[illegible]
174-78.
([illegible])

Reports no. 174—178

THE DRY MATTER PRODUCTION OF EUROPEAN BEECH

(Reprint from Det forstlige Forsøgsvæsen i Danmark, XXI, 1954)

LOSS OF BRANCHES IN EUROPEAN BEECH

BY

CARL MAR: MÖLLER, D. MÜLLER
AND JÖRGEN NIELSEN

LOSS OF BRANCHES IN EUROPEAN BEECH

BY

CARL MAR: MÖLLER, D. MÜLLER AND JÖRGEN NIELSEN

Division of Forestry, Royal Veterinary and Agricultural College, Copenhagen, and Laboratory of Plant Physiology, University, Copenhagen.

Received for publication Oct. 29, 1953.

Introduction. The equation for production of dry matter by forest trees can be formulated as follows: *Annual net increment = gross production less loss of roots, branches, leaves, bark and fruits less loss by respiration in root, stem, branches and leaves.*

This production equation of dry matter was first established by Boysen Jensen (1910, p. 57). In several publications, some in collaboration with Müller, Boysen Jensen has attempted to establish the individual quantities of the equation as it applies to young European beech *(Fagus silvatica L)* and young European ash *(Fraxinus excelsior L.)*. Later, Möller & Müller (1938) and Möller 1946) have tried to determine especially for older beech the quantities in the equation of dry matter production.

In regard to *loss of branches* the following investigations have so far been published: Boysen Jensen & Müller (1927, p. 231) have estimated the loss of branches in young beech and ash on the assumption that every year, branches from the growth of a year die, mainly due to lack of light. Hence, the loss of branches during a year for the individual test-tree is estimated to be equal to the dry matter of the branches of the lowest branch-bearing year's shoot. The authors, however, are of opinion that the values determined in this way are too high, because the number of twigs for each year undoubtedly increases somewhat in the course of years, so that on an average not all the branches of a whole year's growth are pruned off. On the other hand, the natural pruning of twigs and side branches which takes place in the top above the lower branches (lowest branch-bearing year's shoot) has not, as emphasized by Möller (1946, p. 37), been taken into account.

Möller (1946, p. 179) has tried to determine the loss of branches on the principle that between the ground and the canopy of trees in a forest there is an empty space which must once have been full of branches. Similarly, there are in each individual tree crown empty spaces which have formerly been full of side-branches and twigs. It must, therefore, according to the author, be possible to find an approximate expression for the total loss of branches up to this time, on condition that: 1) It becomes possible to determine the "pruning space" for each standing tree, and for each individual tree cut in the course of time through thinnings. This space in the individual tree narrows downwards and is upwards limited by the growing top and it encloses the varying volumes of the top during the growth of the tree, 2) An expression can be found for the former contents of now naturally pruned branches and twigs in this space.

The »content of pruned branches« in per cent should be equal to the percentage of living branches in the canopy. Besides this must be added a value of the same numerical magnitude, as a certain pruning of branches and twigs has taken place in the living crown. Figures for the mass of living branches in the canopy are available. From the forest increment tables containing the wood volume factors and especially the factors of trees taken by thinning, Möller was able to calculate the quantity of the loss of branches. In this way he came to the following general expression for the self-pruning of branches:

$$A = 0.5 \cdot M \cdot (1 \text{ minus } k)$$

where A is the pruning of branches per ha expressed in m^3, k is the average crown ratio and M is the net increment in stem and branches expressed in m^3 per ha. If M is given as the increment of the stand from the beginning, A will give the total pruning of branches from the beginning. If M is given as the annual net increment of the stand for a shorter period, the formula will give the average annual pruning of branches during the period.

As will be seen, the two above mentioned methods used by Boysen Jensen & Müller (1927) and by Möller (1946) are more or less based on approximations and involve a possibility for essential miscalculations. Therefore, though the loss of branches is only 5—10 per cent of the gross production, it is considered worth while to establish some empirical figures for the loss of branches in beech. On this basis it is also possible to estimate the sources of error in the above mentioned methods.

The sample plot. With the approval of Boysen Jensen a stand of European beech was selected. This stand which is compartment 84 in »Lille Bögeskov« is located 8 kilometer northeast of Sorö in the center of Zealand, Denmark (55° 29'N, 11° 38'E). The stand is composed of 90 per cent beech and 10 per cent European ash *(Fraxinus excelsior L)* and is the same forest stand in which Boysen Jensen and Müller established sample plots for their analyses of production of dry matter (Boysen Jensen & Müller 1927, Boysen Jensen 1930). The beech trees were about 45 years old in 1946, when the experiment was established.

