MINIREVIEW

Soil Carbon Dynamics after Forest Harvest: An Ecosystem Paradigm Reconsidered

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ABSTRACT

In one of the most influential studies in the recent history of forest ecology, W. W. Covington (1981) described a pattern in organic matter storage in the forest floors of northern hardwood stands as a function of date of harvest. We review the history of the use and misuse of Covington's curve, describe the studies that tested and failed to support early interpretations of the curve, and provide some alternate interpretations. The curve suggested that forest floor organic matter declines by 50% within 20 years after harvest, and this decline was attributed to accelerated decomposition and changes in litter inputs after harvest. Subsequent studies showed that decomposition rates of surface litter generally decrease after clear-cutting, but accelerated decomposition remains possible in the Oe and Oa horizons. Changes in litter inputs are still difficult to evaluate, because the rate at which woody debris enters the forest floor is unknown. Although Covington attempted to minimize variation due to mechanical disturbance during logging, a reasonable alternative explanation for low organic matter in the forest floor of young stands is that surface material is mixed into mineral soil during harvesting operations. The pattern of forest floor organic matter in stands of different ages may be partly due to changes over time in logging technology and the intensity of biomass removal, in addition to successional effects. It is important to distinguish between mechanisms that release carbon to the atmosphere and those that transfer it to the mineral soil before making inferences about nutrient cycling and carbon sequestration.

Key words: forest floor; Covington; decomposition; forest harvest; chronosequence; soil carbon model; soil organic matter; paradigm.

INTRODUCTION

Organic matter in forest soils is important to nutrient cycling, hydrologic cycles, forest productivity, and the global carbon (C) budget. Globally, soils contain more C than any other terrestrial C pool (Schlesinger 1977; Jobággy and Jackson 2000), and the forest floor is the most dynamic part of soil organic matter. Estimates of the effect of forest harvest on soil C storage are critical to predictions of both local ecosystem sustainability and global C exchange with the atmosphere. Forest harvest may have a significant effect on forest floor structure and function through mechanical disturbance, inputs of logging slash, alterations in litter production, and leaching of dissolved organic matter, as well as the alteration of temperature and moisture regimes.

Measuring the response of soil C to treatments over long time scales is feasible but highly demanding (for example, see Johnson and others 1995; Trettin and others 1999), and estimates are urgently
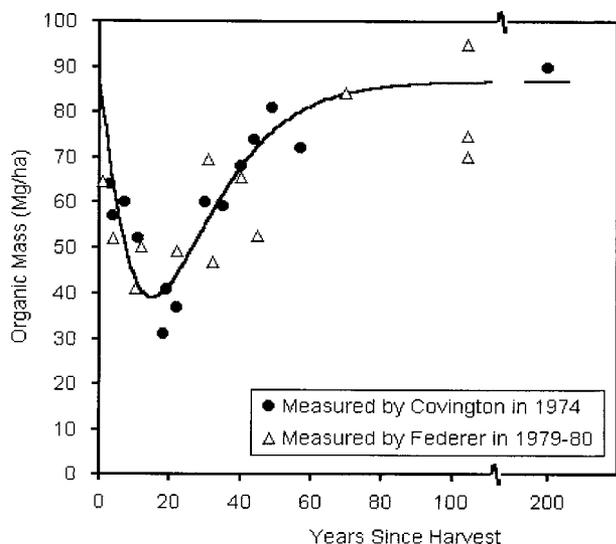
Figure 1. Organic mass of the forest floor in Covington's study (1981) and Federer's additional stands (1984). Covington's curve describes forest floor organic matter (Mg/ha) as $-5.25 \, t^{1.24} \exp(-0.0649 \, t^{1.063}) + 86.75$, where t = time since logging (years).

required for the effective design of environmental policy. It is impractical to wait for decades to obtain those estimates. For this reason, a chronosequence approach is attractive, in which sites of different ages are assumed to represent points in time in the development of individual sites. Because the sites are separated in space and studied at the same time, with changes over time inferred, this technique is called a "space-for-time substitution". Chronosequence approaches have provided valuable insight into patterns of forest succession and soil development (Cowles 1899; Billings 1938; Dickson and Crocker 1953; Crocker and Major 1955; Crews and others 1995; Lichter 1998), but they can be subject to error in the space-for-time substitution if sites differ in respects other than their age. To avoid this problem, researchers try to minimize sources of variation other than time by selecting sites that are similar in other respects.

One of the most influential chronosequence studies in the recent history of ecosystem science is that of W. W. Covington (1981). Covington curve described differences in organic matter storage in the forest floors of northern hardwood forests that had been harvested at different dates over the past century (Figure 1). This study concluded that forest floor mass declined sharply following harvest, with 50% of forest floor organic matter lost in the first 20 years. The apparent losses of organic matter were attributed to increases in decomposition rates and

decreases in litter inputs as the ecosystem reorganized.

The Covington study was conducted within a narrow range of elevation, aspect, and forest and soil type in central New Hampshire, but the interpretation of a dramatic rate of C loss has been widely applied. The Covington curve has been used to estimate the effects of harvest on soil C storage in the Pacific Northwest (Harmon and others 1990), the tropics (Lugo and Brown 1986), North and South America (Cooper 1983), Finland (Liski and Westman 1997), and throughout the temperate zone (Houghton and others 1983). It has been used to estimate nutrient accumulation (Yanai 1992) and release from the forest floor (Hornbeck and others 1986) and to validate simulation models (Aber and others 1978; Pastor and Post 1986). It is so widely believed that it is used without citation (Barnes et al. 1998, p 516) which accords it the status of a paradigm in ecosystem science.

It is perhaps surprising that the mechanisms underlying Covington's curve are still not well understood. Fortunately, the impressive magnitude of the reported C loss inspired a multitude of studies. Some researchers attempted to verify Covington's curve, using chronosequences, repeated measures, and comparisons of cut and uncut stands. Others looked for changes in decomposition rates or litter inputs after harvest, the mechanisms emphasized by Covington. Alternate explanations for Covington's curve were proposed, including the movement of forest floor material into mineral soil and changes in logging practices over time. In this paper, we review Covington's study, its influence, the many subsequent experimental studies, and various attempts to simulate Covington's results with models. We present a new modeling exercise that includes some alternative mechanisms. We conclude that more research is still needed to understand forest floor dynamics following disturbance.

