Decomposer invertebrate populations in U.S. forest biomes

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With 3 figures

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1. Introduction

Decomposition, as an ecosystem process, is effected by microflora and invertebrates in a synergistic manner. The microflora are capable of accomplishing decomposition, albeit slowly, in the absence of the invertebrate animals (Kurčeva 1960, 1964), and typically are responsible for more than 90 % of the CO_2 evolved in forest decomposition (Reichle et al. 1975). The invertebrates are known to stimulate microbial respiration (Ausmus et al., in press) possibly by improvement of substrate through fragmentation (Edwards and Heath 1963; Wallwork 1970), chemical as well as physical changes (van der Drift and Witkamp 1960; McBrayer 1973a). or regulation of growth phases (Ausmus 1974). Consequently, understanding the composition, population dynamics, and activity of soil invertebrates is essential to understanding the dynamics of forest decomposition. This paper reports on decomposer invertebrate work supported by the two forest biome projects of the U. S. IBP. Much of the detailed information from these studies, beyond the scope of this paper, will be published elsewhere. This paper will concentrate on comparisons of numbers of invertebrates among sites and relate population densities to site factors. It will also indicate two interesting corollaries which became apparent during these studies, vertical migration cycles and interactions between mesofauna and microfauna.

2. Methods

Six sites studied represented natural states of coniferous forest (H. J. Andrews Experimental Forest, Oregon), managed coniferous forest (Cedar River Research Area, Washington), unmanaged cove hardwood forest (Oak Ridge National Laboratory, Tennessee), mature mixed oak forest (Coweeta Hydrologic Laboratory, North Carolina), young plantation pine (Coweeta) and fire-maintained pine (Santee Experimental Forest, South Carolina). Each study lasted approximately one year. A summary of sites, forest types and investigators is given in Table 1. Questions regarding specific studies should be addressed to the principals.

The Coweeta Hydrologic Laboratory, U.S. Forest Service (U.S.F.S.), is located in the Nantahala Mountains, a part of the southern Applachians. Elevation ranges from 685 m to 1600 m with slopes > 50 %. Precipitation ranges from 175 cm $yr.^{-1}$ at lower elevations to 235 cm $yr.^{-1}$ at 1800 m. Precipitation is well distributed throughout the year with < 2 % occurring as snowfall. Watershed (WS) 18 probably has never experienced logging and definitely has had neither cutting nor burning since 1924 (Gist 1972). The vegetation is a mixed oak-hickory association. Prior to the introduction of chestnut blight in the 1930's, American Chestnut [*Castanea dentata* (Marsh.)] was a dominant canopy species. Watershed 17 is adjacent to WS 18 and contains an 18-year-old, white pine (*Pinus strobus* L.) plantation, planted to simulate a common eastern community type (Cornaby 1973).

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Table 1. Summary of decomposer invertebrate studies in the forest biomes of the U.S. International Biological Program

Site	Forest type	Investigators
H. J. Andrews Experimental Forest Oregon	mature Douglas fir	Y. KITAZAWA, G. W. KRANTZ, H. J. JENSEN, J. G. WERNZ, T. KITAZAWA
Cedar River Research Area Washington	plantation Douglas fir	same as above
Coweeta Hydrologic Laboratory North Carolina	mature mixed oak	C. S. GIST
Coweeta Hydrologic Laboratory North Carolina	plantation white pine	B. W. CORNABY
Santee Experimental Forest South Carolina	mature loblolly pine	L. J. METZ
Oak Ridge National Laboratory Tennessee	cove hardwood	J. F. MCBRAYER, J. M. FERRIS

The Santee Experimental Forest (U.S.F.S.) is located on the lower coastal plain near Charleston, South Carolina. Elevation is 8.4 m and annual precipitation averages 134 cm. Loblolly pine (*Pinus taeda* L.) forest are fire-maintained sub-climaxes in what is commonly considered an oak climax region. Controlled burning experiments have been conducted at Santee Experimental Forest for over twenty years (METZ and FARRIER 1973). The data reported here are from a fire-excluded control plot which has now developed a dense, hardwood understory.

