

Studies on Characteristics of *Pinus densiflora* Forest in Kangwon Province (II). Constructive and Maintenance Respiration as Related to Growth of Saplings^{1*}

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江原道 소나무林的 特性에 관한 綜合的 研究(II) 幼齡木의 生長에 따른 構成呼吸과 維持呼吸^{1*}

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ABSTRACT

Respiration and growth rates of leaves, branches, stems and roots of 2 to 11-yr-old red pine trees (*Pinus densiflora*) were examined and applied to Thornley's growth equation, $R = (\frac{1 - Y_g}{Y_g}) \frac{dW}{dt} + mW$. The conversion efficiency of substrates (Y_g), maintenance respiration coefficients (m), relative growth rates (μ) were estimated. The efficiency of conversion of substrates (Y_g) was 0.3637g/g dw/yr and the maintenance respiration coefficient (m) was 0.094g/g dw/yr. The relative growth rate (μ) was remarkably reduced with age from 0.90 (2-year-old) to 0.33 (11 year-old). The Ratio of gross respiration (R) per gross photosynthesis (P_g), R/P_g showed the range of 0.6~0.7 and annually 64% of P_g was spent for constructive respiration. The 3.4% of dry weight of whole tree was spent for maintenance respiration.

要 約

소나무 幼齡木의 生長에 따른 器官別 呼吸速度를 赤外線 CO₂ 가스 分析機로 測定하여, 이 基礎資料를 Thornley의 生長式 $R = (\frac{1 - Y_g}{Y_g}) \frac{dW}{dt} + mW$ 에 適用, 構成呼吸에 關係되는 物質轉換效率(Y_g), 維持呼吸係數(m), 그리고 相對生長速度(μ)를 推定하였다. 物質轉換效率 Y_g 는 0.3637g/g dw/yr, 維持呼吸係數 m 는 0.094g/g dw/yr, 그리고 相對生長速度 μ 는 0.90(2年生)에서 0.33(11年生)까지 年齡增加에 따라 현저히 減少하는 傾向을 보였다. 또, 소나무 幼齡木의 總光合成量(P_g)에 대한 總呼吸量(R)의 比率(R/P_g)은 0.6~0.7이었으며, 年間 P_g 의 64%가 새로운 物質을 構成하는 構成呼吸으로 消費되었고, 體重(乾物重)의 3.4%가 維持呼吸으로 消費되었다.

¹ 接受 1994年 1月14日 Received on Jan. 14, 1994.

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* 本 研究는 '92년도 韓國學術振興財團 大學附設研究所 學術研究助成費 支援 연구과제의 일부임.

Introduction

The quantitative difference between photosynthesis and respiration indicates the growth of plant. Based on this clear and simple concepts, many reporters used to analyze the biomass in many species of plants(Tatsuhara, 1992 ; Thornley, 1976 ; Takao and Minowa, 1993). Either in trees, the basic concepts of growth model, i.e. the quantitative difference between input and output of carbon dioxide indicates the growth of plant, are not different from that of herbaceous plants. The process of biomass production of trees, however, is more complex and takes longer than that of herbage and the quantity of consumptive organs such as stem, branch and root are especially large. Thus the loss of energy from nonphotosynthetic organs affects heavily on the growth of trees. Furthermore, as the central portion of stem is transformed into heartwood containing physiologically inactive cells, the respiration rate per weight or unit volume is remarkably declined. Therefore, in trees, the growth model in which the growth is expressed by input and output of biomass according to photosynthesis and respiration cannot be explained easily.

Kira and Shidei(1967) mentioned about forest volume increment as follows. If a forest exceeds a certain age, the stand leaf biomass will indicate constant value, and then the respiration of leaf and the gross biomass production of forest will be proportional to leaf biomass. But both the amount of nonphotosynthetic organ and its respiration are increased with age. Therefore, an old stand's net production which is indicated by the difference between gross photosynthesis and gross respiration of that stand is decreased with age and finally becomes zero and thereafter the total volume of that stand maintains always constant value.

