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# *THE DRY MATTER PRODUCTION OF EUROPEAN BEECH*



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The dry matter production — the net growth — of living organisms, is the gross production minus loss of dry matter. The equation for the production of dry matter in trees is:

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

This equation was first formulated by Boysen Jensen (1910) (see also Boysen Jensen 1932). To illustrate the equation Möller (1946) drew diagrams of the dry matter production of various species of trees. These diagrams are, naturally, defective; because the different quantities were not determined with the same accuracy. During 1947—49, the authors made more accurate analyses of some of the quantities to determine dry matter production of beech[1]). Beech (*Fagus silvatica L.*) is the most important forest tree in Denmark.

The analyses were made in 4 even-aged stands of beech in central Zealand, Denmark (55°31'N, 11°46'E) resp. 8, 25, 46 and 85 years old. The site indexes according to Möller (1933) were respectively about 2 and 1.3 and 1.5 and 2.0. The site index 1.3 has an annual net-increment of 16.1 $m^3$ per ha or 229 cu.ft.

[1]) See Möller, Müller & Nielsen (1954 a and b), and Müller, (1954 a).

TABLE 1.

Extract from yield table of Danish beech site index 2.0 (Möller 1933). All figures refer to the condition of the stand midway between thinnings.

| Age in years | Height in m | Diameter in cm 1.3 m above ground | (1 hectare) Number of stems | (1 hectare) Basal area $m^2$ | (1 hectare) Total Volume cu. m. |
|---|---|---|---|---|---|
| 25 | 8.2 | 7.6 | 3800 | 17.7 | 107 |
| 46 | 16.2 | 17.6 | 960 | 23.2 | 226 |
| 85 | 25.9 | 36.1 | 260 | 26.9 | 401 |

per acre in 25-year-old beech; the site index 1.5 (between "excellent" and "good") has an annual net-increment of 15.5 $m^3$ per ha or 222 cu.ft. per acre in 46-year-old beech and the site index 2.0 ("good") has an annual net-increment of 10.9 $m^3$ per ha or 155 cu.ft. per acre in 85-year-old beech forest. For the ages in question each individual quantity of the equation of dry matter production, all per hectare, has been calculated, and all have been referred to Danish site index 2 ("good"). The figures concerned are represented in tables 1 and 3. Table 1 shows the volume factors (o. b.) for Danish beech forest of site index 2 ("good"). Table 3 contains the individual quantities of the equation of dry matter production refering to Danish beech forest of site index 2. The dry matter production graph for beech (fig. 1) has been drawn on the basis of the figures in Table 3.[1])

The stands analysed to procure the figures in Table 3 are described in the treatise: Möller, Müller & Nielsen: Respiration in Stem and Branches of Beech, 1954. The 8-year old stand of beech is not mentioned in the article, and is therefore briefly described below:

The stand of 8-year-old beech was a dense, natural reproduction of seed origin in a shelterwood forest i. e., a forest with some few 120-year-old trees, about 100—120 $m^3$ per ha, and a dense undergrowth of reproduction of seed origin. The stand of 8-year-old beeches grew in the Enemärket Forest, Sorö 2nd forestdistrict, 55°31'N, 11°36'E, 10 km west of Allindelille Fredskov in central Zealand, Denmark. The height of the stand was 1.7 m, the number of seedlings was 510.000 per ha; freshweight of stems and branches 31.6 t, dry-weight 16.75 t per ha; the leaves had a dry-weight of 2.1 t per ha. The loss of dry matter by respiration in stems and branches was 0.627 t per ha in July at 16.1°. The yearly loss of dry matter by respiration in stems and branches is 2.27 t per ha or 13.5 per cent of the dry weight in stems and branches.

[1]) Sabroe (1947) has given a general survey of forestry in Denmark with a comprehensive list of Danish literature on forestry.

TABLE 2.

