Coarse Woody Debris in Managed Central Hardwood Forests of Indiana, USA

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ABSTRACT. We evaluated the volume of down deadwood (DDW) and the basal area of standing deadwood (SDW) from a chronosequence of 110 silvicultural openings and 34 mature stands (72–105 years old) across three Ecological Landtype Phases (ELTP; wet-mesic bottomlands, mesic slopes, and dry-mesic slopes) in southern Indiana, USA. The volume of DDW decreased with increasing opening age and was lower in clearcuts than in group-selection openings. Openings on mesic slopes and bottoms contained greater volumes of DDW than openings on dry-mesic slopes. Regardless of age and ELTP, openings contained low volumes of highly decayed DDW. The volume of small-diameter DDW decreased rapidly with increasing stand age across all three ELTPs. Mature stands contained low total volumes of DDW (maximum of 22.4 ± 5.1 m^3 ha^{-1}) and low volumes of both highly decayed and large-diameter DDW. Most of the dead trees in silvicultural openings were small diameter and did not contribute significantly to DDW volume. SDW basal area was very low in mature stands (maximum of 1.4 ± 0.5 m^2 ha^{-1}), suggesting that little mortality has occurred. Our results suggest that even and uneven-aged silviculture in hardwood forests have differing impacts on the volume and distribution of coarse woody debris (CWD). In addition, the mature stands that dominate forests across much of the Central Hardwood Region of the eastern United States contain relatively little CWD compared to younger and old-growth stands. FOR. SCI. 50(6):781–792.

Key Words: Central Hardwood Region, deadwood volume, snags, even and uneven-aged silviculture, ecological classification.

COARSE WOODY DEBRIS (CWD), including dead trees (standing deadwood; SDW) and fallen logs (down deadwood; DDW), is an important structural and functional component of forest ecosystems. CWD provides habitat for a variety of vertebrate species including salamanders (Dupuis et al. 1995) and small mammals (Loeb 1999, Bowman et al. 2000). It also provides important food and habitat for insects and other invertebrates (Hammond

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1997), and serves as substrate for a variety of fungi species (Hagen and Grove 1999). In addition, CWD creates regeneration niches for plants that establish either on logs and stumps (Palmer 1987, McGee and Birmingham 1997) or within refugia from herbivores created by downed trees and tip-up mounds (Rooney 1997, Long et al. 1998). DDW also reduces the rates of runoff and erosion from slopes (Hagan and Grove 1999) and creates habitat for aquatic and semi-aquatic organisms by increasing the structural complexity of stream substrates and increasing the deposition of sediments (Lisle 1995).

Because of the relatively slow decay rate of large CWD in hardwood forests, organic material in the form of snags, fallen trees, and decaying logs exerts considerable ecological influence on a site for decades, or even centuries (Van Lear 1996). McFee and Stone (1966) observed that yellow birch (*Betula alleghaniensis* Britt.) CWD persists for a century or more in mature northern hardwood forests. As CWD decomposes, nitrogen and other nutrients are immobilized by microorganisms and later released for plant growth through mineralization (MacMillan 1981). Although the nutrient concentration of woody material is low relative to that of leaves and fine roots, the persistence of CWD amplifies its importance as a component of the biological and biochemical nutrient cycles (McFee and Stone 1966, Idol et al. 2001).

Because forest management directly affects the volume, size structure, and distribution of CWD in forests (Spies et al. 1988), stands may have altered CWD dynamics and ecological relationships after treatment. Harvesting typically reduces the volume of large-diameter CWD by removing large trees that would otherwise die (Green and Peterken 1997) or altering the size distribution and decay dynamics of down deadwood through the addition of small-diameter, nondecayed logging slash (Jenkins and Parker 1997, Fraver et al. 2002). Harvesting may also have a secondary effect on aquatic ecosystems by reducing the amount (Silsbee and Larson 1983) and diameter (Lee et al. 2002) of CWD in streams.

Regardless of forest type, CWD accumulation follows the same general sequence after stand reinitiation. CWD biomass is high immediately after disturbance, declines during stem exclusion (Oliver and Larson 1996), and increases in old-growth forests (McCarthy and Bailey 1994, Goebel and Hix 1996, Sturtevant et al. 1997, Hely et al. 2000, Muller 2003). Although changes in CWD volume and decay stage with increasing stand age have been well documented, the relationship between forest management and the volume of CWD within silvicultural openings has received little study. Specifically, more information is needed about how different silvicultural techniques influence the amounts, decay stages, and diameter distributions of CWD and how these characteristics change through time.

During the past 30 years, two major silvicultural techniques, selection cutting and clearcutting, have been used in southern Indiana forests and throughout the Central Hardwood Region. Selection cutting on state forest land has consisted mostly of single-tree selection (removal of individual mature trees; Nyland 1996) and group-selection openings (removal of mature trees in a small group; Nyland 1996) of less than 2 ha. Clearcutting in the Hoosier National Forest (HNF) in southern Indiana has generally produced openings greater than 4 ha. Management and economic constraints differ for these two management techniques and may influence which trees are selected for cutting and how much residual material is left on site after harvest.

Over the past two decades, the use of ecological classification systems (ECS) has increased on public lands (Spies and Barnes 1985, Van Kley et al. 1994, Carter et al. 2000). Because they are composed of repeating map units that represent stable abiotic components and associated biota, these classifications offer a means to quantify variation in forest composition, productivity, and ecological processes across regional landscapes (Barnes et al. 1982). However, although the development, composition, and productivity of vegetation on ECS mapping units have been examined (Goebel and Hix 1996, Jose and Gillespie 1997, Jenkins and Parker 1998), little attention has been paid to how CWD varies with forest management on ECS units. As ecological classification systems are increasingly used in management decisions, understanding how CWD varies with management across units becomes more important.

Van Kley et al. (1994) developed a multifactor ECS for the Hoosier National Forest and surrounding areas in southern Indiana. Within this system, the broadest unit of classification is the Ecological Landtype (ELT), which is differentiated based on variations in vegetation and topography. Each ELT is further divided into several Ecological Landtype phases (ELTPs) based on more refined differences in vegetation, soils, and physiography. In this study, we sampled CWD in silvicultural openings and mature stands across three ELTPs that represent a gradient of site quality and moisture availability: *Platanus/Asarum* wet-mesic bottomlands, *Fagus-Acer saccharum/Arisaema* mesic slopes, *Quercus alba-Acer saccharum/Parthenocissus* dry-mesic slopes. These three ELTPs are a major focus of forest management in southern Indiana.

