

LITTER PRODUCTION AND ACCUMULATION IN
NATURALLY SEEDED, OLD-FIELD, VIRGINIA PINE
(PINUS VIRGINIANA MILL.) STANDS

by

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INTRODUCTION

Virginia pine (Pinus virginiana Mill.) occurs widely as a pioneer species with a range of approximately 200 miles either side of the Appalachian Mountain Range and includes the Piedmont of Virginia and North Carolina. This species is commonly found on abandoned fields, borrow pits, roadsides and other disturbed sites. Prior to about 1910 Virginia pine was not considered for commercial use. There has been increasing utilization of Virginia pine for pulp wood and saw-timber as other species of pine were and are harvested at rates exceeding growth. The widespread distribution of Virginia pine coupled with increasing harvest rates makes this species one whose impact on site development is important.

Virginia pine frequently becomes established on sites where the litter-layer is absent or the mineral soil contains inadequate amounts of organic matter. Litter-fall is a process that results in site modification by the establishment of a litter-layer which is subject to decomposition and movement into the soil horizons thereby increasing the amount of organic matter in the mineral soil as well as releasing nutrients for continued forest growth. The litter-layer also acts as a buffer protecting the underlying soil from fluctuating temperatures and from the erosive forces of rainfall.

The objective of this study was to measure litter-fall and litter-accumulation in a series of naturally seeded, old-field, Virginia pine stands and to use this data to develop a model which characterizes the accumulation and decomposition of Virginia pine litter in the study area.

LITERATURE REVIEW

Litter-fall is the detritus (leaves, needles, twigs, bark, fruit, cones, seed, etc.) added to the litter-layer from the above ground portion of the forest. The average oven-dry weight of litter production in the warm temperature zone between latitudes 30° and 40° has been estimated to be 5.5 metric tons/ha/yr (Bray and Gorham, 1964). This litter comprises 3.6 metric tons/ha/yr leaves and 1.9 metric tons/ha/yr other material (twigs, bark, fruit, cones, seed, etc.). Rodin and Bazilevich (1967) reported that litter-fall does not vary greatly from community to community in coniferous forests. They indicated that the coniferous forest produces between 2 and 7 metric tons/ha/yr of litter-fall and that needles make up 53-90% of the total with the higher percentages tending to young stands. At or beyond stand maturity total litter production may increase and the contribution of non-needle material will attain a larger percentage of the total. McGinnis (1958) reported litter production in a 15-year-old Virginia pine stand as 4.5 metric tons/ha/yr of which 3.8 metric tons/ha/yr was needles and 0.7 metric tons/ha/yr was non-needle material.

Heyward and Barnette (1936) concluded that stand density of long-leaf pine (Pinus palustris Mill.) did not have any consistent relationship to litter production for stands of 889, 1161, 1947 and 2402 trees/ha. Bray and Gorham (1964) pointed out that if a closed-canopy forest is thinned there is an initial decrease in litter production which is roughly proportional to the degree of thinning, but that as the canopy recloses production will increase to former levels.

The pine forests of the temperate zone normally exhibit a seasonal pattern of needle litter-fall with the maximum occurring in late summer or autumn (Miller and Hurst, 1957; Ando, 1970; Moir, 1972; Nemeth, 1973). Erratic fall of relatively fresh litter (green needles, live twigs and branches) frequently results from wind and rain storms.

The litter-layer or forest floor is made up of organic matter (living and dead) and mineral matter. Variations in weight, thickness and water storage of the litter-layer exist within and between stands and have been explained on the basis of species, stand density, age, site, and climate (Alway, et al., 1933; Kittredge, 1948; Metz, 1954; Mader and Lull, 1968; Wooldridge, 1970; Metz, et al., 1970). When comparing the organic matter weight of the litter-layer the total weight of forest floor is preferable to subdividing litter into individual layers, based on stage of decomposition, because separation is often very difficult (Metz, et al., 1970).

Replenishment and decomposition of the forest floor is a dynamic phase of the forest ecosystem. Development and maintenance of the litter-layer is critical in preventing overland-flow and erosion on forested watersheds (Loudermilk, 1930; Lull and Reinhart, 1972). The rate of rehabilitation of waste-lands and eroded areas varies with the quantitative and qualitative litter producing capacity of the invading vegetation (Daubenmire, 1953). Metz (1954) pointed out that the weight of the forest floor is a reflection of the decomposition rate and that pine litter decomposes at a slower rate than does that of hardwoods.

A volatile matter weight (loss on ignition at 525°C) of 16.54 mt/ha

and litter-layer depth of 2.79 cm was found by Metz, et al. (1970) for a 16-year-old plantation of Virginia pine with an average diameter breast height of 12.19 cm, average height of 11.28 meters and density of 2,990 stems/ha. Litter-layer organic matter content averaged 29 mt/ha and 6.35 cm deep for 65 white pine (Pinus strobus L.) stands, in Massachusetts, ranging from 34 to 96 years in age and 21.12 to 70.94 m²/ha basal area (Mader and Lull, 1968). Litter-layer depths of 6.60 cm, 3.81 cm, and 2.79 cm for stands of loblolly pine (Pinus taeda L.), shortleaf pine (Pinus echinata Mill.) and white pine respectively were reported by Metz et al. (1970).

