CHANGES IN ABOVEGROUND BIOMASS AND NUTRIENT CONTENT ON WALKER BRANCH WATERSHED FROM 1967 TO 1983[1/]

Dale W. Johnson, Gray S. Henderson, and W. F. Harris[2/]

Abstract.--The increment of forest biomass and nutrient content on Walker Branch Watershed, Tennessee, from 1967 to 1983 was interrupted by two insect outbreaks. An outbreak of the southern pine beetle in the early 1970s and an outbreak of the hickory borer in the late 1970s to early 1980s killed a number of shortleaf pine (Pinus echinata) and hickory (Carya spp.) respectively. Yellow-poplar (Liriodendron tulipifera) growth increased over this 16-year period, especially in response to the mortality of shortleaf pine. The net result of these events was little change in total biomass but a substantial shift in species composition (from pine to yellow-poplar) in the Pine forest type over this period. No species has yet responded to the mortality of hickory.

Due to the shift in species composition in the Pine type, calcium and magnesium accumulation rates in biomass increased but foliage biomass decreased over the inventory period. There was little change in foliage biomass or nutrient content in other forest types, despite hickory mortality, since mortality occurred primarily among large trees having low foliage-to-woody-biomass ratios.

The insect attacks, combined with apparently natural self-thinning, caused a large increase in standing dead biomass and in nutrient return via tree fall. This increased rate of return will substantially alter forest floor nutrient content and availability, especially with regard to calcium (where the calcium content of standing dead currently equals forest floor calcium content) and nitrogen (where inputs of woody litter will substantially alter carbon to nitrogen ratios).

Keywords: Walker Branch, Tennessee, pine, yellow-poplar, hickory mortality

---

[1/] Paper presented at the Sixth Central Hardwood Forest Conference, Knoxville, TN, February 24-26, 1987.

[2/] Dale W. Johnson, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831; Gray S. Henderson, School of Forestry, University of Missouri, Columbia, MO 65201; W. F. Harris, National Science Foundation, Washington, DC 20550.

INTRODUCTION

It has been known for decades that forests obtain most of their nutrients by recycling. Consequently, much study has been devoted to the annual cycling of nutrients in forest ecosystems (e.g., Cole and Rapp 1981). On the other hand, studies of long-term nutrient increments in perennial tissues are relatively rare. Although they constitute only a small proportion of total annual uptake, nutrient increments are important indices of net nutrient demand by the forest ecosystem. Nutrient increments must be obtained from outside the annual nutrient cycle, i.e., from atmospheric inputs or from the soil rather than from litterfall, crownwash, or root turnover return. If atmospheric inputs cannot compensate for nutrient increments, then the soil is "mined". Thus, long-term trends in nutrient increments can be of considerable importance to long-term soil nutrient status.

Because of the time spans involved in measuring biomass and nutrient increments, investigators must often resort to the chronosequence approach, in which comparisons are made of stands of differing age, but whose soil and site types are assumed to have been similar at one time (Ovington 1962, Rennie 1955, Switzer and Nelson 1972, Turner 1981, Miller 1981). Stone (1975) points out the many potential pitfalls in taking the chronosequence approach. Nevertheless, Switzer and Nelson (1972), Turner (1981), and Miller (1981) have convincingly shown three basic phases of nutrient accumulation during stand development in coniferous, even-aged, monoculture forests. From stand establishment until canopy closure, the forest is in a phase of maximum net nutrient accumulation in vegetation, primarily because nutrient-rich foliar tissues increase. After canopy closure, foliar biomass stabilizes and nutrient accumulation slows to a relatively low rate since biomass increment occurs primarily in nutrient-poor woody tissues. During this phase, leaf litterfall stabilizes also, a nutrient cycle develops, and the forest floor increases up to a steady-state value whose magnitude is determined by the rates of litterfall and decomposition (Olson 1963). The last cycling stage is one of increased tree mortality due to senscence and self-thinning, resulting in the increased return of woody tissue to the forest floor, which in turn may lead to sufficient immobilization of nitrogen to cause nitrogen deficiencies late in the stands' life (Turner 1981, Miller 1981).

Little is known about patterns of nutrient accumulation in uneven-aged, mixed species forests, although much has been written about changes in biomass and productivity during succession in uneven-aged forests (see review by Peet, 1981). Several hypotheses have been advanced to describe patterns in biomass and productivity during forest succession including 1) a smooth buildup in biomass in logistic fashion up to an asymptote, 2) maximum biomass accumulation during late successional stages followed by a breakup and decline to a lower level in the climax community, 3) a peak biomass as in 2) followed by a series of damping oscillations about an equilibrium value (a result of a shifting mosaic patchwork of vegetation of differing ages within the landscape, and 4) a peak biomass followed by a decline due to reduced nutrient availability as nutrients become tied up in the forest floor, as decribed by Turner (1981) and Miller (1981).

