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The Decomposition of Branch-Wood in the Canopy and Floor of a Mixed Deciduous Woodland

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Summary. The pattern of decomposition of branch-wood greater than 2 cm diameter is described for a one hectare site at Meathop Wood, Cumbria, based on studies carried out as part of the IBP between 1967 and 1972. Three phases of decomposition are recognised. Following the death of branches in the canopy and their colonisation by fungi, decomposition proceeded at an average annual loss rate of about 8.4%. Wood at branch-fall had on average lost about 40% of its original dry weight. On the forest floor the average annual rate of weight lost to decomposition was 17.1%. This could be divided into two phases; fungi were predominant initially but shortly after branch-fall invasion by wood-boring animals occurred. The average annual branch-fall between 1967 and 1971 was 31.5 $g \cdot m^{-2}$. The standing crop of dead branch-wood on the forest floor was estimated in 1971 to be 203.3 $g \cdot m^{-2}$. Assuming steady state this implies an annual turnover of 15.5% of the standing crop which is in good agreement with the observed decomposition rate.

Considerable differences in the rates of decay were observed between individual branches. No significant differences were found between branches of the four main "species" of tree investigated (*Quercus robur* plus *petraea, Fraxinus excelsior, Betula pendula* plus *pubescens, Corylus avellana).*

Introduction

Until recently the functioning of the detritus-based food web has been a comparatively neglected part of production ecology. During the integrated ecosystem studies of the International Biological Programme however there has been an attempt to correct this imbalance and some progress has been made in unravelling the complexities of decomposition processes and quantitatively assessing their significance in ecosystem structure and dynamics (Rosswall and Heal, 1975; Witkamp, 1976).

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The main inputs to the decomposer sub-system in woodland ecosystems are dead materials from the trees—leaves, roots, reproductive structures, stems and branches. This paper reports investigations of some of the major features of the decomposition of the branch component. Bray and Gorham (1964) estimated that branch-wood may form up to 30% of the litter fall in most types of temperate forest, yet this resource has been largely ignored in decomposition studies in comparison with leaves. This studies reported here concern quantitative aspects of the death, fall, and decay of branch-wood greater than 2 cm in diameter. This size limit is arbitrary, material of smaller diameter being described as "twigs", and regarded as having potentially different decomposition characteristics (Healey and Swift, 1971). Similarly, dead stem wood, which is relatively infrequent in the study site, has been excluded from consideration in this report. A more comprehensive account embracing these materials will be published as part of the report of the Meathop Wood IBP Project. Later papers will consider the communities of organisms, and the nutrient dynamics associated with the decomposition of wood.

Methods

Site. The studies were carried out between 1967 and 1974 as part of the IBP Project at Meathop Wood, Cumbria, Grid Reference SD 435795. The dominant trees are oak (*Quercus petraea* (Mattuschka) Liebl. and *Q. robur* L.), ash, (*Fraxinus excelsior* L.), birch, (*Betula pendula Roth* and *B. pubescens* Ehrh.), with an understory of hazel, (*Corylus avellana* L.). Characteristics of the soils and primary production of the site have been described by Satchell (1970). Most of the studies described here were carried out on the type hectare established for the main IBP project but in order to reduce the disturbance resulting from destructive sampling methods some experiments were located in a 5 m wide transect adjacent to the western margin of the hectare, which was divided into twenty-two 5 × 5 m plots. The comparability of this site with the type hectare is shown in Table 1 on the basis of the standing crops of trees and shrubs in the two sites determined by the regression methods described by Bunce (1968). These data reveal that although the total standing crops are broadly similar the species composition does show some marked differences.

States of Decay. The state of decay of a piece of wood may be ascertained by determination of its *relative density* (RD) (Healey and Swift, 1971). The RD of living wood varies between species, and may vary within species in relation to site differences or position in the tree. Variation in the RD of living branch wood in the selected size range was however small both within and between species for the Meathop site (Table 4). The RD distribution of living wood was therefore used as a base-line for comparison with samples taken from various stages of the decay process. The RD of branches was estimated from subsamples not greater than 10 cm long by the calculation of the ratio of dry weight at 80° C to volume. The volume was estimated either by the weight of water displaced or by measurement of the length and diameter of the subsample in the field. There was no significant difference between the mean RD of two samples of living wood in which the volume was estimated by the two different methods. In addition to the RD measurements the branches from the litter layer were examined for the intactness of their bark. The *bark cover* was scored on a percentage basis in 10% intervals ranging from no bark present (0%) to bark completely intact (100%).

