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ABSTRACT

Pitch pine seedlings were grown at constant temperature and photoperiod. Net CO_2-uptake h^{-1} g^{-1} leaves decreased steadily during ontogeny until leaf production ceased. Thereafter, there was no change or a slight increase. Though the ontogenetic pattern was the same in populations native to different geographic areas, there were differences among populations in the rate of CO_2-uptake. Root respiration, calculated from the difference between CO_2-uptake and net assimilation rate, accounted for 6 to 69 per cent of diurnal assimilation.

Growth of shoots and roots was episodic and out of phase. Spurts of growth could be forecast by high rates of respiration 4 weeks earlier, probably because high-energy syntheses precede the processes of cell elongation and cell wall formation. Maintenance and constructive respiration were substantially higher for the shoots (85 per cent leaf tissue) than for the roots. Constructive respiration was proportional to photosynthesis.

INTRODUCTION

In the field, net assimilation rate (NAR) of first year loblolly pine (*Pinus taeda* L.) seedlings declined with age (Ledig and Perry, 1969). It is generally accepted that net photosynthesis also decreases at some point during the first year of growth (Bormann, 1956, 1958). Pines progress through several distinct leaf stages during their first year; cotyledons are followed by primary leaves and eventually, secondary leaves. Each leaf type is morphologically and anatomically distinct. Primary leaves have higher rates of CO_2-uptake than secondary leaves, perhaps explaining the decrease in rate of CO_2-uptake with age (Bourdeau and Mergen, 1959; Wright, 1970). But there was also an initial decrease in CO_2-uptake in Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], which progresses directly from cotyledons to leaves of adult form (Krueger, 1963; Sorensen and Ferrell, 1973). In Douglas-fir the decrease in CO_2-uptake is probably attributable to increased shading within the expanding crown and leaf ageing. It is important to characterize such ontogenetic patterns carefully if tree growth is to be modeled as an aid to management and breeding (Ledig, 1974*b*).

Root respiration also presents a problem in modeling the carbon economy of a plant. Root respiration is usually evaluated in nutrient solution by polarographic methods, or in air, either by O_2-consumption determined manometrically, or by CO_2-efflux determined with an infra-red gas analyzer. All direct methods measure respiration in an environment differing greatly from the relatively stagnant, CO_2-rich, soil atmosphere. The frequent use of detached roots is also suspect because root respiration is dependent on ambient conditions in the shoot (Osman, 1971; Poskuta, Barankiewicz, and Antoszewski, 1971; Szaniawski and Adams, 1974).

In theory, both root and shoot respiration can be partitioned into a component for maintenance of old tissue and a component for growth or construction of new tissue (Baker, Hesketh and Duncan, 1972; McCree, 1970; Monsi and Murata, 1970). Though maintenance and constructive respiration are important parameters in growth modeling, there are no estimates available for tree species.

We followed ontogenetic changes in pitch pine (*Pinus rigida* Mill.) under constant conditions by parallel measurement of CO_2-exchange and growth analysis. Three populations or provenances of pitch pine were compared to determine whether genetic differences existed and to broaden the scope of the investigation. Respiration of roots growing in a relatively natural, undisturbed environment was calculated from rates of CO_2-exchange of the shoot and NAR, providing a standard for comparison of rates measured directly. Respiration was partitioned into maintenance and constructive components for roots and shoots separately, and the relationship of constructive respiration to photosynthesis was examined.

MATERIALS AND METHODS

Seed was collected from two trees in each of three geographically distant stands (Table 1). For the purposes of this study, seed was bulked within stand, using equal numbers of seed from both of the mother trees.

Seed was stratified in damp peat for 20 days, then sown into plastic pots ca. 7·6 cm (3 in) wide by 15·2 cm deep, and covered with 2 cm of white quartz sand. The soil mix was loam, peat and sand in a 1:1:1 ratio. The pots were placed in a growth chamber with photoperiod of 15 h and day:night temperatures of 32:29 °C, relative humidity of 75% ± 5%, and light of 11 800 lx (1100 ft candles). Seedlings were thinned to 2 per pot before overlap occurred. Because of mortality or inadequate germination, there was occasionally only one seedling per pot.