The water storage capacity of the litter-layer serves as a moisture source for the roots of trees growing in it as well as providing a favorable medium for organisms responsible for the decomposition of organic matter. Clary and Ffolliott (1969) showed that the water storage capacity of a ponderosa pine (Pinus ponderosa Laws.) stand in Arizona was .223 cm for a 4.06 cm deep litter-layer. Bernard (1963) reported a water storage capacity of .127 cm for a 1.78 cm deep pine-oak litter-layer in New Jersey. The water storage capacity of the litter-layer of a 12-year-old loblolly pine plantation was .229 cm in a 5.08 cm layer of decomposed needles (Metz, 1958).

METHODS

Stand Selection and Measurement

The stands of old-field Virginia pine used in this study are located in the foothills of the Blue Ridge Mountains at the Reynolds Homestead Research Center, Critz, Virginia. A series of four naturally seeded stands were selected. Stand I (youngest) contained approximately 136,000 stems per hectare and because of this extremely high stocking stand measurements of DBH, density, height and age at the base were obtained for five, .25 m², randomly selected quadrates. The presence of cut Virginia pine stumps in Stand I indicated that the current stand was not the first generation to occupy the site after it was abandoned for agricultural use. A tally of the number of stumps and their diameters was taken in three, 2 x 5 meter plots selected at random in the stand. In Stands II through IV, 1/40 ha plots were established, DBH measured on all trees while total height and age at the base were determined on five harvest trees per stand, representing the range of diameters in each plot. Two plots were established in Stand II, one of which had been thinned to 50% of its original basal area three months prior to the start of this study.

Understory vegetation was sparse or absent in these stands and was not inventoried.

Litter-fall Collections

Ten litter traps, .25 m² area with 4 cm sides, were placed at random in each plot in stands II through IV. Ten litter traps, 154 cm² in area

with 1 cm sides, were placed at random within stand I. Small traps were necessary in stand I since tree density precluded the use of larger traps. Trap construction was plastic with perforated bottom for the small traps while the larger traps were of plastic screening and wood.

Litter-fall was trapped from fall 1970 to fall 1971. Stand I traps were not moved during the collection period because of stand density and configuration. The traps in stand II through IV were repositioned at random after each collection. Intervals between collections varied from 5 to 61 days with the shorter periods occurring when litter-fall was greatest. The material collected was separated into brown needles, green needles, and non-needle material. In this study non-needle material represents twigs, bark, cones, seeds, and needles and leaves of species other than Virginia pine. The amount of green needles, collected for any one interval, was very small so this material was composited into 2 samples, each representing 5 traps, before weighing. The same combining procedure was used for non-needle material. The litter was oven dried at 70°C to a constant weight. Loss on ignition was obtained using ground samples and a muffle furnace set at 525°C until combustion was complete (3 to 6 hours).

Litter-Layer Collections

Ten, 154 cm² in area, randomly selected samples of the litter-layer were obtained from each stand in the spring after the litter-fall collections had begun. After a 4.14 cm rain and the application of an additional 5 liters of water to approximately a .20 m² area over each sample point, a plastic container with a 154 cm² opening was driven to mineral

soil (open end down) and left over-night to allow for gravity drainage to occur. The litter-layer was then removed, placed in a plastic container, sealed and weighed. The samples were dried at 70°C to a constant weight. The depth to mineral soil was measured at the mid point of each side of the hole left by removal of the sample. There was no observed compaction of the remaining litter-layer resulting from the process required to remove the litter-layer samples.

Loss on ignition of the litter-layer was obtained as described above except a longer period (4 to 8 hours) for complete combustion was required. A fire in the drying ovens where the samples were being stored prior to the loss on ignition test reduced the number of samples to seven from stand I, nine from stand IIA, eight from stand IIB, seven from stand III and nine from stand IV.

RESULTS

Stand Characteristics

Stand age ranged from 7 to 36 years, at the base of the main stem, and mean diameter breast height from 1.19 cm to 12.60 cm for the youngest and oldest stands respectively (Table 1). The number of stems per hectare varied from 136,000 in the youngest stand, which is abnormally high, to 2,500 in the oldest stand. Maximum height of 14.52 meters was found in the oldest stand while maximum basal area of 33.40 m²/ha occurred in the 19-year-old stand. The results of the sampling of the cut stumps in the youngest stand revealed that the previous stand contained approximately 5,000 stems/ha, with a mean diameter of 11.7 cm. An age estimate at time of cutting of the previous rotation on the youngest stand site was obtained by deriving relationships of age to diameter and age to density for the three oldest unthinned stands and applying these to the cut stump data and averaging the results over all six solutions to give an estimated age of 27 years.

Litter-fall

Annual total litter-fall (dry weight) ranged from 2.90 mt/ha to 5.49 mt/ha (Table 2). The greatest amount of total litter-fall occurred in the oldest stand. Brown needle litter-fall (dry weight) for the year ranged from 2.31 mt/ha to 3.37 mt/ha. The largest amount of litter-fall as brown needles occurred in the 19-year-old stand. Brown needles contributed from 50.5% to 82.1% of the total yearly litter-fall while green leaves accounted for 1.4% to 10.4% and non-needle material made

Table 1. Characteristics of four, old-field Virginia pine stands.

