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RESPIRATION IN STEM AND BRANCHES OF BEECH

BY

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1. *The problem.* The production of dry matter — the net growth — is gross production minus loss of dry matter, all three quantities being measured in units of dry weight. The gross production depends practically solely on the photosynthesis; at any rate, the mineral nutrients taken up from the soil amount to less than 5 % of the dry matter. The effect of the mineral nutrients on the production of dry matter is caused mainly by the influence of mineral nutrients on photosynthesis (Müller 1932, Müller & Larsen 1935). The losses of dry matter are due partly to loss of roots, branches, leaves, fruits and, in some trees, of bark also, partly to loss of dry matter by respiration in root, stem, branches, leaves and fruits. The *production of dry matter or the net production* appears as a difference between two quantities: the gross production and the losses of dry matter. The production of dry matter may be negative for a while, for instance during the night, and in the case of deciduous trees in the period from defoliation to leafing. If, however, the dry matter production of an individual is negative for a long period, the individual will perish.

The equation for the production of dry matter in forest may be formulated in the following way:

Annual increment (dry matter production) =
gross production minus (loss of roots, branches, leaves, bark and fruits + loss of dry matter by respiration in root, stem, branches and leaves).

An equation of this type for the dry matter production was first advanced by B o y s e n J e n s e n (1910 p. 57, see also 1932). In several papers (1927 together with M ü l l e r and 1930) he has tried to determine in young stands of *Fagus silvatica* and *Fraxinus excelsior* each of the quantities of this equation. Later M ö l l e r & M ü l l e r (1938) and M ö l l e r (1946) have tried to determine the quantities of the equation, especially in older beech. In beech of the age of up to 60 years the loss of fruits and bark is negligible.

The size of the dry matter production depends on all the quantities entering into the equation of dry matter production. In the determination of dry matter production it is therefore necessary to determine the single entries in the equation. In that way only it will be possible to see why the production of matter under certain circumstances is large, under other circumstances small. *Only by analyses of the dry matter production is it possible to learn the reasons for the variations in the size of production of dry matter.*

One of the big quantities in the equation of dry matter production is the loss of dry matter through respiration in stem, branches, and twigs. We are of opinion that the determination of this quantity deserves a new investigation in continuation of our previous investigation. Further we have taken up the question of the respiration in relation to weight and body surface. This question is touched by M ö l l e r (1946, l.c. p. 216 ff), but has scarcely been mentioned elsewhere in plant physiological literature, whereas there is an extensive literature about the relation between respiration, weight and body surface in animals, cf. the recent comprehensive review by H e m m i n g s e n (1951).

In the following pages we will analyse the respiration in stem and branches of beech-trees (*Fagus silvatica*), 25, 46 and 85 years old on the basis of measurements made in July and August 1947 and 1948.

2. *Description of sample plots.* A survey of the wood volume factors of the three sample plots is given in table 1. The same stands of beech were used for the investigations the results of which are to be found in three papers appearing in this volume of the periodical: Det forstlige Forsøgsväsen i Danmark.

TABLE 1.

Wood volume factors of sample plots in Allindelille Fredskov and Lille Bøgeskov, Zealand, Denmark. Measured with Schulzes wooden caliper, and American forest service standard hypsometer. Site index, total volume increment and form factors according to Möller (1933).

- 1) Sample plot *Allindelille, compart. 16*: 22-year-old beech. Site index 1.8. Annual volume increment 14.7 m³ per ha. Measured Aug. 14, 1950.
- 2) Sample plot *Allindelille, compart. 5*: 25-year-old beech. Site index 1.3. Annual volume increment 16.1 m³ per ha. Measured Aug. 5, 1947.
- 3) Sample plot *Lille Bøgeskov, compart. 84*: 46-year-old beech. Site index 1.5. Annual volume increment 15.5 m³ per ha. Measured Aug. 3, 1947.
- 4) Sample plot *Allindelille, compart. 22*: 85-year-old beech. Site index 2.0. Annual volume increment 10.9 m³ per ha. Measured July 27, 1947.

	Number of stems	Diameter in cm on bark in 1.3 m height	Per 1 ha		Form factor o. b.	Total volume m ³
			Basal area m ²	Height in m		
1) <i>Allindelille, compartm. 16</i>						
Beech, upper level	93	42.0	12.9	27.0	0.57	198
— subsidiary levels .	11400	4.1	15.1	7.3	0.80	88
<i>Fraxinus excelsior</i>	1204	3.8	1.4	6.8	0.81	8
Total	12697	—	29.4	—	—	294
2) <i>Allindelille, compartm. 5</i>						
Beech	7300	5.8	19.1	9.6	0.73	134
3) <i>Lille Bøgeskov, compart.84</i>						
Beech, upper level	1020	16.8	22.8	17.8	0.58	234
— subsidiary levels .	2090	5.6	5.1	9.2	0.70	33
Total	3110	—	27.9	—	—	267
4) <i>Allindelille, compartm. 22</i>						
Beech, upper level	242	34.2	22.2	26.0	0.58	335
— subsidiary levels .	78		0.8	12.1		6
Total	320	—	23.0	—	—	341

22-year-old beech. Compartment 16 in Allindelille Fredskov in the centre of Zealand, Denmark (55° 31'N, 11° 46'E). The stand was mixed with European ash, *Fraxinus excelsior*. Annual total volume increment 14.7 m³ per ha or 210 cu ft/acre, site index 1.8. From this plot only some of the beeches were selected for leaf-analysis.

25-year-old beech. Compartment 5, Allindelille Fredskov.

Annual total volume increment 16.1 m³ per ha (230 cu ft/acre), site index 1.3. *Forest floor and ground flora*: Mull (mild humus) and brown earth 48 cm deep; under that compact late senonian limestone ("skrivekridt") almost without roots. pH 5.9 in a depth of 5—10 cm, measured with glass-electrode in Dec. 1949. The ground flora was composed of *Anemone nemorosa* and *Mercurialis perennis*.

46-year-old beech. The stand, with a 10 percent admixture of European ash, *Fraxinus excelsior*, was situated in compartment 84, Lille Bøgeskov, 8 km northeast of Sorø in the centre of Zealand, Denmark (55° 29' N, 11° 38' E), the very stand in which Boysen Jensen had sample plots for his studies in 1923—29 on production of dry matter (Boysen Jensen & Müller 1927, Boysen Jensen 1930). In this stand was also the sample plot where we determined the loss of branches in the years 1947—1952 (Möller, Müller & Nielsen 1954). Annual volume increment 15.5 m³ per ha (222 cu ft/acre), site index 1.5. *Forest floor and ground flora*: 10 cm mull (mild humus) changing to a rootfilled dark-brown brown-earth of moraine clay. The thickness of the brown-earth was about 50 cm. The subsoil was gleyed clay (blue moraine clay) very rich in chalk. pH 5.2. in a depth of 5—10 cm, measured with glass-electrode Dec. 1949. In the ground flora, *Anemone nemorosa* and *Lamium galeobdolon* were prevailing; in spots occurred *Asperula odorata*, *Melica uniflora* and *Oxalis acetosella*.

