

## Predicting fine root production and turnover by monitoring root starch and soil temperature

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To determine how the longevity of fine roots (those without secondary thickening) is controlled, shoots of Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) seedlings were exposed to light or maintained in darkness while roots were maintained at 10, 20, or 30°C. Fine root maintenance respiration rates, estimated from rates of starch and sugar depletion in the seedlings maintained in darkness, ranged from 0.83 to 3.25 mg starch g dry weight<sup>-1</sup> day<sup>-1</sup>. At 20 and 30°C, starch deposition was curtailed and previously deposited starch was used to maintain the older roots, whether current photosynthate was entering the root system or not. On the other hand, at 10°C starch was deposited in the roots whenever the root systems grew. Based on these results, we suggest that starch deposition in a fine root occurs only when the root is being formed and the root carbon balance is positive. Starch is subsequently respired to meet maintenance requirements exclusively. A simple means of estimating root biomass production and turnover based on root starch and soil temperature is described and compared with field estimates.

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Pour déterminer comment est contrôlée la longévité des racines fines, des pousses de semis de douglas (*Pseudotsuga menziesii* Mirb. (Franco)) furent exposées à la lumière ou gardées à l'obscurité, alors que les racines furent maintenues à 10, 20 ou 30°C. Les taux de respiration d'entretien des racines fines, estimés à partir des taux d'utilisation de l'amidon et des sucres dans les semis maintenus à l'obscurité, variaient de 0,83 à 3,25 mg d'amidon g de matière sèche<sup>-1</sup> jour<sup>-1</sup>. À 20 et 30°C, la déposition d'amidon fut restreinte et l'amidon déposé antérieurement fut utilisé pour le maintien des racines plus âgées, que les produits courants de la photosynthèse soient transférés ou non au système racinaire. Par ailleurs, à 10°C l'amidon fut déposé dans les racines quand le système racinaire était en croissance. En se basant sur ces résultats, nous croyons que la déposition d'amidon dans une racine fine se produit seulement lorsque la racine est en voie de formation et que le bilan du carbone de la racine est positif. L'amidon est par la suite respiré uniquement pour assurer le maintien de la racine. On décrit ici un moyen simple d'estimer la production et le turnover de la biomasse racinaire, basé sur la teneur en amidon des racines et la température du sol, et on compare cette estimation aux mesures obtenues au champ.

[Traduit par le journal]

### Introduction

It has long been known that fine roots, or feeder roots, are responsible for the majority of nutrient and water uptake by trees (Lyr and Hoffman 1967; Trappe and Fogel 1977). The physiological costs of maintaining a fine root system are, however, remarkably high (Keyes and Grier 1981; Ågren *et al.* 1980; Grier *et al.* 1980). Although fine roots may constitute less than 1% of the total biomass of a mature tree, they may account for as much as two-thirds of annual biomass production (Grier *et al.* 1980). This is attributed largely to their short lifetimes; fine roots may be replaced (turn over) two to three times each year (Persson 1979; Santantonio 1982), or perhaps even more (Head 1973; Persson 1978). These findings are important to foresters and production ecologists because biomass production below ground, coming from a finite supply of photosynthate, substantially reduces production above ground (Keyes and Grier 1981).

Consequently, what determines the life-span of fine roots is a key physiological question of great ecological significance. Drought and carbohydrate exhaustion have been suggested as possible causes of fine root death (Persson 1979, 1980; Santantonio 1982). A previous study found that the life-span of fine roots was unaffected by the normal range of drought conditions, but that root mortality closely followed the exhaustion

of starch and sugar reserves (Marshall 1984). Starch and sugar are respired to provide the energy required for the maintenance of enzymatic machinery and membrane transport systems in all living tissue, growing or nongrowing. Maintenance respiration rates increase exponentially with temperature (Lawrence and Oechel 1983; Amthor 1984).

Total respiration rates of actively growing tissue are much higher than the maintenance respiration rate because additional CO<sub>2</sub> is released in biosynthetic processes associated with growth. The respiratory cost of a given unit of tissue, termed "growth respiration," is not related to temperature and depends only on the chemical composition of the tissue (Penning de Vries *et al.* 1974; McDermitt and Loomis 1981). Growth can, of course, be curtailed, but a tissue will die if its maintenance requirements are not met.

Seedling physiologists have long been aware of the importance of starch reserves for supporting maintenance respiration (Winjum 1963). Nursery seedlings are commonly stored under cold, dark conditions for several months prior to planting. Loss of reserves during storage has been demonstrated (Ronco 1973; Ritchie 1982) and these losses have been implicated in poor root regeneration and poor seedling survival following planting (see Ritchie 1982).

Reserves are used for growth as well as maintenance. Shoot growth in conifers has been shown to utilize stored reserves (Gordon and Larson 1970). Similarly, two recent studies have concluded that root growth is associated with reductions in root

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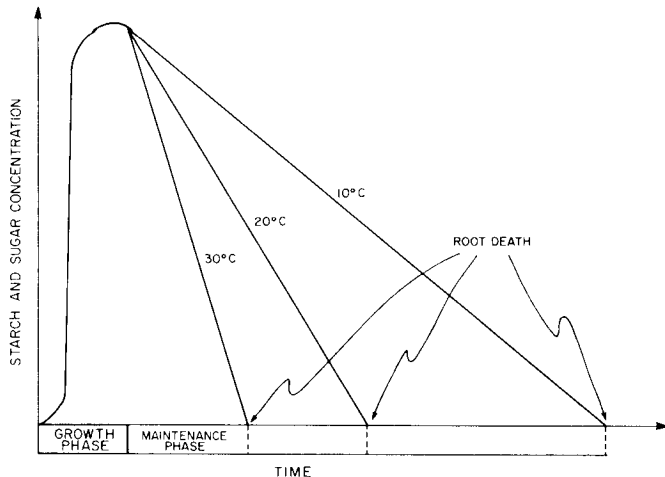


FIG. 1. Hypothesized starch and sugar dynamics of a fine root, showing differences in life-span associated with root temperature.

starch concentrations (Ford and Deans 1977; Ericsson and Persson 1980). These studies, however, did not clearly distinguish whether starch reserves were depleted from all roots or only from those of large diameter.