Standing Crops. The standing crop per unit area of dead branch-wood was determined for the canopy and for the forest floor. In the canopy dead wood can be distinguished as that present as dead trees and that present as dead branches on trees that are still living. Only the latter category is considered here: the dead tree standing crop was equivalent to about 14% of this component. A set of sample trees covering the range of stem girths of the trees in the type hectare was selected at random from the woodland outside the hectare. All branches without

Table 1. Standing crops ($g \cdot m^{-2}$) of trees and shrubs on the wood decay site compared with the type hectare

	Oak	Ash	Birch	Hazel	Other[a]	Total
Wood site (W)	4,618	2,581	1,808	726	1,405	11,159
Hectare (H)	5,033	3,779	1,646	1,426	498	12,382
Ratio (W/H)	0.92	0.68	1.10	0.51	2.82	0.90

[a] Mainly Sycamore and Hawthorn

Table 2. Regression parameters for estimation of dead branch weight on living trees
Regressions: in form $ln\ (y) = a + b\ (ln x)$; where x = stem diameter in cm; y = total weight of dead wood in kg

Species		Oak	Ash	Birch	Hazel and other shrubs	Sycamore[a]
Regression constant	(a)	−8.534	−2.860	−5.309	−4.239	−6.456
Regression coefficient	(b)	3.272	1.359	1.807	1.103	2.494
Mean square deviation	(msd)	1.083	0.418	0.379	0.909	1.059
Coefficient of determination	(r^2)	0.81	0.57	0.80	0.70	0.69
Number in sample	(n)	18	14	14	45	23

[a] Regression based on combined oak, ash and birch sample

buds or leaves were removed from each of the sample trees and their fresh weight determined. The dry weight for each branch was estimated by use of a conversion ratio determined from a 10 cm subsample. Regressions were then calculated for each tree species as *ln (total dead branch dry-weight)* on *ln (stem girth at breast height)*. The regression parameters (Table 2) were incorporated in the standard production programmes (Mountford and Bunce, 1973; Satchell, 1970) with the hectare stand inventory to estimate the standing crop of dead branch wood.

Eight of the plots from the wood site were used for the estimation of the standing crop of branches on the forest floor in March, 1971. Each plot was subdivided into strips 1 m wide running at right angles to the transect length. Two strips per plot, selected at random, were cleared of branches by systematic searching of 1 × 1 m quadrats. Each of the branches was labelled, and its species, mean diameter and total length recorded. Where a branch overlapped two squares, or projected out of the sampling strip, the proportion of the length in each location was noted. The diameter and length data were used to calculate the volume of each branch collected. The dry weight of each branch length was estimated by multiplying its volume by a value for its RD obtained from subsamples taken at subterminal locations. Considerable variation in RD along the length of a branch was revealed in a preliminary experiment where 24 branch lengths from the litter, all about 25 cm long, were subdivided into four or five RD subsamples. The mean value for the Coefficient of Variation in RD of the 24 branches was 19.6%. A regression of the total branch RD on the RD of subterminal subsamples for a total of 46 branches showed a significant relationship indicating that a consistent bias was introduced by use of the sub-terminal subsample for RD estimation. Regression parameters were separately calculated for each species and subsequently used to correct the branch RD estimated from subsample RD.

Branch Fall. Twigs and branches longer than 43 cm were collected fortnightly from 15 5 m × 5 m plots located systematically on the type hectare (Sykes and Bunce, 1970). Before sampling began twigs and branches already on the ground were marked so that they could be distinguished from subsequently fallen material. The collections were sorted into species and dried to a constant weight at 105° C. Collections were made over a 4-year period from 1967. From May 1970 to May 1971, diameter measurements were made to determine the fraction of wood litter fall that was > 2 cm diameter. From this a conversion factor was derived for each species which was applied to the data for the full 4-year sampling period.

Decay Rates. Experiments were established to determine the rate of decay of branch-wood in both the canopy and the forest floor environments. In both cases the rate of decay was measured in terms of total weight loss over determined periods of time. Thus the observed decay is a sum of the contributing processes of leaching, microbial catabolism, animal consumption and export.