The cove hardwood site is a small (0.13 ha) sinkhole which is dominated by yellow poplar (*Liriodendron tulipifera* L.). Located on the U.S. ERDA Reservation in the Ridge and Valley Province of east Tennessee, it is a second growth forest ~50 year old. Elevation is 290 m and the 125 cm $yr.^{-1}$ precipitation is well distributed throughout the year. Because of its location in a sinkhole, it receives both moisture and organic matter from the oak-hickory forest on the surrounding slopes (MCBRAYER 1973b).

The H. J. Andrews Experimental Forest is located in the Willamette National Forest of the Oregon Cascades. Elevation within the site ranges from 500—1600 m. Mild wet winters and warm, dry summers are characteristic for the research area. Precipitation ranges from 230 cm at lower elevations to more than 250 cm on higher ridges. Snowpack at higher elevations may reach 3 m during the winter months. The study site is dominated by *Pseudotsuga menziesii* (MIRB.) averaging ~450 years (DYRNESS, FRANKLIN and MOIR 1974).

The Cedar River Research Area is located in the lower Cedar River watershed of western Washington. The research area is covered by terraces formed during the Holder Delta stage of the Fraser glaciation, and elevation rarely exceeds 220 m. Precipitation averages 14 cm, with nearly all of it falling as rain during the winter months. Snow occasionally accumulates to depths of 3 cm, and fog and mist are frequent. Timber stands in the research area include a 45-year-old plantation of *Pseudotsuga menziesii* bordered by a somewhat younger, dense stand of red alder (*Alnus rubra* BONG.). The original forest was removed between 1910 and 1925 (COLE and GESSELL 1968).

Sampling and extraction of mesofauna differed among the sites only in details. Soil and litter samples were taken as a constant dimension of forest floor and volume and extraction was by some modification of Tullgren funnels with cooling to increase the temperature-humidity gradient within the sample. In the Douglas fir forest, 15 samples were taken at each sampling, each 20 cm^2 in area. Each sample was taken in 5 cm depth increments to 15 cm depth. Extraction was for seven days with the funnels being inside refrigerators maintaining 15 °C. The H. J. Andrews forest was sampled seven times and the Cedar River forest four times from August 1972 through July 1973.

Both Coweeta workers took 0.01 m^2 samples and extracted on Tullgren funnels kept at room temperature but with the bases of the vials submerged in cold water. Collecting just the organic layers of the mixed-oak forest floor, GIST took nine samples in each of the four seasons and extracted for five days. CORNABY, working in the white pine forest, took twelve samples in each of the four seasons beginning September 1971 and ending with a second fall sampling in October 1972. Combined L, F and H layers of the forest floor were taken and extraction was for seven days.

METZ stratified samples from the loblolly pine stand into L, F and H organic layers plus the surface 3 cm of the A_1 soil horizon. Each sample was 20 cm^2 in area. Fifty-four samples were taken on each of twelve sampling dates and extracted for seven days on the MURPHY (1955) modification of Tullgren funnels.

Twenty soil cores were taken each month for one year from the cove hardwood forest by MCBRAYER. Each core had a surface area of 20 cm^2 and volume of 300 cm^3 and included both organic and mineral soil horizons. Extraction was for 72 hours on refrigerated Tullgren funnels.

posite, one-liter sample each month at Oak Ridge. Each sample was processed by a combination of decanting, sieving and Baermann funnel extraction. KITAZAWA and associates sampled the mature fir forest eleven times and the fir plantation four times. Each sample consisted of fifteen 25 cm^3 replications at each of four, 4 cm deep, increments. Extraction was for one week using Baerman funnels.

Macrofauna were sampled at Oak Ridge by taking ten 0.1 m^2 litter samples monthly with Tullgren extraction for 72 hours. The white pine stand at Coweeta was sampled five times by removal of twenty-four 1 m^2 litter samples. Samples were hand-sorted to assess populations. The mixed oak stand was sampled for macroarthropods by means of a grid of 25 pit-fall traps within a 25 m^2 area enclosed by an aluminium foil barrier and covered with a sticky resin to discourage migration.

The mature fir forest was sampled seven times and the plantation four times for macroarthropods. Each sample consisted of fifteen replicates of 625 cm^2 to a depth of 20 cm, including mineral soil. Samples were first hand-sorted and then extracted with large Tullgren funnels.

