

STUDIES ON THE RESPIRATION RATE IN THE
DIFFERENT PARTS OF THE ROOT SYSTEMS OF PINE AND
SPRUCE SEEDLINGS AND ITS VARIATIONS
DURING THE GROWING SEASON

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Preface

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Introduction

Studies on the respiration of conifer roots are so far relatively limited in number. EIDMANN (1943) made weight analytical studies on the rate of respiration in the root systems of various tree species, and also studied the periodic changes in respiration. According to him, the root systems of trees respire at a higher rate than those of many other higher plants. He compared the respiration rates of the root systems of various deciduous and coniferous trees and found differences among tree species in this respect.

Even earlier, ÅLVİK (1939) had carried out similar experiments using the manometric technique. He compared the respiration rates of $1/2$ to 1-year-old spruce and pine root systems to the respiration rate of the shoots and found approximately the same rates.

The experiments on the respiration of mycorrhizae can also be regarded as studies on conifer root respiration. ROUTIEN and DAWSON (1943) and KRAMER and HODGSON (1954) studied respiration in mycorrhizal and uninfected short-roots. LAFOND (1951) studied the effect of various humic extracts on the respiration of *Pinus banksiana* root tips.

On the basis of respirometric experiments, HARLEY and McREADY (1950) found that mycorrhizal roots absorb the phosphorus ion better than do the uninfected roots. KRAMER and WILBUR (1949) came to the same conclusion. It has also been observed (LUNDEGÅRDH 1955, STREET 1962) that the absorption of nutrient ions and the respiration of root cells are essentially correlated processes.

According to VOIGT (1953), respiration depends on the age of the roots, and the young roots of pine have higher rates than the old ones. MIKOLA (1953) also found the respiration of mycorrhizae to be correlated with age. The correlation between age and the respiration of tissues in various other parts of trees has also been investigated. For instance, ZELAWSKI (1960 a) has studied the respiration of oak (*Quercus pedunculata*) branches and stems.

KELLER and WEHRMANN (1963) studied the correlation of root respiration to assimilation and nutrient uptake from the soil and compared root respiration in pine and spruce to each other, and to the results presented by EIDMANN (1943). According to them, after EIDMANN's study very little progress has been made in forest-tree root respiration studies.

On the basis of respiration experiments it is possible to describe root vitality,

not only in terms of the uptake of nutrient ions and water, but also of the root growth rate. Several research workers have examined the growth of the root systems of various tree species and especially its periodism. For example, LADEFOGED (1939) studied the periodism of the growth of the spruce root system and its correlation to soil temperature and moisture. He found the same growth rhythm in both seedlings and old trees.

In this study, an attempt has been made to use the manometric Warburg technique in studying the growing season variations in the respiration rates of the roots of 1-to 3-year-old seedlings of pine (*Pinus silvestris*) and spruce (*Picea abies*) grown in a nursery soil. The results have been compared to earlier growth studies (LADEFOGED 1939, LAIHO and MIKOLA 1964, LYR and HOFFMANN 1965). These experiments have also explored the possible differences between the tree species, and the effect of the growing medium on respiration.

The respiration rates in both short-roots, most active in the uptake of nutrients, and long-roots, separately for the elongating tips and the hardening basal parts, have also been investigated. In addition, before it was possible to solve these problems, several preliminary experiments to adopt to modify techniques were necessary.

Method of study

The Warburg method and its use

The so-called Warburg method, in which gas exchange is measured as pressure changes (UMBREIT *et al.* 1951) has been used in this study. The method has been extensively used in physiological, medical, biochemical, and other studies, and recently it has been used successfully also in the field of forest biology.

Among the first research workers to experiment with the Warburg apparatus in studying soil respiration, CHASE and GREY (1953) and ROVIRA (1953) deserve mention. More recently, MEYER (1959 and 1960) has studied the rates of decomposition especially humus and mull. HINTIKKA (1964), among others, has measured litter decomposition respirometrically. On the use of the Warburg apparatus in respiration experiments on forest tree tissues, studies have been published mainly on the respiration of the trunk, branches, leaves, buds, or seed (ZELAWSKI 1960 a, b, c, and d, FISCHER 1961, MATILE and FREY-WYSSLING 1962, MATLIE 1962, v. SCHÖNBORN 1964).

In respiration studies on the roots of conifers, the Warburg technique has been used by ÄLVIK (1939), ROUTIEN and DAWSON (1943), LAFOND (1951), and MIKOLA (1953).

The Warburg apparatus used in this study was the model V85 (manufactured by B. Braun, Melsungen). Fourteen reaction flasks could be fastened to the apparatus at a time. Thus, since there were two thermobarometers and 4–6 flasks

contained parts of the same sample, 2 to 3 different replicated samples could be studied at a time. Two ml of distilled water were pipetted to each flask containing the samples, and then 0.2 ml of 10 % KOH-solution and a piece of filter paper were placed into the central well of flasks measuring oxygen uptake.

The seedlings were taken intact from the seedbeds. An attempt was made to select seedlings growing close to each other and with shoots of about the same size and appearance. Each sample consisted of four such seedlings. The roots were washed in a water jet with care to remove all soil particles and avoiding their breaking. After washing, the root systems were cut into three parts with a knife: short-roots (Sr), long-root tips (Lrt) (length 1–5 cm), and long-root basal parts (Lrb). (In the third summer, the study material consisted only of long-root segments with numerous numbers of short-roots.) The division is based on the different functions of the different parts of the root systems. The long-roots fasten the shoot to the site and transport nutrients from the roots to the shoot through the abundant xylem tissues (HATCH and DOAK 1933). The short-roots are mainly responsible for the uptake of water and nutrients. The elongation of the root system occurs only near the root-tips, thus the tips of the long-roots differ functionally from the basal parts. With the increasing age of the root system, different changes occur in the long-roots than in the short-roots (LOBANOW 1960). BJÖRKMAN (1942) classified the short- and long-roots by their length. LAIHO (1963) classified them according to their branching. In this study, unbranched roots under 1 cm in length were considered short-roots, branched mycorrhizae were, however, counted as single short-roots.

The gas quantities were calculated as microliters (μ l) per hour and per milligram of oven-dry sample at 25°C. In studies carried out with the Warburg apparatus, this is a commonly used unit of measurement (e.g. ZELAWSKI 1960 a, b, c, d, MEYER 1959, 1960). ROUTIEN and DAWSON (1943) calculated the respiration rates per unit root length which according to LAFOND (1951) and MIKOLA (1953) is probably not the best possible unit of measurement; they recommend the use of the dry weight. The surface area would be the best unit to correlate with respiration, but it is difficult to measure (EIDMANN 1943, MIKOLA 1953). The sample volume was estimated, where needed, as ten times the dry weight. The results were interpreted statistically with the help of the analysis of variance and the t-test.