To follow the rate of decay in the canopy branches of each species, 50 cm in length, were suspended in the canopy with polythene twine. One end of each branch was coated with Bitumastic paint, the other being left open for colonisation by micro-organisms. Prior to suspension the fresh weight of each branch was determined. A fresh weight/dry weight conversion factor was obtained from a subsample taken from the end of these branches and used to determine the dry weight of the branch. Regression analysis of actual branch weight on estimated dry weight again showed a consistent bias. The regression parameters were therefore used to predict the branch dry weight from the subsample weight. Samples of branches were removed from the canopy at three or six monthly intervals for a period of 3 years from March, 1971.

To determine the rate of decay of wood on the forest floor, one hundred- and seventy-five branches (22 oak, 48 ash, 66 birch and 39 hazel) from the standing crop survey described above, were labelled and replaced in the litter in the same metre square from which they were originally recovered. At sixmonthly intervals over the two-year period from April 1971 a sample comprising one-quarter of the branches in each species was recovered. The length, mean diameter, and dry weight were determined. From these measurements the actual RD was calculated for comparison with the initial RD estimated during the standing crop survey.

Results

Standing Crops. Estimates of the total standing crops of dead wood for the type hectare are given in Table 3.

States of Decay. Samples for the living wood and dead standing wood were taken from branch-wood of trees selected at random within the type hectare.

The state of decay at litter-fall was estimated on subsamples taken from all branches >2 cm diameter falling into the branch litter-fall plots over a two-year period from May, 1969. In the second half of this survey period, branches were taken from two additional plots on the wood-decay site in order to increase the sample size for birch and hazel branches which were relatively infrequent on the type hectare. RD data for branches on the forest floor (litter) were taken from a sample of 210 RD estimates made during a survey of microflora and microfauna in branch-wood. This was subdivided into branches which had been invaded by wood-boring fauna and those which had not. The mean values for each of the four main species at each of these significant stages of decay are given in Table 4. By comparison of the RD at each stage with that of living wood it is possible to estimate the extent of decomposition that has taken place and this is shown as the fraction of weight remaining. The heterogeneity of RD at each stage of decay is indicated by the standard errors but is illustrated in more detail for the total wood by the histograms in Figure 1. Although the RD is heterogeneous at all stages this variation increases considerably as decomposition proceeds; the coefficient of variation in RD of living branches was 9.9% ($n=87$) but at litter-fall it was 33.3% ($n=130$) implying that branches enter the litter layer at varying stages of decay. The mean RD at litter fall for the different species implies an average loss of between 33 and 51% of the dry weight of the branches in the canopy.

Table 3. Standing crops of dead branch-wood on the type hectare ($g \cdot m^{-2}$)

	Oak	Ash	Birch	Hazel	Other[a]	Total
Branches in canopy	316.4	83.8	15.0	54.9	9.5	479.6
Branches in litter (wood site)	26.2	59.0	42.4	24.4	6.2	158.2
Branches in litter (type hectare)[b]	28.6	86.1	38.6	47.8	2.2	203.3
Confidence interval[c]	20.5	59.6	20.0	25.5	1.7	63.5

[a] Includes unidentified branch-wood litter
[b] Converted from the wood site figure by use of the site/hectare ratio for tree standing crop given in Table 1
[c] 95% confidence interval based on variance between 85 $1 m^2$ quadrats

Table 4. States of decay of samples of branch-wood taken at various stages of the decomposition process.

		Relative density $g \cdot m^{-3}$				
		Oak	Ash	Birch	Hazel	Total
Living branches	Mean	0.574	0.552	0.543	0.558	0.560
	SE	0.011	0.008	0.020	0.013	0.006
	n	29	29	9	20	87
Standing dead branches	Mean	0.390	0.419	0.537	0.420	0.418
	Se	0.015	0.015	0.020	0.030	0.010
	n	75	30	17	16	138
	Wt/Wo[a]	0.68	0.76	0.99	0.75	0.75
Branch fall	Mean	0.281	0.371	0.330	0.293	0.318
	SE	0.014	0.013	0.027	0.026	0.009
	n	50	37	14	25	126
	Wt/Wo	0.49	0.67	0.61	0.53	0.57
Uninvaded in litter	Mean	0.266	0.282	0.260	0.268	0.268
	SE	0.042	0.022	0.014	0.017	0.070
	n	15	25	37	47	124
	Wt/Wo	0.46	0.51	0.47	0.48	0.48
Invaded in litter	Mean	0.189	0.181	0.215	0.172	0.190
	SE	0.024	0.027	0.023	0.016	0.011
	n	15	14	27	30	86
	Wt/Wo	0.33	0.33	0.40	0.31	0.34