In this study, we test the following hypotheses: (i) that the growth of fine roots is accompanied by starch accumulation rather than depletion, (ii) that a fully developed fine root meets its maintenance requirements wholly from its starch and sugar reserves, and (iii) that the root dies when its starch and sugar reserves are exhausted (Fig. 1). A corollary of these hypotheses is that soil temperature controls fine root turnover through its effect on maintenance respiration. To evaluate these hypotheses, we conducted an experiment in which light and soil temperatures were controlled and starch and sugar concentrations were monitored in fine roots. From the results of this experiment, a model was developed to predict fine root production and turnover in two field studies, the first with Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) forests growing over a range of soil moisture regimes (see Santantonio 1982) and the second with a young Scots pine (*Pinus sylvestris* L.) stand growing in the boreal climate of Sweden (see Ericsson and Persson 1980).

### Materials and methods

Two-year-old Douglas-fir seedlings, grown from seed collected in 1981 near Vernonia, OR (46° N, 123° W), were used as experimental material. Mycorrhizal infection was low at the beginning of the experiment. In March 1983, the seedlings were carefully washed free of soil and transplanted into washed river sand in 550-cm<sup>3</sup> plastic tubes. A small amount of root growth had already begun prior to the replanting. The seedlings were then grown in a cold frame until treatments began.

In early April, as buds were beginning to swell, the seedlings in their plastic tubes were transferred into metal boxes filled with sand. The boxes were placed into stirred water baths at temperatures of 10, 20, and 30°C ( $\pm 0.5^\circ\text{C}$ ) to alter maintenance respiration rates of the root systems. Temperatures in the tubes were equal to those in the water baths except in the uppermost centimetre or two of sand. The water baths were in a growth chamber maintained at an average temperature of  $21.0 \pm 0.5^\circ\text{C}$  and a relative humidity between 70 and 100%. Light levels, provided by fluorescent light supplemented by 300-W Sylvania incandescent bulbs, ranged from 90 to 120  $\mu\text{E m}^{-2} \text{s}^{-1}$  for 16-h days.

At the time of transfer into the growth chamber, half of the seedlings in each temperature treatment were covered by an aluminum

foil sleeve with a volume of about 500 cm<sup>3</sup>. All foliage was tucked up into the sleeve and the sleeve was pushed down to ground level, effectively excluding all light.

Seedlings were not fertilized during the experiment to favor root growth and starch accumulation (Etter 1969; Ariovich and Cresswell 1983). Seedlings were watered whenever soils dried to 2 cm below the surface; watering schedules were adjusted as necessary after each seedling harvest. Average watering intervals varied: 21 days for the covered seedlings at 10°C, 12 days for the uncovered seedling at 10°C, 11 days for the covered seedlings at 20°C, 10 days for the uncovered seedlings at 20°C, and 9 days for the covered and the uncovered seedlings growing at 30°C. In the 10 and 20°C treatments, soil was always moist at harvest so watering was presumably adequate. In the 30°C treatments, however, soils dried quickly and watering intervals were necessarily decreased in the course of the experiment.

Harvest intervals were chosen to match estimated rates of starch depletion based on prebudsbreak starch concentrations measured by Ericsson and Persson (1980) and fine root respiration rates presented by Ågren *et al.* (1980). The first harvest was made just before seedlings were transferred into the growth room.

At the start of the experiment only 10 seedlings were analyzed. These 10 seedlings represented initial conditions in separate analyses of variance for each of the soil-temperature treatments. Although none of the seedlings had yet been shielded from light, the seedlings were arbitrarily divided into five covered and five uncovered so that the first harvest could be included in the analyses of variance. As the experiment progressed, the sampling intervals were adjusted to accommodate differences in growth rates and the long life of seedlings under dark conditions. At 10°C, the last harvest was made after 140 days, whereas at 20 and 30°C final harvests were made after 120 and 60 days, respectively.

Five covered and five uncovered seedlings were chosen at random from each water bath at each harvest date. Because seedlings had not been planted at uniform depths, we divided the plant into root and shoot sections immediately above the first lateral root. Root systems were carefully washed. Roots were then divided into three classes: (i) coarse roots, those roots showing evidence of secondary thickening, specifically, shreds of the periderm overlying a lighter, woodier bark, (ii) old fine roots, those roots without evidence of secondary thickening that appeared to have been present before planting, and (iii) new fine roots. Old fine roots were separated from new fine roots by their darker color, lack of root hairs, more basipetal position, and smaller diameter than fine roots produced more recently.

Samples were dried in a forced-draft oven at 70°C, weighed, and ground to pass a 40-mesh sieve. Samples of 100 mg of the dried, ground tissue were extracted with 100% acetone to remove chlorophyll and other pigments (W.D. Loomis, Oregon State University, Corvallis, OR, personal communication). This extraction removed no detectable sugar or starch. Sugars were then extracted with hot 80% ethanol three to four times until the extract was colorless. This procedure is similar to the Soxhlet extraction (Anonymous 1980). The ethanol extract was cleared first with 100 mg insoluble polyvinylpyrrolidone and then with 100 mL saturated lead acetate solution (Sanderson and Perera 1966). Sugars were determined colorimetrically by the anthrone reaction (Yemm and Willis 1954; Hansen and Moller 1975). Labile polysaccharides were extracted from the ethanol-extracted residue using 35% perchloric acid (Hansen and Moller 1975) on an orbital shaker for 16 h. Quantities of labile polysaccharides, which were mostly starch (Marshall 1984), were determined colorimetrically with anthrone (Yemm and Willis 1954; Hansen and Moller 1975). The perchloric acid extracted 40 mg g dry weight (DW)<sup>-1</sup> of carbohydrates other than starch in all tissues throughout the experiment (Marshall 1984). Perchlorate-extractable carbohydrate concentrations were, therefore, corrected to yield starch concentrations and are expressed in their corrected form throughout this paper. Because of experimental error in determining amounts of background carbohydrates and starch, some values were slightly below zero after this correction.