85-year-old beech. The stand in Allindelille Fredskov, compartment 22, was composed of very fine beech. Annual volume increment above ground 10.9 m³ per ha (156 cu ft/acre); site index 2.0. *Forest floor and ground flora*: Mull (mild humus) on brown earth 40—60 cm deep; under that a compact late senonian limestone ("skrivekridt") with only very few roots. The distance from the surface of the soil to the limestone varies from 26 to more than 80 cm. In the neighbourhood of the test trees we measured distances of 40 cm, 66 cm and more than 80 cm between the surface and the limestone. pH 7.7 in a depth of 5—10 cm, measured with glass-electrode in Dec. 1949. The ground flora was rich in species: *Actaea spicata*, *Anemone hepatica*, *Asperula odorata*, *Cephalanthera damasonium*, *Fraxinus excelsior* (young reproduction of seed origin), *Hedera helix*, *Hordeum europaeum*, *Lactuca muralis*, *Mercurialis perennis*, *Neottia nidus-*

avis, *Oxalis acetosella*, *Paris quadrifolia*, *Pulmonaria obscura*, *Viola silvestris*. R a u n k i æ r (1935) has given a thorough account of the herbaceous flora of Allindelille Fredskov, which is interesting because of the density of its species and its 12 species of orchids, e. g. *Cephalanthera damasonium*, *Cephalanthera rubra*, *Epipogium aphyllum* and *Ophrys insectifera*. O l s e n (1943) has described some glades in the forest.

When judged from the ground flora, all four sample plots in the two forests belong to what R ü b e l (1932) calls Fagetum asperulosum.

3. *Description of the single trees.* The single trees investigated are described in table 2. The tree-numbers are the same as used in the papers: D. M ü l l e r : Die Blätter und Kurztriebe der Buche, 1954, and D. M ü l l e r : Die Atmung der Buchenblätter, 1954. With the exception of tree no. 17, which was an intermediate tree, all the other trees were representative of the dominant trees.

Further explanation of table 2: In the description of the single trees, the heading: Compartment refers to the above descriptions of compartment 5, 16 and 22 in the forest of Allindelille Fredskov and of compartment 84 in the forest of Lille Bøgeskov. The heading: m³ branches 0—1 cm means m³ branches with a diameter less than 1 cm, m³ branches 1—3 cm means branches with diameter over 1 cm and under 3 cm etc. The heading: Wood volume m³ means total volume above ground minus leaves.

TABLE 2.

Description of the beech-trees analysed. The head: Compartment, refers to table 1 with description of sample plots.

Beech No.	1	2	3	4	14	18	19
Date of felling	11/8 48	17/8 48	9/8 49	29/7 47	12/8 50	24/7 47	26/7 47
Compartment	22	22	22	22	22	22	22
Age in years	90	86	85	85	85	80	80
Diameter in cm in 1,3 m height	32.5	32.0	30.4	34.0	31.7	33.3	32.9
Height, m	23.8	25.8	25.6	25.9	24.1	26.4	26.1
Bole-height, m	14.7	11.8	10.3	11.1	8.8	11.2	11.7
Maximal crown-diam., m	6.5	6.3	6.4	8.8	4.6	6.6	6.6
Form factor of total volume	0.580	0.577	0.578	0.543	0.56	0.645	0.554
Total volume of stem, m ³	0.970	1.004	0.888	1.093	0.91	1.189	1.053

TABLE 2 (continued).

<i>Beech No.</i>	1	2	3	4	14	18	19
m ³ branches 0—1 cm	0.033	0.026	0.033	0.037	—	0.037	0.030
- — 1—3 -	0.046	0.049	0.057	0.052	—	0.067	0.052
- — 3—5 -	0.035	0.052	0.046	0.034	—	0.077	0.038
- — 5—7 -	0.033	0.057	0.013	0.025	—	0.073	0.038
- — 7—10 -	0.023	—	—	0.033	—	0.038	0.016
- — 10—15 -	0.007	—	—	—	—	—	—
Total volume of branches, m ³	0.178	0.184	0.149	0.181	0.15	0.292	0.174
Total volume, m ³	1.148	1.188	1.037	1.274	1.06	1.481	1.227
Leaves, fresh weight, kg	24.5	15.9	23.1	41.2	19.9	23.6	24.6
Leaf area (one-side measure) in m ²	187	138	138	—	—	—	—
Mast, fresh weight, kg	—	12.5	—	—	—	—	—
<i>Beech No.</i>	5	6	7	8	9	10	11
Date of felling	16/8 48	2/8 47	4/8 47	7/8 48	10/8 48	14/8 48	10/8 47
Compartment	84	84	84	5	5	5	5
Age in years	47	46	46	28	28	28	24
Diameter in cm in 1,3 m height	17.0	15.3	18.7	7.5	6.7	7.2	7.3
Height, m	16.9	17.3	18.1	10.9	11.5	10.2	11.0
Bole height, m	7.4	8.8	6.9	4.8	—	5.0	5.1
Maximal crown-diam., m	4.4	3.4	3.9	2.0	1.8	3.1	3.0
Form factor of total volume	0.559	0.579	0.556	0.652	0.629	0.650	0.686
Total volume of stem, m ³	0.1738	0.1626	0.2317	0.0260	0.0223	0.0214	0.0269
m ³ branches 0—1 cm	0.0086	0.0077	0.0135	0.0025	0.0018	0.0019	0.0023
- — 1—3 -	0.0163	0.0103	0.0270	0.0025	0.0010	0.0024	0.0024
- — 3—5 -	0.0035	0.0038	0.0033	—	—	—	—
- — 5—7 -	—	—	—	—	—	—	—
- — 7—10 -	—	—	—	—	—	—	—
Total volume of branches, m ³	0.0284	0.0218	0.0438	0.0050	0.0028	0.0043	0.0047
Total volume, m ³	0.2022	0.1844	0.2755	0.0310	0.0251	0.0257	0.0310
Leaves, fresh weight, kg	6.7	7.1	7.5	1.6	1.4	1.0	1.7
Leaf area (one-side measure) in m ²	59	—	—	13	10	8	—
Mast, fresh weight, kg	1.3	—	—	—	—	—	—

TABLE 2 (continued).

<i>Beech No.</i>	12	13	15	16	17
Date of felling	8/8 47	9/8 47	13/8 50	11/8 50	11/8 50
Compartment	5	5	5	16	16
Age in years	24	22	29	24	19
Diameter in cm in 1,3 m height	8.1	8.3	10.5	6.2	3.2
Height, m	10.1	10.7	12.5	8.6	6.6
Bole height, m	5.1	3.7	6.3	4.3	4.2
Maximal crown-diam., m	3.7	3.6	—	—	1.8
Form factor of total volume	0.762	0.752	0.636	0.852	—
Total volume of stem, m ³	0.0304	0.0321	0.0590	0.0177	—
m ³ branches 0—1 cm	0.0038	0.0048	0.0044	0.0020	—
- — 1—3 -	0.0053	0.0060	0.0053	0.0025	—
- — over 3 cm	—	0.0008	—	—	—
Total volume of branches, m ³	0.0091	0.0116	0.0097	0.0045	—
Total volume, m ³	0.0395	0.0437	0.0687	0.0222	0.0029
Leaves, fresh weight, kg	2.4	2.3	3.5	1.5	0.2
Leaf area (one-side measure) in m ²	—	—	28	13	2
Mast, fresh weight, kg	—	—	—	—	—