Some of the overall patterns in nutrient cycling noted in even-aged monoculture forests (i.e., the stabilization of foliar biomass and development of nutrient cycles after crown closure) may also occur in uneven-aged, mixed-species forests, but other aspects of stand development are more complex. For instance, different species within the same forest may vary considerably in nutrient concentrations, both in foliage and woody tissue (e.g., Marion 1979; Johnson et al. 1982). Thus, differential changes in growth (as well as succession) may alter rates of nutrient accumulation even during the second, most stable phase of stand development. Succession from coniferous to deciduous species or vice versa may also lead to changes in foliage biomass, even after crown closure. Disruptions to stand development, such as insect and disease outbreaks, may have quite different consequences in the two forest types being discussed here. In even-aged, monoculture forests, such occurrences could cause large gaps to develop, thus allowing a new stand to grow. In uneven-aged, mixed-species forests, differential species' susceptibility to pathogens may either alter or accelerate the pattern of natural species succession without the development of large gaps and new stands.

Previous studies on Walker Branch Watershed (WBW), Tennessee have indicated that calcium (Ca) increments in oak and hickory woody biomass were quite large relative to atmospheric inputs and soil supplies (Henderson et al. 1978; Cole and Rapp, 1981). Changes in soil Ca status have been noted in selected intensively-studied plots on WBW where biomass Ca increment was high and soil Ca was low (Johnson et al., in press). However, Ca increments had declined from the late 1960's to early 1980's because of reduced growth and increased mortality due to insect attacks.

This paper describes the results of a much more extensive inventory of changes in biomass, species composition, and nutrient increment in forests on Walker Branch Watershed, Tennessee, from 1967 to 1983. The changes in five contrasting forest types (ranging from an even-aged coniferous to an uneven-aged mixed deciduous forest) in response to natural succession and insect (bark beetle) outbreaks are documented and compared with the previously described general patterns of stand development.

SITES

Walker Branch Watershed is a 97.5-ha forested catchment located near the city of Oak Ridge, in eastern Tennessee. The watershed is underlain by dolomite, from which the residual soils were formed (predominantly Typic Paleudults of the Fullerton and Bodine series). Vegetation is primarily oak-hickory (Quercus spp.-Carya spp.), with scattered pine (Pinus echinata Mill. and P. virginiana Mill.) on the ridgetops and mesophytic hardwoods (predominantly Liriodendron tulipifera L. and Fagus grandifolia Ehrh.) in protected coves and stream bottoms. The mean basal area is about 23 m^2/ha. Precipitation averages 151 cm/year, with about 57 percent draining to streams (Henderson et al. 1977). Detailed descriptions of Walker Branch Watershed and the four originally-defined major forest types are given by Grigal and Goldstein (1971). The four originally-defined forest types include Oak-Hickory (Quercus-Carya spp.), Chestnut Oak (Q. prinus), Yellow-Poplar (Liriodendron tulipifera) and Pine (P. echinata and virginiana).

The oak-hickory forest type consists primarily of hickory (Carya glabra and C. tomentosa) chestnut oak (Quercus prinus) white oak (Q. alba) and red maple (Acer rubrum) with lesser amounts of sourwood (Oxydendrum arboreum), blackgum (Nyssa sylvatica), yellow-poplar (Liriodendron tulipifera) and (in descending order of importance) occasional shortleaf pine (Pinus echinata), red oak (Q. rubra), black oak (Q. velutina) with dogwood (Cornus florida) in the understory. These forests occur on both ridgetops and on slopes. The chestnut oak type consists primarily of chestnut oak with (in descending order of importance) lesser amounts of white oak, hickory, red maple, shortleaf pine, blackgum and sourwood. This forest type occupies relatively dry sites near ridgetops. The yellow-poplar type consists primarily of yellow-poplar with lesser amounts of hickory and in descending order of importance occasional white oak, red maple, red oak, and sourwood. These forests occur primarily along streams an in valleys (Grigal and Goldstein, 1971) but are invading dry, ridgetop pine-type forests as well. The pine type consists primarily of shortleaf pine with lesser amounts of yellow-poplar and (in descending order of importance), very occasional hickory, red maple, and dogwood. These forests occur primarily on steep slopes. The loblolly pine type is a 2.5 ha plantation of Pinus taeda planted in 1949 on a ridgetop in the northwest corner of the watershed. The stand consists almost entirely of loblolly pine with an occasional invading yellow-poplar and dogwood in the understory.

METHODS

Aboveground biomass was determined on permanent inventory plots as described by Harris et al. (1973). Measurements of diameter breast height (dbh) taken in 1967, 1970, 1973, 1979, and 1983 for the west branch of the watershed were used in this comparison. Biomass was estimated from the pine, hardwood, and yellow-poplar equations given by Sollins et al. (1973), except in the case of loblolly pine, for which the equations developed by Van Lear et al. (1984) were used. Crosschecks of these regressions, performed by destructively sampling 5 loblolly pine trees on a site near Walker Branch showed that they gave accurate estimates of loblolly pine biomass in our area (D. W. Johnson, unpubl. data). Nutrient content was obtained by multiplying the biomass of each component (foliage, branch, bole) in each of 20 major species (constituting over 95 percent of the total biomass on the watershed) by nutrient concentrations in that component and species. Nutrient contents of minor species (for which concentration data were not available) were estimated by multiplying the biomass of each component by the biomass-weighted average concentration for that component in all other species for which concentrations were known. The magnitude of error introduced by estimating nutrient concentrations of these species in this way is unknown. Overall consequences to this study are probably small, however, due to the minor contribution of these species to stand biomass. Nutrient concentrations were determined from destructive sampling on both Walker Branch (Henderson et al. 1978) and a nearby whole-tree harvesting site (Johnson et al. 1982). These sampling results were pooled since they did not give significantly different values for the species analyzed. Pie-shaped sections of woody tissues and samples of July 1982 foliage were analyzed for N, P, K, Ca and Mg. Plant tissues were dry-ashed overnight at 520°C. The ashed samples were digested with 1 N HCl and diluted to volume using deionized distilled water. The P, Ca, and Mg were analyzed using flame atomic absorption. Ammonium and phosphorous were determined using an automated colorimetric procedure. A block digestion technique was used to digest plant tissues to be analyzed for total Kjeldahl nitrogen.

