

Effects of silvicultural practices on carbon stores in Douglas-fir – western hemlock forests in the Pacific Northwest, U.S.A.: results from a simulation model

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Abstract: We used a new model, STANDCARB, to examine effects of various treatments on carbon (C) pools in the Pacific Northwest forest sector. Simulation experiments, with five replicates of each treatment, were used to investigate the effects of initial conditions, tree establishment rates, rotation length, tree utilization level, and slash burning on ecosystem and forest products C stores. The forest examined was typical of the Cascades of Oregon and dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg). Simulations were run until a C steady state was reached at the landscape level, and results were rescaled relative to the potential maximum C stored in a landscape. Simulation experiments indicated agricultural fields stored the least (15% of the maximum) and forests protected from fire stored the greatest amount (93% of the maximum) of landscape-level C. Conversion of old-growth forests to any other management or disturbance regime resulted in a net loss of C, whereas conversion of agricultural systems to forest systems had the opposite effect. The three factors, in order of increasing importance, most crucial in developing an optimum C storage system were (i) rotation length, (ii) amount of live mass harvested, and (iii) amount of detritus removed by slash burning. Carbon stores increased as rotation length increased but decreased as fraction of trees harvested and detritus removed increased. Simulations indicate partial harvest and minimal fire use may provide as many forest products as the traditional clearcut – broadcast-burn system while increasing C stores. Therefore, an adequate supply of wood products may not be incompatible with a system that increases C stores.

Résumé : Nous avons utilisé un nouveau modèle, STANDCARB, pour examiner les effets de différents traitements sur les réservoirs de carbone (C) dans le secteur forestier du Pacifique Nord-Ouest. Des expériences simulées, avec cinq répliques pour chaque traitement, ont été utilisées pour étudier les effets des conditions initiales, du taux d'implantation des arbres, de la longueur de la période de révolution, du niveau d'utilisation de l'arbre et du brûlage à plat sur les réserves de C dans l'écosystème et dans les produits forestiers. La forêt examinée était typique des Cascades de l'Oregon et dominée par le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.). Les simulations ont été arrêtées lorsque le niveau de C atteignait l'état d'équilibre à l'échelle du paysage. Les résultats ont été exprimés relativement au maximum de C pouvant être stocké dans un paysage. Les expériences simulées indiquent que les terres agricoles stockent le moins (15% du maximum) de C et que les forêts protégées du feu stockent la plus grande quantité (93% du maximum) de C à l'échelle du paysage. La conversion des vieilles forêts à tout autre régime d'aménagement ou de perturbation entraîne une perte nette de C, alors que la conversion des systèmes agricoles aux systèmes forestiers a l'effet opposé. Les trois facteurs les plus importants pour développer un système de stockage optimal de C sont par ordre d'importance : (i) la longueur de la période de révolution, (ii) la quantité de matière vivante récoltée et (iii) la quantité de débris éliminés par brûlage à plat. Les réserves de C augmentent lorsque la longueur de la période de révolution augmente mais diminuent lorsque la proportion des arbres récoltés et des débris éliminés augmente. Les simulations indiquent que la coupe partielle et l'utilisation minimale du feu peuvent fournir autant de produits forestiers que le système traditionnel de coupe à blanc et de brûlis extensif tout en augmentant les réserves de C. Un approvisionnement adéquat en produits forestiers peut donc ne pas être incompatible avec un système qui augmente les réserves de C.

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Introduction

Since forests are a critical part of the carbon (C) cycle, their management has important implications for the concentration of the greenhouse gas carbon dioxide in the atmosphere (Houghton and Woodwell 1989; Sedjo and Solomon 1991; Shulze et al. 2000). Of all the terrestrial biomes, forests and their associated detritus and soils have the greatest

potential to store and cycle C (Post et al. 1990; Dixon et al. 1994). The degree to which this potential is being met, however, is a long-standing question (Baes et al. 1977; Dale et al. 1991; Post et al. 1990; Dixon et al. 1994) that has taken on increased importance in the wake of the Kyoto Protocol (UNFCCC 1997). Clearing of forests for agriculture (Houghton et al. 1983; Hall and Uhlig 1991), harvesting for commercial forest products (Cooper 1983; Houghton et al. 1983, 1987; Harmon et al. 1990), and the removal of non-commercial products such as fuel wood (Brown et al. 1991; Houghton 1991) have all reduced the amount of C stored in forests. Other management activities such as afforestation, fertilization, and protection from fire and insects may have increased the amount of C stored by forests (Tans et al. 1990; Kauppi et al. 1992; Cias et al. 1995; Pacala et al. 2001). The effect of other common practices such as thinning and species replacement is uncertain, as the focus of past research on those treatments has been on harvestable volume and economic value but not C sequestration.

