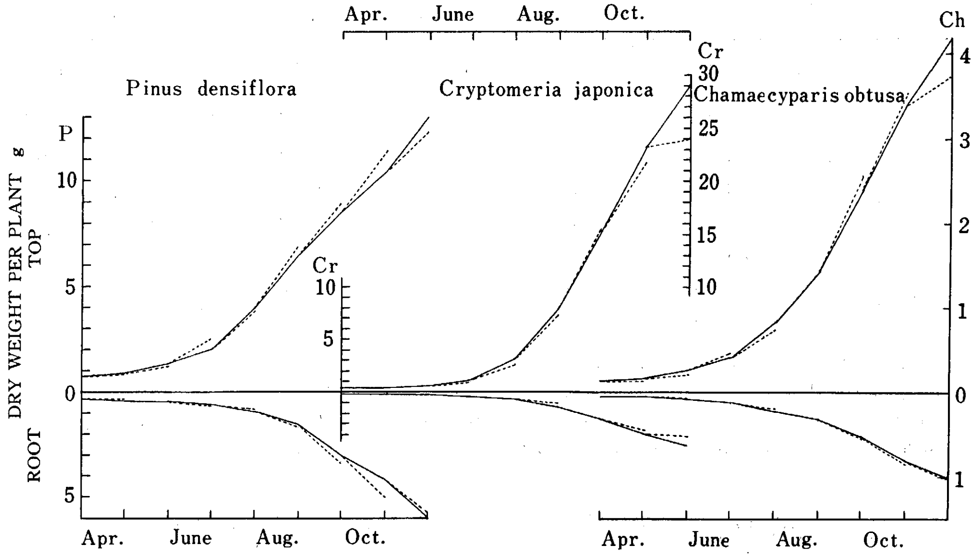

Fig. 74. Seasonal course of growth in dry weight in 1960 measured directly (solid lines) in comparison with that calculated (broken lines).

other, while in the spring and the late fall differ markedly. The difference in spring may be related with (1) an error in the direct measurement of growth resulting from a low rate of dry weight increment, and (2) a greater difference between the temperature at 20 cm above the ground used for the calculation and that at a lower height which has a closer relation to the CO_2-exchange of seedlings. And in the late fall, at emporary rise in photosynthetic capacity resulting from a duration of warmer day may be supposed as a cause of the difference.

In the estimation of dry matter production based on the direct determination of living biomass is required a measurement of the dry weight lost by the fall of needles, twigs and barks and the die of a part of root. But in 1-year-old seedlings dealt with here, these losses are small and are not taken into consideration in the calculation. For instance in *P. densiflora,* the fall of needles throughout the growing season amounts to 0.1 to 0.2 g in dry weight which is a quite small percentage to its entire needle.

The seasonal changes in income, outgo and gain may differ from year to year as shown in the difference between two periods, April, 1960 to March, 1961 and April, 1961 to March, 1962. But the discussions on this point are not made here because of lack of data over a long period.

2) Difference among species

In table 15 are summarized the distribution ratios of respiratory losses and gain (growth) to the annual photosynthetic products. Though the three species differ from each other in photosynthetic response to environmental factors, these differences are not markedly reflected in the dry matter production under the nursery conditions. In each of the three species, from 50 to 60 percent of the annual income are distributed to the dry weight increment. The ratio of respiratory loss of the root to the total outgo

Table 15. Distribution ratio of outgo and gain in percentage to net annual income.

Species	Period, April to March in the next year	Outgo by respiration				Gain, dry weight increment
		R_1*	R_2**	R_1+R_2	$(R_1'+R_2)$***	
P. densiflora	1960/61	21.6	18.6	40.2	(57.8)	59.8
	1961/62	25.7	25.0	50.7	(67.4)	49.3
Cr. japonica	1960/61	26.7	12.2	38.9	(60.1)	61.1
	1961/62	30.5	13.2	43.7	(64.7)	56.3
Ch. obtusa	1960/61	23.6	18.3	41.9	(60.3)	58.1
	1961/62	28.6	23.7	52.3	(68.8)	47.7

* Respiratory loss of the top in the night.

** Respiratory loss of the root throughout the day.

*** Distribution ratio of respiratory loss of the top throughout the day (R_1') and R_2 in percentage to gross annual income including respiratory loss of the top in the daytime.

differs with different species. In *P. densiflora* because of its larger root system and in *Ch. obtusa* because of its higher respiratory rate, the ratio is higher than in *Cr. japonica.*

The differences in distribution of surplus product among the various parts of seedling have influence on further growth. A vigorous photosynthetic production based on expanding photosynthetic system may be expected from a larger share of surplus product allotted to the growth of needles. In this view, a higher distribution ratio of root growth in *P. densiflora* may be at a disadvantage in dry matter production as compared with two other species. But the rapidly developed root system of *P. densiflora* is effective against drought (Satoo 1956) and also may be favorable to make photosynthesis under deficient water conditions.

The balance of dry matter production differs with different species, and internal and external factors. According to the table summarized by Müller (1960), the ratio of respiratory loss of many plant species ranged from 20 to 72 percent of the annual gross production, in which were quoted the values of forest trees ranging 29 to 60 percent (Polster 1950) and of European beech stands of various age ranging 39 to 49 percent (Möller, Müller & Nielsen 1954). In addition to the above-mentioned ratios were obtained recently the following values: 50 percent in dominant tree and 60 percent in supressed one of *Abies Mariesii* in a 20-year-old *Abies* stand (Kuroiwa 1960b); 72 percent in an evergreen broadleaved tree stand (Kimura 1960); 50 percent in artificial communities of *Helianthus tuberosus* (Hogetsu *et al.* 1960); and 65 percent in *Sasa kurilensis* community (Oshima 1961). The values of respiratory loss, R′+R in table 15 show that 1-year-old seedlings of the three species belong to a higher respiratory consumer.

Tranquillini (1959b) studied the dry matter production of young trees of *Pinus cembra* and showed that the respiratory losses amounted to about 38 percent of the annual gross production, which were made up as follows; the aerial part respired 20 percent in the daytime and 7 percent in the night, the subterranean part less than 6 percent, and the entire part during the period buried under the snow less than 6 percent. He (Tranquillini 1962a) also studied 2-year-old *Larix decidua* and 5-year-old *Pinus cembra* and indicated that 8 to 9 percent of the net production were consumed by the nocturnal respiration of aerial part in growing season. The three species in this work are remarkably high in respiratory loss as compared with the species studied by TRANQUILLINI, even though he (TRANQUILLINI 1962b) underestimated the respiratory loss in subterranean part. In addition to the difference of species, that of temperature conditions may be pointed out as a cause of this difference.