Net biomass and nutrient accumulation over the 1967 to 1983 inventory period were calculated based on difference in biomass, assuming biomass-weighted average nutrient concentrations in a given species remained constant over time. No relationship was found between dbh and nutrient concentration in any species or plant component; thus, there was no justification for assuming that concentration did vary with time. However, changes in concentration occurring in conjunction with tree age could have remained undetected in these analyses and may be a source of error in calculations of average annual accumulation.

RESULTS AND DISCUSSION

The 1983 biomass and nutrient content, average annual increment in live trees, and average annual mortality for the five major forest types on Walker Branch Watershed are given in Table 1. The loblolly pine plantation and, to a lesser extent, the mature natural pine forest types had generally lower nutrient contents than the three hardwood types, and this was in part due to the relatively low tissue nutrient concentrations in Pinus species compared to the hardwood species present (Table 2). However, the largest differences among these five forest types were in Ca content (Table 1) which was primarily due to the high Ca concentrations in oak and hickory species (Table 2). Average annual transfer of biomass and nutrients to dead wood via mortality from 1967 to 1983 were often greater than or equal to average annual increments of biomass and nutrients in live trees over the same period (Table 1). This was especially marked in the Pine, Oak-Hickory and Loblolly Pine types. In the Pine and Oak-Hickory types, the high mortality was due to two major insect outbreaks which reduced the steady increment of biomass and nutrients in these forest types (fig. 1). An outbreak of the southern pine beetle in the early 1970s caused considerable mortality of shortleaf pine. This was followed by a steady decline in annual increments in the pine type from 1970 to 1983 most likely due to competition from invading hardwoods (figs. 1 and 2). An outbreak of the hickory borer in the mid to late 1970s caused considerable mortality of hickory and a sudden reduction in annual increments in the yellow-poplar, chestnut oak and (especially) oak-hickory types from 1979 to 1983 (figs. 1 and 2).

In contrast to what occurred in natural shortleaf pine, the bark beetle attacks in the Loblolly Pine type (plantation) were relatively mild and the increased mortality is thought to have been the result primarily of self-thinning. The basal area of the Loblolly Pine type in 1973 (at age 24) (33.5 m^2/ha) was 60 percent greater than that considered optimal for loblolly pine in this region (21 m^2/ha; D. M. Bradburn, pers. comm.) and far greater than that of any other forest type (23.4, 23.3, 22.2 and 23.0 m^2/ha for the Pine, Yellow-Poplar, Oak-Hickory, and Chestnut Oak types, respectively in 1973). By 1983, the loblolly stand had thinned considerably (28.3 m^2/ha) but still remained somewhat overstocked.

Although live pine and hickory biomass decreased, yellow-poplar biomass increased, particularly in the Yellow-Poplar and Pine types (fig. 3). There was an inverse relationship between pine and poplar biomass in the Pine

Table 1. Biomass and nutrient content of live trees in 1983, average annual increment in live trees and average annual mortality from 1967-1983 in five forest types on Walker Branch Watershed, Tennessee

Forest Type	Biomass mg/ha	N	P	K	Ca	Mg
		kg/ha				
			Live trees (1983)			
Pine	144 ± 7	295 ± 15	24 ± 1	182 ± 9	562 ± 36	48 ± 2
Yellow-poplar	186 ± 11	410 ± 24	32 ± 2	225 ± 15	944 ± 80	73 ± 4
Oak-hickory	164 ± 8	357 ± 16	27 ± 1	207 ± 9	1076 ± 53	54 ± 2
Chestnut oak	198 ± 8	433 ± 17	31 ± 1	222 ± 8	1267 ± 50	52 ± 2
Loblolly pine	171 ± 14	279 ± 29	24 ± 2	165 ± 18	363 ± 72	52 ± 6
			Average Annual Increments, 1967-1983			
Pine	1.0 ± 0.06	2.1 ± 0.1	0.16 ± 0.01	0.03 ± 0.08	7.1 ± 0.3	0.5 ± 0.02
Yellow-poplar	2.7 ± 0.10	5.4 ± 0.3	0.43 ± 0.02	1.88 ± 0.16	8.8 ± 0.8	0.8 ± 0.05
Oak-hickory	1.5 ± 0.07	2.7 ± 0.2	0.22 ± 0.01	-0.26 ± 0.10	0.8 ± 0.6	-0.19 ± 0.03
Chestnut oak	2.5 ± 0.08	5.0 ± 0.2	0.36 ± 0.01	1.73 ± 0.10	13.4 ± 0.5	0.36 ± 0.02
Loblolly pine	0.5 ± 0.30	1.4 ± 0.6	0.14 ± 0.05	0.4 ± 0.40	1.5 ± 1.6	0.2 ± 0.12
			Average Annual Mortality			
Pine	4.3 ± 0.4	6.9 ± 0.7	0.53 ± 0.06	4.9 ± 0.5	1.19 ± 1.2	1.1 ± 0.10
Yellow-poplar	2.6 ± 0.3	4.8 ± 0.6	0.38 ± 0.05	3.3 ± 0.5	15.7 ± 2.8	0.9 ± 0.20
Oak-hickory	3.2 ± 0.3	6.4 ± 0.5	0.48 ± 0.04	5.1 ± 0.5	27.9 ± 2.7	2.7 ± 0.10
Chestnut oak	1.9 ± 0.2	3.7 ± 0.4	6.3 ± 0.03	2.5 ± 0.3	14.3 ± 1.4	0.7 ± 0.07
Loblolly pine	7.6 ± 1.2	10.2 ± 1.5	0.89 ± 0.14	6.2 ± 1.0	15.1 ± 2.8	2.1 ± 0.30