Stand	Notes	Age Years	No. Trees Per ha.	Height m.	Basal Area ^{1/} m ² /ha	Average ^{1/} Diameter cm.
I	2nd stand ^{2/}	7 ^{3/}	136,000	2.56 ^{3/}	15.12	1.19
IIA	-	13 ^{4/}	8,280	7.06 ^{4/}	25.51	5.69
IIB	Thinned	13 ^{4/}	3,160	7.74 ^{4/}	16.11	7.90 ^{5/}
III	-	19 ^{4/}	7,120	9.68 ^{4/}	33.40	7.31
IV	-	36 ^{4/}	2,500	14.52 ^{4/}	31.61	12.60

^{1/}At a point approximately 1.36 meters above the ground.

^{2/}Previous stand estimated to have been harvested at age 27, density 5,000 trees/ha, and 11.7 cm. average diameter.

^{3/}Determined by five, .25 m², harvest quadrates.

^{4/}Determined by five harvest trees per stand, representing the range of diameters in each plot.

^{5/}Residual trees only.

Table 2. Estimated annual litter-fall in four old-field Virginia pine stands.

Stand	Age	Stocking Stems/ha	Brown Needles ^{1/}		Green Needles ^{2/}		Non-needle ^{2/}		Total ^{2/}	
			mt/ha (Dry Weight)	% of Total	mt/ha (Dry Weight)	% of Total	mt/ha (Dry Weight)	% of Total	mt/ha (Dry Weight)	
I	7	136,000	2.38 ^c	± 0.249	82.1	.04	1.4	.48	16.5	2.90
IIA	13	8,280	3.31 ^a	± 0.229	77.9	.43	10.1	.51	12.0	4.25
IIB	13	3,160	2.31 ^c	± 0.146	78.0	.30	10.2	.35	11.8	2.96
III	19	7,120	3.37 ^a	± 0.184	66.1	.54	10.4	1.19	23.3	5.10
IV	36	2,500	2.77 ^b	± 0.308	50.5	.31	5.6	2.41	43.9	5.49

^{1/} Brown needle means with the same super scripts are not significantly different using Duncan's Multiple Range Test at the .05 significance level. The 95% confidence interval is included.

^{2/} Statistical analysis not performed due to compositing of samples.

up 11.8% to 43.9%. The fraction of litter-fall in brown needles decreased with increasingly older stands, green needles was lowest in the youngest stand while non-needle material increased as stand age increased (Figure 1).

Thinning in the 13-year-old stand caused a marked reduction in all components of the litter-fall when compared to the unthinned stand (Table 2) but the fraction that each component made to the total was only slightly changed.

Maximum litter-fall occurred in the months of September through December (Figure 2). During this period 62.5% to 67.1 % of the annual brown needle litter fell while green needles and non-needle material contributed a considerably smaller fraction to the yearly totals (Table 3).

The fraction of each component of litter-fall when computed as a weighted monthly average over all stands varied throughout the year (Figure 3). Brown needles consistently accounted for the major fraction of the litter-fall except in the month of January. Total needle-fall (brown plus green) constituted, however, the greatest fraction for all months.

The yearly distribution of green needle litter-fall tended to be greatest during the period December through March when from 25.0% to 61.3% of the yearly total occurred. The non-needle material falling during this interval accounted for 35.4% to 56.3% of the annual total of such material (Table 4).

Litter accumulating on the forest floor increased to a maximum dry matter, volatile matter, depth and maximum cm of water storage capacity