EIDMANN (1962) dealt with the seedlings of seven conifers and showed that the ratio of respiratory loss in root ranged from 30 to 40 percent of that in entire individual in September. The corresponding rates of the three species are 48 percent in *P. densiflora,* 46 percent in *Cr. japonica* and 57 percent in *Ch. obtusa.* In the same report, he calculated the respiratory consumption of 4-year-old seedlings of conifers using the ratio between respiratory rate of aerial and that of subterranean part, and obtained 40 percent in *Pseudotsuga taxifolia,* 50 percent in *Picea excelsa* and 60 percent in *Pinus sylvestris* as a ratio of respiratory loss to annual gross production. These ratios are near to those of the three species studied here.

SUMMARY AND CONCLUSIONS

It is sufficient to know that *Pinus densiflora* (Akamatu), *Cryptomeria japonica* (Sugi) and *Chamaecyparis obtusa* (Hinoki), important forest trees in Japan, differ from each other in their behavior to environmental factors. In this study the rates of CO_2-exchange under various conditions were measured mainly on the 1-year-old potgrown seedlings, and the differences in photosynthesis, respiration and dry matter production were compared with the already known ecological and silvical characters of each species.

The main part of this report consists of seven chapters. In the first four chapters, Chapter I to IV were studied the differences of species in photosynthetic response to light, temperature and soil moisture. In Chapter V, the seasonal variations in photosynthetic production were estimated under the nursery conditions, and the causes of seasonal change were studied in each species. In the last two chapters, after the estimation of respiratory loss in Chapter VI, the dry matter production of the seedling grown individually in the nursery was computed in Chapter VII, and the causes responsible for the productivity difference were discussed.

I) Outline of Each Chapter

Chapter I: The diurnal variations in photosynthetic rate were observed in the open at various times of the year. The photosynthetic rates were obtained by means of an infrared gas analyzer which measured continuously CO_2 concentration of the air before and after passing over the seedling in the assimilation chamber. To protect the sample plant against overheating, the assimilation chamber was enveloped in the water jacket acting as a filter and a cooler.

By the difference in photosynthetic response to environmental factor are divided the daily courses of photosynthesis into two types, the summer type in growing season and the winter one in winter. In the former, the levels of photosynthesis on the daily march are closely related with a few environmental factors, especially with light intensity at each time, while in the latter a fairly relationship between light intensity and photosynthetic rate is disturbed by the appearance of a remarkable midday drop and a change in photosynthetic capacity. In *P. densiflora,* the daily courses are the summer type for the period April to November, and the winter one from December to early in April. But, in *Cr. japonica* and *Ch. obtusa* the winter type appears earlier, in October and November.

In growing season, the daily courses of photosynthesis fluctuate with the change in light intensity all day long on cloudy days. On bright and clear days, the flat-topped diurnal curves are observed, and sometimes the midday drops to varying extent appear. Among the species differs the midday drop in frequency of occurrence and in extent of decrease; seldom and slight in *P. densiflora,* not often and moderate in *Cr. japonica,* and often and marked in *Ch. obtusa.*

Chapter II: Since the artificial light possibly differs from the natural one, the photosynthetic responses to light intensity were studied using the data in the open described in Chapter I. After converting into the rate at constant temperature of 20℃, the daily course of summer type was arranged in the relation between light condition and photosynthetic rate.

The increasing rate of CO_2-uptake with light intensity in a lower range is lower in *P. densiflora,* than in two other species. On clear days is reached light-saturated photosynthesis at about 30 k lux in *P. densiflora,* and at about 20 k lux in *Cr. japonica* and *Ch. obtusa.* The degree of depression in apparent photosynthesis due to excessive light intensity, which corresponds with the midday drop, is marked in *Ch. obtusa,* moderate in *Cr. japonica* and slight in *P. densiflora.* These differences among species well correlate with the degree of tolerance of each species.

The relation of horizontal light intensity to photosynthetic rate on clear days differs from that on cloudy days. The difference may be caused by the discrepancy between the light intensity measured with the luxmeter and that received actually with each part of photosynthetic organ.

Chapter III: At different seasons of the year, the determinations of the photosynthetic response to temperature were made under the controlled conditions. The effect of temperature differs with different seasons. In growing season, the apparent photosynthesis of the three species increases with temperature to the maximum at about 20℃. Further rise of temperature causes a reduction of CO_2-uptake. *Cr. japonica* and *Ch. obtusa* are marked for their post-maximal declination of photosynthesis as compared with *P. densiflora.* Apparent photosynthesis of *P. densiflora* reaches its upper limit between 45 and 50℃, while that of two other species between 40 and 45℃. In the field is found positive apparent photosynthesis down to few degrees below zero. In winter, the decrease in photosynthetic rate due to above-optimal temperature begins at a lower temperature, and optimum and maximum temperatures become lower.

Chapter IV: The effect of drying of soil on apparent photosynthesis was studied under the controlled conditions. The photosynthetic response to decreasing soil moisture differs with different species. The decrease in photosynthetic rate at the initial stage of drying of soil is only apparent in *P. densiflora,* while that at the advanced stage is very marked in *Cr. japonica*, marked in *Ch. obtusa* and moderate in *P. densiflora.*

To make clear the cause of these differences, the changes in water content and rate of transpiration were studied. In *P. densiflora,* an earlier beginning of stomatal closure at the initial stage of drying may be related with the earlier depression in photosynthetic rate. And less marked decrease in photosynthetic rate of this species at the advanced stage may be partly attributed to the slower pace of water loss of seedling resulting from a rapid closing of stomata and a lower rate of cuticular transpiration, and partly attributed to a relatively high rate of photosynthesis of the dehydrating seedling. On the other hand, in *Cr. japonica* the stomatal movement is less sensitive to dehydration and the unchanged photosynthetic rate at the beginning of drying decreases rapidly with rapidly decreasing water content of the seedling. In *Ch. obtusa,* the stomata begin to close at a lower water content but close perfectly at a higher one in comparison with *Cr. japonica,* and the pace of decrease in photosynthesis is intermediate between two other species.