We will address three main questions in this article. First, how does the amount of CWD (DDW volume and SDW basal area) in openings vary with opening age and silvicultural treatment? Second, does the amount of CWD in openings vary with ELTP? Third, does the amount of CWD vary between ELTPs in the mature stands that dominate the forest matrix of southern Indiana?

Methods

Between 1994 and 1996, we sampled 110 silvicultural openings (commercial group selections and clearcuts) on the Pleasant Run Unit of Hoosier National Forest (HNF), Morgan-Monroe State Forest, and Yellowwood State Forest in southern Indiana. Thirty-four mature stands also were sampled on the Pleasant Run Unit of HNF. Plots were sampled across three ELTPs as delineated by Van Kley et al. (1994).

Description of Study Sites

This study was conducted in hardwood forests of south-central Indiana, USA. Parent materials in this area are dominated by Mississippian age sandstone, siltstone, and shale (Van Kley et al. 1994). Soils are mostly acid silt loams (Udalfs and Udulfs) derived from acid bedrock and a small amount of loess (Homoya et al. 1984). Deeply dissected uplands composed of steep slopes and narrow hollows dominate the topography of the area. Annual precipitation ranges from 112 to 137 cm and temperature averages from 13 to 16° C (McNab and Avers 1994).

Hoosier National Forest–Pleasant Run Unit

The Pleasant Run Unit of the HNF (26,900 ha) is located in south-central Indiana approximately 16 km southeast of Bloomington (39°10′ N, 86°35′ W). Much of the area incorporated into the HNF since 1935 was highly depleted and abandoned farmland with highly disturbed natural plant communities (Jenkins and Parker 2000). The mature 72–105-year-old stands we sampled have been unmanaged since their incorporation into HNF. Living basal area in these stands ranged from 23.6 m^2ha^{-1} on wet-mesic bottomlands to 26.8 m^2ha^{-1} on dry-mesic slopes (Jenkins 1998). Clearcutting has been the most common harvest method used on the HNF, although there has been little harvesting since the mid-1980s. Harvesting operations on HNF and state forests are not highly mechanized because crews typically use only chainsaws and skidders (Jayson Waterman, Indiana Division of Forestry, Nov. 17, 2003). According to HNF stand records, the clearcuts we sampled ranged in size from 4 to 20 ha, and in age from 9 to 27 years.

Yellowwood State Forest and Morgan-Monroe State Forest

Yellowwood State Forest and Morgan-Monroe State Forest are compositionally similar hardwood forests located in south-central Indiana. Morgan-Monroe State Forest (9,430 ha) is located approximately 15 km north of Bloomington along the Morgan-Monroe County line (39°25′ N, 86°25′ W). Yellowwood State Forest (8,700 ha) is located approximately 16 km east of Bloomington in Brown County (38°50′ N, 86°30′ W). Since the 1960s, harvests on these two State Forests have been conducted mostly through single-tree and group selection on a 20–30-year cutting cycle. According to state forest records, the group-selection openings we sampled ranged in size from 0.07 to 1.6 ha, and in age from 8 to 26 years.

Description of ELTPs

CWD was sampled across three ELTPs that represent common phases of three broader ecological landtypes; bottoms, mesic slopes, and dry slopes. These three ELTPs are described below and represent a gradient of site moisture availability. In addition, they are a major focus of forest management in southern Indiana.

Platanus/Asarum Wet-Mesic Bottomlands

This ELTP (hereafter wet-mesic bottomlands) is a phase within the Bottomlands ELT and typically occurs in the narrow bottoms of intermittent to perennial streams at low elevations (190–200 m) with slopes of less than 5%. Soils are deep compared to other ELTPs (13 ± 4 cm) and overlay bedrock of weathered siltstone ~1 m below the surface. Dominant overstory species include sugar maple (*Acer saccharum* Marsh.), American sycamore (*Platanus occidentalis* L.), and American beech (*Fagus grandifolia* Ehrh.). The subcanopy is typically dominated by saplings of sugar maple, American beech, and white ash (*Fraxinus americana* L.), with paw paw (*Asimina triloba* (L.) Dunal), musclewood (*Carpinus caroliniana* Walt.), and flowering dogwood (*Cornus florida* L.) also common.

Fagus-Acer saccharum/Arisaema Mesic Slopes

This ELTP (hereafter mesic slopes) is a phase within the Mesic Slopes ELT and typically occurs on steep slopes (35 ± 10%) at moderate elevations (190–260 m). Aspect is generally northerly and ranges from 315 to 135°. Soils are derived mainly from weathered siltstone with bedrock depths of <1 m and an average A-horizon depth of 6 ± 1 cm. Sugar maple, tulip poplar (*Liriodendron tulipifera* L.), American beech, and northern red oak (*Quercus rubra* L.) typically dominate the overstory of this ELTP. The understory is dominated by sugar maple and American beech, with slippery elm (*Ulmus rubra* Muhl.), flowering dogwood, and ironwood (*Ostrya virginiana* K. Koch) also common.

Quercus alba-Acer saccharum/Parthenocissus Dry-Mesic Slopes

This ELTP (hereafter dry-mesic slopes) is a phase within the Dry Slopes ELT and occurs mostly on southerly (135–315°) aspects. Elevation typically ranges from 160 to 240 m and slopes average 23 ± 9%. Soils are typically silt-loam formed from weathered sandstone. The A-horizon depth of this ELTP is the shallowest of the three we studied, with an average depth of 4 ± 3 cm. The overstory of this ELTP is dominated by white oak (*Quercus alba* L.), with black oak (*Quercus velutina* Lam.) and sugar maple as common associates. Sugar maple typically dominates the understory, with American beech, flowering dogwood, and red maple (*Acer rubrum* L.) as common associates.

Field Sampling

We sampled 49 clearcuts, 61 group-selection openings, and 34 mature stands. Mature stands ranged in age from 72–105 years. Because there was no major cutting on the HNF between 1986 and 1996, we did not sample any openings less than 8 years in age to ensure that opening ages were compatible between group selections and clearcuts. On wet-mesic bottomlands, we sampled 12 clearcuts, 16 group selections, and 10 mature stands. On mesic slopes, we sampled 18 clearcuts, 28 group-selection openings, and 12 mature stands. On dry-mesic slopes, we sampled 19 clearcuts, 17 group selections, and 12 mature stands.