The experiments were analyzed as nine separate, completely ran-

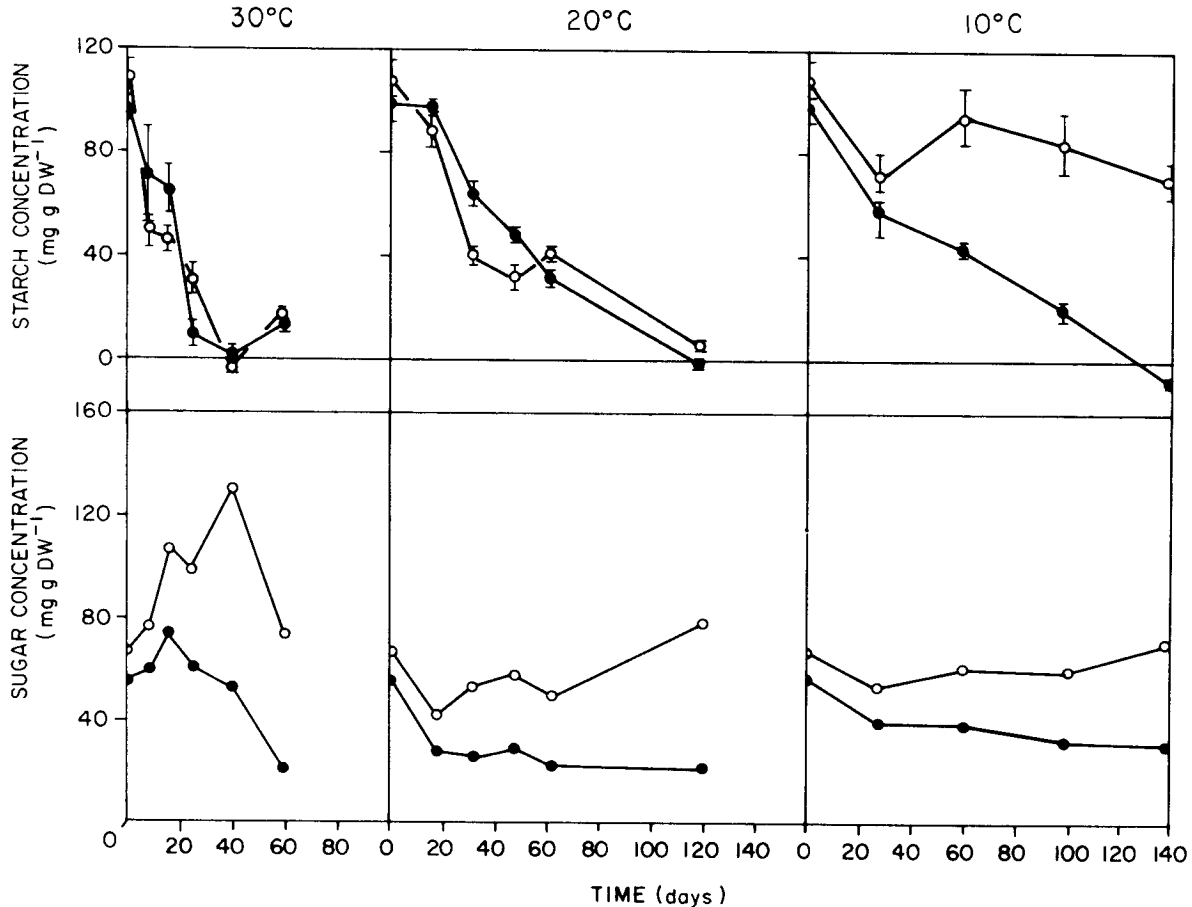


FIG. 2. Starch ( $\bar{x} \pm SE$ ) and sugar concentrations of old fine roots from seedlings grown at specified soil temperatures and exposed to light (○) or maintained in darkness (●).

domized designs, one for each combination of tissue type (shoots, coarse roots, and old fine roots) and temperature (10, 20, and 30°C). Harvest date and light treatment were analyzed as treatments in a factorial design (Steel and Torrie 1980). New fine root samples were composited because amounts from individual trees were generally too small for starch analysis; therefore, they were excluded from the analysis of variance for starch concentrations. Comparisons among subsequent harvests and between dark-grown and light-grown seedlings within a harvest were made using the least significant difference test (Steel and Torrie 1980).

Maintenance respiration rates were calculated by observing the decrease in total carbohydrate reserves (sugar and starch) in covered seedlings exposed to different root temperatures. The first harvest was excluded because respiration rates often respond to sudden changes in temperature (Smakman and Hofstra 1982). The last harvest was excluded because the depletion of starch and sugar was generally already complete. This procedure yielded estimates that were approximately equal to measured rates of CO<sub>2</sub> efflux from root systems (J. D. Marshall, unpublished). Regression lines were fitted to the starch and sugar depletion data and slopes and intercepts were compared using covariance analysis (Neter and Wasserman 1974).

With regression analysis we predicted fine root growth from net changes in fine root starch concentration for the roots from the 10°C treatment. Net daily rates of change in starch concentration were calculated by comparing mean starch contents of subsequent harvests and dividing by the interval between the harvests. We compared these predictions with measured changes in relative growth rates of roots obtained from differences in mean root weight between subsequent harvests (Evans 1972). New fine roots and old fine roots were combined in this analysis.

## Results

Analyses of variance of starch concentrations and weights measured the importance of light, harvest date, and the interaction between light and harvest date for each combination of plant components and root temperatures. In the analysis of starch concentrations (Table 1), interactions between light level and harvest date were significant ( $\alpha = 0.01$ ) for shoots and fine roots at all temperatures. The significance of the interaction for the coarse roots was demonstrated at 10°C, but not at 20 or 30°C. At 20 and 30°C, the effect of light alone was not significant for either the fine or coarse roots. For roots at 10°C, however, as well as for shoots at all temperatures, light effects were very highly significant ( $\alpha = 0.001$ ).

The above results can be interpreted by examining the interaction means, shown in Figs. 2, 3, and 4. Some starch concentrations shown in Figs. 2, 3, and 4 are negative because the values were corrected for mean levels of nonstarch carbohydrate. The significance of the interactions for the old fine roots at 20 and 30°C is due to the covered and uncovered seedlings being alternately higher than one another as the experiment progressed (Fig. 2). This may be attributable to our inability to consistently separate the root fractions from one harvest to the next. It may also be attributable to the conversion of starch to sugars in the light treatments in the early harvests. In either case, the differences between covered and uncovered seedlings are small relative to the decline in starch concentration over time.