Preliminary experiments

The study was carried out in the laboratory of the Forestry Field Station of the University of Helsinki situated about 200 km north of Helsinki. The seedlings were from the Hyytiälä nursery of the Korkeakoski State Forest District. The data are from the summers 1963, 1964, and 1965.

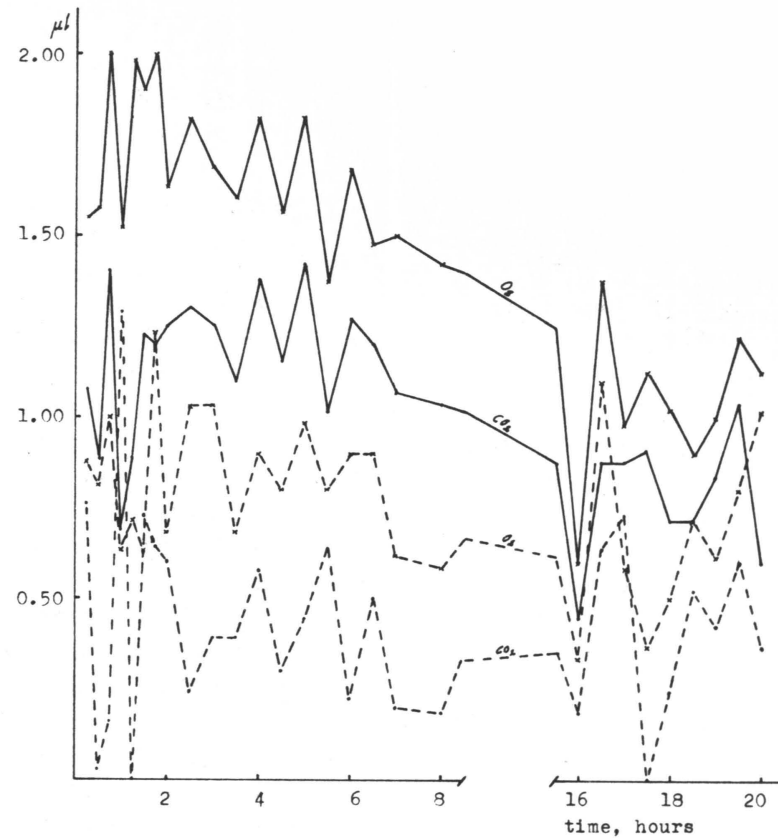


Figure 1. Respiration intensity in «good» (—) and «poor» (---) pine mycorrhizae.

At the start, it was necessary to carry out certain preliminary experiments for the evaluation of methods and development of techniques. First, the changes in the root respiration rate in the Warburg apparatus during a given time were studied. For this purpose, so-called «good» and «poor» pine mycorrhizae were selected, using the classification of MIKOLA and LAIHO (1962). Figure 1 shows the changes in the O_2 uptake and CO_2 release in these samples during 20 hours.

The results showed huge variations in the beginning of the experiment and then a slight leveling off. The general 20-hour trend in the oxygen uptake of the «good» mycorrhizae was downward, but in the CO_2 release it rose a little in the beginning, then gradually decreased, at a rate, however, that was slower than the oxygen uptake. The oxygen uptake of the «poor» mycorrhizae slowly decreased, but the carbon dioxide release rate remained relatively constant. These observations led to the conclusion that before undertaking actual measurements it would be preferable to allow respiration to level off in the samples for

about 45 minutes. This schedule was followed also in the later measurements. The readings were taken after one and two hours after closing the manometers.

In order to study respiration in the different parts of the root system, it was necessary to separate the short-roots, the long-root tips and the long-root basal parts. This separation involved cutting roots into segments. To find out the effect of cutting on the respiration rate, eight replicate runs were made both on intact root systems and on cut parts from similar seedlings (table 1).

Table 1. Respiration in intact and cut root systems of spruce and pine seedlings $\mu l/mg/hr.$

Seedling type	Intact			Cut			$100 \cdot \frac{[1]}{[3]}$	$100 \cdot \frac{[2]}{[4]}$
	[1] O_2	[2] CO_2	RQ	[3] O_2	[4] CO_2	RQ		
2-yr spruce	0.43	0.44	1.02	0.52	0.64	1.28	83	69
» »	0.40	0.40	1.00	0.47	0.51	1.09	85	78
1-yr spruce	0.82	0.70	0.85	1.05	0.94	0.90	78	74
2-yr pine	0.75	0.69	0.92	0.88	0.89	1.01	85	78
» »	0.78	0.69	0.88	0.88	0.87	0.99	85	79
» »	0.56	0.51	0.91	0.70	0.77	1.10	80	66
» »	0.43	0.41	0.95	0.52	0.53	1.02	83	77
1-yr pine	0.61	0.59	0.97	0.79	0.79	1.00	77	75

The average respiration of intact root systems was 82 per cent for O_2 uptake and 75 per cent for the CO_2 release of the totals calculated for the corresponding cut root systems; thus cutting the root system affected oxygen uptake less than carbon dioxide release. The difference between the averages is statistically significant. These values are in good concordance with those published by ZELAWSKI (1960 a) and ZIEGLER (1956) who show the limiting effect of the bark on the stem and the branches. ZIEGLER showed that the removal of the bark increased respiration in the branches by 33-39 %. DeLONG *et al.* (1930) noticed that one cut increased respiration in fruit tree branches by 5-8 %.

The increase in respiration resulting from cutting the roots is naturally a pathological phenomenon caused by the damaging of the tissues. The main factor involved is the surface area of the cut. From the cut surfaces, oxygen can diffuse into the tissues, increasing the respiration rate. In the long-roots, the surfaces resulting from both cutting the roots into pieces and from cutting off the short-roots make a considerable damaged-tissue area. In the short-roots, only the single point of severance from the long-root has to be considered as contributing to the increased respiration.

The RQ (CO_2/O_2) values also demonstrate the larger increase in carbon dioxide release than in oxygen uptake. For this reason, and since it is easier in the apparatus to determine oxygen uptake than carbon dioxide release,

oxygen uptake is believed to be a better expression of the respiration rate than is carbon dioxide release. The result also indicates that when handling the seedling unnecessary breaking of the roots should be avoided.