As similar concepts, Khilmi(Takahasi, 1965) interpreted that the growth of stand volume could be explained by the difference between input and output of solar energy. He claimed that, after the crown closure, the solar energy(λ) reaching to the forest canopy maintains constant value, and proposed the energy balance equation as following relationship :

$$\lambda = \lambda_1 + \lambda_2 \dots\dots\dots ①$$

where λ_1 is the total energy spent for growth process ; λ_2 is the energy spent for the formation of new tissue and organ. In here, if λ is proportional to stand volume(V), Khilmi's equations are given as following equation ② and ③(Takao and Minowa, 1993).

$$\frac{dV}{dt} = A(\lambda - BV) \dots\dots\dots ②$$

$$V = A - (A - V_0)e^{-B(t-t_0)} \dots\dots\dots ③$$

where A and B are constant, t_0 is the beginning stand age, V_0 is the stand volume at $t=t_0$.

This growth model is assumed to be generated by the hypothesis that the energy of forest canopy received from sun is nearly constant in any stand and light intensity does not differ within crown. He interpreted that absorbed solar energy in low growth stand was more easily exhausted with respiration than high growth stand. On the basis of these hypotheses, we could make a misconception that even in such stand as the photosynthesis is completely stopped, the same energy is absorbed by the canopy and it is consumed vastly in soil's surface (Yahata, 1986).

Thornley(1970) proposed a new growth model based on the conception that the difference between the photosynthetic energy and the respiratory energy is the chemical energy fixed in plant. On the basis of this theory, he thought that the growth is remained energy except the energy consumed for conversion of substrates and maintenance of plant body from photosynthetic substrates, and derived equation ④.

$$\frac{dW}{dt} = Yg(Pg - m \cdot W) \dots\dots\dots ④$$

where W is dry weight of plant, m is the maintenance respiration rate, Yg is the conversion efficiency of substrates into plant dry matter. Pg is the gross photosynthesis. And the resolution of equation ④ is equation ⑤(Hesketh et al. 1971 ; Yahata, 1979).

$$W = \frac{Pg}{m} \{1 - \exp[-m \cdot Yg(t)]\} \dots\dots\dots ⑤$$

In here, equation ④ and ⑤ are similar growth model to Khilmi's equation ② and ③.

The purpose of this study was to estimate maintenance and constructive respiration, and to report about relative growth and photosynthesis in young

Table 1. The description of uninvestigated stands of *Pinus densiflora* forest located in the Chunchon-Gun.

Plot no.	Stand age year	Density no./ha	Height range m	Stump diameter range cm	Crown width		Slope	Altitude m
					Min. cm	Max. cm		
1	2- 3	26,400	0.08-0.17	0.14-0.33	3- 5	4-10	22	190
2	4- 5	24,000	0.26-0.36	0.47-0.55	9-11	15-22	23	210
3	6- 7	24,000	0.57-0.70	0.95-1.21	21-28	39-41	25	190
4	8- 9	25,200	1.00-1.14	1.83-2.10	40-48	50-60	23	200
5	10-11	22,400	1.37-1.72	2.55-3.13	58-73	87-92	26	210

red pine trees with Thornley's growth model(1970) which is more reasonable and concrete than Khilmi's. This study is second series of "The studies on characteristics of *P. densiflora* forest in Kangwon province" (Han et al. 1993). In the First series, the authors had made local stem volume tables with relative growth equations.

Materials and methods

1. Investigation of dry weight growth in each organ

The study site was natural red pine stands located in Jeongjokri and Keoduri, Sindongmyun, Chunchon, Kangwon province. Sampling was carried out on the basis of stand age, for various age classes were required. The range of tree ages is 2 to 11. The outline of sampled plots are shown in Table 1.

In this study, 120 sample trees(10~20 trees in each age) were selected.

Whole trees were dug out and divided in each organ and fresh weights of each organ were measured in the field. Each organ was carried to laboratory and oven-dried for 5 days at 80°C. Mean dry weights of leaf, branch, stem, root of trees are indicated in Table 2.

Dry weight was highest in leaf and then in stem, branch and root in order. As for the increment of dry weight in each organ, until 10 years, the leaf increment was most large. But in 11 year old trees, stem increment was most large among all organ.

2. Measurement of respiration of organs

For the measurement of respiration rate, 30 trees were sampled(3 per each age) and the measurement of the respiration rate of each organ was carried out by turns using the assimilation chamber made of acryl (10cm×13cm×20cm), and the concentration of CO₂ was measured by infrared CO₂ gas analyzer(ADC, MK₃). The respiration rate of stem and branch had been measured in the assimilation chamber after its leaves were removed. Roots were dug up and washed out with water, and then its respiration rates were measured in the assimilation chamber.