3. Results and discussion

3.1. Densities

Populations of decomposer invertebrates are not static but may vary as much as fourfold on an annual basis (Table 2). The range of variability is not constant between ecosystem types and, consequently, annual means offer the best ground for comparison. By first comparing the so-called natural systems, it can be seen that the densities found in the eastern cove hardwood forest are quite similar to the western Douglas fir forest. The oak forest is similar when corrected for exclusion of soil forms. Net primary productivities do not differ significantly among the three, being in the range of 1.3 to 1.4 kg dry matter $yr.^{-1}$ and, presumably, annual decomposition approaches net primary productivity, since each represents the final stage of the local sere.

Successional stages, including plantations, attain maximum productivities within a relatively short period but standing crop increases well beyond the attainment of maximum productivity (WHITTAKER 1970). This implies that decomposition is less than net production during the development of a forest and if there is less to decompose, one would expect fewer organisms to decompose it. This is exactly what is seen in comparing the Douglas fir plantation to the mature, 450-year-old stand. At almost all samplings, populations at Cedar River were approximately 50% of those at the H. J. Andrews forest.

The white pine plantation at Coweeta is adjacent to the mature oak stand and replaced an oak stand presumably identical to its neighbor. Maximum and mean densities were ~50% of those in the oak forest although the minimum densities were similar. More im-

Table 2. Seasonal densities of soil and litter arthropods in six contrasting forests of the United States

Forest	Density ($10^4/m^2$)					Data points
	Spring	Summer	Fall	Winter	Annual mean	
Mixed oak[1])	8.0 (11.4)	2.8 (4.0)	9.5 (13.8)	5.8 (8.3)	6.5 (9.3)	4
Plantation white pine[1])	4.0	3.6	3.1	3.7	3.6	4
Mature loblolly pine[2])	10.7	10.4	26.5[3])	14.4	13.7	12
Cove hardwood	10.2	6.0	12.2	7.1	9.7	12
Mature Douglas fir	7.4	4.6 (1972) 12.3 (1973)	8.7	10.7	8.8	7
Plantation Douglas fir	6.6	2.6	2.8	5.1	4.3	4

1) forest flor only, ( ) = estimated density including soil forms
2) microarthropods only.
3) minimum density, 6.2×10^4, occurred late summer/early fall

Taxa	Mature mixed oak		Plantation white pine	
	biomass (mg m^{-2})	%	biomass (mg m^{-2})	%
Collembola	502	46.5	170	3.7
Cryptostigmata	192	17.6	650	14.3
Mesostigmata	37	3.4	70	1.5
Aranea	150	13.8	120	2.6
Chilopoda	5	0.5	—	—
Diplopoda	35	3.2	3170	69.5
Tettigoniidae	10	0.9	120	2.6
Pulmonata	150	13.8	250	5.5

portantly, the arthropods present on the two watersheds differ taxonomically and in the relative proportions of higher taxa (Table 3). For example, Collembola dominated the pine plantation fauna, comprising 46.5% of the biomass. In the oak forest, Collembola averaged only 4% of the decomposer invertebrate biomass which was dominated by millipedes. Conifer litter is more slowly decomposed than deciduous litter (Miller 1974) as a result of relatively low base status and the presence of relatively more recalcitrant materials such as waxes, resins and lignin. Different substrates require different strategies and, consequently, the presence of different fauna on adjacent watersheds is not surprising. This brings us to a possible explanation for the consistently higher invertebrate densities in the loblolly pine forest. The forest is now a mature subclimax and has a dense, hardwood understory. Consequently, litter production from the pines is at the maximum and there is an increasing annual input from the deciduous species. If differing species of invertebrates are involved in decomposition of the two kinds of litter, it is possible that the higher densities result both from the diversity of substrate (yielding more kinds of animals) and the abundance of mate rial to decompose (supporting more individuals). This hypothesis is supported by additional data of Cornaby et al. (in press).

It has been said that litter decomposes at a rate directly related to the number of invertebrate animals in the litter and underlying soil (Edwards et al. 1970). Our results would tend to rephrase the statement to say that the numbers of invertebrate animals present is dependent upon the amount and decomposability of the litter present.