Estimated figures for volume of roots and loss of dry matter by respiration in roots and by loss of roots. Danish beech, site index 2.0. All figures per ha.

| Age in years | *a* Volume and weight of roots | | *b* | *c* | *d* |
|---|---|---|---|---|---|
| | $m^3$ | tons dry matter | Tons dry matter by loss of roots per year | Tons dry matter lost by respiration in roots per year | Annual loss of dry matter by respiration in per cent |
| 8 | 6.0 | 3.4 | 0.1 | 0.5 | 13.5 |
| 25 | 21.4 | 12.2 | 0.2 | 0.7 | 5.8 |
| 46 | 45.2 | 25.8 | 0.2 | 0.9 | 3.5 |
| 85 | 80.2 | 45.6 | 0.2 | 0.9 | 2.0 |

*Root.* Volume and dry weight of roots, loss of roots and respiration of roots are given in Tables 2 and 3 and are unfortunately based on a rather rough estimate. The root volume is estimated at 20 per cent of the total aboveground volume (stems, plus branches, but minus leaves). The loss of dry matter by respiration in roots is estimated to be of the same annual quantity percentagewise as the respiration in stem, plus branches[1]). Finally the annual loss of roots in 46-year-old beech is estimated at 0.8 per cent of the root dry matter or 0.2 ton. This is the same loss of dry matter as the loss of branches amounts to in per cent of the aboveground volume (stem, plus branches, but minus leaves). The big roots are to be considered as the main stem of the root. It should be pointed out that the values in Table 2 which are included in Table 3 are all based on estimates.

*Loss of branches* in Table 3 is estimated at 0.5—1.0 ton dry matter per year. In the investigations on loss of branches an annual loss of 0.8 per cent of the aboveground volume, leaves

[1]) Eidman (1943) found a high respiration rate in 1—4 year old plants including two year old beech trees. The roots in these had an average respiration rate of 30 mg $CO_2$/24 hr/qm/20° C/1 g dry matter in roots. Using the same method of calculating loss of dry matter by respiration as we used in connection with the aboveground parts, we obtain an annual dry weight loss from respiration in roots of 1.27 kg per kilo of dry root weight. This represents a tenfold increase in respiration over young branches below 1 cm in diameter which are themselves respiring at a rather high rate. It should be emphasized, however, that Eidman's values apply solely to the roots of very young trees. Such young plants have many very thin roots and the thickest roots are only a few mm in diameter; they are thinner than the branches under 1 cm diameter. That is why the high respiratory activity of such young root system is comprehensible.

excepted, or 1.0 ton dry matter was found for 45—51-year-old beech, Danish site index 1.2[1]) (Möller, Müller & Nielsen 1954 b). We do not claim that this figure is also valid for younger or older stands or for other site indexes. But instead of operating with an annual loss of 0.8 per cent of the aboveground volume, we have preferred to estimate the branch loss at 1.0 ton dry matter per year for 25- and 46- and 85-year-old beech.

*Loss of leaves.* According to Möller (1946) there is an average of 2.7 tons of dry matter of leaves per ha beech-wood or 6.8 tons fresh-weight. Beech leaves contain on an average 49.0 g dry matter per square meter of leaf area (only one surface measured) and 39.7 per cent dry matter.

*Loss of dry matter by respiration.* Above we have given an account of the estimated annual loss of dry matter by respiration

TABLE 3.

The individual quantities in the equation of dry matter production of Danish beech, site index 2.0. All figures are tons dry matter per ha per year. 1 ton dry matter in root, stem and branches = 1.75 $m^3$. g results from the addition of the figures in column a to f.

| Age in years | a Loss of roots | b Loss of branches | c Loss of leaves | d Loss of dry matter by respiration in | | | e Increment below ground | f Increment above ground | g Gross-production |
|---|---|---|---|---|---|---|---|---|---|
| | | | | root | stem and branches | leaves | | | |
| 8 | 0.1 | 0.5 | 2.1 | 0.5 | 2.3 | 3.6 | 0.8 | 4.0 | 13.9 |
| 25 | 0.2 | 1.0 | 2.7 | 0.7 | 3.5 | 4.6 | 1.6 | 8.0 | 22.3 |
| 46 | 0.2 | 1.0 | 2.7 | 0.9 | 4.5 | 4.6 | 1.6 | 8.0 | 23.5 |
| 85 | 0.2 | 1.0 | 2.7 | 0.9 | 4.6 | 4.6 | 1.2 | 6.2 | 21.4 |

in roots. Here we shall discuss the calculation of the annual loss of dry matter by respiration in stem, branches, and leaves:

*Respiration in stem and branches* has been investigated by the authors (1954 a). We found that the annual loss of dry matter by respiration in stem and branches amounts to: 3.5 tons or 5.8 per cent of the dry matter in stem and branches of 25-year-old beech, 4.5 tons or 3.5 per cent in the case of 46-year-old beech and 4.6 tons or 2.0 per cent in the case of 85-year-old beech.

*Respiration of leaves.* Müller (1954 a) reported as follows: 1 kg beech leaves (397 g dry weight) loose 683 g dry matter by

[1]) Site index 1 = excellent; site index 2 = good.

respiration in the period from leafing to leaf-fall, that is from May 11, to October 21. Hence, the loss of dry matter by respiration from 2.7 (resp. 2.1) tons of leaves (dry weight) amounts to 4.6 (resp. 3.6) tons of dry matter per ha in the period from May 11, to October 21.

*Explanation to Graphic presentation of dry matter production of beech, fig. 1:* The upper heavy curve indicates the gross production. This reaches a climax at the age of 40—60 years. When it is at its maximum it is 23.5 tons dry matter per ha per year. The area between the upper heavy curve and the middle heavy curve is the loss of dry matter by respiration in leaves and by the shedding of leaves. It may be said that the middle heavy curve shows the net production of the leaves, i. e. the dry matter which is given off to the tree by the leaves. This annual net production of the leaves in tons of dry matter per ha is: 8.2 t for 8-year-old, 15.0 t for 25-year-old, 16.2 t for 46-year-old and 14.1 t

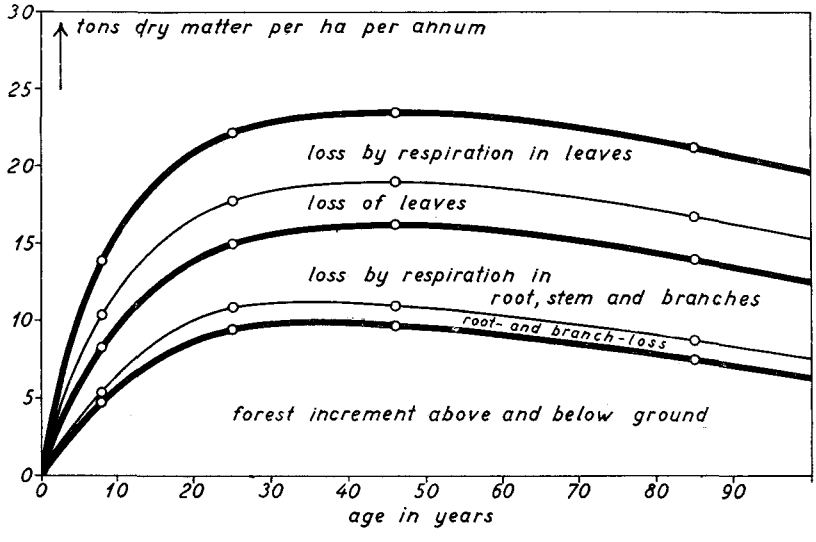


*Fig. 1.* Graphic presentation of dry matter production of European beech *Fagus silvatica L.* The figures represent Danish beech woods, site index 2, cf. table 3. *Ordinates:* Tons dry matter per hectare per annum. *Abscissae:* Age in years. — The upper heavy curve shows gross production. The middle heavy curve shows the net production of leaves. The area between the upper and the middle heavy curves shows the loss of dry matter by respiration in leaves and by shedding of leaves. The heavy curve at the bottom of the graph shows forest increment (current annual increment) above and below ground.

TABLE 4.