Chapter V: The seasonal variations in photosynthetic rate were studied on the seedlings grown in the nursery. The increase in photosynthetic capacity starts with little at February or March, and becomes rapid and marked with the lapse of time. The maximum rate of photosynthetic capacity is attained from midsummer to early fall, and then the rate begins to decrease and reaches its minimum in midwinter. In *P. densiflora* the rise in spring appears earlier and the decline in fall later, and the rate of decrease in winter is smaller than in two other species.

The daily rates of photosynthesis in the nursery were estimated by the use of light- and temperature-curves of photosynthesis, seasonal changes in photosynthetic capacity, and records of horizontal radiation intensity and air temperature at 20 cm above the ground. In order to make clear the cause of seasonal variations were made the calculations based on the four different assumptions. The daily photosynthetic rate is lower in early spring and rises with the increase in photosynthetic capacity towards summer, but the rise is checked by above-optimal temperatures in midsummer. With further progress of season, the effects of higher temperatures gradually fade out, while those of reduction in photosynthetic capacity and of decrease in radiation intensity due to low altitude of sun become conspicuous, through which the rate is depressed and reaches the minimum in winter.

The weight of each cause for decrease of daily photosynthetic rate in the open varies with the species, but the seasonal change in photosynthetic capacity is the most effective in each of the three species. The effect of radiation intensity is remarkable in *P. densiflora,* while that of temperature is marked in *Cr. japonica* and *Ch. obtusa.* The relatively high photosynthetic rate of *P. densiflora* in the open may be mainly attributed to its higher photosynthetic capacity extending over a long period of the year and less sensitiveness of photosynthesis to above-optimal temperatures in summer.

Chapter VI: The rates of respiration of the seedlings were determined at different seasons. The respiratory rate per unit dry weight of the top at 20℃ shows a steady level throughout the year except an increase in spring associated with the elongation of new shoot. The seasonal variations in the root differ from those in the top, and the rate is lower in winter.

The daily rates of respiration in the nursery were estimated by the use of seasonal change in respiratory rate per unit dry weight, temperature-curve of respiration, and records of temperature at 20 cm above and below the ground. Owing to the increase in respiratory rate connecting with elongation of new shoot and higher air temperatures, the rate of the top is higher from late spring to early fall. The lower rates of the root in winter are caused by the decrease in unit rate of respiration and the lower soil temperatures. In the annual rate of respiration of the top, the rate in the daytime is about twice as large as that in the night in each species.

Chapter VII: The surplus production of an individual seedling was calculated as a balance between the income estimated in Chapter V and the outgo in Chapter VI. The estimations were made on the seedlings having average dimensions. The calculated dry matter increments and the corresponding direct determined ones of the seedling grown in the nursery agree with each other from summer to the middle of fall, and differ in spring and late fall.

The gain per individual seedling is higher in fall and lower in winter. For the period August to November, 70 to 80 percent of the annual surplus product are gained in each of the three species. The ratio of respiratory consumption is lower from summer to fall and higher in winter. In midwinter the seedlings are not able to synthesize enough foods to compensate for the respiratory losses. In each species, from 50 to 60 percent of the annual income are distributed to the dry weight increment.

II) Difference among Species in Relation to Silvical Character

P. densiflora, as compared with the other two species is intolerant and is able to establish under severe conditions in open land as a pioneer. It seems that this character of the species is reflected in its ability to carry on photosynthesis at higher light intensities, over a relatively wide temperature range and at lower soil moistures.

In *P. densiflora,* a relatively high capacity for regulating water balance and a rapidly developing root system are effective against drought and also may be favorable for photosynthesis under arid conditions. But these characters of *P. densiflora,* an earlier decrease in photosynthetic rate at slightly below the field capacity associating with an earlier stomatal closure, and a smaller share of surplus product allotted to the growth of photosynthetic organ connecting with a higher distribution ratio of root growth, may be at a disadvantage as compared with two other species in photosynthetic production under relatively moist conditions.

The difference between *Cr. japonica* and *Ch. obtusa* in photosynthetic response is not remarkable as compared with that between *P. densiflora* and two other species. But the characters of two species appear in their differences in degree of depression in photosynthetic rate at above-optimal light intensities and at the advanced stage in drying of soil.

Though the three species differ from each other in photosynthetic responses, these differences are not markedly reflected in dry matter production in the nursery under adequate soil moisture conditions. Here, only light, temperature and soil moisture are taken up as important environmental factors governing photosynthesis. In addition to these, mineral nutrition and also various environmental factors acting for a longer term may be of interest in an explanation for the difference in character of species, on which would need further investigations.

In this work were made the studies on isolated grown individuals. Therefore the results obtained here are available for the seedlings grown in nursery, but to the forest trees, the application of findings is limited. It is desirable that further studies on older trees not only at individual level but also at community level would be made.

As a difference of growing condition between seedling and mature tree is pointed out the effect of temperature at different height above the ground. As described in Chapter V, the higher temperatures in summer caused the depression in apparent photosynthesis. Since the air temperature in the daytime becomes higher with approaching to the ground, the degree of depression in photosynthesis may be remarkable in the seedlings. In table VI and VII, the rates of photosynthetic production estimated by the use of air temperature at 150 cm above the ground are compared with those at 20 cm high. A similar difference is expected also in the effect of lower temperatures in winter. The minimum temperature becomes lower with nearing the ground, and the depression in photosynthetic capacity may be marked in the seedlings. In comparison with 1-year-old seedlings treated here, more remarkable depressions in photosynthetic production in summer and in photosynthetic capacity in winter are probably expected in seedlings at the first year after their emergence.

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アカマツ・スギ・ヒノキ１年生ナエのCO_2同化・呼吸・生長（あらまし）

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しらべたこと

わがくにの重要な造林樹種である，アカマツ・スギ・ヒノキの１年生ナエについて，同化・呼吸・乾物収支の面から，樹種の特性をしらべた。この報告のおもな部分であるⅠ～Ⅶ章は，３つにわけられる。第１はⅠ～Ⅳ章で，わりにかぎられた条件のもとでハチウエナエについて，光・温度・水分と同化量の関係が，樹種によって，どうちがうかをしらべた。第２はⅤ章で，苗畑の条件のもとでの同化量の季節変化をしらべ，その原因の検討をつうじて，各因子の影響の樹種間の差をかんがえた。第３はⅥ・Ⅶ章で，呼吸量をはかり，呼吸によってつかわれる同化生産物の量を推定して，乾物収支量の計算をおこない，苗畑にそだつナエについて物質経済の面から，いろいろとかんがえた。