4. *Methods of felling, cutting into sections and estimation of leaf area.* Each tree was felled at about 9 a. m. Immediately after the felling the tree was measured for stereometric determination of volume. The part of the stem taller than 1.3 m was divided into 2 m sections or in 1 m sections, resp. in the cases of 85-year-old beeches and in the cases of younger beeches. The stem below the height of 1.3 m was divided into 4 equally big sections. The volume of the sections was calculated by means of the Huber formula (Danish: Midtfladeformlen). All the branches were cut off and divided into diameter-classes: Branches of more than 10 cm, of 10—7, 7—5, 5—3, 3—1 cm diameter and branches of less than 1 cm diameter. The class: Branches of less than 1 cm diameter comprised all leaf-bearing branches. The leaf-bearing branches were made up in several bundles, if possible each con-

taining a quota of the branches from the upper, the central, and the lower part of the crown. All the bundles having been weighed, one was picked out for the estimation of leaf-weight and leaf-area; all the leaves in this bundle were picked off, a piece of work absorbing quite a deal of time, taking four persons 1—2 hours. On being picked off, the leaves were divided into two portions: 1) The leaves from the long shoots having the youngest annual shoot longer than 0.5 cm and 2) the leaves from the dwarf shoots having the youngest annual shoot shorter than 0.5 cm. Then the leaves and the branches — now without leaves — were weighed separately. The total weight was less than that of the bundle; this loss of weight was due to the transpiration from the leaves, and the weight of the leaves was corrected accordingly. Through the analysis of the selected bundle the total leaf-weight and leaf-area of the tree was calculated on the assumption that all the bundles contained the same quota of leaves.

The leaf-area was determined on leaf samples with a fresh weight of 10—20 g. as follows: The leaves were placed on positive printing paper for dry development, exposed to light for a short time, and the pictures of the leaves were then developed in NH_3 -vapour. The pictures of the leaves were cut out and weighed, and from the area-weight of the paper — frequently estimated — the leaf-area was calculated. *All leaf-areas are given as one-side-measures*, i. e. the total leaf-area (top side + under side) is twice as big as the figure stated.

Suitable pieces for the determination of respiration were sawn off stem and branches. Fresh weight, specific gravity, and dry weight of selected specimens were determined. As table 3 shows, the specific gravity of stem and branches of beeches increases upwards in July-August, from about 1.00 at the base of

TABLE 3.

Diam. in cm		Specific gravity of stem sections of beeches					Specific gravity of branches of beeches		
		30	25—20	20—15	10—5	7—9	5—3	3—1	1—0
Beech No.	18	1.09	—	1.12	1.15	—	1.09	1.09	—
—	19	0.98	1.04	—	—	1.10	—	1.09	1.12
—	4	1.00	1.04	1.06	1.12	1.15	1.12	—	1.16
—	6	—	—	1.00	1.08	—	—	1.13	1.11
—	7	—	—	0.95	1.12	—	1.08	1.07	—
—	12	—	—	—	1.07	—	1.12	—	—

the stem till about 1.10 in branches and twigs. The stereometric measurement was compared with the values calculated from weight and specific gravity. There was a fair agreement between the values calculated in these two different ways.

Finally the surface of the tree was determined: stem, branches of the different diameter classes separately. Especially the estimation of the surface of the smallest twigs was a rather laborious task. The results are given in table 4.

TABLE 4.
Surface of stem and branches of beeches.
The no.s refer to table 2.

<i>Beech No.</i>	4	18	19	6	7	11	12	13
Age in years	85	90	80	46	46	24	24	22
Surface in m ²								
of stem	16.1	17.9	16.8	5.8	6.3	1.8	1.8	1.9
branches 0—1 cm	27.7	28.2	23.1	6.2	12.6	2.1	3.5	4.2
— 1—3 -	12.0	16.2	12.1	2.7	6.3	0.8	1.5	1.6
— 3—5 -	3.4	7.8	3.8	0.4	0.4	—	—	0.1
— 5—7 -	1.8	4.9	2.5					
— 7—10 -	1.5	1.3	0.8					
Total surface of branches, m ²	46.4	58.4	42.3	9.3	19.3	2.9	5.0	5.9
Total surface of stem+branch., m ²	62.5	76.3	59.1	15.1	25.6	4.7	6.8	7.8

5. *Determination of the respiratory activity.* This determination took place in the forest itself in a small laboratory built for such purposes. We used four cylindrical, galvanized iron-containers. The dimensions of the containers were:

Height	Diameter	Volume
130 cm	17 cm	30.0 litre
150 -	26 -	80.6 -
152 -	33 -	166.8 -
133 -	57 -	332.8 -

The inside of the containers was coated with paraffin and they could be closed with a lid fitting in a water-trap as shown in fig. 1. Through a hole in the lid a rubber-stopper was inserted with a barometric tube reaching somewhat below the middle of the container. Through this tube air-samples for air analysis were drawn.

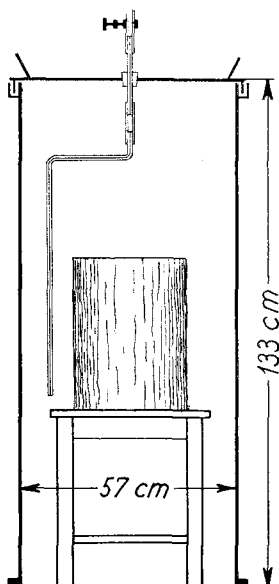


Fig. 1. Diagram of container, volume 332.8 litre, for determination of the respiration in thick stem sections, diameter more than 15 cm. The container is furnished with a wooden stand on which is placed a stem section 30 cm diameter, 40 cm length.

Immediately after the felling, the stems of the 85-year-old beeches were cut into pieces of 20—35 cm diameter, 35—45 cm length, and 25—40 kg fresh weight. The cut surfaces were carefully covered with a thick layer of waterfree lanolin¹⁾, which is impermeable to CO₂. Afterwards one of the stem sections was placed on a wooden stand in such a manner that it was in the centre of the largest container. In the same way the other containers were filled. In the second largest container a stem section of about 20 kg.s fresh weight was placed, and in the two smallest containers 3—6 kg thin stems, branches or twigs were placed, each diameter-class in its separate container. The younger beeches of 25 and 46 years of age were treated correspondingly. When a stem section or a number of branches of convenient volume had been placed in a container, the lid was put on and the

¹⁾ A 6 mm thick layer of lanolin is impermeable to CO₂. In an experiment we found that during 50 hours the loss of weight from bottles with the same bottle-neck diameter and filled with CO₂ was: 1) closed with a rubber-stopper 5.4 mg, 2) closed with a paraffined cork-stopper 0.5 mg, and 3) closed with a 6 mm thick layer of lanolin 0.0 mg.

water-trap filled with water. After about 2 hours the barometric-tube was opened for adjustment of pressure, the thermometres were read, and an air-sample for the first analysis was taken. During the following hours air-samples were drawn at intervals and analysed for content of CO_2 by means of a Haldane apparatus for air analysis.

