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SEASONAL AND ANNUAL VARIATION IN LITTER FALL IN A BEECH STAND 1967—75

SÆSON- OG ÅRSVARIATION I LØVFALDET I EN BØGEBEVOKSNING 1967—75

BY

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1. INTRODUCTION

Several authors stress the importance of litter fall as the major pathway for energy and nutrient transfer in woodland ecosystems. In 1967—75 the litter fall in a Danish beech stand was recorded in terms of dry weight and biocontent. This investigation was a part of the Danish contribution to IBP/PT, viz. an integrated analysis of a beech forest ecosystem. The fall of beech seeds in the site was analysed by Nielsen (in press a) and the nutrient content of the litter fall, nutrient cycling, and nutrient turnover by *Andersson* (in prep.).

Litter production of the world forest ecosystems was reviewed by *Bray and Gorham* (1964), who present a great deal of information on the amount of litter produced in different types of forests throughout the world, e.g. temperate deciduous forests. Recently, *Jensen* (1974) discussed the tree leaf litter fall in forest stands.

Investigations on the litter production of the European beech (*Fagus silvatica* L.) have been carried out by several authors; a century ago *Ebermayer* (1876) studied the chemical composition of beech litter and since that time many ecological aspects of beech litter fall have been considered, cf. *Danckelmann* (1887), *Møller* (1929, 1945), *Møller et al.* (1954 a, b), *Bonnevie-Svendsen and Gjems* (1957), *Jaró* (1958), *Zangiyev* (1960), *Chalupa* (1961), *Donov* (1964), *Myczkowski* (1967), *Mason* (1970), *Heller* (1971), *Nihlgård* (1972), *Anderson* (1973 b), and *Phillipson et al.* (1975).

The litter fall reported in the present paper was recorded throughout the year for a period of nine years; thus seasonal as well as annual variation in litter fall is considered (cf. *Ovington* 1963, *Bray and Gorham* 1964, *Carlisle et al.* 1966, *Newbould* 1967). Further, the litter fall data contribute to an estimate of the food resources of phyllophagous insects and to an analysis of the annual variation in primary consumption in the site (*Nielsen* in press b).

2. SITE DESCRIPTION

The investigations were carried out in the mixed coastal forest Hestehaven (176 ha) near Rønde, 25 km NNE of Aarhus, Eastern Jutland, Denmark. The IBP research site is 3 ha of pure beech (*Fagus silvatica* L.) situated about 500 m from the sea and 100 m from agricultural land. The site slopes from the northwest to the southeast, from a maximum altitude of 27.5 m to 10.7 m above sea level.

The soil is a grey-brown podzolic ("Parabraunerde") resting on moraine material deposited during the Würm glaciation. The litter horizon is rather sharply separated from the surface soil. There is no significant accumulation of litter on the soil surface from year to year. The surface soil is a mull and the subsoil is more or less clayey.

The vegetation consists of three main strata: an overstory layer of beech (i.e. trees > 20 m), an understory layer of beech (i.e. trees < 20 m, DBH > 4 cm), and a field layer composed by herbs and natural reproduction of ash (*Fraxinus excelsior* L.), maximum height about 0.5 m. Natural reproduction of beech is scarce (cf. *Nielsen* in press a).

The overstory beech trees are about 90 years old, Danish site class 1.3, density 191 trees ha^{-1}, average height 29.8 m, crown depth 14.3 m, mean crown width 9.4 m, average diameter (DBH) 43.1 cm, basal area 27.9 m^2 ha^{-1}, and volume 498 m^3 ha^{-1}. In the understory, the density of beech trees is 174 trees ha^{-1}, average height 9.1 m, average diameter (DBH) 9.7 cm, basal area 1.3 m^2 ha^{-1}, and volume 9.0 m^3 ha^{-1}; stand closure (overstory and understory) about 125 %. The last cutting was carried out during the winter 1966—67.

Predominant plant species in the herb layer are *Anemone nemorosa* L., *Melica uniflora* Retz., *Asperula odorata* L., *Hordeum europaeum* (L.), *Circaea lutetiana* L., *Carex sylvatica* Huds., *Veronica montana* L., and *Ficaria verna* Huds. (cf. *Hughes* 1975); the flora indicates the presence of a common beech mull.

Climatic measurements were obtained from local meteorological stations, situated about 10 km from the research site. Generally, the annual precipitation is 550—600 mm, and the mean annual temperature is 7.3°C. The length of the growing season (= days > 10°C) is 145—150 days (1969—71) and the mean temperature and precipitation of this period are 14.1°C and 275 mm.

3. METHODS

The litter fall was estimated by means of litter traps made from cheese cloth bags suspended from hoops, attached to two wooden posts; the bags were pegged. In 1967—68 20 litter traps (diameter 48 cm) were used and from 1969 onwards, 48 traps (diameter 58 cm) were arranged in a stratified random pattern in the research site.

In 1967 the litter traps were placed in position just before the main leaf fall in October, and emptied in late October and November. As pointed out by *Ovington* (1963) autumn collections result in gross underestimates of litter production (generally autumn litter fall represents 75—80 % of annual total). The autumn leaf fall in 1967 was further checked by estimating the biomass of current year leaf litter accumulated on the forest floor; 20 litter samples were collected at random (sample unit 1 m^{-2} of forest floor). The values for the preceeding months were interpolated on values from the succeeding years and the total annual leaf fall 1967 was calculated.

In 1968 litter traps were tended in June, twice in October, and in late November, in 1969—71 weekly from April to December, and occasionally during the winter and early spring. In 1972—75 the traps were emptied in late June, and at 2—4 occasions during September—December. The fall of branches, viz. components > 0.58 m was measured yearly 1969—75 in 6 squares (10 × 10 m), tended biannually.

The litter trap material was divided into leaves, buds, budscales, flowers, cupules, seeds, and twigs. Detrital components e.g. wood-fragments and bark were included in the fraction twigs, thus bits of branches remaining on the trees, crumbling away gradually, were also estimated. The fall of moss, lichens, and frass was generally negligible, however, in 1971 the latter fraction was estimated (cf. *Nielsen* in press b).

The litter components were oven-dried to constant weight at 105°C and weighed. Each fraction was bulked on a monthly and/or yearly basis and the total dry weight (g m^{-2}) of each component was calculated. From each litter fraction subsamples drawn at random were used for the measurement of calorific and nutrient content, primary consumption, etc. Plant material used for calorimetry was dried in a vacuum-oven at 60° to constant weight and ground in a mill. The ash-free dry weight was estimated by oxydizing the organic material in a muffle furnace at 550°C. Energy values were measured by means of an adiabatic bomb calorimeter (Gallenkamp Autobomb).

The leaf area was measured annually by preparing leaf photostats, which were cut out and weighed or measured by means of a planimeter; every year 50 subsamples of autumn leaves (sample unit 100 leaves) were treated. The average leaf area referring to one side of the lamina (excluding petioles) was calculated. Finally, the leaf samples were dried at 105°C to constant weight and weighed. Based on the number of leaves m^{-2} and the average leaf area, the leaf area index (LAI) of the site was calculated.

4. RESULTS AND DISCUSSION

4.1. Variation between years.

Table 1 presents the annual input of litter (d.w.) in the research site 1967—75. Deciduous (vegetative and reproductive plant parts) as well as perennial tissue (woody litter) are shed.