We estimated DDW volume within a circular 500-m^2 plot. We placed the plot within the center of smaller openings and randomly within larger openings and mature stands. Within each plot, we measured the midpoint diameter and length of all down deadwood 10 cm or greater in diameter. Each log was visually classified into one of five decay stages (adapted from Maser et al. 1979, Pyle and Brown 1998) (see Table 1, Figure 1). Decay stages ranged from 1 (freshly fallen) to 5 (near complete decomposition). No decay stage 1 material was found in any of the plots. If a log contained more than one decay stage, we measured it as separate segments by decay stage. The diameter at breast height (dbh) of all standing dead trees ≥10 cm was also measured.

Data Preparation and Analysis

Volume (m^3) of each log was determined using the equation for the volume of a cylinder. Because highly decayed logs are typically oval shaped in cross-section, this equation may over estimate the volume of decay stage 4 and 5 material. However, it is widely used and allows for quick field measurements (e.g., Spetich et al. 1999, Idol et al. 2001). Volume and abundance (logs ha^{-1}) of CWD in each plot was determined for each decay stage. For graphical comparison, DDW volume was also determined for four midpoint diameter classes: 10–20, 21–30, 31–40, and 41–50 cm. Because large-diameter DDW is important to many organisms, we performed statistical analysis (discussed below) on volumes in two diameter classes (10–40 and >40 cm). These classes were selected for ease of comparison with other studies in the eastern United States (e.g., Goodburn and Lorimer 1998). In addition, the basal area (m^2 ha^{-1}) of standing dead trees was calculated for each plot. All values were converted to a per-hectare basis.

Table 1. Characteristics of DDW decay stages adapted from Maser et al. (1979) and Pyle and Brown (1998).

Decay stage description
Stage 1
Bark firmly attached
Exposed wood not stained by weathering
Log is round
Small branches present
Log is resting on surface
Primary surface substrate: sound bark
Stage 2
Bark not firmly attached, patchy
Exposed wood may be bleached
Log is round
Small branches absent
Wood is mostly solid
Log is resting on surface
Primary surface: hard wood, decayed bark
Stage 3
Bark generally absent, but may be present in patches
Log structure is solid, not brittle, firm when kicked
Dry log surface flaky
Wet log surface spongy
Log partially sunk into ground
Primary surface substrate: soft wood
Stage 4
Log is no longer solid, although some fairly solid segments remain
Log breaks into pieces when kicked
Log oval or flattened, one third or more sunk into ground
Primary surface substrate: spongy or powdery wood
Stage 5
Log is flat, mostly sunken into the ground
Log is soft and powdery in texture
Log is often obscured by litter
Primary surface substrate: loosely aggregated blocks

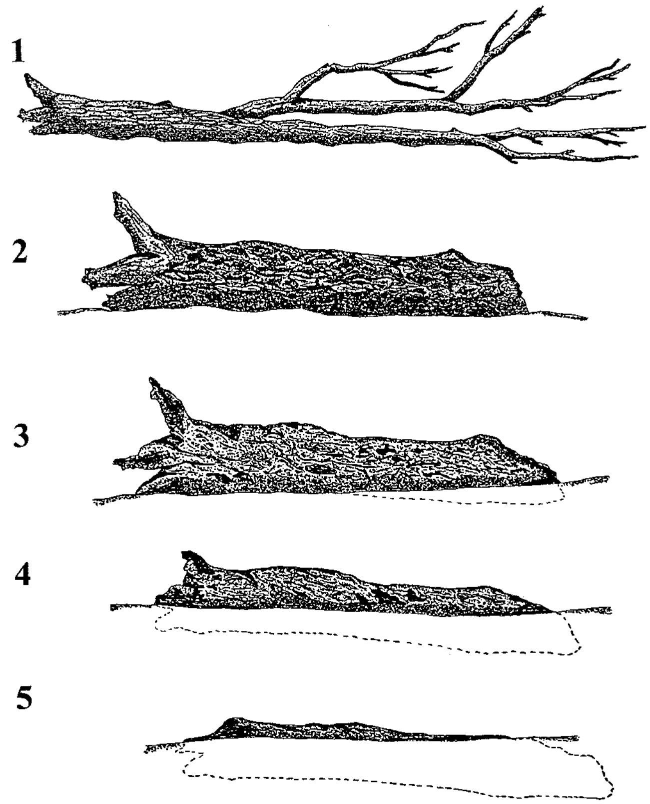

Figure 1. Decay stages of DDW measured in the field. Stages were adapted from those of Maser et al. (1979) and Pyle and Brown (1998).

We used a combination of multiple linear regression techniques to evaluate the influence of opening type (group selection or clearcut), opening age, and ELTP on the volume and abundance of DDW and the basal area of SDW. Square root and natural log transformations on the response variables were used to homogenize variances when necessary. Plots of studentized residuals versus fitted values were used to assess the regression assumption of constant variance (Neter et al. 1996). Residual plots and standard techniques were used to screen for and evaluate the influence of potential outliers (Netter et al. 1996). Opening type and ELTPs were represented by *K*-1 categorical variables, where *K* was the number of classes (Neter et al. 1996). Categorical variables in this case have a value of 1 if true and 0 if false. A significant categorical variable in the final model indicates that that category has a significantly different intercept term than the baseline condition, which is represented by the category that was omitted. By multiplying a categorical variable by the continuous age variable, it is also possible to evaluate whether the slope term associated with the continuous variable varies significantly between categories (Chatterjee and Price 1991).

To reduce our full model, which included opening type, opening age, ELTP, and their respective interaction terms, we used a backwards stepwise regression procedure (Minitab 12.23, 2000). The criteria for a variable to stay in the model were set at $P \leq 0.05$. Once a reduced model was identified, we did a forward check by reentering each independent variable back into the regression and evaluating its significance based on its P-value ($\alpha = 0.05$). This final check allowed us to evaluate the contribution of each variable to the final model and identify variables that might be significant, but were removed during the stepwise procedure. All predictors in the final models were significant at $P \leq 0.05$. Variance inflation factors (VIF) were used to detect whether independent variables in the final models had strong linear associations. We used the criteria suggested by Neter et al. (1996) to evaluate multicollinearity based on the mean VIF of the predictors. Models with mean VIFs considerably greater than 1 are considered to have significantly collinear variables. Mean VIFs for all of our final models were very close to 1 (Table 2). Normal probability plots of residuals were inspected to assess the normality of the error terms. Mean VIFs, F-statistics, and other regression diagnostics for each final model are provided in Table 2.