When we measure the respiration rates of organs, we controlled the temperature at about 18±0.1°C by water circulator(Yamato, CTE-22W). Temperatures of leaf, branch, stem, root were measured by thermocouple and pen recorder. The chamber was supplied with air that saturated with moisture. The velocity of supplied air was 1 to 2l/min. The air in

Table 2. Mean dry weight of each organ in *Pinus densiflora* saplings(W indicates mean dry weight and L, S, B, R, C means leaf, stem, branch, root and consumptive organ. Δ means increment per 1 year). Unit : g/tree

Age(n)	W _L	W _S	W _B	W _R	W	W _C	ΔW _L	ΔW _S	ΔW _B	ΔW _R	ΔW
2(20)	0.257	0.096	-	0.103	0.456	0.199	0.222	0.069	0	0.074	0.365
3(20)	1.283	0.391	0.204	0.339	2.217	0.934	1.026	0.295	0.204	0.236	1.761
4(10)	3.687	0.953	0.667	0.764	6.071	2.384	2.404	0.562	0.463	0.425	3.854
5(10)	5.020	1.897	1.332	1.190	9.439	4.419	1.333	0.944	0.665	0.426	3.368
6(10)	12.429	7.613	4.562	2.589	27.193	14.764	7.409	5.716	3.230	1.399	17.754
7(10)	25.252	13.121	7.635	4.435	50.443	25.191	12.823	5.508	3.073	1.846	23.250
8(10)	42.007	30.386	14.120	8.745	95.258	53.251	16.755	17.265	6.485	4.310	44.815
9(10)	66.724	54.373	33.814	11.727	166.638	99.914	24.717	23.987	19.694	2.982	71.380
10(10)	127.297	94.762	59.313	28.847	310.219	182.922	60.573	40.389	25.499	17.120	143.581
11(10)	157.406	141.656	88.582	47.764	435.408	278.002	30.109	46.894	29.269	18.917	125.189

chamber was circulated by a fan.

Results and Discussion

1. Growth and respiration rate

The respiration rates of each organ are shown in table 2. It was measured at 18°C, which was the mean temperature of growing season(Apr. ~Oct.) during 10 years(1980~1989) in Chunchon area. Leaf dry matter showed the highest value among all organs, and then in stem, branch and root in order. In 3 year-old red pine stands, allocation rate(%) of each organ was 58 : 9 : 18 : 15 in leaf : branch : stem : root, whereas in 11-year-old stands, allocation rate was 36 : 20 : 33 : 11. In here, we can find that allocation rate of root in 3-year-old stand is higher than that of branch, and then allocation rates of stem and branch are increased with age. Yi et al. (1993) reported that, in 14 to 63-year-old red pine stands located in Kangwon province, average allocation rate(%) of stem, branch, leaf was 63 : 21 : 16 in Chunchon, 63 : 24 : 13 in Inje, 78 : 14 : 8 in Pyungchang, 68 : 19 : 13 in Myungju, and they noted that allocation rate was highest in stem and lowest in leaf. Therefore, it was certain that there were prominent differences of allocation rates between young and old stands.

On the other hand, it could be observed that, based on the same temperature(18°C), respiration rate was highest in leaf, and then in branch, stem and root in order. Respiration rates of conductive organ tended to decrease with age. But the respiration rates of leaves showed the value of 0.65mgCO₂/

g/h regardless of age, for almost all leaves of red pine trees were 1 or 2-year-old and the ratio of live cell to dead cell was constant.

2. Estimation of maintenance and constructive respiration

If Pn is net photosynthesis of plant, it could be expressed according to equation, Pn=dw/dt and Pn=Pg-R. Therefore, Equation ⑥ was derived from Thornley's equation ④ mentioned above.

$$R = (1 - Y_g) P_g + m Y_g W \dots\dots\dots ⑥$$

where, R : respiration rate of plant per unit dry weight and time. This equation is similar to the equation ⑦, which expressed respiration of clover and derived by McCree(1969).

$$R = k P_g + c W \dots\dots\dots ⑦$$

where, k is a constant as energy efficiency used for plant formation in the gross photosynthesis ; c is a maintenance respiration coefficient used for plant maintenance and equal to mYg in equation ④ and ⑥.