There are conflicting results for stand-level analyses on the optimum strategy to conserve or absorb C. Many of these differences stem from the way woody slash is treated. Studies excluding woody slash and soils have typically found most management treatments such as clear-cutting to increase C stores (Birdsey 1992), whereas those studies that include these pools do not (Harmon et al. 1990; Krankina and Harmon 1994). Disagreement over the role of plantations in C balances has also occurred in stand level analyses. Conversion of older forest to younger forests has generally been shown to release C to the atmosphere (Cooper 1983; Cropper and Ewel 1987; Harmon et al. 1990; Dewar 1991; Schulze et al. 2000). On the other hand, intensive management practices including the creation of plantations are assumed by many to increase C stores in forests (Johnsen et al. 2001; Kauppi et al. 1992; Kershaw et al. 1993; Sedjo and Solomon 1991). These differences stem in part from the selection of the initial conditions. Establishing plantation forests on a site with degraded soil or that has been deforested can result in a significant uptake of C. Planting the same forest on site formally occupied by old-growth can result in a significant loss to the atmosphere depending on the type and age of the forest.

In this paper a new model, STANDCARB, is used to examine the effects of silvicultural and other treatments on the dynamics of living and dead pools of C in a forest stand. This model avoids many of the problems associated with past models and analyses. The majority of past models used to examine stand-level C dynamics have been analytical models (Cooper 1983; Dewar 1991). While these models can be used to analyze many general aspects of C dynamics, they have difficulty with complicated or real life situations such as thinning and slash removal. Ecological process models (Cropper and Ewel 1987), while more realistic in terms of ecosystem processes than analytical models, are also limited because they usually simulate a fixed mixture of species. This means that fundamental processes such as species succession or replacement due to silvicultural activity can not be included in these simulations. STANDCARB was designed to overcome these restrictions by incorporating the features of a gap simulation model (Urban 1993; Urban et

al. 1993) with an ecological process model (Harmon et al. 1990).

The following paper briefly describes the STANDCARB model and then uses it to examine the effect of various treatments on C stores in Pacific Northwest forests. Treatments examined include the effect of (i) initial conditions, (ii) interval between harvests, (iii) regeneration rates, (iv) thinning, and (v) partial cutting. While some of these treatments have been explored in the past, they have been conducted using different modeling approaches. By using a single model, we can systematically explore potential differences in the treatments and not differences in model structure.