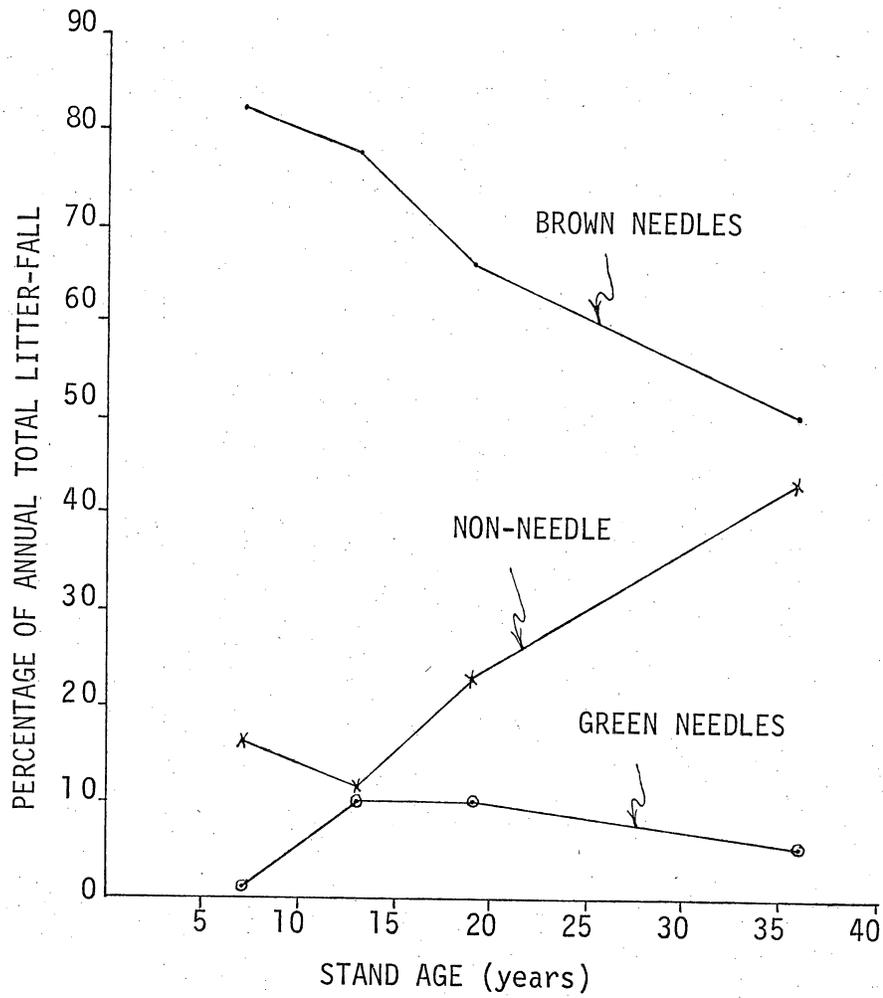


Figure 1. Components of litter-fall as a percentage of annual total litter-fall in four unthinned old-field Virginia pine stands.

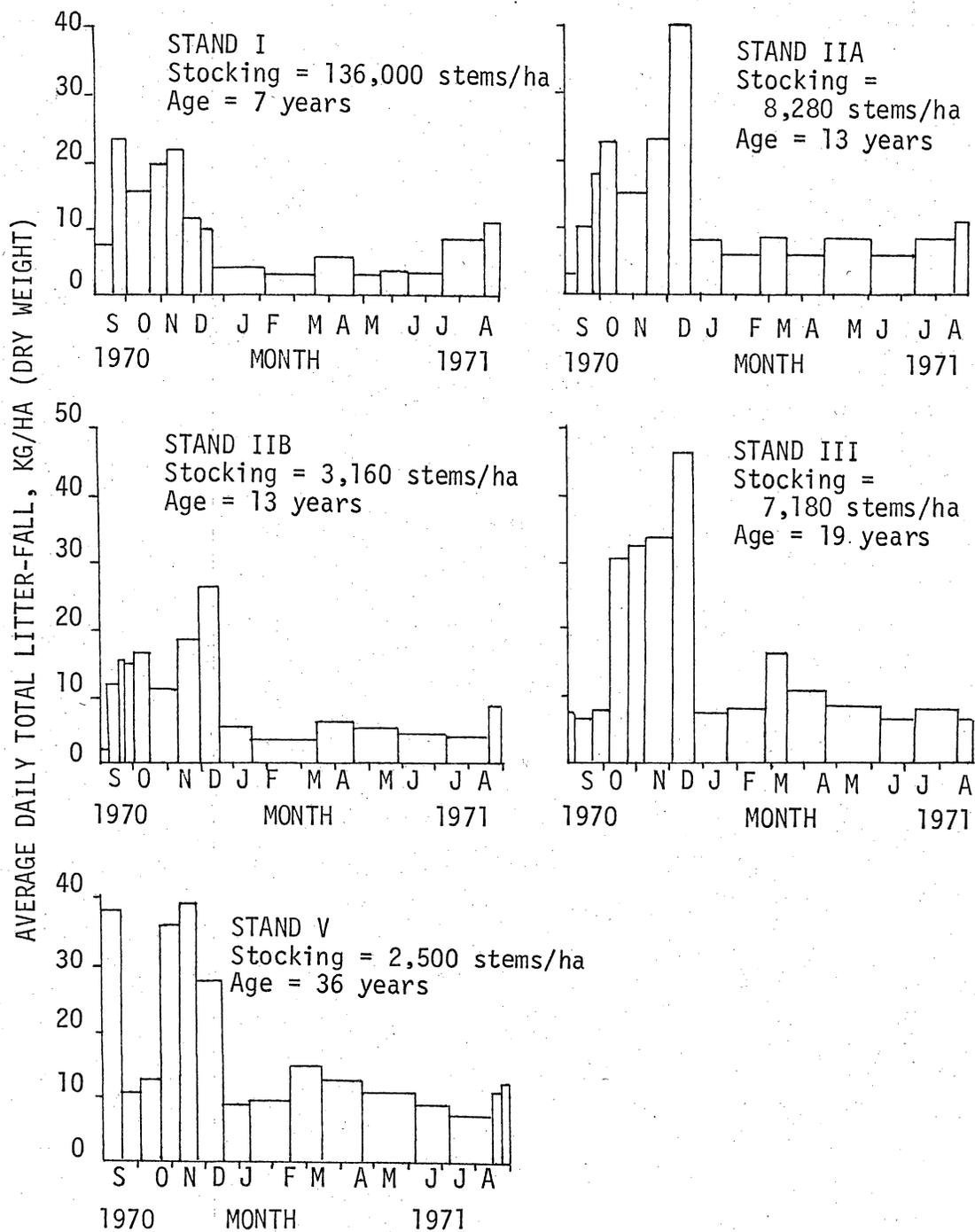


Figure 2. Annual distribution of average daily total litter-fall per collection interval in old-field Virginia pine stands.