On the other hand, we can derive equation ⑧, because of Pg=Pn+R.

$$R = \left(\frac{1 - Y_g}{Y_g} \right) P_n + m W \dots\dots\dots ⑧$$

We can rewrite equation ⑧ to equation ⑨(Thornley, 1976 ; Thornley and Hesketh, 1972).

$$\frac{R}{W} = \left(\frac{1 - Y_g}{Y_g} \right) \frac{1}{W} \cdot \frac{dw}{dt} + m \dots\dots\dots ⑨$$

Many authors insisted that the relationships between $\frac{R}{W} \sim \frac{1}{W} \cdot \frac{dw}{dt}$ is curvilinear(Thornley, 1970) or linear(Chanter, 1977 ; Kimura et al., 1978 ; Mariko, 1988 ; Walker and Thornley, 1977 ;

Table 3. The growth and respiration of *Pinus densiflora* saplings. W is the dry weight : R is the respiration rate. Each value is a mean of 10 to 20 samples.

Age year	Leaf		Branch		Stem		Root		Total	
	W g	R mgCO ₂ /g/h	W g	R mgCO ₂ /g/h	W g	R mgCO ₂ /g/h	W g	R mgCO ₂ /g/h	W g	R mgCO ₂ /g/h
2	0.278	0.65	-	-	0.086	0.40	0.092	0.31	0.456	0.45
3	1.284	0.65	0.204	0.53	0.390	0.25	0.339	0.16	2.217	0.39
4	3.628	0.65	0.691	0.36	0.974	0.15	0.778	0.08	6.071	0.31
5	4.870	0.65	1.182	0.22	1.747	0.12	1.640	0.06	9.439	0.26
6	12.429	0.65	4.562	0.11	7.613	0.09	2.589	0.04	27.193	0.22
7	25.252	0.65	7.635	0.10	13.121	0.07	4.435	0.03	50.443	0.21
8	21.822	0.65	13.934	0.08	30.201	0.05	9.301	0.02	95.258	0.20
9	71.792	0.65	31.214	0.06	51.773	0.04	11.859	0.02	166.638	0.19
10	127.437	0.65	59.469	0.05	94.917	0.04	28.396	0.01	310.219	0.18
11	157.406	0.65	88.582	0.05	141.656	0.03	47.764	0.01	435.408	0.18

Yahata, 1979). Therefore, we can easily estimate the conversion efficiency of substrates(Yg) and maintenance respiration coefficient(m).

In order to estimate the parameters of equation ⑨ in Chunchon red pine trees, dry weights(W), specific growth rates($\frac{1}{W} \cdot \frac{dw}{dt}$), specific respiration rates(R/W) according to age were shown in Table 3. In here, specific growth rates and specific respiration rates tended to decrease with age.

On the basis of data in table 4, the relationship of equation ⑨ was shown in Fig.1. The equation of regression line obtained from Fig.1. is equation ⑩.

$$\frac{R}{W} = 1.7497 \frac{1}{W} \cdot \frac{dw}{dt} - 0.0940 \dots\dots\dots ⑩$$

Therefore, Yg obtained from equation ⑩ was 0.3637g/g dw/yr and m was 0.094g/g dw/yr. In here, 1-Yg is equal to k of McCree's equation ⑦, and we can get K=0.6364. It means that about 64% of annual gross photosynthesis(Pg) is used in constructive respiration. The annual maintenance respiration was 0.094g/g dw/yr. In McCree's equation ⑦, maintenance respiration coefficient c is same value of m·Yg in Thornley's equation ⑥(c=0.094×0.3637=0.0342). Consequently, it can be said that young red pine trees in Chunchon area spent 3.4% of dry weight for maintenance respiration annually. These values were smaller than Yahata's report in which Yg was 0.38 and m was 0.1236 in a mature Japanese cedar forest in Kagosima. The cause of this is considered as that the maintenance respiration rate of trees in Chunchon was lower than that of trees in Kyushyu, southern Japan because of the differences of living temperatures and tree ages.

Referring the similar estimation method of Yg and m, Mariko(1988) indicated the relationships between plant respiration rate(r) and relative growth rate RGR) in a period of Δt=t₂-t₁. The Mariko's equation was expressed in equation 11.

$$\frac{1}{t_2-t_1} \int_{t_1}^{t_2} r dt = \frac{K}{t_2-t_1} \int_{t_1}^{t_2} (RGR) dt + m \dots\dots\dots ⑪$$

In here, r is correspond to specific respiration rate (R/W) and RGR is equal to $\frac{1}{W} \cdot \frac{dw}{dt}$. From this, assumong r and RGR are annual mean value, the equation ⑪ is equal to Thornley's equation ⑨. In equation ⑪, if we plot annual specific respiration rate($\int_{t_1}^{t_2} r dt$) on Y axis and annual specific growth rate($\int_{t_1}^{t_2} (RGR) dt$) on X axis, the slope coefficient

