Landscape patterns of change in coarse woody debris accumulation in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky[1]

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Abstract: Forest disturbance was evaluated in an old-growth forest on the Cumberland Plateau in southeastern Kentucky using a 10-year history of coarse woody debris (CWD) accumulation. CWD averaged 21.8 Mg/ha in 1989 and 29.6 Mg/ha (36% increase) in 1999. In both years, *Quercus montana* Willd. and *Fagus grandifolia* Ehrh. were the two dominant components of CWD; however, over the 10-year interval, *Tilia heterophylla* Vent., *Carya glabra* (Mill.) Sweet, and *Acer saccharum* Marsh. increased significantly, while *Quercus alba* L. declined. CWD occurrence had a highly skewed frequency, which is consistent with the idea that gap dynamics dominate the disturbance patterns of temperate old-growth forests. However, CWD composition bore limited relationship to overstory species composition or to the dynamics of gap creation. Further, while CWD showed no relationship to forest community (i.e., landscape position) in 1989, it was strongly related to community in 1999. The increase in CWD mass and changing importance of landscape position appear to have occurred in the absence of extrinsic disturbance factors. Thus, in old-growth deciduous forests of the temperate region, autogenic disturbance appears to occur at two scales: (*i*) the patch dynamics of individual tree mortality and (*ii*) landscape-scale patterns of mortality that are determined by species composition and differing patterns of mortality among species.

Résumé : Les perturbations en forêt ont été évaluées dans une forêt ancienne située sur le plateau de Cumberland, dans le Sud-Est du Kentucky, en utilisant des données sur l'accumulation des débris ligneux grossiers (DLG) pendant une période de 10 ans. Les DLG atteignaient en moyenne 21,8 $Mg \cdot ha^{-1}$ en 1989 et 29,6 $Mg \cdot ha^{-1}$ en 1999, soit une augmentation de 36 %. *Quercus montana* Willd. et *Fagus grandifolia* Ehrh. dominaient chaque fois la composition des DLG. Cependant, au cours de l'intervalle de 10 ans, la proportion de *Tilia heterophylla* Vent., *Carya glabra* (Mill.) Sweet et *Acer saccharum* Marsh. a augmenté de façon significative tandis que celle de *Quercus alba* L. a diminué. L'occurrence des DLG suivait une fréquence fortement décalée, ce qui est consistant avec l'idée que la dynamique des trouées domine les patrons de perturbation dans les forêts anciennes tempérées. Cependant, la composition des DLG était peu reliée à la composition en espèces de l'étage dominant ou à la dynamique de formation des trouées. De plus, alors que les DLG montraient peu de relation avec la communauté forestière, (c.-à-d. la position dans le paysage) en 1989, ils étaient fortement en lien avec la communauté en 1999. L'augmentation de la masse des DLG et le changement d'importance de la position dans le paysage semblent être survenus en l'absence de facteurs extrinsèques de perturbation. Par conséquent, dans les forêts anciennes décidues de la région tempérée, les perturbations autogéniques semblent survenir à deux échelles : (*i*) la dynamique parcellaire de la mortalité des arbres individuels et (*ii*) les patrons de mortalité à l'échelle du paysage qui sont déterminés par la composition en espèces et les patrons de mortalité qui diffèrent selon l'espèce.

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Introduction

Interpretations of forest disturbance have frequently focused on the distinction between allogenic and autogenic quasi-internal disturbance. While stand-replacing allogenic disturbance is an event of far-reaching impact on structure and dynamics of many forest systems (Oliver 1981; White 1979), mesic temperate forests are often characterized by gap phase dynamics in which mortality of single trees dominates the pattern of turnover and recovery (Runkle 1985). The shifting mosaic model of forest dynamics (Bormann and Likens 1979) and numerous studies of gap dynamics (Lorimer 1977, 1980; Picket and White 1985; Poulson and

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Platt 1996; Runkle 1990) imply a degree of homogeneity in old-growth forests, such that gap disturbance has equal probability of occurrence across the landscape. Thus, the occurrence of gaps should be randomly distributed across the landscape of old-growth forests. However, overstory species are not necessarily randomly distributed across the landscapes of old-growth forests, and differences in species behavior (maximum age, depth of rooting, response to stress, etc.) may strongly influence gap formation, leading to spatially heterogeneous patterns of disturbance.