Seasonal distribution of decomposer invertebrates varied among sites according to local climatic differences. Within the southeastern states, invertebrate populations tended to be bimodal with lows during late winter when the soil was both cold and saturated and in late summer when sustained high evapo-transpiration had reduced soil and litter moistures to an annual minimum. Douglas fir forests exist in a temperate, marine climate characterized by a winter rainy season and a summer drought. Consequently, the decomposer invertebrates tended to show a single annual cycle which was attributable to moisture availability.

3.2. Vertical distributions

Decomposer invertebrates migrate from the litter layers into the mineral soil and back with both circadian and annual cycles. Fig. 1 illustrates the seasonal vertical distribution of oribatid mites in the loblolly pine plantation. The L layer is a dry zone of undecomposed needles which never contains more than 3% of the oribatid population. The F layer is the zone of active decomposition and the H layer represents highly decomposed material of little nutritive value to the mites. The F layer is subject to occasional desiccation while the colloidal nature of the H layer retains moisture even in the driest part of the year. Consequently, the F layer is the layer of choice because the preferred food is there but the H layer becomes a zone of refuge when the F layers drys out. The oribatids tend to be found in the F layer during the wetter period of May to September and in the H layer during the drier autumn.

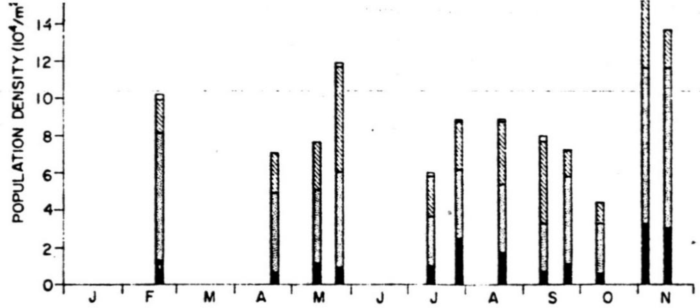

Fig. 1. Vertical distributions of oribatid mites in the forest floor of a loblolly pine plantation near Charleston, South Carolina.

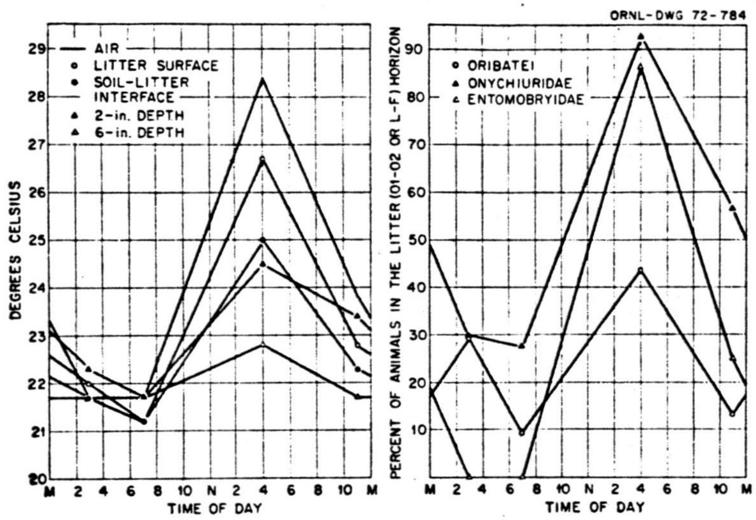

Fig. 2. Circadian vertical migrations of soil and litter microarthropods are apparently influenced by temperature profiles. Data are from August in a cove hardwood forest near Oak Ridge, Tennessee.

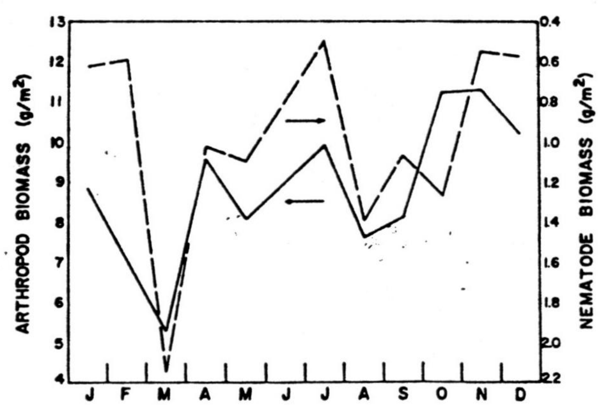

Fig. 3. Interaction of microarthropod and nematode biomass on a seasonal basis. Data are from a cove hardwood forest near Oak Ridge, Tennessee.

batid mites are less mobile and ranged from 10% to 42% in litter over the same period. Also, the oribatids are a more diverse group having many members which seldom enter the litter layers (LUXTON 1972).

