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**DYNAMICS OF COARSE WOODY DEBRIS
IN NORTH AMERICAN FORESTS:
A LITERATURE REVIEW**

TECHNICAL BULLETIN NO. 877

MAY 2004

by
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Acknowledgments

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PRESIDENT'S NOTE

In sustainable forestry programs, managers consider many ecosystem components when developing, implementing, and monitoring forest management activities. Even though snags, downed logs, and stumps have little economic value, they perform important ecological functions, and many species of vertebrate and invertebrate fauna are associated with this coarse woody debris (CWD). Because of the ecological importance of CWD, some state forestry agencies have promulgated guidance for minimum amounts to retain in harvested stands.

It is important that regulatory guidance and management plans for CWD be based on sound understanding of the factors that control CWD dynamics. Thus, this technical bulletin provides information on methods for assessing CWD, the processes that affect CWD inputs, outputs, and nutrient dynamics, and the range of dynamics under various situations. It also identifies important topics for future research.

Based on this review of literature, it is apparent that CWD dynamics are highly influenced by site-specific considerations. The rates at which snags and downed logs are created and decay vary by tree species and age, which in turn are influenced by site characteristics (e.g., growth potential, frequency and intensity of disturbances); small-scale spatial variation is often evident in CWD abundance and dynamics. Thus, factors related to CWD accumulation must be assessed on a site-by-site basis before CWD prescriptions or descriptions can be made accurately.

A handwritten signature in black ink, appearing to read "Ron Yeske", is positioned above the printed name.

Ronald A. Yeske

May 2004

MOT DU PRÉSIDENT

Dans les programmes d'aménagement forestier durable, les gestionnaires tiennent compte de bien des éléments d'un écosystème lorsqu'ils conçoivent, appliquent et surveillent les activités de gestion de la forêt. Malgré leur peu de valeur économique, les chicots, les billes gisant sur le sol et les souches accomplissent des fonctions écologiques importantes, car de nombreuses espèces animales vertébrées et invertébrées sont liées à ces débris ligneux grossiers (DLG). Un certain nombre d'états ont publié des directives en vue de conserver une quantité minimum de DLG dans les peuplements récoltés en raison de leur importance écologique.

Il est essentiel que les directives émises par règlement et les plans de gestion des DLG soient fondés sur une bonne compréhension des facteurs qui régissent la dynamique des DLG. Ce bulletin technique fournit donc de l'information sur les méthodes d'évaluation des DLG, les mécanismes qui influencent leur formation, leur enlèvement, la dynamique des nutriments qu'ils contiennent, et sur la diversité des forces en jeu selon les différentes circonstances. Le rapport dresse aussi la liste des principaux sujets de recherche subséquente.

Cette revue de la littérature permet de constater que la dynamique des DLG est fortement influencée par les conditions propres au site. La vitesse de formation et de pourriture des chicots et des billes au sol varie en fonction de l'essence de l'arbre et son âge qui, à leur tour, sont influencés par les caractéristiques du site (par ex., le potentiel de croissance, la fréquence et l'intensité des perturbations). Les variations spatiales à petite échelle sont souvent manifestes dans la dynamique et l'abondance des DLG. En conséquence, les facteurs liés à l'accumulation des DLG doivent être examinés au cas par cas avant d'être en mesure de décrire des DLG ou d'émettre une prescription de façon précise.



Ronald A. Yeske

Mai 2004

DYNAMICS OF COARSE WOODY DEBRIS IN NORTH AMERICAN FORESTS: A LITERATURE REVIEW

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ABSTRACT

Coarse woody debris (CWD), which is commonly defined as snags, downed logs, and stumps that persist in the ecosystem for some time, has become an important consideration in forest management. Management plans for CWD should be based on sound understanding of the factors that control CWD dynamics. This report provides information on methods for assessing CWD, the processes that affect CWD inputs, outputs, and nutrient dynamics, and the range of dynamics under various situations.

There is no uniform minimum size class at which woody material is considered to be CWD, and that minimum size likely depends upon the site-specific decomposition rate. Most surveys distinguish a range of decay states for downed logs and snags. The most general classification is simply “sound” versus “rotten.” A more detailed scheme defines decay classes based on characteristics such as number of branches, presence of bark, loss of top, and bole integrity.

When sampling CWD, pieces of CWD encountered in plots or along transects may be collected and weighed. More generally, however, volumes are estimated and converted to mass via wood density measurements obtained from the study site or from previously published data. Regardless of the measurement scheme, the precision when projecting estimated CWD quantities to larger areas depends upon the sample size and the inherent variability in CWD quantities. Planar intercept transects appear to be a fast and reliable method for collecting data related to downed log accumulations under a variety of conditions. A triangle of transects provides good coverage and is relatively easy to set up in the field. Permanent sample plots also should include counts and diameters of snags and live trees by species. Repeated surveying of sample plots on some regular cycle (annually, every 3 years, every 5 years, etc.) would provide useful data on dynamics.

The rates at which snags and downed logs are created vary by tree species and age, which in turn are influenced by site characteristics (e.g., growth potential, frequency and intensity of disturbances). Therefore, the reported rates at which snags and downed logs are created vary widely from site to site, and small-scale spatial variation is generally apparent. Temperature and moisture are important controls of decomposition rates. Log diameter affects decomposition both through the surface area to volume relationship and water content. Species differences in size and log constituents, including proportion of bark, heartwood, and sapwood, and wood chemistry, also influence decomposition partly by controlling the rate of insect incursion.

The processes that determine CWD dynamics are tree mortalities, snag retention, and downed log decay rates. However, these rates vary by species, type of mortality, and site characteristics; it is not easy to summarize them or to generalize over various forest types. For example, on some sites reported CWD accumulation has followed a U-shaped timeline, but has not on others. Some sites reach an equilibrium quantity of CWD, but others do not. Disturbance regime, species and site characteristics and other factors related to CWD accumulation must be assessed on a site-by-site basis before CWD prescriptions or descriptions can be made accurately. CWD studies should include more than just snapshots of CWD quantities; they also should include information about the processes underlying those quantities.

The reported amounts of mineral nutrients in CWD and flux rates vary substantially by the specific mineral nutrient and by type of material (bark versus wood), stage of decomposition, and decomposer organisms. For example, N may initially be leached from CWD, but taken up immediately by microbes and fungi and released only after substantial decay. However, the conditions under which this pattern occurs are not clear. The relatively small pool size of nutrients in CWD versus soil components suggests that CWD may not be a major source of nutrients for many forests. However, CWD still may be an important long-term reservoir of nutrients. Managers should account for the potential role of CWD in long-term nutrient dynamics of forests, but more needs to be known about this interaction.

Coordinated research efforts would help improve understanding of the processes that control CWD dynamics. A network of field monitoring sites established cooperatively among the forest products industry, federal agencies, and state agencies, and using compatible methodology would provide a set of comparable data that would allow investigators to assess the relative importance of climate, forest type, management history, and other factors. A modeling network also would provide data with which to parameterize models that could be used by managers to conduct “what-if” analyses for CWD quantities under various proposed management plans. However, we found few publications related to CWD modeling, and there also is a need to improve the tools available for modeling CWD dynamics. No studies found in this review addressed the role of snags as lightning attractors (e.g., the effect of a large snag on a ridge top) or in altering fire regimes. In addition, questions remain about how much CWD is needed to maintain habitat of particular wildlife species. Some studies have shown that guidelines for snag retention were not met even in old-growth sites. However, manipulative studies to test adequacy of particular quantities of CWD appear to be rare, although admittedly such studies were not the objective of this review.

KEYWORDS

coarse woody debris, decay classes, decomposition, decay rates, dynamics, input rates, literature review, methods, nutrient flux, nutrient content, research, sampling

RELATED NCASI PUBLICATIONS

Technical Bulletin No. 775 (January 1999). *Assessing effects of timber harvest on riparian zone features and functions for aquatic and wildlife habitat.*

Technical Bulletin No. 514 (February 1987). *Managing Oregon's riparian zone for timber, fish and wildlife.*

**LA DYNAMIQUE DES DEBRIS LIGNEUX GROSSIERS
DANS LES FORETS DE L'AMERIQUE DU NORD:
UNE REVUE DE LA LITTERATURE**

BULLETIN TECHNIQUE NO. 877
MAI 2004

RÉSUMÉ

Les débris ligneux grossiers (DLG) sont généralement définis comme étant des chicots, des billes gisant au sol et des souches qui subsistent dans l'écosystème pendant quelques temps. Ils sont devenus d'importants éléments à considérer dans la gestion des forêts. Les plans de gestion devraient être basés sur une bonne compréhension des facteurs qui régissent la dynamique des DLG. Ce rapport fournit de l'information sur les méthodes d'évaluation des DLG, les mécanismes qui influencent leur formation, leur enlèvement, la dynamique des nutriments qu'ils contiennent, et sur la diversité des forces en jeu selon les différentes circonstances.

Il n'existe pas d'uniformité dans la définition de la dimension minimum à partir de laquelle du matériel ligneux est considéré comme un DLG, et ce minimum dépend vraisemblablement de la vitesse de décomposition propre au site. La majorité des études font une distinction entre billes au sol et chicots et présentent divers régimes de pourriture pour chacun. La classification la plus générale est simplement « sain » versus « pourri ». Il existe aussi un schème plus détaillé qui définit des classes de pourriture selon des caractéristiques comme le nombre de branches, la présence d'écorce, la destruction de la cime et l'intégrité du tronc.

Lors de l'échantillonnage de DLG, les morceaux de DLG trouvés dans des points d'observation écologique ou le long de transects peuvent être recueillis et pesés. Cependant, de façon générale, les volumes sont estimés et convertis sous forme de masse à l'aide des mesures de densité du bois obtenues du site étudié ou de données déjà publiées. Peu importe la méthode de mesure, la précision de la transposition des quantités estimées de DLG à des superficies plus grandes dépendra de la taille de l'échantillon et de la variabilité inhérente des quantités de DLG. Les transects planaires semblent constituer une méthode fiable et rapide de cueillette de données pour l'accumulation de billes au sol sous diverses conditions. Les transects triangulaires fournissent une bonne couverture et sont plutôt faciles à mettre en place sur le terrain. Les mesures dans les placettes-échantillons permanentes devraient aussi inclure le nombre et le diamètre des chicots et des arbres vivants et ce, selon l'essence. L'échantillonnage répété de placettes-échantillons selon un certain cycle régulier (annuel, triennal, quinquennal, etc.) fournit des données utiles sur la dynamique du site.

La vitesse de formation des chicots et des billes au sol varie en fonction de l'essence de l'arbre et son âge qui, à leur tour, sont influencés par les caractéristiques du site (par ex., le potentiel de croissance, la fréquence et l'intensité des perturbations). Par conséquent, la vitesse de formation de ces débris fluctue d'un site à l'autre, et les variations spatiales à petite échelle sont souvent manifestes. La température et le taux d'humidité jouent un rôle important dans la vitesse de décomposition. Les variables qui agissent sur la décomposition d'une bille de diamètre donné sont la relation qui existe entre son volume et sa surface de même que sa teneur en eau. Les différences qui existent entre les essences en termes de taille, de composantes (entre autres la proportion d'écorce, de duramen et d'aubier), et de chimie du bois influencent également en partie la décomposition en contrôlant le nombre d'incursions des insectes.

Les mécanismes qui gouvernent la dynamique des DLG sont la mortalité des arbres, la rétention des chicots et la vitesse de pourriture des billes au sol. Par ailleurs, cette vitesse varie en fonction de l'essence de bois, le type de mortalité et les caractéristiques du site. Il n'est donc pas facile de résumer ces mécanismes et de généraliser pour divers types de forêt. Dans certains sites, par exemple, l'accumulation de DLG évolue selon une courbe de temps en forme de U, ce qui n'est pas le cas dans d'autres sites. Quelques sites atteignent l'équilibre en matière de quantité de DLG, mais d'autres n'y parviennent pas. Le régime des perturbations, le type d'essence de bois, les caractéristiques du site et autres facteurs liés à l'accumulation des DLG doivent être examinés au cas par cas avant d'être en mesure de décrire des DLG ou d'émettre une prescription de façon précise. Les études de DLG devraient être plus qu'un portrait instantané des quantités de DLG ; ils devraient aussi inclure de l'information sur les mécanismes à la base de ces quantités.

Les quantités de minéraux dans les DLG et leur flux varient de façon substantielle en fonction du type d'élément nutritif et de matériel ligneux (écorce versus bois), du stade de décomposition et des organismes responsables de la décomposition. Par exemple, au début, de l'azote peut s'échapper des DLG par lessivage, mais être repris immédiatement par les microbes et les champignons, et relâché seulement lorsque la pourriture est avancée. Par contre, les conditions sous lesquelles se produisent ces réactions ne sont pas claires. Les DLG contiennent des quantités plutôt faibles d'éléments nutritifs par rapport aux quantités dans le sol. Il semblerait donc que les DLG ne soient pas une source majeure de nutriments pour de nombreuses forêts. Néanmoins, ils peuvent quand même être un important réservoir d'éléments nutritifs à long terme. Les gestionnaires devraient tenir compte du rôle potentiel des DLG dans la dynamique à long terme des nutriments dans les forêts. Il reste toutefois beaucoup de travail à faire pour mieux connaître ces interactions.

Des efforts de recherches coordonnées entraîneraient une meilleure compréhension des mécanismes qui régissent la dynamique des DLG. Si l'industrie des produits forestiers, les agences fédérales et les états mettaient conjointement sur pied un réseau de surveillance de terrain et utilisaient des méthodes compatibles, on obtiendrait une série de données comparables qui permettraient aux chercheurs d'évaluer l'importance relative du climat, du type de forêt, de l'historique de gestion et autres facteurs. Un réseau de modélisation apporterait aussi des données qui alimenteraient des modèles pour les gestionnaires qui voudraient faire des simulations sur la quantité de DLG en fonction de différents plans de gestion. D'ailleurs, nous avons trouvé peu de documents sur la question. Il faudrait également perfectionner les outils actuels de modélisation de la dynamique des DLG. La présente analyse n'a pu identifier aucune étude qui abordait le rôle des chicots comme pôle d'attraction de la foudre (par ex., l'effet d'un gros chicot sur la cime d'une crête) ou comme élément d'altération du régime d'un feu de forêt. De plus, il subsiste des questions sur la quantité de DLG requises pour maintenir l'habitat d'une espèce faunique particulière. Certaines études ont démontré que les directives sur la rétention des chicots n'avaient pas été respectées, même dans des forêts anciennes. Les études manuelles de vérification de la pertinence de quantités spécifiques de DLG semblaient rares, quoique de telles études ne faisaient pas partie des objectifs de la présente étude.

MOTS CLÉS

débris ligneux grossiers, classes de pourriture, décomposition, vitesse de pourriture, dynamique, vitesse de formation, revue de la littérature, méthodes, flux des nutriments, contenu en nutriments, recherche, échantillonnage

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique No. 775 (janvier 1999). *Assessing effects of timber harvest on riparian zone features and functions for aquatic and wildlife habitat.*

Bulletin technique No. 514 (février 1987). *Managing Oregon's riparian zone for timber, fish and wildlife.*

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DYNAMICS OF COARSE WOODY DEBRIS IN NORTH AMERICAN FORESTS: A LITERATURE REVIEW

1.0 INTRODUCTION

Coarse woody debris (CWD)—woody material that persists on the forest floor—has become an important issue in forestry management. CWD is an important habitat component for some terrestrial wildlife species, and its role in helping maintain biological diversity of forests perhaps generates the strongest impetus for considering CWD in management plans. Other issues driving concern about CWD include its potential roles as structure in fish habitat and as a nutrient reservoir for forest sustainability. Also, CWD is sometimes viewed as an indicator of old-growth conditions, a structural class in which there is growing public interest. On a broader scale, concern over atmospheric CO₂ content and global climate change has directed research into the carbon dynamics of forests and the role of CWD. Despite this growing attention to CWD, several introductory forestry texts still have no index entry for coarse woody debris.

Management plans for CWD should be based on sound understanding of the factors that control CWD dynamics. To promote improved understanding of CWD dynamics, we reviewed more than 150 articles that appeared in refereed journals and government publications between 1985 and 1999. Some simply report quantities of CWD in particular forests, while others answer specific questions regarding mechanisms of snag and downed log recruitment and decomposition. Several important reviews already have been conducted on various topics related to CWD. Harmon et al. (1986) describe the various ecological roles of CWD and factors that control the additions and losses of CWD. Caza (1993) and Stevens (1997) provide an overview of information about CWD in British Columbia forests, Lofroth (1998) provides an overview of the “dead wood cycle,” and Hagan and Grove (1999) discuss the role of CWD in forest ecology.

The various types of CWD in the forest are now seen as an important part of forest diversity (Maser et al. 1988). Structural diversity can be enhanced, for example, as shade suppression yields whole standing dead trees and ice damage yields downed branches. Windthrow adds to spatial diversity through the downed bole, the tipup mound, the pit, and damage to neighboring trees. Different sizes and species of trees decay at different rates, creating variety in substrates on the forest floor and, thus, the diversity of organisms that use CWD as habitat.

CWD is now an important part of assessing forest resources, and silvicultural prescriptions sometimes are developed to maintain particular levels of this “legacy” material (Kohm and Franklin 1997). For example, Graham et al. (1994) made recommendations on CWD management by using mycorrhizal fungi as an indicator of adequate quantities of CWD for nutrient cycling. Based on comparisons to unmanaged forests, Keddy and Drummond (1996) suggested that natural eastern deciduous forests would typically be expected to have >20 Mg/ha CWD. They considered forests with 10-20 Mg/ha CWD to be intermediate and forests with <10 Mg/ha CWD to be low CWD forests and, thus, “altered.”

One should keep in mind, however, that CWD may not be an equilibrium process. Therefore, any particular CWD target quantity would apply only to a particular stage in forest dynamics and only at a particular spatial scale. Also, in some systems, old-growth represents a particular stage of the forest dynamics, not necessarily an equilibrium condition that must be maintained.

1.1 Overall Goal of the Review

This review is designed as a guide to recent (1985 to 1999) literature related to CWD dynamics in forests of the U.S. and Canada. The important ecological role of CWD as habitat and its role in lakes, rivers, and streams were not subjects of this review and have been discussed elsewhere. For example, Freedman et al. (1996) recently reviewed the relationships between CWD and wildlife, McMinn and Crossley (1996) reviewed the effects of CWD on biological diversity in southern forests, deMaynadier and Hunter (1995) discussed relationships between forest management (including CWD) and amphibians, and Maser and Sedell (1994) described the role of CWD in rivers, lakes, and the ocean.

Because CWD is a relatively new research topic, investigators have not settled on a set of core questions that studies should address (or even whether the term CWD should include snags). Research objectives, measurement techniques, and even units of measure vary across studies. Thus, generalizations, even geographic comparisons of CWD accumulation, are problematic. However, the major questions around CWD dynamics can be addressed, and that information can be used to design specific studies and monitoring programs.

The goal of this review was not to recommend how much CWD should be left after logging operations in particular forests. While that is an important question, the answer cannot be provided in this type of report because the answer depends on the particular ecological functions of most concern, the particular forest type and structure, and other site-specific considerations. Rather, this report provides information on methods for assessing CWD, the processes that affect CWD inputs, outputs, and nutrient dynamics, and the range of dynamics under various situations. Most studies reviewed in this report were not designed to test specific hypotheses, and few were controlled studies. Thus, quantitative conclusions about specific factors controlling CWD dynamics are not always available.