Forest Floor Defined

In many forests, surface layers rich in organic matter, referred to as "the forest floor", accumulate atop and sometimes in the upper portion of the mineral soil. This surface organic layer is highly active in C and nutrient cycling and potentially more responsive to change than are stocks of organic matter in mineral soils, which accumulate over long time periods and change only slowly (Currie 1999; Currie and others 2002).

The term "forest floor" has been variously defined, with important aspects frequently undefined. All researchers include the O (organic) horizon in their definitions of the forest floor, but some also

include an A horizon when present. The O horizon consists of three layers, defined by rubbed fiber content: the Oi, or fibric, layer of relatively unde-composed litter (formerly the L, or litter, layer); the Oe, or hemic, layer of partly decomposed but still recognizable litter (formerly the F, or fragmented, layer); and the Oa, or sapric, layer containing well-decomposed material whose origin can no longer be identified (formerly the H, or humus, layer) (Soil Survey Staff 1975). The A horizon is an organic-rich horizon in the upper mineral soil, which is not classified as an organic horizon because it contains less than 20% organic C by weight. Because this threshold must be determined in the lab, field dis-tinctions between the Oa and A horizons can be difficult and subjective (Federer 1982).

Fine and coarse woody debris are included in the forest floor to varying degrees by different research-ers. When forest floor samples are dried and then ground, twig and small branch litter can easily be included. When forest floor samples are sieved (mesh sizes in use vary from 2 to 8 mm), material too coarse to pass the sieve is excluded. However, decomposed woody material can be forced through the sieve, and considerable force is generally used, such that most buried woody debris usually passes regardless of the mesh size. Woody debris that is buried but not included in the forest floor escapes many ecosystem budgets of C and nutrient pools.

Finally, both live and dead fine roots are gener-ally included in measurements of the forest floor, although ecosystem budgets claim them for the liv-ing biomass pools. They are ground in any sample processed by grinding, and they are brittle enough to pass a sieve in dried samples processed by sieving. Like woody debris, fine roots present a small but systematic source of error in interpreting the dy-namics of the forest floor in the context of ecosys-tem budgets.

The Covington Study

Covington's study was conducted in the White Mountains of New Hampshire in the context of the Hubbard Brook Ecosystem Study. The Hubbard Brook Experimental Forest was established in 1955 by the US Forest Service to study the hydrology of small catchments. In 1963, the project was ex-panded to consider questions of nutrient budgets and cycling, and the Hubbard Brook Ecosystem Study was formally established as a cooperative endeavor between the Forest Service and professors from Dartmouth College, including Herb Bormann and Gene Likens.

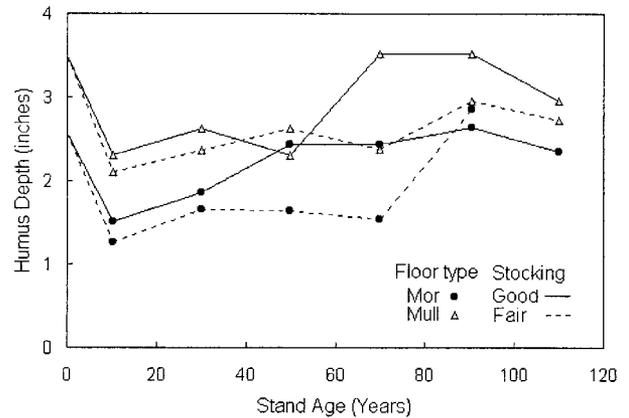In 1965, one of the Hubbard Brook catchments (W2) was clear-cut, and regrowth was prevented

Figure 2. Humus depth as a function of stand age as reported by Sartz and Huttinger (1950). Note that the points for year zero were not observations, but were supposed to describe the humus depth of the former stand prior to logging. The interval up to the first obser-vations was called "a period of organic decomposition following logging."

for 3 years by herbicides. By the time Wally Cov-ington started graduate school in 1972, the loss of nutrients and organic matter from this site was exciting interest. Dominski (1971) reported that the forest floor had declined by 3 cm or 24% (Bormann and Likens 1979), and decomposition of soil organic matter, especially the forest floor, was thought to be the primary source for the increased nutrient ex-port in stream water (Bormann and Likens 1979). Earlier chronosequence studies (Sartz and Hut-tinger 1950; Trimble and Lull 1956) had also re-ported forest floor losses after harvest (Figure 2). Covington decided to devote his dissertation work (Covington 1977) to the pattern of organic matter storage in the forest floor (Covington 1981) and litterfall (Covington and Aber 1980) following dis-turbance, using a chronosequence approach.

After some exploratory sampling, Covington was convinced that spatial variation in the forest floor was so great that even quite large differences be-tween sites would not be statistically detectable with random sampling. He decided to use a re-stricted stratified-random sampling approach to de-termine the parameters for the shape of the re-sponse surface. He avoided streams, rocks, stumps, root crowns, coarse woody debris, skid trails, other disturbed areas evidenced by abnormal horizona-tion, and pits and mounds caused by individual treefall (Covington 1981).

Covington found a dramatic difference in the amount of forest floor organic matter in stands of different ages (Figure 1). The oldest stands had the most, and the stands aged 18–22 years had the

least. He interpreted this pattern as resulting from two primary factors: accelerated decomposition after harvest and changes in woody litter inputs over time. Covington's 1981 paper is frequently cited as evidence of changes in decomposition rates or litter inputs, although there are other possible explanations for the pattern he observed.

Covington fit a least-squares curve to forest floor organic mass as a function of stand age using a gamma function, a complex curve that allowed some ecological interpretations. The curve started at the value of the asymptote approached in old stands, then decayed exponentially and recovered through logistic growth. Because this model has five parameters and there were a total of 14 stands, the choice of curve was not meant to be statistically justified. But it made explicit a function that could be applied to predict C and nutrient storage in the forest floor following disturbance, and the provision of an equation likely contributed to the curve's wide application.

Long before it was published in *Ecology* (Covington 1981), Covington's curve had a widespread influence. An important pathway of influence was the reproduction of Covington's woody litter, leaf litter, and forest floor curves in the second book on the Hubbard Brook Ecosystem Study, *Pattern and Process in a Forested Ecosystem* (Bormann and Likens 1979). This classic work expanded upon Covington's 1977 conceptual model of ecosystem development following disturbance, which consisted of degrading (age 0–15 years), rapidly aggrading (age 15–64 years), and slowly aggrading phases (age 64–200 years). Bormann and Likens's reorganization phase was the degrading period in which net ecosystem productivity was negative due to decomposition of dead wood and forest floor organic matter that exceeded the rate of living biomass accumulation (Covington 1977).