4.1.1. Deciduous litter.

The annual amount of leaf material shed ranged from about 243 to 303 g m^{-2}, the maximum : minimum ratio being 1.2. Based on beech stand

Table 1. Annual litter fall in a 90 years old beech stand, Hestehaven, Denmark 1967—75. Dry weight g m^{-2}(±SD) (untransformed data) and biocontent (10^5 J m^{-2}).

Tabel 1. Årlige løvfald i en 90årig bøgebevoksning, Hestehaven, Danmark, 1967—75. Tørvægt g m^{-2}(±SD) (utransformerede data) og energiindhold (10^5 J m^{-2}).

Litter component	1969	1970	1971	1972	1973	1974	1975	Average
Leaves g m^{-2}	289.2 (±32.77)	242.9 (±37.22)	281.8 (±33.32)	291.2 (±35.33)	273.9 (±45.45)	249.8 (±18.06)	289.8 (±26.63)	278.9
Blade 10^5 J m^{-2}	60.1	50.4	58.5	60.5	56.9	51.9	60.2	57.9
Budscales g m^{-2}	31.1 (± 3.67)	24.6 (± 2.10)	35.4 (± 3.10)			26.2 (± 2.91)		29.3
Knopskæl 10^5 J m^{-2}	6.1	4.8	7.0			5.1		5.8
Flowers g m^{-2}	18.9 (± 6.29)	3.3 (± 2.10)	2.8 (± 1.66)			21.0 (± 6.34)		11.5
Blomster 10^5 J m^{-2}	3.8	0.7	0.6			4.2		2.3
Cupules g m^{-2}	86.5 (±34.34)	15.9 (±11.54)	16.3 (±16.03)		19.5 (±14.20)	142.5 (±56.24)	0.3 (± 0.95)	46.8
Skåle 10^5 J m^{-2}	16.6	3.0	3.1		3.7	27.3	0.06	9.0
Seeds g m^{-2}	34.3 (±14.94)	3.6 (± 4.19)	3.5 (± 3.76)	2.1 (± 2.68)	3.8 (± 2.77)	53.5 (±16.08)	0	11.8
Bog 10^5 J m^{-2}	7.8	0.8	0.8	0.5	0.9	12.1	0	2.7
Twigs g m^{-2}	39.7 (±31.98)	20.3 (±24.38)	63.8 (±41.79)	32.9 (±31.42)	31.3 (±34.29)	15.1 (±36.61)	16.0 (±13.90)	31.3
Kviste 10^5 J m^{-2}	8.3	4.2	13.3	6.9	6.5	3.1	3.3	6.5
Branches g m^{-2}			31.9	59.7	52.5	28.5	85.4	51.6
Grene 10^5 J m^{-2}			6.7	12.4	10.9	5.9	17.8	10.8
Total woody g m^{-2}			95.7	92.6	83.8	43.6	101.4	83.4
Ved, ialt 10^5 J m^{-2}			20.0	19.3	17.4	9.0	21.1	17.4
Total non-woody g m^{-2}	460.0	290.3	339.8			493.0		
Løvfald ÷ ved 10^5 J m^{-2}	94.4	59.7	70.0			100.6		
Total non-leaf g m^{-2}			153.7			286.8		
Løvfald ÷ blade 10^5 J m^{-2}			31.5			57.7		
Total all g m^{-2}			435.5			536.6		
Total 10^5 J m^{-2}			90.0			109.6		

Leaves 1967 288.6 g m^{-2}(59.9 × 10^5 J m^{-2}); 1968 302.9 g m^{-2}(±50.09) (62.9 × 10^5 J m^{-2})
Seeds 1967 2.1 g m^{-2}(±1.59) (0.5 × 10^5 J m^{-2}); 1968 3.5 g m^{-2}(±3.91) (0.8 × 10^5 J m^{-2})

data from *Ebermayer* (1876) *Bray and Gorham* (1964) calculated a maximum : minimum ratio of 1.3. The total annual leaf litter production in 1967 was estimated by adding the autumn leaf fall of about 246 g m^{-2} and an average leaf fall May—September 1969—71 of 41 g m^{-2} (cf. p. 18). The average annual beech leaf litter fall 1968—75 was about 279 g m^{-2}.

From the European continent *Ebermayer* (1876) reported an annual leaf fall of 337 g m^{-2} in 60—90 years old beech stands and 327 g m^{-2} in stands aged > 90 years. However, since this leaf material was collected from the forest floor at various times during the year, the results of *Ebermayer* (op. cit.) may be defective. Further, records of 157—286 g $m^{-2}yr^{-1}$ (*Bonnevie-Svendsen and Gjems* 1957), 200—270 g $m^{-2}yr^{-1}$ (*Chalupa* 1961), about 260 g $m^{-2}yr^{-1}$ (*Donov* 1964), and about 290 g $m^{-2}yr^{-1}$ (*Myczkowski* 1967) are presented. In German beech stands (age 60—120 years) the annual leaf fall ranged from about 300 g to 340 g $m^{-2}yr^{-1}$ (Heller 1971) and in a 90 years old beech stand in Southern Sweden a leaf fall of about 348—372 g $m^{-2}yr^{-1}$ was estimated (*Nihlgård* 1972). *Møller* (1945), studying the leaf litter fall in several Danish beech stands in relation to tree age, found an annual leaf fall ranging from 153 to 331 g $m^{-2}yr^{-1}$. Based on 12 records of leaf litter fall in a number of 85—95 years old beech stands studied by *Møller* (op. cit.) the average annual leaf litter production approximates about 250 g $m^{-2}yr^{-1}$. From a beech stand in England *Mason* (1970) recorded an annual leaf litter fall of about 338 g m^{-2}. According to *Mason* (op. cit.) the average leaf litter production of twelve studies in European beech stands was 260 g $m^{-2}yr^{-1}$. The average annual leaf litter production in the Hestehave beech stand is definitely within the range of litter fall data presented from European beech stands, apparently being close to the average of these and of Danish stands (age 85—95 years).

The significance of weight loss from leaf material trapped was considered. A certain proportion of the weight loss from decomposing leaf litter is due to abiotic weathering processes (cf. *Witkamp and Olson* 1963, *Anderson* 1973a). *Kirita and Hozumi* (1969) studied the significance of aerobic leaching of water soluble material in litter fall studies in a tropical rain forest and proposed a correction factor to account for the weight loss. This correction may be of minor significance in cool-temperate beech and oak forests (*Kirita and Hozumi* 1969); however, in studies on the litter fall in a mixed deciduous forest stand in Southern Sweden, *Andersson* (1970) drew the attention to the effect of leaching, when there are long time intervals between the emptying of litter traps.

In 1969—71 the litter traps in Hestehaven were emptied weekly, thus the weight loss due to leaching of accumulated leaves is negligible and no correction is needed. In the summer of 1968 and 1972—74, the leaf litter accumulated during 2—3 months. Based on the correction factor of *Kirita* *and Hozumi* (1969) summer weight loss from leaf litter trapped in Hestehaven July—August amounts to about 5 % of the initial weight, corresponding to an underestimate of leaf fall of < 1 g m^{-2}. A similar weight loss from the non-leaf fraction would be expected, however, no correction factor could be suggested.