We have organized the review around factors that influence CWD dynamics. A general, conceptual description of CWD input/output processes is straightforward. Stated simply, trees die, fall over, and decay. Thus, any factor that influences tree species composition, productivity, size, mortality, or decomposition will influence CWD dynamics. Harmon et al. (1986) described the processes involved in the movement of trees through the stages of live, snag, downed CWD, and decomposed material, and the factors that influence those transformations. Rates of CWD input are affected by the interaction of climate, tree size, agents of mortality (e.g., wind, disease, fire, stem exclusion), and the susceptibility of different species to those agents. Successional status influences the species composition of the forest. The interactions of climate, snag/log size, and resistance to decay affect the rates of decomposition and transition from snag to downed log. A succession of decomposer organisms and changing substrate quality affect the decomposition rates of CWD. Management practices influence CWD inputs/outputs directly (e.g., fire, harvesting) or indirectly through other factors (e.g., productivity, size, mortalities, microclimatic conditions, species composition). Of course, these factors and their interactions are best understood and managed on a site-specific basis.

1.2 Review Methods

The articles discussed in this review were identified through three search strategies. First, we searched two computer-based literature databases (TREE and Current Contents) and the Internet using a wide set of key words, including debris, detritus, forest floor, forest dynamics, mortalities, snags, downed logs, nutrient dynamics. Second, we manually searched the tables of contents of journals that routinely report CWD research (e.g., *Canadian Journal of Forest Research*, *Ecology*, *Forest Ecology and Management*) and catalogs of U.S. and Canadian Forest Service publications.

Finally, the literature cited section of articles found through these searches provided additional articles. Student theses and other unpublished research reports were not included.

Those interested in CWD also should be aware of three other sources of information. Two sources are a “dead tree” website (<http://www.for.gov.bc.ca/research/deadwod>) maintained by the Canadian Forest Service, and an Internet-based discussion group of about 150 participants that has been active since late 1999 (http://www.egroups.com/group/dead_wood). A third source of information is a conference (The Ecology and Management of Dead Wood in Western Forests) sponsored in November 1999 by the Western Section of The Wildlife Society, at which more than 80 papers were presented. Abstracts are available at <http://www.tws-west.org/deadwoodabstracts.html>.

2.0 METHODS USED TO STUDY CWD

In this section, we review approaches to defining CWD and methods that have been used to estimate CWD quantities, characterize its condition (e.g., decay class), assess input/output rates, and measure nutrient content. We also suggest a survey scheme.

2.1 Defining CWD

CWD is commonly defined as snags, downed logs, and stumps that persist in the ecosystem for some time. However, there is no uniform minimum size class at which woody material is considered to be CWD, and that minimum size likely depends upon the site-specific decomposition rate. For example, a 2.5-cm diameter stick in a dry oak forest in Missouri may persist for several years, and thus be considered as CWD. On the other hand, a 2.5-cm stick of red alder in a Pacific Northwest forest would decay rapidly and probably would not be defined as CWD. Harmon et al. (1986) suggested 7.5 cm as the minimum size of CWD in western North America and 2.5 cm elsewhere in North America. A lower limit of length may be included in the definition of CWD (e.g., minimum length 1 m), but no uniform standard exists.

2.2 Decay Classes of CWD

The value of a particular piece of CWD as habitat or a nutrient reservoir depends on its state of decomposition. Thus, most surveys distinguish a range of decay states for downed logs or snags. The simplest classification is simply “sound” versus “rotten.” A more detailed scheme defines 5 decay classes of downed boles (see Table 2.1). While Class I refers to new material and Class V to the oldest, specific definitions of decay classes may vary by forest type. Pyle and Brown (1998) found that decay classes could be visually assessed quickly and accurately. Because some heterogeneity occurs within logs, investigators may even consider recording the different decay classes encountered along the length of each log (Pyle and Brown 1999).

For snags, decay classes have been defined according to characteristics such as number of branches, presence of bark, loss of top, bole integrity (e.g., Maser et al. 1979). However, the characteristics used in classifying material into decay classes often vary with tree species and site conditions.

Table 2.1 Example Definition of Coarse Woody Debris Decay Classes
(from Goodburn and Lorimer 1998)

Class	Characteristics
I	tight bark, no visual decay
II	some bark slippage, incipient decay of sapwood
III	decay obvious in outer layers, pointed metal rod penetrates more than half the radius
IV	some of outer xylem layers missing, decay extended well toward core, metal rod penetrates clear through bole
V	organic debris collapsed to ground level and mixing with soil, little structural integrity

2.3 Estimating CWD Quantities

Caza (1993) and Harmon and Sexton (1996) describe general methods for estimating quantities of CWD. Units for describing CWD quantities include counts (e.g., areal density of snags and logs), volume (m³/ha), surface area (m²/ha), projected area (m²/ha), percent cover, and mass (Mg/ha). Methods of sampling include fixed area plots or line transects. No single method is appropriate for all studies. Rather, the costs and benefits of more detailed vs. faster sampling schemes should be assessed for each study.

Pieces of CWD encountered in plots or along transects may be collected and weighed. More generally, however, volumes are estimated and converted to mass via estimates of wood density obtained from the study site or from previously published data. Wood density can be calculated from mass and volume measurements taken from sections of selected pieces of CWD. Wood volume can be measured by displacement of water or other media (e.g., small seeds). Because wood density values depend on tree species and state of decay, separate density values usually are required for each species in the various states of decay.

Volume of CWD pieces may be estimated by measuring the length and diameter of CWD encountered in area plots or along transects. The approach that investigators choose may depend upon the tradeoff between complexity of measurement in the field and the potential for added accuracy. If a cylindrical shape is assumed, only midpoint diameter and length are needed to compute volume. For more accurate volume estimates, other geometric shapes can be used. If logs are assumed to be the shape of the frustum of a cone, both end diameters should be measured. For a twice-tapering shape, end diameters and diameter at any point where diameter changes abruptly must be measured. For elliptical cross sections, major and minor axes should be measured. An estimate of total CWD volume within a plot may be calculated by summing the estimated volume of each piece of CWD encountered.

Rather than estimate the volume of each piece of CWD, investigators may use several quicker, simpler methods. Harmon and Sexton (1996) measured only the diameter of each piece of CWD encountered at the planar intercept along line transects. They computed total volume for the transect using the formula, $V = \pi^2 * (\Sigma d^2 / 8L)$, where d is the diameter of the piece of CWD, corrected if

necessary for elliptical cross section and L is the transect length. Prisms (Harmon and Sexton 1996) and relascopes (Gove et al. 1999) provide even faster means of assessing CWD. Detailed guidelines for using the relascope method and formulae for estimating CWD quantities from relascope data are provided by Gove et al. (1999) and Stahl (1998).

2.4 Statistical Estimation of Plot Totals

Regardless of the measurement scheme, the quantities of CWD measured within the sampling areas often are projected to the entire study area. The precision of the result depends upon the sample size and the inherent variability in CWD quantities, which can be high. Based on data reported from old-growth sites in the central U.S., Shifley and Schlesinger (1994) reported that as many as 200 0.1-ha plots may be necessary to achieve sampling error of 10% of actual snag density. They suggested that >300 plots may be necessary to achieve sampling error of 10% for estimating volume of CWD >10 cm diameter, but 25% error may be possible with sample sizes up to 55 plots. Shifley and Schlesinger (1994) also reported that it may be necessary to use 1,500 plots to achieve 25% sampling error for each decay class of CWD. This is not to suggest that all studies must have such large sample sizes, but rather to indicate that study objectives must be set realistically. Precise estimates of mean CWD volumes for each decay class over a large area may not be realistic.

Bull, Holthausen, and Marx (1990) assessed the effect of plot size and sampling method on snag density in northeastern Oregon. An intensive search yielded actual snag densities, which were used to compare results from plots of various sizes and plotless techniques (i.e., relascope). Their recommendations were to use plots sufficiently large to reduce the statistical variability in snag counts within each plot, specifically 0.4-ha plots or a prism-factor of 5 for sampling large areas (e.g., >1,000 ha) and where snag densities are 1.7-4.9 snags/ha. One plot per 3.6-9.7 ha was found to be sufficient to estimate snag density within 25% of the actual mean 95% of the time for target areas 1,298-1,392 ha. Bull, Holthausen, and Marx (1990) suggested that, with small target areas or sparse snags, a complete count should be done. In areas with high density of live trees, they suggested that prisms not be used because snags may be hard to see. The authors also recommended caution in applying these results to different types of forests and different situations. Each situation calls for a careful consideration of the information needs and costs.

A combination of plot sizes can be useful for different kinds of information. Because the sampling intensity for a desired level of precision depends on the variability in the system, some studies have used fewer, larger quadrats for some variables and more, smaller quadrats for other variables. For example, volume of downed logs 10-20 cm diameter may be measured in 900-m² quadrats while volume of larger (and thus less common) logs may be measured in 2,500-m² quadrats that subsume the smaller, nested quadrat (e.g., Spies, Franklin, and Thomas 1988).

Orientation of transect lines may affect the precision and accuracy of estimates. Transect lines can be randomly oriented, oriented according to the direction that most logs lie, or systematically oriented. A triangular arrangement of transect lines appears to prevent orientation bias when logs are not oriented randomly (Bell et al. 1996). However, lengths of the transect lines and number of lines again depend on the inherent variability of the system. Surveyors may inadvertently deviate from the established transect line to avoid or seek out logs, which may add to variance. But, one study found no overall bias in average results (Ringvall and Stahl 1999).

2.5 Assessing CWD Input Rates

Inputs to CWD (i.e., tree mortalities, toppling rates for live or dead trees, branch fall) can be estimated by a time series or by a chronosequence (Harmon and Sexton 1996). The time series, which is a prospective study, involves monitoring an established study site over time (i.e., monitoring

over time at a given space). A chronosequence is a retrospective study, in which space substitutes for time. In other words, different sampling points are selected to represent different ages. This substitution of space for time is often used in successional studies as well.

A time series of repeated measurements offers the obvious advantage of a known history, but data are not available for many years. A chronosequence is convenient and data are available immediately. However, there often is uncertainty about the ages of study stands and individual logs, and about whether initial and post-disturbance climatic conditions were actually similar at the different sites.

In a retrospective study, investigators generally determine creation times of the individual pieces of CWD or the disturbance time of sites. If the disturbance history of a site is known (e.g., time of fire or insect outbreak), that information is used. If the date is not known or dates are needed for individual pieces of CWD, investigators may use dendrochronology of downed logs, ages of trees growing on nurse logs, dendrochronology of neighboring live trees (to evaluate years of competitive release due to gap formation), or scars on surviving trees that indicate toppling of a log. Investigators also may use decay class to predict age of CWD, if all CWD of a given decay class can be assumed to be within the same age range. Because decay class is relatively simple to estimate, this method can be a convenient way to assess the ages of downed logs.

2.6 Assessing Output Rates

CWD accumulation is a function of input rates and output rates. As previously discussed, inputs are derived from tree mortalities, toppling of live or dead trees, and branch fall. Outputs are generally through decomposition, but fire, downslope movement, and other disturbances (e.g., site preparation activities) also may remove CWD from a site. Outputs through decomposition can be assessed prospectively or retrospectively (Harmon and Sexton 1996). Decomposition rates are typically estimated retrospectively by correlating estimated ages of downed logs with decay class of the logs. The most common technique is to develop an exponential regression model of wood density based on material age (e.g., $Y_t = Y_0 * e^{-kt}$, where Y_t is density at age t , Y_0 is initial density, k is the decay constant estimated by the regression procedure, and t is age). The decay constant represents the amount of material lost per unit of time; thus a larger constant represents faster decay. One problem with this model is that decay rates differ substantially between material suspended above the forest floor (e.g., by neighboring trees) and material in contact with the forest floor. Time spent suspended generally cannot be estimated for a given log.

If all material is considered together, the model is called a single exponential model. However, logs represent heterogeneous substrates (namely outer bark, inner bark, sapwood, and heartwood), each of which differs in concentration of lignin, cellulose, and nutrients. Decomposition times for these various substrates differ and multiple exponential models of decay may be necessary to accurately depict log decomposition (Schowalter 1992). When this approach is taken, overall decomposition is modeled as the sum of the decay of each component.

Decomposition also can be measured by monitoring a cohort of logs placed on the forest floor (e.g., Harmon and Sexton 1996) or by using a chronosequence (e.g., Harmon, Cromack, and Smith 1987). In a cohort study, subsamples of the logs are measured at given time intervals for density, insect activity, etc. Because the initial status of the logs is known and because the time frame is known, these studies provide the most reliable information on decay rates. Still, data are not available until several years have lapsed. Alternatively, a chronosequence study consists of comparing downed logs of different known age, with age estimated from time since treefall, stand age, dendrochronology, etc.

Means, Cromack, and MacMillan (1985) described a number of difficulties associated with using the chronosequence/retrospective approach. For example, when using this approach, the decay curve is typically inferred from a set of density values from logs of various ages. But the initial density is usually unknown for each log. Instead, an average density of sound wood of that species is used. But those density values are known to vary. For instance, coefficients of variation of 10% have been estimated for density of sound Douglas fir logs (*Pseudotsuga mensezii*). Residence times (i.e., the time since the bole has died) can be inferred in a number of ways, but one cannot know the length of time the log (or section of log) spent suspended above the forest floor. Estimates of residence times based on ages of nursed logs may be quite variable, especially because trees growing in shade may not form growth rings every year. Stand age may be confounded with residence time if older logs that fell earlier in stand development represent smaller trees or tree species that decay more rapidly than trees present in the current stand. Logs that decay rapidly may be lost to the study, resulting in an underestimate of average decay rates. Finally, interior tissues of larger logs may not be colonized by microbes for several decades, which could lead to underestimation of decay rates for that wood. Despite these difficulties, retrospective studies may be the only way to gain information on decay rates when data from earlier years are not available.

Another limitation of retrospective studies is that methods that estimate decomposition only from changes in wood density generally overlook the role of CWD fragmentation (Harmon and Sexton 1996). On the other hand, prospective studies can provide this and other information. For example, Harmon (1992) described a long-term log decomposition study at the Andrews Experimental Forest in Oregon designed to answer several important questions. In 1985, a total of 530 logs that were 45-65 cm diameter and 5.5 m long were placed in six old-growth forest sites. Logs were Douglas fir, Pacific silver fir, western hemlock and western red cedar. Physical and chemical characteristics of the outer bark, inner bark, sapwood and heartwood were determined. The study was designed with 18 sampling times over a 200-year period to test the specific hypotheses that: 1) decay resistance of heartwood is the principal factor behind the differences in decay resistance of different species; 2) time lags in colonization by decomposer organisms control decay rates and, thus, a single exponential decay model with decay slowing over time may not be appropriate; and 3) invertebrate boring into logs speeds microbial colonization. A portion of the logs were enclosed in insect excluding mesh to test the influence of insects on decay.

Because prospective and retrospective studies each have their relative merits for estimating CWD output rates, a method that combines the two may be advantageous. Harmon, Krankina, and Sexton (2000) have described a combined method: a chronosequence resampled after some time. This approach, which the authors termed “decomposition vectors,” appears to combine the convenience of a chronosequence study with the greater certainty of a prospective study.

2.7 Nutrient Content

Nutrient flux between CWD and soil is an important process. CWD may act as a nutrient source through mineralization or by hosting N-fixing organisms. CWD also may act as a nutrient sink by immobilization. Studies have quantified this flux by analyzing the nutrient content of logs by decay class in a chronosequence or by analyzing experimental logs in a time series.

Nutrient content of CWD (typically N, P, K, Ca, Mg, Mn, Na) is measured using standard analytic techniques (e.g., AOAC methods), and the resulting concentrations usually are expressed on a mass or volume basis (mg/g or mg/ml). Total quantity can be obtained by multiplying concentration by estimated total mass or volume. The concentrations themselves may be of interest for determining substrate quality, while the total quantity may be of interest for assessing the nutrient pool represented by CWD.

Decomposer or microbial activity also can be directly measured. For example, N-fixation has been assessed by acetylene reduction (e.g., Sollins et al. 1987). Measurements of microbial activity under varying temperature and moisture conditions in controlled environment chambers can discern the effects of environmental conditions on this aspect of nutrient flux.

Finally, CO₂ efflux has sometimes been measured to assess decomposition rates and evaluate the role of CWD in modifying atmospheric CO₂ content. One convenient way to measure CO₂ efflux in the field is by using a respiration chamber that contains a CO₂ trap (e.g., soda lime – see Marra and Edmonds 1996).

2.8 Recommendations for Sampling CWD

Given the importance of CWD to forest ecosystem processes, CWD quantities are sometimes specified in management goals. Thus, forest managers need a convenient measurement scheme that provides useful data. Such data collection also may help researchers better understand the role of species, site conditions, and management actions on CWD accumulation.

Planar intercept transects appear to be a fast and reliable method for collecting data related to downed log accumulations under a variety of conditions. A triangle of transects provides good coverage and generally can be established without too much difficulty around permanent sample quadrats or points. However, the length and number of such transects depends on the variability of the site, the precision of estimation required, and the resources available for the survey effort. A five-part classification scheme is quick and reliable for characterizing the decay class of downed logs encountered along transects. Although no one plan for sampling effort can be developed for all purposes, the use of consistent field methods and consistent units when measuring and reporting CWD (e.g., m³/ha) would facilitate comparisons across sites.

Permanent sample plots also should include counts and diameters of snags and live trees by species. Repeated surveying of sample plots on some regular cycle (annually, every 3 years, every 5 years, etc.) would provide useful data on dynamics. Again, the frequency of sampling would depend on the nature of the site (e.g., frequency, extent and intensity of disturbances) and resources available. Detailed studies of decay rates and nutrient flux are likely beyond the resources and the data requirements of routine sampling for forest monitoring.

Given the range of methods for studying CWD, studies can be designed from simple, one-time descriptions of CWD quantities to complete studies of CWD dynamics and nutrient flux. Detailed descriptions of methods are provided in the studies cited in the following sections.

3.0 INPUT RATES OF CWD

CWD originates from live trees or standing dead trees (snags) that fall apart or fall over. Obviously, stand structure has a major effect on CWD dynamics. However, to more adequately describe CWD dynamics, one must also describe the mechanisms that generate snags and that topple snags and live trees. Quantities of CWD reported in the literature are reported in Table 3.1.

In harvested stands, the slash and stumps from timber harvesting contribute to CWD. The type of harvest and subsequent site preparation activities determines the amount of CWD added to the forest floor and the amount of pre-existing (legacy) CWD left on the forest floor. For example, whole-tree harvests often create less CWD than other forms of harvesting.