The preliminary experiments also included determinations the vitality changes of the seedling roots during the time of storage. This experiment was carried out in the summer of 1965. The seedlings were lifted on September 6 so that as much as possible of the root systems was left intact. The sample seedlings were 2-year pine, grown for one year under a plastic shelter and the other in the open, in fertilized peat. After lifting, the seedlings were stored in closed plastic bags. About a third of these bags was kept at room temperature (about 20°C), a third in a refrigerator (at about +3°C) and the remainder in a freezer unit (at about -30°C). To provide a basis for comparing vitality changes due to storage, root respiration was studied immediately after lifting on samples of long-root pieces with a great number of attached mycorrhical short-roots. The storage times were 10, 19, and 30 days. The seedlings stored at -30°C were kept at room temperature for about 5 hours before the measurements.

In each case (figure 2), seedling vitality decreased during storage as shown by the decreased uptake of oxygen in the roots. The decrease was the most marked in the seedlings kept at the lowest temperature. In general CO₂ release decreased at a slower rate than O₂ uptake. However, during 10 days in the refrigerator (+3°C), no significant changes occurred. The phenomenon is similar to change in the respiration intensity as a function of the time of measurement. Gas exchange in the roots of the seedlings stored at room temperature increased after 19 days, probably because of increased microbial activity. The results suggest that storage of seedlings for a fairly long time at a temperature close to freezing is possible without appreciably changing the root vitality

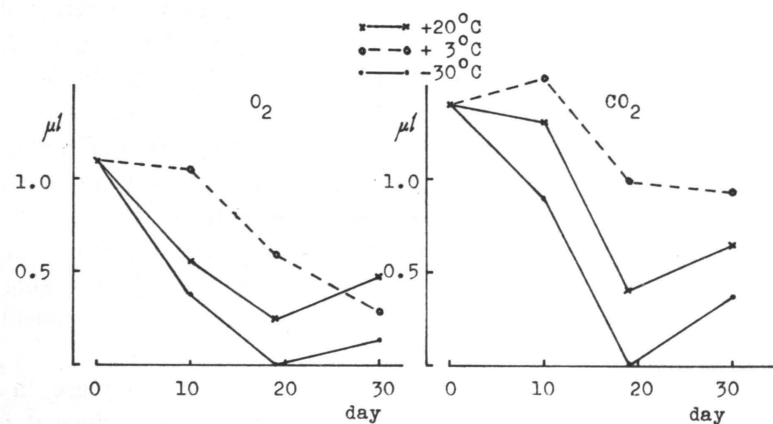


Figure 2. The effect of seedling storage on root respiration ($\mu\text{l}/\text{mg}/\text{hr}$).

Standardized experimental conditions

Lifting and taking the seedlings from their natural environment to the laboratory for respiration studies may have changed respiration intensity. This possible change was not assessed in the study; lifting was considered as affecting all seedlings in a similar way. Neither has the effect of temperature on root respiration been studied; all determinations were made at the same temperature, +25°C.

Preliminary tests indicated the need standardizing the experimental conditions to offset the initially high respiration rate induced by cutting, by allowing the sample flasks to be agitated in the water bath, with the manometers open, for 45 minutes.

The amounts of sample material in the flasks varied because respiration was simultaneously measured for the whole root system. This procedure avoided the possible difficulties resulting where separate roots exhibit different growth rates thus naturally affecting root respiration, as LADEFOGED (1939) found true even for a single seedling.

The short-root subsamples varied on an average between 10–20 mg/flask, those for the long-root tips between 15–30 mg, and those for the basal parts of the long-roots between 20–80 mg depending on the age and growth rate of the seedlings. In the third summer, the study was limited to the periodism of root respiration; the material studied consisted of long-root segments (2–4 cm long) with a large number of short-roots. An attempt was made to keep these amounts constant, averaging about 5 mg/flask.

Evaluation of the method

In analytical studies on respiration, whether gravimetric or colorimetric, only the released carbon dioxide can be measured. The uptake of oxygen, an essential part of respiration, remains unmeasured. When the number of oxygen molecules taken up in respiration equals that of the released carbon dioxide molecules, i.e. the $RQ = 1$, it does not matter which gas is measured. This is generally the case in the oxidation of carbohydrates (COLLANDER 1944). However, if other processes than direct oxidation are also involved in tissue respiration, the ratio of the gas quantities may change.

With gas manometric and gas volumetric methods, both carbon dioxide release and oxygen uptake can be measured, and our data from the respiration process is considerably more complete. In addition, as shown earlier, O₂ uptake seems to be a better measure of respiration than CO₂ release both because of the relative simplicity of the method and because the cutting of the roots affects the CO₂ release to a greater extent than the O₂ uptake.

The laboratory conditions are standard for the work with the Warburg

apparatus. Therefore the measured rates do not correspond to respiration *in situ*; they have to be regarded only as relative values. Gas exchanges has to be determined with the apparatus from relatively small samples; therefore great accuracy is required in the use of the method.

Results and discussion

Respiration intensity in the different parts of the root system

The roots need energy mainly for water and nutrient uptake and growth. The energy requirements is met through respiration. In numerous studies, nutrient uptake on one hand and growth and respiration on the other have been found to be strongly correlated in the root systems of trees. Nutrient absorption is most intensive in the short-roots. This is due to the large amount of physiological activity in the root tips (KRAMER and KOZLOWSKI 1960), associated with a concomitant retardation of growth in the zone from the tips to the basal parts. STEWARD *et al.* (1942) and STREET (1962) have found the meristems to be most active in water and nutrient uptake. According to this study, respiration intensity is the greatest in pine and spruce short-roots (table 2) but also considerable in the long-root tips at the points of elongation.

Table 2. Respiration ($\mu\text{l}/\text{mg}/\text{hr}$) in the different parts of 1–2-year pine and spruce seedling root systems.

Part of root system ¹	O ₂			CO ₂			RQ		
	pine	spruce	F	pine	spruce	F	pine	spruce	F
Sr	1.79	1.75	0.02	1.68	1.57	0.07	0.92	0.94	0.00
Lrt	1.10	1.20	0.21	1.03	1.08	0.05	0.92	0.94	0.00
Lrb	0.65	0.76	0.21	0.89	0.90	0.00	1.64	1.31	3.44
F	7.66**	9.45**		3.78*	6.95**		20.21***	8.17**	
LSD ₀₅ . .	0.42	0.33		0.42	0.27		0.19	0.15	

¹ Sr short-roots
Lrt long-root tips
Lrb long-root basal parts

The values given in table 2 are average respiration rates for the different parts of the root systems of 1- to 2-year pine and spruce, measured from eleven sample lots. The replicated samples were taken simultaneously during the first autumn and second summer. The values from the first autumn are given in this connection since they are of about the same magnitude as the corresponding values for the following early summer.