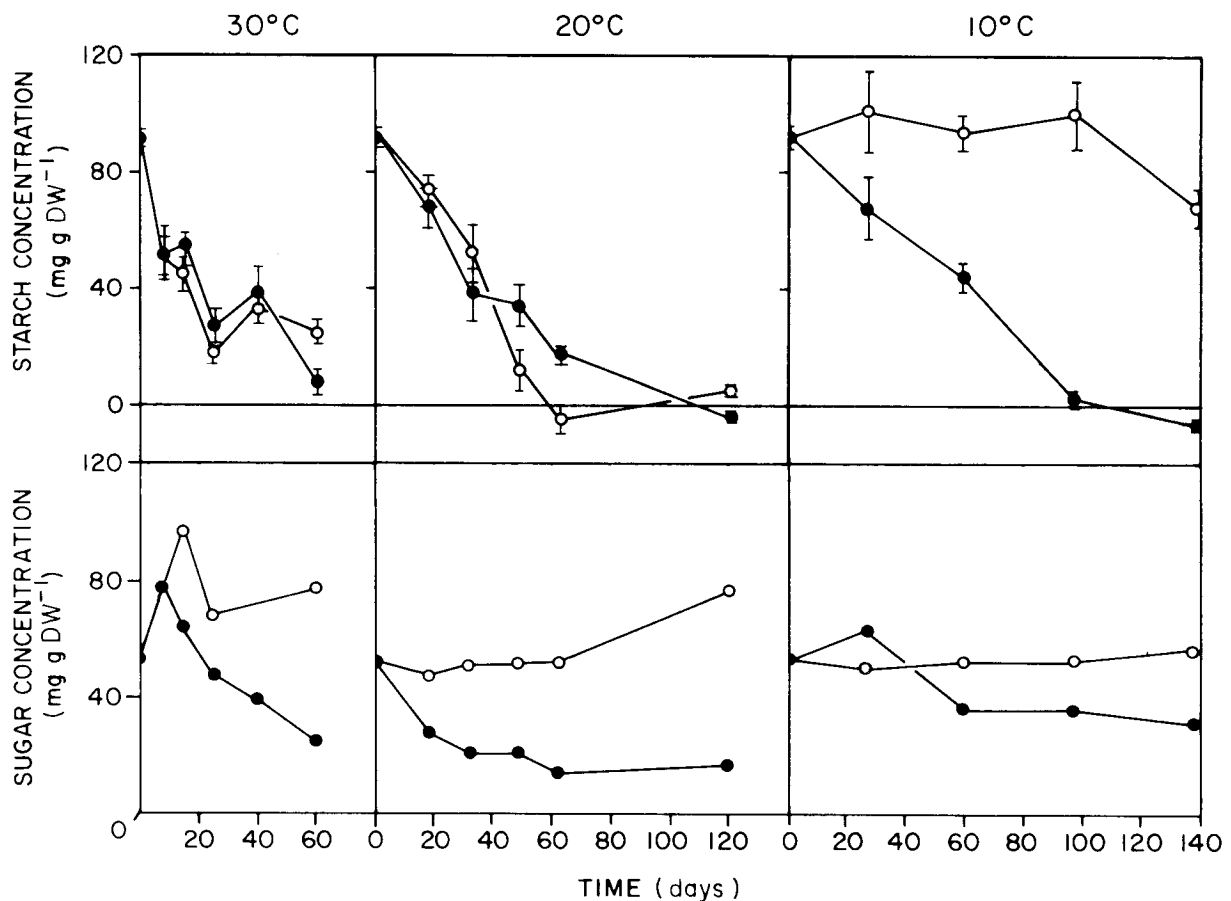


FIG. 3. Starch ( $\bar{x} \pm SE$ ) and sugar concentrations of coarse roots (with secondary thickening) from seedlings grown at specified soil temperatures and exposed to light (open symbols) or maintained in darkness (closed symbols).

TABLE 1. Tests of significance of *F*-tests from analyses of variance for starch concentrations of seedling components

Root temp. (°C)	Light	Harvest	Light × harvest
Shoots			
30	***	***	***
20	***	***	***
10	***	***	***
Coarse roots			
30	NS	***	NS
20	NS	***	NS
10	***	***	***
Old fine roots			
30	NS	***	***
20	NS	***	***
10	***	***	***

NOTE: NS, not significant at 0.01 level; \*\*\*, significant at 0.001 level.

At 10°C, however, starch concentrations of the roots were definitely affected by light conditions (Figs. 2, 3, and 5). Starch concentrations in old fine roots of covered and uncovered seedlings declined in parallel between harvests one and two (Fig. 2). Between harvests two and three, however, the starch concentration of the fine roots increased in the light-

grown plants. Starch concentrations of the coarse roots in the light did not fall significantly below prebudbreak level until the final harvest (Fig. 3). Thus, we explain the light effect shown in the analysis of variance for fine and coarse roots at 10°C (Table 1) as being due to consistently higher starch concentrations in the root systems of the light-grown seedlings.

From a maximum starch concentration of 288 mg g DW<sup>-1</sup>, shoots of the covered seedlings declined sharply over the first 30 days, then continued to decline much less sharply until day 100, when all starch was depleted (Fig. 4). The new shoot tissue produced during the first 30 days represented 20.3 ± 1.4% ( $\bar{x} \pm SE$ ) of the weight of the old tissue. Starch concentrations of the shoots of the light-grown seedlings declined less steeply and increased to over 160 mg g DW<sup>-1</sup>, later to fall again.

We also calculated an analysis of variance on the weights of seedling components for each combination of light treatment and harvest date at the different soil temperatures (Table 2). The light level by harvest date interaction was always significant for the shoots, coarse roots, and new fine roots. For the old fine roots, however, the light by harvest date interaction was never significant and the effects of light treatments were inconsistent.

In the covered seedlings, weights of all seedling components remained essentially unchanged, although there were downward trends in weights of all components except the new roots, probably as a result of starch depletion (Table 3). Shoot weights of the uncovered seedlings increased significantly, but not until shoot elongation had ceased and starch levels had