As an illustration of analysis and calculation, it may be stated as follows: A stem section of beech, fresh weight, 33.55 kg, diameter 34.0 cm, length 36 cm, no red heartwood, was placed in container 4, volume 332.8 litres. From this volume we subtract 16.7 litres, which is half the volume of the stem section¹⁾ and 7.5 litres, which was the volume of the wooden stand. Consequently the real volume, i. e. the effective volume was 308.6 litres, and reduced to 0° , 760 mm = 279.6 litres, the temperature being 20° C and the pressure 756 mm at the closing of the container before the first analysis. An analysis at 2 p. m. gave 0.14 p. ct. CO_2 , an analysis at 7 p. m. gave 0.33 p. ct. CO_2 . The increase of CO_2 0.19 p. ct., which means that there has been formed $279.6 \times 0.0019 = 0.531$ litres CO_2 at 0° , 760 mm. 1 ml CO_2 at 0° , 760 mm weighs 1.95 mg, which means a production of 1.035 g CO_2 in 5 hours at 20° .

6. Conversion to loss of dry matter of the figures for CO_2 given off.

When the amount of CO_2 given off has been determined, the figures are converted to CO_2 given off per 30 days. The figure arrived at is reduced to the mean temperature of the month. This reduction is the most disputable of the calculations. Firstly, it was difficult under the working conditions in the forest to keep the temperature fairly constant. We had to use the mean temperature calculated on the basis of the maximum and minimum thermometers in the containers. Secondly the amounts of CO_2 given off must be reduced to the mean temperature of July i. e. 16.1° C. This reduction was made on the assumption that the simultaneous relative rise of temperature and respiration is the same for peas as for beech stems, an assumption which is scarcely wrong. For the reduction we used the curve given on fig 2

¹⁾ As correction for the amount of CO_2 , which remains dissolved in the water of the wood, we add half the volume of the wood to the air volume.

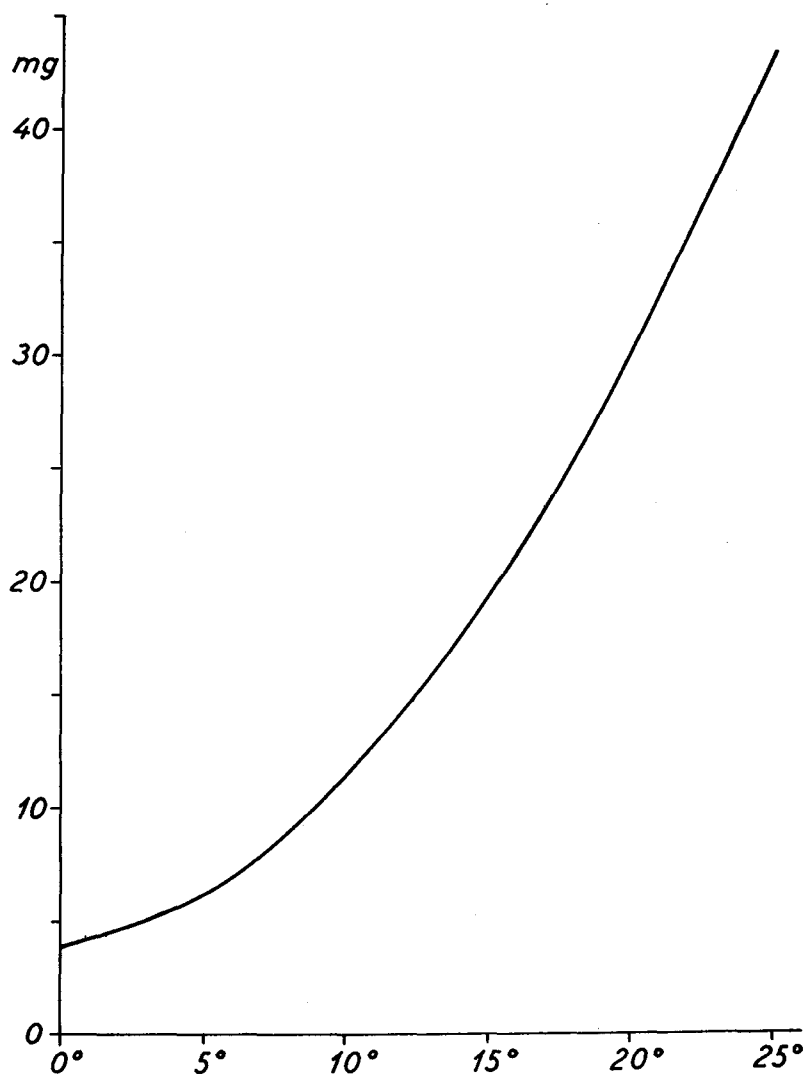


Fig. 2. Kuijper's curve giving the respiration of germinating peas as a function of temperature. Ordinate: mg CO₂ given off per 100 (that is about 75 g.) germinating peas per hour. Abscissæ: Temperature in degrees C.

which shows the dependence upon temperature of the respiration in germinating peas (K u i j p e r 1910). In the above-mentioned case the respiration was found to be 1.035 g CO₂ per 5 hours at 20°, that is 149.0 g CO₂ per 30 days at 20°. According to fig 2 this is reduced to 105.6 g CO₂ per 30 days at 16.1° C.

The amount of CO₂ is then converted a) into kg CO₂ given off per m³ stem or branches in July at 16.1°, b) into kg dry matter per m³ stem or branches per year, and c) into loss of dry matter per year in per cent of dry matter.

a) *Conversion to kg CO₂ given off per m³.* In connection with the determination of respiratory activity, the fresh weight and often also the specific gravity of the stem sections and branches were determined. In tables 5 and 6, however, m³ stem and branches is in all cases calculated from the fresh weight by estimating the specific gravity of branches at 1.10 and that of stems at 1.05. In the example given, the respiration was 105.6 g CO₂ per 30 days at 16.1° C in a stem section of 33.4 kg fresh weight = 31.8 litres, i. e. 3.3 kg CO₂ given off per m³ stem per 30 days at 16.1° C.

b) *Conversion to loss of dry matter in kg per m³ stem or branches per year.* The amount of CO₂ given off by respiration may be converted to loss of dry matter in one of the following ways: α) One may assume that it is mainly carbohydrate with the composition C₆H₁₀O₅ (100 g starch contain 44.4 g C) that is dissimilated (katabolised) by respiration in beech stems. The fact that the respiratory quotient for young beech stems is nearly 1 (Boysen Jensen & Müller 1927) points in that direction. When using this as a basis for the calculation, one finds that 1 kg CO₂ given off corresponds to a loss of dry matter of 0.614 kg. β) Or one may calculate the loss of dry matter from the content of C in stem and branches. According to Ebermayer (1876 p. 77—78) beech wood contains 50 p. ct. C. From this we calculate that 1 kg CO₂ given off corresponds to a loss of dry matter of 0.546 kg¹). This method of calculation was used for the present treatise, as the calculation based on C-content is the most correct. It is true that glucose with 40.0 p. ct. C, sucrose (saccharose) with 42.1 p. ct. C and starch and hemicelluloses with 44.4 to 45.5 p. ct. C are katabolised — broken

¹) Instead of dry matter Polster gives kg C only. His figures can be converted into dry matter by multiplication with 2.

down — by respiration; but as the percentage of C is maintained constant, the calculation on the basis of C-content must be the most correct. So the present and the following treatises differ from the papers by Boysen Jensen & Müller (1927) and Möller & Müller (1938), both of which use as a basis for the calculation the fact that 1 kg CO₂ corresponds to a 0.614 kg. loss of dry matter. The figures for loss of dry matter in the papers mentioned should therefore be multiplied by 0.889 (sc. 54.6 : 61.4) to be comparable with the values given here.