In forested ecosystems, disturbance creates a legacy, not only in the gap that is produced but also in the coarse woody debris (CWD) that is left behind. Because of its somewhat slower rate of disappearance, CWD serves as a longer record of disturbance than actual gaps within the canopy, which are rapidly filled by ingrowth. CWD has been well recognized as an important component of ecosystem structure and function, playing roles in carbon and nutrient storage, hydrologic response, and seedling establishment, and providing physical structure for higher trophic levels (McFee and Stone 1966; Franklin et al. 1987; Harmon et al. 1986; Harmon and Chen 1991). Global patterns of CWD mass indicate large accumulations in cool coniferous forests of high latitudes, intermediate accumulations in temperate regions, and low accumulations in moist tropical regions (Harmon et al. 1986; Muller and Liu 1991; Tritton 1980; Uhl and Kauffman 1980). However, these patterns are complex and are regionally modified by temperature and moisture regime, with greater accumulations occurring in drier and (or) cooler habitats (Harmon et al. 1995). Successional patterns of CWD accumulation have also been documented using chronosequences and suggest general patterns in temperate forests of high accumulations in disturbed stands followed by low accumulations in aggrading stands and finally level and intermediate accumulations in mature stands (Idol et al. 2001; Spetich et al. 1999; Spies et al. 1988). Such successional patterns reflect the impacts of allogenic disturbance and subsequent stand regeneration. However, to date, repeated measures of CWD in old-growth forests have not been used to evaluate stand dynamics.

In old-growth forests, CWD has been used as a standard against which the influences of natural disturbance and forest management can be evaluated (Keddy and Drummond 1996; Hale et al. 1999; McGee et al. 1999). However, the dynamics of CWD in these forests and the distribution of those dynamics in relation to landscape position and forest community have been little studied. Change in CWD amount over time may be one of the strongest measures of the dynamics of forest structure, since CWD is a short-term record of canopy disturbance. Changes in CWD are often presumed to be a product of either stochastic allogenic events such as windthrow (Putz and Sharitz 1991) and ice damage (Rebertus et al. 1997; Mou and Warrillow 2000) or autogenic processes of old-growth forests resulting from characteristics such as advancing age or variation in productivity (Romme and Martin 1982). In the absence of exceedingly long-term studies, disturbances by stochastic events or internal processes are impossible to distinguish except in the most extreme cases, such as Hurricane Hugo (Putz and Sharitz 1991) and the 1998 ice storm throughout the northeastern United States and southeastern Canada (Rhoads et al. 2002). Further, internal processes likely predispose a forest to susceptibility to stochastic events. Regardless of cause, changes in CWD should provide a measure of recent canopy disturbance.

An old-growth mixed mesophytic forest in southeastern Kentucky provides a unique opportunity to investigate landscape patterns of forest dynamics using short-term changes in CWD accumulation. To accomplish this, changes in total CWD accumulation and proportion of individual species as well as changes in the relationship between landscape position and CWD amounts were evaluated over a 10-year period of study.

Study site and previous investigation

The Lilley Cornett Woods Appalachian Research Station (37°05′N, 83°00′W, Roxana Quadrangle) in southeastern Kentucky contains an old-growth mixed mesophytic forest that is representative of the forests of the Rugged Eastern Section of the Cumberland Plateau (Braun 1950). The very steep and highly dissected terrain of the area supports diverse vegetation (Martin 1975; Muller 1982) with strong gradients related to slope position, soil moisture, and nutrient availability. Three forest communities have been described: beech forests occur on lower slopes and are dominated by *Fagus grandifolia* Ehrh., sugar maple – basswood stands are on midslopes on north- and east-facing aspects and are dominated by *Acer saccharum* Marsh. and *Tilia heterophylla* Vent., and chestnut oak – red maple forests are found on upper slopes, ridgetops, and midslopes of south and west aspects and are dominated by *Quercus montana* Willd. and *Acer rubrum* L. (Muller 1982).