Extrapolation to the Global Scale

Covington's curve was applied to the global C budget almost immediately, and in some cases, extrapolated to the whole soil profile rather than just the forest floor. Woodwell and others (1978) provided an early rough estimate of the global C balance of terrestrial systems. They estimated that agricultural clearing and forest harvest caused the loss of perhaps 2.0 (0.5–5.0) Pg C y^{-1} from detritus and humus, citing only Covington's 1977 thesis as evidence that forest harvest causes a substantial net loss of soil organic matter. To improve these estimates, Moore and others (1981) developed a bookkeeping model to reconstruct the effects of historical land-use change on the global C budget.

Houghton and others (1983) described this model in detail, and Woodwell and others (1983) highlighted results from both studies. The bookkeeping model uses a series of idealized curves to describe the temporal patterns of C loss and recovery in vegetation and soils after forest harvest and conversion to agriculture. The effect of forest harvest on temperate forest soils (a 50% loss over 10 years) was largely based on Covington's curve, but this loss was applied to the whole top 1 m of soil rather than just the forest floor. The lost C was assumed to be released to the atmosphere and amounted to a net release of 0.34 Pg C y^{-1}, or 50% of the net flux from harvested and regrowing forests (Houghton and others 1983). Houghton and others (1983) acknowledged that their extrapolation to the whole soil profile was highly uncertain, and subsequent versions of the model reduced the assumed effect to 20% loss (Houghton and others 1987), or no effect of forest harvest on forest soils (Melillo and others 1988; Houghton 1995). This influential family of models extrapolated the Covington curve far beyond its intended range of sites and soil depths, with important implications for understanding of the global C budget.

Covington's curve has indirectly influenced other large-scale C budgets. To augment US Forest Service measurements of C sequestration in trees with estimates of changes in detrital pools, Birdsey (1992, 1996) referred to the model results of Pastor and Post (1986) and the model assumptions of Moore and others (1981) and Houghton and others (1983), all of which derived largely from interpretations of Covington's work, as justification for assuming that 20% of mineral soil C is lost following harvest and intensive site preparation in southern forests. In addition, forest floors were assumed to lose two-thirds of their preharvest C stock in all regions but the south, where it was assumed that site preparation practices caused the loss of the whole forest floor. These assumptions spread to Russia, as Kolchugina and Vinson (1993) provided early estimates of forest C sequestration for the former Soviet Union by applying Birdsey's (1992) rates of whole-system C accumulation to Russian forests. The estimates of both Birdsey (1992) and Kolchugina and Vinson (1993) were included in the synthesis of forest C sinks in the Northern Hemisphere by Dixon and others (1994), a widely cited reference for global-scale forest C uptake.

OBSERVATIONAL TESTS OF THE CURVE

Covington's curve had such important implications for C budgets and nutrient cycling that it inspired a

burst of research activity. Critics and enthusiasts sought to replicate Covington's curve through additional chronosequence work, to document changes by resampling individual sites over time or by comparing treated with untreated sites, and to test the mechanisms thought to be responsible for losses of forest floor mass after harvest.

Replicating the Chronosequence

Tony Federer sought to test Covington's findings using a less biased sampling scheme. He undertook a replication of the study (Federer 1984), visiting sites meeting the same criteria but sampling systematically. Covington had measured 14 stands in 1974. Federer sampled six stands in 1979 and seven more in 1980, only one of which coincided with Covington's. It was difficult to find additional stands in the age range predicted to have the least forest floor, because clear-cutting was not common in the region in the 1940s and 1950s. This made it impossible at the time to better test Covington's curve with more extensive sampling.

Federer's results supported some aspects of the Covington curve, but not others (Figure 1). The oldest of Federer's stands had the most massive forest floors and those between 10 and 32 years old had the least (Federer 1984), but the magnitude of implied decline (36%, or approximately 30 t/ha) was much less than Covington's 50% (approximately 40 t/ha). Federer suggested that some of the loss of forest floor organic mass might be due to mechanical disturbance rather than decomposition, which would have quite different implications for global C budgets.

Resampling the Chronosequence

A test of whether the chronosequence truly represented a developmental time series became possible once enough time had elapsed to allow significant progression of stands along the time axis. Covington's sampling scheme required judgment to exclude pits, mounds, and other anomalies, which would have been difficult to replicate. Fortunately, six of Federer's stands at the Bartlett Experimental Forest were permanently marked (Federer 1982), and the other seven were readily relocated. To assure consistency of sampling methods over time, Federer participated in resampling his chronosequence in 1994 and 1995, 15 years after the original sampling (Yanai and others 1999, 2000).

Covington's curve provided a testable prediction of the change expected for each stand, based on its age at the 2 sampling dates (Figure 3). Three stands were in the age range for which the curve described
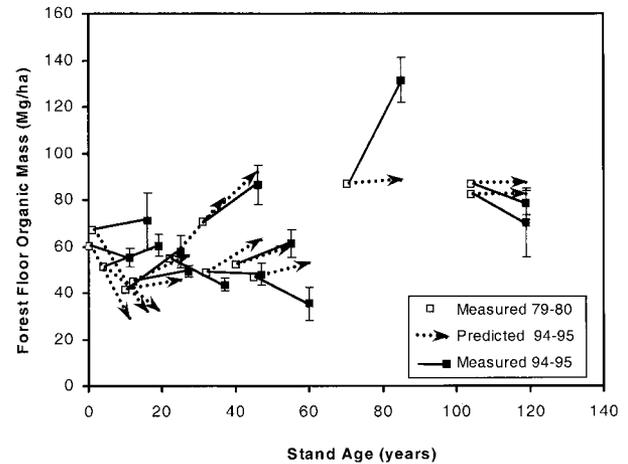

Figure 3. Predicted and observed changes in forest floor organic mass in Federer's chronosequence (1984). These values differ from those reported by Yanai and others (1999, 2000) because a previous error was corrected in the calculation of organic fraction. The starting points differ slightly from Federer's report (see Figure 1) because the archived samples were reanalyzed with the newer samples.

losses of 37%–52% of forest floor organic mass over a 15-year period. Middle-aged stands were predicted to gain organic matter by 1994–95, while the oldest stands should have achieved steady state, with organic matter essentially unchanged.