The individual quantities in the equation of dry matter production of Danish beech, site index 2.0. All figures in per cent of gross production.

| Age in years | a Loss of roots | b Loss of branches | c Loss of leaves | d Loss of dry matter by respiration in | | | e Increment below ground | f Increment above ground |
|---|---|---|---|---|---|---|---|---|
| | | | | root | stem and branches | leaves | | |
| 8 | 0.4 | 3.6 | 15.1 | 3.6 | 16.5 | 25.9 | 5.8 | 28.8 |
| 25 | 0.9 | 4.5 | 12.1 | 3.1 | 15.7 | 20.6 | 7.2 | 35.9 |
| 46 | 0.8 | 4.3 | 11.5 | 3.8 | 19.2 | 19.6 | 6.8 | 34.0 |
| 85 | 0.9 | 4.6 | 12.6 | 4.2 | 21.5 | 21.5 | 5.6 | 29.0 |

for 85-year-old beeches, site index 2. The leaves, therefore, synthesize between 8.2 and 16.2 tons of dry matter annually per ha for the production of buds, branches, stems and roots. Of this amount, about 40 per cent is lost by respiration in roots, stem and branches and by loss of roots and branches.

The heavy curve at the bottom of the graph shows the annual forest increment above and below ground. We have estimated the annual increment in dry matter of roots at 20 per cent of the increment of aboveground volume. The increment in $m^3$ is quoted from M ö l l e r (1933) and the conversion to dry matter was done by making 1 $m^3$ root, stem or branches volume equal to 0.57 tons of dry matter.

The following percentages of gross organic matter production in beech remain as forest increment above end below the ground after respiration and physical losses:

| Age | Per cent forest increment |
|---|---|
| 8 years | 34 |
| 25 — | 43 |
| 46 — | 41 |
| 85 — | 35 |

## DISCUSSION

More than 50 per cent of the photosynthates used for stem growth are built up in leaves on dwarf shoots (M ü l l e r 1954b). The large gross production of a beech forest is due partly to the big leaf area and partly to the 5-months long period of activity.

On the other hand photosynthesis per leaf area per hour is not great in beech leaves. Boysen Jensen (1929 and 1932 p. 44) found in the most pronounced sunleaves of beech a maximum real photosynthesis of 3.5—4 mg $CO_2$ per 50 $cm^2$ leaf area (one surface only) per hour at 20° and a $CO_2$-pressure of 0.228 mm. The corresponding value for the most pronounced shadowleaves is 1.2 mg $CO_2$. The values, especially the value for the sunleaves, are perhaps somewhat too small. Polster (1950) found that the real photosynthesis was 4.9 mg $CO_2$ (highest daily value) resp. 3.6 mg $CO_2$ (mittlere Tagesleistung) per 50 $cm^2$ leaf area (one surface only) per hour in 8-year-old isolated beech trees.

The most significant feature of the graphic presentation of dry matter production is: *the decrease of dry matter production in stands of older beech is partly due to a decrease in gross production and partly to a slight increase of loss of dry matter.* The loss of dry matter increases only a little from the time the stand is 25 years old until it is 85 years old. It increase from 12.7 tons dry matter per ha and year in 25-year-old beeches, to 13.9 tons in 46-year-old beech and to 14.0 tons in 85-year-old beech. But the gross production of the 85-year-old stand is smaller. The two factors, increasing loss of dry matter, and decreasing gross production, combine to cause decreasing annual increments. The decrease of gross production is solely caused by a diminished photosynthesis. The reason why photosynthesis is diminished in older stands is, we dare assume, a more and more unfavorable water balance. A favorable water balance is one of the conditions for a maximum photosynthesis. There is less reason for assuming that deficiency in nitrogen or ash constituents is the cause of decreased gross production in older stands. The fact that the leaves of a tree inherit a number of mineral constituents from the leaves of the preceding year, diminishes the requirement of the older trees for inorganic nutrients from the ground.

The diagram of dry matter production, which Möller (1946) has given, is reproduced in several papers and books, e. g. by Baker, Polster and Walter. We hope that the graph in its present form will replace the older diagram.