Eighty permanent 0.04-ha plots established in Big Everidge Hollow have provided a framework for analysis of vegetation patterns and dynamics, soil properties, litter fall, production of secondary chemicals, and spatial patterns of CWD accumulation (Muller 1982; Muller and Martin 1983; Muller et al. 1987; Muller and Liu 1991). Ten plots were established randomly in each of eight topographically defined strata to ensure adequate sampling of the full range of sites within the watershed (further details available in Muller 1982; Muller and Liu 1991). In 1989, CWD on all plots was quantified (Muller and Liu 1991). Over the entire watershed, CWD averaged 21.8 Mg/ha, with the greatest amounts occurring in the chestnut oak – red maple forest community (27.1 Mg/ha) and somewhat lesser amounts occurring in the beech and sugar maple-basswood communities (17.0 and 20.7 Mg/ha, respectively). Although not statistically significant, this distribution of CWD suggested greater amounts on more exposed drier sites dominated by oaks and red maple. All but four of the plots contained some measurable CWD; however, the accumulation was patchily distributed throughout the watershed with 10 of the 80 plots containing 39% of the total measured mass. Similarly, while the accumulated CWD was composed of 23 species, six species accounted for >75% of the accumulation. With the exception of *Castanea dentata* (Marsh.) Borkh., which has not grown a tree-sized stem in the area since the introduction of chestnut blight in the 1940s, the species composition of CWD generally resembled the species composition of the overstory.

Materials and methods

In 1999, a resurvey of CWD on all 80 plots was conducted. Sample methods followed those of Muller and Liu (1991). CWD (woody material not incorporated into the forest floor or humus) over 20 cm in diameter was measured. Each piece was identified to species, categorized as a branch fragment, log, or snag, and assigned a decomposition class based on characters of bark slippage and depth of decay. Individual pieces were measured for overall length and diameter at each end and in the middle. Volume was determined for each portion of the individual pieces assuming that it was a segment of a cone of known length and end diameters. Mass was determined for each piece using previously determined densities (see Muller and Liu 1991).

The large increase in highly decomposed materials (class IV) (Table 1) led to considerable difficulty in identifying CWD to species, both in the field and in the laboratory. In particular, four out of 39 pieces of *Acer* and seven out of 25 pieces of *Carya* could not be identified to species. Additionally, several pieces of *Quercus* could not be distinguished further than the two subgenera *Leucobalanus* (including *Quercus alba* L. and *Q. montana*, 59 out of 178 pieces) and *Erythrobalanus* (*Quercus coccinea* Muenchh., *Quercus rubra* L., and *Quercus velutina* Lam., 17 out of 74 pieces). Finally, difficulties in distinguishing extremely decomposed *Quercus* and *C. dentata* led to an increase in estimated *C. dentata*.

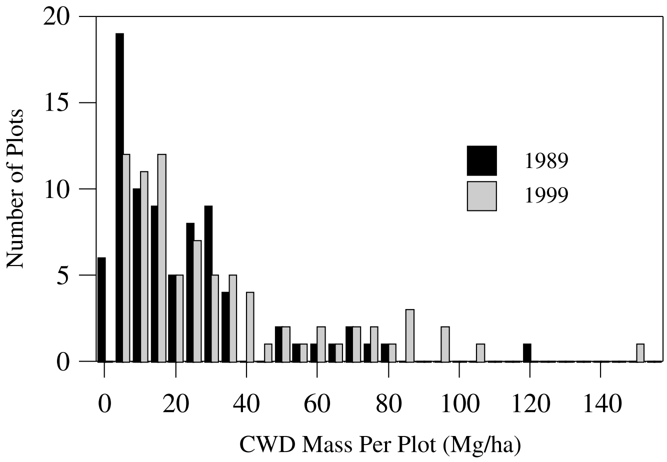
The data (CWD volume and mass) were summarized on each of the sample plots by species and for all species combined. Because of highly skewed distributions, the data were analyzed nonparametrically. Differences between years were analyzed using the Wilcoxon paired-sample test and differences among communities were analyzed using the Kruskal–Wallis test. However, to make meaningful comparisons with other studies and to consider CWD in the context of ecosystem dynamics, mean values are presented with the maximum value as a measure of the range of variation. Aboveground living biomass of all stems >20 cm diameter at breast height was calculated using the generalized equation of Monk et al. (1970) for boles and large stems of southern Appalachian hardwoods.

Table 1. Distribution of coarse woody debris (CWD) among coarse woody debris types and decomposition classes at Lilley Cornett Woods, southeastern Kentucky, in 1989 and 1999.