3.3. Nematodes versus microarthropods

One of the more tantalizing observations emerging from these studies was an apparent interaction between microarthropods and nematodes in the cove forest (Fig. 3). The biomass of nematodes virtually mirrored the biomass of microarthropods throughout the year. That is, when microarthropods were abundant, nematodes were not. and vice versa. The correlation coefficient, −0.602, is significant ($P < 0.05$). Terrestrial nematodes are, in fact, aquatic organisms which operate in the interstitial soil water. Water-logging of soils in winter, while suppressing microarthropods, might increase habitat available to certain nematode species and could explain the strong interaction into March. The interaction remains strong through the summer while soil water is a nearly constant 35%. As the soil begins to dry in late summer, both nematodes and microarthropods decline and this similarity reduces the value of the overall negative correlation coefficient. Our data are not yet complete enough to place too much confidence in this relationship, but if the hypothesis is verified, it would indicate resource partitioning leading to an area rich in theoretical implications.

Similar interactions were not observed in the Douglas fir forests. Because of the seasonality of moisture availability, populations of both microarthropods and nematodes were related to moisture. Nematode numbers ranged from a low of 6.0×10^5 m^{-2} in August to a high of 2.2×10^6 m^{-2} in April with an annual mean of 1.3×10^6 m^{-2}. By contrast, the cove hardwood forest, with well-distributed precipitation, averaged 2.5×10^6 nematodes m^{-2} with a range of 1.1×10^6 to 6.9×10^6.

4. Summary and conclusions

The range of forest-floor invertebrate population densities reported in the literature is approximately 2×10^3 m^{-2} (BORNEBUSCH 1930) to 8×10^5 m^{-2} (MURPHY 1953) for temperate regions. All of the studies reported here fall within that range, but that really doesn't tell us very much. That range incorporates not only actual differences in densities but seasonal variations and differences in efficiency of estimation as well. The studies reported here represent a higher level of comparability by the inclusion of seasonal variation and the use of essentially the same estimation techniques.

That diverse forest types having similar litter production rates should produce similar invertebrate densities and that successional forests having lesser litter production should produce lower densities tends to point to litter production as the determiner of invertebrate populations, rather than the number of invertebrates present determining litter standing crops. But why should a forest in transition from conifer to hardwood have the highest densities of all? We suspect that the fauna associated with the decomposition of loblolly pine has experienced a significant increase over the younger, more-vigorous stage as pine litter fall increases due to the maturation and incipient decline of that component of the forest. In addition, the annual input of deciduous litter supports a separate fauna which is rapidly approaching its maximum density. We would be eager to see this hypothesis examined more closely.

Vertical migrations of decomposer invertebrates is viewed as a strategy to exploit a resource occurring in an intermittantly unfavorable environment. Unpublished work by one of us (J. F. McB.) has previously demonstrated that these organisms are relatively insensitive to thermal gradients when the normally concomitant humidity gradient is neutralized. Thus, it would appear that the environmental clue for vertical migrations is the moisture gradient and that the strong correlation with temperature (Fig. 2) is a secondary relationship.

Finally, there is a temptation to overindulge in speculation on the relationship between nematodes and microarthropods in the cove hardwood forest. Where climatological parameters permit the year to be partitioned by different functional groups, several advantages accrue to the popuedaphic microarthropods either feed directly on bacteria or harvest bacteria along with the plant remains they ingest. The activity pattern shown in Fig. 3 could result in reduced competition. It is also possible that the negative correlation is purely coincidental since the data represent only one year. Nevertheless, we find the data to be provocative and look forward to further clarification of cause and effect.

5. Literature

AUSMUS, B. S., 1974. Litter and soil microbial dynamics in a deciduous forest stand. Ph. D. Thesis, University of Tennessee. 183 pp.