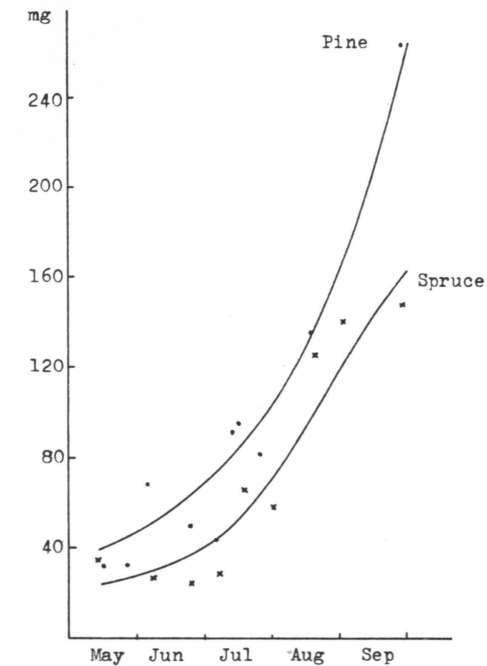


Figure 3. Average weight increase in the entire root systems of 2-year seedlings during the 1964 growing season.

When the oxygen uptake rate per weight unit in the pine seedling short-roots is given the value 100, the rate in the long-root tips is 61 and in the basal parts 36. The corresponding values for spruce are 100, 69, and 43. The relative carbon dioxide release rates are different for the basal parts of the long-roots: pine 53, and spruce 57, when the corresponding CO₂ release from the short-roots is 100.

It can be seen that especially the carbon dioxide release rate in the basal parts of the long-roots is relatively greater than the oxygen uptake. This is best described by the RQ value. In pine and spruce short-roots it is 0.9, but in the basal parts of the long-roots it is considerably greater, 1.3–1.6.

When the respiration rates of the tree species were compared on the basis of the dry weight of the different root system parts no significant difference was found between them. However, in the respiration rates per total root system a difference can be seen; this result stems from the different size of the seedlings, the root systems of pine being clearly larger (figure 3). Thus, the pine root system respiration rate is greater than that of spruce, especially during the second autumn.

In comparing the respiration rates of different transplants of tree species grown in mineral soil EIDMANN (1943) found that when the relative rate for

the pine root system per dry weight was 100, spruce had a carbon dioxide release rate of 47. Unfortunately, the transplants he studied were of different ages, the pines being 2-year-old and the spruces 3-year-old. The root systems of the pine and spruce seedlings studied by KELLER and WEHRMANN (1963) had respiration rates 3 to 4 times greater than those used by Eidmann. The authors ascribe the difference to the younger age of the plants in their experiments. Also the faster growth rate of these seedlings may have influenced the results.

Respiration in different-aged root systems

MIKOLA (1953) has found in his experiments that young mycorrhizae have twice the respiration rate of old ones. According to BJÖRKMAN (1956), two-year-old mycorrhizae are scarcely active. Also VOIGT (1953) considers age to decrease respiration. HATCH (1937) and HARLEY (1959) showed that during the first growing season, nutrient uptake by seedlings depends largely on the long-roots, but their importance decreases with increasing age; during the second growing season it is still, however, considerable. With increasing age, the long-roots lignify and surface tissues become suberized, which decreases respiration. This is also shown by this study in table 3 and figure 4.

Table 3. Rate of respiration ($\mu\text{l}/\text{mg}/\text{hr}$) in the different parts of 1-, 2-, and 3-year-old pine and spruce seedling root systems.

	Part of root system	Pine					Spruce				
		1-yr	2-yr	3-yr	F	LSD.05	1-yr	2-yr	3-yr	F	LSD.05
O ₂	Sr	3.70	1.50	1.20	19.58*	0.55	2.45	1.76	1.25	2.32	
	Lrt	1.82	1.00	0.39	14.71*	0.32	1.67	0.88	0.78	1.31	
	Lrb	1.08	0.61	0.16	11.33*	0.23	0.98	0.49	0.35	2.75	
	F	15.83*	11.50*	31.88*			1.71	9.50	10.25*		
	LSD.05 . .	0.64	0.26	0.17				0.27*			
CO ₂	Sr	2.95	1.50	1.16	12.93*	0.43	1.83	1.54	0.91	1.80	
	Lrt	1.40	1.04	0.72	4.00		1.35	0.85	0.68	0.96	
	Lrb	0.99	0.83	0.76	1.50		1.40	0.59	0.41	11.20*	0.32
	F	30.71*	2.40	2.40			0.35	3.77	43.33**		
	LSD.05 . .	0.32						0.07			

The differences between the different parts of the root systems of the 1- to 3-year-old seedlings are statistically significant in that with the increasing age of the seedling, the respiration rate per unit weight of pine roots decreases considerably; in spruce, the decrease is smaller but still noticeable. The samples were taken twice during August and September 1963, simultaneously from all seedlings, which were grown in mineral soil in the open. The decrease in the

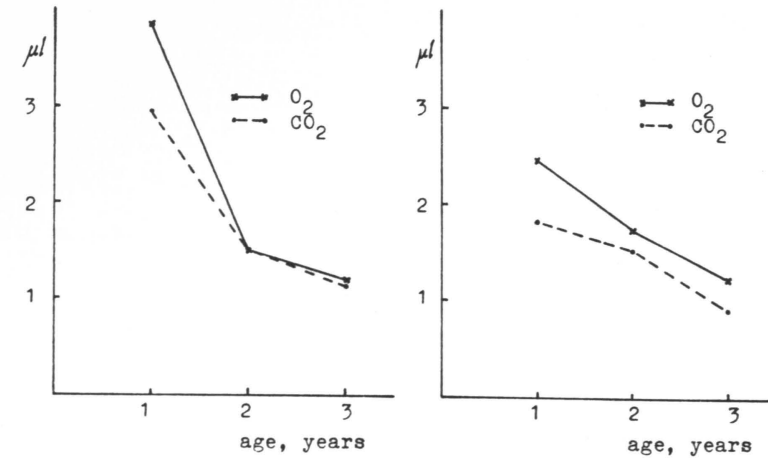


Figure 4. Rate of respiration ($\mu\text{l}/\text{mg}/\text{hr}$) in the short-roots of different-aged pine (left) and spruce seedlings.

short-root respiration rate with seedling age is at least partly due to the preponderance of young short-roots in 1-year seedlings in contrast to a number of old ones in 2-year seedlings, and still more old ones in 3-year seedlings. The result could have been different, if only the short-roots of the same growing season were studied from all seedlings.

Similar differences have been observed in the respiration rates of the different parts of the root system (page 12).

