September 1994

Sustainable Management of Temperate and Subtropical Plantation Ecosystems

Proceedings of Sino-America Forestry Technology Cooperation Workshop, January 11-12, 1993 Taipei, Taiwan, ROC

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editors

Taiwan Forestry Research Institute
Taipei, Taiwan, Republic of China

Funding for this workshop was provided by
Council of Agriculture, ROC

THE BIOLOGICAL SIGNIFICANCE OF COARSE WOODY DEBRIS IN FOREST ECOSYSTEMS

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INTRODUCTION

Clearcut harvesting, with residual removal and prescribed burnings, is one of the major causes of ecosystem disturbances in the Pacific Northwest forests, and exerts a significant impact on forest ecosystem structure and function that can affect the long-term forest productivity. In the absence of vigorous tree roots, soil nitrification and denitrification accelerate, resulting in losses of N and nitrate leaching (Adamson *et al*., 1987; and Likens, 1979; Frazer *et al*., 1990; Dutch and Ineson, 1990). Increased sulfate adsorption in soil due to acidification following nitrification is coupled with leaching of nutrient cations and Al (Johnson *et al*., 1982; Mitchell *et al*., 1989). Tree removal also induces reduction of siderophores which are important in the iron nutrition of both the microorganisms and tree growth (Perry *et al*., 1984).

Clearcut harvesting reduces nitrogen input from nitrogen fixation (Jurgensen *et al*., 1992); it reduces mycorrhiza formation (Harvey *et al*., 1980) and mycorrhizae-associated nitrogen-fixing microbes (Li and Hung 1987; Li and Castellano 1987; Li *et al*., 1992). N_2 fixation by free-living soil bacteria also is reduced (Jurgensen *et al*., 1989).

Clear-cutting decreases soil organic matter content, especially where logs and tops are removed from the cutting area (Mroz *et al*., 1985; Cromack *et al*., 1979; Wallace and Freedman, 1986). This results in site deterioration by lowering soil cation exchange capacity, reducing moisture retention, and increasing soil compaction. Thus, coarse woody debris---harvest residues and standing dead or unmerchantable trees---left undisturbed on harvested areas can ensure adequate supplies of soil organic matter and serves as wildlife habitat.

STRUCTURAL DIVERSITY OF COARSE WOODY DEBRIS

Disturbances such as, fires, windstorms, insects, diseases, suppression and competition create the coarse woody debris that becomes important structural components of the forest. In plantations, clearcutting leaves relative small amounts of coarse woody debris--branches and small-diameter tops; Large accumulation of coarse woody debris, however, occurs in old growth forests.

Coarse woody debris performs various ecological functions between the time it falls on the forest floor and the time it is finally incorporated into soil. Through biological, chemical and physical processes, structural diversity of coarse woody debris can be recognized into five classes based (Table 1) on its physical characteristics (Maser *et al*., 1988).

Table 1. A 5-class system of decay based on fallen Douglas-fir trees*.

Characteristics	Decay class				
of fallen trees	I	II	III	IV	V
Bark	Intact	Intact	Trace	Absent	Absent
Twigs, 1.18 inches (3cm)	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Color of wood	Original color	Original color	Original color to faded	Light brown to reddish brown	Redbrown to dark brown
Portion of free on ground	Tree elevated on support points	Tree elevated on support points but sagging slightly	Tree is sagging near ground	All of free on ground	All of tree on ground
Invading roots	None	None	In sapwood	In heartwood	In heartwood

*From Maser *et al*., 1988.

BIOLOGICAL FUNCTIONS OF COARSE WOODY DEBRIS

Coarse woody debris provides habitat, shelter, protective cover and resource for many animals in natural forests. Many forest-dwelling small mammals eat mycorrhizal fungi and disperse the mycorrhizal fungal spores through their feces (Castellano *et al.*, 1989; Maser *et al.*, 1978) in forests. Animal feces have been shown to contain N_2-fixing microbes (Li *et al.*, 1986a; 1986b), which play a vital role for tree reestablishment and the maintenance of ecosystem productivity.

Numerous tree species can grow on coarse woody debris. In the Pacific Northwestern North American, *Picea sitchensis* and *Tsuga heterophylla* area commonly found growing on coarse woody debris; *Alnus rubra* , *Pseudotsuga menziesii*, and *T. placata* also can grow on it (Harmon *et al.*, 1986). The forest type of *P. sitchensis-T. heterophylla* has 94-98% of the tree seedling growing on coarse woody debris that occupies only 6-11% of the forest floor (Graham and Cromack, 1982). Ninety-eight percent of *T. heterophylla* seedlings in an old-growth *Pseudotsuga-Tsuga* forest are rooted on coarse woody debris that covers only 6% of the forest floor (Christy and Mack, 1984); and 75% of the tree seedlings grow on woody debris that occupies only 9% of forest floor of *Piece-Abies* forests in British Columbia (Smith, 1955).