[a] *Wt/Wo* = Mean RD of sample/Mean RD of living wood = Fraction of weight remaining

The distribution of bark cover among 230 branches from the litter is shown in Table 5. Although there is a significant correlation between the state of decay and the amount of bark lost from the branches, the most significant feature of the data is the very large proportion of branches showing a totally intact bark cover. This amount to 40% of the branches examined and implies

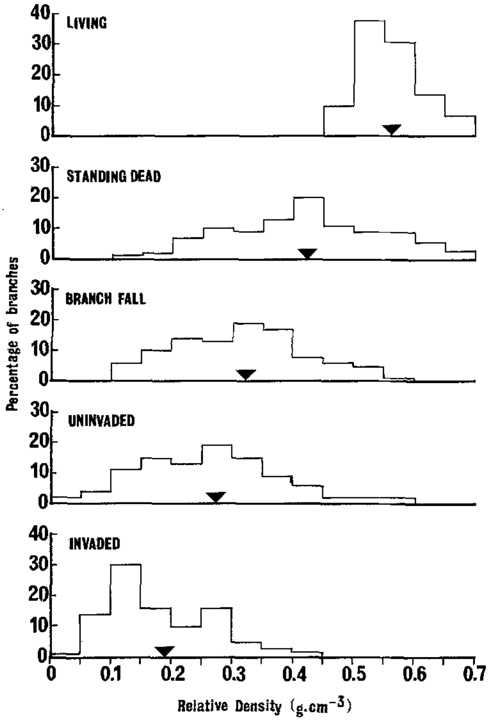

Fig. 1. Distribution of states of decay within samples of branches of all species taken at various stages of the decomposition process. The mean RD is indicated by the arrow in each case. Numerical data for this, the standard errors, and the number in each sample are given in Table 4

Table 5. The relationship between the percentage of bark remaining and the state of decay of branches in the litter[a]

Bark cover %	100	90	80	70	60	50	40	30	20	10	0
Mean RD ($g \cdot cm^{-3}$)	0.338	0.252	0.131	0.221	0.243	0.164	0.141	0.196	0.232	0.188	0.156
n	98	51	23	11	8	3	4	8	3	3	18

[a] Correlation coefficient for (Bark%: Mean RD) $r=0.712$ $Sr=2.107$

Table 6. Fall of branch-wood on the type hectare summarised by year and species ($g \cdot m^{-2} \cdot yr^{-1}$)

	Oak	Ash	Birch	Hazel	Total
1967	5.3	4.6	1.9	1.3	13.1
1968	5.9	9.0	3.5	10.9	29.3
1969	8.6	17.1	6.1	5.2	37.0
1970	8.3	21.4	4.6	12.4	46.7
4 yr mean[a]	7.0±0.83	13.0±3.8	4.0±0.9	7.5±2.6	31.5±7.1

[a] Mean± SE calculated on the four year totals

Table 7. Decomposition rates (fraction of weight lost per year) for the four main species in canopy and litter environments

		Decomposition rate *b.*	Significance *Fs.*	Intercept *a.*	Significance *t.*
Oak	Canopy	0.088	2.31 ns	0.93	0.34 ns
	Litter	0.067	0.49 ns	0.82	1.18 ns
Ash	Canopy	0.019	0.14 ns	0.87	0.96 ns
	Litter	0.165	11.36[a]	0.87	1.23 ns
Birch	Canopy	0.130	7.57 (ns)	0.92	0.69 ns
	Litter	0.148	45.77[c]	0.93	1.27 ns
Hazel	Canopy	0.098	9.05[a]	0.99	0.15 ns
	Litter	0.280	9.26 (ns)	0.83	0.91 ns
Total	Canopy	0.084	10.89[b]	0.93	1.02 ns
	Litter	0.171	197.02[c]	1.00	0.08 ns

Significance levels: ns = not significant; (ns) = significant at $P=0.10$
[a, b, c] Significant at $P=0.05$, 0.01 and 0.001 respectively
See text for explanation of significance tests

that whatever protection from invasion by animals and fungi is given by the presence of bark is largely retained until a late stage of decomposition.