A square sample plot 20 × 20 m, i.e. 400 m^2, was marked and enclosed. The stand was measured on the 5th of August 1948. The figures, converted into one hectare, are given in *table 1.* The site-index was 1.2. The current annual increment was 16.4 m^3 per ha or 235 cu ft/acre.

TABLE 1.

Wood volume factors of the sample plot in Lille Bögeskov at Sorö. Beech, Fagus silvatica, 47 years old. Danish siteclass 1.2. Area 400 m^2 (20×20 m). Measured Aug. 5, 1948 with Schulzes wooden caliper and american forest hypsometer. Form factors according to Möller (1933). Total volume increment 16.4 m^3 per ha per year (235 cu feet/acre).

All figures per ha.

	Number of stems	Diameter in cm on bark at 1.3 m height	Basal area m^2	Height in m	Form factor o. b.	Total volume m^3
Beech, upper level	725	19.3	21.1	19.0	0.60	241
» subsidiary level	2500	4.0	3.2	6.5	0.84	17
European ash ...	75	17.4	1.8	18.5	0.61	20
Total	3300	—	26.1	—	—	278

Forest floor and ground flora of the sample plot have been described by Boysen Jensen & Müller (1927) as follows: 10 cm mull (mild humus) with gradual change to a rootfilled, darkbrown brown earth (Braunerde), soil originating from moraine clay. The thickness of the brown layer was about 50 cm. The subsoil was moraine clay rich in lime. pH which was 5.2 at 5—10 cm depths was measured with glass electrode in Dec. 1949. The prevailing herbs were in 1947—1950 just as in 1927 *Anemone nemorosa* and *Lamium galeobdolon. Asperula odorata, Melica uniflora* and *Oxalis acetosella* appeared in spots. Besides these *Mercurialis perennis, Vicia sepium, Pulmonaria obscura, Carex silvatica* and *Ranunculus auricomus* were recorded in 1924.

Method. The method for direct determination of loss of branches is outlined by Möller (1946 p. 197). He writes: »An area of 0.01—0.1 ha according to the age of the stand, is swept clean and the surface tramped firm. All the branches and twigs fallen down in this area are to be picked up and measured«. The sample plot of 400 m^2 was fenced after the thinning in the spring 1946 and all the leaves and branches were removed. The tramping of the surface was superfluous since the surface was rather firm. Moreover, a tramping of the surface might have hurt or had a restrictive influence on the roots. Then, with intervals of two months, all branches and twigs were picked up and brought to the Laboratory of Plant Physiology in Copenhagen. There the volume of all the branches was measured. For this purpose we used a cylindrical xylometer, height 110 cm, inner diameter 25 cm, with an overflow pipe, so that the displaced water could run into a graduated cylinder. Then all the branches were dried at 100°C until they reached constant weight. From these two measurements was calculated the loss of branches in m^3 per ha and in tons dry matter per ha. The figures are given in *table 2.*

Sources of error. The method which was used will probably give too low result for the following reasons: 1) When the branches are collected most of them are dry, and their volume is therefore smaller than when they still were on the trees, 2) Some of the branches have lost part of the bark, which causes loss of volume and weight, 3) Bits of branches may remain on the tree and crumble away gradually since the branches may not be pruned off in their entirety, 4) In most of the branches bacteria and fungi have caused an initial decomposition, which brings about a loss of weight and partly of volume. This is true especially as far as the bark is concerned. The natural pruning of branches in beech depends simply on a certain decomposition of the wood. Whereas the specific gravity of fresh branches after drying is 0.57, some of the branches (volume about 200 ml) picked up had a specific gravity after drying of only 0.22. The best preserved branches had a specific gravity after drying of 0.60. It can be seen that the deterioration involves a reduction in dry weight. These branches, therefore, have an inferior value as fuel. A parallel investigation by H o l m (1938) brings out that firewood which has remained for an abnormally long time in the forest decreases both in weight and in value as firewood, 5) When the volume of branches is measured in water, some water will penetrate into the branches. This water will not be included while measuring the volume of displaced water, 6) Some of the pruned stumps of branches and dwarf shoots may be left on the ground when the branches are collected. The average age of dwarf shoots on beech trees was found to be 8 years. The total dry weight of the live dwarf shoots of beech is approximately 0.4 ton per ha. The annual loss of dry matter of dwarf shoots, therefore, ought to be of the 0.05 tons order of size[1]).

One factor which may cause higher values of the results is the activity of earthworms which may have the effect that some mineral particles may adhere to branches and twigs and thus cause an increase of the dry weight of these.