同化量・呼吸量の測定には赤外線ガス分析器をつかった (Fig. 1, 2, 61)。同化箱は大小ふたつのプラスチック製の透明円筒をかさねたもので (Fig. 3, 4)，あいだに水をながして同化室の気温上昇をふせいだ (Fig. 5, 6)。

わかったこと

同化量の日変化　季節によってちがい，夏型と冬型にわけられる。夏型の日変化 (Fig. 8～10) では，同化量は，そのときどきの光のつよさと温度でほぼきまる。日変化の経路は，はれの日には台形となり，ヒノキでは日中低下のみられることがおおいが，アカマツではあまりめだたない (Fig. 11)。冬型の日変化 (Fig. 12～15) では，温度の影響によるいちじるしい日中低下や (Fig. 12)，同化能力の変化 (Fig. 16, 17) のため，同化量は，そのときの光のつよさや温度だけではき

まらない。夏型の日変化は 4～11 月，冬型の日変化は 12～4 月はじめにみられるが，スギ・ヒノキでは 10・11 月にも冬型のことがある (Fig. 19～22)。

光のつよさと同化量 人工光源は自然光とくらべて，ちがう点がおおいので，野外でえた夏型の同化量の日変化の資料をもとにして，両者の関係をもとめた。水平面日射量 (Fig. 24)，水平面照度 (Fig. 32)，太陽高度 (Fig. 35) のいずれをとっても，アカマツはスギ・ヒノキにくらべて，光のつよさの増加にともなう同化量の上昇がゆるやかである。光飽和がみられる水平面照度は，はれの日で，アカマツ 30k lux，スギ・ヒノキ 20k lux である。スギとヒノキ，とくにヒノキでは，つよい光のもとで同化量の低下がみられる (Fig. 36)。

水平面照度と同化量の関係は天候によってちがう (Fig. 27, 29)。そのおもな原因として，照度計の受光面と同化器官の受光面の形状のちがいが，かんがえられる (Fig. 30)。

温度と同化量 この関係は季節によってかわり，春～秋と冬にわけられる (Fig. 37)。春～秋の最適温度は3樹種とも 20℃ ちかくである。アカマツは，スギ・ヒノキにくらべて，それより温度が上昇したばあいの同化量のへりかたがゆるやかで，最高温度は，アカマツ 45℃ 以上，スギ・ヒノキは 40～45℃ である。最低温度は，あまり同化能力のさがっていない状態では，3樹種ともマイナス数度である。冬には最適・最高温度とも，春～秋よりもひくくなる。

土の水分と同化量 アカマツは土の水分が野外容水量よりすこしへると，同化量がさがりはじめる。これはナエの含水率のわずかな低下によって，気孔がとじはじめるためとかんがえられる (Table 2, 3)。気孔のうごきにともなって蒸散量はへり，またクチクラ蒸散量もちいさいので (Fig. 43)，土がかわいてもアカマツの含水率は，なかなかさがらず (Fig. 39, 44)，3樹種のなかで，もっともひくい土の含水率まで，みかけ同化量がプラスであった (Fig. 40)。スギはアカマツにくらべて，土の乾燥にたいする蒸散量の調節がおくれ，クチクラ蒸散量もおおきい。このため土のかわきはじめには，同化量はほとんどかわらないが，ある程度まで土の含水率がさがると，ナエの水分条件が急速にわるくなり，同化量は急激にさがる。ヒノキの同化量の変化は，土のかわきはじめはスギにちかいが，ナエの水分調節がうまくいくために，みかけ同化量がマイナスになる土の含水率は，スギよりもひくい。

同化量の季節変化 同化能力は3樹種とも春から夏にかけてあがり，夏から秋のはじめに最高，それからさがり冬には最低になる (Fig. 46)。アカマツは，ほかの2樹種にくらべて，同化能力のたかい期間がながく，冬の低下の程度もすくない。

同化能力の季節変化，日射量・気温の記録などをつかって，苗畑の条件のもとでのナエの日同化量を計算した。日同化量は春から夏にかけてふえ，秋から冬にかけてへり，冬はすくない (Fig. 59, Table Ⅲ)。季節変化の最大の原因は同化能力の変化で，太陽高度（日長）の変化と毎日の天候の変化による日射量の増減がそのつぎになる (Fig. 60, Table 9)。毎日の天候による日射量の変化と気温の変化の影響の順位は，アカマツでは日射量が，スギ・ヒノキでは気温がさきになる。夏は同化量がおおいが，たかい気温の影響がなければ，もっと値はふえるであろう。冬に同化量がひくいのは，同化能力の低下とひくい太陽高度による日射量の低下が，おもな原因になっている。春さきの 3～4 月ごろは，日長・気温などの条件はよいが，同化能力がひくいので同化量がすくない。アカマツの同化量がスギ・ヒノキにくらべて，1年をつうじてたかい水準にあるのは，同化能力のたかい期間がながいことと，夏の高温の影響がすくないためである。

呼吸量 地上部の単位呼吸量 (20℃) は，メがのびる時期にその前後よりたかくなり，冬になってもあまりかわらない (Fig. 63)。地下部の単位呼吸量の季節変化は，地上部とはかなりちがう (Fig. 66)。

単位呼吸量の季節変化，気温・地温の記録などから，苗畑でのナエの呼吸量を計算した (Fig. 71, Table IV)。地上部の呼吸量は，春のおわりから秋のはじめにかけてたかい。この期間には，メがのびる単位呼吸量のたかい時期と，それにつづく気温のたかい時期がふくまれる。冬は地上部・地下部とも呼吸量はひくい。地上部の年呼吸量を昼と夜にわけると，3樹種とも昼間の呼吸量は夜間の約2倍になった。

物質収支と乾物生長　苗畑にそだつ平均のおおきさのナエについて (Fig. 68, 69)，まえにえた苗畑での単位量あたりの日同化量・呼吸量から，個体あたりの毎日の収支量をもとめ，炭素含量 (Table 13)・分配率 (Fig. 70) などをつかって乾物増加量を計算した。その結果と実際にナエをほりとってしらべた乾物増加量は比較的よくあう (Fig. 74, Table V)。秋から夏にかけては同化量のうち呼吸によって消費されるわりあいがすくないが，冬から春のはじめにかけては大部分が呼吸につかわれる (Fig. 73)。同化量から呼吸量をひいた収支量は秋に最高になり，冬にはマイナスになることもおおい (Fig. 72)。1年間を3つにわけると，1年生ナエでは年収支量の7～8割が8～11月の期間にえられる (Table 14)。1年分をまとめると，3樹種とも同化量のうちの5～6割が，乾物増加にむけられる (Table 15)。