In 1967—74 the total annual fall of beech leaves in the research site ranged from 3400—4300 leaves m^{-2} (average about 3900 leaves m^{-2}). The mean leaf area ranged from 14.6 cm^2 to 16.8 cm^2 (Table 2), average 15.5 cm^2. The LAI ranged from 5.0 to 6.9 (Table 2); however, a distinct seasonal

Table 2. Nos of leaves (m^{-2}), average leaf area (cm^2), and leaf area index (LAI) ($m^2 m^{-2}$) in a 90 years old beech stand, Hestehaven 1967—74.

Tabel 2. Antal blade (m^{-2}), gennemsnitlige bladareal (cm^2) og samlede bladareal ($m^2 m^{-2}$) i en 90 årig bøgebevoksning, Hestehaven 1967—74.

Year *År*	Nos of leaves m^{-2} *Bladantal m^{-2}*	Average leaf area *Gennemsnitlige bladareal* $cm^2 \pm$ SE	LAI (m^2m^{-2}) *Samlede bladareal m^2m^{-2}*
1967	3500	16.4 ± 0.78	5.7
1968	4300	15.6 ± 0.80	6.7
1969	4100	15.0 ± 0.78	6.1
1970	3400	14.7 ± 0.54	5.0
1971	4000	16.8 ± 0.73	6.9
1972	4100	14.6 ± 0.49	6.4
1973	3900	—	6.1
1974	3500	15.5 ± 0.77	5.4

variation in the leaf area index of the beech canopy was observed (*Nielsen* in press b). The number of leaves recorded from Hestehaven is within the range observed by *Knuchel* (1914), *Burger* (1950), and *Myczkowski* (1967) in European beech stands, viz. 2300—4300 m^{-2}. The number of leaves m^{-2} recorded in the research site falls in the upper part of the range, viz. 2300—4100 leaves m^{-2}, observed in Danish beech stands, age 80—200 years (*Møller* 1945), or even somewhat higher. The estimates of average area of beech leaves in Hestehaven approximated the lower end of the range of beech leaf areas recorded in other beech stands. In stands age 80—200 years, *Møller* (1945) recorded a mean leaf area of 15.2—19.0 cm^2; in a Swedish beech stand the average leaf area was 20.8 cm^2 (*Nihlgård* 1972). Apparently, the photosynthetic surface of the Hestehave stand is composed of a high number of fairly small leaves.

On a world-wide basis leaf surface area in deciduous broadleafed forests ranges from 4 to 6 $m^2 m^{-2}$ (*Tadaki* 1966), being about 6 in deciduous forests of the cool temperate zone (*Kira and Shidei* 1967). In beech forests in Japan the LAI ranged from 5.5 to 11.3 being 5.6 in 85 years old stands (*Nomoto* 1964). In a number of European beech stands the LAI ranged from about 5.0 to 8.5 (*Burger* 1950, *Jaró* 1959, *Chalupa* 1961, and *Myczkowski* 1967). In a Swedish beech stand the LAI was approximately 2.9, or based on litter values about 3.4 (*Nihlgård* 1972). In Danish beech stands (age 80—200 years) a LAI of 4.0—7.0 was recorded; in 90 years old stands the LAI was 5.0—7.0 (*Møller* 1945). The LAI of the research site is within the range presented by *Møller* (op. cit.).

The annual amount of budscales shed ranged from about 25 to 35 g m^{-2} (Table 1) corresponding to a maximum : minimum ratio of 1.4. The average 1969—71 is about 30 g $m^{-2}yr^{-1}$, which corresponds to the fall of budscales and flowers recorded in mature beech woodland in England (*Mason* 1970). In a coppiced *Fagus*-site in England, *Anderson* (1973b) recorded about 40 g of budscales m^{-2}, whereas *Møller* (1945) and *Myczkowski* (1967) present much lower values, viz. 2—3 g m^{-2}. The fall of budscales is a rough index of the autumn litter fall, and the variation in leaf fall between years 1969—71 is broadly reflected in the fall of budscales (Table 1). This indicates that, to a large extent, annual leaf production is already determined early in the season, at the time of leaf-out, and is not particularly sensitive to environmental conditions during the growth period.

In the litter trap material reproductive plant parts were represented by male flowers, cupules, and seeds. The annual input of flowers ranged from 2.8 to about 21 g m^{-2} (maximum : minimum ratio 7.5), cupules from 0.3 to 143 g m^{-2} (maximum : minimum ratio about 475), and seeds from zero in 1975 to 53.5 g m^{-2} (maximum : minimum ratio ∞) (cf. *Nielsen* in press a). The amounts of flowers and cupules shed in 1970 and 1971 were not significantly different, however, a considerably higher fall was observed in 1969. *Myczkowski* (1967) recorded a fall of beech flowers of 2.9 g $m^{-2}yr^{-1}$. The fall of beech seeds 1967—75 was discussed by *Nielsen* (in press a). Generally, the seed fall represented about 1 % of the leaf fall, however, in the mast years 1969 and 1974 12 and 21 %, respectively. In 1971 and 1974 seed fall made up 0.5 and 10 % of the total litter fall (including branches).

4.1.2. Perennial tissue.

The annual fall of twigs in Hestehaven ranged from 15 to 64 g m^{-2} (Table 1); the maximum : minimum ratio was 4.3. The annual fall of branches > 58 cm length 1971—75 ranged from 29 to 85 g m^{-2}; the maximum : minimum ratio was 2.9; no distinct trends in the size class distribution of branches recorded in the sample plots were observed. The diameter of about 84 % of the branches was < 10 mm. The total fall of twigs and branches ranged from about 44 to 101 g $m^{-2}yr^{-1}$. *Myczkowski* (1967) recorded a fall of beech twigs and bark litter of about 75 g $m^{-2}yr^{-1}$ and

Mason (1970) about 59 g $m^{-2}yr^{-1}$. In a 50 years old beech stand *Møller et al.* (1954a) recorded a branch and twig loss of 120 g $m^{-2}yr^{-1}$. In their investigation on loss of branches in beech forests (45—51 years old) an annual loss of 0.8 % of the volume of stems and branches, corresponding to 12.8 % of the annual wood increment or about 4 % of the annual gross production (d.m.) was found (*Møller et al.* op. cit.). In beech stands 25—85 years old an annual branch loss of about 100 g $m^{-2}yr^{-1}$ was estimated (*Møller et al.* 1954b). In the research site the annual increment in stems 1969—72 represents 14.8 m^3 ha^{-1} (*Henriksen*, unpublished). 1 m^3 of beech wood corresponds to 0.6 t dry matter (*Møller* 1965), thus an annual branch loss of about 110 g $m^{-2}yr^{-1}$ would be expected; this estimate corresponds fairly well with the annual fall of woody litter actually recorded in Hestehaven 1971—73, and 1975, viz. about 80—100 g m^{-2} (Table 1).

The maximum : minimum ratio of the total fall of twigs and branches was 2.3; however, when major woody components are included, wood fall can be very erratic, being heavily influenced by the fall of a single tree trunk. Actually, during recent years a number of understory trees have fallen down, and the fall of a few overstory trees heavily attacked by the beech coccus (*Cryptococcus fagi* Bärenspr.) has been recorded. No one of these erratic events has been recorded by the litter traps or sample plots used. In 1971 the number of standing dead or dying trees and dead stems in the forest floor was counted and in 1975 (April) the total number of fallen logs was recorded. Based on allometrics the volume of dead stems fallen was estimated and converted to dry weight. In the period 1967—71 a fall of 18 understory trees was recorded, corresponding to an annual input of woody litter of about 4 g m^{-2} (d.w.) and in 1971—75 about 47 understory trees had fallen, corresponding to an annual input of woody litter of about 11 g m^{-2}. Apparently, the contribution of fallen trees to the input of woody litter in the site is increasing.