Table 2. Nutrient concentrations in foliage, branch and bole tissues of major tree species on Walker Branch Watershed (percentage of dry weight)

Tissues	Tree species							
	Black gum	Yellow-poplar	Hickory	White oak	Chestnut oak	Shortleaf pine	Red maple	Loblolly pine
					N			
Foliage	1.50 ± 0.00	1.58 ± 0.14	1.40 ± 0.04	1.78 ± 0.28	1.48 ± 0.08	0.84 ± 0.02	1.28 ± 0.08	1.07 ± 0.15
Branch	0.27 ± 0.02	0.24 ± 0.03	0.28 ± 0.07	0.24 ± 0.05	0.24 ± 0.06	0.26 ± N.D.	0.20 ± 0.07	0.22 ± 0.01
Bole	0.17 ± 0.006	0.18 ± 0.01	0.19 ± 0.04	0.16 ± 0.02	0.18 ± 0.02	0.11 ± 0.01	0.17 ± 0.04	0.09 ± 0.02
					P			
Foliage	0.11 ± 0.003	0.11 ± 0.004	0.10 ± 0.006	0.13 ± 0.006	0.11 ± 0.004	0.09 ± 0.03	0.10 ± 0.005	0.09 ± 0.03
Branch	0.03 ± 0.009	0.02 ± 0.005	0.02 ± 0.008	0.02 ± 0.01	0.02 ± 0.005	0.02 ± N.D.	0.02 ± 0.006	0.03 ± 0.006
Bole	0.018 ± 0.005	0.01 ± 0.001	0.01 ± 0.003	0.009 ± 0.003	0.01 ± 0.002	0.008 ± 0.007	0.02 ± 0.004	0.01 ± 0.003
					K			
Foliage	1.18 ± 0.02	0.94 ± 0.11	0.92 ± 0.14	1.09 ± 0.05	0.93 ± 0.04	0.68 ± 0.01	0.67 ± 0.07	0.53 ± 0.16
Branch	0.26 ± 0.17	0.15 ± 0.19	0.30 ± 0.31	0.18 ± 0.18	0.11 ± 0.07	0.15 ± N.D.	0.19 ± 0.19	0.13 ± 0.04
Bole	0.11 ± 0.02	0.06 ± 0.06	0.18 ± 0.08	0.07 ± 0.06	0.06 ± 0.06	0.10 ± 0	0.08 ± 0.007	0.06 ± 0.01
					Ca			
Foliage	1.09 ± 0.03	1.65 ± 0.11	1.61 ± 0.17	1.10 ± 0.15	0.83 ± 0.05	0.25 ± 0.02	0.79 ± 0.08	0.25 ± 0.05
Branch	0.71 ± 0.26	0.30 ± 0.20	1.41 ± 0.68	0.89 ± 0.29	0.65 ± 0.32	0.30 ± N.D.	0.40 ± 0.28	0.27 ± 0.05
Bole	0.91 ± 0.35	0.31 ± 0.17	1.08 ± 0.14	0.72 ± 0.26	0.67 ± 0.11	0.19 ± 0.01	0.44 ± 0.19	0.09 ± 0.03
					Mg			
Foliage	0.31 ± 0.02	0.41 ± 0.04	0.31 ± 0.02	0.15 ± 0.008	0.16 ± 0.02	0.11 ± 0.02	0.17 ± 0.01	0.10 ± 0.01
Branch	0.02 ± N.D.	0.06 ± N.D.	0.05 ± N.D.	0.05 ± N.D.	0.04 ± N.D.	0.04 ± N.D.	0.02 ± N.D.	0.05 ± 0.006
Bole	0.05 ± 0.001	0.03 ± 0.01	0.07 ± 0.02	0.02 ± 0.005	0.01 ± 0.002	0.02 ± N.D.	0.02 ± 0.003	0.03 ± 0.008

type, indicating that poplar growth increased in response to pine mortality. The net effect was a fairly stable biomass and nutrient content but a significant change in species composition in the Pine type (fig. 4). From 1967 to 1983, yellow-poplar increased from 14 to 37 percent of the total biomass, and pines decreased from 74 to 42 percent of the total biomass in the Pine type. As the pines dropped out and were replaced by Yellow-poplar in the Pine type, foliage biomass declined (fig. 5) because of inherent differences in the foliage biomass of these species (e.g., the pines retain 2 to 3 years' needles, whereas the yellow-poplar retains only one year's set of leaves). In the other forest types, foliage biomass remained relatively stable. The stability of foliage biomass in the Oak-Hickory type, despite the large biomass loss due to hickory mortality, is due to the deaths of primarily large trees having low foliage-to-wood biomass ratios. Note the convergence of foliage biomass in the Pine type with that in the other deciduous forest types as deciduous species succeed pines (fig. 5).