Ad 1. This source of error (the loss of volume caused by the drying of the branches) is eliminated in the following way: From a beech of the same size as the dominant trees of the sample plot, but outside this, the following branches were cut:

Average diameter cm	Weight kg	Volume litre
0—1	0.90	0.870
1—3	1.70	1.870
3—5	0.33	
Total:	2.93 kg =	2.74 litre.

[1]) 50 to 90 per cent of the leaves of beech are placed on dwarf shoots. On the trees from the sample plot it was found that on an average 80 per cent, or about 2 tons of leaves (dry matter) are placed on the dwarf shoots. Through some determinations it was found that 4.8 g of dwarf shoots (dry matter) carry 22.9 g of leaves (dry matter). Consequently the total dry weight of dwarf shoots is about 0.42 tons per ha. The annual loss of dwarf shoots should therefore be approximately 0.42 t : 8 = 0.05 tons.

The sample of branches was kept for six months under similar conditions as the branches which are on about to fall from the tree through natural pruning. After this time interval the dry weight was found to be 1.59 kg and the volume 2.38 litre.

In order to convert the cubic meter volume for pruned branches to cubic meter volume for fresh branches, the former has been multiplied with $\frac{2.74}{2.38} = 1.15$. These converted values are shown in table 2: *m^3 corrected.*

Ad 2 and 3. At the time it was not possible to establish any correction factors for these errors. It is however estimated that these errors are relatively small.

Ad 4. All the samples of naturally pruned branches had during the whole period of 6 years (cf table 2) a dry weight of 460 kg per m^3 (corrected) fresh volume. According to Boysen Jensen & Müller (1927 p. 259) the content of dry matter in stems and branches of young beeches is 570 kg per m^3. The difference is most likely caused by microbial action in the pruned branches. It seems feasible to eliminate this error by multiplying all the dry matter values found by $\frac{570}{460} = 1.24$. The corrected figures are shown in table 2 under the heading: *dry matter corrected.*

Ad 5. According to earlier experience in measuring the solid contents of branches and other woody objects the error mentioned may be considered negligible, if the xylometer measurements are carried out quickly. An estimate of the quantity of water absorbed can be obtained by checking water level immediately after the branches have been submerged and then observe the quantity of water and rate of absorption as it takes place. According to tests made the error does not exceed 2 per cent.

Ad 6. The fact that not all the smallest branches were collected may create an error of some importance. Some time after the ordinary gathering of branches was finished, a very thorough gathering was made of the smallest branches on five plots of 1 m^2 each. In this way some very small branches and stumps of branches were gathered with the following result:

Plot A	(1 m^2)	=	10 ml
— B	—	=	21 -
— C	—	=	19 -
— D	—	=	9 -
— E	—	=	8 -
		Average	13.4 ml = 0.134 m^3 per ha.

The dry matter collected from these 5 m^2 was 24.46 g = 0.049 t per ha. (At the ordinary gathering of branches just before there was 0.303 m^3 = 0.161 t of dry matter per ha.) If this material was present at the time of the first gathering, it would naturally constitute an error. If the small twigs and stumps of branches are actually pruned off in the course of a period of only two months, the amount of branches not being collected, will constitute $6 \times 0.134 = 0.8$ m^3 or 0.3 t of dry matter per ha per year.

In order to get a more exact expression of the amount of the smallest twigs, which may not have been collected in the original gathering, a new procedure was followed. Just after the branches were collected on Oct. 15th and Dec. 15th 1949 a thorough gathering of the smallest twigs was initiated on the above mentioned five plots of 1 m^2 each, with the following result:

		Oct. 15th 1949	*Dec. 15th 1949*
Plot A	(1 m^2)	5 ml	5 ml
— B	—	6 -	6 -
— C	—	5.5 -	7 -
— D	—	5 -	10 -
— E	—	4 -	2 -
	Mean	5.1 ml	5.9 ml.

The October 15th collection equals 0.051 m^3 or 0.025 t of dry matter per ha, which is 15 per cent of the main gathering, while the December 15th equals 0.059 m^3 or 0.031 t of dry matter per ha, which is 8 per cent of the main gathering.

It is interesting to note that the finest twigs contain only 370 g of dry matter per litre which is less than the bigger branches. The reason for this may be that the smaller twigs have a higher bark content and also that the smallest twigs are especially exposed to disintegration through microbial action.

The dry matter was determined after the measurements of the volume. The error arising from adherent earth-particles must therefore be negligible since most of these probably would be washed off while the wood had been placed in the water.