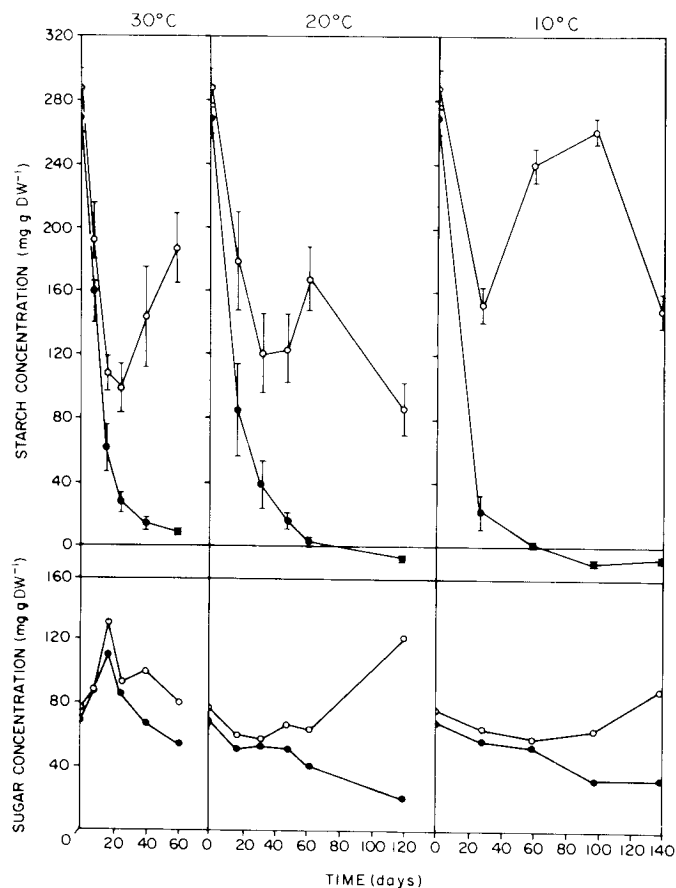


FIG. 4. Starch ( $\bar{x} \pm SE$ ) and sugar concentrations of shoots of seedlings grown at specified soil temperatures and exposed to light (○) or maintained in darkness (●).

begun to recover. Coarse root and new root weight in uncovered seedlings rose significantly following the increase in shoot weight. There were no consistent increases in weight of old fine roots in seedlings exposed to light.

Relative growth rate was regressed against change in starch concentration for composited new and old fine roots grown at 10°C under light (Fig. 6). The relative growth rate is negative when no growth occurs because respiration of reserves results in weight loss. As hypothesized, fine root growth was associated with starch deposition. In slow-growing roots, small decreases in the average starch concentration sometimes resulted when starch losses in maintenance respiration exceeded starch gains associated with growth.

Maintenance respiration rates of each of the seedling components were calculated by linear regression of mean starch and sugar concentration against time for each temperature treatment, using only the covered seedlings. There were no differences among the slopes and intercepts of the starch and sugar depletion curves for the shoots. The slopes and intercepts were not all significantly different for the roots at different temperatures; the separate equations are presented, however, because the slopes are our best estimates of maintenance respiration rates (Table 4). The regression equation predicting maintenance respiration rates ( $R_m$ , milligrams  $CH_2O$  per gram DW per day) from root temperatures ( $T$ , degrees Celsius) is

$$[1] R_m = 0.408e^{0.0685T}$$

The  $R^2$  of this equation is 0.99. The  $Q_{10}$  value of  $R_m$  is 1.98.

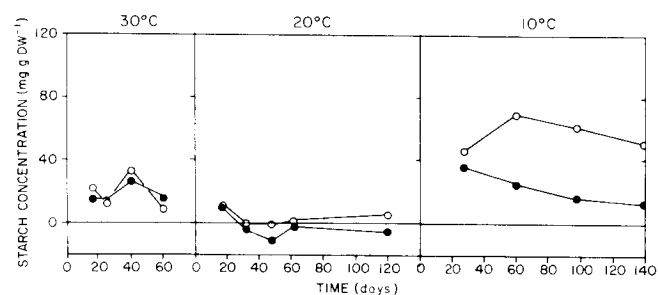


FIG. 5. Starch concentrations of new fine roots (grown after treatment began) from seedlings at specified soil temperatures and with shoots exposed to light (○) or maintained in darkness (●).

TABLE 2. Tests of significance of  $F$ -tests from analyses of variance for weights of seedling components

Root temp. (°C)	Light	Harvest	Light × harvest
Shoots			
30	***	**	***
20	***	**	**
10	***	NS	***
Coarse roots			
30	NS	**	**
20	***	***	***
10	***	***	**
Old fine roots			
30	NS	**	NS
20	NS	***	NS
10	**	***	NS
New fine roots			
30	***	***	***
20	***	***	***
10	***	***	***

NOTE: NS, not significant at 0.01 level; \*\*, significant at 0.01 level, but not at 0.001 level; \*\*\*, significant at 0.001 level.

In the shoots and in roots at 30°C, covering the seedlings significantly reduced sugar concentrations, but only after all starch had been depleted. After starch exhaustion, sugar concentrations in the shoots declined from  $65.5 \pm 4.9$  to  $29.3 \pm 4.2$  mg g DW<sup>-1</sup> ( $\bar{x} \pm SE$ ) (Fig. 4); this difference is significant at the 0.01 level. In roots from the 30°C treatment, sugar concentrations declined after starch exhaustion from  $59.7 \pm 3.6$  to  $23.0 \pm 2.0$  mg g DW<sup>-1</sup> (Figs. 2 and 3), a difference also significant at the 0.01 level. In the roots growing at 10 and 20°C, differences in sugar concentration after starch depletion were not significant; however, there were significant declines in sugar concentration shortly after seedlings were covered. These roots declined from  $59.5 \pm 3.5$  mg g DW<sup>-1</sup> at the first harvest to  $27.9 \pm 1.7$  mg g DW<sup>-1</sup> afterward; this difference was significant at the 0.001 level. Although the measured sugar concentrations did not fall to zero, the sugar concentrations measured at the end of the experiment were equal to those of dead roots in another experiment (23 mg g DW<sup>-1</sup>; Marshall 1984). Considering the likelihood of fungal decomposition of complex carbohydrates in the dead tissue, it would be sur-

TABLE 3. Weights (milligrams) of various components harvested at selected dates following seedling exposure to specified light and soil-temperature conditions

Soil temp. (°C)	Harvest (days)	Shoots		Coarse roots		Old fine roots		New fine roots	
		Dark	Light	Dark	Light	Dark	Light	Dark	Light
10	0	1640a	1650a	229a	175a	629a	716a	35a	27a
	28	1110a *	2040a	251a	309a	412a	467b	43a	47a
	60	1330b *	2620b	283a	436b	372b *	593b	87a *	271b
	98	1290b *	2670b	337a	472b	485b	511b	96a *	324b
	140	845b *	2730b	248a *	482b	336c	485b	122a *	640c
20	0	1640a	1650a	229a	175a	629a	716a	35a	27a
	17	1420a	1720a	248a	287b	538a	537b	64a	86a
	32	1250a *	2000a	298a	339b	486a	569b	88a	121a
	48	1300a *	2090a	350a	408b	426a	552b	128a	217a
	62	1210a *	2530b	233b *	493b	397a	435b	123a *	347b
	120	1500a *	2560b	296b *	571b	549b	435b	90a *	416b
30	0	1640a	1650a	229a	175a	629a	716a	35a	27a
	8	1500a	1590a	321a	233a	575a	393b	76a	69a
	16	1400a	1610a	262a	286a	577a	397b	56a	102a
	25	1360a	1570a	277a	243a	520a	398b	52a	103a
	40	1470a *	2140b	313a	368a	519a	464b	63a *	158a
	60	1150a *	2210b	260a *	452a	411a	454b	77a *	278b