樹種間のちがいと生態的な性質との関係

アカマツは陽樹で，いわゆる先駆者として裸地や尾根すじのような，きびしい立地条件のもとでも生育の可能な樹種である。対照的な樹種であるスギにくらべてアカマツは，よりつよい光まで有効に同化作用に利用することができ，かなり土がかわいても，またかなり温度がたかくなっても，ある程度の同化作用をいとなむことができる。冬の同化能力の低下のちいさいことからみて，低温の影響もすくない。こうした性質が，日射量はおおいが，はげしい温度変化や土の乾燥がおこりやすい裸地のような立地での生育を可能にしているとかんがえられる。

アカマツは土の水分の変化に敏感に反応し，ナエの含水率の低下がふせがれるが，それにともなって同化量もいくらかさがる。また同化生産物のうち，地下部をつくるのにまわされるわりあいがおおきい。アカマツのこのような性質は乾燥した立地での生育には有利だが，スギの生育に適した，たとえば沢ぞいの比較的水分条件にめぐまれた立地での同化生産には不利なようにおもわれる。

同化作用にみられるスギとヒノキのちがいは，スギとアカマツのばあいほど，いちじるしくはない。ヒノキはスギにくらべれば，乾燥した立地への造林が可能であるが，土の水分と同化量の関係には，こうした性質の差がみとめられた。

ここでは，光のつよさ・温度・土の水分の3条件と同化量の関係をしらべた。しかし，いろいろな立地条件のもとでしめされる各樹種の特性を，同化生産の面からうらづけするには，栄養条件や，ながい期間にわたる光や水分条件の影響なども，とりあげなければならない。

この報告では，土の水分が適当な状態にある苗畑の条件のもとでの同化量を推定し，乾物収支の計算をおこなった。このような条件のもとでは，各因子と同化量の関係にみられた樹種間の差は，あまりきわだって，でてこなかった。各樹種の生態的性質との関係をしるためには，さらにいろいろな栽培条件をくみあわせて，しらべなければならない。

ここでの材料は，個体の状態にある1年生ナエであった。林分やもっとおおきな樹木では，結果がかわることもあるとおもわれる。ナエのばあいと，おおきな樹木のばあいのちがいのひとつとして，ナエではたかさがひくいために，地表面ちかくの変化のはげしい温度条件の影響をうけやすいことが，かんがえられる。

APPENDIX (Tables)

Table I. Horizontal radiation intensity and temperature at 20 cm above or below the ground at Tokyo University Forest Experiment Station, Tanasi, Tokyo for the period April, 1960 to March, 1962.

Year	Month	Radiation (g cal/cm²)		Mean temperature (℃)		
		Monthly total	Daily mean	+20 cm		−20 cm
				Daytime	Night	Whole day
1960	Apr.	11,884	396.1	17.7	12.2	16.1
	May	13,456	434.1	22.5	17.1	20.2
	June	11,495	383.2	25.9	21.2	23.2
	July	13,512	435.9	30.9	25.1	27.5
	Aug.	13,423	433.0	31.0	25.7	28.3
	Sep.	9,466	315.6	27.5	23.1	26.3
	Oct.	8,258	266.4	21.6	16.3	20.7
	Nov.	6,346	211.5	16.4	10.8	15.8
	Dec.	6,619	213.5	11.3	2.7	10.4
1961	Jan.	7,325	236.3	8.6	1.7	8.0
	Feb.	8,812	314.7	10.9	0.7	8.8
	Mar.	10,139	327.0	13.4	6.7	11.5
	Apr.	12,674	422.5	20.4	13.1	16.7
	May	12,954	417.9	24.2	18.2	21.2
	June	11,823	394.1	26.9	21.8	24.5
	July	13,679	441.3	32.9	27.5	29.9
	Aug.	11,707	377.6	32.2	26.8	29.9
	Sep.	11,163	372.1	31.0	24.8	28.5
	Oct.	6,505	209.8	23.3	20.1	22.9
	Nov.	7,122	237.4	17.9	12.4	17.5
	Dec.	7,100	229.0	12.5	4.5	12.2
1962	Jan.	7,790	251.3	9.8	1.3	9.4
	Feb.	8,786	313.8	13.2	3.4	10.2
	Mar.	10,656	343.7	14.9	7.0	12.9

Table II. Duration of temperature (T), radiation intensity (R), and the both at the same time (T and R) favorable for attaining photosynthetic rate above 90 percent of the maximum. Figures in parentheses are the values calculated with the temperature-curve of photosynthesis in winter.

Species	Year	Month	Photoperiod	T	R	T and R
Pinus densiflora	1960	Apr.	393	369	154	152
		May	435	387	191	143
		June	436	325	148	59
		July	444	179	181	13
		Aug.	418	152	197	14
		Sep.	372	260	118	40
		Oct.	350	326	116	104
		Nov.	309	292	88	88
		Dec.	304	221 (240)	105	102 (103)
	1961	Jan.	311	160 (188)	108	97 (105)
		Feb.	304	194 (209)	143	139 (142)
		Mar.	371	282	143	139
		Apr.	393	380	172	162
		May	435	364	181	113
Cryptomeria japonica	1960	Apr.	393	336	155	143
		May	435	331	192	108
		June	436	270	176	51
		July	444	113	214	27
		Aug.	418	98	217	8
		Sep.	372	188	143	24
		Oct.	350	308	142	116
		Nov.	309	275	110	108
		Dec.	304	179 (238)	125	113 (120)
	1961	Jan.	311	117 (188)	134	98 (127)
		Feb.	304	158 (209)	155	135 (151)
		Mar.	371	233	168	157
		Apr.	393	344	206	169
		May	435	319	204	95
Chamaecyparis obtusa	1960	Apr.	393	320	122	105
		May	435	313	135	89
		June	436	267	138	37
		July	444	113	164	26
		Aug.	418	98	157	7
		Sep.	372	188	121	17
		Oct.	350	303	127	102
		Nov.	309	242	98	93
		Dec.	304	137 (180)	118	93 (98)
	1961	Jan.	311	71 (140)	122	57 (107)
		Feb.	304	122 (181)	149	110 (138)
		Mar.	371	191	142	125
		Apr.	393	327	157	133
		May	435	310	164	74

Table III. Sum of apparent photosynthesis per month and cause of depression of the rate in the open as compared with the maximum one.