Both pine and hickory mortality have caused a substantial accumulation of biomass and nutrients in standing dead trees (fig. 6). Thus, total net aboveground biomass and nutrient increment declined from 1979 to 1983 as a result of hickory mortality, and most net increment went into standing dead. Although estimates in fig. 6 are too large, to the extent that decay and loss of limbs are not accounted for (foliage is deleted, but standing dead biomass and nutrient content are estimated from regressions and nutrient concentrations in woody tissues of live trees), it is clear that localized areas will receive substantial return of woody litter and nutrients as these trees fall over the next few years.

Nutrient return via tree fall increased significantly from 1970 to 1983 as a result of increased mortality (fig. 7). Return in the Pine type peaked from 1973 to 1979 and seems to be declining now that the beetle kill has run its course. Return in the Oak-Hickory type is increasing and will continue to increase as standing dead trees and additional hickory mortality contribute to woody return to the forest floor. The return in the Loblolly Pine

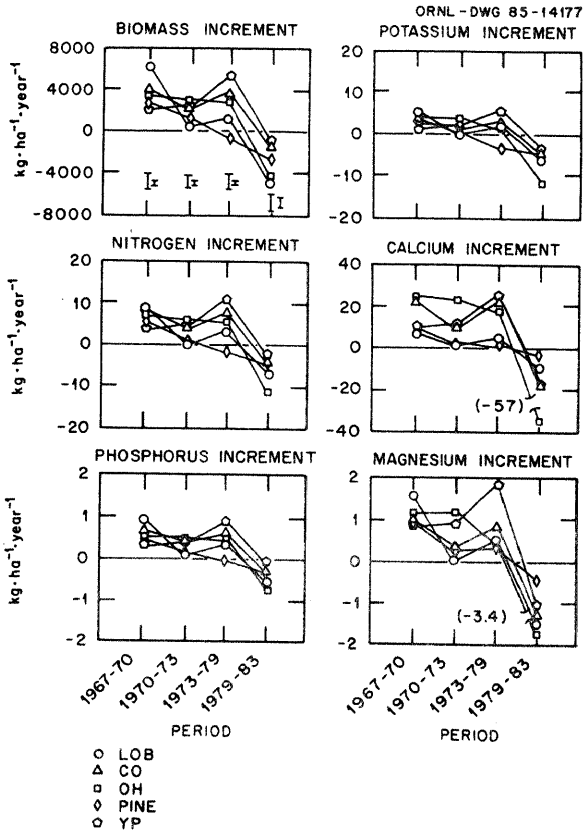

Fig. 1. Live biomass increment and N, P, K, Ca and Mg increment in live biomass in five forest types on Walker Branch Watershed. LOB = loblolly pine plantation, CO = chestnut oak, OH = oak-hickory, YP = yellow-poplar, and PINE = native pine-hardwood. The ranges (largest and smallest) of standard errors of biomass estimates among plots in a forest type are shown for each year.

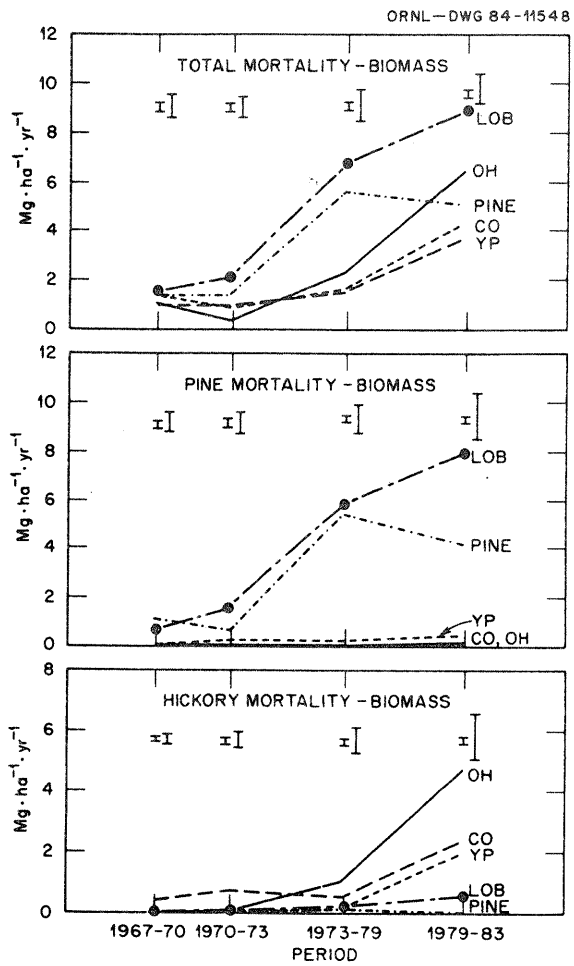

Fig. 2. Total mortality, mortality of Pinus spp., and mortality of Carya spp. in five forest types of Walker Branch Watershed. (See fig. 1 for legend).

type was very high from 1979 to 1982. During this period, mortality also increased (fig. 2), but standing dead biomass decreased. Thus, it is apparent that loblolly pines do not remain standing long after death, compared to shortleaf pine and hickory (figs. 2 and 7).