NOTE: Significant differences ( $\alpha = 0.01$ ) in root biomass observed between progressive sampling dates for a given treatment are denoted by a different letter (a, b, or c). Differences ( $\alpha = 0.01$ ) between light and dark treatments on the same sampling date are denoted by an asterisk.

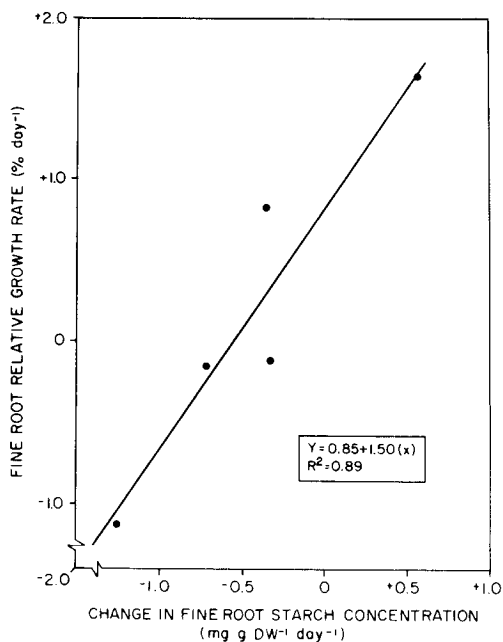


FIG. 6. Relative growth rate of fine roots maintained at 10°C predicted from net changes in starch concentrations.

prising if the sugar concentrations could be forced to zero under any circumstances.

By the date of the final harvest, all seedlings maintained in darkness had died. Though the 1-year-old foliage remained green and apparently unwilted under the aluminum sleeves, it quickly withered and browned upon exposure to light.

### Discussion

The hypothesized pattern of starch deposition and depletion presented in Fig. 1 can be tested with regard to the foregoing

TABLE 4. Regression equations that describe depletion of starch and sugar in seedlings maintained in darkness

Material	Temp. (°C)	Intercept (mg CH <sub>2</sub> O g DW <sup>-1</sup> )	Slope <sup>a</sup> (mg CH <sub>2</sub> O g DW <sup>-1</sup> day <sup>-1</sup> )	R <sup>2</sup>	n
Coarse roots	30	191a	-2.53a	0.93	4
	20	183a	-2.10a	0.91	4
	10	176a	-1.03b	0.98	3
Old fine roots	30	217a	-3.25a	0.86	4
	20	189a	-1.53a	0.96	4
	10	165a	-0.83b	0.95	3
Shoots before bud set	21	338a	-7.87a	0.94	5
Shoots after bud set	21	162b	-1.07b	0.94	6

NOTE: Values in the same column followed by a different letter are significantly different at  $\alpha = 0.01$ .

<sup>a</sup>Slopes are estimates of maintenance respiration rates.

results. Starch concentrations increased proportionally to root growth at 10°C, although during periods of slow root growth, starch losses in respiration sometimes exceeded starch gains in growth. Starch deposition was not observed in growing roots at higher temperatures (20 and 30°C), despite rapid root growth at these temperatures. These soil temperatures exceed the 3-year maximum of 16.4°C measured at 20 cm depth by D. Santantonio (unpublished) in three Douglas-fir stands in western Oregon. Because such high soil temperatures would lead to very high maintenance respiration rates and because light levels used in these experiments were rather low, the seedlings at the high temperatures probably had low carbon balances and were unable to provide sufficient photosynthate for starch synthesis (Kramer and Kozlowski 1979). While carbon balances as low as these are probably seldom observed in the field, they offered

us an opportunity to trace the depletion patterns of the starch that was already present in the seedlings at the beginning of the temperature treatments.

Once deposited, starch was not augmented or replaced in a given root. Despite significant amounts of root growth in the uncovered seedlings, the light effect on starch concentration of fine roots at high temperatures was nonsignificant (Table 1) and starch depletion in the roots of covered and uncovered seedlings at 20 and 30°C was similar (Figs. 2 and 3). If the sugars transported from the shoot to support root growth were also available to the nongrowing roots, we reason they would have been used for maintenance, reducing starch depletion in the uncovered plants relative to that in the covered plants. Also, light effects would have been significant in the analyses of variance (Table 1). Moreover, differences in starch concentrations between covered and uncovered seedlings would have been more pronounced and the starch concentrations of the uncovered plants would have been consistently higher than those of the covered plants at all temperatures as the experiment progressed. Since none of the above occurred (Figs. 2 and 3), we conclude that starch in nongrowing fine roots is not augmented from other sources. Rather, current photosynthate is used almost exclusively for growth of new fine roots and, if the carbon balance permits, for starch deposition in new fine roots. The dependence of root growth on current photosynthate has been noted before (Richardson 1958; Zaerr *et al.* 1973; van den Driessche 1978).