Obviously, tree fall is extremely variable, however, on an average the annual input of tree trunks 1967—75 represents an amount of woody litter of about 8 g m^{-2} (d.w.), which should be added to the amount of twig and branch litter shed 1971—75 (Table 1); thus the total amount of woody litter ranges from about 50 to 110 g $m^{-2}yr^{-1}$. In 1971—73 the stem fall represents 7—8 % of the total annual fall of woody litter. Finally, during 1970—75 one whole overstory tree and the canopies of three other ones fell down, corresponding to an erratic and highly aggregated input of woody litter of about 2.4 t ha^{-1}.

4.1.3. Total litter fall.

In 1971 and 1974 the total annual fall of all litter components ranged from about 435 to 537 g m^{-2}, the maximum : minimum ratio being 1.2. The biomass of the total litter fall recorded from Hestehaven is lower than that recorded by *Mason* (1970) in an English beech stand (584 g $m^{-2}yr^{-1}$) and by *Nihlgård* (1972) in a beech stand in Southern Sweden (520—630 g m^{-2} yr^{-1}), but distinctly higher than the average litter fall of 30 European beech sites, viz. 360 g $m^{-2}yr^{-1}$ (data from *Bray and Gorham* 1964, *Myczkowski* 1967, *Mason* 1970, and *Nihlgård* 1972). The total annual litter fall in Hestehaven exceeds the annual litter production of 320 g m^{-2} for deciduous angiosperms in the Northern Hemisphere (*Bray and Gorham* 1964). However, due to the considerable divergence resulting from lack of standardization in methodology and especially in the collection of woody litter, comparative litter fall studies are often defective.

The maximum : minimum ratio for the beech stand in Hestehaven indicates that the year to year difference in total litter fall is fairly small being within the deciduous angiosperm range of 1.1—1.8 and close to the *Fagus silvatica* ratio of 1.3 (*Bray and Gorham* 1964).

In the present study beech leaves made up 47—65 % of the total litter fall. *Bray and Gorham* (1964) and *Rodin and Bazilevich* (1967) present data on the percentage of leaves in the total litter fall in deciduous forests; however, comparisons require a knowledge of the number of litter components considered in each particular study. In beech litter fall studies in Europe the percentage of leaves ranged from 58—92 % (*Bonnevie-Svendsen and Gjems* 1957, *Myczkowski* 1967, *Mason* 1970).

In a discussion of the percentage of non-leaf litter, the heterogeneity of litter fall data available should also be considered and in some cases non-leaf components and woody litter are mixed. In 1971 and 1974 the total fall of non-leaf litter was about 154 and 287 g $m^{-2}yr^{-1}$ corresponding to 35 and 53 % of tree litter shed. On an average, non-leaf litter makes up about 30 % of the total angiosperm litter, or about 21 % for cool temperate angiosperm woodland (*Bray and Gorham* 1964). Non-leaf litter values of 37—45 % of the total litter fall was recorded by *Carlisle et al.* (1966), *Sykes and Bunce* (1970), and *Mason* (1970).

In the research site the ratio of non-leaf components to leaves in litter was about 0.5 in 1971, however, in the mast year 1974 1.1; according to *Kira and Shidei* (1967) this ratio is generally 0.5, sometimes approaching 1 in some climax forests.

According to *Myczkowski* (1967) and *Mason* (1970) the fall of beech flowers and budscales made up 1.6 % and 5.2 % of the total litter fall; in the present study, the fall of these components ranged from about 28 to 50 g $m^{-2}yr^{-1}$, which corresponds to 9—10 % of the total litter fall (branch loss not included). In 1971, when fall of branches is considered, budscales and flowers made up about 9 % of the total litter fall, this percentage being considerably higher than those quoted above.

In 1971 the total wood fall in percent of total litter fall and of leaf fall was 22 % and 34 %; in 1974 8 % and 18 %, respectively. In temperate woodlands the wood fall generally represents 18—39 % of the total litter fall and 27—78 % of the leaf fall (*Carlisle et al.* 1966, *Duvigneaud and Ambroes* 1969, *Sykes and Bunce* 1970, *Hughes* 1971, *Gosz et al.* 1972, *Nihlgård* 1972, *Rochow* 1974, and *Christensen* 1975). On an average, the relative abundance of woody litter in the research site is close to the percentages reported for the stands studied by *Hughes* (1971), *Nihlgård* (1972) and *Christensen* (1975); however, it is distinctly lower than most of the earlier records from the temperate zone.

In Hestehaven 1971 seed made up < 1 % of the total litter fall and in 1974 about 10 % (cf. *Nielsen* in press a).

4.2. Seasonal variation.

Table 3 presents the monthly fall of beech litter components (< 58 cm) in terms of dry weight (g m^{-2}). The phenology of beech litter fall 1969—71 was analysed and in Fig. 1 the seasonal production of beech litter components as a percentage of their annual production is presented. In October—November 215—238 g m^{-2} of beech leaves were shed, corresponding to 80—90 % of the annual leaf fall (Table 3, Fig. 1), and in all three years nearly all leaf litter had fallen by the end of November. The number of attached dead leaves observed on beech during the winter is negligible. About 50 % of the beech leaves in Danish beech stands are shed about the first of November (average of about 20 years, *Møller* 1965), cf. Fig. 1. In beech stands in Sweden, England, and Czechoslovakia the fall of beech leaves peaked in October — early November (*Nihlgård* 1972, *Mason* 1970, *Anderson* 1973b, *Chalupa* 1961). Thus only small variation in the main phenology of leaf litter fall is observed between the European beech sites.

In October 1969 and 1970 the fall of beech leaves showed distinct maxima of 65—75 % of the yearly total of leaf litter. In September 1969 > 14 %, a fairly high proportion of the autumn leaf fall, occurred. Moisture stress may indicate the beginning of leaf senescens and abscission (*Addicott and Lyon* 1973). The summer and early spring of 1969 were dry (precipitation Ødum 1969: 125 mm, 1970: 208 mm, 1971: 240 mm), however, the fairly high leaf fall in September 1969 is not necessarily explained by moisture stress, since in spite of an extremely hot and dry summer 1975 (record of this century) only about 9 % of the total annual leaf fall occurred in September.

A progressive mortality of beech leaves occurs from leafing until senescence, and a pre-autumnal fall of green leaves may be caused by premature abscission induced by low light intensities in the low canopy. In the present study, the summer fall (May—August) of green leaves made up 10—25 g

Table 3. Monthly fall of beech litter components in Hestehaven, 1969—71 (— means negligible quantity recorded). Only components < 58 cm considered.
Tabel 3. Månedlige fald af forskellige komponenter af nedfaldsløv, bøg, Hestehaven 1969—71 (— betyder registrering af ubetydelige mængder). Kun fraktioner < 58 cm medregnet.