The total effect of the errors will be as follows: The error caused by loss of volume of the branches is considered eliminated through the correction described above. The effect of loss of bark and stumps of branches left on the trees can hardly amount to more than 5 per cent. The effect on dry matter content through deterioration by bacteria and fungi must be considered eliminated through the correction factor described above. The error due to absorption of water during the measuring of volume is at most 2 per cent. The amount of the smallest branches having escaped the gathering is supposed to be about 10 per cent of the main gathering.

The loss of branches found by the investigation from 1947 to 1952. On the above mentioned sample plot and using the procedure described previously the loss of branches in beech was determined during the 6 years from 1947 to 1952. The results are given in table 2. The figures under the heading "m^3 correct-

TABLE 2.

Loss of branches in European beech, 45—51 years old, in Lille Bögeskov in the centre of Zealand, Denmark. All figures per ha. Thinned in July 1946, December 1949 and January 1953.

		t dry matter	t dry matter corrected	m^3	m^3 corrected	
1947	15/12 1946—15/2 1947	0.022	0.027	0.040	0.046	
	15/2 1947—15/4 1947	0.161	0.200	0.303	0.349	
	15/4 1947—15/6 1947	0.038	0.047	0.077	0.089	
	15/6 1947—15/8 1947	0.014	0.017	0.023	0.026	
	15/8 1947—15/10 1947	0.067	0.083	0.118	0.136	
	15/10 1947—15/12 1947	0.069	0.086	0.146	0.168	
	1947	0.371	0.460	0.707	0.814	
1948	15/12 1947—15/2 1948	0.133	0.165	0.256	0.295	
	15/2 1948—15/4 1948	0.086	0.107	0.146	0.168	
	15/4 1948—15/6 1948	0.067	0.083	0.112	0.129	Two
	15/6 1948—15/8 1948	0.124	0.154	0.243	0.280	heavy
	15/8 1948—15/10 1948	0.346	0.429	0.645	0.743	storms
	15/10 1948—15/12 1948	0.292	0.362	0.643	0.740	in Sept.
	1948	1.048	1.300	2.045	2.355	

TABLE 2.
(Continued).

		t dry matter	t dry matter corrected	m³	m³ corrected	
1949	15/12 1948—15/2 1949	0.135	0.167	0.248	0.286	
	15/2 1949—15/4 1949	0.086	0.107	0.155	0.178	
	15/4 1949—15/6 1949	0.085	0.106	0.151	0.174	One
	15/6 1949—15/8 1949	0.148	0.184	0.261	0.300	heavy
	15/8 1949—15/10 1949	0.176	0.218	0.330	0.380	storm the
	15/10 1949—15/12 1949	0.395	0.490	0.725	0.835	3. of Oct.
	1949	1.025	1.272	1.870	2.153	
1950	15/12 1949—20/2 1950	0.042	0.052	0.080	0.092	
	20/2 1950—17/4 1950	0.052	0.064	0.100	0.115	
	17/4 1950—15/6 1950	0.054	0.067	0.099	0.114	
	15/6 1950—15/8 1950	0.063	0.078	0.113	0.130	
	15/8 1950—14/10 1950	0.161	0.200	0.296	0.340	
	14/10 1950—18/12 1950	0.070	0.087	0.125	0.144	
	1950	0.442	0.548	0.813	0.935	
1951	18/12 1950—19/2 1951	0.024	0.030	0.051	0.059	
	19/2 1951—15/4 1951	0.010	0.012	0.020	0.023	
	15/4 1951—16/6 1951	0.077	0.095	0.147	0.169	
	16/6 1951—15/8 1951	0.107	0.133	0.222	0.255	
	15/8 1951—16/10 1951	0.036	0.045	0.075	0.086	
	16/10 1951—17/12 1951	0.242	0.300	0.498	0.573	
	1951	0.496	0.615	1.013	1.165	
1952	17/12 1951—25/2 1952	0.029	0.036	0.055	0.063	
	25/2 1952—15/4 1952	0.018	0.022	0.029	0.033	
	15/4 1952—14/6 1952	0.075	0.093	0.148	0.170	
	14/6 1952—15/8 1952	0.040	0.050	0.081	0.093	
	15/8 1952—15/10 1952	0.099	0.123	0.201	0.231	
	15/10 1952—15/12 1952	0.038	0.047	0.082	0.094	
	1952	0.299	0.371	0.596	0.684	

ed" are the result of a multiplication by the constant factor 1.15 of the values from the collected material (see above). The figures in the column "dry matter corrected" have resulted from multiplication by 1.24 of the dry matter values from the collected branches (see above).