To further clarify apparent differences among ELTPs, we refit each model with each of the other ELTPs representing the baseline condition. This was done because the K-1 categorical variables used in the initial variable-reduction procedures are each compared to a base condition represented by the ELTP that was omitted. This allowed us to refine our final equations so that ELTPs that were not significantly different from each other were combined into the baseline condition.

This regression approach provides a more detailed analysis of the relationship between DDW and silvicultural opening age than a more traditional analysis of variance (ANOVA) in which the continuous age variable would be collapsed into classes. Quantitative concomitant variables can be incorporated by using ANCOVA. However, an important ANCOVA assumption is that all treatment regression lines have the same slope (Neter et al. 1996). Scatter plots of treatment effects versus silvicultural opening age suggested that the rate of decline in DDW with advancing opening age was not constant between treatments. Therefore, ANCOVA was not appropriate for this analysis.

Because organisms that use DDW often require material of different sizes or degrees of decay, we performed separate analyses for each decay stage (2–5) and two diameter class (10–40 and >40 cm). Initial analysis showed no significant relationships for decay stages 2, 4, and 5. Therefore, we combined decay stages into two broader classes, low decay material (stages 2 and 3) and high decay material (stages 4 and 5). The total aggregate volume and abundance of DDW logs were also examined.

Initial analysis showed a negative relationship between silvicultural opening type and DDW volume, suggesting that group selection and clearcuts contained different volumes of DDW. We ran further analyses to determine what DDW characteristics explained the larger volume of DDW in group-selection openings. We used t-tests to compare the diameter and length of logs in group selections and clearcuts. The Kolmogorov-Smirnov test with Lilliefors' correction was used to test data normality (Neter et al. 1996), and the Levene median test of homogeneity was used to test for equal variances (Neter et al. 1996). Both tests

Table 2. Final regressions equations of DDW volume ($m^3\ ha^{-1}$) and abundance ($logs\ ha^{-1}$) and SDW basal area (BA, $m^2\ ha^{-1}$) versus ELTP, opening age (AGE, years), and opening type.

Equation	F-statistic	Adj. R^2	$\bar{V}IF$	P-value
$\ln(\text{total volume}) = 6.68 - 0.275\ DM - 0.977 \ln(AGE) - 0.559\ CC$	27.68	0.42	1.07	<0.001
$\ln(\text{volume decay class 2\&3}) = 6.74 - 1.24 \ln(AGE) + 0.196\ (M * \ln(AGE)) + 0.666\ CC$	24.26	0.39	1.07	<0.001
$\ln(\text{volume small-diameter logs}) = 4.80 - 0.0795\ AGE - 0.353\ CC$	28.34	0.33	1.1	<0.001
$\ln(\text{volume large-diameter logs} + 1) = 2.58 - 1.37\ CC$	43.78	0.29[a]	—	<0.001
$\ln(\text{total abundance}) = 7.36 - 0.497 \ln(AGE)$	18.27	0.14	—	<0.001
$\ln(\text{abundance decay class 2\&3}) = 7.41 - 0.649 \ln(AGE)$	16.31	0.13	—	<0.001
$\ln(\text{abundance small-diameter logs}) = 7.28 - 0.510 \ln(AGE)$	15.30	0.12	—	<0.001
$\text{sqrt}(\text{abundance of large-diameter logs}) = 7.28 - 2.51\ CC$	27.24	0.20	—	<0.001
$\ln(\text{total BA SDW} + 1) = -1.38 + 0.643 \ln(AGE) - 0.0988\ B * \ln(AGE) + 0.698\ CC$	28.33	0.43	1.07	<0.001

[a] R^2 values are presented for simple linear regressions.
Categorical variables (1 if category, 0 otherwise) for individual ELTPs were coded as follows: bottoms = B, mesic slopes = M, and dry mesic slopes = DM. To test whether individual slope terms were significant, categorical variables were multiplied by continuous variables and their significance in each regression was evaluated. Categorical variables were also used in the same manner to denote the type of silvicultural opening. Because there were only two types of openings, clearcuts are denoted by CC = 1 and group selections are denoted by CC = 0. Only significant relationships are presented ($P <$ 0.05). Average variance inflation factors ($\bar{V}IF$) are provided for variables in multiple regressions. $n = 110$ for all regressions. See text for definitions of decay and diameter classes.

showed that the data did not significantly violate assumptions ($P > 0.05$).

We used Kruskal-Wallis one-way ANOVA on ranks to compare DDW volume and SDW basal area across ELTPs in mature stands. Before between-group comparisons, we used the Kolmogorov-Smirnov test with Lilliefors' correction to test normality and the Levene median test to test for equal variances. Although variances among ELTPs did not differ significantly for DDW volume ($P = 0.464$) or SDW basal area ($P = 0.359$), data were not normally distributed for either DDW or SDW ($P < 0.001$ for both). Because of this violation of the assumption of normality, we used the nonparametric procedure. Separate analyses were conducted for total DDW volume, small-diameter DDW volume, large-diameter DDW volume, low-decay DDW volume, high-decay DDW volume, and basal area of SDW. Because none of the ANOVA analyses was significant ($P > 0.05$), no post hoc multiple comparisons were made.

Results

DDW Volume and Abundance Versus Silvicultural Opening Type

Our results suggest that group selection and clearcutting have produced different volumes of DDW in regenerating stands (Figures 2 and 3). Overall, total volume of DDW was greater in group-selection openings than in clearcuts (partial $F_{1,106} = 20.8$, $P < 0.001$, Table 2), suggesting that a greater volume of DDW remains in group selections after harvest. Group-selection openings also contained a greater volume of low-decay material (decay classes 2 and 3) than did clearcuts (Figure 3; partial $F_{1,106} = 16.8$, $P < 0.001$). The volume of high-decay DDW (decay classes 4 and 5) was not significantly correlated with opening type (overall $F_{1,108} = 1.24$, $P = 0.269$). Overall, openings contained greater volumes of low-decay material than high-decay material.