Instead of following Covington's curve, there was little pattern in the observed changes in forest floor mass as a function of stand age (Figure 3). The three youngest stands, which were predicted to show rapid losses, did not, and they differed significantly from the predictions ($P < 0.01$). The forest floors in the older stands remained more massive than those in the younger stands, but there was no significant change in the four stands that were predicted to increase their mass by 24%–46%. As discussed below, changes in logging practices over time may partly explain the pattern of forest floor mass observed by Covington.

Resampling of Individual Sites

Monitoring individual sites over time is an alternative to the chronosequence approach to studying forest succession. Inspired by Covington's curve, investigators at a variety of sites measured forest floor mass before and after logging. These studies sometimes found gains rather than losses and often suggested soil mixing as a mechanism for mass loss from the forest floor, rather than increased decomposition rates.

At the Coweeta Experimental Forest in the

southern Appalachians, clear-cutting with and without residue removal both resulted in increased forest floor masses 4–7 years after harvest (Mattson and Swank 1989). After a whole-tree harvest at an oak site in Virginia, forest floors mass increased immediately relative both to preharvest conditions and to a paired uncut site and declined within 2 years to preharvest levels (Johnson and others 1985). Three northern hardwood stands in Michigan had 42%–71% losses of forest floor mass 1.5 years after harvest, which was attributed in part to mixing with mineral soil; there was no continued mass loss in the next year (Mroz and others 1985). Fifteen years after whole-tree and sawlog harvest treatments at Oak Ridge, Tennessee, the C content of the forest floor did not differ from preharvest conditions or by harvest treatment relative to unharvested plots (Johnson and Todd 1998).

Closer to where Covington developed his curve, an experimental watershed at the Hubbard Brook Experimental Forest (W5) was clear-cut in 1983–84. The treatment was a whole-tree harvest with little slash remaining on site, which should have maximized the possibility of observing a loss of organic matter from the forest floor. Three years after the harvest, changes in forest floor and mineral soil C were not statistically detectable (Huntington and Ryan 1990). By 8 years after harvest, stocks of C in the forest floor had declined by 27% from preharvest values ($P = 0.05$) (Johnson 1995; Johnson and others 1995), but not by the 44% predicted by the Covington curve for 8 years postharvest. Field incubations of forest floor blocks indicated that 23% of forest floor C disappeared by 7 years postharvest (Johnson and others 1995). Even though new litter inputs were excluded from these blocks, their rate of mass loss was still slower than that predicted by the Covington curve.

Comparisons of Paired Stands, Cut and Uncut

Comparing forest floors in cut and uncut stands is another approach to testing the predictions of Covington's curve. Although the pre- and postcut comparisons described above did not consistently find mass loss from the forest floor, two studies have found multiple harvested stands to have considerably less massive forest floors than nearby uncut stands. In West Virginia, nine cut stands had on average 35% less forest floor organic mass than the paired uncut stands 0.5–23 years after harvest (Mattson and Smith 1993). In northwestern Quebec, four harvested stands had about half as much forest floor mass as four uncut stands 5–12 years after cutting (Brais and others 1995). However, not

all such comparisons have shown such dramatic differences. In a northern mixed forest in Ontario, the forest floor in a conventionally clear-cut stand had more organic matter 3 years after harvest than in adjacent uncut and whole-tree harvested stands (Hendrickson and others 1989). These tests of the Covington curve reported changes in mass of the forest floor; whether the differences are due to loss to the atmosphere depends on the mechanism of loss.

TESTING THE INITIAL INTERPRETATION OF THE CURVE

Accelerated Decomposition

It had long been asserted, but without experimental tests, that increased moisture and temperature following logging should accelerate decomposition rates (Lutz and Chandler 1946; Moller 1954; Hart 1961; Witkamp 1971). However, litter decomposition experiments following the 1981 publication of the Covington curve instead found the opposite.

In a southern Appalachian hardwood forest, decomposition rates of leaves of three hardwood species were slower in a clear-cut than in an adjacent uncut site 8 years after clear-cutting (Blair and Crossley 1988). Densities of microarthropods, important to decomposition in these systems, were also lower in the clear-cuts (Mattson and Smith 1993). In an oak forest in Wisconsin, mass loss from litterbags was slower in a clear-cut than in an uncut stand 5 to 7 years after harvest (Yin and others 1989). In a coastal montane coniferous forest on Vancouver Island, mass loss of needle litter was slower in harvested plots than in old-growth forest (Prescott 1997). In 14 sites across British Columbia, pine litter decomposed less rapidly in clear-cut than in paired uncut stands; rates of mass loss from aspen litter or forest floor material were not significantly affected by clear-cutting (Prescott and others 2000). In all these cases, the authors attributed slower decomposition in clear-cuts to drier surface conditions. Clear-cutting in an east Texas bottomland hardwood forest increased soil temperature and reduced moisture in the top 15 cm of mineral soil (Londo and others 1999). Clear-cutting at Oak Ridge, Tennessee, increased soil temperature to 15 cm; soil was drier at a depth of 3 cm but wetter at 15-cm depth (Edwards and Ross-Todd 1983). At an oak forest in Virginia, clear-cutting increased both temperature and moisture at 2.5-cm depth in the mineral soil (Johnson and others 1985).

Although process studies have demonstrated that litter decomposition does not generally increase af-

ter clear-cutting, particular responses will depend on climate and litter quality (Meentemeyer 1978; Moorhead and others 1999) and patterns of succession (Hughes and Fahey 1994), with accelerated decomposition perhaps more likely at higher latitudes (Yin and others 1989). In addition, although litterbag studies have generally found that decomposition rates are reduced after logging, it is not clear that the decomposition of the whole forest floor is described by such techniques. Cellulose in litterbags incubated at the interface of the Oe–Oa horizons decomposed more rapidly in clear-cut sites than in uncut sites on Vancouver Island, British Columbia, although there was no difference in litterbags incubated between the Oi and Oe horizons (Binkley 1984). Because the Oa is usually the most massive of the forest floor horizons, the effect of canopy removal is probably more important on conditions there than it is on conditions at the surface. It seems plausible that decomposition rates could decrease at the surface due to drying, while increased temperature or moisture could simultaneously promote decay at depth.

Changes in Litter Inputs

Change in the rate of litter inputs to the forest floor was another mechanism originally thought to control the shape of the Covington curve (Covington 1981). Even if decomposition rates were unaffected by clear-cutting, the hiatus in litter inputs that follows canopy removal should cause some decline in forest floor mass. After a delay, resumption of litter inputs by the regenerating stand should then cause forest floor masses to rise again.