From the figures in table 2, the mean quantities have been calculated for loss of branches during the winter- and summer half-years. These figures are given in table 3.

TABLE 3.

Loss of branches at beeches in the different seasons.
Corrected figures.

	Winter half-year $^{15}/_{10}$—$^{15}/_{4}$		Summer half-year $^{15}/_{4}$—$^{15}/_{10}$	
	t dry matter per ha	m^3 per ha	t dry matter per ha	m^3 per ha
1947	0.31	0.56	0.15	0.25
1948	0.63	1.20	0.67	1.15
1949	0.76	1.30	0.51	0.85
1950	0.20	0.35	0.35	0.58
1951	0.34	0.66	0.27	0.51
1952	0.11	0.19	0.27	0.49
Average	0.39	0.71	0.37	0.64

From these two tables the following can be seen: Under the given conditions the annual loss of branches in European beech, 45—51 years old (Danish site-index 1.2) was on an average 1.35 m^3 or 0.76 tons of dry matter per ha (19.3 cu ft/acre). During the thinning, however, some branches, which would not have pruned off until the following years, were torn off[1]). Together with the trees felled some dead, but not yet pruned branches, were removed. These dead branches must be included in the amount of branches lost, since they do not belong to what is commonly considered increment. As the investigation was not started until after the thinning in July 1946, we have no figures for the branches lost during this tinning. However, during the thinning made in Dec. 1949 the following determinations were made: 1) The dead branches broken off due to the thinning, 2) The dead branches still sitting on the trees cut during the thinning.

The following figures, calculated per ha, were found:

	tons of dry matter	tons of dry matter corrected	m^3	m^3 corrected
Ad 1	0.450	0.558	0.805	0.926
Ad 2	0.123	0.153	0.198	0.228
Total		0.711		1.154

[1]) The increasing shading towards the end of the period between thinnings should not influence the loss of branches, when thinnings are made every 3 years.

Since the thinnings made during 1946 and 1949 were of about the same intensity, only the 1949 data are used. If 1.15 m^3 is added to the figure for volume of pruned branches collected during the first year a figure is obtained which is a little smaller than the figures obtained for the collections from the following years. Correspondingly it is estimated, that to the figures for loss of branches in 1950 there should be added 1.15 m^3 or 0.71 tons of dry matter, so that the total loss of branches in 1950 was 2.09 m^3 or 1.26 tons of dry matter per ha.

For the first thinning period of 3 years there is consequently — including the corrections for thinning — an average annual loss of branches of 2.16 m^3 or 1.21 tons per ha. For the second thinning period of 3 years there is — including correction for thinning — an average annual loss of 1.31 m^3 or 0.75 tons per ha. The lower values for the second period of thinning are mainly due to the low figures for the year 1952.

For the whole period from 1947 to 1951 for 45—51 years old European beech the annual loss of branches is found to be 1.74 m^3 per ha (24.9 cu ft/acre) or 0.98 tons of dry matter per ha.

As mentioned above, the values found are too small, even after the corrections. The error in the measurement of the volume amounts to about 2 per cent, the effect of loss of bark and uncollected stumps of branches to about 5 per cent, and finally the smallest twigs, which escaped collection to about 10 per cent. The result of all this is that an allowance of 15—20 per cent must be made to the total result. Therefore, it is estimated that the real loss of branches — including the dead and torn-off branches from the thinning — is as follows: 2.1 m^3 or 1.2 tons dry matter per ha per year (found as an average for a period of 6 years). These figures are considered to be valid for a Danish beech forest 45—50 years old with a Danish site-index of 1.2[1]). This corresponds to an annual loss of branches of 0.8 per cent of the total volume of stem + branches or 12.6 per cent of the annual increment in stem and branches.

Older determinations of loss of branches. Møller (1946 p. 179—201) has earlier investigated the figures for loss of branches for forest stands in Denmark. These figures for European

[1]) Annual increment in stem + branches for a stand of European beech 47 years old and Danish site-index 1.2 is 9.4 tons of dry matter per ha or 16.4 m^3 per ha (235 cu ft/acre).

TABLE 4.

Annual loss of branches at beech-stands, per ha.