		Leaves *Blade* g m^{-2}	Budscales *Knopskæl* g m^{-2}	Twigs *Kviste* g m^{-2}	Flowers *Blomster* g m^{-2}	Cupules *Skåle* g m^{-2}	Seeds *Bog* g m^{-2}	Monthly total *Månedlig total* g m^{-2}
April *April*	1971	0.4	0.2	8.5	—	0.4	—	9.5
May *Maj*	1969							
	1970	1.0	21.0	2.1	0	2.8	—	26.9
	1971	1.1	31.2	2.2	1.6	0.9	—	37.0
June *Juni*	1969	2.8	28.8	4.0	16.1	0.4	0	52.1
	1970	2.7	2.2	0.9	3.1	1.7	—	10.7
	1971	1.9	2.2	1.9	1.2	0.7	0	7.9
July *Juli*	1969	2.8	1.0	0.6	2.5	1.5	0	8.4
	1970	1.5	0.6	2.9	0.2	1.2	—	6.4
	1971	12.4	0.6	17.5	—	1.3	0.2	32.0
August *August*	1969	4.3	0.2	0.9	0.2	2.3	0.2	8.1
	1970	4.8	0.5	2.6	—	1.0	—	9.0
	1971	10.1	0.2	0.5	—	0.2	—	11.0
September *September*	1969	41.3	0.8	22.9	—	37.7	10.2	113.0
	1970	18.4	0.3	1.9	—	1.9	0.8	23.3
	1971	18.9	—	1.7	—	2.4	0.6	23.7
October *Oktober*	1969	220.4	0.3	7.0	—	16.0	17.1	260.8
	1970	163.8	—	7.7	0	6.1	2.6	180.2
	1971	116.4	0.8	23.6	—	10.0	2.7	153.5
November *November*	1969	17.5	—	4.2	0	28.5	6.8	57.0
	1970	50.7	0	2.2	0	1.1	—	54.1
	1971	120.6	0.2	7.6	0	0.4	—	128.8
December *December*	1971	—	0	0.3	0	—	—	0.3

m^{-2}, corresponding to 3.5—9.0 % of the total annual leaf fall (Table 3, Fig. 1). The leaf fall in July and August 1971 was higher than that observed during the same period 1969 and 1970 (Table 3, Fig. 1). Wind speed is counted as one of the factors influencing leaf fall. An analysis of the amount of leaf litter recorded weekly in July 1971 shows that nearly all leaf litter material was shed in a windy period, when wind speeds of 20—25 knots (BF 5—6) were recorded. Further, the majority of the leaves shed during July 1971 were attacked by the fungus *Gloeosporium fagicolum* Pass (Melanconiales). Leaf abscission is a common response to infection by pathogenic microorganisms, and beech leaves attacked by *G. fagicolum* are shed during the summer (*Schwerdtfeger* 1970). In late August 1971 a new peak of leaf fall occurred on a single windy day (wind speed 17 knots, BF 5).

In Denmark the beech is generally fully leafed in mid-May (*Møller*

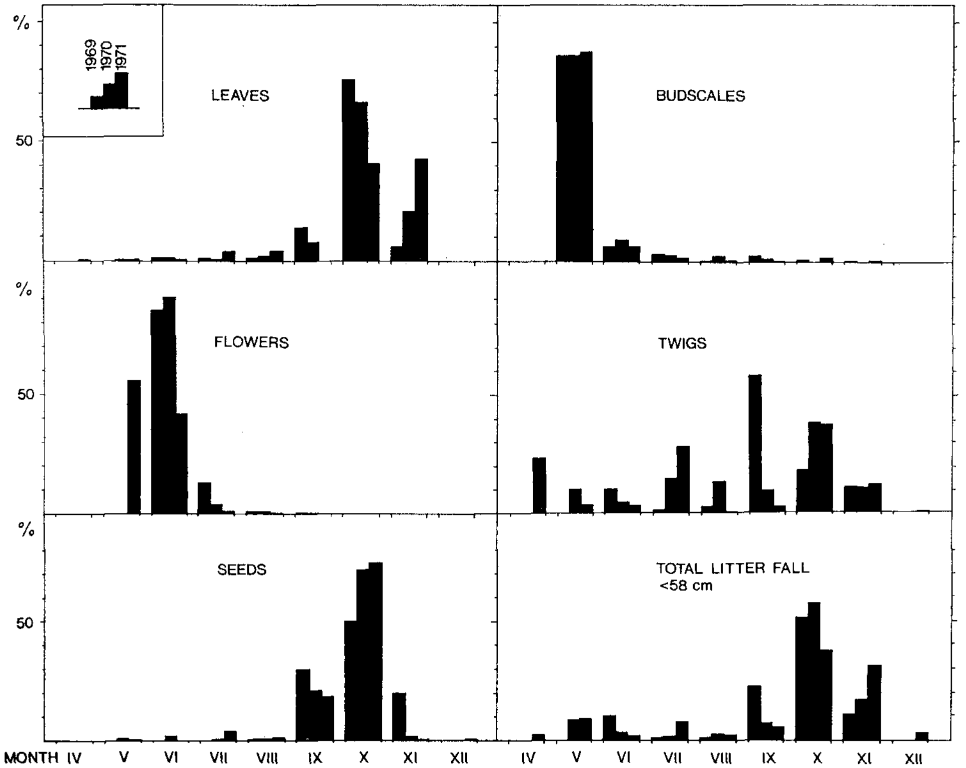


Fig. 1. The phenology of litter fall, Hestehaven 1969—71. The monthly production of beech litter components (< 58 cm) as percentage of their annual production (dry weight).

Fig. 1. Løvfaldets fænologi, Hestehaven 1969—71. Den månedlige produktion af komponenter kortere end 58 cm udtrykt i procent af årsproduktion af de pågældende fraktioner.

Leaves = *blade,* budscales = *knopskæl,* flowers = *blomster,* twigs = *kviste,* seeds = *bog,* total litter fall = *totale løvfald (baseret på tørvægt).*

1965); in Hestehaven about 85—90 % of the budscales (20—30 g m^{-2}, cf. Table 3) were shed in May, generally, about 6—9 % in June and smaller amounts during the next months (Fig. 1). In a British beech stand about 86 % of budscales and flowers were shed during May (*Mason* 1970). In the study carried out by *Anderson* (1973b) the budscale fall was limited to the spring months; however, in the study of *Mason* (op. cit.) as well as the present study the budscales fell throughout the year (except for the period December—April), which may indicate the extent to which leaf replacement occurs during the growing season (cf. *Anderson* 1973b).

Generally, beech flowers were recorded in the litter from May to September, with a distinct peak in spring and early summer (Fig. 1). *Mason* (1970) recorded a peak fall of flowers in May. In Denmark the flowering of beech generally occurs in the latter three weeks of May (*Holmsgaard and Olsen* 1960). According to *Nielsen* (in press a) the major period of seed fall is September—October or September—November (cf. Fig. 1, Table 3).

The seasonal variation in the input of twigs (< 58 cm) was irregular (Fig. 1, Table 3). *Carlisle et al.* (1966) observed maximum values of wood fall in September—November, *Mason* (1970) recorded a peak fall of twigs in September, amounting to 35 % of the annual total, whereas *Sykes and Bunce* (1970) found that twig and branch litter showed no tendency to fall in any particular month. Several authors e.g. *Bray and Gorham* (1964), *Carlisle et al.* (1966), *Gosz et al.* (1972), and *Rochow* (1974) point out the relationship between maximum wind speed and peak values of wood fall; however, in some forest ecosystems the fall of woody litter cannot be explained by the wind factor alone (cf. *Christensen* 1975). In July 1971 the high input of twigs is correlated with a windy period in mid-July. The total input of twigs July 1971 represents 17.5 g m^{-2} (Table 3); in the week 13.—21. VII an input of about 17 g m^{-2} was recorded, viz. about 94 % of the monthly total (Wind speed 20—25 knots, BF 5—6). Further, in October 1971 the twig fall is distinctly associated with strong winds, thus of a monthly total of 23.6 g m^{-2} (Table 3), about 20 g m^{-2} or 83 % were recorded during a single week (wind speed about 17 knots, BF 5). Presumably, all wind forces greater than or equal to 5 BF (17 knots) may affect the rate of wood fall by mechanical breakage (cf. *Christensen* 1975).