The southern pine beetle and hickory borer outbreaks have considerably affected nutrient distribution and accumulation rates on the watershed over the last 16 years. There is every reason to believe that such outbreaks occurred in the past also, especially following droughts. Craighead (1949) states, in reference to eastern U.S. bark beetles, that ". . . almost without exception outbreaks of these insects occur during a period of deficient rainfall. This is particularly true of the southern pine beetle, the hickory bark beetle and species of Ips" (p. 48). Droughts did occur during the spring of 1969 [the Palmer Drought Index (PDI) was -2 until June] and in the late summer of 1980 through early spring of 1981 (PDI < -2 from August 1980 until April 1981), which may have contributed to the insect outbreaks. Other stresses, such as air pollution, may also have contributed, but we have insufficient data to so determine. Studies of acid deposition effects in Chestnut-Oak and Yellow-Poplar stands indicate that no chronic nutritional problems have developed or will develop in the near future as a result of acid deposition (Richter et al. 1983, Johnson and Richter 1984). Studies on the effects of gaseous air pollution (e.g., O_3 or SO_2 damage) on tree susceptibility to insect attacks have not as yet been made. At this point, drought seems to be the most likely triggering mechanism for the beetle attacks.

The long-term effects of the hickory borer outbreak are as yet unknown, but the southern pine beetle outbreaks have caused a rapid shift in species composition toward yellow-poplar. This trend, if it continues, will result in

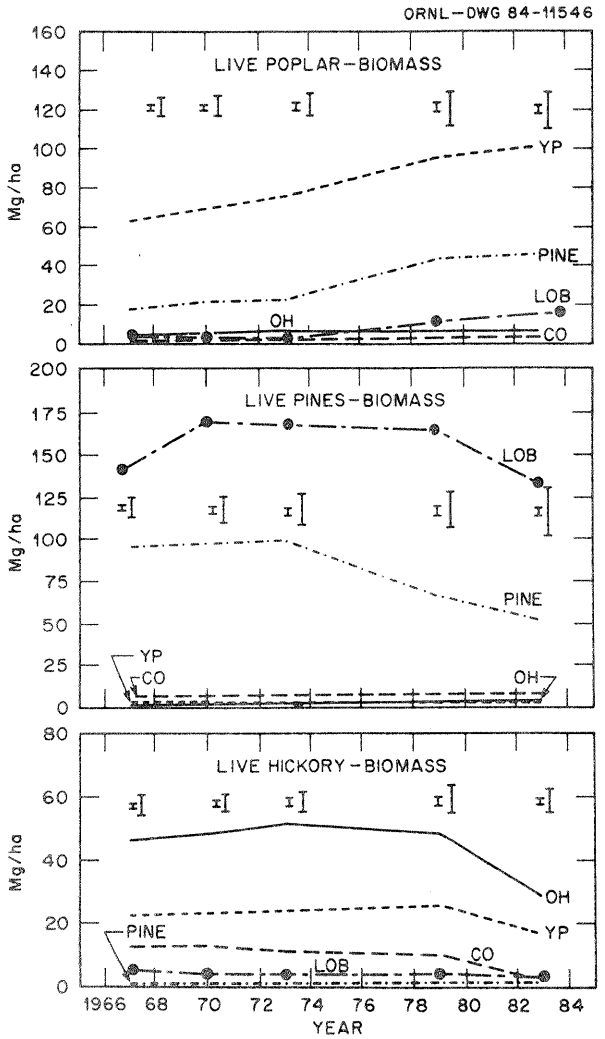

Fig. 3. Live biomass of yellow-poplar (Liriodendron tulipifera), pines (Pinus spp.), and hickory (Carya spp.) in five forest types on Walker Branch Watershed. (See fig. 1 for legend).

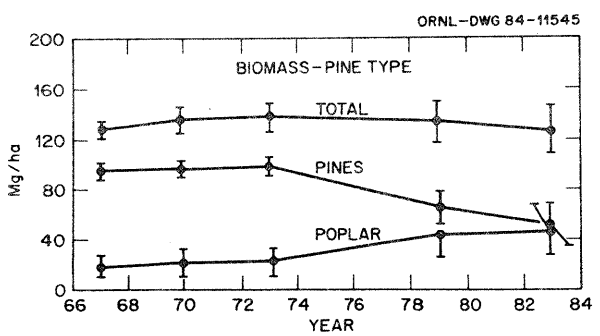

Fig. 4. Total biomass, pine biomass, and yellow-poplar biomass in the Pine forest type. Standard errors of biomass estimates among plots are shown.

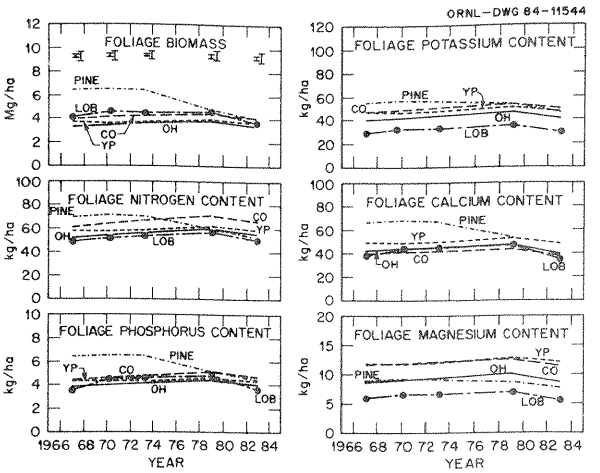

Fig. 5. Foliage biomass and foliage N, P, K, Ca, and Mg content in five forest types on Walker Branch Watershed. (See fig. 1 for legend).