	1989		1999	
	Mg/ha	%	Mg/ha	%
CWD type				
Logs	14.5	67	20.9	70
Fragments	2.1	10	3.3	11
Snags	5.2	24	5.5	19
Total	21.8		29.7	
Decomposition class				
I	7.0	33	6.7	24
II	7.9	37	5.5	19
III	2.3	11	7.0	23
IV	4.4	20	10.3	34
Total	21.6		29.7	

Note: Differences in column totals are the result of rounding errors.

Fig. 1. Frequency distribution of coarse woody debris (CWD) occurrence on eighty 0.04-ha plots in Big Everidge Hollow at Lilley Cornett Woods, Letcher County, Kentucky.



Results

CWD in 1999 exhibited a marked increase from the 1989 estimate. Although amounts on individual plots were in the same range as for the previous sampling (0.3–146.3 versus 0–120.3 Mg/ha in 1989) (Fig. 1), CWD over the watershed averaged 103.5 m^3/ha and 29.7 Mg/ha versus 65.4 m^3/ha and 21.7 Mg/ha in 1989. This represents a 58% increase in CWD volume (p = 0.006) and a 36% increase in CWD mass (p = 0.091) over the 10-year sampling interval. The distribution of CWD among debris types was also generally similar among years. Logs accounted for 67% of the total mass in 1989 and 70% in 1999, branch fragments 10 and 11%, respectively, and snags 24 and 19%, respectively (Table 1). However, strong differences were observed in the distribution of CWD among decomposition classes in the two surveys. In 1989, the two more thoroughly rotted classes (III and IV) accounted for 31% of the total accumulation, while in 1999, these same classes accounted for 58% of the total (Table 1).

The overall increase in CWD reflected variable proportions of individual species among years (Table 2). A total of 23 species were part of the accumulated CWD in 1989 and 29 species in 1999. In 1989, >75% of the accumulated CWD was accounted for by only six species: *Q. montana* (24.8%), *F. grandifolia* (15.6%), *Q. alba* (11.9%), *C. dentata* (10.6%), *Q. velutina* (8.7), and *Q. rubra* (6.9%). However, in 1999, a comparable proportion of the total accumulation was composed of nine taxa: *Q. montana* (19.5%), *F. grandifolia* (12.7%), *C. dentata* (9.3%), *T. heterophylla* (6.9%), unidentified *Leucobalanus* (6.7%), *Carya glabra* (Mill.) Sweet (6.1%), *Q. alba* (5.6%), *Liriodendron tulipifera* L. (5.1%), and *A. saccharum* (4.8%). Species that accounted for more than 10% of the net change between 1989 and 1999 (8.0 Mg/ha) included *T. heterophylla* (1.5 Mg/ha), *L. tulipifera* (1.2 Mg/ha), and *A. saccharum* (0.8 Mg/ha). *Quercus alba* declined by 0.93 Mg/ha; however, all *Leucobalanus* increased by

Table 2. Average species composition of coarse woody debris (CWD) mass (>20 cm in diameter) in 1989 and 1999 on eighty 0.04-ha sample plots in Big Everidge Hollow at Lilley Cornett Woods, southeastern Kentucky.