TABLE 1. *Pitch pine provenances used in this study*

Name	County	State or Province	Stand ID No.	N. Lat.	W. Long.	Elev. (m)
St. Chrysostôme	Chateauguay	Quebec	17	45°06′	73°54′	69 (225 ft)
Great Egg Harbor River	Atlantic	New Jersey	34	39°30′	74°46′	9 (30 ft)
Peak Creek	Pulaski	Virginia	54	37°02′	80°50′	677 (2220 ft)

At 66, 94, 121, 158, and 185 days after germination, the rate of CO_2-exchange was measured using six pots from each of the three populations. The above-ground portions of the seedlings were sealed in a plexiglass cuvette. The rate of CO_2-exchange was determined over the interval 280 to 320 p.p.m. with an infra-red gas analyzer operated in a closed system. Procedures were similar to those described in Ledig and Clark (1972). CO_2-uptake was measured under conditions corresponding to day temperature and light intensity in the growth chamber, that is 32 °C and 11 800 lx. CO_2-evolution from the shoot was measured in the dark at 29 °C. Because of a missing value, the CO_2-exchange data was analyzed on a plot mean basis with 3 sources × 5 dates.

Following each CO_2-exchange measurement, the seedlings were harvested. Roots were washed from the soil and separated from stem and leaves. Dry weights were determined after several days of drying at 90 °C.

RESULTS

The rate of CO_2-uptake decreased by 50 per cent from day 66 to day 121 (Fig. 1a). Thereafter it increased slightly to day 185. Analysis of variance indicated significant differences

among populations. The northernmost population, St. Chrysostôme, had consistently lower rates of CO_2-uptake than the southernmost population, Peak Creek. The Great Egg Harbor River population had the highest rates of CO_2-uptake until 121 days when its relative superiority disappeared. However, the population × date interaction was not statistically significant.

The rate of shoot respiration increased to a maximum from day 66 to 94, then decreased to near minimal values by day 121 [Fig. 1b]. Although the pattern seemed to vary among populations, there were no statistically significant differences.

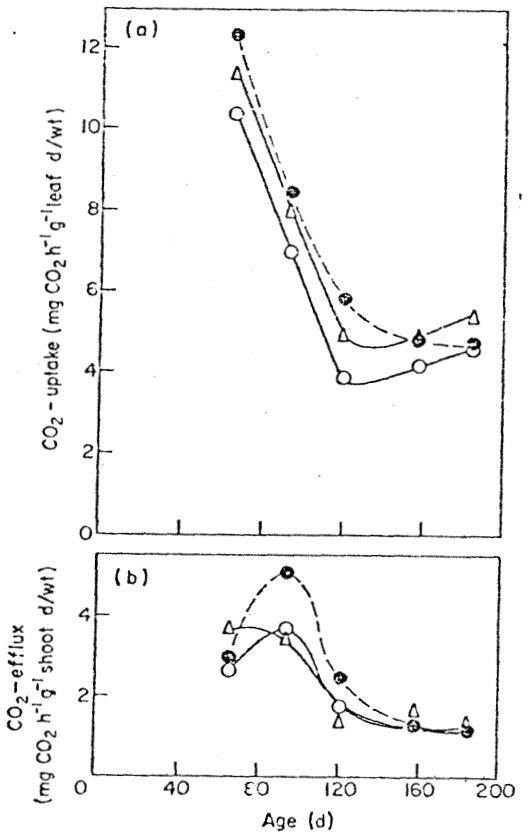

FIG. 1. CO_2-exchange in seedlings of three pitch pine populations ($n = 6$). (*a*) Rate of net CO_2-uptake of shoots at 11 800 lx and 32 °C. (*b*) Rate of CO_2-efflux of shoots at 29° C in the dark. —●— Great Egg Harbour River, NJ;—Δ— Peak Creek, VA; —○— St. Chrysostôme, Quebec.