The effect of the growing medium on respiration

The effect of the growing medium on the respiration rates of the different parts of the root systems of 2-year pine seedlings is shown in table 4. The root systems were sampled ten times, simultaneously from seedlings grown in mineral soil and in peat.

Table 4. Rate of respiration ($\mu\text{l}/\text{mg}/\text{hr}$) in the different parts of the root systems of pine seedlings grown in peat (P) and mineral soil (M).

Part of root system	O ₂			CO ₂			RQ	
	P	M	F	P	M	F	P	M
Sr	1.50	1.61	0.15	1.40	1.38	0.00	0.93	0.86
Lrt	0.81	0.90	0.48	0.76	0.86	1.25	0.94	0.96
Lrb	0.43	0.37	0.67	0.70	0.64	0.67	1.49	1.73
F	17.35***	21.33***		13.64***	24.00***			
LSD.05	0.27	0.22		0.27	0.16			

Similar differences among the respiration rates of the different parts of the root systems can be seen as previously shown (tables 2 and 3). In this case, however, the growing medium has not affected the respiration rate of the root system.

Variations in the respiration rate during the growing season

From several growth studies (LADEFOGED 1939, LAIHO and MIKOLA 1964, LYR and HOFFMANN 1965), we know that the growth of the root systems of trees is rhythmic. It can be expected that root respiration follows approximately the same rhythm as root growth.

Respiration rate variations were studied during two summers in the different parts of the root systems of pine seedlings grown in the open in peat and in mineral soil, and of spruce seedlings grown in peat. In the summer of 1965, the respiration rate variations were also studied in the root systems of two-year-old pine and spruce seedlings grown under plastic for the first year and in the open during the second, in fertilized ground peat, in long-root segments with numerous short-roots. The results are given in tables 5—7 and figures 5—7.

During the first year the root respiration rate of the seedlings decreased from the middle of the summer toward autumn (figure 5). During the second growing season, respiration was considerable around the middle of May and then decreased very slowly to the middle of October. The respiration rate in the different parts of the root system varied in a similar way, but the variation in the basal parts of the long-roots was not so great as in the other parts. In the short-roots of pine seedlings in contrast to those of spruce the respiration rate in September deviated most from the rate in the basal parts of the long-roots.

Table 5. Respiration rates ($\mu\text{l}/\text{mg}/\text{hr}$) at different times during the growing season in the different parts of the root systems of pine seedlings grown in the open in mineral soil.

Part of root system	1963					1964										
	31.7.	2.9.	15.9.	8.10.	6.11.	14.5.	20.5.	4.6.	23.6.	3.7.	21.7.	29.7.	17.8.	1.9.	29.9.	
O ₂	Sr	4.18	3.21	2.05	1.96	1.69	1.23	3.29	1.83	1.41	1.63	1.74	1.29	1.41	1.15	1.10
	Lrt	2.08	1.55	1.11	0.92	0.88	0.75	1.54	0.91	0.71	1.00	1.06	1.11	0.80	0.75	0.40
	Lrb	1.29	0.87	0.94	0.49	0.31	0.26	0.70	0.47	0.33	0.33	0.54	0.41	0.32	0.25	0.13
CO ₂	Sr	3.37	2.69	1.34	1.94	1.53	1.28	2.27	1.61	1.25	1.41	1.50	1.12	1.29	1.05	1.02
	Lrt	1.78	1.25	0.99	0.96	0.92	0.91	0.98	0.83	0.72	0.75	1.01	1.13	0.83	0.81	0.61
	Lrb	1.42	1.10	1.05	0.88	0.43	0.72	0.75	0.62	0.56	0.75	0.84	0.77	0.66	0.60	0.33
RQ	Sr	0.77	0.84	0.65	0.99	0.91	1.04	0.69	0.88	0.89	0.87	0.86	0.87	0.91	0.91	0.93
	Lrt	0.75	0.81	0.89	1.04	1.05	1.21	0.64	0.91	1.01	0.75	0.95	1.02	1.04	1.08	1.53
	Lrb	0.67	1.26	1.12	1.80	1.39	2.77	1.07	1.32	1.70	1.73	1.56	1.88	2.06	2.40	2.54