Table 3.1 CWD Quantities Reported in the Literature by State/Province

State or Province	CWD Type	CWD Material	CWD Quantity ^a	CWD Size Class	Citation
NB	conifer	snags + logs	29.6 t C/ha		Fleming and Freedman (1998)
WI, MI	hardwood	snags + logs	11.3 t C/ha		Tyrell and Crow (1994a)
	Hardwood / hemlock	snags + logs	84-200 m ³ /ha	>10/20 cm dia	
IN, IL, IA, MO	oak/hickory	logs	1.8-28.3 Mg/ha	>20 cm dia	Spetich et al. (1999)
		snags	21.4 m ³ /ha	>10 cm dia	
		snags	11 pct of live stems		
IL	mesic forest	logs	60.3 m ³ /ha		Roovers and Shifley (1997)
		snags	99 snags/ha		
MO	oak	snags	2.5 m ³ /ha BA		Shifley et al. (1997)
		logs	81.2 m ³ /ha		
KY	beechn/maple	snags + logs	10 pct of live stems		
TN	maple forest	CWD	0-240 m ³ /ha	>20 cm dia	Muller and Liu (1991)
			0-120 Mg/ha		
			14.2 Mg/ha	>3 cm dia	
			19.3 Mg/ha	all	
VA	chestnut/oak and oak/hickory	snags	41 pct cover	all	Rosenberg, Fraser, & Stauffer (1998)
			0.8-2.2 pct cover	>4 cm dia	
			160 snags/ha	>3 cm dia	
NC	pine-hardwoods	snags + logs	7.7-15.7 Mg/ha	>7.5 cm dia	Vose et al. (1999)
SC	Piedmont	snags	20-35 snags/ha	>10.2 cm dia	Moorman et al. (1999)

(Table continued on next page. See note at end of table.)

Table 3.1 (Continued)

State or Province	CWD Type	CWD Material	CWD Quantity ^a	CWD Size Class	Citation
FL	pine plantation	Snags	10.6 snags/ha	>12.7 cm dia	Land, Marion, & O'Meara (1989)
AB	hardwood	snags	18-100 snags/ha	>9.1 cm dia	Lee (1998)
CO	Englemann spruce/sub-alpine fir	CWD	1-21 pct cover	>4 cm dia	Roovers and Rebertus (1993)
			142 snags/ha		
			19 snags/ha	>48 cm dia	
AZ	ponderosa pine	snags	5 snags/ha		Ganey (1999)
	mixed conifer		29 snags/ha		
AZ	pine/oak	snags	0-40 snags/ha	>30 cm dia	Rabe et al. (1998)
		logs	4-26 logs/ha	>25.5 cm dia	
BC	interior	snags	25-275 snags/ha	21-35 cm dia	Clark et al. (1998)
			20 snags/ha	>35 cm dia	
WA	subalpine forest	snags	5-51 snags/ha		Flanagan, Morgan, & Everett (1998)
WA, OR	various	snags	2.5-47 snags/ha	>28 cm dia	Ohman, McComb, & Zumravi (1994)
WA	subalpine	snags	57 snags/ha		Flanagan, Morgan, and Everett (1998)
WA, OR	various	snags	2-47 snags/ha		Ohman, McComb, & Zumravi (1994)
CA	various	snags	4-6 L snags/ha	>12.7 cm dia	Jimerson (1989)
			34-100 S snags/ha		
CA	various	snags	7-91	>8 cm dia	Morrison et al. (1986)
CA	mixed conifer	snags + logs	29-400 Mg/ha	>15 cm dia	Harmon, Cromack, & Smith (1987)
AK	various SE AK	snags + logs	1.5 -203 Mg/ha	>7.5 cm dia	Larson (1992)

^a Direct comparisons among study results are problematic due to varying definitions of CWD and different sampling methods.

Aside from harvesting, other factors such as shading, pathogens, fire, wind, ice, and drought can add to CWD by causing tree mortalities. The importance of these various factors varies by geography, stand age, stand composition, and other site factors. The interaction of these factors often results in substantial spatial and temporal variation in quantities of CWD, especially by decay class. Some of these disturbance factors are large-scale and infrequent (e.g., stand-replacing storms or fires), while others are small-scale and frequent (e.g., single tree deaths due to shading). In other words, snags and downed logs may be created in pulses or continually. Forests subject to small- and large-scale natural disturbances may be valuable comparison sites for the relative importance of these factors. However, efforts to study this issue are difficult because natural disturbance regimes have long been suppressed in many forests. Therefore, the role of gap phase dynamics and stand-replacing fires in generating CWD remains unclear in some geographic regions such as the southeastern U.S. (Van Lear 1996).

3.1 Sources of Tree Mortality and Effects on CWD Input Rates

Major disturbances that cause pulses of mortality and subsequent large inputs of CWD include ice storms (Rebertus et al. 1997), insect outbreaks (Fleming and Freedman 1998), and unusually strong windstorms (Roovers and Rebertus 1993; Onega and Eickmeier 1991). More frequent but less intense disturbances include lightning strikes, chronic pathogen incidence, and environmental stress (McCune, Cloonan, and Armentano 1988).

These sources of mortality exhibit strong spatial and temporal variation. For example, windthrow mortality may be more important on soggy, bottomland soils than on upland soils (McCune, Cloonan, and Armentano 1988). Mortalities and subsequent CWD inputs can be very localized, due to factors such as the death of a single, large tree. In one study, the death of one tree accounted for 75% of the CWD input over a 12-year period (Onega and Eickmeier 1991). Therefore, input data collected for only a few years at small spatial scales may not accurately reflect long-term averages over large areas.

3.2 Effects of Fire

Fires can have numerous effects on tree dynamics. Fires can kill large trees, thereby creating snags. On the other hand, fire can consume snags and down wood. Fires also can thin a stand, thereby reducing mortalities in some size classes of trees. From the opposite perspective, suppression of fire can increase stem exclusion, thus increasing inputs of small diameter CWD (Spetich et al. 1999). Fire can increase recruitment of snags, especially in combination with drought, but can also increase decay rates of snags (Morrison and Raphael 1993).

The effects of a specific fire on CWD dynamics depend on the intensity of the burn, which depends on fuel, weather, and the history of fire in the forest. The effect of the fire on a specific snag or live tree also depends on the characteristics of that tree. For example, Horton and Mannan (1988) found that loss of snags depended on decay class and on the diameter of the snags, with a greater loss for larger snags. If larger trees survive the fire but smaller ones are killed, the size class distribution will shift to more but smaller snags (Horton and Mannan 1988). The authors recommend that plans for prescribed fires incorporate methods for retaining snags and downed CWD. Specifically, in forests in which the silvicultural treatments have reduced snag abundance, they recommend that fuel breaks be created around snags of each decay class to prevent snag loss during the burn.

Reported responses of CWD to fire have been highly variable. Fires added CWD in a jack pine forest (Niemuth and Boyce 1998), but mass of downed logs remained similar after a fire in a pine-hardwood forest in the southern Appalachians of North Carolina (Vose et al. 1999). Differences in fire history were cited as a factor in differences in CWD inputs in the Pacific Northwest (Spies,

Franklin, and Thomas 1988). Specifically, CWD volume generally was greater in Washington and Oregon Cascades sites than in Coastal Range sites, although some of the smallest values for CWD in old growth (74 Mg/ha) were observed on six sites in the Oregon Cascades. These regions have different fire histories, partly due to moisture regimes. Topographic position and aspect also affected CWD quantities, perhaps due to combined effects of moisture regime and fire frequency.

3.3 Effects of Tree Species, Tree Size, and Forest Type on Tree Mortalities and Snag Persistence

Tree species differ in mortality rates, in the time period they persist as snags, and in their susceptibility to different forms of disturbance (Moorman et al. 1999; Goodburn and Lorimer 1998; Raphael and Morrison 1987). For example, Lee (1998) found that paper birch snags did not persist as long as snags of other species in boreal forests. Raphael and Morrison (1987) found that pine snags decayed more rapidly than fir snags in the Sierra Nevada Mountains of California. Specifically, a greater proportion of fir snags remained in decay Class I and II than did pine snags (Figure 3.1). Across all tree species, recruitment rates averaged 4.2 snags/ha/yr and snags fell at an average rate of 1.4 snags/ha/yr. Thus, the snag population was increasing, mainly in smaller diameter Jeffrey pine. Mortalities of Jeffrey pine were greater than for other species primarily due to Jeffrey pine beetles. A Leslie matrix population model predicted an increase of CWD for about 100 years, after which CWD was projected to reach a steady state. However, the authors noted that the assumption of constant transition probabilities was not realistic.

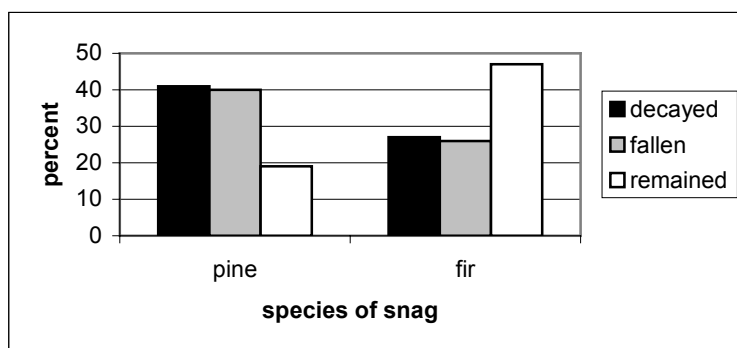


Figure 3.1 Fate of Class I and II Snags after 5 Years in the Sierra Nevada (data from Raphael and Morrison 1987). (“Decayed” refers to conversion to Class IV or V snags; “remained” refers to snags remaining in Class I or II.)

Size of tree also affects mortality. Small diameter trees may have greater mortality rates than large diameter trees (Runkle 1991). However, there also may be a minimum size threshold beyond which mortality rate begins to increase with diameter (Volk and Fahey 1994).

As a result of differences among tree species (and also due to site effects), snag populations (e.g., species composition, densities, volume) can vary widely among different cover types. In old-growth hardwood/hemlock forests, mortality rates were lower for hemlocks than for yellow birch, but hemlocks were more susceptible to uprooting (Tyrrel and Crow 1994a). Stands with hemlocks had greater snag densities than did hardwood-only stands (Goodburn and Lorimer 1998). Because yellow birch snags are persistent, the proportion of yellow birch snags can be greater than their proportion of live trees. In maple/beech forest, short-lived trees such as black cherry, basswood, aspen, and birch had mortality rates greater than 70%, while hemlock, beech, sugar maple, and white ash had mortality rates less than 60% (Volk and Fahey 1994).

In Arizona, median snag densities ranged from 5 snags/ha in ponderosa pine to 29 snags/ha in Douglas fir/white fir/mixed conifer stands (Ganey 1999). Interestingly, the authors reported that few of their unlogged sites met the U.S. Forest Service recommendations for snags, suggesting that USFS snag retention policies may be overly stringent. In another study in Arizona, Rabe et al. (1998) reported that ponderosa pine/grassland sites had more snags (2 snags/ha) and more downed logs (6.3 logs/ha) than ponderosa pine/gambel oak stands (1 snag/ha, 4 logs/ha).

In South Carolina Piedmont forests, more snags occurred in upland hardwood (35.6 snags/ha) and cove hardwood (31.9 snags/ha) than in pine hardwood (28 snags/ha) or in pine plantations (20.2 snags/ha) (Moorman et al. 1999). Snag densities generally were highest in young or intermediate-aged stands within each forest type in the latter study.

In the Sierra Nevada Mountains of California, CWD mass (logs and snags) varied widely among forest types (Harmon, Cromack, and Smith 1987), ranging from 29 Mg/ha on Jeffrey pine sites to 400 Mg/ha on riparian giant sequoia sites (Figure 3.2). Snags accounted for varying amounts of the CWD: 2.4% of the CWD mass on Jeffrey pine sites, 4% on giant sequoia sites, and 25 to 57% on concolor fir sites. The very large amount of CWD on the riparian giant sequoia site was due mainly to giant sequoia logs. These results illustrate the influence of forest type and stand characteristics on input and output rates. For example, the low productivity and higher decay rates of Jeffrey pine likely led to low CWD accumulation in that forest type.

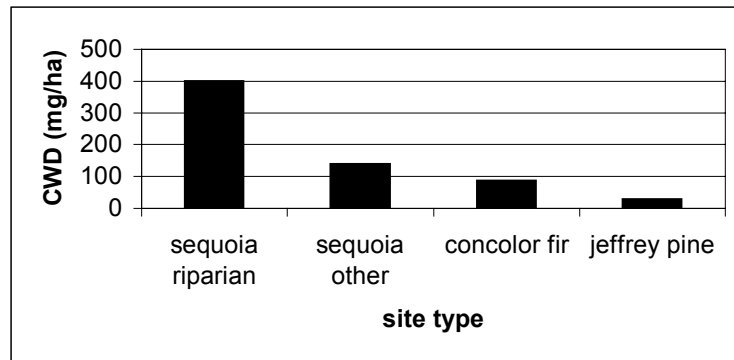


Figure 3.2 CWD Mass (Snags + Downed Logs) across Site Types in the Sierra Nevada (data from Harmon, Cromack, and Smith 1987).

In southeast Alaskan forests, CWD accumulation ranged from 1.5 Mg/ha in shore pine/crowberry sites to 151 Mg/ha in western hemlock-red cedar/blueberry sites (Larson 1992). Type of CWD varied among sites as well. All of the logs in western hemlock/Alaska cedar plots were rotten, but none of the logs in shore pine/crowberry stands were. Cutover western hemlock/Alaska cedar stands averaged 203 Mg/ha of downed logs, while old-growth stands of the same forest type averaged 55 Mg/ha. Approximately 60% of logs were rotten in both groups.

Snag densities varied widely with forest type on a large range of sites in Washington and Oregon (Ohman et al. 1994). The lowest density of snags was in old growth ponderosa pine sites (2.5 snags/ha); the greatest density of snags was in the oldest age-class temperate coniferous forest (47 snags/ha).

In northern California, snag density was greatest in Shasta red fir stands, and least in tan oak/Douglas fir stands (Jimerson 1989) (Figure 3.3). Moisture likely differed among sites. Snag composition generally followed a shade tolerance gradient; Douglas fir accounted for most snags overall (36%) followed by white fir (29%).

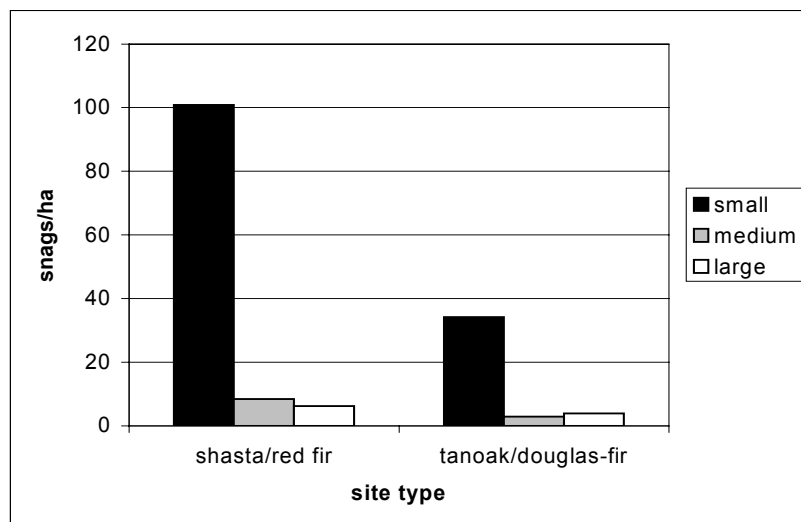


Figure 3.3 Density of Different Snag Size Classes across Site Types in Northern California (data from Jimerson 1989)

In summary, the recruitment of trees into snags and the persistence of the snags clearly varies by species and, therefore, by cover type. Species differ in longevity, size at maturity, susceptibility to mortality agents, decay resistance, and other factors that determine the likelihood of dying or toppling. For example, in northern mixed forests, some species are known as snag formers (e.g., yellow birch) while others are known as topplers (e.g., eastern hemlock). Forest managers should understand these inherent differences among tree species and the factors that influence CWD dynamics (e.g., disturbance regimes, weather patterns), and stand descriptions and management guidelines should take these differences into account.

3.4 Effects of Site Productivity and Stocking on Tree Mortalities

Site productivity affects CWD by controlling species composition, the volume potential, the size of trees, and the rate of self thinning (Sturtevant et al. 1997). The rates of tree mortality and snag creation typically increase with productivity and stocking rate due to increased stem exclusion (Volk and Fahey 1994; Spetich et al. 1999). Trees not only grow faster on a high productivity site, but also can achieve higher stocking rates, thereby accelerating the rate of snag creation. For example, a high-quality balsam fir stand in Newfoundland would produce 8-cm diameter CWD 48 years after disturbance, while a low-quality site would require 78 years (Sturtevant et al. 1997).

More and larger snags and downed logs were found on high productivity sites than on low productivity sites in old-growth stands in Indiana, Illinois, Iowa, and Missouri (Spetich et al. 1999). Total dead wood volume was well correlated with potential productivity. Size of CWD also varied by productivity, with maximum downed log volume in the 45- to 65-cm diameter class on the highest productivity site, but in the 25- to 45-cm diameter class for the lowest productivity site.

Stocking rate appears to be positively related to tree mortality. For example, in maple/beech forests in New York, mortalities were greatest (63%) in an uncut plot and lower in plots that received timber improvement cuts 53 years earlier (Volk and Fahey 1994). The lowest mortalities (38%) were in the stand with the lowest initial stocking rate (Volk and Fahey 1994).

3.5 Effects of Stand Age

Stand age affects tree mortality and snag retention due to tree aging and structural and compositional changes associated with succession. For instance, in chestnut-oak and oak-hickory forests in southwestern Virginia, the proportion of larger diameter snags increased with age (Rosenberg, Fraser, and Stauffer 1988). However, total snag density remained similar across age classes (160 snags/ha), probably because large snags persist longer than small snags.

In midboreal hardwood forests in Alberta, total snag densities were greater in stands ≥ 40 years old compared to younger stands (Lee 1998). Snag densities were 18 snags/ha in 20- to 40-year-old stands, and 62-100 snags/ha in older stands. No differences in snag density were apparent among stands 40, 60, 80, and 100+ years old. As stands aged, snag species shifted from quaking aspen and balsam poplar to white spruce and paper birch. Size of snags changed with stand age, too, with more small snags in younger stands. As mortality switched from self-thinning to deaths of canopy trees, the size distribution of snags approached that of live trees. Snag input rates increased steadily with stand age, but rates of snag fall down generally declined with stand age up through 80-year-old stands, then increased with further stand development.

The sizes of snags varied by stand age in interior spruce, subalpine fir, and lodgepole pine stands in west central British Columbia (Clark et al. 1998). Across all stand ages, smaller snags (6-20 cm diameter) were most common. The abundance of moderately-sized snags (21-35 cm diameter) declined with age to 100-year-old stands, but then increased with age (Figure 3.4). The oldest stands had more large snags (≥ 36 cm diameter) than did other ages of stands (20 snags/ha in stands 200 years old). Although a general pattern was apparent, snag quantities varied widely within age groups. For example, snag density ranged from 78-500 snags/ha in stands 124 and 127 years old.

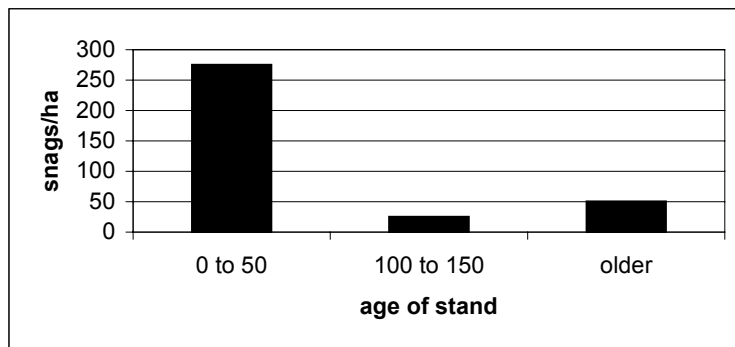


Figure 3.4. Density of Moderately Sized (21-35 cm Diameter) Snags in Stands of Different Ages in West-Central British Columbia (data from Clark et al. 1998)

Snag recruitment increased then decreased with stand age in a subalpine forest in central Washington (Flanagan, Morgan, and Everett 1998). Dominant species were white bark pine, subalpine larch, subalpine fir, mountain hemlock, and silver fir, depending on site. Snag density increased up to the understory reinitiation stage (average of 42 snags/ha for dominant and codominant trees and almost

15 snags/ha for intermediate-suppressed trees) then declined to old-forest stage. Large-scale disturbances were not common (i.e., very little logging and no fires for at least 100 years). The greatest agent for tree mortality was weather-related removal of crowns by snow, wind, or ice. Root disease, bark beetles, and suppression were other common causes of mortalities. Cause of mortality affected snag longevity; trees killed by weather remained standing longer than those killed by pathogens.