	CWD					Overstory biomass				
	1989		1999			1979		1989		
Species	Mg/ha	%	Mg/ha	%	Net change	Mg/ha	%	Mg/ha	%	Net change
Quercus montana	5.4 (70.3)	25.0	5.8 (69.6)	19.5	0.4	48.0	21.5	54.3	23.2	6.2
Fagus grandifolia	3.4 (41.3)	15.6	3.8 (49.1)	12.7	0.4	59.3	26.6	48.0	20.5	–11.3
Castanea dentata	2.1 (25.0)	9.7	2.8 (51.1)	9.3	0.7					
Tilia heterophylla	0.5 (28.2)	2.4	2.0 (25.2)	6.9	1.5	6.9	3.1	9.3	4.0	2.4
Leucobalanus[a]			2.0 (64.1)	6.7	2.0					
Carya glabra	1.1 (57.5)	5.0	1.8 (59.6)	6.1	0.7	6.3	2.8	7.0	3.0	0.7
Quercus alba	2.6 (50.0)	11.9	1.6 (57.9)	5.6	–0.9	12.6	5.7	17.8	7.6	5.2
Liriodendron tulipifera	0.3 (41.2)	1.4	1.5 (39.0)	5.1	1.2	15.1	6.8	15.6	6.6	0.5
Acer saccharum	0.6 (19.6)	2.7	1.4 (91.1)	4.8	0.8	12.1	5.4	12.1	5.1	0.0
Quercus rubra	1.5 (19.4)	7.1	1.3 (8.7)	4.5	–0.2	8.0	3.6	11.6	4.9	3.6
Quercus velutina	1.9 (13.2)	8.6	1.3 (20.1)	4.5	–0.5	13.0	5.8	9.2	3.9	–3.8
Nyssa sylvatica	0.1 (16.4)	0.3	0.7 (51.9)	2.5	0.7	5.0	2.2	6.6	2.8	1.6
Erythrobalanus[a]			0.7 (16.3)	2.4	0.7					
Robinia pseudoacacia	0.2 (5.1)	0.8	0.6 (16.5)	2.1	0.4	1.0	0.4	0.8	0.4	–0.2
Miscellaneous species[b]	2.0 (16.4)	9.5	2.1 (40.0)	7.2	0.1	35.7	16.0	42.2	18.0	6.5
Total	21.6 (120.3)		29.6 (146.3)		8.0	223.1		234.5		11.4

Note: As a measure of the range of variation, maximum CWD values are given in parentheses. Also shown is overstory biomass for boles and large stems (>20 cm in diameter) for the two inventories prior to the CWD measurements (1979 and 1989). Total CWD volume was significantly different between the two years (p = 0.006); however, the significance was only marginal for total CWD mass (p = 0.091).

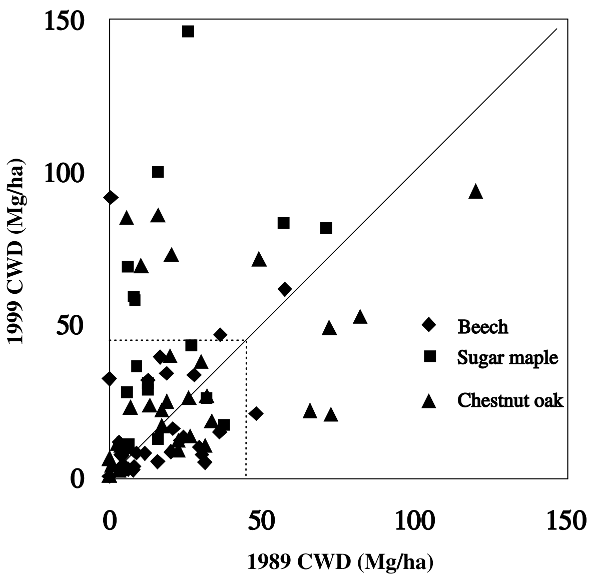
[a]*Leucobalanus* and *Erythrobalanus* included highly decomposed material that could not be identified further than these two subgenera of *Quercus*.

[b]Miscellaneous species included *Sassafras albidum*, *Morus rubra*, *Acer rubrum*, *Aesculus octandra*, *Amelanchier arborea*, *Betula nigra*, *Carya cordiformis*, *Carya ovata*, *Carya tomentosa*, *Cornus florida*, *Fraxinus americana*, *Juglans nigra*, *Magnolia acuminata*, *Nyssa sylvatica*, *Pinus* spp., *Quercus coccinea*, and *Oxydendrum arboreum*.

1.5 Mg/ha, suggesting that difficulties in making final determination of identification may have accounted for much of this apparent decline. Conversely, *C. dentata* increased, impossibly, by 0.7 Mg/ha. Unidentified *Erythrobalanus* also declined by 0.7 Mg/ha, suggesting that errors in field identification of the exceedingly well-decomposed *Erythrobalanus* may account for the apparent increase in *C. dentata*.