The three primary categories of litter inputs to the forest floor are foliage, fine roots, and dead wood. Investigators knew 20 years ago that inputs of foliar litter recovered fairly rapidly after logging in northern hardwoods (Marks 1974; Covington and Aber 1980), so this input could not explain the timing of the Covington curve. Inputs of fine-root litter were less well understood, so in an attempt to explain the Covington curve, it was suggested that they were reduced for decades following harvest (Aber and others 1978). However, recent studies have shown that fine-root production and mortality are higher in recently cut than in undisturbed oak (Yin and others 1989) and oak–hickory forests (Idol and others 2000). Since fine-root production in mature northern hardwood forests rivals to foliar production (Fahey and Hughes 1994), and 50% of fine roots occur in the forest floor (Fahey and others 1988), the dynamics of root litter are potentially important in the effort to explain changes in the forest floor.

To explain the steep apparent rise in forest floor mass after year 20 (Figure 1), Covington (1981) suggested that inputs of woody litter might rise substantially, both because of the breakdown of large logging slash and because the regrowing forest reaches a stem exclusion phase, providing woody debris to the forest floor. The effect of such a pulse of woody debris on the forest floor is difficult to assess, however, because the rate at which woody litter in various size classes enters into measurements of the forest floor is not well known. After a clear-cut in which all the trees were left in place, 90% of the mass of dead boles had disappeared after 23 years (Arthur and others 1993), with an unknown fraction entering the forest floor. In a mixed oak forest in Tennessee, 85% of harvest residue decomposed within 15 years after clear-cutting (Johnson and Todd 1998). In North Carolina, two-thirds of the mass loss from recognizable woody debris was through mineralization, while solution fluxes of dissolved organic matter accounted for less than 10% of the mass loss, and fragmentation (including bark sloughing) accounted for the remainder (Mattson and others 1987). Some fraction of the fragmented material is also respired over time. Wood decay is highly variable among vegetation types and climates (Harmon and others 1986) and relative to the position of the wood above or on the soil (Johnson and Todd 1998).

ALTERNATIVE EXPLANATIONS

Accelerated decomposition has been the most common interpretation of the apparent loss of forest floor organic matter following harvest, but there are several alternative explanations for this pattern. The magnitude of the estimated loss depends on the curve fit to the data, and the equation used by Covington is a complex one. The assumed starting point appears too high, perhaps due to mixing of forest floor material with the mineral soil. An additional complication is that the degree of mixing is likely to have varied over the chronosequence, because of changes in harvest practices over time.

An Ambitious Curve Fit

Although the chronosequence approach focuses on stand age as an explanatory variable, many other factors affect soil properties, such as tree species, microclimate, microtopography, soil texture, and parent material. These factors introduce spatial variation in soil properties, which can confound the space-for-time substitution unless there is a sufficient number of sites to clearly distinguish pattern

from random variation. The form of the Covington curve, with its exponential decrease and asymptotic recovery, was based on ecosystem theory rather than statistical parsimony. An overly complex curve is likely to find pattern in random spatial variation, and Covington's equation fit 14 points with five parameters. The Covington curve's loss of 50% of forest floor organic matter, or about 45 Mg/ha, in the years following disturbance has two main causes for uncertainty. First, forest floor organic content can easily vary by 20–30 Mg/ha among stands of approximately the same age (Figure 1). Second, where forest floor material has been mixed with the mineral soil, the assumed starting point immediately postdisturbance is too high.

Mixing or Movement into Mineral Soil

Contemporaries of Covington such as John Aber and others (1982) and Tony Federer (1984) recognized the possible importance of mixing forest floor material into the mineral soil. It has long been recognized that forest operations often disturb soils (Nyland 2001). A study of 13 partially cut hardwood stands in New York found that skid trails covered an average of 38% of the area, with 99% of skid trail area disturbed (Nyland and Gabriel 1971). Three whole-tree harvested sites in New England had mineral soil exposed in 8%–18% of the area; some type of disturbance affected 71%–92% of the area (Martin 1988). In a study designed to follow the fate of the missing forest floor, Ryan and others (1992) found mineral soil exposed in 25% of a whole-tree harvested watershed (W5) at Hubbard Brook. Buried organic horizons were found in 10% of the area.

Disturbance that leaves mineral soil at the soil surface reduces the organic mass of the forest floor as typically defined and measured. If mineral soil is deposited on the soil surface, the former O horizon is a buried horizon and is not collected by standard sampling methods. If forest floor material is mixed with mineral material such that the organic C is less than 20% of the mass, it is classified as mineral soil. In the study mentioned above, Ryan and others (1992) found enough organic matter buried and mixed with mineral soil to account for the loss from the forest floor.

Initial mixing of forest floor into mineral soil could explain why the young stands of the Covington and Federer chronosequences fall well below the starting point of the Covington curve (Figure 1). The curve fit assumes that immediately following harvest, a stand begins with mass matching that of mature forest stands and loses mass via decomposition. This assumption was also made by Sartz and

Huttinger (1950) and Trimble and Lull (1956) (Figure 2). None of these chronosequences provides evidence for the assumed high forest floor mass or thickness immediately after harvest. Forest floor mass or thickness in sites aged 1–4 years were only about 75% of the values of mature, unharvested sites (Figures 1 and 2), leaving open the possibility that logging disturbance causes burial of the forest floor and that the initial decomposition rate is overestimated by these curves. The distinction between respiring the forest floor and moving it into the mineral soil is obviously critical for accurate accounting of C.

In addition to CO_2 mineralization and mechanical mixing, losses of C from the forest floor after harvest can result from erosion or from increased leaching of dissolved organic C (DOC). Leaching of DOC from the forest floor transfers C to mineral soils, where it is largely retained (McDowell and Likens 1988; Qualls and others 1991; Currie and others 1996). DOC production and leaching is sensitive to any changes in hydrologic fluxes or mineralization rates of litter or humus (Kalbitz and others 2000). Root trenching increased losses of DOC from the forest floor (Cronan and others 1992), and DOC leaching from the Oa horizon increased by 15–20 kg C ha^{-1} y^{-1} relative to a control watershed in the 8 years following the harvest of W5 at Hubbard Brook (Johnson and others 1995). However, the generality of any changes in DOC fluxes after forest harvest is uncertain, because other studies have found either increases, decreases, or no change (Kalbitz and others 2000).