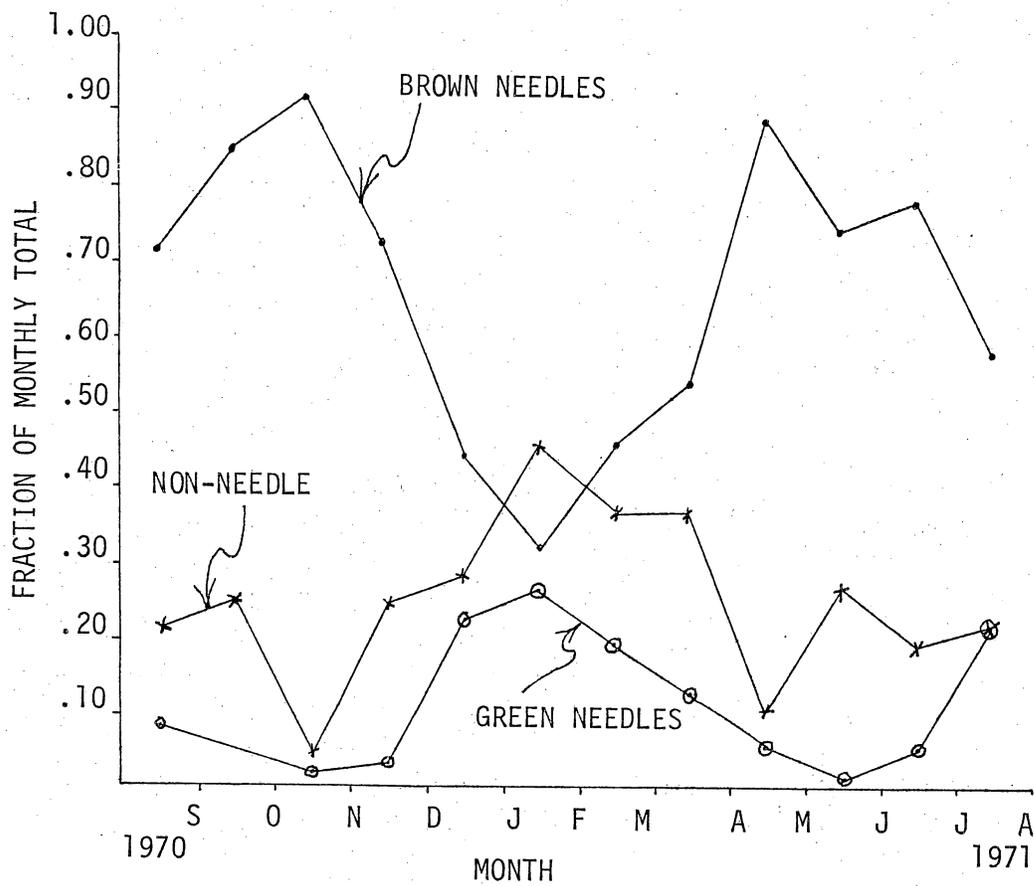


Figure 3. The fractional contribution of brown needles, green needles, and non-needle material per month as a weighted average in four old-field Virginia pine stands.

Table 3. Total litter-fall, brown needle litter-fall, green needle litter-fall, and non-needle litter-fall for the period September - December, 1970.

Stand	Brown Needles ^{1/}		Green Needles ^{2/}		Non-Needle ^{2/}		Total ^{2/}		
	mt/ha (Dry Weight)	% of yearly brown Needles	mt/ha (Dry Weight)	% of yearly green Needles	mt/ha (Dry Weight)	% of yearly Non-needle	mt/ha (Dry Weight)	% of yearly TOTAL	
I	1.50 ^c	± 0.203	63.0	.02	50.0	.19	39.6	1.71	59.0
IIA	2.07 ^a	± 0.197	62.5	.10	23.2	.19	37.3	2.36	55.5
IIB	1.55 ^c	± 0.149	67.1	.10	33.3	.18	51.4	1.83	61.8
III	2.19 ^a	± 0.177	65.0	.12	22.2	.51	42.8	2.82	55.3
IV	1.79 ^b	± 0.294	64.6	.08	25.8	1.27	52.7	3.14	57.2

^{1/} Brown needle means with the same super scripts are not significantly different using Duncan's Multiple Range Test at the .05 significance level. The 95% confidence interval is included.

^{2/} Statistical analysis not performed due to compositing of samples.

Table 4. Green needles and non-needle litter-fall for the period December through March 1971.

Stand	Green Needles ^{1/} mt/ha (Dry Weight)	Percent of Yearly Green Needles	Non-Needle ^{1/} mt/ha (Dry Weight)	Percent of Yearly Non-Needle
I	.01	25.0	.17	35.4
IIA	.23	53.5	.22	43.1
IIB	.17	56.7	.15	42.8
III	.31	57.4	.67	56.3
IV	.19	61.3	.78	32.4

^{1/}

Statistical analysis not performed due to compositing of samples.

in the 36-year-old stand (Table 5). The 7-year-old stand had exceptionally high values of dry matter, volatile matter, depth and maximum cm of water storage for its age which can be explained by the existence of a previous Virginia pine stand on the site. Greatest maximum water storage per centimeter of depth occurred in the thinned stand and is probably due to the compaction resulting from trampling during the thinning operation.

The ratio of litter-fall to litter-layer decreased with increasing stand age in the unthinned primary stands (Figure 4).

Table 5. Dry matter weight, volatile matter weight, depth, maximum centimeters of water storage, and maximum centimeters of water storage per centimeter of depth, with 95% confidence limits, in four old-field Virginia pine stands.