The time trend for snag abundance varied by forest type on a range of sites in Washington and Oregon (Ohman et al. 1994). Density of snags increased with stand age in conifer-hardwood forests (2.1 snags/ha in youngest stands to 12 snags/ha in the oldest stands) and temperate conifer forests (2.9 snags/ha in youngest stands to 47 snags/ha in oldest stands). However, in temperate conifer forests, snag density declined at the open sawtimber age. For ponderosa pine and mixed conifer forests, there was no consistent pattern between snag density and stand age. But for both forest types, snags were most abundant in the oldest stands. In part, snag density differed among stand ages because all snags in the youngest forest stands were remnant and the number of remnant snags depended on disturbance history. Large snags were not recruited until stands reached large sawtimber or mature stage. Ohman et al. (1994) considered snag densities on this site inadequate to meet habitat requirements for cavity-nesting species.

In northeastern Wisconsin and northern Michigan, snags generally declined in density, basal area, and volume with age of old-growth hardwood-hemlock forests (Tyrell and Crow 1994a). However, total CWD accumulation increased with stand age (stand ages ranged from 193-358 years). Total volume of CWD increased linearly with stand age from 84.5 m³/ha in the younger stands to 200 m³/ha in stands 150-200 years old. Hemlock CWD volume increased with stand age but not all species did. Downed log mass increased with stand age from 1.8 Mg/ha in younger stands to 28.3 Mg/ha in older stands. Advanced decay classes of logs became more common with increased stand age.

Part of the effect of stand age observed by Tyrell and Crow (1994a) was due to successional differences. Paper birch and white pine were the major snag species in younger stands and yellow birch was the most common snag species in older stands. Hemlock snags increased in basal area with stand age. White cedar and balsam fir were present as snags in all ages of stands. Hemlock accounted for a greater proportion of downed logs in older stands than in younger stands, approaching the relative area of hemlock in the live tree basal area. The steady increase in CWD volume may have been related to increased size of hemlock with stand age.

In summary, there is no consistent relationship between snag creation/retention and stand age for all forest types or stands. Species and site characteristics interact to control the temporal patterns of mortalities and snag persistence. Managers must assess these factors on a site-specific basis when trying to understand or predict the temporal pattern of snag recruitment or loss.

3.6 Spatial Variability in CWD Input

The factors that determine snag creation and snag and tree fall vary spatially as well as temporally. This variation in factors that create CWD has important implications for CWD dynamics in the landscape and associated wildlife species. Some wildlife species actually may benefit from a patchy distribution of snags and logs. Intensity of sampling for CWD also must consider the degree of spatial variation. For example, a high degree of spatial variation necessitates a large sample size to obtain desired confidence intervals for means.

A large degree of spatial variation in CWD has been reported in several studies, but only a few studies have focused specifically on quantifying the degree of spatial variability or its causes. Land,

Marion, and O'Meara (1989) found strong, small-scale variability in snag abundance in a pine plantation on a pulpwood rotation. Twenty-five percent of all snags occurred in clusters (mean cluster size was 4.4 snags). Land, Marion, and O'Meara (1989) attributed these clustered mortalities to beetle attacks.

Muller and Liu (1991) noted that in an old-growth forest in the Cumberland Plateau of southeastern Kentucky, spatial variation in CWD dynamics reflected gap dynamics. Mean CWD volume was 66.3 m³/ha (21.8 Mg/ha), but the distribution of CWD was very patchy. Most plots contained very little CWD and 10 of the 80 plots contained almost 40% of the total CWD observed. Most CWD (68%) was in decay Class I or II and species composition of CWD matched that of the canopy. One artifact of older disturbance was apparent, though. American chestnut contributed 11% of CWD even though no live trees >10 cm diameter were present, reflecting its low rate of decomposition and former dominance in the canopy.

Morrison et al. (1986) observed strong spatial variation in snag abundance in forests near Tahoe, California. Snags were most abundant near water and natural openings. Site type, which varied across the landscape, also affected snag density. Density of snags at least 8 cm diameter ranged from 6.8 snags/ha in Jeffrey pine stands to 81 snags/ha in red fir/white fir stands.

Spies and Cline (1988) reported that up to half of the total CWD across an area may be concentrated in less than one-fifth the area. This patchy distribution of CWD may arise from the patchy distribution of the large trees that contribute large quantities of CWD and the patchy distribution of tree mortalities. For example, wildfires often burn in patches of varying intensity.

3.7 Summary

The rates at which snags and downed logs are created vary by tree species and age, which in turn are influenced by site characteristics (e.g., growth potential, frequency and intensity of disturbances). Therefore, the rates at which snags and downed logs are created vary widely from site to site and small scale spatial variation is generally apparent. Any descriptions of CWD inputs must be site-specific.

4.0 OUTPUTS OF CWD

The major CWD output processes are decomposition (carbon mineralization) and fragmentation. Decomposition is driven by microbial activity, the rate of which depends upon temperature, moisture, and substrate quality (e.g., C:N ratio). Decomposition rates are generally expressed as percent of density or total mass loss over time, as a rate constant in an exponential decay equation, or as a half-life (see Section 2).

Differences in decomposition rates related to temperature and moisture regimes can be seen by comparing CWD losses across geographic areas. Of course, because geographic areas also differ in tree species, some of the geographic differences may be related to substrate quality. Thus, geographic differences are most easily seen when comparing decay rates among regions for the same species. Substrate differences are best illustrated by differences in decay rates of different species within geographic areas. Decay rates would be expected to increase with growing season temperature and moisture availability, but rates may be relatively slow in very moist conditions due to decay resistance of dominant trees (e.g., Douglas fir in the Pacific Northwest or eastern white cedar in a Michigan swamp). Overall summaries of decay rates are presented in Table 4.1.

Table 4.1 Reported Decomposition Rates

State/ Province	Forest Type	Decomposition Rate	Citation
AB	lodgepole pine/Eng. spruce	23 to 200+ yr half-life depending on site	Johnson and Greene (1991)
BC	Douglas fir	32 yr half-life	Stone et al. (1998)
BC	lodgepole pine	3 to 170+ yr half-life depending on site	Wei et al. (1997)
CA	mixed conifer	14 yr half-life	Harmon, Cromack, & Smith (1987)
CO	lodgepole pine/Eng. spruce	40 pct volume remaining after 140 yr	Brown et al. (1998)
IL	silver maple	8 yr half-life	Cheung and Brown (1995)
IN	beech/maple	48 to 60 yr half-life depending on species	MacMillan (1988)
LA	river basin	8 to 13 yr half-life	Rice et al. (1997)
MI, WI	hemlock/hardwood	33 yr half-life	Tyrrel and Crow (1994b)
MN	aspen/spruce/pine	9 to 16 yr half-life depending on species	Alban and Pastor (1993)
NC	various Appalachian	8 to 9 yr half-life	Mattson, Swank, & Waide (1987)
NH	maple/yellow birch/beech	7.2 y half-life	Arthur, Tritton, & Fahey (1993)
NY	sugar maple/beech/hemlock	40 to 80% mass remaining after 2 yrs	Sinsabaugh et al. (1992)
OR	Douglas fir	82 yr half-life	Means, MacMillan, & Cromack (1992)
OR	lodgepole pine	26 yr half-life	Busse (1994)
OR, WA	Douglas fir	24 yr half-life	Spies, Franklin, & Thomas (1988)
OR, WA	Douglas fir, w. hemlock	70 to 77 yr half-life	Sollins et al. (1987)
TN	sugar maple	6 to 11 yr half-life	Onega and Eickmeier (1991)
WA	various	20 to 77 yr half-life depending on species	Erickson, Edmonds, & Peterson (1985)
WA	w. hemlock/Douglas fir	3 to 4 g CO ₂ /m ² /d	Marra and Edmonds (1994, 1996)

4.1 Decay Rates in Midwestern and Northeastern U.S. Forests

Warm summers and adequate moisture availability yield relatively fast decomposition rates for CWD in the midwestern and northeastern U.S. For example, decay rates of CWD were rapid in a New Hampshire maple/yellow birch/beech forest (Arthur, Tritton, and Fahey 1993). Total CWD mass declined by 89% of the original mass by 23 years post-cutting. This decline represents a half-life of 7.2 years and a decay constant (k) of 0.096 per year. Decomposition rates varied by species. Beech decayed most rapidly followed by maple, yellow birch, and ash (which decayed slowest). Wood densities for the various decay classes of the 23-year-old downed boles also indicated this rapid decay rate. The largest drop in density (a 50% decline) was from living to decay Class I boles. Density continued to decline steadily and the most decayed class (i.e., Class IV) had only about one-sixth the density of living boles. This loss of density was consistent across species.

Decay rates were slower for old-growth hemlock/hardwood forests in northern Michigan and northern Wisconsin (Tyrrel and Crow 1994b). The decay rate for downed hemlock logs was $k = 0.021$ (33 yr half-life). Site-to-site variation suggested that origin of logs controlled decay rate. Decay rates were slower on a site where most downed logs originated from blowdown ($k = 0.012$), compared to the other sites where downed logs may have been partially decayed as snags before falling. Downed logs took 30 to 48 years to convert from Class I to Class V, with longest times required for the conversion from Class II to III (Figure 4.1). Hemlock logs took up to 200 years to lose structural definition.

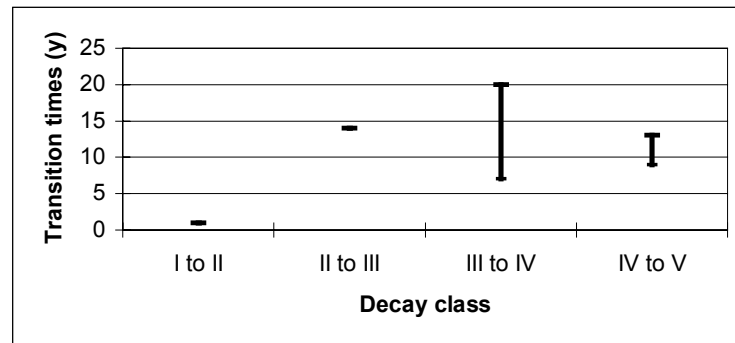


Figure 4.1 Transition Times for Logs in Old-Growth Hemlock/Hardwood Forests in Northern Michigan and Northern Wisconsin (data from Tyrrel and Crow 1994b). (Figure represents reported ranges of values for Class III to IV and IV to V; Class I to II and II to III are single data points.)

CWD decayed rapidly in central Illinois bottomlands (Cheung and Brown 1995). Silver maple logs (the dominant canopy species) lost 25% of their initial mass after 3.5 years of decomposition. Bark decomposition accounted for most of this loss. Only minor losses of sapwood or heartwood occurred. All bark that was rotten at the beginning of the study had decomposed by the end of the 1.5-year study. Decomposition rate of whole logs was $k = 0.089$. Leaching and respiratory losses accounted for most of this loss. Fragmentation accounted for only about 10% of the loss, as suggested by the lack of invertebrate activity observed on the logs.

In western New York, decomposition rates of paper birch wood varied from site to site in sugar maple/beech sites and hemlock sites (Sinsabaugh et al. 1992). Decomposition rates were much slower on riparian sites than upland sites (Figure 4.2), and were not steady year to year. Instead, a time lag was apparent in which decomposition rates remained low for a few years, then increased.

In Indiana, decay rates varied by species in an old-growth oak/hickory/maple/beech forest (MacMillan 1988). Beech was much more persistent than maple (Figure 4.3)

Decomposition also varied by species in coniferous forests in Minnesota (Alban and Pastor 1993). Fourteen years after felling, quaking aspen, white spruce, red pine, and jack pine retained their bark and shape but became soft and crumbly. No roots were present in the 14-year-old downed logs. Decomposition rates were slowest for jack pine and fastest for aspen (Figure 4.4). Decay rates did not vary by initial diameter or initial chemical composition of boles.

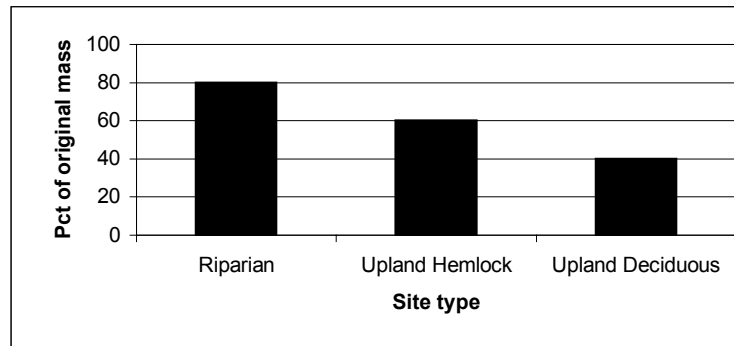


Figure 4.2 Decomposition of Paper Birch Wood in Sugar Maple/Beech Sites and Hemlock Sites in Western New York (data from Sinsabaugh et al. 1992). (Values represent percent of original mass remaining after 24 months.)

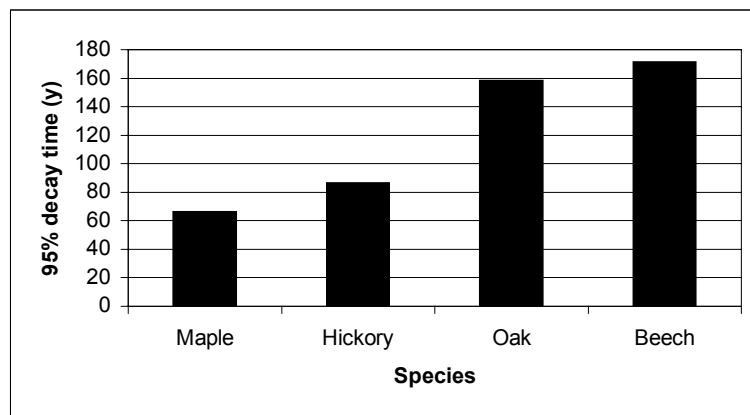


Figure 4.3 Decay Rates in an Old Oak/Hickory/Maple/Beech Forest in Indiana (data from MacMillan 1988). (Data represent time required for 95% loss of material.)

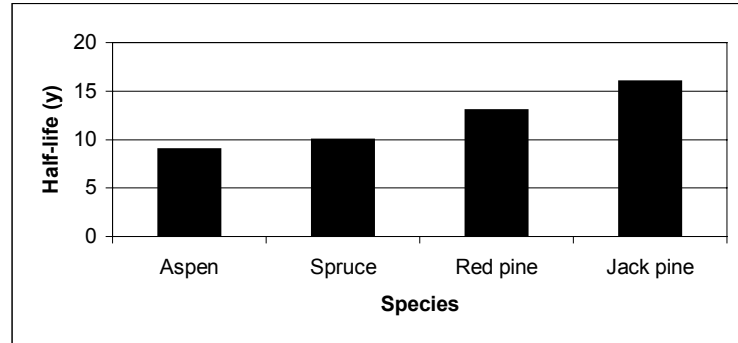


Figure 4.4 Decomposition (Half-Life) of Various Species in Coniferous Forests in Minnesota (data from Alban and Pastor 1993)

4.2 Decay Rates in Rocky Mountain Forests

Moisture conditions may not be as optimal for decomposition in montane forests of the Rocky Mountains compared to the central and western U.S. Some Rocky Mountain forests tend to be quite dry in the summer, while others are cool and moist.

In Alberta, snags and downed logs decayed slowly in lodgepole pine/Engelmann spruce stands (Johnson and Greene 1991). In fact, snags did not decline in mass over time, but downed logs did. Decay constants for downed lodgepole pine boles decreased with stand age, ($k = 0.017$ and $k = 0.0299$ on 58-year-old sites versus $k = 0.0035$ on a 222-year-old site). Engelmann spruce decayed more rapidly than lodgepole pine.

The low decay rate of snags reported by Johnson and Greene (1991) may have been due to their low moisture content (<20% of dry weight). Because snags decayed so slowly on these sites, falldown rates were constant with snag age rather than increasing with decay over time. Lower decomposition rates of CWD in the older sites may have been due to generally cooler conditions on the floor of an older stand and a shorter snow-free period. Fallen boles may have been too moist for rapid decomposition in these cool conditions. Diameter of fallen boles did not seem to affect decomposition rate.

Source of CWD may affect decay rates in Rocky Mountain forests. Windthrown logs decayed slowly in lodgepole pine/Engelmann spruce forests in Colorado (Brown et al. 1998). After 140 years, 40% of the original wood volume was still present. This slow rate of decomposition may have been due to rot resistance of lodgepole pine (i.e., many resin ducts and heartwood high in polyphenols) and the initial sound condition of logs in the study (i.e., death was due to toppling, not rot).

4.3 Decay Rates in Southeastern U.S. Forests

Relatively fast decomposition rates would be expected in the warm, moist conditions of southern forests. Decomposition rates for CWD were relatively fast in a sugar maple forest in the Blue Ridge Mountains near Nashville, Tennessee (Onega and Eickmeier 1991). Snag and downed log decomposition rates (k) were 0.062 and 0.11, respectively, representing half-lives of 11.2 years and 6.3 years, respectively.

In southern Appalachian forests of North Carolina, decomposition rates for downed logs also were rapid over a six-year period (Mattson, Swank, and Waide 1987). Hardwood-hemlock, oak-hickory, and hardwood-pine sites were clearcut with most of the biomass left in place. Wood density declined rapidly ($k = 0.083/\text{yr}$ for downed logs, $k = 0.077/\text{yr}$ excluding bark). No fragmentation of wood was observed; thus, all of the loss was attributed to density loss (i.e., CO_2 efflux and dissolved organic C). CO_2 efflux was 2,715 kg C/ha/yr and was greatest in the summer. Dissolved organic carbon flux was 147 kg C/ha/yr. Thus, C loss clearly accounted for most of the density loss. Loss rates varied by species, degree of ground contact, and occurrence of fungi.

In Louisiana, CWD left by Hurricane Andrew in the Atchafalay River Basin also decayed rapidly (Rice et al. 1997). Yearly decay rates of pumpkin ash logs were $k = 0.05$ to 0.081 , and varied with ground contact and level of damage (Figure 4.5). C loss closely matched the loss of density.