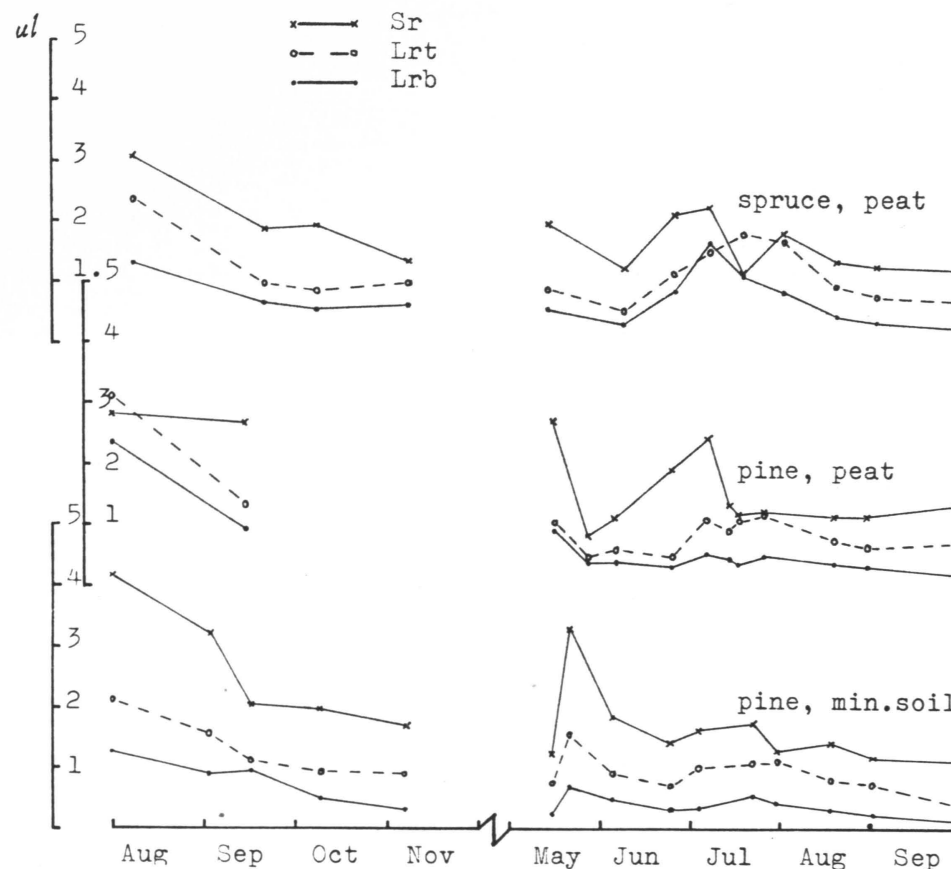


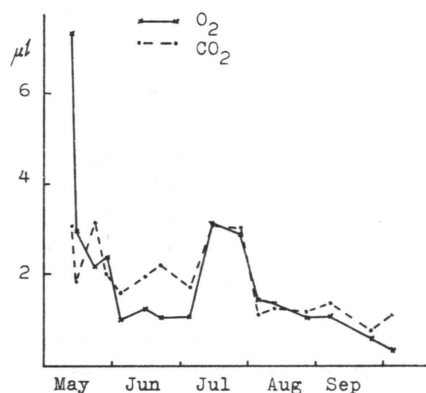
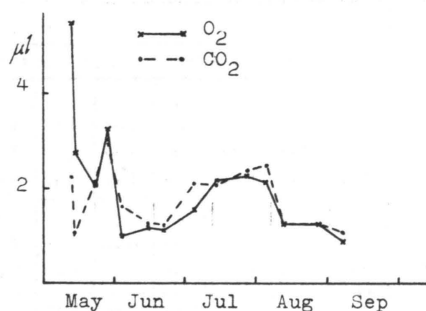
Figure 5. Oxygen uptake ($\mu\text{l}/\text{mg}/\text{hr}$) variations in the different parts of the root systems during the first two growing seasons.

Table 6. Respiration rates ($\mu\text{l}/\text{mg}/\text{hr}$) at different times during the growing season in the different parts of the root systems of pine seedlings grown in the open in peat.

Part of root system	1963		1964											
	30.7.	14.9.	15.5.	26.5.	5.6.	24.6.	6.7.	13.7.	16.7.	25.7.	18.8.	29.8.	28.9.	
O ₂	Sr	2.79	2.68	2.71	0.80	1.10	1.92	2.46	1.35	1.17	1.25	1.13	1.15	1.32
	Lrt	3.11	1.34	1.06	0.47	0.58	0.48	1.09	0.91	1.09	1.17	0.78	0.65	0.73
	Lrb	2.34	0.95	0.92	0.40	0.38	0.33	0.52	0.44	0.39	0.50	0.35	0.32	0.20
CO ₂	Sr	3.01	2.23	2.15	1.17	1.05	1.88	2.22	1.18	0.97	1.03	1.11	1.09	1.29
	Lrt	3.33	1.12	0.73	0.63	0.56	0.43	0.89	0.88	1.06	1.12	0.71	0.65	0.77
	Lrb	2.24	1.26	0.72	0.73	0.46	0.51	1.02	0.90	0.88	0.95	0.70	0.59	0.46
RQ	Sr	1.08	0.83	0.79	1.46	0.95	0.98	0.90	0.87	0.83	0.82	0.98	0.95	0.98
	Lrt	1.07	0.84	0.69	1.34	0.97	0.90	0.82	0.97	0.97	0.96	0.91	1.00	1.05
	Lrb	0.96	1.33	0.78	1.83	1.21	1.55	1.96	2.05	2.26	1.90	2.00	1.84	2.30

Table 7. Respiration rates ($\mu\text{l}/\text{mg}/\text{hr}$) at different times during the growing season in the different parts of the root systems of spruce seedlings grown in the open in peat.

	Part of root system	1963				1964								
		7.8.	20.9.	7.10.	7.11.	13.5.	8.6.	25.6.	7.7.	18.7.	1.8.	19.8.	2.9.	29.9.
O ₂	Sr	3.04	1.86	1.95	1.33	1.97	1.21	2.11	2.23	1.19	1.83	1.35	1.25	1.21
	Lrt	2.36	0.97	0.85	0.98	0.78	0.52	1.16	1.52	1.83	1.70	0.94	0.78	0.68
	Lrb	1.31	0.65	0.51	0.62	0.52	0.32	0.85	1.67	1.12	0.84	0.45	0.33	0.25
CO ₂	Sr	1.32	2.34	1.91	1.44	1.72	1.32	1.95	1.83	1.27	1.65	1.44	1.19	1.20
	Lrt	1.93	0.76	0.84	1.15	0.68	0.74	0.69	1.14	1.76	1.66	1.03	0.80	0.72
	Lrb	1.60	1.20	0.74	0.69	0.64	0.39	0.75	1.75	1.23	0.94	0.57	0.47	0.36
RQ	Sr	0.43	1.26	0.98	1.08	0.87	1.09	0.92	0.82	1.07	0.90	1.07	0.95	1.01
	Lrt	0.82	0.78	0.99	1.17	0.87	1.42	0.59	0.75	0.96	0.98	1.10	1.03	1.06
	Lrb	1.22	1.85	1.45	1.11	1.23	1.22	0.88	1.05	1.10	1.12	1.27	1.42	1.44

Figure 6. Respiration rate ($\mu\text{l}/\text{mg}/\text{hr}$) variations in long-root segments (Sr + Lrt) from 2-year-old pine seedlings.Figure 7. Respiration rate ($\mu\text{l}/\text{mg}/\text{hr}$) variations in long-root segments (Sr + Lrt) from 2-year-old spruce seedlings.

According to figures 6 and 7, the respiration rate variation during the growing season 1965 was similar to that of the previous summer. Respiration was greatest in the beginning of the summer, early in May. Unfortunately it was impossible to run the experiments early enough to be able to follow the increase in the respiration rate early in spring; however, the rates of respiration for the roots of the pine seedlings grown in the open in mineral soil indicate (figure 5) a very rapid increase in the rate in the spring. The variation during the growing season is similar in pine and spruce root systems. The periodism of respiration has been studied by EIDMANN (1943) on intact root systems. Table 8, showing the CO₂ release variations in the root systems of 2-year pine and 3-year spruce transplants, has been taken from his paper. Early in spring the CO₂ release rate is high, but in June it decreases, rises again in July and is still fairly high even in October. But Eidmann's experiments were carried out in Halstenbek, NW-Germany so the high October activity is not surprising.

Table 8. Respiration rate ($\text{mg CO}_2/\text{g}/\text{day}$) in transplant root systems during the growing season in Halstenbek (EIDMANN 1943).

Tree species	Month					
	April	May	June	July	August-September	October
»Ost»-pine	62.7	64.5	61.2	86.4	49.7	62.3
»Rhein»-pine	44.0	49.0	23.5	48.2	60.6	48.4
Spruce	24.4	30.6	14.0	40.3	30.0	29.0

The rhythm of respiration during the growing season at northern latitudes is thus very similar to the growth rhythm of the roots. According to LADEFOGED (1939), the following rhythm is followed by the growth of spruce (*Picea abies*) roots: The growth increases to the middle of May and decreases after that. Another increase occurs at the end of July; some increase is still seen in September. LAIHO and MIKOLA (1964) have found a similar growth rhythm in Finland in pine (*Pinus silvestris*) and spruce seedlings. According to LYR and HOFFMANN (1965), pine root growth is greatest in July, shoot growth in May.