The limits of significance associated with the fall of twigs in July 1970 and 1971 indicate a marked difference in the spatial distribution of twig fall in July 1970 and 1971. In the latter year the distribution of twig fall was fairly regular, representing a general loss of woody litter due to high wind speed, whereas in July 1970 the erratic fall of a single big branch in a litter trap represents 81 % of the monthly total.

In the period May 1970 to June 1971, a total fall of branches > 58 cm of about 32 g m^{-2} was recorded (Table 1); 28 g m^{-2} or about 88 % of the total fall of branches was recorded during summer and autumn (June to December 1970). In the period June to December 1971 a branch fall of about 22 g m^{-2} was recorded, corresponding to about 37 % of the annual branch fall. In the branch fall December 1970 to June 1971 no material > 3.0 cm diam. was recorded. In the material shed June—December 1970 and 1971 the size class > 3.0 cm represented about 35 % and 18 %; apparently, the majority of larger branches shed fell during the autumn. *Gosz et al.* (1972) recorded a branch fall of 75 % during the winter months; during this period the branches are brittle and more easily broken. In 45—51 years old beech stands no conspicuous difference in branch fall in the winter half-year (mid-October to mid-April) and in the summer half-year (mid-April to mid-October) was observed (*Møller et al.* 1954a).

In September—December 76—88 % of the total litter fall (< 58 cm) was recorded (Fig. 1) or about 250—430 g m^{-2} (Table 3).

4.3. The energy content of litter components.

Table 4 presents the average calorific content (± SE) of litter components, based on dry weight. Seeds represent components of high calorific value (22635 J g^{-1}), twigs and leaves are of intermediate calorific value, viz. about 20835 J g^{-1} and 20755 J g^{-1}, respectively, whereas flowers, budscales, and cupules are of low calorific value, viz. about 19160 J g^{-1} — 20165 J g^{-1}. On an average the calorific value of all beech litter components analysed is about 20530 J g^{-1}.

Table 4. Energy content of beech litter fractions (dry weight).
Tabel 4. Kalorieindhold af fraktioner af nedfaldsløv, bøg (baseret på tørvægt).

Litter fraction *Fraktion*	Nos of pellets *Antal prøver*	Energy content *Energiindhold* J g^{-1} ± SE
Seeds *Bog*	17	22635 ± 251.2
Twigs *Kviste*	15	20836 ± 125.6
Leaves *Blade*	71	20753 ± 83.7
Flowers *Blomster*	9	20167 ± 251.2
Budscales *Knopskæl*	9	19623 ± 125.6
Cupules *Skåle*	15	19163 ± 293.1

A calorific value of beech leaves of about 20755 J g^{-1} (d.w.) is within the range demonstrated by a number of authors e.g. *Myczkowski* (1967) and *Runge* (1971). However, *Ovington and Heitkamp* (1960) recorded a calorific value of beech leaves of about 19640 J g^{-1} (d.w.), viz. considerably lower than the records mentioned above. The energy content of oak leaves was about 20680 J g^{-1} (*Carlisle et al.* 1966). Obviously, the calorific value of beech leaves changed seasonally (*Nielsen* in press b); similar seasonal changes in calorific value were observed in leaves of oak (*Carlisle et al.* op. cit.) and alder and birch (*Hughes* 1971).

The calorific value of beech twigs (20835 J g^{-1}) is within the range of that of oak twigs (about 20300—21020 J g^{-1}, average 20725 J g^{-1}) (*Carlisle et al.* 1966). However, the energy content of beech budscales (about 19625 J g^{-1}) and male flowers (about 20165 J g^{-1}) is significantly lower than that of the corresponding oak litter components, viz. 20390 and 21100 J g^{-1}, respectively (cf. *Carlisle et al.* 1966).

Compared with the calorific value of beech seeds recorded by other authors, the biocontent of seeds from the research site is fairly low (cf. *Nielsen,* in press a).

The biocontent of the annual litter fall in the Hestehave beech stand made up about 90—110 $\times$ 10^5J m^{-2} (Table 1). The leaf litter fall represented 50—63 $\times$ 10^5J $m^{-2}yr^{-1}$ (average about 58 $\times$ 10^5J $m^{-2}yr^{-1}$) or about 65—70 % of the biocontent of the total litter fall, however, in 1974 (mast year) the leaf fall made up about 45 %. Budscales contributed about 5—7 $\times$ 10^5J $m^{-2}yr^{-1}$ (average about 6 $\times$ 10^5J $m^{-2}yr^{-1}$) and reproductive plant material (flowers, cupules, and seeds) about 5—45 $\times$ 10^5J $m^{-2}yr^{-1}$; generally, the latter components contributed < 10 % of the annual litter fall biocontent, however, in the mast year 1974 about 40 %. The biocontent of woody litter fall (twigs and branches) was 9—21 $\times$ 10^5J $m^{-2}yr^{-1}$, representing about 20 % of the beech litter biocontent (1974 < 10 %). Presumably, the biocontent of beech stems falling erratically contributes about 1.0 $\times$ 10^5J $m^{-2}yr^{-1}$. The non-leaf litter shed amounts to about 30—58 $\times$ 10^5J $m^{-2}yr^{-1}$ or 30—35 % of all litter biocontent (1974 > 50 %).