All three populations followed nearly the same growth curve. At the end of the experiment, differences in dry weight between the largest and smallest population were less than 10 per cent of the mean. Therefore, results were pooled (Fig. 2). The rate of dry weight growth was nearly linear for the entire period, but growth of leaves and roots was obviously episodic. During the first interval (66 to 94 days) root growth was rapid while leaves were slowly increasing in dry weight. Between 94 and 158 days, root growth was nil and root weight may even have declined while leaves increased rapidly in dry weight. Finally, in the period from 158 to 185 days, buds had been set, top growth ceased, and leaf weight actually decreased because of the loss of older primary leaves. However, the rate of total dry weight growth continued unabated due to rapid root growth.

NAR was calculated on a leaf dry weight basis as instantaneous values (Ledig, 1974*a*) from polynomials fitted to total and leaf dry weight. The data suggested a quadratic relationship for total dry weight and cubic relationships for leaf and root dry weight (Fig.

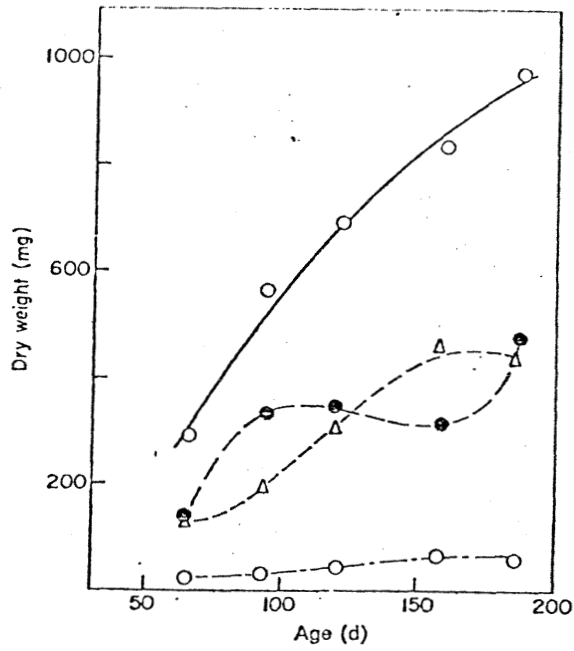

FIG. 2. Fitted curves for total dry weight growth and growth of leaves, roots, and stem of pitch pine seedlings at 32:29 °C day:night temperatures and 11 800 lx. Note alternating periods of leaf and root activity ($n = 18$). —○— Total; —●— Roots; --△-- Leaves; —○— Stem.

2). NAR decreased throughout the experimental period, unlike CO_2-uptake in which the ontogenetic decline was halted at 121 days (Fig. 3 and Table 2).

To make rates of CO_2 exchange and *NAR* comparable, the rate of CO_2-exchange was calculated on a daily basis and converted from g CO_2 to g d. wt. The conversion was accomplished by multiplying the rate of CO_2-uptake in the light by the number of hours of light (15 h), subtracting the rate of dark respiration multiplied by hours of dark (9 h), and multiplying the difference by 0·55:

$$NAR_T = 0{\cdot}55(15P - 9R_T),$$

where NAR_T is net assimilation rate of the shoot; P is net CO_2-uptake of the shoot in the light; and R_T is dark respiration of the shoot. The constant 0·55 is the inverse of the empirical ratio of gC g^{-1} seedling d. wt., multiplied by 12/44, the proportion by weight of C in CO_2. The value 0·55 was rather constant throughout ontogeny in seedlings of both Japanese black pine (*Pinus densiflora* Sieb. et Zucc.) and cryptomeria (*Cryptomeria japonica* D. Don; Negisi, 1966). A similar value (0·54) was calculated for one-year old aspen (*Populus tremuloides* Michx.) grown in controlled environments (Bate and Canvin, 1971). NAR_T as calculated from CO_2-exchange showed a more pronounced reversal of the ontogenetic decline after 121 days (Fig. 3) than rate of CO_2-uptake alone (Fig. 1a). At all points, NAR_T exceeded *NAR*. The difference should be due primarily to losses of C as CO_2 by root respiration.