In the example given above we found an output of 3.3 kg. CO₂ per m³ per 30 days at 16.1°, which corresponds to a loss of dry matter of $3.3 \cdot 0.546 = 1.80$ kg dry matter. The figures for this loss of dry matter in July will not be found in the tables, because the losses of dry matter in July have been converted to loss of dry matter per year by multiplication with 3.62. In the investigations by Boysen Jensen & Müller (1927), it was shown that 27.62 p. ct. of the annual loss of dry matter by respiration took place in July. That is our reason for multiplying the loss of dry matter in July with 3.62 in order to find the annual loss of dry matter by respiration. In the example given we find the annual loss of dry matter to be $1.80 \times 3.62 = 6.5$ kg.

c) *The annual loss of dry matter in per cent.* From the annual loss of dry matter calculated per m³ of stem and branches, we have calculated the loss of dry matter in p. ct. In all cases we have estimated the content of dry matter to be 53.0 p. ct. of the fresh weight. In the example given we find: 1 m³ stem = 1050 kg. fresh weight = 556.5 kg dry matter, of which the annual loss of dry matter by respiration amounts to 6.5 kg or 1.2 p. ct.

d) *Errors.* It is difficult to estimate the errors of our determinations. The errors due to traumatic stimulus from the cut surfaces are negligible, because the effect of traumatic stimulus is appreciable in the neighbourhood of the cut surface only (Müller 1924, Opitz 1931). The most uncontrollable factor was, as mentioned, the temperature during the determinations. If the analysis of respiratory activity is to be repeated, it should be done in thermoregulated containers. The agreement between the various determinations proves that the error scarcely exceeds 10 p. ct.

7. *Loss of dry matter by respiration in stem and branches of beech, Fagus sylvatica.* The results of our determinations

TABLE 5.

				kg CO ₂ given off per m ³ in July at 16.1°	Annual loss of dry matter by respiration in kg per m ³ stem or branches
<i>25-year-old beech</i>					
<i>Beech 12</i>	Branches	under 1 cm diam.		36.8	72.6
	—	1—3 —		18.8	37.1
	Stem	8 —		15.0	29.1
<i>Beech 13</i>	Branches	under 1 —		29.6	58.6
	—	1—3 —		19.9	39.3
	Stem	8.0 —		13.2	26.1
<i>Beech 11</i>	Branches	under 1 —		39.7	78.4
	Stem	4.6 —		18.2	36.0
	—	7.2 —		13.0	25.8
<i>46-year-old beech</i>					
<i>Beech 6</i>	Branches	under 1 cm diam.		37.5	74.1
	—	1—3 —		17.4	34.4
	Stem	5.5 —		19.0	37.6
	—	7.3 —		10.1	20.0
	—	12.1 —		7.6	15.0
	—	14.1 —		8.8	17.4
	—	16.0 —		6.4	12.6
<i>Beech 7</i>	Branches	under 1 cm diam.		34.9	69.0
	—	1—3 —		10.5	20.8
	—	3—5 —		15.6	30.8
	Stem	9.4 —		10.8	21.3
	—	12.3 —		7.3	14.4
	—	16.1 —		4.8	9.5
	—	18.7 —		5.4	10.7
<i>85-year-old beech</i>					
<i>Beech 19</i>	Branches	under 1 cm diam.		48.5	95.9
	—	1—3 —		11.6	22.9
	—	3—5 —		4.6	9.1
	—	7—9 —		6.3	12.5
	Stem	24.6 —		4.6	9.1
	—	26.4 —		2.8	5.5
	—	28.5 —		2.6	5.1
	—	34.1 —		4.1	8.1
<i>Beech 4</i>	Branches	under 1 —		32.1	63.5
	—	— 1 —		45.8	90.5
	—	1—3 —		12.0	23.7
	—	1—3 —		12.6	24.9
	—	3—5 —		6.1	12.1
	—	5—7 —		7.8	15.4
	—	5—7 —		6.6	13.0
	—	7—9 —		7.5	14.8

TABLE 5.
continued.

			kg CO ₂ given off per m ³ in July at 16.1°	Annual loss of dry matter by respiration in kg per m ³ stem or branches
	Stem	15.6 cm diam.	7.7	15.2
	—	21.4 —	5.0	9.9
	—	25.7 —	3.6	7.1
	—	31.2 —	3.5	6.9
	—	34.0 —	3.5	6.9
Beech 1	Stem	26.2 —	4.6	7.6
	—	26.2 —	3.1	
Beech 2	Stem	32.7 —	3.5	7.3
	—	32.7 —	3.9	

of the respiration in stem and branches are given in table 5 and graphically in fig 3. In fig 3 the abscissæ are diameters of the individual wood samples and the ordinates are kg CO₂ given off per m³ in July at 16.1°. Samples from stem and branches respectively are given with different signatures. Fig 3 shows:

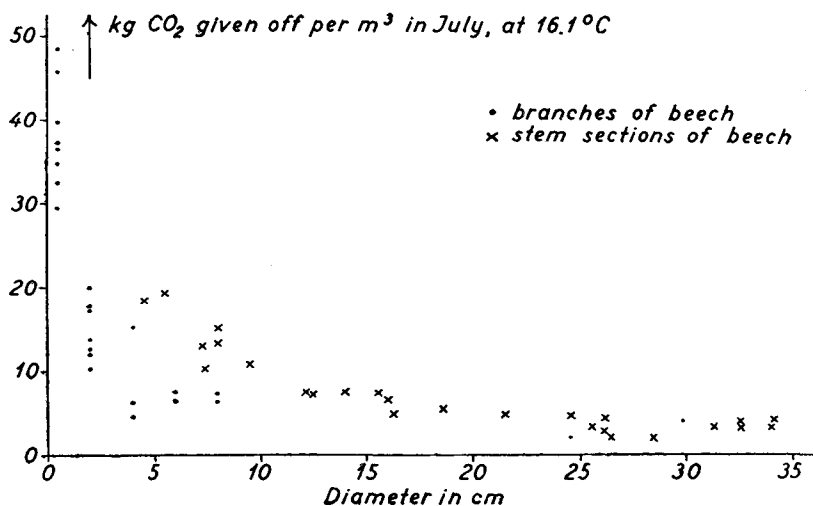


Fig. 3. Respiration in sections of stems and branches of different diameter of beech, *Fagus sylvatica* (cf table 5). Ordinate: kg CO₂ given off per m³ in July at 16.1°. Abscissæ: Diameter of stems and branches in cm.

- a) In stems as well as in branches the respiratory activity decreases with increasing diameter.
- b) In the diameter interval between 4.5 and 8 cm, where we have measurements from stems as well as from branches, the respiratory activity is highest in the stem sections, probably because branches are older, i. e. have narrower rings and smaller increment than stems of the same diameter.

Further, the total annual loss of dry matter by respiration in stem and branches is calculated according to the arrangement of the wood in diameter classes, as given in table 2. This calculation is made separately for each diameter class by reading on the smoothened curves of fig 3 the loss of dry matter by respiration per m³ separately for the various diameter classes. The

TABLE 6.
Respiration of the single trees.