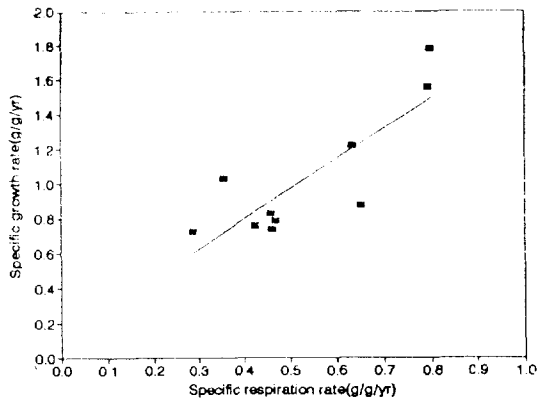


Fig. 1. Specific growth rates against specific respiration rates in *Pinus densiflora* saplings (R squared=0.689006).

Table 4. Time course of specific growth rates and specific respiration rates of whole plant in *Pinus densiflora* saplings.

Age (year)	Dry matter W (g)	Specific growth rate $\frac{1}{w} \frac{dw}{dt}$ (g/g/yr)	Specific respiration rate R/W (g/g/yr)
2	0.456	0.801	1.779
3	2.217	0.794	1.555
4	6.071	0.635	1.221
5	9.439	0.357	1.032
6	27.193	0.653	0.876
7	50.443	0.461	0.832
8	95.258	0.471	0.785
9	166.638	0.428	0.758
10	310.219	0.463	0.738
11	435.408	0.288	0.727

K and m on Y axis could be easily obtained. And because K is equal to $(1-Y_g)/Y_g$, Y_g is estimated accordingly.

The value of Y_g obtained from above equations has meaning as follows. CO_2 absorbed in leaves by photosynthesis is converted to end substrates composed of high energy substrates such as carbohydrates, proteins, lipids, oils and fats, terpenes, lignin etc., and these substrates formation need many molecular energy such as ATP and $NADPH_2$ through the process of biosynthesis. If the process of biosynthesis is known, molecular weights of ATP and $NADPH_2$ required by final products could be artificially calculated.

The molecular weight of ATP and $NADPH_2$ per unit weight of end substrates is not affected by environmental factor. According to Oikawa(1979) and Penning de Vries(1975a), it is noted that the efficiency of conversion of substrates was not influenced by temperature or environmental factors and decided by chemical construction rate of end substrates. If the chemical construction rate of substrates of plant is constant, respiration energy which needed in transformation from CO_2 to plant body is constant. Penning de Vries(1975a) calculated the efficiency of conversion of substrates through clarifying the chemical process from initial photosynthates to end substrates. He calculated the efficiency of conversion of substrates which needed in making 1g of end substrates from 1g of initial photosynthates (glucose) and said that it was 0.616~0.404 in nitrogenous compounds, 0.826 in carbohydrates, 0.330 in lipids, 0.465 in lignin, 1.104 in organic acid. It is obvious that the larger molecular numbers the compounds have, the smaller its efficiency is. Therefore, the plant with high molecular compounds like fats and lignin must have lower conversion efficiency of substrates than the plant with low molecular compounds like carbohydrates and the former spends large respiration energy in making end substrates.

The efficiency of conversion of substrates, $Y_g (= 0.36)$ of red pine is less than that of cotton boll ($Y_g = 0.74$). It means that red pine's end substrates was composed of high molecular compounds which require more substrates conversion energy than cotton boll.

Penning de Vries(1975a) said that in order to

produce 1000g of end substrates, the sunflower absorbed 2235g of CO_2 in photosynthesis and released 506g of CO_2 in respiration of various production process. According to his calculation, it means that in constructive respiration the sunflower spends 27% ($506g/2235g = 0.227$) of CO_2 absorbed in photosynthesis. And this value is similar to clover's 25% calculated by McCree(1969) as mentioned above.

While, maintenance respiration rate m has meanings as follows. Penning de Vries(1975b) said that maintenance respiration was different from constructive respiration. The maintenance respiration energy is spent in maintaining ion concentration of cells to proper levels and transforming enzymes in the process of maintaining plant body. Accordingly, the respiration energy of the organ which does not grow or does not transport substrates belong to maintenance respiration.