Root respiration was calculated using the following model for *NAR*:

$$NAR = 0{\cdot}55(15P \cdot W_N - 9R_T \cdot W_N - 24R_R W_R)/W_N,$$

where *NAR*, P, and R_T are as defined above, W_N and W_R are leaf and root dry weight respectively, and R_R is the rate of root respiration in mg $CO_2 h^{-1}$ g^{-1} root d. wt. Solving for R_R:

$$R_R = [0{\cdot}55(15P - 9R_T) - NAR](W_N/W_R)[1/(0{\cdot}55)(24)].$$

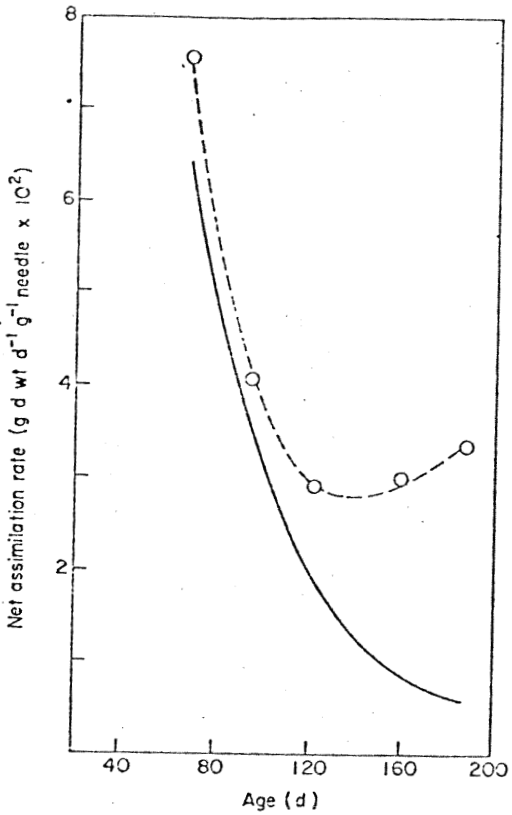

FIG. 3. The decline in *NAR* of pitch pine seedlings with age compared to changes in NAR_T calculated from CO_2-exchange of the shoot (see text). --o-- NAR_T; —— NAR.

TABLE 2. *Growth analysis parameters for pitch pine seedlings*

	Age (days)				
	66	94	121	158	185
Relative growth rate ($g\ g^{-1}\ d^{-1}$)	0·027	0·013	0·003	0·004	0·003
Net assimilation rate ($g\ g^{-1}\ d^{-1}$)	0·064	0·037	0·018	0·009	0·006
Leaf weight ratio ($g\ g^{-1}$)	0·418	0·360	0·447	0·518	0·461

The error of estimate was determined by calculating root respiration for each of the three provenances separately and computing the variance. Root respiration and shoot respiration were decidedly episodic (Fig. 4). When shoot respiration was high, root respiration was low and vice versa.

DISCUSSION

The lack of any difference in growth among the three populations was surprising. In the nursery, there were substantial differences in height among these populations when they were one year old (unpublished data). In general, height growth decreases with increasing latitude. The pronounced sensitivity of northern populations of pitch pine to decreasing day-length (Vaartaja, 1959) may explain the variation observed in the field.

TABLE 3. *Rates of root respiration in woody plants, grouped by technique of measurement. Rates cited for highest temperature reported* ⩽ 32 °C