Changes in Logging Impacts over Time

One of the weaknesses of the chronosequence approach to studying forest floor dynamics is that the nature of the logging treatment has changed over time. The oldest stands in the Covington and Federer chronosequences were probably logged by hand, with the boles removed from the site with horses. The stands in which Covington found the lowest forest floor mass—those that were 10–30 years old in 1974—were harvested between 1944 and 1964. This period coincided with the use of crawler tractors, which were introduced in this region after World War II and were replaced by rubber-tired skidders during the 1960s. One important difference between the effects of horses, tractors, and rubber-tired skidders is the degree of mechanical disturbance of the forest floor. In an Idaho study, soil displacement was greater following tractor logging than skidder logging (Clayton 1990).

Another difference between logging treatments over time is the market for wood products, which

influences the amount of material removed in logging and the amount left behind to decompose and rebuild the forest floor. Increasing the intensity of harvest removals also increases soil disturbance because more of the land area is traversed by logging equipment (Martin 1988). In a literature review, Martin (1988) concluded that the extent of disturbance had increased over time in New England, coincident with changes in technology and the increase in harvest intensity. Both factors, temporal change in the amount of mixing of forest floor into mineral soil and an increase in biomass removals, could contribute to the pattern observed by Covington, in which recently harvested stands have less forest floor mass than those harvested long ago.

ATTEMPTS TO MODEL THE CURVE

Previous Modeling Efforts

Covington's study took place just prior to a period of rapid progress in the development of biogeochemical process models. The chronosequence of forest floor masses was considered a valuable data set for model development and testing (Aber and others 1978; Pastor and Post 1986, 1988). The modeling approaches developed during this period contributed to the extended influence of the Covington curve.

JABOWA and FORTNITE.   John Aber and others made two early efforts to model ecosystem processes after harvest, including changes in forest floor mass. In the first model (Aber and others 1978), empirical curves describing litter inputs through time in three shade tolerance categories of vegetation were linked with a new model of decomposition processes. Foliar litter was assigned decomposition rates by shade tolerance class, to allow simulation of the effect of rapidly decomposing litter from early successional species. The model used litterfall data from Covington's chronosequence plots to parameterize the recovery of foliar production to 80% of preharvest litterfall flux within 5 years (Covington and Aber 1980). Inputs of fine roots and woody litter were described as theoretical curves in the model, based on best contemporary estimates in the absence of field data. Fine-root litter was assumed to begin at zero and rise linearly over a period of 30 years. Woody litter inputs were assumed to have a maximum rate of increase in year 30, as suggested by JABOWA simulations (Covington 1981).

Using these temporal patterns of litter inputs, the model simulated a rapid increase in forest floor mass beginning about 25 years after harvest (Aber

and others 1978). However, the model did not reproduce the Covington curve's severe minimum. The model then calculated the degree to which decomposition would need to increase following harvest in order to match the minimum of the Covington curve. This exercise generated a "decomposition multiplier" that began with a 30% increase in decay rates and returned linearly to zero by 38 years after harvest.

The second modeling effort produced FORTNITE (Aber and others 1982), a model that used the gap model JABOWA (Botkin and others 1972) to produce more mechanistic inputs of litterfall to the decomposition and forest floor model described above. Inputs of fine-root litter recovered rapidly after harvest, consistent with the rapid rise in foliar litter inputs. FORTNITE produced a curve of forest floor mass after harvest that declined more rapidly than that predicted by the previous model (Aber 1979) or by the Covington curve, reached a minimum proportionally higher than in the Covington curve and subsequently rose more slowly than both the previous model predictions and the Covington curve. The authors concluded, "It is difficult to explain how the forest floor could continue to decline for 20 years when leaf and presumably fine root litter recover very rapidly. Changes in the distribution of fine root litter or in the rate of mixing between forest floor and mineral soil could be important here" (Aber and others 1982).

LINKAGES.   LINKAGES (Pastor and Post 1986) expanded on the successional forest dynamics of the JABOWA (Botkin and others 1972), FORET (Shugart and West 1977), and FORTNITE (Aber and others 1982) models. LINKAGES also expanded on some of the decomposition processes from FORTNITE, broadening the set of ecological interactions to include soil texture and water use by vegetation. Again, the Covington (1981) and Federer (1984) chronosequence data were viewed as providing a check on the simulations. The model produced a mean response of an initial postharvest decline in forest floor mass that was much less steep than that of the Covington curve (Figure 4). There was a sharp rise to a peak in forest floor mass 30–40 years after harvest, due to inputs of woody stems during the stem exclusion phase of forest development.

LINKAGES included a postharvest multiplier of decay rates (1.0 to 2.0) (Pastor and Post 1986), similar to the one explored by Aber and others (1978). This multiplier depends on the ratio between current leaf area and that of a closed canopy and on the water-holding capacity of soil, which allows variability among sites. Still, LINKAGES did
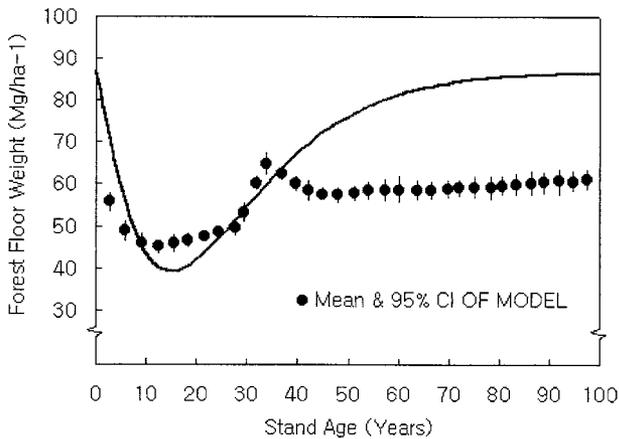
Figure 4. A comparison of the results of the LINKAGES model (Pastor and Post 1986) with Covington's curve (1981).

not simulate the depth of Covington's curve (Figure 4). In model simulations, this multiplier had only a minor effect on decay rates (J. Pastor personal communication), possibly because canopy recovery was so rapid.

A key feature of LINKAGES is that it was intended to represent landscape-level averages, not actual trajectories for any particular forest stand. Pastor and Post (1986) emphasized two important sources of variability. First, simulated declines in soil organic matter after harvest were closely related to initial stocks of soil organic matter, which could result from the particular histories of each stand. Second, successional trajectories could differ among stands and have major impacts on both preharvest levels and postharvest trajectories of forest floor mass (Pastor and Post 1986). Aber and others (1982) also emphasized the importance of variable successional trajectories.