5. CONCLUSION

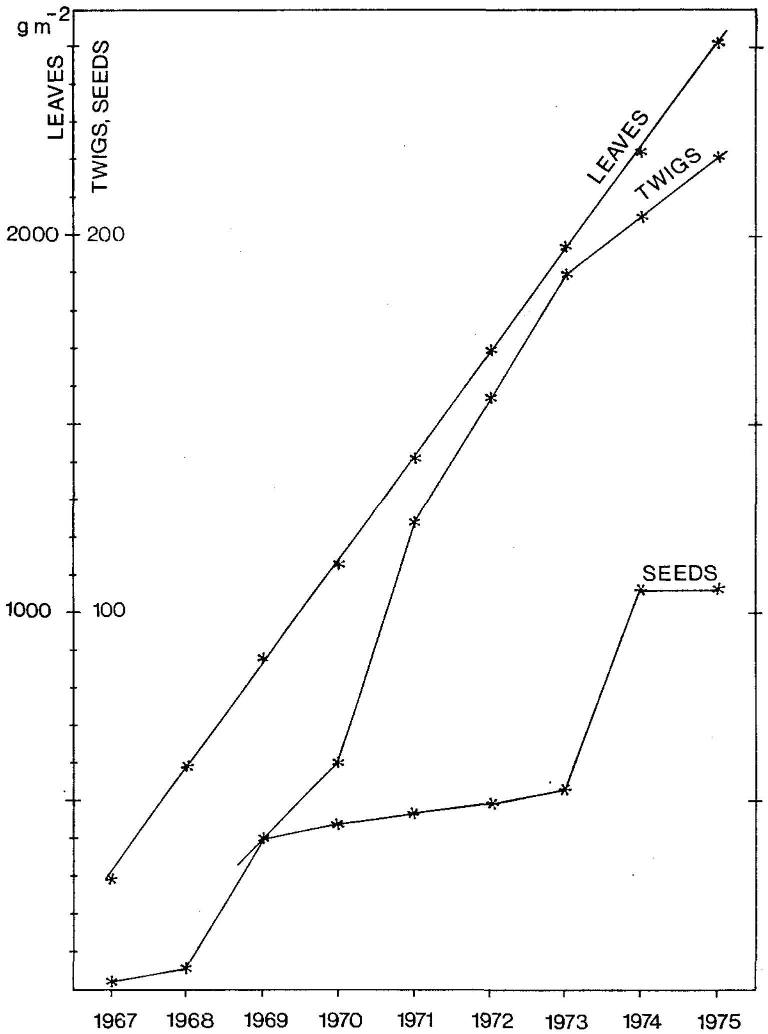
The fall of leaf litter in the Hestehave beech stand is within the range of leaf fall data presented from European beech stands, being close to the average of these and of Danish stands (age 85—95 years). The fall of budscales is higher than most other European records. The fall of twigs and branches and the relative abundance of woody litter, viz. 8—22 % of all litter is distinctly lower than most of the records from temperate deciduous forests. The seed production and the quality and calorific value of the seeds shed are low. The fall of total tree litter, viz. 435—535 g $m^{-2}yr^{-1}$ is distinctly higher than the average litter fall of 30 European beech sites, viz. 360 g $m^{-2}yr^{-1}$, and higher than the annual litter production of 320 g m^{-2} for deciduous angiosperms in the Northern Hemisphere. The discrepancy is largely explained by lack of standardization of litter fall studies.

The contribution of ground vegetation to total litter fall in the site was about 162 g $m^{-2}yr^{-1}$ (*Hughes* 1975), corresponding to about 40 % of the average annual production of tree litter components (< 58 cm) or 30—37 % of total tree litter production (including branches, root loss not considered).

The annual litter fall represents an energy transfer of about 90—110 $\times$ 10^5J m^{-2} of which biocontent the leaf fall makes up 65—70 % (in a mast year about 45 %); in mast years the fall of reproductive plant material may contribute as much as 40 % of the annual litter fall biocontent. The quantities of nutrients falling in the beech litter are presented by *Andersson* (in prep.); preliminary data suggest an annual transfer in litter fall of approximately: C 1600 kg ha^{-1}, N 30—40 kg ha^{-1}, Na 2 kg ha^{-1}, K 9 kg ha^{-1}, Ca 35 kg ha^{-1}, Mg 5 kg ha^{-1}, P 2 kg ha^{-1}, and Mn 2 kg ha^{-1} (data from *Andersson*, unpublished).

A distinct long term constancy in the annual fall of leaves and budscales is observed, the maximum : minimum ratios being 1.2 and 1.4, respectively. A higher annual variation in the fall of twigs (maximum : minimum ratio 4.3), and branches (maximum : minimum ratio 2.9) occurs and the fall of trees is extremely erratic. A conspicuous annual variation is observed in the fall of reproductive plant parts viz. flowers (maximum : minimum ratio 7.5), cupules (maximum : minimum ratio 475), and seeds maximum : minimum ratio ∞). The annual variation in the fall of some litter fractions 1967—74 is presented in Fig. 2 in which the cumulative totals (g m^{-2}) are shown; the long term constancy in the fall of beech leaves, the higher annual variation in the amount of twigs shed, and the record of distinct peak years in seed production (mast years) is emphasized. The conspicuous annual variation in the fall of woody litter and reproductive plant parts again stress the importance of litter fall studies lasting several years.

The composition of the monthly litter fall changes seasonally (Table 3, Fig. 3). In May the litter fall is dominated by budscales (75—85 %). A proportion of cupules of the preceeding year is often shed during next spring and summer; in June mainly budscales (20—55 %) and flowers (15—30 %) are shed. The calorific content of budscales is fairly low (Table 4), however, *Anderson* (1973) pointed out that budscales may have considerable ecological importance to some forest floor animals, e. g. as cryptic micro-habitats, oviposition sites, or pupal and moulting chambers. *Carlisle et al.* (1966) pointed out that although the small non-leafy components mainly falling in spring and early summer accounted for only about 15 % of the dry weight of oak litter, they contained about 30 % of the nitrogen, 40 % of the phosphorous and 25 % of the potassium in all types of litter. In Hestehaven the annual input of budscales and flowers averaged about 40 g m^{-2} (cf. Table 1) or 7—10 % of the total annual litter fall. Assuming that the high nutrient content observed in small non-leafy fractions of oak litter is also valid for the comparable beech litter components, the latter should be taken into account in studies on the nutrient cycling in beech forest ecosystems, especially when the seasonal variation in nutrient transfer is considered. During the period of beech flowering large amounts of pollen are observed in the litter traps, however, for a quantitative estimate, specific pollen traps are required. In litter fall studies this reproductive plant component is generally neglected, although it is shed in tremendous quantities; in beech, 100 flowers produce 1—1.6 cm^3 of pollen (*Stanley*



F i g. 2. The annual variation in the fall of beech leaves, twigs, and seeds, Hestehaven 1967—75; cumulative totals (g m^{-2}, dry weight).

F i g. 2. Årlige variation i nedfald af bøgeblade, kviste og bog, Hestehaven 1967—75; kumulative værdier (g m^{-2}, tørvægt).
Leaves = *blade,* twigs = *kviste,* seeds = *bog.*

et al. 1973). The ecological significance of pollen in the acceleration of litter decomposition in the forest floor was suggested by *Stark* (1972). In the litter fall of July the relative abundance of budscales and flowers generally declines strongly; a summer peak in the fall of twigs may occur. Preautumnal fall of beech leaves only represents 3.5—9.0 % of annual total; however, the chemical properties, nutritive value, and decomposition rate