Branch Litter Fall. The annual fall of branch wood over the four year sampling period is shown in Table 6 together with an annual mean estimated on the basis of the four years of sampling. Comparison with the data for the forest-floor standing-crops of Table 3 shows that in all cases the standing-crops are in excess of the annual branch-fall. If it is assumed that the standing crop has reached a steady state (i.e. is not accumulating or declining) then an estimate of the implied annual fractional weight loss (K,) can be made using the formula $K=L/X$ where L=annual litter fall and X= litter standing crop at steady state (Jenny et al., 1949; Olson, 1963). These computed estimates are given in Table 8. The value $3/K$ is an estimate of the time for turnover of 95% of the annual litter fall and is also quoted in Table 8.

Rates of Decay. Decomposition rates were computed for each species separately and for the total branch-wood for each of the two decomposition experiments. A Model I regression employing replicated Y values for each X value was used (Sokal and Rohlf, 1969, p. 428). The equation tested was $\ln Y=a+bX$ where Y=fraction of weight remaining ($=Wt/Wo$, see Table 4) and X=time in years ($=t$). The semi-logarithmic form is that normally assumed for decomposition studies (Minderman, 1968) and the slope (b) is termed the *fractional weight loss* ($g \cdot g^{-1} \cdot yr^{-1}$). Agreement with this model was tested by computation of the variance ratio F_S) of linear regression over deviations from regression. Comparisons between pairs of regression coefficients were made by the method

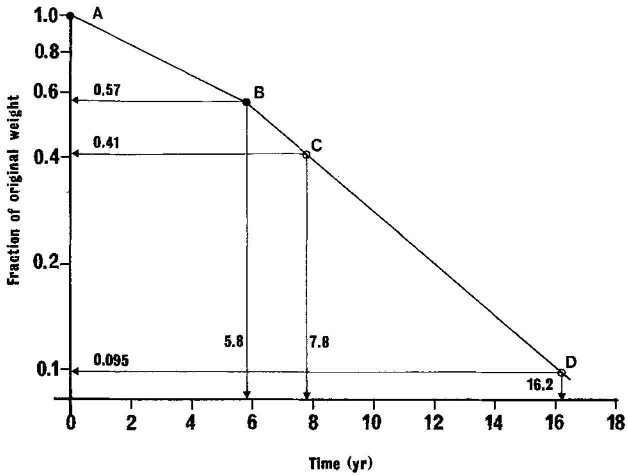

Fig. 2. Pattern of decomposition of branch-wood at Meathop. The decay curves are plotted from the regression equations for total branch-wood given in Table 7. Four identifiable stages of decomposition are indicated on the curves; *A* branch death; *B* branch fall; *C* animal invasion; *D* arbitrary termination point (equivalent to RD=0.05 $g \cdot cm^{-3}$) at which incorporation of the residues of decomposition into the general soil and litter environment can be said to have become a dominant factor. Full discussion of these points is given in the text

described by Sokal and Rohlf (1969, p. 450). The significance of deviation of the intersect (*a*) from the expectation that it would equal *ln* 1.0 (i.e. zero) was evaluated by the t-test method of Snedecor and Cochran (1969 p 166). The computed values of *b* and *a* and the results of the tests of significance are given in Table 7 for each of the species and for the total branch-wood.

No significant deviations of the intersect from a *Y* value of 1.0 were found. This suggests that the initial stage of decomposition in all cases is consistent with the subsequent pattern of weight loss. In the canopy experiment significant agreement with the semi-logarithmic regression equation was found only for the total wood and hazel; birch was significant only at the 10% level. In the litter total, birch and ash were significant beyond 5% and hazel at 10%. The oak curve in the litter was particularly variable and the estimated rate was much lower than that of the other species. Comparisons of the significant regression coefficients showed no significant differences between species in either canopy or litter. Decomposition rates in the canopy were in all cases except oak slower than in the litter but the difference was only significant at the 10% level for the total branch wood and was insignificant for birch.