An Additional Modeling Exercise

We undertook a new modeling exercise using the DocMod model (Currie and Aber 1997) to explore the dynamics of the forest floor in the region of New Hampshire represented by the Covington curve. This model contains many processes in common with models mentioned above, with three important differences: Our model allows mixing of forest floor and mineral soil during harvest, it contains no increase in decay rates following harvest, and it excludes coarse woody litter (more than 5 cm in diameter).

Model Structure. We linked the forest production model PnET (Aber and Federer 1992) and the decomposition model DocMod, as done previously by

Currie and Aber (1997). PnET has been used to model forest production across the region (Aber and others 1995). DocMod was developed to model litter decay, humification, and DOC production in the forest floor. The interactions of litter quality and climate in controlling litter decay in DocMod have been tested in a blind model comparison against field data in four biomes (Moorhead and others 1999).

We adapted the linked PnET–DocMod to the analysis of forest floor mass after harvest. We used PnET to estimate steady-state values of foliar, fine-root, and woody litter production. DocMod then used these litter inputs to reach a steady-state forest floor mass before simulating a harvest. In the simulated harvest, fine woody debris (less than 5 cm in diameter) and O-horizon material were mixed downward into mineral soil, a fraction of the living aboveground foliage and woody tissue (less than 5 cm in diameter) was added to the forest floor from slash, and dying roots were added as litter to forest floor and mineral soil horizons.

The main process we sought to explore was the mixing of organic and mineral soil during logging. We also included two other processes not represented in previous models. First, we included the leaching of DOC from the forest floor to deeper soil horizons, which amounts to a transfer of C equivalent to 10%–25% of foliar litterfall. Because soluble organics are somewhat stabilized in mineral soils, this amounts to a substantial sink for C in mineral soil over the lifetime of a forest stand. We also included a positive feedback of root litter inputs to the forest floor, with more fine roots present in a thicker (more massive) forest floor; however, in our simulations, forest floor mass was relatively insensitive to this feedback.

Model Parameterizations and Calibrations. To parameterize the postharvest time series in foliar litter inputs, we used the observations of Bormann and Likens (1979), in which inputs rise within 4 years of clear-cutting to about 80% of closed-canopy values and reach closed-canopy values within 28 years. Our simulated inputs of fine-root litter recovered at the same rate as foliar litter inputs. Foliar litter quality, a determinant of decay rates in DocMod, was parameterized to species in the region (Currie and Aber 1997) and distributed through time among three successional classes, as in Aber and others (1978).

For inputs of woody litter, we used a sigmoidal curve beginning with zero inputs after logging, as did Aber and others (1978). However, our curve rose to its maximum and steady-state value in year 30, as opposed to year 60, our woody litter inputs
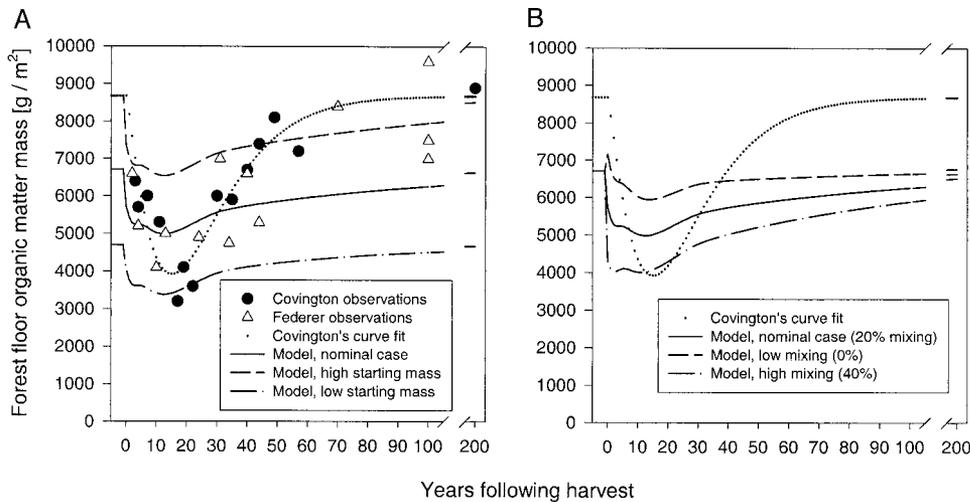
Figure 5. Comparisons of measurements and models of organic mass of the forest floor after harvest. (**A**) Covington's (1981) and Federer's (1984) measurements shown together with Covington's empirical curve fit, and three simulations of the linked PnET–DocMod models. Model results derive from three different preharvest values of organic mass as steady-state values: our nominal case (6700 g OM/m²), a higher value (8675 g OM/m²) used by Covington (1981), and a lower value (4725 g OM/m²) for illustration. All three simulations used a rate of mixing of 20% of O-horizon organic mass during harvest. (**B**) Model results from three simulations using our nominal steady-state value of organic mass (6700 g OM/m²), with three different rates of mixing during harvest: 0, 20%, and 40%.

and woody detrital pools included only material less than 5 cm in diameter, and we allowed 25% of these woody inputs to be eventually incorporated into forest floor mass. We assumed that longer time periods are required after clear-cutting before larger-size classes of woody stems are produced, lost as litter, and decomposed sufficiently to enter measurements of the forest floor.

Of the main processes controlling forest floor mass, the rates of wood fragmentation and humification and the rates of humus turnover are the most poorly known. After the PnET–DocMod link was structured and parameterized, the decay rate of fine woody debris was adjusted to produce a steady-state pool amounting to 455 g/m² (ash-free), the value obtained in a mixed hardwood forest in central Massachusetts (Currie and Nadelhoffer 2002). Second, three decay rates of humus in the Oa horizon were selected to produce three steady-state values in forest floor mass for the same litter input. The first mass value was 6.7 kg/m², the mean of seven measurements obtained over a 21-year period at W6 at Hubbard Brook (Yanai and others 1999). For the second mass value, we used 8.7 kg/m², the asymptotic value of Covington's (1981) curve. For purposes of illustration, we chose a third value, 4.7 kg/m², which was equally far below the first value.

We ran the model using these three steady-state values of mass, assuming that 20% of the harvested

biomass is left on site as slash and that 20% of O-horizon mass is mixed downward during logging (Figure 5A). We also ran the model for three rates of soil mixing: 0, 20%, and 40%, with initial forest floor mass and humus decay rate held constant (Figure 5B).