In both years, there appeared to be a break in the highly skewed distribution of CWD among plots at 45 Mg/ha, with many plots containing CWD less than this amount and a scattered few containing greater amounts (Fig. 1). In 1989, 10 plots containing more than 45 Mg/ha accounted for 39.2% of the total CWD for the watershed. In 1999, 18 of the 80 plots fit this criterion and accounted for 57.8% of the total. Over all 80 plots, occurrence of CWD in 1989 was not necessarily a good predictor of CWD in 1999 (Fig. 2). Numerous plots contained <45 Mg/ha in both samplings, suggesting that 0–45 Mg/ha may represent a base range that characterizes much of the landscape in an old-growth mixed mesophytic forest. However, six of the 10 plots containing CWD in amounts >45 Mg/ha in 1989 were associated with low amounts in 1999, suggesting that even large amounts of CWD are rapidly decomposed. Conversely, plots with CWD >45 Mg/ha in 1999 generally contained small amounts in 1989, suggesting that at any given point in the landscape, CWD accumulations are temporally episodic. Large inputs, which cannot be maintained indefinitely, are rapidly decomposed, creating a cyclical pattern of accumulation. The one

Fig. 2. Occurrence of coarse woody debris (CWD) mass in 1989 and 1999 and among three forest communities on eighty 0.04-ha plots in Big Everidge Hollow at Lilley Cornett Woods, Letcher County, Kentucky. The broken line identifies an apparent break in CWD distribution that occurs at ~45 Mg/ha. The solid line represents equality of mass in both 1989 and 1999.



exception to this pattern was a south-southwest-facing (aspect 195°) midslope plot in which a large accumulation (>93 Mg/ha) occurred in both years. This plot was dominated in both years by a single log (*Q. montana*) that was held off of the ground by the locally steep undulating topography and accounted for 57.9% of CWD mass in 1989 and 43.4% in 1999.

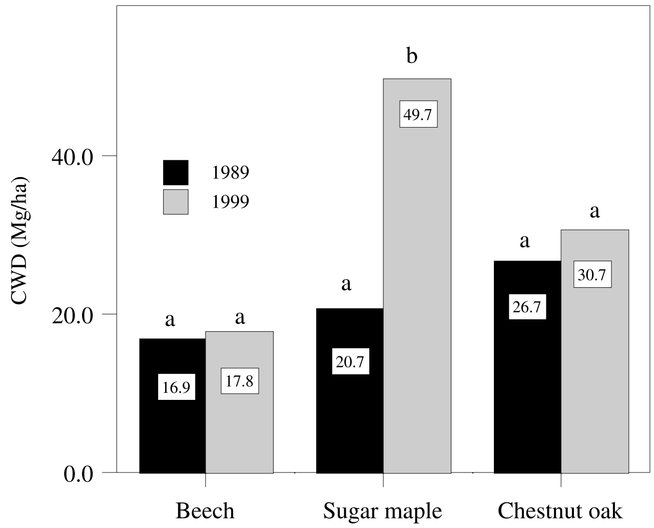
Although it might be expected that CWD would be negatively correlated with basal area of living trees, these two variables were unrelated ($p > 0.1$) with the following exceptions. Five plots with particularly high basal area (>50 m^2/ha) had generally low CWD (<23 Mg/ha). However, one plot with especially high CWD (146.2 Mg/ha) still had average basal area (23.8 m^2/ha).

In 1989, the patchy distribution of CWD occurred throughout the landscape and did not vary with forest community ($p > 0.05$) (Fig. 3), although there was an apparent trend towards larger CWD amounts on the more exposed and drier chestnut oak – red maple plots. However, in 1999, CWD exhibited strong patterns of distribution among forest communities ($p < 0.01$), with greatest amounts occurring in the midslope sugar maple – basswood community and least in the lower-slope beech community ($p < 0.01$) (Fig. 3). In beech plots, CWD mass remained essentially constant, exhibiting an insignificant increase of only 0.9 Mg/ha (5.3%) ($p > 0.05$). This overall change, however, did include a significant change in *Q. alba*, which declined from 1.9 to 0.1 Mg/ha. The slight overall increase observed in beech plots was accounted for by small increments in a variety of species. CWD in sugar maple – basswood plots increased by 140.0% over the 10-year period ($p < 0.01$) (Fig. 3). Those species whose CWD changed more than 10% of the 1989 average (20.7 Mg/ha) were *T. heterophylla* (increased from 1.3 to 9.6 Mg/ha), *Q. montana* (from 0 to 7.00 Mg/ha), *C. glabra* (from 0.2 to 3.7 Mg/ha), *L. tulipifera* (from 0.3 to 3.3 Mg/ha), *A. rubrum* (from 0 to 2.3 Mg/ha), and *Nyssa sylvatica* Marsh. (from 0.3 to 2.4 Mg/ha). In chestnut oak – red maple plots, CWD increased insignificantly by 3.9 Mg/ha overall (14.6%) ($p > 0.05$), and changes >10% of the 1989 average (27.1 Mg/ha) included only unidentified *Leucobalanus*, which increased from 0 to 3.2 Mg/ha.