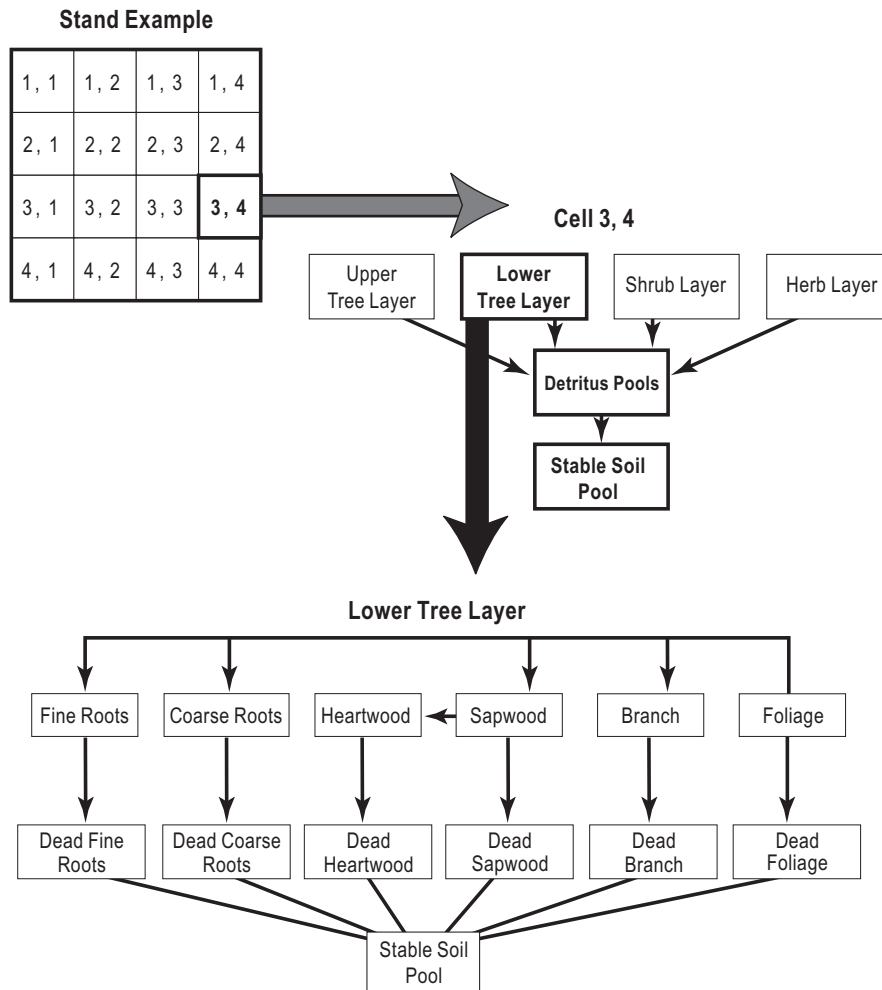
Model overview

Detailed documentation of the model including example input and output files is available from the senior author at request (Harmon et al. 1996c) or via Web site (<http://www/fsl.orst.edu/lter/pubs/modelsfr.htm>). The object of STANDCARB is to simulate the accumulation of C over succession in mixed-species, mixed-aged forest stands. The current version of the model is parameterized for stands in the Pacific Northwest and can be used to investigate the stand-level effects of various regeneration strategies, effects of thinning, patch cutting, tree species replacement by design or by natural succession, slash burning, and wildfires. As in many C models, STANDCARB does not include the effects of nutrient cycling. This means that we assume that nutrient stores will not be influenced by the treatments enough to lead to major changes in site productivity. STANDCARB provides output on 10 live state variables, nine "dead" state variables, and three state variables related to the volume harvested. The state variables are saved as means and standard errors of the mean for each year.

STANDCARB is programmed in C++ and uses difference equations on an annual time step for all variables, except those used to estimate the effects of climate on tree establishment, growth, and decomposition. These climate-related variables are calculated on a monthly time step. Spatially, STANDCARB is designed to simulate the dynamics of a number of cells within a stand. Each cell represents the area occupied by a single, mature tree (in these particular simulations an area of approximately 0.04 ha), although depending on age a cell can represent either a cohort of trees or a single tree (see below). Within a cell, spatial arrangement of trees is not considered. This approach allows the model to have flexibility in terms of species mixtures and (or) tree ages, and allows the user to estimate the degree of spatial variation among cells within a simulation.

STANDCARB uses a number of levels of organization to estimate changes in C stores within a stand (Fig. 1). A stand is composed of a number of cells, each which contains up to four layers of vegetation, six detritus pools, and a stable soil C pool. The four layers of vegetation that can occur in each cell are upper trees, lower trees, shrubs, and herbs. The two tree layers can have different species, whereas the shrub and herb layers are viewed as single "species". Each cell can have any combination of layers except that lower trees can only occur when upper trees are present. Each of the layers can potentially have six live parts: (i) foliage, (ii) fine roots,

Fig. 1. Overall conceptual structure of the STANDCARB model showing the relationship between the stand, cells, plant layers, layer parts, and detritus pools.



(iii) branches, (iv) sapwood, (v) heartwood, and (vi) coarse roots. In addition to these parts, bole, aboveground, belowground, and total live mass are derived from combinations of these parts. Each of the live parts of each layer contributes material to a corresponding detritus or dead pool. Thus, foliage adds material to the dead foliage, fine roots to dead fine, etc. Finally, all the detritus pools in a cell can potentially add material to a stable soil pool.

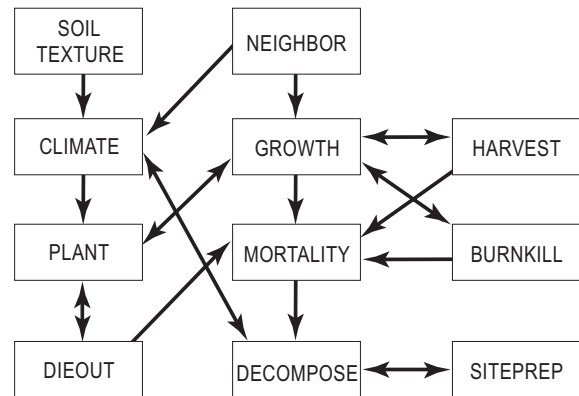
Module descriptions

STANDCARB contains 11 major modules that perform specific functions (Fig. 2). The following section describes the purpose and calculations of each module.

PLANT AND DIEOUT modules

The PLANT and the DIEOUT modules allow STANDCARB to simulate species replacement during succession. These modules determine the “birth” and “death”, respectively, of plant layers and are the most analogous to those found in a typical gap model (Urban and Shugart 1992). The PLANT module determines when herb, shrub, upper tree, or lower tree layers establish in a cell and deter-

Fig. 2. Major modules in the STANDCARB model and the flow of information among them.



mines which tree species will establish in a cell depending upon the local abundance of species as well as the light, temperature, and moisture conditions present as predicted by the NEIGHBOR and CLIMATE modules. The DIEOUT module determines when the upper tree layer needs to be replaced given that trees have a finite life-span. Trees are rep-

resented by a cohort of multiple individuals until they reach an age when self-thinning would leave a single tree. This is also the age when tree crowns reach their maximum extent. Tree mortality at this point means that the upper tree layer has to be replaced by the PLANT module.