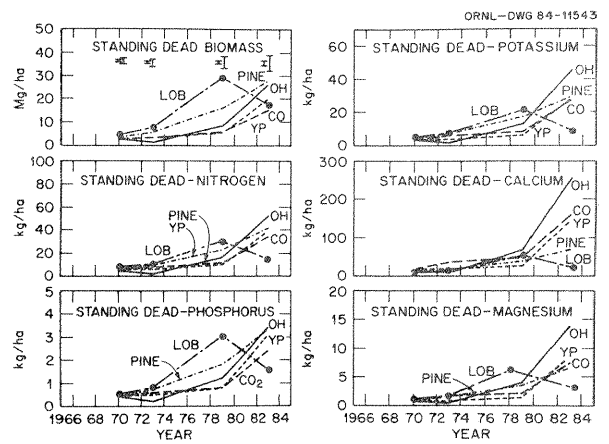

Fig. 6. Biomass N, P, K, Ca, and Mg content in standing dead trees on Walker Branch Watershed. (See fig. 1 for legend).

long-term increases in Ca and Mg increment in what were formerly pine stands. This trend is somewhat evident already in that Ca and Mg increment in live trees remained near zero, while the biomass, N, P, and K increment decreased from 1967 to 1983 in the Pine type (fig. 2).

SUMMARY AND CONCLUSIONS

Insect attacks and overstocking have altered what had been a steady increment of biomass and the rate of nutrient accumulation in the biomass of forests on Walker Branch Watershed, Tennessee. Mortality of shortleaf pine in response to a southern pine beetle outbreak in the early 1970s facilitated and apparently hastened the natural succession of

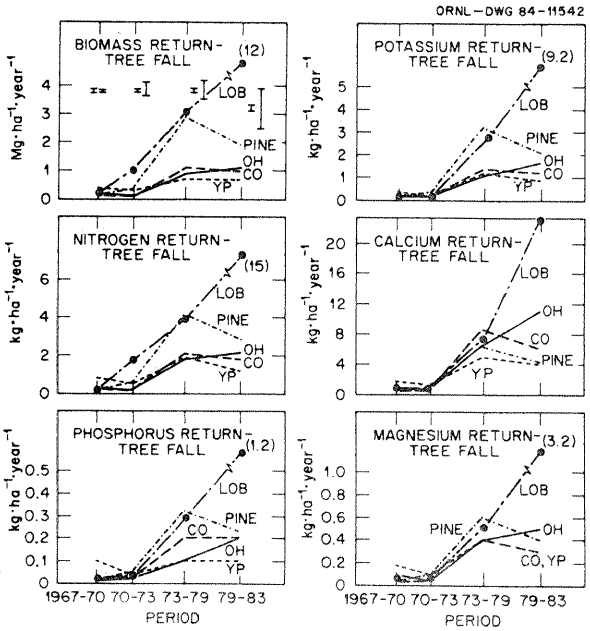

Fig. 7. Return of biomass, N, P, K, Ca, and Mg via tree mortality in five forest types on Walker Branch Watershed. (See fig. 1 for legend).

pine to hardwood in what was formerly the Pine forest type. Loblolly pine was less affected by the beetles, but loblolly pine mortality increased from 1973 through 1983 in an apparent self-thinning response to overstocked conditions. Yellow-poplar growth increased over the entire watershed during this period, especially in response to shortleaf pine mortality. In what was formerly the Pine forest type there was a large change in species composition from shortleaf pine to yellow-poplar dominance, which resulted in a reduction in foliage biomass, N, P, and Ca (but not K or Mg) content, but very little net change in total biomass and nutrient content in total biomass. No species has yet responded to hickory mortality.

Mortality of shortleaf pine, loblolly pine, and hickory resulted in very marked increases in standing dead biomass, nutrient content in standing dead biomass, and nutrient return via tree fall. Return of K and Ca via tree fall will considerably increase the forest floor content of these elements. Also, the return of woody biomass having wide C:N and C:P ratios may significantly alter N and P availability, especially in localized areas.

The insect attacks were preceded, and probably stimulated, by droughts, but other contributing factors, such as air pollution, cannot be excluded. The long-term effects of these attacks on the productivity of these forests remain to be seen; however, if current trends continue, the invasion of yellow-poplar is likely to increase productivity, perhaps up to pre-beetle-attack levels, in what was formerly the Pine type.

As of 1983, the rather large net annual increments of Ca in biomass reported earlier for Walker Branch Watershed (31 $kg \cdot ha^{-1} \cdot yr^{-1}$ in aboveground biomass; Henderson et al. 1978) had been drastically reduced, primarily due to hickory mortality resulting from a hickory borer outbreak. Calcium (and other nutrients) in standing dead biomass will be returned to the forest floor and most certainly will contribute to the Ca requirements of the remaining live trees. The spatial distribution of woody litter return in relation to living trees taking up large amounts of Ca is not necessarily optimal for such a long-term Ca recycling, however. Further inventories of biomass and nutrient changes coupled with more intensive soil resampling programs are planned to monitor biomass and nutrient redistribution trends in the future.