A. *Pinus densiflora.*

Year	Month	Sum of apparent photosynthesis*	Ratio to the maximum (2,978.7)**	Cause of depression***			
				Photosynthetic capacity	Photoperiod	Radiation	Temperature
1960/61	Apr.	1,009.4	33.9	61.7	13.9	21.4	3.0
	May	1,392.3	46.7	37.8	2.8	50.1	9.3
	June	1,930.7	64.8	29.1	4.5	44.9	21.5
	July	2,016.2	67.7	2.8	0	38.1	59.1
	Aug.	1,859.0	62.4	5.0	13.4	34.2	47.4
	Sep.	1,535.1	51.5	15.5	29.0	30.0	25.5
	Oct.	1,354.2	45.5	28.0	40.4	26.5	5.1
	Nov.	855.1	28.7	38.6	43.8	15.3	2.3
	Dec.	373.7	12.5	53.8	39.0	1.1	6.1
	Jan.	79.3	2.7	58.7	29.3	6.4	5.6
	Feb.	138.5	4.6	65.1	28.6	1.0	5.3
	Mar.	388.9	13.1	66.4	16.6	13.4	3.6
1961/62	Apr.	1,083.9	36.4	66.4	15.0	15.3	3.3
	May	1,384.7	46.5	37.5	2.7	49.2	10.6
	June	1,899.8	63.8	28.2	4.3	46.6	20.9
	July	1,931.7	64.9	2.6	0	33.2	64.2
	Aug.	1,754.4	58.9	4.6	12.1	36.5	46.8
	Sep.	1,555.0	52.2	15.8	29.6	22.1	32.5
	Oct.	1,107.2	37.2	22.8	33.0	36.9	7.3
	Nov.	941.6	31.6	42.2	47.9	8.6	1.3
	Dec.	397.1	13.3	56.2	40.8	0.7	2.3
	Jan.	86.6	2.9	61.9	30.8	3.5	3.8
	Feb.	139.0	4.7	65.2	28.6	2.9	3.3
	Mar.	415.5	13.9	69.8	17.4	10.5	2.3

B. *Cryptomeria japonica.*

Year	Month	Sum of apparent photosynthesis*	Ratio to the maximum (3,832.0)**	Cause of depression***			
				Photosynthetic capacity	Photoperiod	Radiation	Temperature
1960/61	Apr.	536.2	14.0	73.0	10.7	13.0	3.3
	May	1,094.3	28.6	64.7	2.0	20.3	13.0
	June	1,944.0	50.7	47.7	2.8	20.3	29.2
	July	2,349.4	61.3	10.2	0	22.5	67.3
	Aug.	2,127.4	55.5	0	11.0	25.3	63.7
	Sep.	1,931.9	50.4	17.9	24.9	31.8	25.4
	Oct.	1,094.2	28.6	53.0	24.5	17.2	5.3
	Nov.	306.1	8.0	59.6	27.0	11.1	2.3
	Dec.	186.7	4.9	62.2	29.8	3.5	4.5
	Jan.	65.9	1.7	62.0	25.7	3.2	9.1
	Feb.	31.5	0.8	65.0	23.8	4.6	6.6
	Mar.	152.7	4.0	69.7	13.5	11.8	5.0
1961/62	Apr.	565.2	14.7	76.1	11.2	9.1	3.6
	May	1,229.6	32.1	72.5	2.3	14.0	11.2
	June	1,957.6	51.1	48.1	2.9	26.3	22.7
	July	2,115.0	55.2	8.8	0	17.3	73.9
	Aug.	2,074.3	54.1	0	10.6	25.3	64.1
	Sep.	1,760.4	45.9	16.2	22.6	17.4	43.8
	Oct.	926.2	24.2	46.6	21.5	24.3	7.6
	Nov.	339.0	8.8	63.8	28.9	5.7	1.6
	Dec.	197.3	5.1	64.7	30.9	1.4	3.0
	Jan.	72.7	1.9	65.8	27.4	0.1	6.7
	Feb.	33.3	0.9	67.3	24.6	3.8	4.3
	Mar.	164.4	4.3	73.4	14.2	9.6	2.8

Table III. (continued).

C. *Chamaecyparis obtusa.*

Year	Month	Sum of apparent photosynthesis*	Ratio to the maximum** (3,652.0)	Cause of depression***			
				Photo-synthetic capacity	Photoperiod	Radiation	Temperature
1960/61	Apr.	559.0	15.3	71.8	9.8	14.0	4.4
	May	1,265.0	34.6	67.4	2.1	18.6	11.9
	June	1,831.9	50.2	52.7	3.0	18.8	25.5
	July	2,029.2	55.6	12.0	0	17.6	70.4
	Aug.	1,940.3	53.1	0	11.5	22.3	66.2
	Sep.	2,033.2	55.7	8.4	26.0	37.2	28.4
	Oct.	1,367.2	37.4	45.0	25.9	22.0	7.1
	Nov.	487.6	13.4	51.5	25.9	12.7	9.9
	Dec.	227.6	6.2	60.1	28.4	5.1	6.4
	Jan.	43.0	1.2	59.1	22.8	5.3	12.8
	Feb.	19.4	0.5	63.3	21.3	6.6	8.8
	Mar.	172.4	4.7	68.3	11.7	12.9	7.1
1961/62	Apr.	587.1	16.1	74.7	10.2	10.7	4.4
	May	1,316.1	36.0	70.2	2.2	12.9	14.7
	June	1,756.1	48.1	49.7	2.8	21.6	25.9
	July	1,740.3	47.7	10.2	0	13.8	76.0
	Aug.	1,827.3	50.0	0	10.8	20.9	68.3
	Sep.	1,693.0	46.4	6.8	21.0	18.4	53.8
	Oct.	1.170.3	32.0	39.2	22.6	29.7	8.5
	Nov.	588.6	16.1	58.6	29.4	9.1	2.9
	Dec.	236.0	6.5	61.5	29.1	4.9	4.5
	Jan.	49.4	1.4	63.8	24.6	2.9	8.7
	Feb.	21.4	0.6	67.0	22.5	5.7	4.8
	Mar.	183.7	5.0	71.2	12.1	12.0	4.7

D. Values in the winter months calculated by the use of temperature-curve of photosynthesis in winter.

Species	Month 1960/61	Sum of apparent photo-synthesis*	Ratio to the maximum**	Cause of depression***			
				Photo-synthetic capacity	Photoperiod	Radiation	Temperature
Pinus densiflora	Dec.	394.1	13.2	55.9	40.6	1.1	2.4
	Jan.	81.6	2.7	59.8	29.7	6.5	4.0
	Feb.	141.8	4.8	66.1	29.1	1.0	3.8
Cryptomeria japonica	Dec.	191.1	5.0	63.2	30.3	3.6	2.9
	Jan.	70.7	1.8	64.5	26.8	3.4	5.3
	Feb.	33.0	0.9	66.9	24.5	4.7	3.9
Chamaecyparis obtusa	Dec.	226.4	6.2	59.8	28.3	5.1	6.8
	Jan.	46.8	1.3	61.7	23.9	5.5	8.9
	Feb.	20.1	0.6	64.4	21.8	6.8	7.0

* Rate (mg CO_2/g d.w. of top/month) in the open estimated in calculation (d).