Species	Respiration (mg CO_2 h^{-1} g^{-1} d. wt.)	Temperature (°C)	Details of measurement	Author
			IRGA, CO_2-efflux in soil	
Populus tremuloides Michx.	1·27	20	Attached root systems of 1-year-old seedlings in soil	Bate and Canvin, 1972
Derris elliptica (Wall.) Benth.	0·3*	27	Attached root systems of 28-month-old seedlings in gravel culture	Huck, Hagemann and Hanson, 1962
			IRGA, CO_2-efflux in air	
Abies mariesii Mast. *Abies veitchii* Lindl.	0·4–1·0	30	Excavated, detached root system of 20-year-old trees in a natural stand	Kuroiwa, 1960
Pinus strobus L.	1·8–3·2†	19	Excavated, detached root systems of 2-year-old, potted seedlings grown outdoors, sampled from May to October	Lister, Slankis, Krotkov and Nelson, 1967
Chamaecyparis obtusa Sieb. et Zucc.	0·4–1·6		Excavated, detached root systems of 1–2-y-old seedlings dug from the nursery, sampled over an entire year	Negisi, 1966
Cryptomeria japonica D. Don	0·2–1·2	20		
Pinus densiflora Sieb. et Zucc.	0·4–1·5			
Pinus strobus L.	0·9–2·6†	25	Excavated, detached root systems of 2-y-old, potted seedlings grown outdoors under various shade treatments, sampled in October	Shiroya *et al.*, 1962
Pinus cembra L.	1·4	30–35	Excavated, detached root systems of young, potted seedlings	Tranquillini, 1959
Pinus sylvestris L.	0·4–1·0	25	Excavated, detached root systems of 1-y-old potted seedlings grown outdoors, sampled from May to October	Zelawski, Kurcharska and Kinelska, 1971
Pinus sylvestris L.	3·2–3·8	25	Detached root systems of 15–20-w-old seedlings grown in nutrient solution	Zelawski and Nalborczyk, 1971
			Manometric, O_2-consumption in air	
Pinus echinata Mill.	5·3–8·3‡	27	Excavated, detached root systems of 45-d-old potted seedlings grown outdoors, sampled in late August	Allen, 1969

Acer rubrum L.	10·1§		Distal 1·5 cm of roots of cuttings grown in growth chamber	Steinbeck and McAlpine, 1966
Liriodendron tulipifera L.	7·4§			
Salix babylonica L.	11·0§	25		
Salix nigra Marsh.	12·7§			
Polarographic, O_2-consumption in solution				
Betula nigra L.	0·9–1·6‖		Distal 6 cm of roots of wild seedlings, 60–120 cm tall, sampled in March and April	Boyer, Romancier and Ralston, 1971
Liriodendron tulipifera L.	1·7–1·9‖			
Salix babylonica L.	0·6–1·1‖	28		
Pinus taeda L.	1·5–1·7‖			
Pinus taeda L.	4·2‖	28	Distal 6 cm of roots of greenhouse-grown seedlings, sampled in mid-winter	
Larix decidua Mill.	0·9–1·4¶		Excavated, attached root systems of seedlings in their second or third year, grown outdoors	Keller, 1967
Picea abies (L.) Karst.	1·9–2·2¶			
Pinus cembra L.	1·4¶	30		
Pinus mugo Turra.	1·1¶			
Pinus strobus L.	1·5¶			
Pinus sylvestris L.	1·5¶			
Tsuga canadensis (L.) Carr.	1·5–2·2¶	19	Attached root systems of 8-month-old seedlings grown in nutrient solution, measured under various levels of shoot illumination.	Szaniawski and Adams, 1974

* converted from μl CO_2 h^{-1} g^{-1} d. wt.
† converted from mg CO_2 h^{-1} g^{-1} f. wt. assuming dry weight is equal to 10 per cent of fresh weight.
‡ converted from μl O_2 h^{-1} 10 mg^{-1} d. wt.
§ converted from μl O_2 h^{-1} mg^{-1} d. wt.
‖ converted from μg O_2 min^{-1} g^{-1} d. wt.
¶ converted from mg O_2 h^{-1} g^{-1} d. wt.