The conversion of shoot reserves to new shoot tissue in the covered seedlings shows that the shoots were operating as essentially independent systems; shoot growth in the dark did not require translocation of reserves from the roots. According to the equation in Table 4, starch and sugar concentrations in the shoots declined by 236 mg g DW<sup>-1</sup> from the beginning of the experiment until bud set. If one assumes that the rate of decline of carbohydrate reserves after budbreak represents the maintenance rate, losses because of maintenance during the period of shoot growth would be 31 mg g DW<sup>-1</sup>, leaving 205 mg g DW<sup>-1</sup> available for tissue synthesis. The new tissue represented 203 (± 14) mg g DW<sup>-1</sup> of old tissue. If the 31 mg g<sup>-1</sup> of starch respired in maintenance is added back into the weight of the old tissue to obtain the original weight of the old tissue, the new growth represents 197 (± 14) mg g DW<sup>-1</sup> of old tissue. Thus, assuming that shoot growth was entirely at the expense of shoot reserves, the conversion efficiency of starch and sugar to new biomass was approximately 96 ± 7%. The decline in sugar concentrations over this period was not significant when averaged across the temperature treatments, so we assumed that the seedlings were mainly converting starch to biomass. The theoretical efficiency of converting starch to cellulose would be 94%, a value obtained by converting the glucose equivalents of Chung and Barnes (1977) to starch equivalents. Conversion efficiencies for synthesis of conifer shoot tissue from starch would normally be much lower, on the order of 71% in *Pinus taeda* (Chung and Barnes 1977); however, if the conversion efficiency of Chung and Barnes (1977) is recalculated assuming that lignin and phenolics were replaced by cellulose as might be expected in etiolated shoots (Hahlbrock and Grisebach 1979), the conversion efficiency would rise to 88%. These data support our contention that in spite of the sink strength of the growing shoot, the reserves used in shoot growth came exclusively or almost exclusively from shoot tissues, leaving the reserves in the fine roots to be used for maintenance processes in the fine roots. The situation with the

reserves of the coarse roots in large trees is less clear (Ericsson and Persson 1980).

The final part of the hypothesis presented in Fig. 1 is supported by our observations that seedlings died only after starch was exhausted and sugar concentrations were as low as can be expected. If the seedlings had died before starch and sugar were exhausted, more starch and sugar would have remained in the dead roots.

The starch and sugar depletion rates measured in this study are similar to the lowest estimates of maintenance respiration in the literature, excepting those for dormant seeds (Penning de Vries 1972). Ledig *et al.* (1976) estimated root respiration as the difference between CO<sub>2</sub> uptake and net assimilation rate in pitch pine (*Pinus rigida* Mill.) seedlings. Just prior to a period of respiratory weight loss in the root systems, they estimated root respiration rates as 3.3 mg CH<sub>2</sub>O g DW<sup>-1</sup> day<sup>-1</sup> at 32°C. Our estimates at 30°C were 3.3 and 2.5 mg CH<sub>2</sub>O g DW<sup>-1</sup> day<sup>-1</sup> for fine and coarse roots, respectively.

Maintenance respiration rates have more typically been reported to be higher than those reported here, ranging as high as 42 mg CH<sub>2</sub>O g DW<sup>-1</sup> day<sup>-1</sup> in root systems of Scots pine (*Pinus sylvestris* L.) (Szaniawski 1981) and from 7 to 16 mg CH<sub>2</sub>O g DW<sup>-1</sup> day<sup>-1</sup> in hardwood species (Lawrence and Oechel 1983). The wide variation in these estimates is attributable partly to differences in respiration measurement procedures. As Ledig *et al.* (1976) observed, respiration rates are sharply increased when roots are excised or removed from soil immediately prior to respiration measurements. Even when CO<sub>2</sub> efflux is measured from intact root systems, as from plants potted in sand (Lawrence and Oechel 1983), the measurements are likely to be overestimates resulting from the contributions of heterotrophs respiring root exudates and decomposing dead tissues.

Methods of estimating respiration owing to maintenance also vary substantially because of differences in the precise definition of what constitutes "maintenance" (Amthor 1984). The method we have used led to a complete cessation of growth and allowed for weight loss as reserves were depleted in respiration. The values reported here should be considered minimum rates of maintenance respiration and are about one-third the maintenance respiration rates of actively growing Douglas-fir seedlings (J. D. Marshall, unpublished).

Root starch deposition appears to be hindered by a low carbon balance. The nonsignificant light effect on accumulation of root starch at 20 and 30°C in our growth-room study indicated that little or no starch was deposited in old fine roots of these root systems as they grew. Moreover, starch concentrations of growing roots at 20 and 30°C never exceeded 30 mg g DW<sup>-1</sup> (Fig. 5) and were not significantly different between covered and uncovered seedlings, even during periods of rapid growth. The extent to which fine roots grow without starch deposition in nature cannot be determined from this experiment, although it would be expected to occur under conditions of high soil temperatures and low photosynthetic rates, leading to low carbon balances. If such root growth occurs, it might result in roots living only 2–3 weeks (Head 1973). This rapid turnover could be advantageous for the seedling in a droughty environment or where extensive feeder root systems are needed to mine limited nutrient resources. Under these conditions, prolonged root life would have a physiological cost but no benefit.

The relation between maintenance respiration and fine root turnover can be tested using data collected in field studies. For

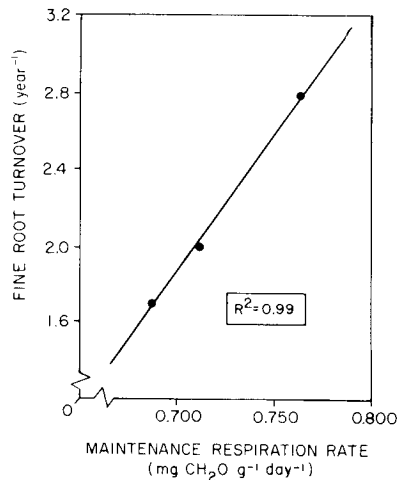


FIG. 7. Regression of fine root turnover rates as measured by Santantonio (1982) against estimated maintenance respiration rates of fine roots.

example, the effect of soil temperature on fine root turnover can be demonstrated from data of Santantonio (1982). He measured soil temperature and fine root biomass and turnover in three Douglas-fir stands on sites he classified by direct measurement as wet, moderate, and dry. Although Santantonio (1982) attributed differences in turnover to differences in soil moisture, Marshall (1984) has shown that soil moisture has little direct effect on root mortality. We summarized Santantonio's (unpublished) soil-temperature data and calculated average root respiration rates on each site using the prediction equation for maintenance respiration presented earlier. As shown in Fig. 7, the maintenance respiration rates predict rates of fine root turnover with an  $R^2$  value of 0.99. Using the maximum range of starch and sugar concentrations of fine roots observed in this study ( $134 \text{ mg g DW}^{-1}$ ) and dividing it by annual mean maintenance respiration on each of Santantonio's sites, we estimate annual turnover rates of  $1.87\text{--}2.08 \text{ year}^{-1}$ , similar in magnitude to Santantonio's measurements ( $1.7\text{--}2.8 \text{ year}^{-1}$ ).