Stand	Age	Dry Matter weight (mt/ha)	Volatile Matter weight (mt/ha)	Depth (cm)	Maximum cm. of water storage (Based on Volatile Matter)	Maximum cm. of water storage per cm. of depth.
I	7	105 ^b ^{1/} ± 38	23.6 ^b ± 8.7	3.45 ^b ± .53	.66 ^c ± .20	.191 ^c ± .032
IIA	13	45 ^c ± 7	17.9 ^c ± 3.5	2.60 ^c ± .41	.54 ^c ± .08	.210 ^c ± .023
IIB	13	43 ^c ± 9	15.0 ^c ± 4.0	1.65 ^d ± .40	.54 ^c ± .12	.330 ^a ± .068
III	19	76 ^{bc} ± 14	33.6 ^b ± 9.0	3.86 ^b ± .66	1.09 ^b ± .19	.282 ^b ± .020
IV	36	139 ^a ± 37	52.0 ^a ± 5.5	5.34 ^a ± .65	1.42 ^a ± .16	.265 ^b ± .044

^{1/} Those means within each column having a common superscript letter(s) are not significantly different using Duncan's multiple range test at the 5% level of significance.

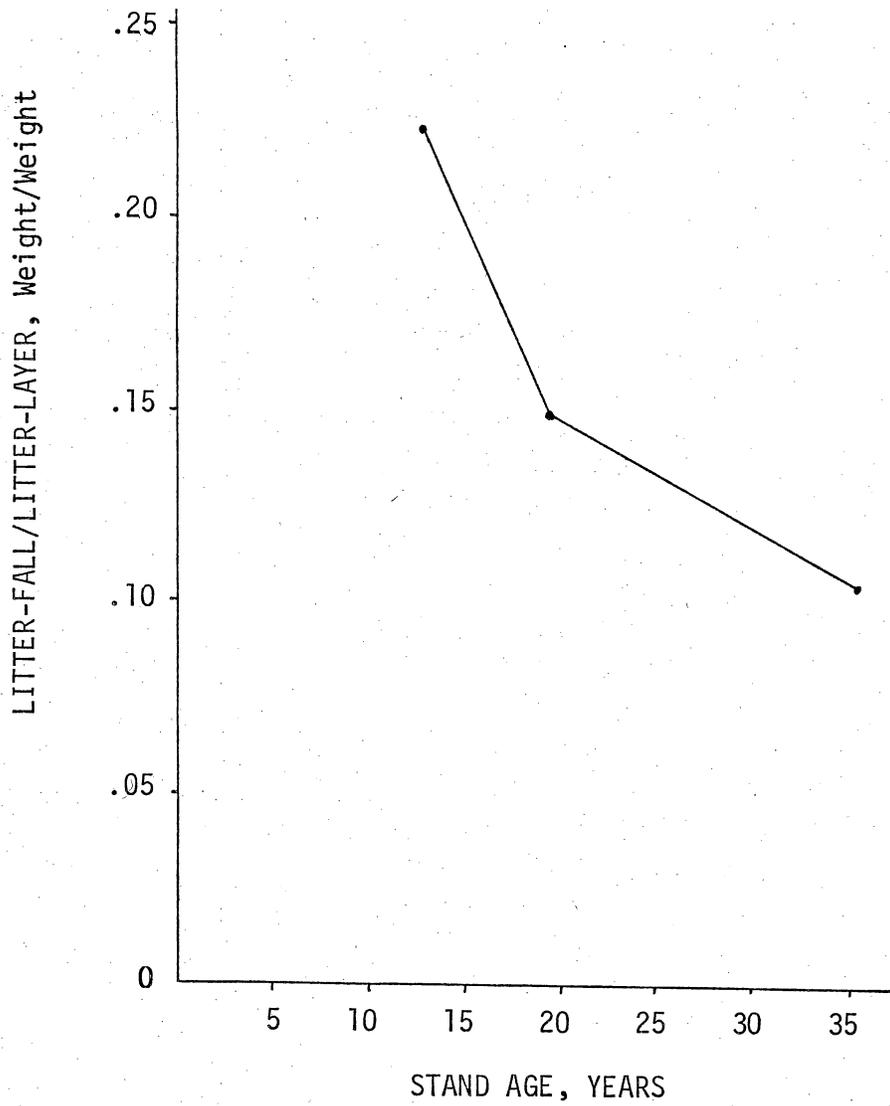


Figure 4. The ratio of litter-fall to litter-layer volatile matter weight in three unthinned old-field Virginia pine stands.

DISCUSSION

Annual production of total litter-fall is within the limits of 2 to 7 metric tons per hectare which is characteristic of the coniferous forest according to Rodin and Bazilevich (1967). The 4.25 mt/ha/yr estimate of total litter production for the unthinned 13-year-old stand is very near the estimate of 4.5 mt/ha/yr for a 15-year-old Virginia pine stand in Tennessee (McGinnis, 1958). The decrease in needles as a fraction of total litter-fall with increasing stand age is indicative of stand maturation (Bray and Gorham, 1964). The seasonal pattern of needle-fall is typical of coniferous species at this latitude (Bray and Gorham, 1964). With the exception of the youngest stand there was a noticeable contribution of green needles in the litter-fall which amounted to 9 percent of the total needle-fall. The relatively small amount of green-needle fall in the youngest stand can be explained by the fact that the stand was surrounded by older, taller stands which offered protection from wind.