The volumes of large-diameter (>40 cm) and small-diameter (10–40 cm) DDW were significantly greater in group selections than in clearcuts (Table 2). The difference in small-diameter DDW volume between group selections

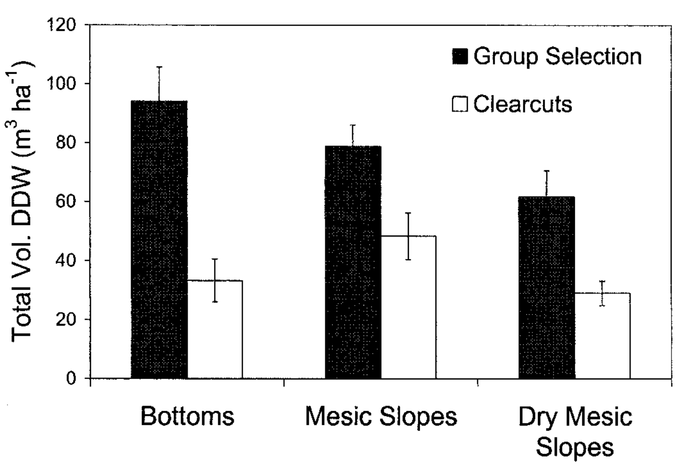

Figure 2. Total volume (mean ± 1 SE) of DDW ($m^3\ ha^{-1}$) in group-selection and clearcut openings across three Ecological Land Type Phases.

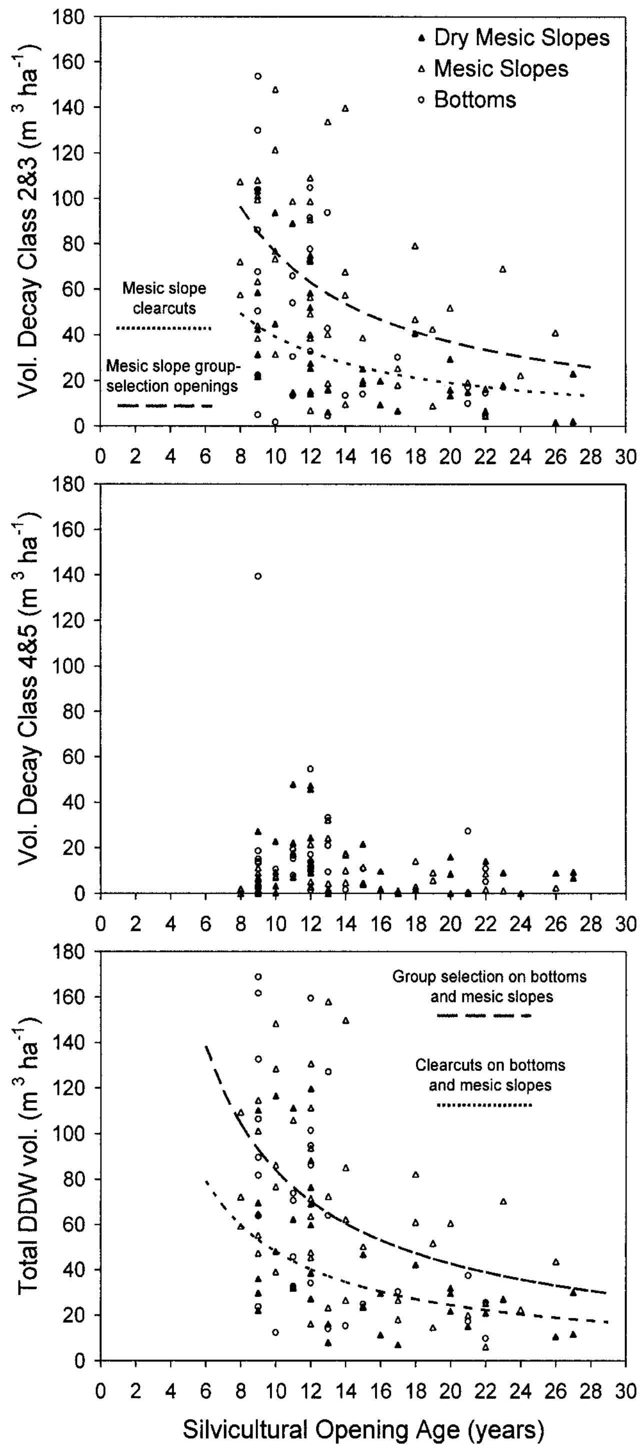

Figure 3. Trends in DDW volume by decay stage as a function of silvicultural opening age. Trend lines represent solutions to equations in Table 2.

and clearcuts (partial $F_{1,107} = 6.29$, $P = 0.014$) was apparent across the range of opening ages examined, but showed some evidence of convergence in older openings (Figure 4). This trend with opening age was not observed for large-diameter DDW (partial $F_{1,107} = 1.23$, $P = 0.268$). On average, group-selection openings contained five times greater volume of large-diameter DDW than did clearcuts, regardless of opening age or ELTP ($23.9 \pm 3.6\ m^3\ ha^{-1}$

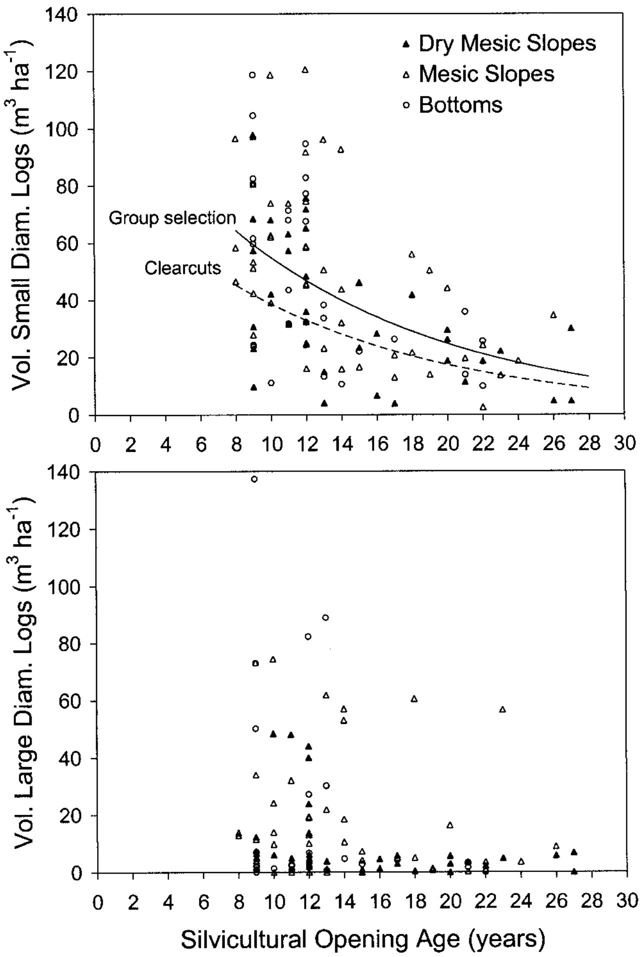

Figure 4. DDW volume (m^3 ha^{-1}) by diameter class (small logs: 10–40-cm diameter; large logs: >40-cm diameter) as a function of opening age. Trend lines represent predicted relationships between volume and opening age. See Table 2 for equation.