Discussion

While the 36% increase in CWD mass over 10 years seems considerable, it does little to change our perceptions of geographic trends in CWD accumulation. Previous evaluation of existing studies of CWD in old-growth deciduous forests of the temperate zone of North America distinguished between larger accumulations (34–49 Mg/ha) in cool temperate forests and lower accumulations (22–32 Mg/ha) in warm temperate forests (Muller and Liu 1991). The present accumulation at Lilley Cornett Woods of 29.7 Mg/ha still falls within the range of warm temperate forests and suggests that the distinction between warm and cool temperate forests is probably valid. However, as observed in this study (Table 1), within any given forest, CWD will fluctuate within the range identified above. Decomposition in these forests is rapid, and large inputs followed by decay can account for the fluctuations observed. Rates of change ($k = -\ln(b_t/b_0)/t$) calculated for each plot over the 10-year period ranged from –0.5 to 0.19. Negative values reflect plots exhibiting a significant increase in CWD, while positive values reflect net loss. The maximum rate of loss ($k = 0.19$) is within the range of decomposition values previously established for hardwood species (Harmon et al. 1986), and the maximum observed increase on a single plot (3.7 Mg = 91.1 Mg/ha) could be accounted for by input from a single tree of 66 cm diameter at breast height (biomass calculated with the generalized equation of Monk et al. 1970). The oscillations that appear to be occurring at the watershed level (Table 1) are probably accounted for by the balance between episodic inputs and decomposition. More important dynamics probably occur at more local scales.

Fig. 3. Average coarse woody debris (CWD) mass (Mg/ha) among forest communities in 1989 and 1999 on eighty 0.04-ha plots in Big Everidge Hollow at Lilley Cornett Woods, Letcher County, Kentucky. Within a year, community types with the different letters superposed were significantly different (Kruskal Wallis, $p > 0.05$). Sample sizes were 31 for beech plots, 17 for sugar maple – basswood plots, and 32 for chestnut oak – red maple plots.



The general lack of relationship between CWD and plot basal area is partially reflective of study design: basal area of living trees includes only those trees located within the plot, while CWD frequently originates from trees located outside of the plot. Because of the relatively small plot size (0.04 ha, diameter = 22.6 m on the horizontal), these edge effects are probably exacerbated. More importantly, however, disturbances creating CWD in these mixed mesophytic forests tend to be characterized by single tree disturbances including canopy breakage and whole-tree blowdowns. At Lilley Cornett Woods, 87% of canopy gaps were created by single tree events and 69% of these events were created by canopy breakage rather than whole-tree blowdown (Romme and Martin 1982). Median size of these gaps was 307 m^2. The patchy distribution of CWD in 1989 and 1999 (Fig. 1) and the lack of relationship between living tree basal area and CWD are consistent with the idea that disturbances in Lilley Cornett Woods, in particular, and old-growth eastern deciduous forests, in general, are driven in part by gap phase dynamics (Barden 1979, 1980; Romme and Martin 1982; Runkle 1981). However, as described below, other aspects of this study suggest that this dynamic follows patterns previously unrecognized.