	Site-index	m^3	tons dry matter	in p.ct of increment in stem and branches	in p.ct of total overground volume minus leaves
Boysen Jensen & Müller 1927.					
Beech, not thinned, 24 years old	1.8	4.2	2.4	29	3.8
» heavily thinned, 24 years old	1.8	2.5	1.4	16	2.9
Oppermann 1915[1])					
Beech, heavily thinned .	1.5	3.3	—	28	—
Helms[1])					
Beech	2.7	2.2	—	27	—
Möller's formula 1946					
Beech, 48 years old ...	1.2	3.7	2.0	23	—
These investigations					
Beech 45-51 years old	1.2	2.1	1.2	12.8	0.8

[1]) According to calculations by Carl Mar: Möller (1946 p. 192), as an average of rotations of resp. 125 years and 100 years.

beech are shown in table 4, in addition to the figures obtained from the present investigation. The latter values are from direct determinations, while Möller's figures are all calculations based on various theories. It is interesting to note that the calculated values are higher than those found through actual measurements.

On two average trees in the immediate vicinity of the sample plot a crown ratio of $k = 0.55$ was measured. Using this ratio in the Möller's formula[2]) (1946, p. 190) the loss of branches is found as follows:

$$A = 0.5 \cdot 16.4 \cdot (1-0.55) \text{ or}$$
$$A = 3.7 \text{ m}^3 \text{ per ha per year.}$$

The average increment of stem + branches per ha of a stand of European beech 47 years old, Danish site-index 1.2, is 16.4 m^3. The figure 3.7 m^3 is much higher than the directly measured loss of branches, which was found to be 2.1 m^3.

[2]) $A = 0.5 \cdot M \cdot (1-k)$.

The reason for the lower values found in the present investigations may partly be due to the fact already mentioned by Möller (1946 p. 199), that the "pruning space", as defined above, is not limited downward by a conical surface but by a neiloid surface, because the relative width of the crown increases with age in accordance with the fact that the ratio: height over diameter in 1.3 m height decreases with age. This means that the pruning space is decreased, a decrease which amounts to 33 per cent, which gives an equivalent decrease in the calculated loss of branches.

It is true, that Möller was of opinion, that this error, although considerable for the individual tree, is of much less importance for the stand, because a reduced relative growth-room for the middle tree will at the same time mean a proportionally bigger number of stems. Although this is naturally correct, it can not alter the fact, that by the determination of the loss of branches in the stand the basis has been the determination of loss in the single tree or more correctly the middle tree, which determination is based on a probably erroneous assumption.

Part of the explanation of the difference between the empirically found loss of branches and that determined by means of Möller's formula may also be seen from the following observation: It seems probable that loss of branches in relation to the increment of stem and branches — which may be called the relative loss of branches — will increase with age due to the fact that a given part of the crown in the older trees is carried by a much greater structure or a much greater system of the crown-supporting tissue than in a young tree. In the early age only small branches are pruned off while in the older age also thick branches will fall off.

On the other hand the speed at which the crown is lifted upward is very much reduced with age.

The problem is complicated, but in any case it does not seem unlikely, that the relative loss of branches will increase with age. If this is the case it is not in accordance with Möller's above mentioned formula for determination of the loss of branches, even if the formula after a correction should be valid for the total loss of branches during the life time of a tree or a stand of trees.

The original intention with M ö l l e r's formula was to determine the loss of branches of an individual tree. Since the total loss of branches of all the individual trees is identical to the loss of branches of the whole stand, the formula should be applicable to a stand of trees, when k (crown ratio) is replaced by an average figure for the crown ratios which the stand has had during its life time.

Furthermore, since the formula specifies that the loss of branches is determined by the increase in volume of stem and branches and by the crown ratio, it should be possible to use the formula for a determination of the loss of branches for a shorter period in the case M means the increase in volume for the same short period. The increase in volume must at any rate influence the loss of branches if regular thinnings are maintained, because the leaf-mass is about constant as found by M ö l l e r (1946). Therefore any regeneration of living crown-parts must result in a parallel loss of crown-parts.

M ö l l e r maintains (1946 p. 194) that because of the variation in frequency of the storms it is impossible to get acceptable results for a short period of one or two years, and emphasized the importance of a steady scale of the intensity of thinning, as any increase or decrease in the intensity of thinning will influence the loss of branches.

As mentioned it is likely that the relative loss of branches increases with age, so that the determination of the annual loss of branches by means of the formula may give too high results for the younger and too low results for the older stands. It would be interesting to have some determination for the loss of branches in stands of beeches 20—30 years old and between 70 and 100 years old. Until such determination are at hand, the constant 0.5 in M ö l l e r's formula should be modified to 0.3. The formula is therefore as follows:

$$\text{Loss of branches } A = 0.3 \cdot M \cdot (1-k)$$

where M is either the total or the annual increment in stem + branches and k is the average crown ratio. The formula is only to be used with great reservation.

The structure of the formula is presumably correct, as it could have been deducted in the same way with neiloid surfaces instead of with conical surfaces as the lower limitation of the

TABLE 5.
Beech, upper level from the border of the sample plot used for the determination of loss of branches.