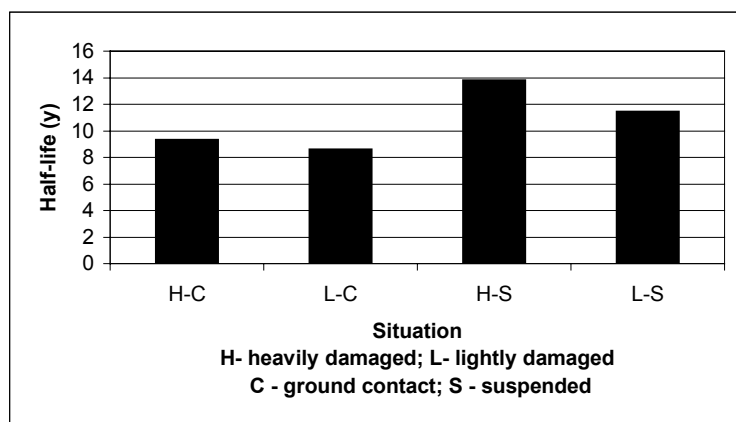


Figure 4.5 Decomposition (Half-Life) of Pumpkin Ash Logs Downed by Hurricane Andrew in Louisiana (data from Rice et al. 1997)

Snags fell apart rapidly in loblolly pine and shortleaf pine plantations in southeastern Arkansas (Cain 1996). Fragmentation rates were greatest in stems <10 cm dbh ($k = 0.76$) and lowest in larger dbh snags ($k = 0.05$). Sixty percent of snags still retained small branches in the crown two years after death. But after an additional year, no small branches were left in the crowns of snags. By three to six years after death, 90% of snags were classified as being in advanced decay.

Decay rates were slow in a sugar maple/red oak/basswood/magnolia forest in the Alleghany Plateau of western Maryland (McCarthy and Bailey 1996). Most downed logs and snags were in decay Classes IV and V with red oak and black locust over-represented as snags and logs compared to their proportion in the canopy. The authors suggested that this nonequilibrium of the canopy and CWD was due to a moderate, stand-wide disturbance in the 1800s and the slow decay rate of old logs.

Fresh oak bolts decomposed faster than fresh pine bolts over an 18-month period in the South Carolina Coastal Plain (McMinn 1998). Oak lost 22% of its original density after 18 months, but pine lost only 10% (bolts were 20 to 30 cm dia). For pine bolts, decomposition decreased with increasing size. Density losses were 28% for the 4-6 cm class, 10% for the 20-30 cm class, and 20% for the 40-50 cm class. No differences in decomposition rates were detected between xeric, mesic, and hydric sites.

Porter et al. (1998) examined bacterial community composition and total bacteria numbers for the initial 16 weeks of decomposition of the oak and pine logs under the three moisture regimes. They

found increased numbers of bacteria over the 16-week time period, but were unable to find any differences in bacterial community composition or numbers between the three moisture regimes. In another aspect of this study, Tainter and McMinn (1999) examined changes in the chemical decomposition of heartwood and sapwood in the pine and oak bolts. In both species, nonstructural carbohydrate concentrations declined over the 16-week period, but structural carbohydrates (cellulose, hemicellulose, or holocellulose) did not nor did wood density. Moisture content declined more rapidly on the drier sites and sapwood dried more quickly than heartwood. Fungi increased over the 16-week period.

Tiarks et al. (1999) reported initial results of a time-series study of decomposition and C and N flux of loblolly pine boles across several sites in the South. Boles 16-37 cm diameter were placed in sites under three intensities of harvest and soil compaction. Over the initial six months of the study, logs had lost 14.6% of their original mass. No differences in decomposition rate, N flux, or C flux were found among the sites. Cumulative C loss through log leachate was 13 g/m² over the 6 months; N loss was 0.27 g/m². Bark beetles occupied the logs within 1 month and wood borers were found 2-3 weeks after placement. Within 6 months, fungi reached the heartwood via the beetle and borer tubes, and termites followed the fungi.

4.4 Decay Rates in U.S. Pacific Northwest and British Columbia Forests

Decomposition and nutrient flux of CWD have been studied extensively in the U.S. Pacific Northwest and British Columbia. Perhaps one reason for the large number of studies is the tremendous accumulation of CWD under natural conditions and the potential impact on this “detrital capital” of some forest management practices. Generally, decomposition rates in the Pacific Northwest and British Columbia are slow. However, widely varying decay rates have been reported, depending on species, temperature, moisture, log size, and log decay class.

4.4.1 Species and Site Differences

Decay rates in the Pacific Northwest and British Columbia vary widely among tree species and sites. In the Sierra Nevada Mountains of California, downed concolor fir logs decayed at a moderate rate in the mixed-conifer forests of the Sequoia National Park (Harmon, Cromack, and Smith 1987). A chronosequence of windthrown logs lost density at a rate of $k = 0.049$, which translates to a half-life of 14 years with 95% of the original mass disappearing by 61 years. Fragmentation apparently was not a major pathway of wood loss during this initial period because volume did not decline appreciably for the first 24 years of decay. Although bark did not decay for the first 8 years, it did fragment rapidly in subsequent years and was mainly gone after 26 years. Decay rates did not differ with log diameter, but appeared to decline with increased annual precipitation.

Harmon, Cromack, and Smith (1987) provided extensive details about the decay process. The decay sequence for concolor fir was in this order: needles fell off, twigs fell off, branches fell off, bark fell off and ants invaded, sapwood became friable, parts of log collapsed and settled to forest floor, heartwood became friable, pieces of wood sloughed off, and cross section became elliptical. The decay continuum was similar for Jeffrey pine, but wood density did not decline with age because its wood sloughed off as it decayed. Only at decay Class IV did decay overtake the remaining wood.

Harmon, Cromack, and Smith (1987) also provided information about the organisms that contributed to decay of CWD. They found that insect excavations increased with log age, with little excavation in logs <6 years old and about 0.7% of the logs excavated per year after that. Insect excavation increased with decay class until Class III. After that point, no insect galleries were seen in Class IV logs (although it would have been difficult to observe galleries due to fragmentation and collapse of the wood). Decomposer organisms moved into logs at about 1 cm of radius per year.

Reported decay rates for Douglas fir have been variable. In Oregon and Washington, decomposition was slow ($k = 0.029$) on moist sites dominated by Douglas fir (Spies, Franklin, and Thomas 1988). In Oregon, Means, MacMillan, and Cromack (1992) also found slow decay rates with a half-life for Douglas fir logs of 82 years ($k = 0.006$ to 0.007). Total biomass per log declined 98% from Class I to Class V, with a 75% loss between Class II and III (the largest drop between consecutive age classes). Wood density declined only by 50% from Class I to Class V, with the largest decline from Class I to Class II (a 25% loss). Time spent in decay classes became progressively longer, and was as long as 219 years in Class V (Figure 4.6). High water content, high C:N ratios, and antidecay compounds in the logs all led to these slow decay rates. C:N ratios started at 620 for logs in decay Class I and dropped steadily to 244 for decay Class V.

Decomposition was much faster in a 90-year-old Douglas fir forest on southern Vancouver Island, British Columbia (Stone et al. 1998). The mean decay constant for all logs was $k = 0.022$. The decay rate decreased with diameter (from $k = 0.067$ for logs <20 cm diameter to $k = 0.012$ for logs >80 cm diameter), and for length classes (from $k = 0.033$ for logs ≤ 3 m long to $k = 0.019$ for logs >9 m long). Decay constants also increased with decay class (Figure 4.7). Because of this rapid decay, only 38 of 186 logs mapped in an initial survey remained after 65 years of decay. Most logs designated at the beginning of the study as rotten and logs that were <20 cm diameter had disappeared by the final survey taken 65 years later.

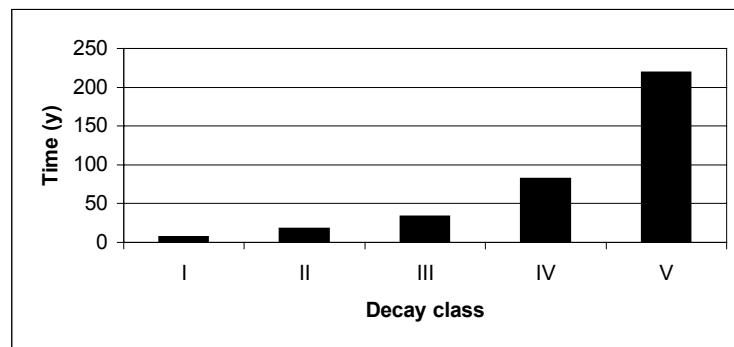
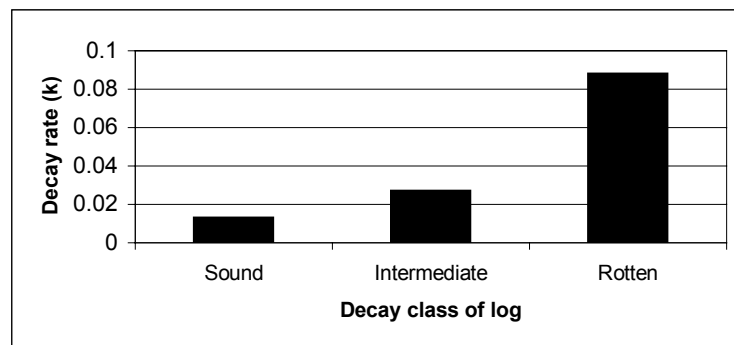


Figure 4.6 Time in Each Decay Class for Douglas Fir Logs in Oregon (data from Means, MacMillan, and Cromack 1992)

Figure 4.7 Decomposition Rates (k) of Douglas Fir Logs in Southern Vancouver Island, British



Columbia (data from Stone et al. 1998)

Decay rates varied by species in old Douglas fir and western hemlock stands in the Cascade Range of western Oregon and Washington (Sollins et al. 1987). Although each species had about the same density for a given decay class, they differed in the time required to reach that decay class. Western hemlock logs reached decay Class III 25 years sooner than Douglas fir and 5 years sooner than western red cedar. Part of this difference among species may have been because western red cedar logs remained suspended above the forest floor longer than the other two species. Nearly all Class II western red cedar logs were still suspended, but most Class II logs of other species were on the ground. All Class V logs found were Douglas fir and all Class V logs were entrenched. Decomposition coefficients differed among species with Douglas fir decaying fastest and western red cedar slowest (Figure 4.8). For all species, sapwood began to decay almost immediately, reaching a density of 0.10 g/ml by decay Class III, at which time the sapwood began to slough off.

Western hemlock also decayed more rapidly than Douglas fir in the Olympic Peninsula of Washington (Marra and Edmonds 1994, 1996). CO₂ loss (“log respiration”) was 4 g CO₂/m²/day for western hemlock and 3 g CO₂/m²/day for Douglas fir).

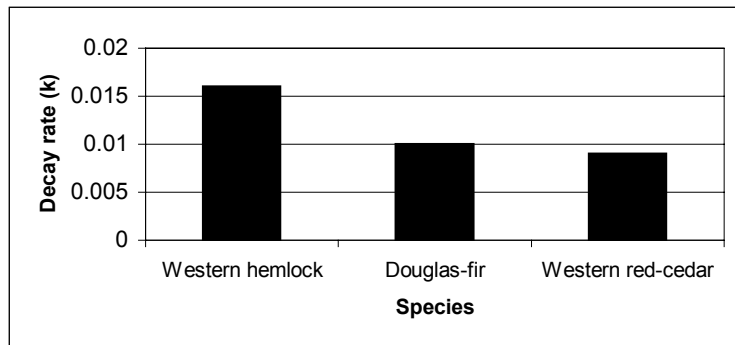


Figure 4.8 Decay Rates in 450- to 750-year-old Douglas Fir and Western Hemlock Stands in the Cascade Range of Western Oregon and Washington (data from Sollins et al. 1987)

Lodgepole pine logs decomposed at a moderate rate in dry forests of central Oregon (Busse 1994). The logs represented mortalities from repeated outbreaks of mountain pine beetle. Decomposition rate was $k = 0.027$ (half-life of 26 yr), and decay Class I boles had the same density as live trees. This lack of decomposition probably was because most Class I boles were suspended above the forest floor by intact branches. The moderate decay rates also were evident in the ages of downed boles (Figure 4.9). For example, downed boles in decay Class IV were only about 38 years old. (These ages did not distinguish time spent suspended vs. on the ground). No relationship was detected between decomposition rate and bole diameter.

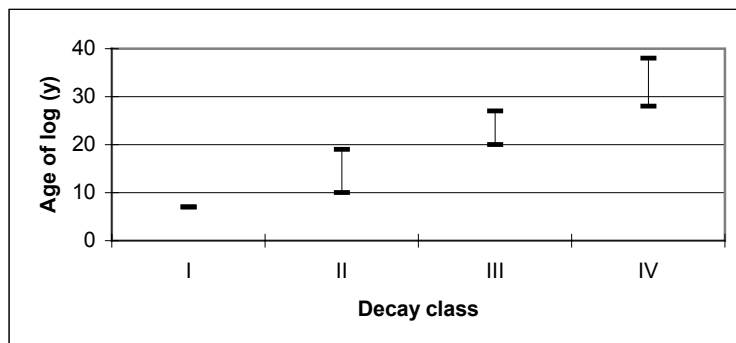


Figure 4.9 Ages of Downed Lodgepole Pine Boles in Dry Forests of Central Oregon (data from Busse 1994). (Figure represents ranges of values with a single datum for Class I.)

Species decayed at different rates on Vancouver Island, British Columbia (Keenan, Prescott, and Kimmins 1993). Cedar decayed most rapidly, and hemlock slowest (Figure 4.10). By decay Class V, density of hemlock boles (the only Class V material) was 0.23 g/ml in old-growth stands and 0.18 g/ml in second-growth stands. Density of decay Class V logs was half that of decay Class I logs.

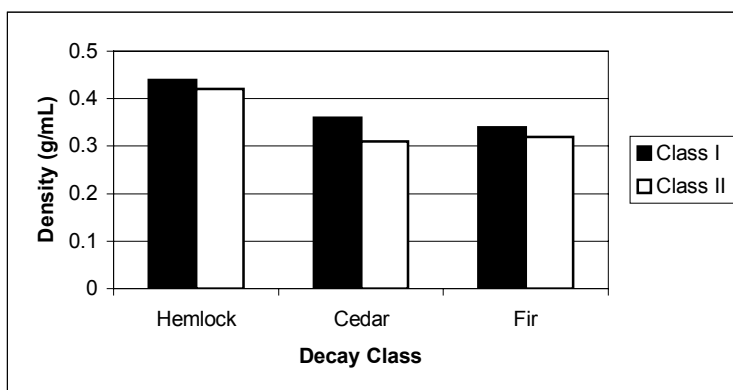


Figure 4.10 Density of Downed Logs on Vancouver Island, British Columbia (data from Keenan, Prescott, and Kimmins 1993)

In Washington, Erickson, Edmonds, and Peterson (1985) found that decay rates differed among species ($k = 0.036$ for western hemlock, 0.037 for Douglas fir, 0.009 for Pacific silver fir, and 0.012 for ponderosa pine). However, because Erickson, Edmonds, and Peterson (1985) measured the species in stands they dominated, they hypothesized that the observed differences were due to climatic differences among sites. Generally, silver fir and ponderosa pine forests are drier than hemlock or Douglas fir forests, and exhibit more extremes in temperature. To test site effects, Erickson, Edmonds, and Peterson (1985) placed red alder branches on each site as a standard material. After two years, the standard material showed the same order of decomposition rates as did the other species. They observed faster decomposition of red alder in western hemlock and Douglas fir stands than in Pacific silver fir stands, and no decomposition in the ponderosa pine forest. Thus,

because none of the species differed in wood constituents, they attributed the observed differences among species to different moisture regimes.

4.4.2 Size and Decay Class

Diameter affected decomposition rates of Douglas fir logs in a controlled study in a northwest Washington forest (Edmonds and Eglitis 1989). Large diameter logs decayed faster than small diameter logs (79.5% of original mass remaining after 10 years for large diameter logs versus 92.3% for small diameter logs). Insect attacks decreased with increasing log diameter, but persisted longer into the season on larger diameter logs. Furthermore, wood borers provided an entrance for brown cubical rot. However, insect activity and decomposition rate were not strongly related. For example, no loss in mass could be detected in logs <5 years old, but there was frass production from these logs. Also, Edmonds and Eglitis (1989) wrapped a subset of logs in screen to exclude Douglas fir beetles. Although ten years after the logs were placed they had lost mass, no difference in mass loss was apparent for screened versus unscreened logs.

In the Olympic Peninsula of Washington, decomposition decreased then increased with decay class (Marra and Edmonds 1994). The authors suggested that the pattern (Figure 4.11) was due to rapid decomposition of labile materials in fresh logs, leaving a higher proportion of recalcitrant material in Class III logs. Decomposition may have then increased as roots and their mycorrhizae invaded older logs. Seasonal differences also were apparent with higher CO₂ loss from June to October and slower rates during November through May, probably due to moisture conditions.



Figure 4.11 CO₂ Loss of Logs by Decay Class in the Olympic Peninsula of Washington (data from Marra and Edmonds 1994)

Marra and Edmonds (1994) found that log diameter was an important control on respiration rates, depending on decay class. Rates increased consistently with diameter for Class I to II western hemlock logs, but rates decreased consistently with diameter for Class III western hemlock logs. No diameter effect was apparent in Class V logs. Decay Class V logs had the highest respiration (4.28 g CO₂/m²/d), which was not statistically different from soil respiration rate (5.22 g CO₂/m²/d). However, the relationship between diameter and respiration rates was unclear. Respiration was sometimes greater for small logs than larger logs, sometimes less in smaller logs. Respiration rates were highest in summer and lowest in winter, but the timing of peak rates depended on species and decay class. Temperature, which affects respiration rates, was more equitable on the forest floor than in downed logs. For example, temperatures in May to August averaged 23°C just under the surface of decay Class III logs, 35°C for decay Class V logs, and only 17.5°C for soil.

The decay class of log affected specific agents of decomposition in old Douglas fir and western hemlock stands in the Cascade Range of western Oregon and Washington (Sollins et al. 1987). The proportion of logs with insect galleries and incursion of roots increased steadily with decay class. The proportion of logs with fungal rhizomorphs increased to decay Class III then declined. No fungal rhizomorphs were detected in western red cedar logs. CO₂ losses (respiration rates) were consistent among species and decay classes, but were greater in summer than in winter. Moisture content increased steadily through the decay classes, averaging 250% and 350% for Class IV logs in summer and winter, respectively, for all species. Sapwood was wetter than heartwood. But, because respiration rates did not vary with moisture content, the authors suggested that percent saturation was more meaningful than moisture content.

In Douglas fir stands in Oregon, Hope and Li (1997) found that logs in Classes IV-V had greater CO₂ efflux rates than mineral soil. Litter had higher rates than the Classes IV-V logs (Figure 4.12). No effects due to elevation or stand age were apparent. CO₂ efflux declined with depth in the soil or logs. CO₂ loss was not due to respiration by roots that grew in the logs, as shown by no difference in trenched versus untrenched logs.

In Washington, Erickson, Edmonds, and Peterson (1985) found that smaller diameter logging debris (1-2 cm diameter) decomposed more slowly than larger diameter material (8-12 cm diameter). However, they attributed observed differences among CWD size classes to site-related differences in moisture. Larger material had greater moisture content in the dry season than did smaller material. Smaller residue dried faster, which often slows decomposition. Material in contact with the ground also had higher moisture content than suspended material.