versus 4.5 ± 1.0 m^3 ha^{-1}). In general, clearcuts contained less volume in all DDW diameter classes than did group-selection openings (Figure 5). Abundance of large-diameter DDW was also significantly greater in group-selection openings than in clearcuts ($P < 0.001$, Table 2). However, abundance of small-diameter and total DDW did not differ between group-selection and clearcut openings (partial $F_{1,107} = 1.30$, $P = 0.258$ and partial $F_{1,107} = 0.176$, $P = 0.676$, respectively).

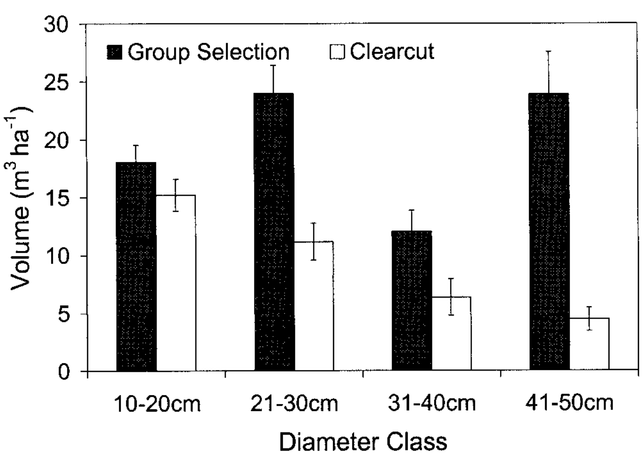

Figure 5. Distribution of DDW volume by diameter class in silvicultural openings (mean ± 1 SE).

The mean length and diameter of logs in group-selection openings were greater than in clearcuts ($t = 3.75$ and $t = 4.21$, respectively; $P < 0.001$ for both). The mean length of logs in group-selection openings was 3.6 ± 0.2 m, compared to 2.7 ± 0.2 m in clearcuts. The mean diameter of logs in group-selection openings was 23.4 ± 0.5 cm, compared to 20.3 ± 0.5 cm in clearcuts.

DDW Volume and Abundance Versus Opening Age

The total volume of DDW declined rapidly with the age of silvicultural openings (Table 2, Figure 3). The volume of low-decay DDW exhibited a trend nearly identical to that of total DDW volume (Figure 3). The volume of high-decay DDW was not significantly related to opening age (overall $F_{1,108} = 3.37$, $P = 0.069$).

We observed a large volume of small-diameter DDW in the silvicultural openings we sampled, but volume declined rapidly with increasing opening age (partial $F_{1,107} = 33.6$, $P < 0.001$, Table 2, Figure 4). The volume of large-diameter DDW was not significantly associated with opening age (partial $F_{1,107} = 1.23$, $P = 0.268$). The total abundance of logs declined significantly over time in all openings (Table 2, Figure 6). The abundance of low-decay DDW exhibited a decline similar to total DDW abundance (Table 2), but the abundance of high-decay DDW was not significantly associated with opening age (overall $F_{1,109} = 0.10$, $P = 0.752$), because losses in this class were offset by new inputs created by decay of existing DDW.

Our results indicate that much of the small-diameter logging slash on a site disappears rapidly with time since

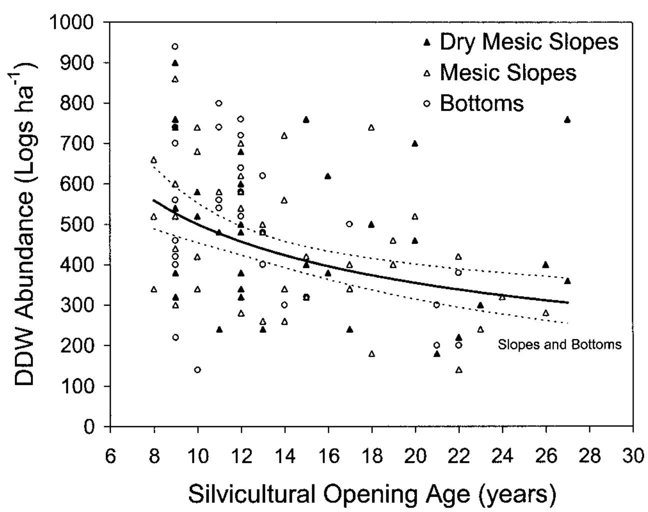

Figure 6. Relationship between the abundance of logs and silvicultural opening age. The trend line illustrates the general decline in abundance of logs with increasing opening age across all three ELTPs. The 95% confidence envelope is bounded by dotted lines. See Table 2 for equation.

harvest (Table 2). Although smaller logs were quickly lost to decay, larger logs were more persistent. We did not observe a significant decline in the abundance of larger logs with increasing opening age (partial $F_{1,107} = 0.44$, $P = 0.512$).

DDW Volume and Abundance Versus ELTP

Silvicultural openings on dry mesic slopes contained significantly lower volumes of DDW than did openings on mesic slopes and bottoms at any given age (partial $F_{1,106} = 4.97$, $P = 0.028$, Table 2). In addition, at a given age, silvicultural openings on mesic slopes contained significantly greater volumes of low-decay material than did openings on other ELTPs (partial $F_{1,106} = 10.6$, $P = 0.001$, Table 2). The volume of large-diameter and high-decay material did not vary among ELTPs (Figures 3 and 4). The abundance of logs also did not vary significantly by ELTP ($P \geq 0.668$).