Discussion

An overall picture of the wood decay process is given in diagrammatic form in Figure 2. This description is compounded from the decay rates of wood of all species from both the canopy and the litter layer experiments (Table 7).

The curves are linked by the observed state of decay for wood at litter fall (Table 4), both curves having been extrapolated to meet at this point. The process of wood decay has been arbitrarily terminated at the state of decay equivalent to an RD of 0.050 $g \cdot cm^3$ as branches of lower RD are rarely found.

The process of decay is summarised as possessing three readily distinguishable stages. The first stage (A to B) is that of decay in the canopy, initiated by the death of the branch. The causes of death have not been studied but they probably include biological agents, such as parasites, and non-biological damage including wind-break. A rough estimate of the annual input (I) due to branch death can be made by means of the equation $I = bX + L$, where b is the decay rate for standing dead wood (Table 7), X is the standing crop of the same component (Table 3) and L is the annual branch fall (Table 6). For the total branch wood this gives an estimate of 71.8 $g \cdot m^{-2} yr^{-1}$ which is less than 1% of the estimated standing crop of the trees and shrubs on the type hectare (Table 1).

Decay in the canopy accounted for some 40% of weight loss on average (Table 4). Visual evidence suggests that this was largely due to fungi although some bark beetle activity was seen in a minority of branches. An interesting implication of this extensive canopy decay is that branch fall figures (such as those quoted by Bray and Gorham, 1964) significantly underestimate the amount of branch-wood entering the decomposer system. Thus the above figure of 71.8 $g \cdot m^{-2} yr^{-1}$ is closer to this amount than is the figure of 31.5 $g \cdot m^{-2} yr^{-1}$ given by the branch fall data. This fact should be borne in mind when assessing the significance of wood in comparison to other resources such as leaves which probably have far lower extents of weight loss prior to fall.

The second phase of decay (B to C) is that which occurs between branch fall and the time of invasion by wood-boring animals. This time was estimated as lying mid-way between the mean RD of invaded and uninvaded wood respectively. For total wood this gives an estimate of 0.229 $g \cdot cm^{-3}$ or after 59% weight loss. The estimated RD for animal entry was remarkably consistent for the four species, ranging from 0.228 to 0.238 $g \cdot cm^{-3}$. The main agents of decomposition in this phase were again presumed to be fungi but the quantitative contribution to overall decay of this phase was relatively small and accounted for only fifteen to twenty per cent of the total weight loss (Fig. 2). The third phase (C to D) is that of internal animal activity and typically shows a progressive fragmentation of the wood and a darkening of its colour. Thus wood approaching the terminal RD of 0.050 $g \cdot cm^{-3}$ has lost all coherence except that maintained by the bark (where present) and has become a mixture of small wood fragments, animal faeces, and amorphous humus. These materials, when released by fragmentation of the bark, would probably not be distinguishable from the general organic matter of the humus horizons of soil.

The failure of the semi-logarithmic decay curve to adequately describe all but a few of the sets of decomposition data is probably in part due to inadequate replication in some of the experiments. Another contributory factor may however be the existence of a high degree of heterogeneity in the wood-decay process. The large extent of variation in RD at litter-fall shows that individual branches enter the forest floor environment at widely differing stages of decay.

Table 8. Estimates of the turnover of dead branches in the litter layer

	Oak	Ash	Birch	Hazel	Total
1. Estimated fractional weight loss[a] ($g \cdot g^{-1} \cdot yr^{-1}$)	0.245	0.151	0.104	0.157	0.155
2. 95% turnover (yr) Based on (1)	12.2	19.9	28.8	19.1	19.4

[a] $K = L/X$ (see text)

They may also vary markedly in the species of organisms colonising them (Swift, 1976). The resolution of the quantitative extent of the implied differences in decay-rate between branches, and of the factors which determine it, depends on the use of more precise and non-destructive methods of following the pattern of decomposition of wood through all its stages.

Two estimates have been made of the annaul fractional weight loss for total branch-wood on the forest floor (Table 7 and Table 8) and give very similar values (0.171 and 0.155 $g \cdot g^{-1} yr^{-1}$ respectively). This may be quite fortuitous as the rates for two of the four individual species differed markedly but in opposing directions, that of oak being higher by the ratio method and that of hazel by the experimental method.

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