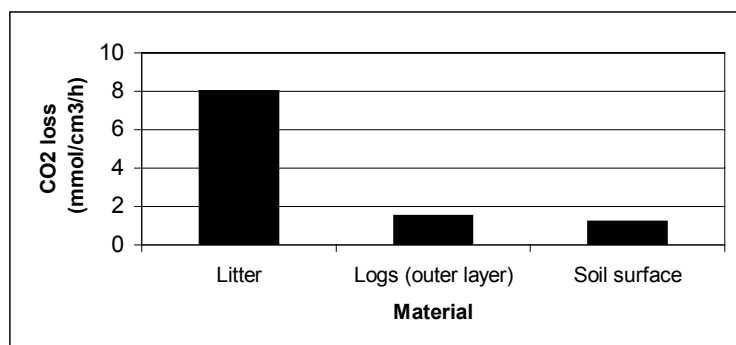


Figure 4.12 CO₂ Loss for Various Materials in Douglas Fir Stands in Oregon (data from Hope and Li 1997)

4.4.3 Wood Chemistry

Species and decay class effects on CWD outputs may be due in part to differences in wood constituents. In the Andrews Experimental Forest in the western Cascades of Oregon, various carbon compounds decayed at different rates in Douglas fir logs (Means, Cromack, and MacMillan 1985). Acid detergent soluble fraction decayed more rapidly than cellulose, and cellulose decayed more rapidly than lignin. Although a single exponential model fit the data well (with $k = 0.007$ and $R^2 = 0.61$), the authors suggested that the summation-exponential model be used for studies in which carbon constituents are of interest. The summation-exponential model accurately reflected the slower decay of lignin and more accurately back-forecast initial densities of sound wood. The single

exponential model did not reflect the rapid initial decay of heartwood and thus, underestimated the initial densities.

Preston, Sollins, and Sayer (1990) also found that cellulose decayed more rapidly than lignins and resins in heartwood of western hemlock and Douglas fir, and that western hemlock decomposed faster than Douglas fir. However, western cedar showed a much different decay pattern with little change in proportion of constituents, even though mass and log volume declined. Little degradation of lignin was apparent in the logs. No increases were observed in chitin, aliphatic substances, or humic substances, indicating no accumulation of fungal or microbial C. Insects, brown rot fungus, and chemical autohydrolysis appeared to be the major decay processes with little further breakdown of lignin, perhaps due to unfavorable environmental conditions.

4.4.4 *Management Effects on Decay Rates*

In lodgepole pine forests of interior British Columbia, harvested sites had higher decay rates than burned sites (Wei et al. 1997). Decomposition coefficients for harvested sites ranged from $k = 0.18$ - 0.21 , and for fire-killed sites from $k = 0.004$ - 0.009 . The observed difference probably was due to at least two factors. First, harvested boles were mainly in contact with the ground, while more of the CWD in burned sites was suspended. Second, the size class distribution of CWD differed between burned and harvested sites. For the wildfire site, logs ≥ 7 cm accounted for 92% of the mass of CWD, but only 52-64% on harvested sites.

Harvesting also affected respiration rates in the Olympic Peninsula of Washington (Marra and Edmonds 1994, 1996). A clearcut site had lower wintertime respiration rates and higher summertime rates than an old-growth site. This pattern suggested that temperature affected decomposition more than moisture because the clearcut was drier and warmer in the summer but wetter and cooler in the winter than the old-growth. This result also suggested that, for this site during this time, excessive moisture did not limit decomposition of CWD. No “case-hardening” was observed for CWD despite warm, dry conditions.

4.5 Summary

Differences in decomposition rates across geographic regions and within regions show that temperature and moisture are important controls of decomposition rates. Log diameter affects decomposition both through the surface area to volume relationship and water content. On drier sites, the lower moisture content may be more important than the larger relative surface area. Species differences in size and log constituents, including proportion of bark, heartwood, and sapwood, and wood chemistry, also influence decomposition partly by controlling rate of insect incursion.

5.0 TEMPORAL DYNAMICS OF CWD

The factors that influence the accumulation of CWD—mortalities, tree sizes, and tree species—change with stand development. Thus, the temporal pattern of CWD may be predictable. Because early-successional species are generally not long-lived, CWD may accumulate through the early stages of stand development. But, early-successional tree species may not grow large and may decay quickly. Thus, CWD may decline as the stand develops and fewer trees die and fall. In later stages of stand development, large late-successional species begin to die or blow down and CWD often begins to accumulate.

This pattern of CWD accumulation is known as the U-shaped timeline. As discussed below, it is a common but not universal pattern. The pattern that actually occurs depends upon the scale and

frequency of disturbances and site and species characteristics. Also, the actual pattern involves more than just total amount of CWD; the size classes and decay classes vary over time as well.

A common question about CWD dynamics is whether CWD inputs roughly match outputs. Does CWD quantity typically reach equilibrium? As shown below, it does not appear that an equilibrium level of CWD is the norm. As with other features of CWD, the answer depends upon specific site characteristics.

Harvesting and other management practices can alter input and output rates and, thus, CWD accumulation. As discussed below, harvested sites may have less CWD at some stages of development than do unharvested sites, and harvested sites often have less older, larger CWD. However, this is to be expected because harvesting usually removes the boles of commercially valuable trees.

5.1 U-shaped Timeline? Sometimes...

Spies and Cline (1988) modeled CWD accumulation in the Oregon Coastal Range using a U-shaped function. They estimated that the initial time of increasing CWD would last about 400-600 years. Then, CWD inputs would decline again as successional trees (e.g., Douglas fir) passed from the stand. They also projected that, as late-successional trees died, CWD would reach a lower, equilibrium quantity. Because Douglas firs are long-lived, they estimated that the later stage may not occur for up to 1,200 years. But, the authors warned that this conceptual scenario may not be common because fires and other disturbances add and take away CWD. For example, recurring fire in young stands can consume CWD and vegetation.

Spies and Cline (1988) used their model to evaluate differences between unmanaged stands and plantations. According to their model, an unmanaged stand has a relatively slower temporal dynamic that spans a wider range of CWD quantities than a plantation which typically passes more quickly through a smaller range of values. In addition, they reported that plantations usually produce smaller trees that disappear faster and legacy CWD in later decay stages may be removed during harvest or site preparation operations. Thus, Spies and Cline (1988) projected that CWD in Douglas fir plantations would vary from a high of 56 Mg/ha immediately after harvesting to a low of 11.2 Mg/ha immediately before harvesting (Figure 5.1).

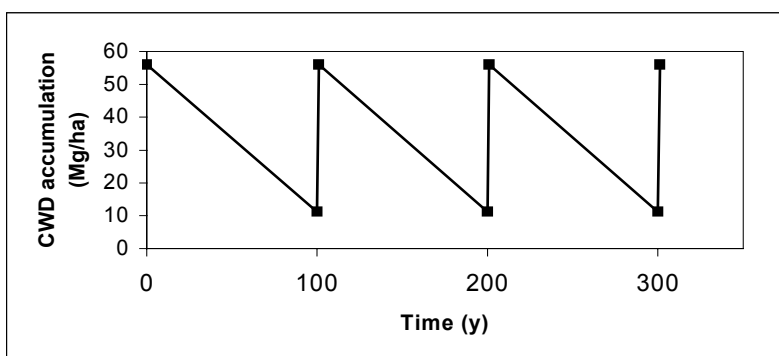


Figure 5.1 CWD Dynamics Produced Using a Simulation Model of Douglas Fir Plantations in the Pacific Northwest (data from Spies and Cline 1988)

Spies and Cline (1988) also described changes in CWD size classes that occurred with stand age. Most of the CWD in young stands was in later decay stages because much of it was legacy CWD from the previous stand. The proportion in later decay stages then generally declined with stand age, but the actual amount of later-stage CWD was steady. This consistency in absolute amount suggests that CWD in later decay classes is a stable, less variable component of the forest ecosystem. Thus, stands with recurring harvest or fire that consumes CWD may not have much legacy CWD.

Stevens (1997) summarized the effects of disturbance frequency on CWD accumulation. In each case, she postulated a U-shaped timeline. But, the specific shape depended on the frequency of disturbance, namely, whether the disturbance regime represents rare stand-initiating events (250- to 350-year return times), infrequent stand-initiating events (200-year return times), frequent stand-initiating events (100- to 125-year return times), or frequent stand-maintaining fires (4- to 50-year return times).

Sturtevant et al. (1997) found the U-shaped timeline in a chronosequence of balsam fir-dominated forests. Compared to recently clearcut stands, CWD volume declined with stand age up to 64-year-old stands (15.2 m³/ha), then increased with stand age up to 80-year-old stand (78.1 m³/ha). CWD volume remained consistent after that time. This timeline seemed to be driven by sound logs; volume of decayed CWD showed no consistent temporal pattern. In this site, CWD declined as legacy and disturbance-generated CWD decayed. The regenerating forest began to contribute new CWD at about 55 years post-disturbance. At that time, CWD accumulated for the next 30 to 40 years, then reached an equilibrium. Snags did not begin to appear until about 60 years post-disturbance.

A U-shaped timeline also was apparent in a New Hampshire maple/yellow birch/beech forest (Gore and Patterson 1986). CWD mass was greatest in a newly cut forest (86.4 tons/ha), declined with stand age through 15- to 45-year-old stands (32 tons/ha), and then increased in the 100-year-old stand (54 tons/ha). The newly cut stand included logging slash and legacy CWD. This material decomposed within 20 years, then early-successional species began to contribute CWD. Later-successional species began to contribute at about 70 years, and by 100 years, decomposition and CWD input were at an equilibrium level of 30-40 tons/ha. In comparison, an uneven-aged stand (harvested using single tree selection with 20- to 25-year cutting cycle) had 42 tons/ha, and uncut stand had 35 tons/ha. Size and decay classes of newly added CWD increased with stand age.

Petranka et al. (1994) found that CWD accumulation followed a U-shaped timeline in lower elevation forests in the Blue Ridge Escarpment of western North Carolina. Dominant trees were oaks, hickories, maples, ashes, basswood, and magnolia. CWD declined with stand age to 79-year-old stands, then began to increase (Figure 5.2). Mean log diameter and proportion of logs in later decay classes also increased with increasing stand age.

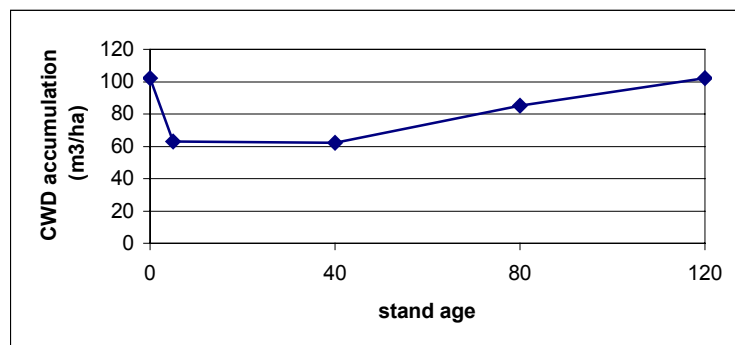


Figure 5.2 CWD Accumulation (Volume) with Stand Age in Lower Elevation Forests in the Blue Ridge Escarpment of Western North Carolina (data from Petranka et al. 1994)

Van Lear and Waldrop (1995) used a FORET-type model to predict CWD loadings in southern forests. Their model predicted a peak of about 50 Mg/ha at about 90 years for mesic forests, then a drop to about 30 at 180 years. Xeric forests were predicted to peak at about 30 Mg/ha at 75 years and then a drop to 25 Mg/ha. With logging slash included, a U-shaped timeline was predicted beginning with 70 and 50 Mg/ha of debris for mesic and xeric forests. The authors stated that more information about input and output rates was required to parameterize the model.

Crooks et al. (1998) tested the prediction of Van Lear and Waldrop (1995) in South Carolina Piedmont forests, and found that CWD followed a U-shaped timeline. CWD was defined as ≥ 2.54 cm diameter. Initial quantities from logging slash were high (10.1 to 14.6 Mg/ha), declined through ages 8-25 years to < 2.2 Mg/ha, then increased through stands aged ≥ 100 years (Figure 5.3). CWD quantities in the oldest stands were 6.7 to 13.4 Mg/ha. In stands ≤ 25 years old, submesic stands generally had more CWD than did stands with more xeric conditions (probably due to more moisture and higher productivity). However, this relationship did not hold true for stands > 25 years old, possibly due to differences associated with succession (e.g., physical characteristics of the stands, changes in species composition, higher decomposition rates). In comparison to the predictions from the model by Waldrop (1996), these forests had less post-logging debris and faster decomposition rates than the model predicted. Although the model predicted a decline in CWD loading after 70 years, only the submesic sites showed a plateau in the field data.



Figure 5.3 Downed Coarse Woody Debris Accumulation in Carolina Piedmont Forests (adapted from Crooks et al. 1998)

CWD also followed a U-shaped timeline in the Allegheny Plateau of western Maryland (McCarthy and Bailey 1994). Sites represented recently clearcut (< 2 years old), pole (15-25 years old), mature (65-90 years old), and old (100-200 years old) stands. Downed log volume and mass were greatest for the recent clearcuts and declined with stand age (Figure 5.4). In contrast, log size and decay class increased with stand age. Several of the large logs were chestnut (presumably killed by chestnut blight) and others were oaks killed by gypsy moth. Snags had a different temporal pattern. Density

of snags increased from recently clearcut to pole (48 snags/ha in clearcut and 1,100 snags/ha in pole stands), then declined for mature and old stands (384 snags/ha in mature stands and 277 snags/ha in old stands). Due to differences in snag diameter with age, basal area of snags steadily increased with stand age (2.2 m²/ha, 2.3 m²/ha, 6.8 m²/ha, and 7.8 m²/ha for recently clearcut, pole, mature, and old stands, respectively). The authors found no large logs in advanced decay, suggesting that the old stands perhaps had not recovered completely from harvesting during the 1800s. The authors recommended that forest management in these areas should plan for incorporation of large logs in later stages of stand development.

In west central British Columbia, CWD showed a U-shaped timeline in interior spruce, subalpine fir, and lodgepole pine stands (Clark et al. 1998). Both basal area of snags and volume of downed logs declined then increased with stand age (Figure 5.5). Snag abundance largely reflected successional status. Stands <200 years old generally had smaller (30-39 cm) spruce snags, while stands >200 years old had larger (> 40 cm) fir snags. Log volumes were too variable for the investigators to detect any clear patterns related to succession.

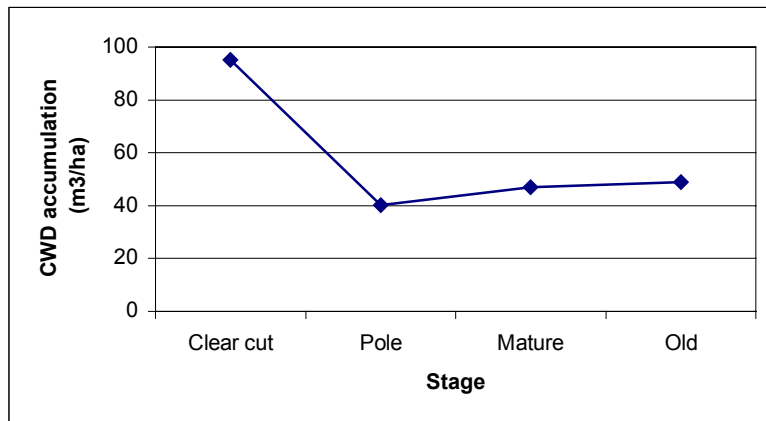
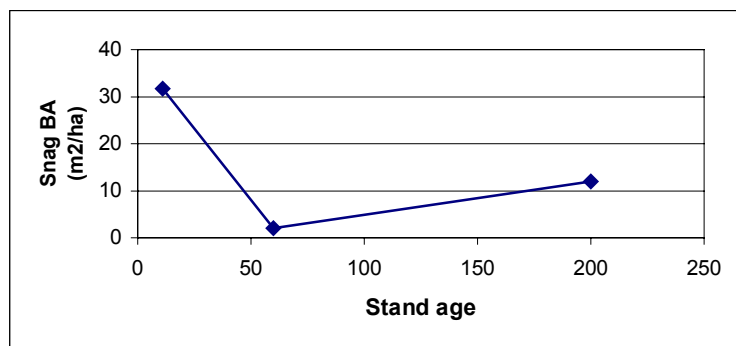
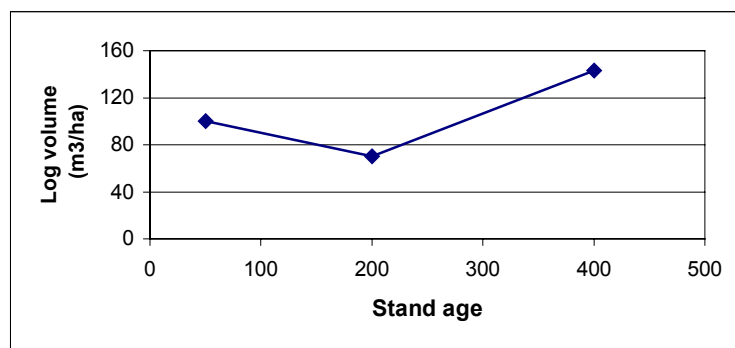


Figure 5.4 Downed Log Volume and Stand Age in the Allegheny Plateau of Western Maryland (data from McCarthy and Bailey 1994)



a.



b.

Figure 5.5 Snag Basal Area (a) and Downed Log Volume (b) in Interior Spruce, Subalpine Fir, and Lodgepole Pine Stands of Different Ages in West Central British Columbia (data from Clark et al. 1998)

On Vancouver Island, British Columbia, the timeline of CWD accumulation varied by site condition (Wells, Trofymow, and MacKinnon 1998). The drier (east) side showed no consistent temporal pattern in accumulation, but the wetter (west) side showed a U-shaped temporal pattern. The west side had higher productivity and, thus, greater CWD mass (17-38 Mg/ha on the east versus 65-191 Mg/ha on the west) and volumes (55 m³/ha to 149 m³/ha on the east, 307 m³/ha to 636 m³/ha on the west). In both areas, younger stands had CWD only in earlier decay classes and older stands had CWD across a range of decay classes. CWD was mainly in smaller size classes in younger sites on the east side, while sizes were more evenly represented in older sites. CWD tended to be larger overall on the west side. Douglas fir was the most common species in CWD on the east side, but western hemlock and western red cedar were the most common species on the west side. Lower growth rates and higher decomposition rates on the drier sites may have accounted for these differences. But the comparison also may have been confounded by the possibility that remaining old-growth on the east side generally occupies lower productivity sites (i.e., higher productivity sites are no longer in old growth).

In Oregon and Washington, a U-shaped timeline also was apparent in moderately moist sites dominated by Douglas fir (Spies, Franklin, and Thomas 1988). CWD quantities were greatest in old

growth (534 m³/ha, 123 Mg/ha), lowest in mature stands (250 m³/ha, 52 Mg/ha), and intermediate in young stands (423 m³/ha, 78 Mg/ha). Of these totals, snags accounted for 41% of the volume and 44% of the biomass. The effect of stand age was more pronounced when the sites were divided into more detailed age classes. Younger stands (60-80 years old) had moderate levels of CWD, moderate-aged stands (80-120 years old) had less, then CWD climbed again to age 400-600 years, at which point it declined again. This pattern was similar in snags and downed logs.

Spies, Franklin, and Thomas (1988) also found that size and age class of the logs varied with stand age. While younger stands had more downed logs and snags, old-growth stands had larger downed logs and snags. In young stands, CWD was primarily in decay Classes III-V (legacy material). However, in mature stands that shifted to a more even distribution across Classes II-V, and in old-growth stands to mainly Classes II and III. Productivity, disturbance history, and other site factors modified this temporal pattern and considerable site-to-site variability was apparent. Because most of the CWD in these sites was Douglas fir, the temporal pattern may have reflected the long-lived, slow-decaying nature of this species. The decline in CWD with age may have been due to the more rapid decay of later successional trees (i.e., silver fir and western hemlock).