SDW Basal Area Versus Opening Type, Opening Age, and ELTP

The basal area of SDW varied with opening type, opening age, and ELTP (Table 2). Wet-mesic bottomlands had significantly lower basal area of SDW than did mesic or dry-mesic slopes (partial $F_{1,106} = 4.54$, $P = 0.036$, Table 2). Across all ELTPs, the basal area of SDW increased with increasing opening age (Table 2). Overall, clearcuts contained greater basal area of SDW than did group selections (partial $F_{1,106} = 40.1$, $P < 0.001$, Table 2). The low basal area of SDW within openings (maximum of 1.4 ± 0.2 $m^2\ ha^{-1}$) revealed that standing dead trees did not contribute greatly to total CWD in these stands.

DDW Volume and SDW Basal Area of Mature Stands

Although DDW volume in mature stands on dry-mesic slopes was twice that of wet-mesic bottoms, the high variability of the data resulted in a lack of statistical significance (Table 3). Generally, mature stands across the three ELTPs had relatively low volumes of DDW compared to silvicultural openings. Most of the DDW we measured was composed of small-diameter and low-decay logs. The basal area of SDW was less than 2 $m^2\ ha^{-1}$ across all three ELTPs, suggesting that there was little input of new DDW in these stands (Table 3).

Discussion

Effects of Management on CWD

Many studies of CWD in hardwood secondary forests of the eastern United States have focused on stands that regenerated after logging in the early twentieth century or after modern clearcutting (e.g., McCarthy and Bailey 1994, Goebel and Hix 1996, Idol et al. 2001). There have been fewer studies comparing CWD inputs after different modern management techniques (Goodburn and Lorimer 1998, Fraver et al. 2002). In northern hardwood forests, Goodburn and Lorimer (1998) found greater amounts of CWD in selection stands than in 65–75-year-old even-aged stands. In the Acadian forest of central Maine, stands managed under an expanding-gap harvesting system contained a greater volume of CWD after harvest (Fraver et al. 2002). Although these and other studies have quantified CWD at the stand level, we were unable to find any studies that compared the amount of CWD within individual openings of differing size.

Surprisingly, we found that different amounts of CWD remained within openings after clearcutting and group-selection harvest. We observed significantly greater volumes of DDW in group selections than in clearcuts. National and state forest records did not show a greater preharvest volume of timber in stands we sampled that received group-selection cutting. Although the total number of logs did not vary significantly between opening types, the length and diameter of logs in group-selection openings were greater than those in clearcuts. Consequently, we found a greater volume of both large- and small-diameter logs in group-selection openings.

There are numerous possible explanations for the higher volume of DDW we observed in group-selection openings. The most likely relate to market forces associated with each harvesting system. In smaller openings, loggers may not use as much of the topwood as loggers harvesting in clearcuts. Hauling out this relatively low-value material may not be economically worthwhile because of the comparatively low volume produced by a dispersed cutting system. In addition, skidding long tree lengths in partially cut stands presents problems because residual trees are often damaged by the skidding operation, and moving skidders between trees is

Table 3. Mean ± 1 SE of total DDW volume, small-diameter DDW volume (10–40-cm diameter), large-diameter DDW volume (>40-cm diameter), low-decay DDW volume (decay stage 2–3), high-decay DDW volume (decay stage 4–5), and standing deadwood basal area (>10 cm dbh) within mature stands on dry-mesic slopes, mesic slopes, and wet-mesic bottoms.

	Dry-mesic slopes $n = 12$	Mesic slopes $n = 12$	Bottoms $n = 10$	P-value
Total DDW	22.4 ± 5.1	19.0 ± 5.5	10.8 ± 3.4	0.287
Small-diameter DDW	21.7 ± 5.1	18.7 ± 5.2	7.8 ± 1.6	0.113
Large-diameter DDW	0.8 ± 0.4	0.3 ± 0.3	2.9 ± 2.9	0.530
Low-decay DDW	18.5 ± 4.8	16.9 ± 5.7	8.5 ± 3.2	0.289
High-decay DDW	3.9 ± 1.3	2.1 ± 0.8	2.3 ± 0.4	0.537
SDW basal area	0.8 ± 0.3	1.4 ± 0.5	0.6 ± 0.4	0.263

All volumes are $m^3\ ha^{-1}$, basal area is $m^2\ ha^{-1}$. Comparisons between ELTPs were made with Kruskal-Wallis one-way ANOVA on ranks, but no significant differences were found.

difficult and time-consuming (American Pulpwood Association 1988). However, the larger volume of this material centralized within clearcuts may make it economically feasible to haul it out for use in pallet bolts and other lower value products. Because Indiana lacks a pulp market, trees less than 30.5 cm dbh are not removed from stands, although they may be cut and left as culls (Jayson Waterman, Indiana Department of Natural Resources, Nov. 17, 2003). To make harvesting more profitable, group selections may also be marked to include more larger and taller trees of better economic value. Regressions that included significant treatment effects explained between 20 and 43% of the variation in the volume and abundance of DDW, suggesting that additional quantitative variables may be necessary to fully explain DDW dynamics in these stands.

The amount of edge around smaller openings may also contribute to their higher volume of DDW. Small openings have a high ratio of perimeter-to-opening area that could increase the influence of deadwood falling into the opening from the surrounding forest matrix. However, we found that the mature forests surrounding openings contain little CWD compared to younger and older forests.

Because of the significantly greater volume of DDW found in group-selection openings, this silvicultural technique has created relatively small isolated pockets of high DDW volume within a matrix of former clearcuts and mature stands that contain relatively little DDW. Although group-selection openings contained a greater volume of large-diameter DDW (>40 cm dbh; Figures 4 and 5, Table 2) than did clearcuts, they did not contain greater volumes of highly decayed DDW. Highly decayed material is viewed as a critical habitat resource for many organisms (Hagen and Grove 1999). For example, other studies have shown that larger logs provide more cover and a longer duration of use for salamanders (Cline et al. 1980) and are a preferred food base for some insects (Hanula 1996). However, low-decay material is not highly used by salamanders (Herbeck 1998), and may not readily be fed upon by some types of forest insects (Graham 1925). The group-selection openings we sampled contained large volumes of decay class 3 material (Figure 3), which may result in greater volumes of high-decay DDW (classes 4 and 5) with decomposition. However, the volume of DDW in group selections >20 years of age was less than 40 $m^3 ha^{-1}$ (Figure 3) and was less than 23 $m^3 ha^{-1}$ in mature stands (Table 3). Although successive group-selection harvests in these stands will once again increase the volume of CWD, large-diameter, highly decayed material will still be lacking.