Beech no.	Age in years	Diameter on bark at 1.3 m height, cm	Height in m	Volume of stem + branches m^3	Volume of branches m^3	p.ct of branches
6	46	15.3	17.3	0.1844	0.0218	11.8
7	46	18.7	18.1	0.2755	0.0438	15.9
5	47	17.0	16.9	0.2022	0.0284	14.0

space in which the branches are pruned. It seems natural that the loss of branches depends partly on the total wood volume produced, partly on the crown ratio.

The percentage of branches. The determination of the loss of branches was carried through mainly with the intention of finding how much dry matter the beech trees lose annually by natural pruning of branches. However, it may also be of interest to see how great a percentage of the total volume of branches is lost by pruning. The volume of branches has been measured on three dominant beech trees, 46—47 years old, standing just outside the sample plot. The result is given in table 5. The percentage of branches has been calculated. This value is the volume of branches in per cent of the volume of stem + branches. The percentage of branches gives a clearer picture of the volume of branches than the branch volume quotient. However, the percentage of branches can be calculated from the branch volume quotient, which is volume of branches divided by volume of stem. The percentages of branches of the beech trees on the border of the sample plot were 11.8 and 15.9 and 14.0 or on an average 14 per cent. The total volume of stem + branches was 278 m^3 per ha; 14 per cent of this value or 38.9 m^3 is the total volume of branches. *The annual loss of branches in this 46 years old beech stand amounted to 5.4 per cent of the total volume of branches.*

In table 6, figures for the percentage of branches in beech are presented. The trees of the ages 25 and 85 years respectively were felled in Allindelille Fredskov and the 46 years old trees were taken from the border of the sample plot in Lille Bögeskov, both localities in the centre of Zealand. The table shows that among trees of the same age those having the greatest diameter also have the greatest percentage of branches. This relationship is well known and is also seen from table 7.

TABLE 6.

Percentage of branches at dominant beech-trees. Percentage of branches = volume of branches in per cent of total volume of stem + branches. A detailed description of the sample plots, where the trees were taken, and of the single trees can be found in Möller, Müller & Nielsen: Respiration in stem and branches of beech. Det forstlige Forsögsväsen i Danmark *21*, 273. *1954*.

Locality	Beech no.	Age in years	Diameter on bark at 1.3 m height, cm	Total volume of the tree (stem + branches) in m^3	per cent of branches	Wood volume in m^3 per ha
Allindelille	13	22	8.3	0.0442	26.1	
Fredskov	11	24	7.3	0.0307	15.3	
compartm. 5	9	28	6.7	0.0251	11.2	
	10	28	7.2	0.0257	16.7	134
	8	28	7.5	0.0310	16.6	
Lille	6	46	15.3	0.1844	11.8	
Bögeskov	7	46	18.7	0.2755	15.9	278
compartm. 84	5	47	17.0	0.2022	14.0	
Allindelille	19	80	32.9	1.273	15.7	
Fredskov	18	80	33.3	1.432	20.4	
compartm. 22	3	85	30.4	1.037	14.4	
	4	85	34.0	1.252	16.8	341
	2	86	32.0	1.188	15.4	
	1	90	32.5	1.148	15.5	
					M = 16.4 %	

Due to the fact that the investigation on the loss of branches in beech was carried out in the same stand that was used in 1923—1930 for the investigation of dry matter production by Boysen Jensen and Müller, it is of interest to study the percentage of branches from 1923 to 1925 when the trees

TABLE 7.

Percentage of branches at beech-trees. Crown class 1 was dominant trees, crown class 2 was codominant-intermediate trees, crown class 3 was suppressed trees. Age of the beeches 22—24 years. Danish site-index 1.8. Calculated from the figures in Boysen Jensen & Müller (1927).

	Per cent of branches at beech from sample plot not thinned	Per cent of branches at beech from sample plot heavily thinned
Crown class 1	18.0	17.3
» » 2	17.5	15.4
» » 3	13.0	10.2

of the sample plot were from 22 to 24 years old. The percentage of branches is calculated from total volume of stem + branches and the branch volume quotient (Boysen Jensen & Müller 1927 p. 259 a. 261) and is here given in table 7. Each figure is the average of about 20 determinations of representative beech trees in the three crown classes: Dominant, codominant-intermediate and suppressed trees.