5.2 ...But Not Always

CWD accumulations do not always follow the U-shaped timeline. Volume of downed logs increased with stand age in cove forests in the Great Smokey Mountains (Busing 1998). Overall, more downed logs were found in old-growth forests >200 years old (161 m³/ha) than in 40- to 70-year-old second-growth stands (50.6 m³/ha), but amounts varied widely (43-208 m³/ha across all stands). Snag density was greater in young stands (31 snags/ha) than in old-growth stands (22.5 snags/ha), but also varied widely (12-33 snags/ha across all stands). Large snags (>50.8 cm) occurred only in old growth (average density 5 large snags/ha).

CWD quantities also generally increased with stand age in southern Appalachian forests in South Carolina and North Carolina (Hardt and Swank 1997). Young stands (i.e., 30-75 years since logging) had ≤ 2.5 snags/ha while mature and old-growth (i.e., 200+ years old) stands averaged 18 snags/ha. A maple-basswood old-growth stand had snags across the range of decay classes. Downed log volumes ranged from 22.4-91.4 m³/ha, with a general increase with stand age. The pattern was variable, though, with one young stand containing the greatest volume and number of downed logs.

In northeastern Alberta, snags and downed logs increased with stand age in boreal forests (Lee et al. 1997). Stands were classified as young (20-30 years old), mature (30- 65 years old), and old (120+ years old). Snag densities increased from young to mature and declined in old stands (33.0, 73.1, and 66.2 snags/ha, respectively). However, the difference between mature and old was not statistically significant. CWD counts were lower in mature than in young or old stands, but mean diameter of CWD was greater in old than in young stands (23.5 cm versus 18 cm). Thus, volume of CWD was greatest in old stands (61 m³/ha, 76 m³/ha, and 101 m³/ha for young, mature, and old stands, respectively). Size distribution of CWD was more even in old stands (120+ years old) than in young (20 to 30 years old) or mature stands (50 to 65 years old). Contributions of pre-fire snags and pre-fire downed logs declined with stand age (Figure 5.6). Logs in advanced decay classes occurred most often in older stands. Most of the downed logs in young stands were in early decay classes (maximum frequency in Classes III and IV and relatively few in Class VII). Most of the downed logs in old stands were in advanced decay (maximum frequency in Class VII). All pre-fire downed logs were at least in decay Class IV in mature stands.

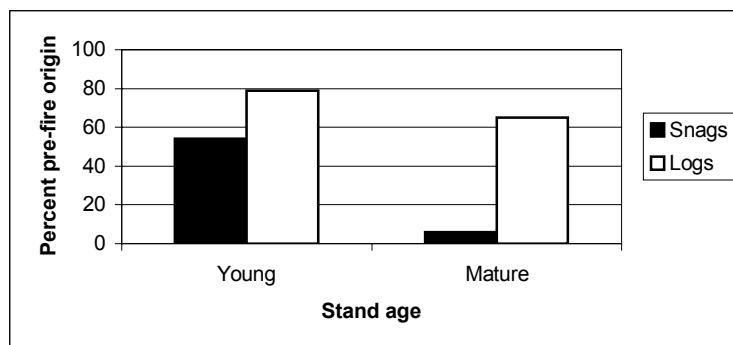


Figure 5.6 Percentage of Snags and Downed Logs That Originated before a Fire in Young (20- to 30-Year-Old) and Old (50- to 65-Year-Old) Boreal Forests of Northeast Alberta (data from Lee et al. 1997)

In New Brunswick, CWD mass increased then decreased with stand age in a chronosequence of conifer and hardwood stands (Fleming and Freedman 1998). The authors reported CWD biomass as tons of carbon per hectare. Stands 55 years old averaged 5 t C/ha, 90-year-old stands averaged 10 t C/ha, and 105-year-old stands averaged only 5 t C/ha.

In northern Ontario, total CWD did not follow any pattern in a chronosequence of white pine, red pine, and jack pine stands (Carleton and Arnup 1993). Variations in stocking rates on the stands may have accounted for the wide variability in CWD over time.

In southeastern Ohio, density and volume of downed logs and snags showed no consistent time patterns in a chronosequence of oak-hickory stands (Goebel and Hix 1996). Snag density was greatest in the 70- to 89-year-old stands (53 snags/ha), then declined to a low of 5 snags/ha for stands 130-149 years old. Snag density was not greater in old-growth than in second-growth stands. Basal area of snags, volume of downed CWD, and size of CWD showed no consistent pattern with stand age. Total CWD (snag plus downed) volume ranged from 2-30 m³/ha. Low productivity of these sites may have limited CWD accumulation, suggesting that CWD quantities may not be an accurate indicator of old-growth status.

5.3 Equilibria of CWD Inputs and Outputs

If ongoing, small-scale, frequent mortalities occur at the same rate that trees are recruited into the older, larger size classes, CWD inputs and outputs may reach equilibrium. Otherwise, larger-scale disturbances may result in pulses of mortalities and CWD (see Section 3).

Whether a system is in equilibrium is an important question for managers. Perhaps the most practical implication is that a system at equilibrium can have a static target. In other words, a particular prescribed quantity of CWD can be a valid goal and a monitoring program need only check periodically to be sure that goal is being met. Managers would then need to continue or impose management actions or processes that maintain that equilibrium. On the other hand, goals and prescriptions for a non-equilibrium system would be more complicated and likely should include separate prescriptions for different structural classes and consideration for the processes that drive non-equilibrium dynamics.

In western Maryland, CWD did not appear to be in equilibrium in an old-growth stand dominated by sugar maple, red oak, basswood, and magnolia (McCarthy and Bailey 1996). The authors cited two

factors as evidence of a lack of equilibrium: the majority of CWD was in decay Classes IV and V; and red oak contributed most of the CWD, but was not the dominant live tree.

In central Illinois, snag inputs and outputs were not at equilibrium in an old-growth forest, as indicated by differences in species composition of snags versus live trees (Roovers and Shifley 1997). More than one-fourth of the snags were elm; white and northern red oak accounted for 45% of snag basal area (mainly from a few large individual snags). Although maple was the dominant living tree, it accounted for only 18% of the snags and less than 5% of total snag basal area. Size distribution of snags closely followed that of live trees.

CWD also did not appear to be in equilibrium in second-growth and old-growth oak/hickory forests in Indiana, Illinois, Iowa, and Missouri (Spetich et al. 1999). Combining the second-growth and old-growth sites, volume of dead wood declined with stand age to a minimum of 20 m³/ha on 60- to 80-year-old stands, then increased with stand age with 100 m³/ha on a 220-year-old stand. But CWD dynamics likely was not in equilibrium — a single windstorm on one site added 20m³/ha of CWD and an ice storm on another site increased downed CWD by 27%.

Some studies, however, have found stands that seemed to be in equilibrium. Sturtevant et al. (1997) found that balsam fir-dominated forests reached an equilibrium amount of CWD after about 100 years. A New Hampshire maple/yellow birch/beech forest also reached equilibrium quantities of CWD (Gore and Patterson 1986).

In northern Michigan and northern Wisconsin, CWD inputs and outputs in old-growth hemlock/hardwood forests appeared to be at equilibrium (Tyrrel and Crow 1994b). An equilibrium model fit observed proportions of the various decay classes in old growth, but not in younger stands. The equilibrium conditions occurred after the dominant canopy trees reached 400 years old and if disturbances were limited to individual tree mortalities. However, large-scale disturbances such as wind storms disrupted the equilibrium. In addition, although proportions of the decay classes may have been at equilibrium, the amount of CWD increased with stand age even among old-growth forests (Tyrell and Crow 1994a).

In Ontario, eastern white cedar forests on cliff faces appeared to be in equilibrium between recruitment and mortality (Kelley and Larson 1997). These forests did not show evidence of any periodic large-scale disturbances. Snag densities averaged 317 stems/ha (24% of all standing stems). High mortality and slow decomposition contributed to this high snag density. Even so, this CWD loading may not be essential for the continued dominance of eastern white cedar because it does not require nurse logs to germinate.

5.4 Comparing CWD Dynamics in Two Distinct Forests

Harmon and Hua (1991) illustrated the processes controlling CWD dynamics by comparing two widely differing old-growth sites: Andrews Experimental Forest in Oregon and a deciduous forest in Changbai Mountain Biosphere Reserve in China. Mortality rates were similar (0.3% to 0.7%). In both sites, normal tree mortality added about as much CWD per year as major disturbances such as windstorms and fire. In other words, while one fire may add up to 1,000 Mg/ha, normal tree mortality could add even more CWD over the 500-year period representing fire return times.

Decay rates were different between the two forests. For example, exponential decay constants for dominant species in the China forest were $k = 0.027$ (*Tilia* spp.) and $k = 0.016$ (*Pinus* spp.) compared to $k = 0.016$ for hemlock and $k = 0.005$ for Douglas fir in the Oregon forest. As the authors indicated, Douglas fir is decay-resistant due to antifungal compounds in heartwood. Weather also was reported as a likely influence on CWD dynamics. The China site was cooler and drier, while the

Oregon site was too wet for efficient decomposition (the fungi involved in decomposition in the Oregon site are obligate aerobes and saturation of the logs limited oxygen content).

Several other differences existed between the two sites. About 30% of CWD loss in the China site was due to fragmentation, and about 50% of the loss in the Oregon site could be attributed to this factor. Up to 57% loss to fragmentation has been reported in the Oregon sites. Slower inputs and faster decomposition yielded less CWD accumulation in the China site.

The authors suggested that the large quantities of CWD in the Oregon site could act as a stabilizing reservoir of N after major disturbances. Newly fallen logs initially would immobilize N, but later slowly release it. The immobilization could possibly act to conserve N in the post-disturbance environment and stabilize the flux of N back into circulation (although phloem may release its nutrients relatively rapidly). The authors stated that two pathways of nutrient release overlooked in some studies are a) fungi that release nutrients from wood to forest floor, and b) fragmentation, which may release nutrients more rapidly than previously assumed.

5.5 CWD Dynamics under Different Management Regimes

Obviously, timber harvesting affects CWD inputs and outputs. Harvests can create CWD by converting live vegetation to dead. Thinning can enhance production of larger trees, some of which may be left for snags and ultimately downed CWD. Thus, management practices may alter the number and size of snags and logs from more and smaller material to less and larger material.

Comparisons of plantations, harvested natural forests, and unharvested stands show that harvested sites often have less accumulation of large CWD than do unharvested sites. Thinning also may reduce CWD accumulation. For example, new black spruce plantations in New Brunswick averaged 10 tons C/ha in CWD, but 20-year-old plantings had only 0.08-0.12 t C/ha of CWD mass (Fleming and Freedman 1998). CWD remaining from the establishment of the plantation decomposed and was not replaced because precommercial thinning reduced stem exclusion mortalities and there was little mortality otherwise.

In Minnesota, Wisconsin, and Michigan, the difference in CWD accumulation between harvesting systems depended on stand development stage in red pine forests (Duvall and Grigal 1999). These stands represented unmanaged natural stands, thinned natural stands, and plantations of various ages. Managed stands had less CWD than unmanaged stands through all stages of stand development. The largest differences were in 125-year-old stands at which point, managed stands had only 50% of the CWD as unmanaged stands of similar age. Unmanaged stands had 800 snags/ha while young (0-30 years old) managed stands had only 1.5 snags/ha. Young managed stands also had 80% less downed log biomass than unmanaged stands. In mature stands, the managed stands had more decay Class I logs and fewer decay Class II and III logs than did unmanaged stands. This distribution of CWD among decay classes was predicted to affect the time required for stands to reach a steady state in CWD quantity. The authors predicted that unmanaged forests would reach 90% of steady state CWD quantities by 100-125 years, but managed forests would require 900-1,200 years to do so.

In northern Michigan and Wisconsin, harvesting reduced accumulation of downed logs (Goodburn and Lorimer 1998). Managed even-aged stands had fewer downed logs than selection-cut stands, which had fewer downed logs than old-growth stands (Figure 5.7). These differences primarily were due to larger-sized pieces in old growth (35% of the logs in old growth were classified as large but only 25% of the logs in selection cut were large). Although proportions of logs in the various decay classes was consistent across harvest systems, old-growth stands had about twice the volume of large logs in advanced decay classes compared to selection-cut stands. The type of CWD varied as well. For old-growth stands, more than 80% of downed CWD was fallen boles; in the selection stands

about 40% of the downed CWD was harvest tops and unmerchantable boles. Lower snag and CWD production in section-managed stands may have been partially due to reduced senescence-related mortalities in managed stands.

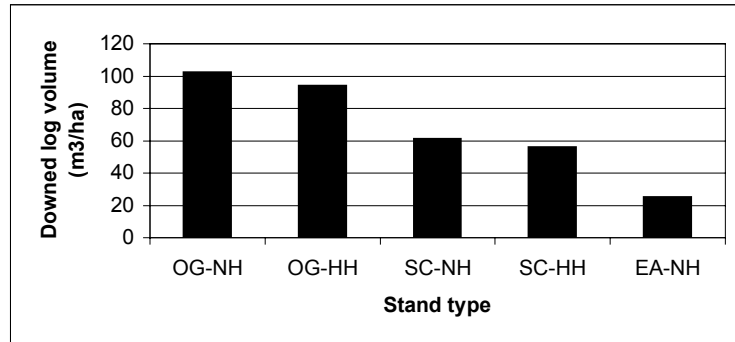


Figure 5.7 Downed Log Volume across Forest Types and Harvesting Types in Northern Michigan and Wisconsin (data from Goodburn and Lorimer 1998). OG = Old Growth, SC = Selection Cut, EA = Even Aged; NH = Northern Hardwoods, HH = Hardwood/Hemlock.

Goodburn and Lorimer (1998) also found that harvest method affected snag density and size. Total density of snags was greater in even-aged stands than in selection-cut or old-growth stands; selection-cut and old-growth stands averaged 38 and 39 snags/ha, respectively, while even-aged stands averaged 90 snags/ha. But old-growth and selection-harvested northern hardwood stands had twice the density of large snags compared to even-aged-managed stands. The similarity between selection-cut and old-growth stands may have been because the selection cuts followed wildlife tree retention guidelines. Very large snags (>65 cm diameter) were absent from the even-aged stand and only at low density in the selection stands. However, each old-growth plot contained at least one very large snag.

In Indiana, Illinois, Iowa, and Missouri, old-growth sites had twice the volume of snags and three times the volume of downed logs as found on second-growth sites (Spetich et al. 1999). The ratio of snags to live trees also was lower on second-growth sites (0.08 versus 0.11, a small but statistically significant difference). But on the higher-productivity sites, second-growth sites had a higher ratio of snags to live trees in the smallest diameter classes (a ratio of 0.20).

In oak forests in Missouri, volume of downed logs was greater in old-growth than in 70- to 90-year-old, second-growth stands (Shifley et al. 1997). Old-growth sites averaged 35.9 m³/ha (ranging from 24-49), twice the value for second growth (average 17.5 m³/ha, ranging from 12-25). This difference was primarily for logs in the later decay classes. In both second-growth and old-growth stands, about half of the downed logs were in decay Class III. But, the old-growth stands had a greater proportion of logs in decay Classes IV and V. The number of live trees and number of snags did not differ significantly between old-growth and second-growth (35 snags/ha and 31 snags/ha, respectively). However, basal area of snags was significantly greater in old-growth stands (Figure 5.8) due to the larger size of snags in old growth. In second-growth stands, 70-80% of the logs were ≤20 cm diameter while the old-growth stands had slightly more downed logs > 20 cm diameter.

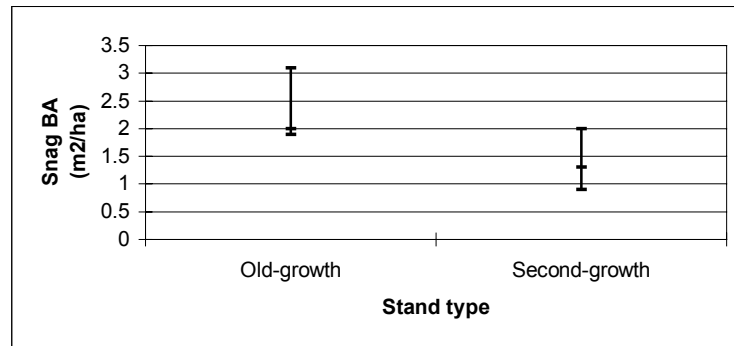


Figure 5.8 Volume of Downed Logs in Old-Growth and Second-Growth Oak Forests in Missouri [Bars represent minimum, mean, and maximum of data reported by Shifley et al. (1997).]

In central Massachusetts, stands thinned 4-12 years prior to the study had fewer snags than unthinned stands in white pine/red oak/maple forests (Healy, Brooks, and DeGraaf 1989). Dead trees accounted for about 20% of all stems in unthinned stands and about 15% of all stems in thinned stands. Snags in unthinned stands were larger than in thinned stands (11.8 cm dbh versus 9.8 cm dbh).

In Montana, CWD quantities increased from second-growth to old-growth stands in Douglas fir/ponderosa pine forests (Lesica et al. 1991). Old-growth sites had more and larger snags and more downed logs (Figure 5.9). Sound logs accounted for 36% of CWD volume in old growth and only 4% in second growth, indicating that downed logs in second growth were mainly from logging some 70 years before.

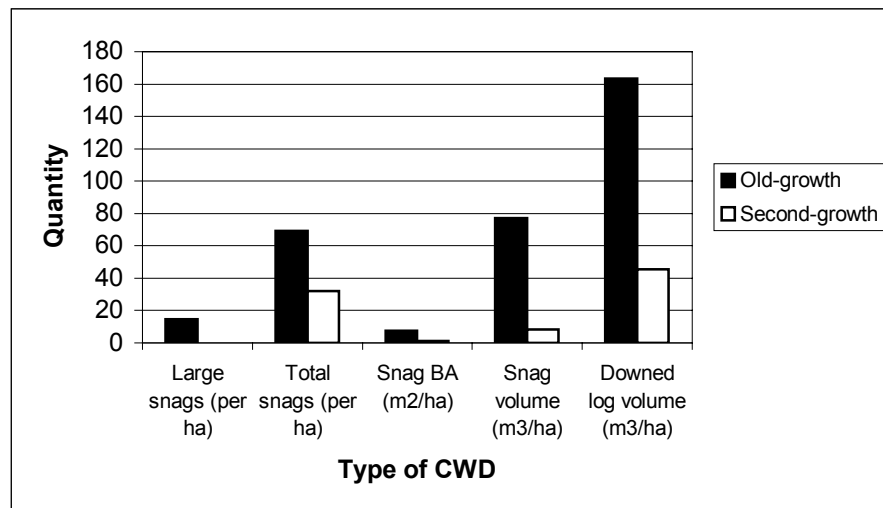


Figure 5.9 CWD Quantities in Old-Growth and Second-Growth Douglas Fir/Ponderosa Pine Forests in Montana (data from Lesica et al. 1991)

5.6 Summary

Although the processes that determine CWD dynamics are easy to define—tree mortalities, snag retention, and downed log decay rates—they are not easy to summarize over various forest types. These rates vary by species, by type of mortality, and site characteristics; accurate generalities cannot be made. For example, some sites follow a U-shaped timeline but others do not. Some sites reach an equilibrium quantity of CWD and others do not. Disturbance regime, species composition, site characteristics, and other factors related to CWD accumulation must be assessed on a site-by-site basis before CWD prescriptions or descriptions can be made accurately. CWD studies should include more than just snapshots of CWD quantities; they also should include information about the processes underlying those quantities.