Assuming that fine roots develop with the same initial starch concentration, it should be possible to estimate fine root biomass production from starch concentration and soil-temperature data. Provided photosynthate is available beyond the immediate needs of the plant, starch deposition occurs in fine roots only during growth or immediately following growth. It is therefore possible to estimate the starch concentration of any cohort of fine roots at any point in time; the procedure would be to simply estimate the sum of maintenance respiration since ingrowth and reduce the root starch concentration by that amount. After deducting maintenance respiration from the initial starch concentration of each cohort, an overall mean starch concentration can be calculated. If the measured starch concentration is higher than that predicted, the difference can be attributed to ingrowth of new roots. The equation is as follows:

$$[2] \quad b_n = \frac{\sum_i (s_i \cdot b_i) + (\bar{s} \cdot b_i)}{\bar{s} - s_n}$$

where  $b_n$  is the new fine root biomass,  $s_i$  is the starch concentration of each cohort of fine roots,  $b_i$  is the biomass of each cohort of fine roots,  $\bar{s}$  is the average starch concentration of all

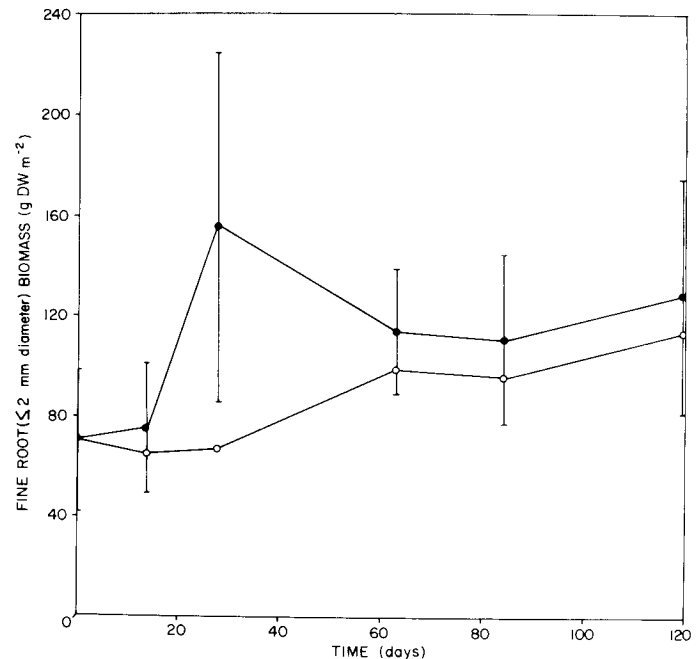


FIG. 8. Predicted (○) and measured (●,  $\bar{x} \pm \text{SE}$ ) fine root biomass from data for control plots of Ericsson and Persson (1980).

fine roots,  $b_t$  is the total fine root biomass, and  $s_n$  is the starch concentration of new fine roots.

The root biomass increment of a given stand can then be estimated for a growing season using the maximum starch concentration observed, usually just before budbreak, as an estimate of new root starch concentration. We have done this using the starch and root biomass data of Ericsson and Persson (1980) from Scots pine stands receiving no treatment (Fig. 8) or receiving daily irrigation and fertilization (Fig. 9). Root respiration rates were obtained from Ågren *et al.* (1980). Root temperatures were estimated using air temperatures at 1 m (Ericsson 1979) increased by 12% to correct for the exponential effect of diurnal temperature fluctuations on maintenance respiration rates (calculated from data of Halldin *et al.* 1980).

With the exception of one point each on Figs. 8 and 9, the biomass predictions fall within the standard errors of the biomass measurements. The lack of agreement at the two points might be attributable to measurement error, particularly given the high variability around the third point in Fig. 8. If the short-lived increase in root biomass shown in Fig. 8 is real, it might be attributed to root growth without starch deposition. In any case, it is encouraging that Eq. 2 was able to estimate biomass fluctuations as well as it did on sites receiving such differing treatments.

Additional studies are needed (i) to determine the extent of root growth without starch deposition and its relation to plant carbon balance, (ii) to compare starch dynamics of mycorrhizal and nonmycorrhizal roots, (iii) to examine detailed patterns of starch accumulation and depletion in the various tissues of roots using <sup>14</sup>C-labeling, and (iv) to field test the ideas presented here with temperature and starch data collected specifically for that purpose.

From our work and from that of others, we conclude that initial starch concentration and soil temperature are key variables in estimating fine root turnover and fine root biomass. By separating growth from maintenance respiration and by knowing the initial amount of starch in new roots, it is possible to

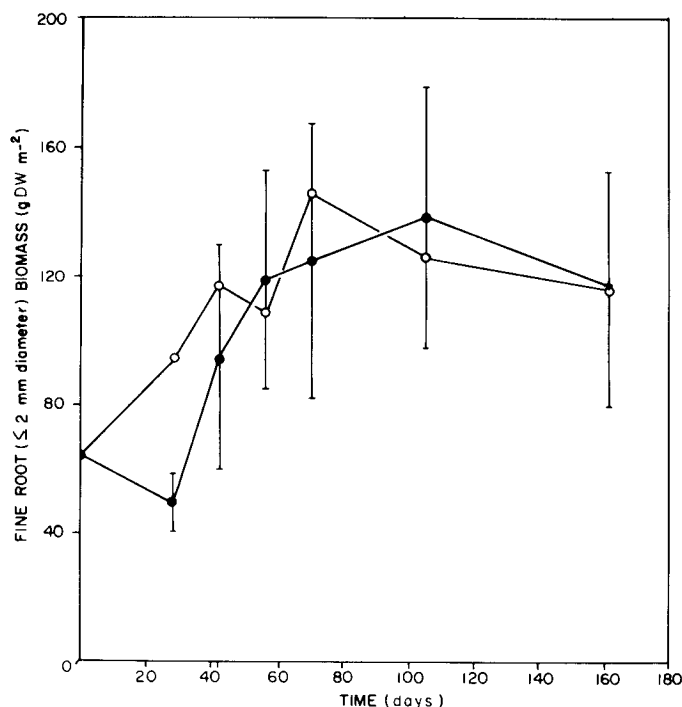


FIG. 9. Predicted (○) and measured (●,  $\bar{x} \pm SE$ ) fine root biomass from data for irrigated and fertilized plots from Ericsson and Persson (1980).

estimate turnover rates and biomass of fine roots within the resolution of present field measurements. Future field studies should include measurements of these variables because of their importance in explaining and predicting fine root growth and turnover.

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