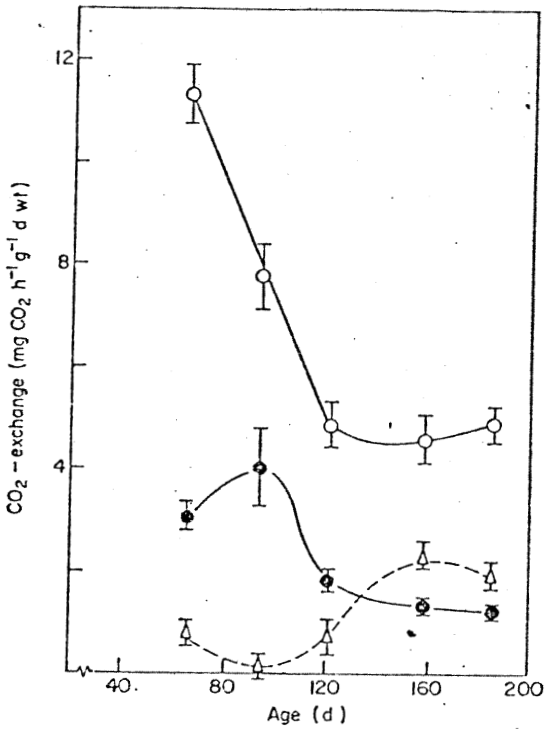

FIG. 4. Rate of net CO_2-uptake at 11 800 lx, respiration of the shoot in the dark (both $n = 18$), and rate of root respiration calculated from NAR and CO_2-exchange data as described in the text ($n = 3$). Note alternating periods of shoot and root activity. Vertical lines indicate $\pm s_{\bar{x}}$. —o— Net Photosynthesis; —•— Shoot respiration; --Δ-- Root respiration.

Obviously, the potential for early growth under the constant conditions used here was not dependent on population.

The distinctly episodic and alternating nature of leaf and root growth is important. An alternating pattern is well-documented in field studies (e.g. Krueger and Trappe, 1967; Friedrich *et al.*, 1973), but our data indicate that it is an inherent rhythm in pitch pine and occurs even under constant conditions. Rather constant relationships between shoot or leaf and root growth rates have been reported (Ledig, Bormann and Wenger, 1970). However, most studies utilized a short period in which alternating patterns of growth were not obvious or long periods during which the general pattern between log(leaves) and log(root) is linear (Ledig and Perry, 1965; Ovington, 1957 analyzed in Ledig *et al.*, 1970). When sampling is frequent and conducted over the equivalent of an entire season, allometric relationships between leaves and root are not so simple.

The ontogenetic decline in net CO_2-uptake continued even after the initiation of secondary leaf production. The decline eventually leveled off, but not until leaf growth had ceased. We suggest that the increase in self-shading as the seedling crown lengthened contributed more to the decline than a change in leaf type. This does not rule out differences in the photosynthetic capacity of cotyledonary, primary, and secondary leaves (Bourdeau and Mergen, 1959; Wright 1970).

NAR of the whole plant continued to decrease even after the ontogenetic decline in the rate of CO_2-uptake by the tops had leveled off. Apparently, respiratory demands of the root increased after shoot growth ceased. Similar patterns in *NAR* were observed in loblolly pine, but could have resulted from temperature acclimation because seedlings were grown outdoors (Ledig and Perry, 1969). The decline in this study occurred under constant conditions, so it was an inherent consequence of the developmental pattern of pine seedlings.

Root respiration calculated from the difference between *NAR* and NAR_T provides a