## SUMMARY

The dry matter production of European beech *(Fagus silvatica L.)* in Denmark was investigated through new analyses of loss of dry matter by loss of branches and by respiration in stem, branches, and leaves. Based upon these analyses we have drawn a *graphic presentation of the dry matter production of beech,* Danish site index 2. The gross production, with 23.5 tons of dry matter per ha per year, reaches its climax at the age of 40—60 years.

The net production in the leaves is the gross production minus (loss of leaves, plus loss of dry matter by respiration in leaves). The net production in the leaves, with 16.2 tons of dry matter per ha per year, reaches its climax at the age of 40—60 years.

From the gross production approximately 60 per cent is lost by respiration in root, stem, branches and leaves and by loss of roots, branches, and leaves. The rest of the gross production, roughly 40 per cent constitutes the forest increment of root, stem and branches.

The decrease of dry matter production in older stands is partly due to a decrease in gross production, and partly to a slight increase of loss of dry matter.


## REFERENCES


*Baker, F. 1950.* Principles of silviculture. 414 p. New York.

*Boysen Jensen, P. 1910.* Studier over Skovträernes Forhold til Lyset. Tidsskr. f. Skovväsen, København, *22,* 1—116.

*Boysen Jensen, P. 1929.* Studier over Skovträernes Forhold til Lyset. Dansk Skovforen. Tidsskr. *14,* 5—31.

*Boysen Jensen, P. 1932.* Die Stoffproduktion der Pflanzen. 108 p. Jena.

*Eidmann, F. 1943.* Untersuchungen über d. Wurzelatmung und Transpiration unserer Hauptholzarten. Schriftenrh. Akad. Deutsch. Forstw. *5,* 1—144.

*Gäumann, E. 1935.* Der Stoffhaushalt der Buche (Fagus silvatica L) im Laufe eines Jahres. Ber. Schweiz. Bot. Ges. *44,* 157—334.

*McFadyen, A. 1950.* Biologische Produktivität. Arch. Hydrobiol. *43,* 166—170.

*Müller, D. 1954 a.* Die Atmung der Buchenblätter. Det forstlige Forsögsväsen i Danmark *21,* 303—318.

*Müller, D. 1954 b.* Die Blätter und Kurztriebe der Buche. Det forstlige Forsögsväsen i Danmark *21,* 319—326.

*Möller, Carl Mar:. 1933.* Boniteringstabeller og bonitetsvise Tilväkstoversigter for Bög, Eg og Rödgran i Danmark. Dansk Skovforen. Tidsskr., København, *18,* 457—513, 537—623.

*Möller, Carl Mar:. 1946.* Untersuchungen über Laubmenge, Stoffverlust und Stoffproduktion des Waldes. Preprint 1945. Det forstlige Forsögsväsen i Danmark *17,* 1—287.

*Möller, Carl Mar: & Jörgen Nielsen. 1953.* Testing of Danish yield tables of 1933 for beech, oak and Norway spruce. Dansk Skovforen. Tidsskr. *38,* 1—176.

*Möller, Carl Mar:, D. Müller & Jörgen Nielsen. 1954 a.* Respiration in stem and branches of beech. Det forstlige Forsögsväsen i Danmark *21*, 273—301.

*Möller, Carl Mar:, D. Müller & Jörgen Nielsen. 1954 b.* Loss of branches in European beech. Det forstlige Forsögsväsen i Danmark *21*, 253—271.

*Polster, H. 1950.* Die physiologischen Grundlagen der Stofferzeugung im Walde. Untersuchungen über Assimilation, Respiration und Transpiration unserer Hauptholzarten. 96 p. München.

*Sabroe, A. 1947.* Forestry in Denmark. A guide to our guests. 2. ed., 114 p. Copenhagen.

*Walter, H. 1951.* Ökologische Pflanzengeographie. Fortschr. d. Botanik *13*, 154—172.

*Wetzel, K. 1941.* Die physiologischen Grundlagen der pflanzlichen Stoffproduktion. Hdb. d. Pflanzenzücht. *1*, 297—359.