Model Results and Interpretation. Our model results show that the rapid drop in Covington's curve cannot be explained by changes in litter inputs as represented here, without increases in decay rates after harvest. Mixing during harvest, on the other hand, can produce a sudden drop in forest floor mass. The steep rise in forest floor mass indicated in years 30–45 in the Covington curve requires an explanation not represented in our model. A change over time in the rate of mixing at harvest, as expected with changes in logging technology, might explain the observed differences between stands harvested at different times (using different curves in Figure 5B to explain different points in Covington's curve). Alternatively, as Covington suggested, coarse woody litter, which was omitted from this model, could play an important role in forest floor recovery.

Today, 20 years after publication of Covington's (1981) results, model validation is still limited by a lack of knowledge of the rates of production, decay, and stabilization of litter following harvest, especially root and woody litter and especially at depth within the forest floor. These limitations make it

difficult even now to produce a model that can distinguish between the possible explanations for Covington's curve.

Lessons Learned

Challenges of the Chronosequence Approach

The main challenge of using a chronosequence to infer changes in ecosystem processes with stand age or time since treatment is that other factors may vary or covary along the chronosequence. For example, a purported accumulation of nitrogen over time in *Pinus radiata* plantations in New Zealand turned out to be due instead to a fertility gradient that coincided with time of planting (Turvey and Smethurst 1988). Stand development in Glacier Bay, Alaska, was determined as much by changes in seed sources over the course of several hundred years as by successional processes (Fastie 1995).

The chronosequence interpretation of Covington's curve (Figure 1) requires an explanation for a dramatic loss and recovery of forest floor mass over time after logging. Increases in decomposition following harvest and delayed resumption of litter inputs may be important mechanisms. Alternatively, the small organic masses in stands harvested between the mid-1940s and mid-1960s might be partly explained by the particular harvesting practices of that time. In addition, model results illustrate the importance of preharvest values of forest floor mass. Because recently logged stands are likely to have been second-growth stands already, they may have started with lower forest floor mass. These differences in treatments and starting conditions could contribute to deviation from the chronosequence assumption that stands followed the same trajectory of development. Changes in CO_2, climate, and other biotic and environmental factors give further cause to doubt that the forest floors of more recently harvested stands will follow the same curve as the oldest stands in the chronosequence. Finally, spatial variation in the landscape introduces a high degree of uncertainty in the space-for-time substitution. These limitations in the chronosequence approach underscore the need for long-term ecosystem studies, especially replicated treatments or reference systems paired with manipulations.

Growth of Knowledge and Remaining Uncertainties

The many studies inspired by Covington's curve have greatly advanced our understanding of factors influencing organic matter storage in the forest floor. However, even the two mechanisms most prominently raised by Covington (1981)—increased decomposition rates and changes in litter inputs—remain uncertain, and new mechanisms have been proposed.

Before Covington's study, it was widely believed that decomposition rates increased after forest harvest; afterward, Covington (1981) was often cited to support this belief. However, subsequent research found, mostly to the investigators' surprise, that litter decomposition did *not* increase after harvest. Nonetheless, studies of litterbags at the soil surface do not reflect conditions deeper in the forest floor. A small increase in decomposition rates in the Oa horizon, which is by far the most massive, could have an effect. This continues to be a key uncertainty.

The role of root litter and woody litter in forest floor dynamics remain difficult to assess. There is now better information on the size of coarse woody debris pools, but rates of woody litter inputs and the rates of fragmentation, decay, and stabilization that control residence time in the forest floor remain relatively unknown.

Research inspired by Covington's curve has introduced new factors into explanations of organic matter storage in the forest floor. Organic matter can be mixed downward into mineral soils during harvesting, which has very different implications for ecosystem C storage than does a loss to decomposition. In fact, organic matter may be more stable in the mineral soil than it would have been in the surface organic layer. Enhanced leaching of dissolved organic matter into mineral soil, where it is largely sorbed and partially stabilized, is another, if minor, mechanism of C transfer out of the forest floor after harvest. Analyses that have used the Covington curve to supply a flux of C to the atmosphere have probably overestimated the effect of forest harvest on the global C budget.

In the absence of a better source, Covington's curve was used for global C accounting of the whole soil profile. Most of these extrapolations have since been corrected, but the influence of the Covington curve persists in ways that can be difficult to identify because it is often not cited directly. Fortunately, better sources are now available. Dale Johnson (1992) reviewed 13 studies and concluded that C stocks in the mineral soil were largely unaffected (less than 10% change) by forest harvest. Johnson and Curtis (2001) augmented this review and conducted a formal meta-analysis of 73 studies. Some

researchers reported increases, others found decreases; the average overall effects were slight. Whole-tree harvest (29 studies) caused a small decrease (6%) in A-horizon C stocks, whereas sawlog harvest (44 studies) resulted in a small (18%) increase, largely in coniferous stands (34 studies). Neither review examined the effects of forest harvest on the forest floor, although Johnson and Curtis (2001) suggested that the amount of harvest residue left behind would be a dominant control. Although the effects of forest harvest on forest floor mass remain equivocal, our current understanding suggests that forest harvest has a much smaller effect on forest floor and soil C pools than was predicted from early interpretations of Covington's curve.

The Influence of a Compelling Interpretation

It is easy to understand why Covington's curve gained so much influence so rapidly. It provided an empirical, quantitative model of an ecosystem pattern that was widely needed but very difficult to verify. The reported loss of 50% of preharvest forest floor organic matter was striking and memorable, and the interpretation seemed reasonable. However, the causes of the differences in forest floor organic matter with stand age cannot be easily explained. As we have outlined here, key processes suggested by Covington more than 20 years ago still remain to be tested adequately.

There are other examples in ecology of paradigms that have been widely influential without having been confirmed by experimental tests. Charlie Hall described the weakness of the data supporting the logistic, Lotka-Volterra, and density-dependent recruitment models (Hall 1988). He attributed the persistence of these models in part to the appeal of simple rather than complex explanations and the power of mathematical descriptions.

The Covington curve is an example from the field of ecosystem science in which a data set, together with a quantitative and mechanistic interpretation, served to synthesize contemporary hypotheses into a paradigm. This paradigm inspired further data collection, hypothesis testing, and the modeling of important patterns and processes, such as decomposition rates, the dynamics of coarse woody debris, and soil disturbance in harvesting operations. Now, 2 decades later, we can appreciate both the achievement this paradigm represents and the fact that future paradigms of the response of forest soils to disturbance will likely incorporate a somewhat revised set of processes.

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