	Tree no.	Diameter in cm in 1.3 m height	Total volume of stem + branches in m ³	Tons dry matter in stem + branches	Annual loss of dry matter in kg by respiration in stem + branches	Annual loss of dry matter by respiration in stem and branches in p.ct. of dry matter in stem and branches
25-year-old beech	12	8.1	0.0395	0.0225	1.25	5.6
	13	8.3	0.0437	0.0249	1.46	5.9
	11	7.3	0.0310	0.0177	1.03	5.8
46-year-old beech	6	15.3	0.184	0.105	3.90	3.7
	7	18.7	0.276	0.157	5.17	3.3
85-year-old beech	19	32.9	1.227	0.699	13.9	2.0
	4	34.0	1.274	0.726	14.2	2.0
	18	33.3	1.481	0.844	16.8	2.0

results are given in table 6 together with the loss of dry matter in p. ct. From this it appears that loss of dry matter in p. ct. decreases with increasing age, as might be expected from fig 3 and fig 4.

Using the annual loss of dry matter given in table 6, we have finally calculated the annual loss of dry matter per ha beech forest, Danish site index 2, for the three age groups: 25, 46 and 85 years. The results of the calculation are shown in table 7, from which it appears that 25-year-old beech loses 5.8 p. ct. dry matter in stem and branches annually by respiration in these

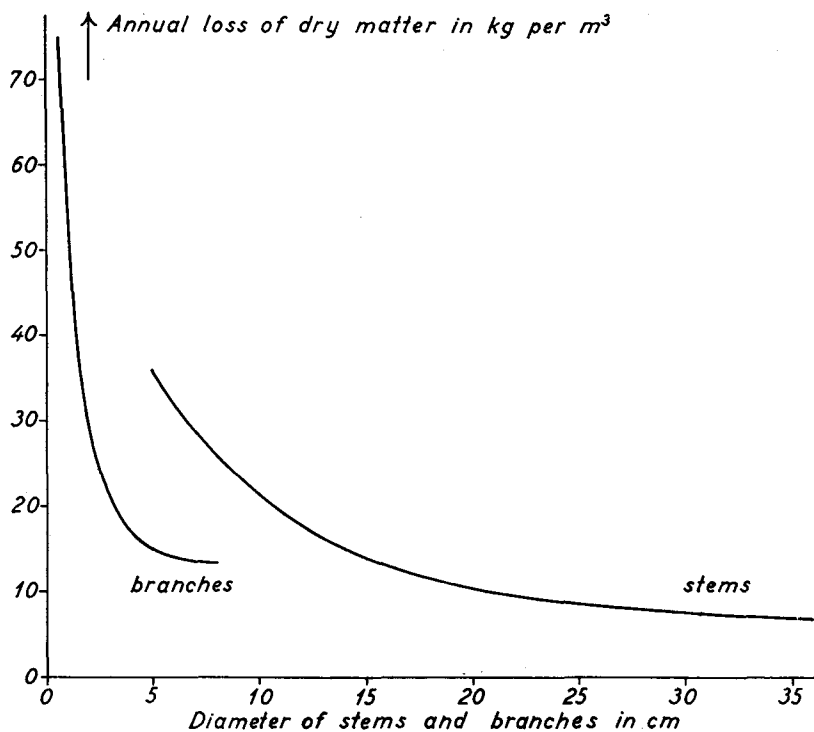


Fig. 4. Annual loss of dry matter in kg by respiration per m^3 of sections of stems and branches of beech, *Fagus sylvatica*. Ordinate: Annual loss of dry matter in kg per m^3 . Abscissæ: Diameter of stems and branches in cm.

TABLE 7.

Danish beechwood, Danish site index 2.0. Loss of dry matter by respiration in stem and branches per year per ha. Total volume is taken from Möller: Boniteringstabeller etc. 1933. The annual loss of dry matter in p. ct. is taken from table 5.

	m^3 stem + branches per ha*)	tons of dry matter in stem + branches per ha	Annual loss of dry matter by respi- ration in stem and branches in p. ct. of dry matter in stem and branches	Annual loss of dry matter by respiration in stem and branches in tons per ha
25-year-old beech	107	61	5.8 %	3.5
46 — —	226	129	3.5 %	4.5
85 — —	401	229	2.0 %	4.6

*) $1 m^3/ha = 14 \text{ cu ft/acre.}$

organs. The corresponding values for 46-year-old beech are 3.5 p. ct. and for 85-year-old beech 2.0 p. ct.

It is of interest to insert these figures for loss of dry matter by respiration into accounts made by G ä u m a n n (1935) of the dry matter economy of beech. G ä u m a n n investigated 105-year-old beeches. Each tree had a total volume of about 2.5 m³ stem + branches or about 1400 kg dry matter. A tree of that kind contained about 87 kg mobilizable carbohydrate¹⁾ in stem + branches; that is 6.2 p. ct. of the dry matter, this amount consisting mainly of saccharose and hemicellulose, and of smaller quantities of glucose and starch. We may assume that the contents in p. ct. of mobilizable carbohydrate in stem and branches are the same in our beeches as in those analysed in Switzerland by G ä u m a n n. Consequently our 85-year-old beeches contain on an average 46 kg mobilizable carbohydrate in stem and branches, the 46-year-old beeches 15 kg and the 25-year-old beeches 1.3 kg. Yet, the content in p. ct. of mobilizable carbohydrate probably decreases with increasing age, so that the calculated values are too small, especially as far as the young beeches are concerned. G ä u m a n n found that 17 p. ct. of the mobilizable carbohydrate in stem and branches is used for leafing²⁾, and 12 p. ct. partly for the formation of the annual ring, partly for root growth. To this we may add that an 85-year-old beech uses about 15 kg annually, a 46-year-old beech about 4.5 kg and a 25-year-old beech about 1.2 kg for respiration in stem and branches. For an 85-year-old beech the balance-sheet looks like this:

Mobilizable carbohydrate in stem and branches		
	of an 85-year-old beech	46.0 kg
Annual use	for leafing	17 p. ct. = 7.8 kg
—	- for annual ring	
	and growth of root ...	12 p. ct. = 5.5 kg
—	- for respiration in	
	stem and branches ...	33 p. ct. = 15.0 kg 28.3 kg
		<hr/> 17.7 kg

¹⁾ i. e. carbohydrate that can be metabolized by leafing, by respiration, by forming the annual ring, etc.

²⁾ According to R a m a n n & B a u e r (1911) 23 to 43 p. ct. of the dry matter in two-year-old beeches is lost by respiration during the leafing.

From this it appears that approximately 60 p. ct. of the mobilizable carbohydrate in stem and branches is transformed annually. The part of the mobilizable carbohydrate in stem and branches which is broken down by respiration in stem and branches, is of the same magnitude as the part used for leafing + formation of annual ring + root growth.

The literature on loss of dry matter by respiration in stem and branches has been reviewed by Möller (1946) and Polster (1950). Investigations younger than 1950 have been carried out by Tranquillini (1952). He found that during the night, in the beginning of October, in a 10 m. high, isolated beech, about 14 p. ct. of the photosynthesis surplus was broken down by respiration in the over-ground part of the tree, the leaves included. As respiration in the day-time is higher than in the night, the loss of dry matter by respiration in the entire over-ground parts is, we presume, at least 25 p. ct. of the gross production by photosynthesis.