The litter-layer volatile matter weight, depth and maximum water storage capacity reported here are comparable in magnitude to the results obtained by others (McGinnis, 1958; Bernard, 1963; Mader and Lull, 1968; Clary and Ffolliott, 1969; Metz et al., 1970). Dry matter weights were considerably higher than the corresponding volatile weights due to incorporation of mineral soil as also was the case found by Metz et al. (1970).

Thus, since these stands generally exhibit characteristics similar to those reported for Virginia pine and other coniferous species it seems appropriate to assume that the series of stands studied represent the normal progression that one stand would undergo over time. With this assumption a model of litter decomposition and accumulation can be developed, using as inputs the volatile weights of the litter-fall and litter-layer of the various stands studied.

Jenny, et al. (1949) and Olson (1963) have considered models of litter accumulation. The usual approach is to assume equilibrium (annual litter-fall equals annual litter-layer decomposition) and stability (rate of decomposition and annual litter-fall both constant). Olson (1963) and Ando (1970) estimated a decomposition rate k for various pine species by:

$$k = L/X_{SS} \quad (1)$$

where L is the annual litter production and X_{SS} is the litter-layer weight at equilibrium and stability. Units such as carbon weight, dry matter weight, volatile matter weight, or energy can be used for L and X_{SS} .

Based on carbon weight data found by McGinnis (1958) and used by Olson (1963) for a 15-year-old Virginia pine stand in Tennessee and solving equation (1), k is estimated as 0.20. Olson (1963) then used the exponential model of Jenny, et al. (1949):

$$X_t = (X_{SS})(1 - e^{-kt}) \quad (2)$$

where X_t is the weight of the accumulated litter-layer at time t , X_{SS} is as previously defined, and e is the base of the natural logarithms. In order to estimate the time to reach 95 percent equilibrium and assuming k remains constant throughout the life of the litter-layer, the following

equation of Jenny (1949) is used:

$$t' = \frac{-\ln\left(\frac{100-95}{100}\right)}{k} = \frac{3.0}{k} \quad (3)$$

where t' is the time required to reach 95 percent equilibrium, k is as previously defined, and \ln is the natural logarithm. Time to 95 percent equilibrium, from McGinnis' (1958) data, for Virginia pine in Tennessee using equation (3) is 15 years.

Using litter-fall and litter-layer data obtained for the unthinned 13 and 36-year-old stands respectively and solving equations (1) and (2) and comparing the results to the observed values of the unthinned stands it is apparent that the fit is poor (Figure 5).

Virginia pine is a species that is short-lived (approximately 90 years) and because of this may never attain equilibrium or stability as defined by Jenny. Even shorter life spans are indicated by Slocum and Miller (1953) who point out that mean annual increment (cubic feet of wood inside bark) culminates at approximately 45 years of age and heart rot is prevalent beyond age 50 for trees growing on old fields in the Piedmont of North Carolina.

The change in amount and composition of litter-fall with stand age and the corresponding changes in the quantity of accumulated litter are further evidence against equilibrium or stability existing in any of the stands monitored in this study so that the method of calculating the decomposition constant k as used by Olson is inappropriate.

Because the previously developed models failed to adequately account for changes in litter-fall and accumulation, three different models were