The rate of respiration, especially oxygen uptake, is at its greatest in the roots at the time of the fastest growth. However, no large changes occur in the rate of carbon dioxide release during the growing season as is also shown by the RQ values (tables 5—7 and figures 6—7). The RQ is at its smallest at the period of large oxygen uptake, thus reflecting not only the rate of growth but also other types of metabolic activity. This reasoning further supported by the fact that the highest RQ and thus a relatively high rate of CO₂ release is found in the basal parts of the long-roots, which do not elongate. On the other hand, elongation is also negligible in the short-roots, in which, however, as has

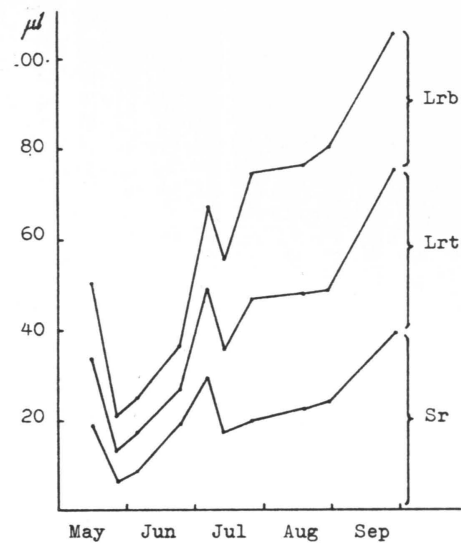


Figure 8. Oxygen uptake ($\mu\text{l/hr}$) changes in the root systems of two-year-old pine seedlings during the growing season.

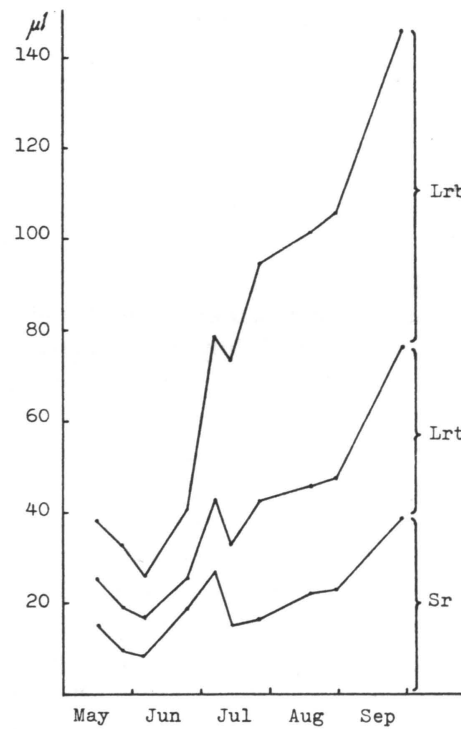


Figure 9. Carbon dioxide release ($\mu\text{l/hr}$) changes in the root systems of two-year-old pine seedlings during the growing season.

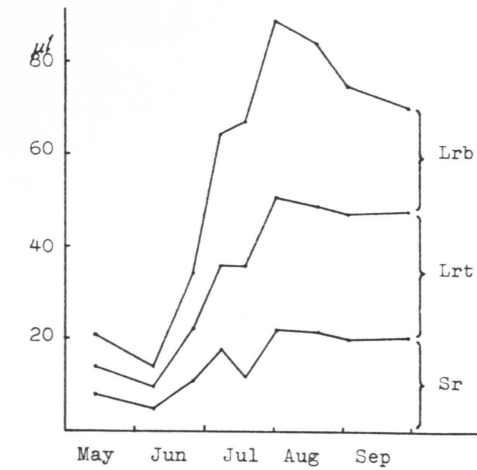


Figure 10. Oxygen uptake ($\mu\text{l/hr}$) changes in the root systems of two-year-old spruce seedlings during the growing season.

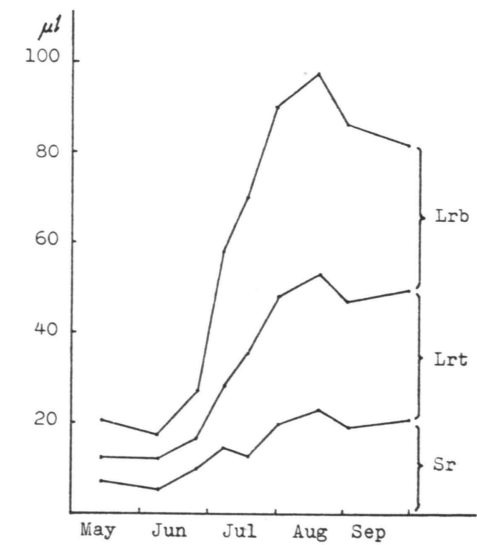


Figure 11. Carbon dioxide release ($\mu\text{l/hr}$) changes in the root systems of two-year-old spruce seedlings during the growing season.

been mentioned previously, the major part of the nutrient and water uptake of the trees occurs.

By measuring the weight changes in the different parts of the root system, the rhythm of respiration in the whole root systems and their parts was also determined. The results are shown in figures 8—11. Due to the weight increase in the root system, the root respiration rate increased in pine seedling to a con-

siderable extent in the autumn of the second growing season. For spruce the situation was different (figures 10 and 11), indicating considerably smaller autumn weight increase to the spruce than the pine root systems. LAIHO and MIKOLA (1964) have found in the latter part of the summer a considerable root weight increase resulting especially from the dicotomous branching of the short-root tips. In spruce similar extensive branching of mycorrhizae in the latter part of the summer has not been found.

The results of this study are for a large part complementary to earlier studies on respiration dealing with root growth and nutrient uptake; they show that the respiration rate in the different parts of the root system is an excellent indicator of the rate of metabolic activity at the time of measurement.