It may be added here that Älvik (1939) and Hagem (1947) in Norway have investigated the dry matter balance in the darkest month of the winter of small evergreen plant specimens, chiefly seedlings of *Pinus silvestris* L and *Picea abies* L. They found an increase in dry matter per 24 h, a positive dry matter balance, even in the darkest days of December. Further it may be added that Printz (1937) has shown that in the winter branches and thin stems of various kinds of soft and hard woods have a higher respiration at e. g. 15° when they for some days have been kept at a temperature about 0°. Such a thermic stimulus has been known from potatoes since the investigations of Müller-Thurgau (1885) and from young branches of *Fagus silvatica* since Simon (1906).

8. *The respiration in proportion to body surface and growth.*

In the zoophysiological literature the question of the relation between respiratory activity and body surface has been treated frequently since Rubner (1883). We shall refer only to the treatises of Bornebusch (1930), Hemmingsen (1950), Krogh (1916), Lehmann (1951) and Zeuthen (1947). As far as trees are concerned, Möller (1946, p. 216 ff) has put forward the hypothesis that the respiration of stem and branches is nearly proportional to the body surface. He writes:

“Dass für den Respirationsverlust nicht die Grösse der Holzmasse massgebend ist, sondern eher die Oberfläche des Stammteiles, ist bestätigt worden...”. “In Wirklichkeit ist es nicht die Oberfläche selbst, welche die Respiration bestimmt, sondern vielmehr die Oberfläche im Zusammenwirken mit einem innerhalb derselben belegenen Holzring von wechselnder Grösse”. “Wie Johansson (1933) gezeigt hat, spielt auch der Zuwachs des Stammteils mit hinein”.

TABLE 8.

	Tree no.	Surface of the single tree in m ²			Fresh weight per tree (stem + branches) in kg	Annual loss of dry matter by respiration in stem and branches in kg
		stem	branches	total		
25-year-old	12	1.81	5.06	6.87	43	1.25
beech	13	1.85	5.80	7.65	47	1.46
	11	1.75	2.84	4.59	34	1.03
46-year-old	6	5.82	9.36	15.18	195	3.90
beech	7	6.25	19.32	25.57	282	5.17
85-year-old	19	16.76	42.31	59.07	1300	13.9
beech	4	16.07	46.40	62.47	1301	14.2
	18	17.89	58.43	76.32	1601	16.8

In order to investigate the correlation of the respiratory activity with the surface we have, on the basis of the figures in tables 4 and 5, for each analysis calculated the respiration per m² body surface in g CO₂ given off in July at 16.1°. The results are given graphically in fig 5, the abscissae giving the diameter. Besides, the analyses from the three different stands are marked separately.

Fig. 5 shows that in the three stands the respiration per m² surface of the stem sections increases a little with increasing diameter. This means that respiration is not quite proportional to surface. If we look at each age separately, we find a stronger increase of the respiratory activity per m² body surface with increasing diameter. Further we see from fig 5 partly that the respiratory activity per m² surface of branches increases rapidly with increasing branch diameter, and partly that it is considerably lower than that of stem sections of the same diameter.

As may be seen from fig 5, certain facts indicate that the respiratory activity of stem and branches depends not only on

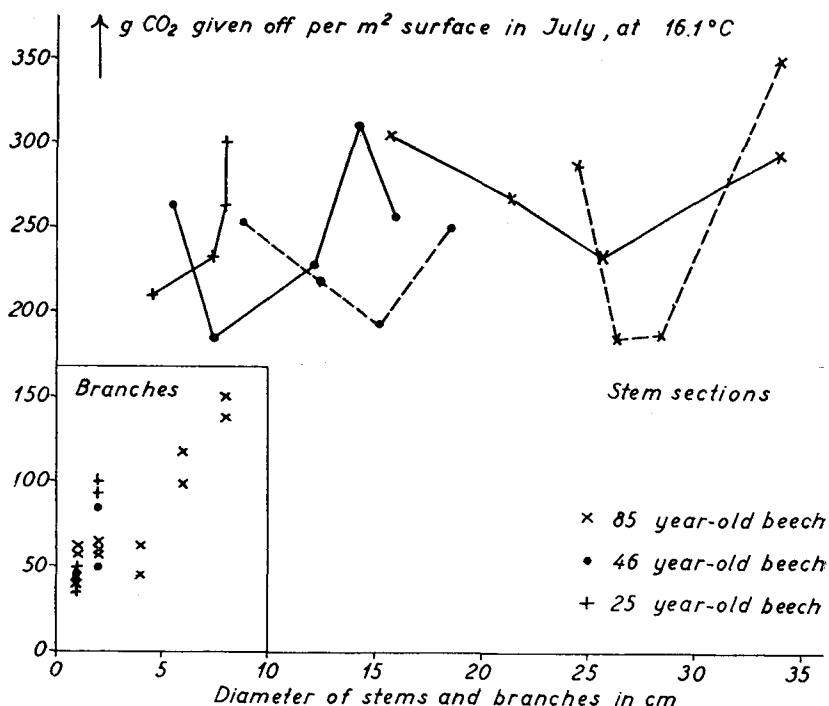


Fig. 5. Respiration of stem and branches of beech, *Fagus sylvatica*, in relation to surface. Ordinate: g CO₂ given off per m² surface in July at 16.1°. Abscissæ: Diameter of stems and branches in cm.

the surface but also on the width of the annual rings. In fig 5 the points representing each of the trees are connected with lines. It appears from this that there is a tendency towards increasing respiratory activity at the basis of the stem, where the diameter is biggest, a decrease in the activity higher up in the stem, and finally in the upmost parts another increase. A similar variation in the widths of the annual ring is found in the stem, cf Möller : Træmålingslære etc. 1951. p. 31.

In the case of branches fig 5 shows, as mentioned above, partly that the respiratory activity per m² is lower than in the case of stem sections with the same diameter, and partly that it increases highly with increasing diameter of the branches.

Hem m i n g s e n (1950) in his survey of respiration in the animal and vegetable kingdom has found that respiration is proportional to a fractional power (n) of the body weight (W)

$$y = k \cdot W^n,$$

where k is the proportionality factor. n is found to be 0.73. In his diagrams p. 11 and p. 17 he has put in the respiration of entire beech trees (stem + branches). The measurements fall remarkably well into line with the metabolism-body-size-relation of poikilothermal (cold-blooded) animals.

9. *The mechanism of respiration.* As far as we know, the gas exchange of the trees takes place solely by diffusion. The distance, through which diffusion has to take place, is not long, because the metabolism — the respiration — which is the cause of the gas exchange, goes on partly in the bark, partly in the cambial cylinder, and partly in the youngest annual rings. The respiration in wood decreases rapidly inwards (Möller & Müller 1938, Goodwin & Goddard 1940). There is a division of labour in the wood, not only between sapwood and heartwood, but also between outer and inner sapwood (Müller 1949). The thickness of the bark¹⁾, which is decisive for the distance through which diffusion has to take place, is small in most species. In beech in Allindelille Fredskov in Denmark the thickness of the bark was between 0.9 and 4 mm (table 9). Gäumann (1935) states that a 105-year-old beech, the stem and branches of which weighed 2650 kg. fresh weight (= 1400 kg. dry weight), had 75 kg. bark (dry weight). Also tropical trees, having presumably a high respiration, have thin bark. Foxworthy (1927) writes that the thickness of the bark in a number of Malayan timber trees is in average 10 mm, maximum over 25 mm and minimum 4 mm. Species with thick bark

TABLE 9.