** Percent of the maximum rate per month in parentheses.

*** Percent of the total depression in each month.

Table IV. Sum of respiration per month.

Species	Year	Month	Respiration (mg CO_2/g d.w./month)			
			Top			Root
			Daytime	Night	Whole day	Whole day
Pinus densiflora	1960/61	Apr.	521.7	263.5	785.2	667.6
		May	871.6	364.2	1,235.8	709.9
		June	751.3	347.8	1,099.1	822.8
		July	872.7	388.1	1,260.8	1,071.9
		Aug.	709.8	370.2	1,080.0	997.2
		Sep.	500.7	338.7	839.4	767.4
		Oct.	349.0	240.6	589.6	464.5
		Nov.	269.7	164.0	433.7	313.4
		Dec.	185.1	75.6	260.7	204.7
		Jan.	144.4	55.5	199.9	133.3
		Feb.	159.3	53.4	212.7	158.3
		Mar.	258.5	110.3	368.8	318.7
		(Total)	5,593.8	2,771.9	8,365.7	6,629.7
	1961/62	Apr.	614.1	282.0	896.1	700.3
		May	949.5	398.3	1,347.8	758.9
		June	792.3	361.4	1,153.7	884.1
		July	951.6	437.8	1,389.4	1,196.4
		Aug.	743.4	391.5	1,134.9	1,071.6
		Sep.	588.6	369.7	958.3	855.6
		Oct.	386.0	315.7	701.7	528.2
		Nov.	291.5	194.7	486.2	350.1
		Dec.	203.9	98.6	302.5	242.6
		Jan.	161.6	59.3	220.9	155.2
		Feb.	195.8	74.2	270.0	154.2
		Mar.	290.9	113.0	403.9	363.2
		(Total)	6,169.2	3,096.2	9,265.4	7,260.4
Cryptomeria japonica	1960/61	Apr.	264.6	133.1	397.7	453.8
		May	672.5	283.5	956.0	825.3
		June	848.6	394.7	1,243.3	736.6
		July	877.4	389.0	1,266.4	676.1
		Aug.	736.3	384.9	1,121.2	820.6
		Sep.	531.0	358.4	889.4	767.6
		Oct.	349.0	240.6	589.6	541.4
		Nov.	227.9	139.9	367.8	417.6
		Dec.	143.3	60.5	203.8	239.2
		Jan.	110.1	45.6	155.7	92.8
		Feb.	125.1	43.5	168.6	92.0
		Mar.	191.8	82.8	274.6	132.0
		(Total)	5,077.6	2,556.5	7,634.1	5,795,0
	1961/62	Apr.	313.9	144.0	457.9	475.9
		May	734.5	308.1	1,042.6	849.7
		June	882.3	409.7	1,292.0	792.0
		July	958.4	431.2	1,389.6	755.4
		Aug.	769.5	407.7	1,177.2	882.3
		Sep.	622.8	391.6	1,014.4	855.6
		Oct.	386.0	315.7	701.7	616.2
		Nov.	255.2	163.7	418.9	479.6
		Dec.	163.6	78.7	242.3	283.0
		Jan.	126.5	49.4	175.9	108.9
		Feb.	156.6	60.2	216.8	105.9
		Mar.	215.3	85.0	300.3	150.7
		(Total)	5,584.6	2,845.0	8,429.6	6,355.2

Table IV. (continued).

Species	Year	Month	Respiration (mg CO_2/g d.w./month)			
			Top			Root
			Daytime	Night	Whole day	Whole day
Chamaecyparis obtusa	1960/61	Apr.	439.9	223.0	662.9	721.3
		May	715.8	296.2	1,012.0	1,085.7
		June	604.9	281.0	885.9	1,043.9
		July	806.6	366.6	1,173.2	1,129.0
		Aug.	785.6	415.4	1,201.0	1,231.1
		Sep.	556.8	376.7	933.5	1,228.8
		Oct.	369.1	253.1	622.2	773.9
		Nov.	227.9	139.9	367.8	443.5
		Dec.	143.3	60.5	203.8	239.2
		Jan.	110.1	45.6	155.7	133.2
		Feb.	119.4	41.8	161.2	117.9
		Mar.	178.9	77.8	256.7	244.2
		(Total)	5,058.3	2,577.6	7,635.9	8,391.7
	1961/62	Apr.	525.4	241.0	766.4	764.4
		May	783.3	325.4	1,108.7	1,158.3
		June	637.2	291.8	929.0	1,117.3
		July	878.0	411.4	1,289.4	1,258.5
		Aug.	822.3	568.4	1,390.7	1,323.6
		Sep.	655.9	411.2	1,067.1	1,370.0
		Oct.	408.3	336.2	744.5	880.4
		Nov.	255.2	163.7	418.9	509.0
		Dec.	163.6	78.7	242.3	283.0
		Jan.	126.5	49.4	175.9	155.3
		Feb.	139.7	57.6	197.3	136.6
		Mar.	199.3	79.3	278.6	277.5
		(Total)	5,594.7	3,014.1	8,608.8	9.233.9

Table V. Balance of dry matter production of an individual seedling in each month.