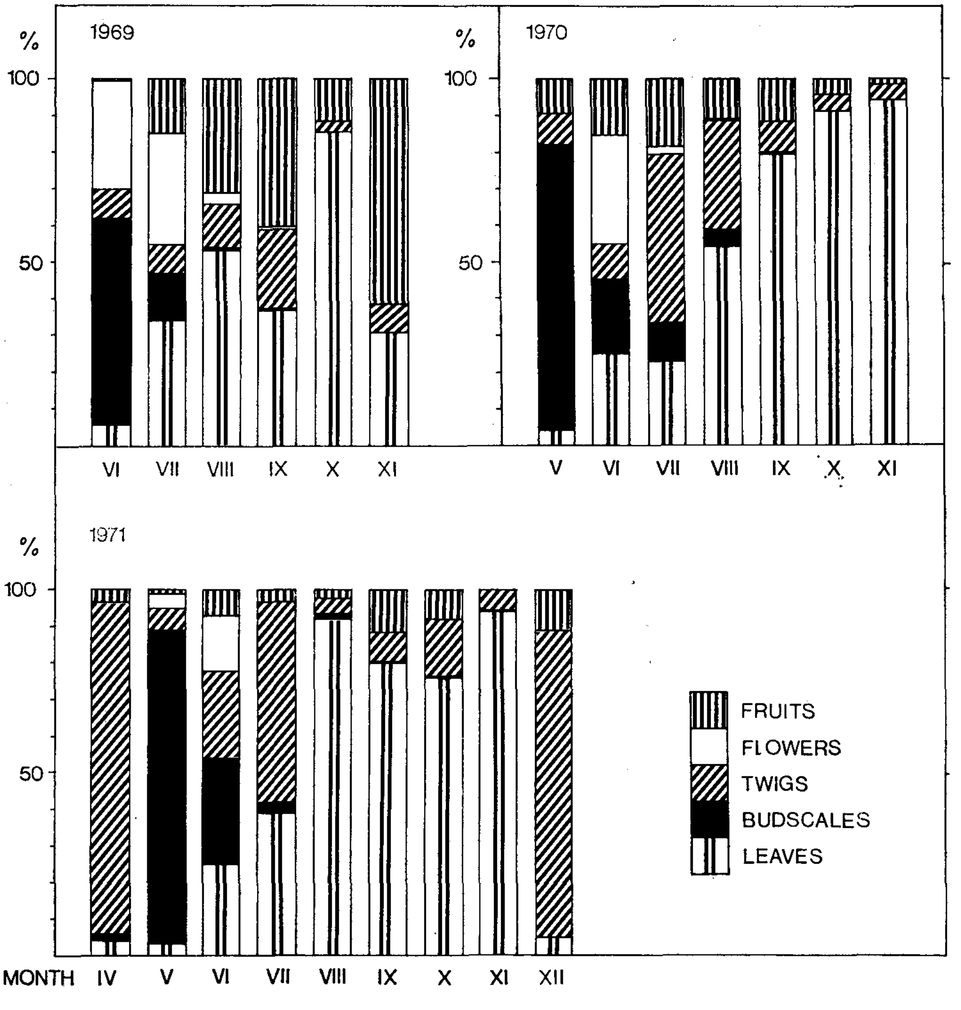


Fig. 3. The relative composition of the monthly litter fall, Hestehaven 1969—71. Only fractions < 58 cm are considered; based on dry weight.

Fig. 3. Den relative sammensætning af det månedlige løvfald, Hestehaven 1969—71. Kun komponenter kortere end 58 cm er taget i betragtning; baseret på tørvægt. Leaves = *blade,* budscales = *knopskæl,* twigs = *kviste,* flowers = *blomster,* fruits = *skåle og bog.*

of leaves shed prematurely differ from that of autumnal leaf litter. In August leaves make up 50—90 % of the monthly litter fall and in September, October and November 30—>90 % of the monthly totals (cf. Table 3, Fig. 3). The relative abundance of twigs in the autumn litter fall varies considerably from about 2 % in October 1969 to about 20 % in September 1969; during the winter and early spring the litter fall is dominated by woody litter (Fig. 3, April and December 1971).

The maximum transfer of organic matter as well as of energy is recorded in October, corresponding to 150—260 g m^{-2} (Table 3) or 30—50 × 10^5J m^{-2}; in the beech stand the autumn litter fall represented 75—90 % of the total amount of organic matter or energy transferred by the annual tree litter fall, further, in autumn the major nutrient transfer in the beech forest ecosystem occurred. In July and August minimum values generally occur, viz. 5—10 g m^{-2} (Table 3) or 1—2 × 10^5J m^{-2}. As pointed out by *Hughes* (1975) half or more of the ground vegetation litter is produced in the first half of the season, especially in June—July. In summer the tree litter production is low, thus the temporal pattern of ground vegetation litter production has important ecological consequences for the soil and the soil organisms.

The spatial pattern of litter fall varies considerably according to component shed, thus the spatial variation of the fall of leaves and budscales is small (SD = 5—20 % of mean), the fall of flowers, cupules, seeds and twigs is more patchy and especially that of the heavy fruit components and twigs (cf. Table 1). The fall of large branches and stems is extremely patchy and in the forest floor these components of woody litter are heavily aggregated, representing distinct centres of activity for invertebrates associated with dead wood.

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SUMMARY

In 1967—75 the range of leaf fall in a 90 years old Danish beech stand was 240—300 g $m^{-2}yr^{-1}$, representing 47—65 % of the total litter fall. The fall of budscales made up 25—35 g $m^{-2}yr^{-1}$, flowers 3—21 g $m^{-2}yr^{-1}$, cupules < 1—143 g $m^{-2}yr^{-1}$ and seeds 0—54 g $m^{-2}yr^{-1}$. In 1967—75 two mast years were recorded. The fall of twigs and branches was 45—100 g $m^{-2}yr^{-1}$; erratic stem fall is discussed. Total wood fall corresponded to 8—22 % of total litter fall and 18—34 % of leaf fall. Generally, fall of woody litter recorded is lower than most earlier records from the temperate zone.

The range of total litter fall was 435—535 g $m^{-2}yr^{-1}$, corresponding to a biocontent of 90—110 × 10^5J m^{-2}. The annual variation in average leaf area, number of leaves m^{-2} and leaf area index is discussed. A distinct long term constancy in the annual fall of beech leaves and budscales was observed. The most conspicuous annual variation was observed in reproductive plant parts shed. The phenology, monthly composition and biocontent of the litter fall are discussed.

RESUMÉ

I årene 1967—75 registreredes løvfaldet i en 90 årig bøgebevoksning i Hestehaven, Rønde, Jylland. Ved løvfald forstås i denne sammenhæng ikke alene bladfald, men nedfald af overjordiske plantedele i almindelighed. Nedfaldet af blade, knopskæl, kviste, blomster, bog og skåle registreredes ved hjælp af løvfangere (diameter 58 cm) og grenfaldet på prøveflader (10 × 10 m). Det årlige nedfald af bøgeblade varierede fra ca. 240 til 300 g m^{-2}, repræsenterende 47—65 % af det totale løvfald; det årlige bladfald i forsøgsområdet var nær gennemsnittet for 30 europæiske bøgelokaliteter og for danske bevoksninger (85—95 år). Faldet af knopskæl udgjorde 25—35 g $m^{-2}år^{-1}$ og af blomster 3—21 g $m^{-2}år^{-1}$, skåle < 1—143 g $m^{-2}år^{-1}$ og bog 0—54 g $m^{-2}år^{-1}$. I perioden 1967—75 registreredes to oldenår. Nedfaldet af kviste og grene var 45—100 g $m^{-2}år^{-1}$; fald af stammer diskuteredes. Det totale vedfald repræsenterede 8—22 % af det totale løvfald svarende til 18—34 % af bladfaldet. Som regel var vedfaldet i forsøgsområdet lavere end de fleste tidligere målte værdier fra det tempererede område. Det totale løvfald udgjorde 435—535 g $m^{-2}år^{-1}$, repræsenterende en årlig energitilførsel på 90—110 × 10^5J m^{-2}. Urtevegetationens årlige bidrag til det totale løvfald svarede til ca. 40 % af det gennemsnitlige nedfald fra bøgen (komponenter < 58 cm) eller 30—37 % af det totale årlige tilskud af organisk materiale fra bøgetræerne (grene medregnet, rodtab ikke taget i betragtning). Årsvariationen i gennemsnitlige bladareal, bladantal m^{-2} og samlede bladareal m^{-2} belystes. Det årlige nedfald af bøgeblade og knopskæl var meget konstant (forholdet mellem maksimum og minimum henholdsvis 1.2 og 1.4). Største årsvariation registreredes i nedfaldet af bog og skåle (maksimum : minimum henholdsvis ∞ og 475). Løvfaldets fænologi og månedlige sammensætning samt komponenternes energiindhold diskuteredes.

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