check on values obtained by more direct gas exchange measurements. Direct measurement of root respiration by CO_2-exchange techniques must always be suspect because the root environment is extensively altered. Root respiration is usually measured by washing the root from the soil and measuring CO_2-efflux in a flowing stream of air. Injury or handling may increase the rate of respiration (Evans, 1972). Measurement of intact roots in soil involves flushing the soil atmosphere with a flowing stream of air (Keller, 1968). With either technique, the normal soil atmosphere, probably CO_2-rich, is destroyed and this might affect respiration. It was encouraging to find that published values (Table 3) were of the same order of magnitude found in this study, suggesting that measurements of root respiration by CO_2-efflux are satisfactory. Rates of respiration reported for whole root systems of pine were in the range of 0·4 to 3·8 mg CO_2 g^{-1} d. wt. h^{-1}, with one exception. The values reported here for pitch pine were very similar, 0·2 to 2·3 mg CO_2 g^{-1} d. wt. h^{-1}. Values reported by Allen (1969) and Steinbeck and McAlpine (1966) in the range 5·3 to 12·7 mg CO_2 g^{-1} d. wt. h^{-1} represented more active tissue; i.e. very young unbranched roots and root tips, respectively. Roots of older seedlings and proximal root portions are more woody and have less respiring tissue for their mass than young roots (Negisi, 1966). Probably, the same explanation applies to the high rates of respiration of wheat roots, 3·6 to 13·5 mg CO_2 g^{-1} d. wt. h^{-1} (Osman, 1971), compared to the rates of perennial strawberry, 0·8 to 2·3 mg CO_2 g^{-1} d. wt. h^{-1}, which is in the range reported for woody plants (Poskuta *et al.*, 1971).

NAR includes a component for nutrient uptake, not accounted for in this study. Assuming that the mineral content of pine seedlings is 10 per cent and that uptake was a constant proportion of dry weight throughout ontogeny, estimates of root respiration would be increased by 5 to 25 per cent, but of course, the pattern would be unchanged.

From the three components, net CO_2-uptake in the light, CO_2-efflux of the shoot in the dark, and CO_2-efflux of the root, a carbon balance-sheet was calculated (Table 4). Although rates of root respiration were not high, roots imposed a major drain on the carbon economy of the seedling because of their mass. At 66 days, 12 per cent of diurnal assimilation was lost by root respiration and the loss increased to 69 per cent by 185 days. Thus any model of growth must include root respiration.

TABLE 4. *Carbon economy of pitch pine seedlings*

Age (days)	Diurnal CO_2 assimilation of shoots in light	Nocturnal CO_2 efflux of shoots in dark		Daily CO_2 efflux of roots		Daily CO_2 balance
	mg	mg	per cent of diurnal assimilation	mg	per cent of diurnal assimilation	mg
66	22·1	4·2	19	2·7	12	15·2
94	22·0	7·9	36	1·4	6	12·7
121	22·6	6·1	27	6·1	27	10·4
158	31·2	6·6	21	17·6	56	7·0
185	32·3	5·5	17	22·2	69	4·6

Dry weight growth and the rate of CO_2-exchange are related in a complex way (compare Figs 2 and 4). At the period marking the commencement of rapid needle growth (94 days), shoot respiration was high, and at the period marking the commencement of rapid root growth (156 days), root respiration was high. Rates of respiration anticipated subsequent changes in growth rate; or in other words, dry weight growth lagged behind changes in respiration. Major metabolic activity preceding spurts of growth was probably involved in synthesis of proteins, nucleic acids and plasmalemma, high energy-requiring syntheses.

Subsequent accumulation of dry weight was largely a measure of cell expansion and the conversion of sucrose to cell wall substance. The conversion of sucrose to polysaccharides may have an efficiency as high as 95 per cent (Barnes, 1972), so respiratory losses during cell wall formation would be low. When rates of respiration were plotted against growth rate one measurement period (ca. 4 weeks) later, the correlation was excellent, but there was no correlation with current growth rate (Fig. 5). The correlation between rate of respiration and rate of growth 2 or 3 weeks later might be better than the correlation with rate of growth 4 weeks later. We used 4 weeks because that was our sampling interval and no interpolation was required.