Year	Month	Photosynthesis mg CO_2	Respiration mg CO_2		Increment		
			Top	Root	Calculated		Measured
		P	Night R_1	Whole day R_2	mg CO_2 $P-R_1-R_2$	mg dry matter	mg dry matter
(*Pinus densiflora*)							
1960/61	Apr.	746	196	224	326	178	310
	May	1,416	370	326	720	393	520
	June	3,630	658	437	2,535	1,384	830
	July	5,889	1,112	790	3,987	2,177	2,300
	Aug.	9,890	1,978	1,223	6,689	3,652	3,140
	Sep.	11,875	2,602	1,708	7,565	4,130	3,410
	Oct.	13,199	2,339	1,856	9,004	4,916	3,020
	Nov.	9,679	1,872	1,546	6,261	3,419	4,380
	Dec.	4,608	932	1,167	2,509	1,370	
	Jan.	978	684	760	−466	−254	
	Feb.	1,708	658	902	148	81	
	Mar.	4,795	1,360	1,817	1,618	883	
	(Total)	68,413	14,761	12,756	40,896	22,329	
1961/62	Apr.	613	159	182	272	149	620
	May	1,517	433	352	732	400	920
	June	4,409	873	644	2,892	1,579	1,550
	July	7,524	1,696	1,259	4,569	2,495	3,250
	Aug.	12,348	2,756	2,047	7,545	4,120	5,100
	Sep.	16,364	3,871	3,360	9,133	4,987	5,900
	Oct.	15,522	4,413	3,163	7,946	4,339	7,000
	Nov.	17,196	3,604	3,359	10,233	5,587	
	Dec.	7,930	1,969	2,576	3,385	1,848	
	Jan.	1,729	1,184	1,648	−1,103	−602	
	Feb.	2,776	1,482	1,638	−344	−188	
	Mar.	8,298	2,257	3,857	2,184	1,192	
	(Total)	96,226	24,697	24,085	47,444	25,906	
(*Cryptomeria japonica*)							
1960/61	Apr.	235	59	55	121	66	10
	May	566	134	123	309	169	320
	June	1,635	337	203	1,095	598	670
	July	4,302	712	314	3,276	1,789	2,360
	Aug.	10,882	1,915	655	8,312	4,538	5,360
	Sep.	21,571	4,006	1,388	16,177	8,833	8,550
	Oct.	20,120	4,536	1,680	13,904	7,592	9,300
	Nov.	7,220	3,304	2,105	1,811	989	6,900
	Dec.	4,470	1,448	1,234	1,788	976	
	Jan.	1,578	1,092	479	7	4	
	Feb.	754	1,041	475	−762	−416	
	Mar.	3,656	1,982	681	993	542	
	(Total)	76,989	20,566	9,392	47,031	25,680	
1961/62	Apr.	717	182	153	382	209	240
	May	1,800	447	445	908	496	430
	June	4,021	867	604	2,550	1,392	730
	July	6,808	1,376	587	4,845	2,645	2,550
	Aug.	13,810	2,728	967	10,115	5,523	5,350
	Sep.	21,725	4,767	1,704	15,254	8,329	7,950
	Oct.	16,764	5,793	2,020	8,951	4,887	4,500
	Nov.	6,755	3,253	1,807	1,695	925	
	Dec.	4,005	1,598	1,098	1,309	715	
	Jan.	1,476	1,003	423	50	27	
	Feb.	676	1,222	411	—957	−523	
	Mar.	3,337	1,726	585	1,026	560	
	(Total)	81,894	24,962	10,804	46,128	25,185	

Table V. (continued).

Year	Month	Photosynthesis mg CO_2	Respiration mg CO_2		Increment		
			Top	Root	Calculated		Measured
		P	Night R_1	Whole day R_2	mg CO_2 $P-R_1-R_2$	mg dry matter	mg dry matter
(*Chamaecyparis obtusa*)							
1960/61	Apr.	79	32	36	11	6	20
	May	224	52	63	109	60	135
	June	634	98	106	430	235	175
	July	1,137	207	165	765	418	540
	Aug.	2,139	459	321	1,359	742	680
	Sep.	3,702	740	490	2,472	1,350	1,180
	Oct.	4,052	759	521	2,772	1,514	1,280
	Nov.	1,914	501	405	1,008	550	950
	Dec.	849	226	244	379	207	
	Jan.	160	170	136	−146	−80	
	Feb.	72	156	120	−204	−114	
	Mar.	643	290	249	104	57	
	(Total)	15,605	3,690	2,856	9,059	4,945	
1961/62	Apr.	82	33	46	3	2	40
	May	268	66	77	125	68	240
	June	815	139	164	512	280	290
	July	1,322	321	258	743	406	480
	Aug.	2,286	553	430	1,303	711	995
	Sep.	3,754	894	706	2,154	1,176	1,145
	Oct.	3,609	1,043	673	1,893	1,034	630
	Nov.	1,948	543	487	918	501	
	Dec.	817	272	300	245	134	
	Jan.	171	171	165	−165	−90	
	Feb.	74	199	145	−270	−147	
	Mar.	636	274	294	68	37	
	(Total)	15,782	4,508	3,745	7,529	4,112	

Table VI. Sum of apparent photosynthesis (mg CO_2/g d.w. of top/month) estimated by the use of air temperature at 150 cm or at 20 cm above the ground.

Year	Month	*P. densiflora*		*Cr. japonica*		*Ch. obtusa*	
		20 cm*	150 cm	20 cm	150 cm	20 cm	150 cm
1961	Apr.	1,083.9	1,089.4	565.2	570.2	587.1	591.0
	May	1,384.7	1,403.3	1,229.6	1,245.5	1,316.1	1,336.5
	June	1,899.8	1,920.3	1,957.6	1,993.8	1,756.1	1,797.5
	July	1,931.7	2,044.1	2,115.0	2,307.3	1,740.3	1,968.6
	Aug.	1,754.4	1,826.4	2,074.3	2,247.0	1,827.3	2,001.1
	Sep.	1,555.0	1,703.8	1,760.4	1,926.5	1,693.0	1,841.2
	Oct.	1,107.2	1,114.6	926.2	932.9	1,170.3	1,177.4

* Height of measuring temperature.

Table VII. Balance of dry matter production of an individual seedling for the period April to October, 1961 estimated by the use of air temperature at 150 cm or at 20 cm above the ground.

Species	Height of measuring temperature	Photo-synthesis mg CO_2 P	Respiration mg CO_2		Increment	
			Top Night R_1	Root Whole day R_2	mg CO_2 $P-R_1-R_2$	mg dry matter
P. densiflora	150 cm	61,922	14,381	11,223	36,318	19,830
	20 cm	58,297	14,201	11,007	33,089	18,067
Cr. japonica	150 cm	71,823	16,570	6,619	48,634	26,554
	20 cm	65,645	16,160	6,480	43,005	23,481
Ch. obtusa	150 cm	13,274	3,126	2,453	7,695	4,201
	20 cm	12,136	3,049	2,354	6,733	3,676