Huston (1996) suggested that the effects of CWD on biodiversity are most prominent in the decomposer food webs, where a complex array of species rely on the energy and structural diversity of forest-floor habitats provided by CWD. The amounts of CWD appropriate for specific forest types are not known, but it appears that, in most cases, insufficient CWD is being recruited in managed forests (Spies et al. 1988, Bunnell et al. 2002). More information is needed to determine what proportion of forested lands can be under intensive management before CWD-dependent species become affected or extirpated (Hagen and Grove 1999).

The results of our study exhibited similar relationships between CWD volume and time since harvest as studies conducted in other parts of the eastern US hardwood forest. In northern hardwood forests, Gore and Patterson (1986) observed much lower DDW volumes in 50-year-old stands than in recent clearcuts and old-growth forests. The high volume of DDW present in recent silvicultural openings results from the addition of postharvest slash and stumps. Our study lacked data from openings 1–8 years in age. However, these younger openings tend to contain even greater volumes of postharvest slash (McCarthy and Bailey 1994). The majority of this DDW input is relatively small in diameter with a large surface area-to-volume ratio that leads to rapid decomposition. Once the majority of this small-diameter material decays, DDW volume gradually declines as stands mature because the volume of DDW input from the developing stand is less than the loss from decomposition. Although mortality does occur in these developing stands, most standing dead trees are small in diameter and the volume of material they produce is negligible compared to the volume of postharvest slash.

Variation in CWD Across ELTPs

Although productivity across the three ELTPs is similar (Jose and Gillespie 1996, Jose and Gillespie 1997), we did observe differences in the volume of DDW among ELTPs. Generally, we observed a greater volume of DDW in silvicultural openings on mesic slopes and wet-mesic bottomlands than on dry-mesic slopes. The relationship between CWD and topography has received little study in the forests of eastern North America. Crooks et al. (1998) observed no changes in CWD with landscape classification units in Piedmont forests of South Carolina. However, in forests of southern Ohio, Rubino and McCarthy (2003) found greater DDW abundance on lower and less steep slopes.

Variations in DDW volume with ELTP may result from differences in species composition and the rate of decomposition among sites. Although the difference was not statistically significant ($P = 0.113$), mature stands on dry-mesic slopes had three times the volume of small-diameter DDW than of those on wet-mesic bottomlands. Lower relative humidity and reduced substrate moisture on dry-mesic slopes may slow decomposition. In addition, these stands are dominated by oak (*Quercus*) species (Jenkins and Parker 1998), which have slower rates of decay than other hardwood species (MacMillan 1988). In silvicultural openings, this trend was reversed. Dry-mesic slopes contained lower volumes of DDW than did mesic slopes or wet-mesic bottomlands. The higher volume of *Quercus* species, which have high value as timber, on dry-mesic slope may have resulted in shorter and fewer slash fragments being left after harvest.

CWD in Mature Stands

The 72–105-year-old mature stands we sampled are in the early stage of understory reinitiation, as defined by

Oliver and Larson (1996). In this stage of stand development, there is little overstory mortality and, therefore, little input of DDW in the form of dead trees. This low mortality contributes to the generally low overall DDW volume in these stands and the low volume of highly decayed and large-diameter deadwood. In our study, we found that mature stands had relatively low basal area of SDW (Table 3) compared to older silvicultural openings, which were still undergoing stem exclusion (mean $= 3.1 \pm 0.7$ m^2 ha^{-1} for openings $\geq$18 years old across all three ELTPs). During late stem exclusion, some input of SDW occurs as trees die from competition and self thinning. Larger canopy trees will begin to lose vigor and die as these stands enter the understory reinitiation stage. As stands enter the old-growth stage, tree-fall gaps will form, further increasing the volume of CWD (McGee 1984, Oliver and Larson 1996, Muller 2003). In old-growth forests of the Midwest, Spetich et al. (1999) observed an average DDW volume of 60.3 m^3 ha^{-1}, over three times the volume we found across mature stands.

Numerous authors have suggested that large-diameter, highly decayed material is very important habitat for many species of vertebrates (Barnum et al. 1992, Dupuis et al. 1995). Mature stands on all three ELTPs had very low volumes of highly decayed and large-diameter DDW and contained little SDW compared to old-growth stands (Spetich et al. 1999). Because stands of this age are dominant across much of the Central Hardwood Region, forests across the Region likely possess limited habitat for these species. Although the volume of large-diameter, highly decayed material increases as forests enter the old-growth stage of development (Muller and Liu 1991, Goebel and Hix 1996, Spetich et al. 1999), more research is needed to determine how forest management can be adapted to increase the availability of CWD in contemporary stands.

Conclusions

Clearcutting and group-selection harvest, two silvicultural systems used throughout eastern North America, have produced different amounts of CWD within openings of southern Indiana. We observed a significantly greater volume of DDW in group-selection openings than in clearcuts. These differences likely relate to market forces associated with each type of harvesting system. Because of the large amount of overlap in holdings among the national and state forests we studied, these different management techniques are producing considerable local variability in DDW volume. Understanding the amount of CWD produced by different management techniques is an important first step in developing management guidelines for retaining sufficient volumes of DDW in managed stands of the Central Hardwood Region. Although guidelines have been developed for the retention of snags (SDW) during harvest on many national forests, guidelines for DDW volume have received little attention (Bunnell et al. 2002).

Based on our results, the volume of DDW remaining within an opening after harvest varies with ELTP. We observed significantly greater volumes of DDW on mesic slopes and wet-mesic bottomlands than on dry-mesic slopes. The prevalence of more valuable oak species on dry-mesic slopes may result in less slash being left on the site after harvest. Because the volume of DDW after harvest does not differ significantly between mesic slope and wet-mesic bottomland stands, these two ELTPs could be considered together when modeling CWD dynamics after harvest or developing guidelines for DDW retention in managed forests.

In our study, we found that the mature 72–105-year-old stands that dominate the forests of the southern Midwest contain little CWD compared to younger stands that develop after management or the Region's few remaining old-growth stands. Generally, the amount of CWD in the openings we sampled declined quickly after harvest and leveled off after ~14 years (Figure 3). This suggests that, under current conditions, stands may remain relatively depauperate of CWD for over a hundred years until canopy mortality and windthrow begin to increase CWD inputs.

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