Our understanding of gap phase dynamics has implied or assumed that these disturbances occur uniformly or at least randomly over the entire forest (Runkle 1985). That is, following the "reorganizing" forces of a stand-replacing disturbance, increasing age of the forest will increase the randomness with which individual trees die and gaps are created (Bormann and Likens 1979). This would suggest that CWD composition should reasonably reflect species composition of the overstory. This has previously been described as being the case at Lilley Cornett Woods (Muller and Liu 1991); however, important differences emerged between the two surveys that suggest that the dynamics of CWD input vary significantly over time. In a reanalysis of the 1989 and 1999 surveys, CWD composition was measured against biomass of overstory stems and boles from the preceding vegetation survey (10 years earlier) (Table 2). In 1989, CWD of several species differed substantially from their proportion of aboveground biomass from 10 years earlier. Those species whose proportion of CWD mass was more than 50% lower than their proportion of stem and bole biomass included *A. saccharum*, *L. tulipifera*, and *N. sylvatica*. These are also species that have fairly high decomposition rates (Harmon et al. 1986). Species whose proportion of CWD was more than 50% greater than their proportion of stem and bole biomass included *Q. alba*, *Q. rubra*, and *Robinia pseudoacacia* L. While these discrepancies might be attributed solely to differences in decomposition rates, they were not consistent with the subsequent survey. In 1999, no species were underrepresented in CWD; however, *T. heterophylla*, *C. glabra*, and *R. pseudoacacia* were all more prominently reflected in CWD than in biomass. The varying amounts of individual species composing CWD suggest a dynamic of tree mortality that is somewhat independent of overstory composition and does not reflect random gap disturbance through the forest.

CWD composition also appears to reflect poorly the actual dynamics of gap creation. Using data collected for the 10-year period of 1973–1982, Romme and Martin (1982) identified *F. grandifolia* as the predominant species contributing to gap formation at Lilley Cornett Woods: it accounted for the creation of 46% of all gaps surveyed. *Fagus grandifolia* was the second most important component of CWD in the 1989 and 1999 surveys (Table 2). Still, it accounted for <17% of CWD in both surveys. In contrast, *Q. montana*, which was the largest component of CWD in both surveys (19–25%), was a very small contributor to gap formation (2% of inventoried gaps; Romme and Martin 1982). Decomposition rates of *F. grandifolia* and *Q. montana* are similar ($k = 0.017–0.019$, half-life = 35–40 years; MacMillan 1986) and do not appear to account for the discrepancy between gap formation and CWD accumulation of these species. This discrepancy between gap formation prior to 1980 (Romme and Martin 1982) and CWD accumulation in 1989 and 1999 (Table 2) again suggests changing patterns of CWD formation among species over time that are not tightly linked to overstory species composition. This, in turn, implies that disturbance in old-growth forests may not be strictly a random event.

Many evaluations of the dynamics of old-growth forests have suggested that topographic influence operates at the level of exposure to allogenic (often construed as stand replacing) disturbance (Kramer et al. 2001; Runkle 1985). Where exposure to catastrophic winds (or presumably fire or ice damage) occurs, gap phase dynamics is precluded because the forest matrix that supports such dynamics is destroyed by those extrinsic events. Where topography limits exposure to intense extrinsic disturbance, gap phase dynamics predominate. The 1989 survey of Lilley Cornett Woods showed that most plots contained a base amount of CWD from 0 to 45 Mg/ha and a few plots contained accumulations in excess of 45 Mg/ha (Fig. 1). While the spatial distribution of this CWD suggested a trend towards higher amounts on drier, more exposed slopes (Muller and Liu 1991) (Fig. 3), this pattern was not significant ($p > 0.1$). Thus, the 1989 survey supported the general idea of gap phase dynamics occurring randomly over the broad expanse of old-growth forests. The current survey suggests other conclusions. While the frequency of CWD accumulation remained highly skewed with many plots containing <45 Mg/ha and a few containing substantially larger amounts (Fig. 1), the topographic distribution was not random. Plots on midslope positions of east- and north-facing aspects (sugar maple – basswood plots) contained significantly larger amounts of CWD than either beech or chestnut oak – red maple plots ($p < 0.01$) (Fig. 3). As noted above, the increase in CWD in these midslope plots was the result of several species; however, *T. heterophylla*, which is generally restricted to these plots, accounted for 28.7% of the increase. Thus, varying patterns of species dynamics may strongly influence topographic patterns of forest disturbance.

A strictly random pattern of gap phase disturbance at Lilley Cornett Woods would be reflected in CWD composition that closely mimics overstory composition and a random pattern of disturbance across the landscape. The observations of this study that (*i*) CWD is not closely linked to overstory composition and (*ii*) CWD amounts across the landscape change significantly with time suggest that the intensity of disturbance may vary among forest types. Thus, the dynamics of gap phase disturbance can be viewed as occurring at two levels: (*i*) the scale of individual trees and the gaps that they create and (*ii*) the scale of forest community or landscape position and the species that it contains.

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