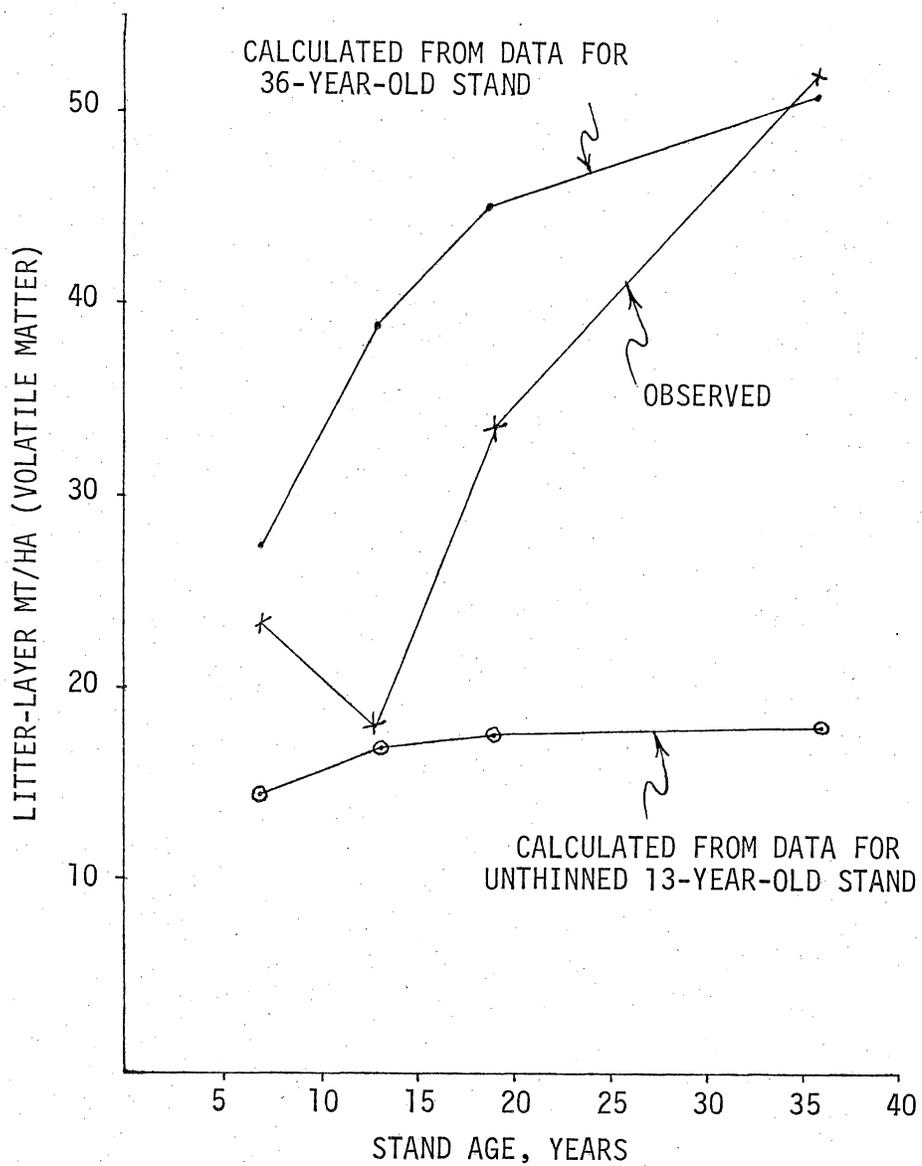


Figure 5. Observed versus calculated values of litter-layer in four old-field Virginia pine stands.

fitted to the data for the unthinned stands age 7 to 35 using an iterative technique (Table 6). The first model assumes that litter decomposes at a fixed annual rate as assumed in previously published models with litter-fall changing with time. The second model assumes in addition, that the decomposition rate of litter decreases linearly as the age of the litter increases. The third model assumes in addition to litter-fall changing with time that the litter is split into two fractions decomposing at fixed, but different, annual rates. The goodness of fit is similar for all three models but with the model assuming litter composed of two separate components each decomposing at a fixed rate is the best. This model most closely approaches reality in that litter-fall is composed of a mixture of different components such as cellulose and lignin which are known to decompose at different rates.

The litter-layer of the youngest stand represents the accumulation from two partial rotations. If no previous stand had existed, a litter-layer of approximately 8 mt/ha would be predicted by each model. Assuming the original stand was cut at age 27, the predicted litter-layer would have been 34-35 mt/ha. The observed litter-layer value of 23.40 mt/ha suggests that the decomposition rate after the harvest of the previous stand increased considerably. Further evidence in support of this view is the substantial decrease in volatile matter weight of the litter-layer after thinning in the 13-year-old stand even after allowing for the simultaneous reduction in litter-fall.

The results of this study suggest that the simplistic model of litter decomposition in the literature is inadequate to explain known

Table 6. Observed and calculated volatile matter weight of litter-fall and litter-layer in four old-field Virginia pine stands.

Stand	Age	Litter-fall mt/ha		Litter-layer mt/ha			
		Observed	Calculated ^{1/}	Observed	Model 1 ^{2/}	Model 2 ^{3/}	Model 3 ^{4/}
I	7	2.33	2.80	23.40	8.78(34.57 ^{5/})	8.40(34.31 ^{5/})	8.37(35.51 ^{5/})
IIA	13	4.14	4.21	17.80	21.79	20.62	20.59
III	19	4.97	4.88	33.50	33.39	31.70	31.79
IV	36	5.34	5.37	51.90	51.13	52.09	51.96

^{1/}Calculation based on non-linear least squares solution.

^{2/}One fraction of the litter-layer and fixed decomposition rate of 0.0860. Minimum residual squares = 16.48.

^{3/}Litter-layer first year decomposition rate of 0.1030 which then decreases by 0.00075 per annum. Minimum residual squares = 11.24.

^{4/}Two fractions of litter-fall, 0.596 and 0.404, the former decomposing at a rate of 0.1515 and the latter at a rate of 0.0404. Minimum residual squares = 10.74.

^{5/}Accumulation when carryover from previous stand is used at the initiation time of existing stand.

data on litter accumulation. Additional studies relating litter decomposition to chemical composition and environmental variables are necessary if an adequate model of litter accumulation is to be developed.

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LITTER PRODUCTION AND ACCUMULATION IN NATURALLY SEEDED,
OLD-FIELD, VIRGINIA PINE (PINUS VIRGINIANA MILL.) STANDS

by

Richard Edward Kreh

(ABSTRACT

Litter-fall and litter-layer data were collected from stands of 7, 13, 19 and 36-year-old naturally seeded, old-field, Virginia pine. The pattern of yearly litter-fall was highly seasonal with maximum needle-fall occurring during the fall months. Estimated annual total litter-fall ranged from 2.90 mt/ha dry weight in the 7-year-old stand to 5.49 mt/ha dry weight in the 36-year-old stand. The percent annual contribution of non-needle material to the total increased from 16.5% in the 7-year-old stand to 43.9% in the 36-year-old stand.

Maximum litter-layer dry matter weight of 139 mt/ha and volatile matter weight (loss on ignition at 525°C) of 52 mt/ha occurred in the 36-year-old stand. The depth and maximum water storage of the litter-layer increased with stand age to a maximum of 5.34 cm and 1.42 cm respectively in the 36-year-old stand.

Several models characterizing the accumulation and decomposition of litter were developed. The best fit model assumes that litter-fall changes with time and that the litter is split into two fractions with each fraction decomposing at a different fixed annual rate. This model

supports the fact that litter-fall is a mixture of different components such as cellulose and lignin which are known to decompose at different rates.