Coarse woody debris is a major source of mycorrhizal fungi. Douglas-fir tuberculate ectomycorrhizae, formed by *Rhizopogon vinicolor*, are common in coarse woody debris. With the supplementary fungal sheaths, tubercles confer added benefit to the tree during water stress or serve as a barrier against entrance by pathogen or aphid attack (Zak, 1971). Growth of *T. heterophylla* on coarse woody debris results in formation of diversity of ectomycorrhizae (Christy *et al.*, 1982; Kropp, 1982a, 1982b, 1982c). Harvey *et al.* (1976) found that the moisture retention capacity of decaying wood makes it increasingly important as a reservoir of biological activity in dry summer months (fig.1). Ectomycorrhizae survive in decaying woody under conditions which are unfavorable in the mineral soil (Harvey *et al.*, 1978; 1979).

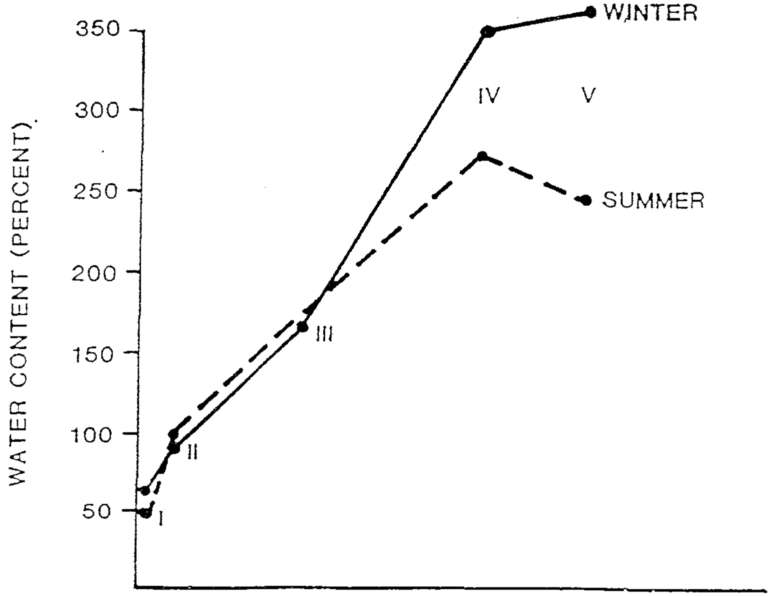

Fig. 1. Moisture content of fallen Douglas-fir trees; each point represents a decay class (Maser *et al.*, 1988).

Lignin in coarse woody debris decays more slowly than cellulose and hemicellulose (Crawford, 1981), leading to an increase in the lignin-to-cellulose ratio as decay proceeds. In undecayed wood, the lignin-to-cellulose ratio ranges from 0.6 to 1.2 for angiosperms and from 0.5 to 0.9 for gymnosperm (Harmon *et al.*, 1986). In undecayed *P. menziesii logs*, the ligin-to-cellulose ratio is about 0.9, increasing to about 1.3, 1.98, and 2.7 after 50, 100, and 150 years of decay, respectively. Lignin finally is incorporated into soil, increasing soil organic content, which supports seedling roots and associated ectomycorrhizae (Harvey *et al.*, 1986, 1987). Soil organic matter also is important for the maintenance of site productivity because of its role in soil water retention, cation exchange, and nutrient supply. P, K, Ca, Mg, Mn, and Na also increase as wood proceed from the least to the most decayed classes (Harmon *et al.*, 1986).These nutrients are essential for microbial and plant growth. Fruiting bodies of mycorrhizal fungi in association with coarse woody debris provide these nutrients to insects, mollusks and mammals (Maser *et al.*, 1979).

Coarse woody debris is the site of nitrogen fixation by asymbiotic organisms. Silvester *et al.*, (1982) showed that N_2 fixation in *P. menziesii* woody debris is microaerophilic. Li and Crawford (unpublished data) demonstrated that most of the N_2-fixers isolated from coarse woody debris are oxygen sensitive for nitrogenase activity. Oxygen concentration in coarse woody debris can be as low as 2% (Paim and Becker, 1963). Wood samples flushed with N_2 can get better nitrogenase activity than the samples determined under ambient atmospheric conditions (Silvester *et al.*, 1982; Li and Crawford, unpublished data). In an old-growth *P. menziesii* ecosystem, total input of N from external sources was estimated at 5 kg ha^{-1} $year^{-1}$ (Sollins *et al.*,1980), additional input by fixation in coarse woody debris would increase ecosystem productivity, as Jurgensen *et al.*, (1992) indicated that large amounts of woody residue left on the harvested site can double the amounts of nitrogen fixation compared with the uncut stand.

Harmon *et al.* (1986) modified a computer model to predict the effects of coarse woody debris on site productivity of a *T. heterophylla* stand of the coastal Oregon. The productivity was monitored over seventeen 30-year rotations, or six 90-year rotations. Productivity of *T. heterophylla* declined quickly if coarse woody debris was removed initially from the stand. The predicted productivity between with and without coarse woody debris was small in the N rich stand but would be greater in a less N rich stand (Harmon *et al.*, 1986).

SUMMARY

Coarse woody debris added to forest floor increases soil organic matter, partly because the well-decayed wood is rich in residual lignin. Soil organic matter is important in maintaining ecosystem productivity because of its role in water retention capacity, nutrient supply and source of mycorrhizal fungi for conifer seedlings. Coarse woody debris creates and maintains structural and biological diversity that contribute forest long-term productivity, because animals, organisms, structure pathways and ecosystem functions are interdependent. Removal of coarse woody debris will reduce these relationships with concurrent reduction of ecosystem processes performed by coarse woody debris.

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