In general, maintenance respiration rate is influenced by environmental factors like light, temperature, humidity and soil nutrients(Oikawa, 1979; Penning de Vries, 1975a; Yahata, 1986). The maintenance respiration rate was higher in a sun leaf than in a shade leaf, and varied with species and organs. For example, the maintenance respiration rate of sunflower was higher than that of corn in the same circumstances and especially low in seed or branch of trees(Penning de Vries, 1975b). The maintenance respiration rate was low in xylem of tree, cotton boll composed of cellulose, seed of starchy cereals(Penning de Vries, 1975b). Because maintenance respiration is related to enzyme transformation, it is influenced by protein content, especially by temperature.

And continuous water stress reduces enzyme activation, but there is an exceptional enzyme. By intense water stress, respiration rates of mature leaves were noticeably reduced, whereas that of young leaves were occasionally increased.(Oikawa, 1979). The deficit of soil nutrients raised expenses of maintenance of cell and the deficit of NO_3^- or SO_4^{2-} raised protein transformation to 2~3 times(Oikawa, 1979). For example, Waring et al.(1985) compared *Pinus sylvestris* grown in cold area of Sweden with *Pinus taeda* grown in warm area of southern part of U.S.A. and found that the maintenance respiration rate of *Pinus taeda* was remark-

Table 5. Time course of gross photosynthesis(Pg), net photosynthesis(Pn), respiration(R) of whole plant in *Pinus densiflora* saplings. C is constructive respiration ; M is the maintenance respiration.
(Pg=Pn+R, Pn=ΔW/Δt. Refer to Table 2)

Age	Pg g/tree/yr	Pn g/tree/yr	R			R/Pg
			C g/tree/yr	M g/tree/yr	C+M g/tree/yr	
2	1.176	0.365	0.768	0.043	0.811	0.69
3	5.208	1.761	3.239	1.208	3.447	0.66
4	11.267	3.854	6.842	0.571	7.413	0.66
5	13.109	3.368	8.854	0.887	9.741	0.74
6	41.575	17.754	21.265	2.556	23.821	0.57
7	65.219	23.250	37.227	4.742	41.969	0.64
8	119.593	44.815	65.824	8.954	74.778	0.63
9	197.692	71.380	119.648	15.664	126.312	0.64
10	372.523	143.581	199.781	29.161	228.942	0.61
11	441.731	125.189	275.614	40.928	316.542	0.72

Table 6. Time course of relative growth rate(μ) in *Pinus densiflora* saplings.

Age	2	3	4	5	6	7	8	9	10	11
μ	0.90	0.82	0.64	0.47	0.52	0.44	0.42	0.40	0.40	0.33

$\mu = Yg(Pg - mW) / W ; Yg = 0.3637 ; m = 0.094$

Specific growth rate(g/g/yr)

ably larger than that of *Pinus sylvestris* in the same temperature.

Table 5 indicates gross photosynthesis(Pg), net photosynthesis(Pn), gross respiration(R), constructive respiration(C), maintenance respiration(M), and R/Pg ratio of young red pine trees in Chunchon. In here, constructive respiration occupy remarkable weights in gross respiration and average of C/Pg ratio was 63.6%. Ratio of gross respiration to gross photosynthesis(R/Pg) showed relatively constant value(0.6~0.7) regardless of age increment and it meant that 60~70% of gross photosynthesis was spent in respiration.

On the other hand, the relative growth rate(μ) of plant was expressed in equation ②(Thornley, 1970).

$$\mu = \frac{1}{W} \cdot \frac{dw}{dt} \dots\dots\dots ②$$

From the relation of equation ⑨, ⑫, and Pn=Pg-R, the equation ⑬ is derived(Thornley, 1971).

$$\mu = Yg(Pg - mW) / W \dots\dots\dots$$

In equation ⑬, If the values of Yg is known, m, gross photosynthesis(Pg), and dry weight(W), relative growth rate(μ) can be estimated. Table 6 showed the variation of values estimated by equation ⑬ in each age. Relative growth rate is remarkably high in very young saplings(0.90 in 2-year-old trees and 0.82 in 3 year-old trees), and then get smaller

with age(0.33 in 11-year-old trees). Relative growth rates in Table 4 were estimated values as related to respiratory loss and photosynthetic production in whole tree organs. Therefore, it implies intensive physiological growth rather than general relative growth model.

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