	Thickness of the bark, i. e. tissues outside the cambial cylinder, in the height of:					
	10 cm	75 cm	5 m	10 m	15 m	19 m
Beech no. 1, 85-year-old	4.0 mm	3.1 mm	2.8 mm	2.5 mm	2.3 mm	2.2 mm
— 30-year-old, 6.3 cm diam. in 1.3 m height	1.2 mm	1.2 mm	0.9 mm	—	—	—
— 30-year-old, 7.3 cm diam. in 1.3 m height	1.1 mm	1.0 mm	0.8 mm			

¹⁾ the bark of a tree is defined as all tissues outside of the cambium.

such as oak and larch are characterized by cracks in the bark, reaching the neighbourhood of the cambium.

Geurten (1950) has found that the diffusion of CO_2 through the bark of various trees are the following in $\text{mg CO}_2/\text{dm}^2/\text{h}$: *Acer pseudoplatanus* 3—18; *Fagus silvatica* 2—19; *Fraxinus excelsior* 1—20; *Quercus robur* 2—26. The two figures state the lowest and the highest daily maximum. For *Fagus silvatica* we have found the following figures (mean from July at 16.1°):

			mg CO_2 diffused through the bark per dm^2/h in July at 16.1°
Twigs under 1 cm	diameter		0.7
— 1—3 cm	—		0.5
Stem 5—10 cm	—		4.9
— 10—20 cm	—		4.3
— 21—34 cm	—		4.0

There are certain signs of partial anaerobic respiration — or intramolecular respiration, to use the old term — in the cambial tissues. Firstly Devaux (1899) and McDougal & Working (1933) have at times found a high percentage of CO_2 and a low percentage of O_2 in air sucked out of trees. In the experiments by Devaux the traumatic stimulus, having great effect on branches, may have influenced the results. McDougal & Working sucked air through bores in various trees. In *Juglans regia* the air in the pneumatic system of the stem consisted of 5—22 p. ct. CO_2 and of 8—15 p. ct. O_2 . In *Quercus agrifolia* CO_2 varied between 1 and 26 p. ct., and O_2 between 11 and 19 p. ct. In *Populus macdougalii* CO_2 varied from almost atmospheric proportions to 18.5 p. ct. and oxygen from 0.0 to 21.2 p. ct. From this we see that the quantity of oxygen in stem for normal respiration may at times be insufficient. Ruhland & Ullrich (1936) and Ruhland & Ramshorn (1938) investigated the respiratory quotient, RQ, of cambial tissues of *Betula alba*, *Populus nigra*, *Syringa vulgaris* and *Tilia pubescens* and *T. tomentosa*. The respiratory quotient, RQ, is $\frac{\text{volume CO}_2 \text{ given off}}{\text{volume O}_2 \text{ taken up}}$. In case $\frac{\text{CO}_2}{\text{O}_2}$ is between 0.5 and 1.0, the oxygen supply is sufficient; in case $\frac{\text{CO}_2}{\text{O}_2}$ is considerably

higher than 1, an incomplete combustion of respiratory material is very likely to go on — along with a normal combustion. Now R u h l a n d and his above mentioned co-workers found RQ to be considerably higher than 1 in the cambial tissues from the above mentioned trees, and they proved, what was already found by D e v e a u x (1899), that there is a certain production of alcohol (ethanol) in the wooden tissues. B o y s e n J e n s e n & M ü l l e r (1927) found RQ to be about 1, but did not investigate stems thicker than 6 cm in diameter. It will be necessary to estimate RQ also in thick stem-sections and in the warm season. It appears that the inward diffusion of oxygen is not sufficient, not even in the thin, apical 15 mm of *Allium*-roots, at any rate not when temperature is more than 20° and the respiratory activity consequently great (B e r r y & N o r r i s). Unfortunately it is impossible to determine by calculation exclusively whether the inward diffusion of oxygen is sufficient (B e r r y & N o r r i s 1949 and G e r a r d 1931).

Trees are the biggest of all living organisms. Such big organisms could not exist were it not that the respiration in great parts of their body was low, e.g. in the older parts of root, stem and branches. This is necessary for two reasons: Firstly, the loss of dry matter by respiration must be reduced; for had the stem the same respiratory activity as the branches under 1 cm diameter, the total gross production would be broken down — burned away — through respiration in stem and branches. Now the loss of dry matter by respiration in stem and branches is only about 20 p. ct. of the gross production (M ö l l e r, M ü l l e r & N i e l s e n 1954). Secondly, an intense air-exchange in a thick stem could hardly take place solely by diffusion through the bark. The low respiratory activity in the old parts of root, stem and branches is obtained by the small amount of living cells in these organs. The many dead cells in the wood correspond in a way to the dead intercellular substance forming the greater part of the supporting tissue of the higher animals. On the other hand, the forming of a body of dead cells is only possible when the cells are protected against decay by some substance. Lignin is the substance that gives the dead cells in the wood their power of resistance.

We beg the "Carlsbergfondet" which has paid the expenses of the investigation, to accept our most respectful thanks. We thank professor, dr. P. Boysen Jensen, whose work on the gross increment and net increment of plants has been the source of inspiration of the investigations, for the warm interest with which he has participated in our work. Also, we are highly grateful to Royal forest supervisor Th. Kaspersen, who has given us indispensable help, and to dr. phil. A. Hemmingsen for discussing with us the problem metabolism/body surface. We are highly indebted to the Rask-Ørsted Foundation for the economic grant to the translation.

SUMMARY

The respiratory activity of stem and branches of European beech, *Fagus silvatica*, has been investigated. This was done by placing 25—40 kg pieces of stems or 3—20 kg branches with the cut surfaces covered with lanolin in containers of 30—330 litre. From time to time air-samples were drawn from the containers and analysed. From the respiratory activity of 25-year-old, 46-year-old and 85-year-old beeches from good sites, the loss of dry matter by respiration was calculated per ha for a Danish beech wood of Danish site index 2 at the ages of 25, 46, and 85 years. The annual loss of dry matter by respiration in stem and branches was as follows in per cent of dry matter in stem and branches: 5.8 per cent, 3.5 per cent, and 2.0 per cent resp. for 25-, 46-, and 85-year-old beeches. The annual loss of dry matter by respiration in stem and branches in tons of dry matter per ha beech wood was: 3.5 and 4.5 and 4.6 tons for resp. 25-, 46-, and 85-year-old beech wood.

A single 25-year-old beech tree had a total volume (stem + branches) of 0.038 m³ (= 0.022 tons of dry matter) and a total surface (stem + branches) of 6.4 m². The annual loss of dry matter by respiration in stem and branches of such a tree was 1.25 kg or 5.8 per cent of the dry matter in stem and branches.

A single 46-year-old beech tree had a total volume (stem + branches) of 0.230 m³ (= 0.131 tons of dry matter) and a total surface (stem + branches) of 20.4 m². The annual loss of dry matter by respiration in stem and branches of such a tree was 4.54 kg or 3.5 per cent of the dry matter in stem and branches.

A single 85-year-old beech tree had a total volume (stem + branches) of 1.327 m³ (= 0.756 tons of dry matter) and a total surface (stem + branches) of 66.0 m². The annual loss of dry matter by respiration in stem and branches of such a tree was 15.0 kg or 2.0 per cent of the dry matter in stem and branches.

Respiration in relation to surface: Fig. 5 shows that the respiration per m² surface of the stem sections increases a little with increasing diameter. This means that respiration is not quite proportional to surface.

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