ACKNOWLEDGMENT

Research supported by the Office of Health and Environmental Research, U.S. Department of Energy under contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. Publication No. 2828, Environmental Sciences Division, Oak Ridge National Laboratory.

LITERATURE CITED

Alban, D. H.
1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Science Society of America Journal 46:853-861.

Cole, D. W., and M. Rapp.
1981. Elemental cycling. In D. E. Reichle (ed.), Dynamic Properties of Forest Ecosystems, pp 341-409. Cambridge University Press, London.

Craighead, F. C.
1949. Insect enemies of eastern forests. U.S. Dept. of Agriculture Misc. Pub. No. 656. U.S. Government Printing Office, Washington, D.C. 679 pp.

Grigal, D. F., and R. A. Goldstein.
1971. An integrated ordination - classification analysis of an intensively-sampled oak-hickory forest. Journal of Ecology 59:481-492.

Harris, W. F., R. A. Goldstein, and G. S. Henderson.
1973. Analysis of forest biomass pools, annual primary production, and turnover of biomass in a mixed deciduous forest watershed. In H. E. Young (ed.), Proc. Int. Union of Forest Res. Organ. Symp., Working Party on Forest Biomass, 20-24 Aug., 1973, pp. 41-64. Univ. of Maine Press, Orono.

"The submitted manuscript has been authored by a contractor of the U.S. Government under contract No. DE-AC05-84OR21400. Accordingly, the U.S. Government retains a nonexclusive, royalty-free license to publish or reproduce the published form of this contribution, or allow others to do so, for U.S. Government purposes."

Henderson, G. S., D. D. Huff, and T. Grizzard.
1977. Hydrologic characteristics of Walker Branch Watershed. In D. L. Corell (ed.), Watershed Research in North America, pp. 195-209. The Smithsonian Institution, Edgewater, Maryland.

Henderson, G. S., W. T. Swank, J. B. Waide, and C. C. Grier.
1978. Nutrient budgets of Appalachian and Cascade region watersheds: A comparison. Forest Science 24:385-397.

Jenkinson, D. S.
1970. The accumulation of organic matter in soil left untended. Commonwealth Bureau of Soil Science Rothamstad Exp. Station Report for 1970. Part 2. pp. 113-137.

Johnson, D. W., G. S. Henderson, and D. E. Todd.
Changes in nutrient distribution in forests and soils of Walker Branch Watershed over an eleven-year period. Biogeochemistry (in press).

Johnson, D. W. and D. D. Richter.
1984. Effects of atmospheric deposition on forest nutrient cycles. Tappi Journal 67:82-85.

Johnson, D. W., D. C. West, D. E. Todd, and L. K. Mann.
1982. Effects of sawlog vs whole-tree harvesting on the nitrogen, phosphorus, potassium, and calcium budgets of an upland mixed oak forest. Soil Science Society of America Journal 46:1304-1309.

Marion, G. K.
1979. Biomass and nutrient removal in long-rotation stands. In A. L. Leaf (ed.), Impact of Intensive Forest Harvesting on Forest Nutrient Cycling, pp. 98-110. State University of New York, Syracuse.

Miller, H. G.
1981. Forest fertilization: Some guiding concepts. Forestry 54:157-167.

Olson, J. S.
1963. Energy storage and the balance of producers and consumers in ecological systems. Ecology 44:322-331.

Ovington, J. D.
1962. Quantitative ecology and the woodland concept. In J. B. Cragg (ed.), Advance in Ecological Research. Vol. 1., pp. 103-192. Academic Press, London and New York.

Peet, R. K.
1981. Changes in biomass and production during secondary succession. Ch. 20. In D. C. West, H. H. Shugart and D. B. Botkin (eds.). Forest Succession: Concepts and Application. Springer-Verlag, New York.

Rennie, P. J.
1955. The uptake of nutrients by mature forest growth. Plant Soil 7:49-95.

Richter, D. D., D. W. Johnson, and D. E. Todd.
1983. Atmospheric sulfur deposition, neutralization, and ion leaching in two deciduous forest ecosystems. Journal of Environmental Quality 12:263-270.

Sollins, P., D. E. Reichle, and J. S. Olson.
1973. Organic matter budget and model for a southern Appalachian Liriodendron forest. EDFB-IBP-73-2. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Stone, E. L.
1975. Effects of species on nutrient cycles and soil change. Phil. Trans. R. Soc. Lond. B 271:149-162.

Switzer, G. L., and L. E. Nelson.
1972. Nutrient accumulation and cycling in Loblolly pine (Pinus taeda L.) plantation ecosystems: The first twenty years. Soil Science Society of America Proceedings 36:143-147.

Turner, J.
1981. Nutrient cycling in an age sequence of western Washington Douglas-fir stands. Annals of Botany 48:159-169.

Van Lear, D. H., J. B. Waide, and M. J. Teuke.
1984. Biomass and nutrient content of a 41-year-old loblolly pine (Pinus taeda L.) plantation on a poor site in South Carolina. Forest Science 30:395-410.