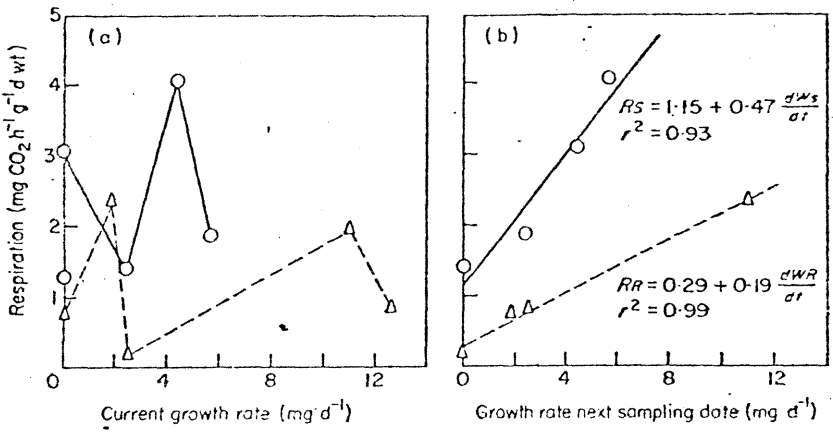

FIG. 5. (*a*) Lack of relationship between the rate of shoot respiration g^{-1} leaf d. wt. versus the rate of d. wt. growth of leaves (dW_L/dt), and rate of root respiration g^{-1} root d. wt. versus the rate of d. wt. growth of the roots (dW_R/dt). (*b*) Rates of shoot respiration and root respiration related to rate of d. wt. growth one sampling period later, demonstrating the lag of d. wt. growth behind respiration.

Figure 5(*b*) can be used to partition respiration into maintenance and constructive components. Maintenance respiration produces the energy to maintain tissue integrity and function. It can be estimated as the rate of respiration when no growth is occurring, 1·15 mg CO_2 h^{-1} g^{-1} d. wt. for shoots and 0·29 mg CO_2 h^{-1} g^{-1} d. wt. for roots. Constructive respiration results from catabolic processes that supply ATP and other intermediates to meet energy requirements for the conversion of carbohydrate to new tissue. The slopes of the relationships in Fig. 5(*b*) indicated that 0·47 mg CO_2 was respired to produce each mg of new shoot and 0·19 mg CO_2 to produce each mg of new roots. Both maintenance respiration and respiration of growing tissues was several times greater in the shoot (which was ca. 85 per cent leaf weight) than in the root—a reasonable result considering the woody nature of the root.

McCree (1970) defined constructive respiration as a function of gross photosynthesis, but Baker *et al.* (1972) questioned this procedure. We tested McCree's hypothesis by comparing constructive respiration to gross photosynthesis calculated as the sum of net CO_2-uptake in the light plus shoot respiration in the dark. Because this method of calculating gross photosynthesis is questionable, we also compared constructive respiration to net photosynthesis (Fig. 6). Constructive respiration was a constant proportion of both net and gross photosynthesis calculated on a daily basis. Such a relationship will not hold for shorter periods because of the lag in transport of photosynthate to the site of respiration.

Unless growth is constant, the technique presented here can be used to estimate maintenance and constructive respiration, important parameters in growth models (Monsi

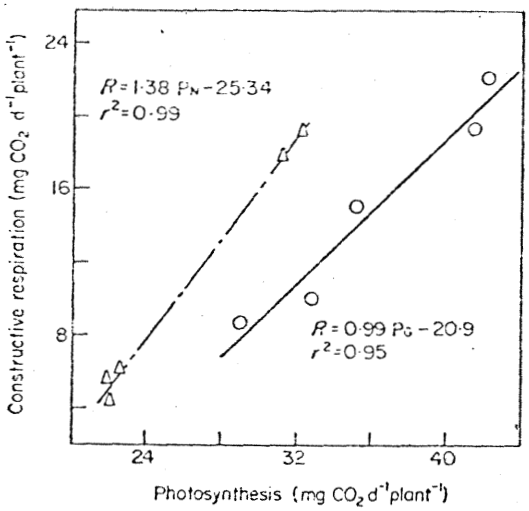

FIG. 6. Data showing that constructive respiration is proportional to net and gross photosynthetic CO_2-uptake.

and Murata, 1970; Baker *et al.*, 1972). It is obvious that maintenance and constructive respiration may be quite different in different tissue types, and growth models should take that into account. Based on the correlation between respiration and photosynthesis, it appears that the level of constructive respiration may be determined by the availability of photosynthate.

ACKNOWLEDGEMENT

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