Mechanism of loss of branches in beech. The small branches and twigs are not pruned by a separation layer as are the small branches and twigs of Quercus a.o. However, near the base of a dead branch there is a "weak spot", where the branch breaks very easily. Gelinsky (1933) has given a clear and thorough account of the mechanism of the natural pruning of branches in beech. What happens is briefly this: Before the branch dies, the formation of annual rings at the base of the branch ceases. Up to 5 annual rings may be missing, when the branch dies. The abscission begins with the formation of a protective layer (Schutzschicht) at the base of the dead branch. After the completion of the protective layer, it takes from 4 to 9 years, before the branch falls off, and as a rule the pruning occurs immediately above the protective layer. In a way it resembles the abscission by a separation layer, however, the conclusive difference is, that the abscission of branches by a separation layer is an active process, a vital function. The abscission of branches in beech is an entirely passive process. The living beech tree does not interfere with the processes going on in the period between the death of the branch and its abscission.

We want to express our appreciation to *Carlsbergfondet* which has paid the expenses of the investigation. To Dr. P. Boysen Jensen, whose work on the production of dry matter of plants has inspired so many investigations, we want to extend our sincere gratitude for the interest with which he has participated in this work. Furthermore, we are highly grateful to the following persons: Mr. Th. Kaspersen, Royal forest supervisor, whose kind co-operation made the investigation possible; Mr. Kr. Jörgensen, forest guard, Lille Bögeskov, who has faithfully undertaken the collection of branches; and mag. agro. H. Lorck and cand. mag. E. Bille Hansen, who have both with great care carried out the determination of volume and dry weight. We are indebted to the *Rask-Örsted Foundation* for the economic grant to the translation.

SUMMARY

Up to now only theoretical calculations have been available for the determination of loss of branches in beech. In the paper by M ö l l e r (1946), the latest calculation together with a survey of the older literature is to be found.

In the present paper the results have been given of direct measurements of the loss of branches in about 50-year-old European beech (*Fagus silvatica*). The sample plot is situated in a forest in the center of Zealand, Denmark, and had Danish site-index 1.2. During 6 years the fallen branches and twigs were collected every 2 months. The volume and dry weight were determined. The sources of error were examined. The errors due to loss of volume by drying and by microbial decomposition are corrected. The corrected values are given in table 2, p. 260. The other errors in the measurements of the loss of branches indicate that the corrected figures should be raised about 20 per cent. In the first and fourth year the loss of branches was influenced by the thinning undertaken prior to the collection. It was found that as an average for the 6 years the annual loss of branches was 1.74 m^3 or 0.98 tons of dry matter per ha. Corrected with 20 per cent the values amounted to 2.1 m^3 or 1.2 tons per ha of dry matter annual. The annual loss of branches, according to the last mentioned figures, was: *0.8 per cent of the total volume above the ground less leaves, or 12.8 per cent of the annual increment in stem + branches, or 4.3 per cent of the annual gross production of dry matter.*

In connection with the determination of the loss of branches the percentage of branches in stands of Danish beech is mentioned in table 5, 6 and 7 on pgs. 267—68. The annual loss of branches was about 5.4 per cent of the total volume of branches on the sample plot. Finally G e l i n s k y's investigation on the mechanism of the abscission of branches of beech trees is reported.

REFERENCES

Boysen Jensen, P.: Studier over Skovträernes Forhold til Lyset. Tidsskrift for Skovväsen, Köbenhavn, *22,* 1—116. *1910.*

Boysen Jensen, P.: Untersuchungen über die Stoffproduktion in jungen Beständen von Esche und Rotbuche II. Det forstlige Forsögsväsen i Danmark *10,* 365—391. *1930.*

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

Boysen Jensen, P. & D. Müller: Untersuchungen über die Stoffproduktion in jungen Beständen von Esche und Rotbuche. Det forstlige Forsögsväsen i Danmark *9,* 221—268. *1927.*

Gelinsky, H.: Die Astreinigung der Rotbuche. Z. Forst- u. Jagdwesen *65,* 289—322. *1933.*

Holm, Folke: Buchenbrennholz. Det forstlige Forsögsväsen i Danmark *15,* 1—16. *1938.*

Mayer-Wegelin, H.: Ästung. 178 p. Hannover *1936.*

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

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

Möller, Carl Mar: & D. Müller: Die Atmung in alten Stammteilen. Det forstlige Forsögsväsen i Danmark *15,* 113—138. *1938.*

Oppermann, A.: Gute dänische Buchenwälder, in drei Ertragstafeln dargestellt. Det forstlige Forsögsväsen i Danmark *4,* 341—380. *1915.*

RESPIRATION IN STEM AND BRANCHES OF BEECH

BY

CARL MAR: MÖLLER, D. MÜLLER
AND JÖRGEN NIELSEN