AUSMUS, B. S., R. FERRIGNI and J. F. MCBRAYER (in press). Microcosm assessment of the role of litter-inhabiting fauna on decomposition processes. Soil Biol. Biochem.

BORNEBUSCH, C. H., 1930. The fauna of forest soil. Forst. ForsVaes. Danm. **11**, 1—224.

COLE, D. W., and S. P. GESSELL, 1968. Cedar River research: a program for studying the pathways, rates and processes of elemental cycling in a forest ecosystem. Univ. Washington Coll. Forest Resources Monograph, Contrib. No. 4, Seattle. 53 pp.

CORNABY, B. W., 1973. Population parameters and systems models of litter fauna in a white pine ecosystem. Ph. D. Thesis, University of Georgia. 98 pp.

CORNABY, B. W., C. S. GIST and D. A. CROSSLEY, Jr., 1975. Resource partitioning in leaf-litter faunas from hardwood and hardwood-converted-to-pine forests. In: F. G. HOWELL, J. B. GENTRY and M. H. SMITH (eds.). Mineral cycling in southeastern ecosystems. ERDA Symposium Series. (CONF-740513). pp. 588—597.

DYRNESS, C. T., J. F. FRANKLIN and W. H. MOIR, 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. US/IBP Coniferous Forest Biome, Ecosystem Anal. Studies Bull. **4**: 123 pp. + viii.

EDWARDS, C. A., and G. W. HEATH, 1963. The role of soil organisms in the breakdown of leaf material. In: J. DOEKSEN and J. VAN DER DRIFT (eds.). Soil organisms. North Holland Publ. Co., Amsterdam. pp. 76—84.

EDWARDS, C. A., D. E. REICHLE and D. A. CROSSLEY, Jr., 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: D. E. REICHLE (ed.). Analysis of temperate forest ecosystems. Springer-Verlag, Berlin. pp. 147—172.

GIST, C. S., 1972. Analysis of mineral pathways in a cryptozoan foodweb. Ph. D. Thesis, University of Georgia. 151 pp.

KURČEVA, G. F., 1960. Rol' počvennych životnych v razloženii dubovogo opada. Počvovedenie **4**, 16—23.

KURČEVA, G. F., 1964. Wirbellose Tiere als Faktor der Zersetzung von Waldstreu. Pedobiologia **4**, 8—30.

LUXTON, M., 1972. Studies on the oribatid mites of a Danish beech wood soil. Pedobiologia **12**, 434—463.

MCBRAYER, J. F., 1973a. Exploitation of deciduous litter by *Apheloria montana* (Diplopoda: Eurydesmidae). Pedobiologia **13**, 90—98.

MCBRAYER, J. F., 1973b. Energy flow and nutrient cycling in a cryptozoan foodweb. Ph. D. Thesis, University of Tennessee. 78 pp.

METZ, L. J., and M. H. FARRIER, 1973. Prescribed burning and populations of soil mesofauna. Environ. Entomol. **2**, 433—440.

MILLAR, C. S., 1974. Decomposition of coniferous leaf litter. In: C. H. DICKINSON and G. J. F. PUGH (eds.). Biology of plant litter decomposition I. Academic Press, London. pp. 105—128.

MURPHY, P. W., 1953. The biology of forest soils with special reference to the mesofauna or meiofauna. J. Soil Sci. **4**, 155—193.

MURPHY, P. W., 1955. Note of processes used in sampling, extraction and assessment of the mesofauna of heathland. In: D. K. McE. KEVAN (ed.). Soil zoology. Academic Press, New York. pp. 338—340.

REICHLE, D. E., J. F. MCBRAYER and B. S. AUSMUS, 1975. Ecological energetics of decomposer invertebrates in a deciduous forest and total respiration budget. In: J. VANĚK (ed.). Progress in soil zoology. Junk B. V. Publ., The Hague. pp. 283—292.

VAN DER DRIFT, J., and M. WITKAMP, 1960. The significance of the breakdown of oak litter by *Enoicyla pusilla*, Burm. Arch. Neerl. Zool. **13**, 486—492.

WALLWORK, J. A., 1970. Ecology of soil animals. McGraw-Hill, London. 283 pp.

WHITTAKER, R. H., 1970. Communities and ecosystems. Macmillan, New York. 159 pp.

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