References

- BJÖRKMANN, E. 1942. Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. Symb. Bot. Upsal. 6:2.
- »— Über die Natur der Mykorrhizabildung unter besonderer Berücksichtigung der Waldbäume und die Anwendung in der forstlichen Praxis. Forstwiss. Cbl. 50:265—286.
- CHASE, F. E., and GRAY, P. H. H. 1953. Use of the Warburg respirometer to study microbial activity in soils. Nature (Lond.) 171:481.
- COLLANDER, R. 1944. Kasvifysiologian perusteet I. Helsinki.
- DELONG, W. A., BEAUMONT, J. H., and WILLAMAN, J. J. 1930. Respiration of apple twigs in relation to winter hardiness. Plant Physiol. 5:509—534.
- EIDMANN, F. E. 1943. Untersuchungen über die Wurzelatmung und Transpiration unserer Hauptholzarten. Schriftenr. der Hermann-Göring-Akad. Deutsch. Forstwiss. 5.
- FISCHER, H. 1961. Weitere Untersuchungen über den Gaswechsel von Blütenblättern. Planta 57:430—443.
- HARLEY, J. L. 1959. The biology of mycorrhiza. London.
- HARLEY, J. L., and MCCREADY, C. C. 1950. The uptake of phosphate by excised mycorrhizal roots of the beech. New Phytologist 52:83—85.
- HATCH, A. B. 1937. The physical basis of mycotrophy in *Pinus*. The Black Rock Forest Bull. 6. New York.
- HATCH, A. B., and DOAK, K. D. 1933. Mycorrhizal and other features of the root system of *Pinus*. J. Arnold Arbor. 14:85—99.
- HINTIKKA, V. 1964. Psychrophilic basidiomycetes decomposing forest litter under winter conditions. Comm. Inst. Forest. Fenn. 59.2.
- KELLER, TH., and WEHRMANN, J. 1963. CO₂-Assimilation, Wurzelatmung und Ertrag von Fichten- und Kiefersämlingen bei unterschiedlicher Mineralstoffernährung. Schweiz. Anst. forst. Versuchsw. Mitt. Bd. 39: 4.
- KRAMER, P. J., and HODGSON, R. H. 1954. Differences between mycorrhizal and nonmycorrhizal roots of loblolly pine. 8th Internat. Bot. Cong. Proc. sec. 13:133—134.
- KRAMER, P. J., and KOZLOWSKI, T. T. 1960. Physiology of trees. New York.
- KRAMER, P. J., and WILBUR, K. M. 1949. Absorption of radioactive phosphorus by mycorrhizal roots of pine. Science 110:8—9.
- LADEFOGED, K. 1939. Untersuchung über die Periodizität im Ausbruch und Längenwachstum der Wurzel bei einigen unsere gewöhnlichsten Waldbäume. Medd. forstl. försögsv. Danm. 16, 1.
- LAFOND, A. 1951. The rate of respiration of jack pine root tips as influenced by extracts from different types of humus. Soil Sci. Soc. Am. Proc. 15:357—359.
- LAIHO, O. 1963. Tutkimuksia mykoritsainfektion synnystä ja kehityksestä sekä kasvinsuojeluaikoiden vaikutuksesta siihen metsätaitarhoissa. Unpublished. Univ. of Helsinki Dep. Silviculture.
- LAIHO, O., and MIKOLA P. 1964. Studies on the effect of some eradicants on mycorrhizal development in forest nurseries. Acta Forest. Fenn. 77. 2.
- LOBANOW, N. W. 1960. Mykotrophie der Holzpflanzen. Berlin.

- LUNDEGÄRDH, H. 1955. Mechanism of absorption, transport, accumulation and secretion of ions. *Ann. Rev. Plant. Physiol.* 6:1—24.
- LYR, H., and HOFFMANN, G. 1965. Untersuchungen über das Wurzel- und Sprosswachstum einiger Gehölze. *Silva Fenn.* 117.4.
- MATILE, PH. 1962. Über die Lichtatmung der Brakteen von *Euphorbia pulcherrima*. *Planta* 58:193—198.
- MATILE, PH., and FREY-WYSSLING, A. 1962. Atmung und Wachstum von Hefe im Licht. *Planta* 58:154—163.
- MIKOLA, P. 1953. Mykoritsain merkitys puiden ravinnonotossa. *Luonnon tutkija* 57:1—6.
- MIKOLA, P., and LAIHO, O. 1962. Mycorrhizal relations in the raw humus layer of northern spruce forest. *Comm. Inst. Forest. Fenn.* 55.18.
- MEYER, F. H. 1959. Untersuchungen über die Aktivität der Mikroorganismen im Mull, Moder und Rohhumus. *Arch. Mikrobiol.* 33:149—169.
- »— 1960. Vergleich des mikrobiellen Abbaus von Fichten- und Buchenstreu auf verschiedenen Bodentypen. *Arch. Mikrobiol.* 35:340—360.
- ROUTIEN, J. B., and DAWSON, R. F. 1943. Some interrelationship of growth, salt absorption, respiration and mycorrhizal development in *Pinus echinata* Mill. *Am. J. Bot.* 30: 440—451.
- ROVIRA, A. D. 1953. Use of the Warburg apparatus in soil metabolism studies. *Nature (Lond.)* 172:29—30.
- V. SCHÖNBORN, A. 1964. Die Atmung der Samen. Untersuchungen über den Einfluss von Wassergehalt und Temperatur auf die Sauerstoff-Aufnahme und Kohlendioxid-Abgabe von Samen, die sich im Zustand der Lebensruhe befinden. BLV. Verlagsgesellschaft. München.
- STEWART, F. C., PREVOT, P., and HARRISON, J. A. 1942. Absorption and accumulation of rubidium bromide by barley plants. Localisation in the root of cation accumulation and of transfer to the shoot. *Plant Physiol.* 17:411—421.
- STREET, H. E. 1962. The physiology of roots. *Viewpoints in Biol.* 1:1—49.
- UMBREIT, W. W., BURRIS, R. H., and STAUFFER, J. F. 1951. *Manometric techniques and tissue metabolism*. 2. ed. Minneapolis.
- VOIGT, G. K. 1953. The effects of fungicides, insecticides, herbicides, and fertilizer salts on the respiration of root tips of tree seedlings. *Soil Sci. Soc. Am. Proc.* 17:150—152.
- ZELAWSKI, W. 1960 a. Changes in wood respiration during the first days after cutting. *Bull. Acad. Pol. Sci.* 8:405—413.
- »— 1960 b. Influence of tissue injury on wood respiration after felling. *Bull. Acad. Pol. Sci.* 8:457—462.
- »— 1960 c. Respiration intensity of oak wood in particular annual rings of sapwood. *Bull. Acad. Pol. Sci.* 8:509—516.
- »— 1960 d. A contribution to the problem of temperature influence on respiratory processes in wood. *Bull. Acad. Pol. Sci.* 8:517—519.
- ZIEGLER, H. 1956. Über den Gaswechsel verholzter Achsen. *Flora* 144:229.
- ÄLVIK, G. 1939. Über Assimilation und Atmung einiger Holzgewächse im westnorwegischen Winter. *Medd. fr. Vestl. forstl. försöksanstalt.* 22.

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