6.0 NUTRIENT FLUX OF CWD

One of the potential ecological roles of CWD is as a nutrient reservoir. CWD can be a source of nutrients that are mineralized during decomposition. CWD also can act as a substrate for N-fixing microbes. But CWD also can be a nutrient sink if, for example, high C:N ratios result in immobilization of N. The flux of nutrients into and out of CWD varies with species of log, conditions of the log (i.e., decay class) and site factors.

It also is important to remember that nutrient concentrations (g/g or g/ml) are only one aspect of nutrient flux. Because mass also changes with decay, the absolute quantity of nutrients (concentration \times mass or concentration \times volume) may have a different temporal pattern than concentration. For example, concentrations of nutrients may increase over time. But if mass decreases fast enough, content of nutrients in the CWD decreases.

6.1 Nutrient Flux in Midwestern Forests

The conditions by which CWD acts as a nutrient source or a sink in midwestern forests are not clear. CWD represented a nutrient sink for N and P in an old-growth, maple-beech forest in Indiana (MacMillan 1988) and a sink for N, Ca, and Mg in coniferous forests in Minnesota (Alban and Pastor 1993). But in the latter study, K was mineralized; P was mineralized in species with high initial P concentration (aspen and spruce) and immobilized in species with low initial concentration (pines). In central Illinois bottomlands, N, Ca, and Mg were immobilized, and P and K were mineralized, with the rates differing for bark, sapwood, and heartwood (Cheung and Brown 1995). In a northern hardwood forest, CWD acted as a nutrient source (Arthur, Tritton, and Fahey 1993).

Species-specific factors, such as wood chemistry and fragmentation rates, likely influence source/sink dynamics. For example, in the study by MacMillan (1988), fragmentation rates were highest for beech and lowest for oak. Initial lignin content was greatest in oak, while initial cellulose content was greatest in maple.

In northern Ontario, N₂-fixation was detected in conifer-hardwood CWD, but rates varied by species and were limited by water and carbon (Hendrickson 1991). N₂-fixation, as measured by acetylene reduction, was greatest in aspen, followed by maple, balsam fir, and jack pine. Paper birch and white pine had no activity. Species exhibiting white rot (aspen, birch) had a greater potential for N₂-fixation than did brown-rotting species (conifers). With advanced decay, white-rotting species showed increased N₂-fixation, but brown-rotting species (especially white pine) did not.

6.2 Nutrient Flux in Rocky Mountain Forests

The role of CWD as a nutrient source or sink also is unclear in Rocky Mountain forests. In southwest Alberta, CWD did not appear to be a substantial source of nutrients in coniferous forests (Laiho and Prescott 1999). Nutrient flux differed by species and by nutrient (Figure 6.1). The authors applied the measured N and P flux rates to CWD input rates measured on these sites and concluded that CWD was not a major source of nutrients in this system.

In Colorado, CWD was an important reservoir for base cations in old-growth Engelmann spruce/subalpine fir forest (Arthur and Fahey 1990). Because cations can be lost easily from the system, this source may have been especially important. In this study, N, P, Ca, and Na increased with decay class; Mg and K decreased with decay. Dead boles accounted for only 7% of N in the system, 5% of P, 12% of Ca, 17% of Mg and 16% of K. However, forest floor components accounted for substantially more.

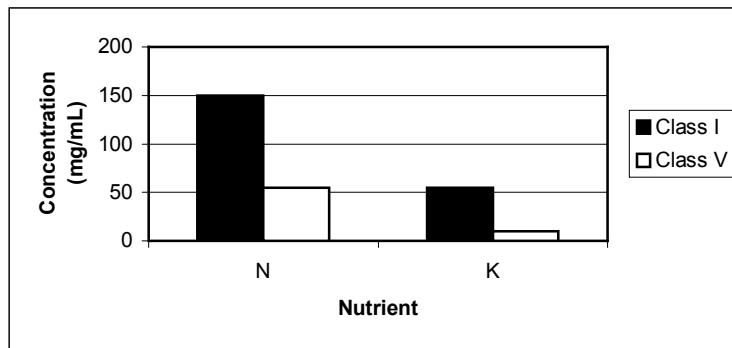


Figure 6.1 Nutrient Concentrations (N and K) in CWD in Southwest Alberta Coniferous Forests (data from Laiho and Prescott 1999)

6.3 Nutrient Flux in Southeastern U.S. Forests

Only one recent study has looked specifically at nutrient dynamics from CWD in the southeastern U.S. (Rice et al. 1997). Hurricane Andrew caused substantial damage to forests in the Atchafalay River Basin in Louisiana. The resulting CWD decayed rapidly and released P, but not N. Flux also differed from outer to inner portions of logs. Over a 30-month interval, up to 75% of the original P content was released from outer portions of logs, but P content increased in inner portions of logs. N was not released; 75-100% of the original N content remained after 30 months. The immobilization of N and its later release as the stand develops may act to conserve N immediately after a disturbance.

6.4 Nutrient Flux in U.S. Pacific Northwest and British Columbia Forests

As with decomposition rates, nutrient flux has been studied extensively in forests of the U.S. Pacific Northwest and British Columbia.

6.4.1 Role of CWD in Nutrient Cycling

Harmon and Hua (1991) suggested that CWD may retain nutrients immediately after a disturbance, but release them as the post-disturbance forest develops. But the mechanisms for nutrient flux in CWD are not well understood. As the authors explained, chronosequence studies are convenient, but

may be misleading because they cannot account for fragmentation. Material lost by fragmentation may be higher-quality substrate than the persisting material (e.g., inner bark versus wood). As a result of looking only at the residual, lower-quality substrate, investigators may underestimate nutrient efflux.

Jurgensen et al. (1997) reviewed the role of CWD in inland forests of the Pacific Northwest while describing effects of timber harvesting on those systems. They reported that woody residue can be a major pool of nutrients in inland Pacific Northwest forests, and that nutrient content increases with stand age as moisture and fire risk moderate. Woody residue decay appears to be driven by invertebrates and white and brown rot fungi; thus, microclimate affects decay rates. They suggested that water and N content generally increase with age of logs. White rot, which starts the decay process, is followed by brown rot. Sapwood is generally attacked by white rot (which eats cellulose and lignin) and heartwood by brown rot (which eats cellulose and modifies lignin). However, this pattern varies by species of fungi and tree. Jurgensen et al. (1997) indicated that N-fixation in CWD, which generally increases with CWD accumulation, can be 50% of all N fixed in a forest.

However, CWD does not always appear to be a major nutrient source in the Pacific Northwest. In western hemlock/western red cedar sites on Vancouver Island, CWD accounted for only 15% of N in the system and 19 to 25% of P (Keenan, Prescott, and Kimmins 1993). The N content of downed logs was 254 kg/ha on old-growth sites and 271 kg/ha on second-growth sites.

An often overlooked nutrient pathway is the release of nutrients from decaying CWD via fungal sporocarps. Mushrooms are an important part of the food supply of some PNW animals. Thus, CWD management may affect this route of nutrient flow. For example, truffle production increased with greater quantity of CWD in a Douglas fir forest in Oregon (Amaranthus et al. 1994).

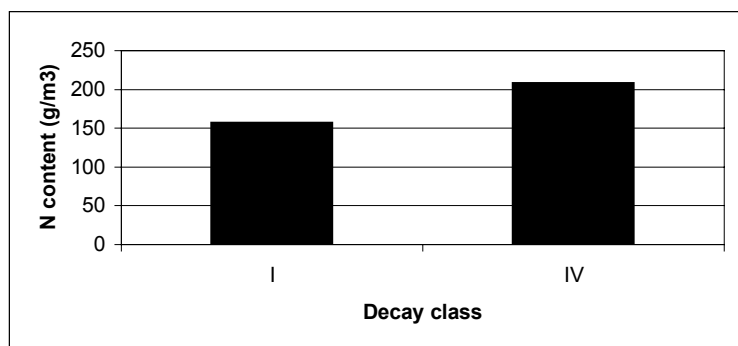
In another study in Oregon, nutrient exports by sporocarps were greater than that from leaching or insect consumption (Harmon et al. 1994). The authors concluded that fungi played two roles in CWD decomposition: immobilizing nutrients in the logs, and subsequently exporting nutrients from the logs via sporocarps. The quantity and type of nutrients exported depended on fungal species, host species, and time. However, in some cases nutrients were exported early in decomposition when nutrients were thought to be immobilized in the CWD, and fungal sporocarps were produced even in the presence of high C:N ratios. Specifically, 2.95% of the N and 6.58% of the P initially in fir logs was exported via sporocarps by the end of 7 years. Sporocarp-mediated export declined by year 7 when sapwood and inner bark decay began. Perhaps N is not immobilized to the extent indicated by chronosequence studies.

6.4.2 Nutrient Gains and Losses

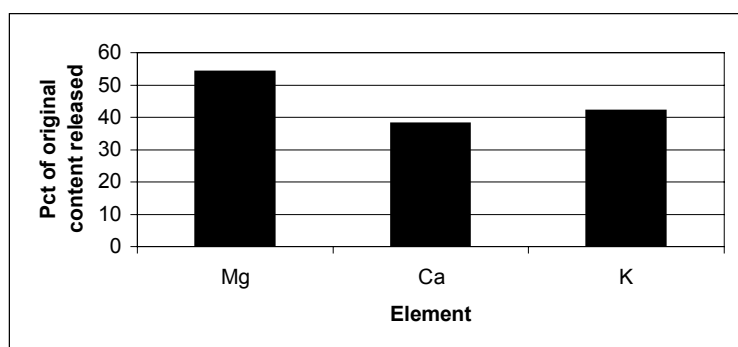
Reported rates of nutrient flux vary by species, log constituents, site, and type of nutrient. Immobilization is common, but nutrients also are mineralized in some situations.

On Vancouver Island, British Columbia, nutrient concentrations increased with age of western hemlock and western red cedar logs (Keenan, Prescott, and Kimmins 1993). N concentration generally remained consistent in Class I and Class II logs but increased from Classes III to IV to V. P concentrations were non-detectable except for Class IV and Class V logs. K concentrations decreased with decay class.

N, P, and Ca concentrations increased steadily with decay class in dry lodgepole pine forests in British Columbia (Wei et al. 1997) and in Oregon (Busse 1994). Although concentrations (g/g) increased in the latter study, volumetric content (i.e., g/m³) increased only for N (Figure 6.2a). Mg, Ca, and K were released (Figure 6.2b).



a.



b.

Figure 6.2 Nutrient Dynamics of CWD in Lodgepole Pine Forests in Oregon (Busse 1994): (a.) Nitrogen Content over Time and (b) Mg, Ca, and K Loss

In the Sierra Nevada Mountains, N concentration increased with decay class in mixed-conifer forests (Harmon, Cromack, and Smith 1987). The increases were nearly threefold (from 0.09 to 0.11% in decay Class I logs to 0.25 to 0.35% in decay Class IV logs).

In western Oregon and Washington, N concentrations also increased with log age in Douglas fir and western red cedar stands (Sollins et al. 1987). The dynamics differed among log components. Initially, bark had greater N concentration than heartwood, but N concentration increased with decay of the heartwood. Ultimately, heartwood had greater N concentrations than bark in the most advanced decay class. P and Mg generally accumulated through Class III, but Na, Ca, and K remained constant. N accumulated more on Douglas fir sites than on western red cedar sites.

In a northwest Washington forest, concentrations of N, P, Ca, and Mn declined over a ten-year period (Edmonds and Eglitis 1989). Of the original mass of N, 17-20% was released. Only Mg was immobilized. C:N ratios increased with decay and bark had greater nutrient content and lower C:N ratios than did wood.

In the western Cascades of Oregon, P, Ca, and Mg increased with decay class (Means, MacMillan, and Cromack 1992). In contrast, K and N decreased. Most K loss was early in decomposition while most N loss was later in decomposition. Na accumulated in early decomposition, then was lost in later stages. Concentrations for all elements except C were lower in logs than in the forest floor. Logs accounted for 28% of all “detrital capital” (the sum of C and nutrients in debris, forest floor, and soil).

In an old-growth forest in the Oregon Cascade Mountains, N was mineralized from downed boles (Hart 1999). The authors estimated that boles contributed 4-6% of the plant-available N. One percent of the total N available in boles was mineralized per year, compared to only 0.4% of total N in the soil. Microbial biomass, microbial respiration, anaerobically mineralizable N, and aerobic net N transformations were all greater in boles than in soil. However, the author had expected microbial activity to be greater in soils than in boles because soils had a lower C:N ratio (117 for boles, 26 for soil). The authors offered two explanations for the higher activity in boles. Boles may have had more readily mineralizable N. Or, the less mineralizable C compounds in boles may have reduced N demand in microbes living in the boles.

Another study in old growth in Oregon (Hope and Li 1997) also found greater N mineralization in downed boles than in soil. In this study, N-fixation rates in downed boles were greater on a young site than on an old-growth site. No clear effects on N flux were apparent for moisture content, substrate type, or root activity.

Edmonds and Eglitis (1989) found that insects did not affect decomposition as shown by a lack of difference between logs screened to exclude insects and control logs. Also, frass did not appear to be a major pathway of nutrient release from decomposing logs. More nutrients were released from litter fall than from frass from decomposing logs. N was released from the decomposing logs, but it may have been from leaching. The authors suggested that N may not have accumulated in logs because there was little opportunity for fungi to import N from adjoining soil. Most fungal decay appeared only in the central portion of the logs.

Rate of N loss from logs may be related to stage of decay. For example, at least two studies have documented no net loss of N until lignin begins to decompose (Berg and McClaugherty 1987; Means, MacMillan, and Cromack 1992). In the latter study, N release occurred after about 44% of the log mass had been lost and the C:N ratio dropped to 411 (initial C:N ratios were greater than 600).

While N may be released by CWD, it may not be immediately available for forest growth. Busse (1994) found that soil microbes quickly immobilized N released from decaying CWD. The ratio of microbial to total carbon (C_m/C_t) was greater under logs than for neighboring soil, regardless of decay class. Although downed wood appeared to have a long-term effect on soil microbial activity, downed wood represented only a small fraction (<3%) of the nutrients in the combined system of CWD, O horizon, and mineral soil. Generally, fungi are very effective at scavenging free N, as shown by the fact that mineral N was not detected in logs with fungal rhizomorphs (Sollins et al. 1987).

6.4.3 Water Dynamics

The water dynamics of CWD can be different than that of soil. For example, boles contained 4-5 times the water content of soil in an old-growth forest in the Oregon Cascade Mountains (Hart 1999). Harmon and Sexton (1995) estimated that 2-5% of incoming rainfall could be intercepted by CWD. Thus, the water dynamics of CWD can affect the water balance of the ecosystem. In turn, the water relations of CWD can influence decomposition rates (too dry as well as too wet), nutrient cycling, and the risk of fire.

Harmon and Sexton (1995) evaluated in detail water dynamics of CWD and its effects on nutrient release. Water dynamics of downed logs varied with tissue (inner bark, outer bark, sapwood, heartwood), species, and decay class. Specifically, moisture content of fir and Douglas fir logs increased with decomposition, with greater moisture content in inner bark than outer bark. Moisture content of sapwood generally increased with decay class, but heartwood did not absorb an appreciable amount of water even after 8 years. In fact, sapwood actually dried out over the 8 years of the study. These moisture trends were not apparent in western red cedar or hemlock.

Harmon and Sexton (1995) also found that less water ran off logs as they decayed. Originally, half the water falling on the logs ran off. But, even after just one year, water began to enter the inner bark layer, and eventually entered and moved through the sapwood. The changes in water uptake affected interception losses and flux of C and nutrients. As water entered and flowed through logs, carbon and mineral nutrients were transferred from the logs to the soil. Flow rates and concentrations of leachate indicated that 0.3-0.45% of the initial carbon content and 0.99-1.86% of the initial N content of logs may have been leached out within the first 8 years of decay. Due to increased water movement through logs and increased mineralization, mass of carbon and nitrogen flowing from the logs increased 10-16 times over the course of the study.

6.5 Summary

The reported amount of mineral nutrients in CWD and the flux rates vary substantially by the specific mineral nutrient and by type of material (bark versus wood), stage of decomposition, and decomposer organisms. For example, N may initially be leached from CWD but taken up immediately by microbes and fungi and then released only after substantial decay. However, the conditions under which this pattern occurs are not clear. The relatively small pool size of nutrients in CWD versus soil components suggests that CWD may not be the major source of nutrients for many forests. However, CWD still may be an important, long-term reservoir of nutrients. Managers should account for the potential role of CWD in long-term nutrient dynamics of forests, but more needs to be known about this interaction. Whether fertilization treatments could compensate for changes in nutrient dynamics was not included in the scope of this review.

7.0 RECOMMENDATIONS FOR FUTURE STUDY

Given the importance of CWD for sustaining wildlife habitat and as a nutrient reservoir, coordinated research efforts likely would improve understanding of the processes that control CWD dynamics. Coordinated field monitoring and simulation modeling should help achieve this goal.

A network of field monitoring sites, established cooperatively among the forest products industry, federal agencies, and state agencies, would facilitate data collection. A set of sites following the same definitions and sampling methods would provide a set of comparable data that would allow investigators to assess the relative importance of climate, forest type, management history, and other factors. For example, CWD planar intercept transects could be established on permanent sample plots to estimate mean downed log volume by decay classes and mean density and basal area of snags. Such data could be made available to the research community.

There also is a need to improve the tools available for modeling CWD dynamics. We found few publications related to CWD modeling. In one such publication, Morrison and Raphael (1993) described the use of Leslie matrix models to describe dynamics between various classes of CWD. Despite this lack of information about modeling CWD, some forest management agencies have added CWD components to growth and yield models. However, most have not published these models. Modeling also is one way to test the level of understanding about processes controlling CWD

dynamics. Furthermore, modeling allows managers to conduct “what-if” analyses for CWD quantities under various proposed management plans. The network of monitoring sites described above could provide data for deriving model parameters and for field testing the models.

A particularly promising modeling approach may be to add snag and CWD components to individual-based forest growth models (e.g., FORET-derived models) so that mortalities generate standing dead or toppled trees. Snags could then be tracked by age and stochastic events could be used to trigger snag fall and windthrow of live trees. Downed logs could then decay under exponential decay models with the decay constants set for species and site. Logs could be classified into decay classes and moved from one decay class to another based on site and species characteristics. (These data would need to be extracted from existing and future studies because such investigations would be beyond the scope of the monitoring network). Model output would represent snag count by size class and downed log counts and mass/volume by decay class. Because individual-based models capture successional behavior and are spatially explicit, temporal and spatial dynamics could be incorporated. Such individual-based models should be more accurate than larger-scaled models based on assumptions such as a simple U-shaped timeline of CWD or a simple exponential decay of a total quantity for CWD output derived from a growth and yield model.

Finally, a number of other questions remain. For example, no studies found in this review addressed the role of snags as lightning attractors (e.g., the effect of a large snag on a ridge top) or in altering fire regimes. Further research is needed into site- and species-specific factors that control CWD dynamics. Questions remain about how much CWD is needed to maintain habitat of particular wildlife species. Some studies have shown that guidelines for snag retention were not met even in old-growth sites. However, manipulative studies to test the adequacy of particular quantities of CWD appear to be rare, although admittedly, such studies were not the objective of this review.

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