GROWTH module

This module calculates the mass of the six live pools of C and is divided into nine functions that perform specific calculations including the absorption of light and foliage growth; the allocation of production to fine roots and woody plant parts; respiration from living parts; heartwood formation; losses from mortality, litterfall, and pruning; calculation of live stores; and conversion of bole mass to wood volume. Each of these functions is invoked for each plant layer present in a cell. Parameters controlling these functions are specific to plant layers, and in the case of trees, species.

The growth of each layer is a function of the amount of foliage present in a layer that is, in turn, dependent on the amount of light absorbed by them. Light is expressed as a percentage of full sunlight, and we assume that taller layers have a competitive advantage over shorter stature layers; if taller layers are present they will absorb light before underlying layers. When the model is run in the cell by cell interaction mode (as it was in these simulations) the light coming into a cell can be reduced by shading from surrounding cells (see NEIGHBOR module). Layers are able to increase their foliage mass until the light compensation point for that layer or species of tree is reached. The amount of light remaining below the foliage of each layer is a function of the mass of foliage of that layer as defined by a Beer–Lambert equation.

We assume that there is a fixed ratio between the mass of fine roots and foliage. This implies that the energy and nutrient gathering portions of plants are in balance. This ratio is life-form specific (herbs, shrubs, and trees) and is assumed to be highest for herbs, intermediate for shrubs, and lowest for trees.

The photosynthate produced by foliage is allocated to the sapwood, branches, and coarse roots by assuming that production of these parts is proportional to the mass of foliage and that the rates of allocation are fixed. The latter assumption is based on the idea that these are structural elements that need to be in balance to function properly. Allocation rates are set to give the proportions of a tree >50 cm diameter at breast height as solved by allometric biomass equations (Means et al. 1994). We used this diameter range, because the proportions of tree parts become relatively stable at this size.

Respiration losses are deducted from the allocation added to woody plant parts. Respiration of all plant parts except heartwood is estimated from their mass and a respiration rate that is a Q_{10} function of mean annual temperature (Ryan 1990). For foliage, fine roots, branches, and coarse roots the fraction that is alive is constant among species and layers. In the case of sapwood, adjustments are made to reflect the varying proportions of the sapwood that is alive (Panshin and de Zeeuw 1970).

The mass transferred from sapwood to heartwood for each tree layer is determined by the rate of heartwood formation and the mass of sapwood. The rate of heartwood formation is parameterized so that the proportion of boles in sapwood

matches the values in mature trees of the various tree species (Lassen and Okkonee 1969).

The change in live stores is calculated at annual time steps from the rates of allocation to the individual parts minus respiration, litterfall, pruning, and mortality losses from competition, small-scale disturbance (see MORTALITY module), timber harvest (see HARVEST module), and fire (see BURNKILL module).

NEIGHBOR module

The purpose of this module is to simulate the interaction among the cells regarding light and is only used when the interactive, multicell mode of the model is run (the mode used in our simulations). The main interaction among cells is one of interception of diffuse and direct radiation. Diffuse radiation can be blocked on all sides, whereas direct radiation is only blocked on the east-, south-, and west-facing directions. The degree of shading is determined by the relative heights of trees in cells and the distance among cells. The height is estimated from the age of the upper tree layer in each cell, and a Chapman–Richards equation that specified the maximum height of a species and the age that maximum was reached. Given that relative differences in tree heights are used to determine shading, the model is relatively insensitive to absolute height. We, therefore, did not vary the maximum height as a function of site index. Foliage is assumed to extend from the ground to the tree top and is evenly distributed over this height. Although this is not the most realistic depiction of foliage distribution, it does result in the competitive effects typical of more complex gap models with less of the computational overhead. Cells are arranged on rectangular grid and effects of cell to cell shading are estimated on eight transect lines. Boundary effects, a problem in all spatially explicit models, were addressed by assuming the surrounding forest was the same as the simulated forest.

MORTALITY module

The mortality rate of foliage, fine roots, branches, and coarse roots when entire trees die and (or) when parts are pruned is determined by this module. Sapwood and heartwood are only transferred to detritus pools when entire trees die. Branches and coarse roots are transferred to detritus pools when both entire trees die and when these parts are pruned. A major assumption of this module is that as the amount of light absorbed by the stand increases, pruning of branches and coarse roots and the mortality rate for entire trees increases. The turnover of foliage and fine roots are constants based on the longevity of these parts. The mortality of upper trees is also dependent upon the time a species has occupied a cell given that each tree has a finite life-span (see the DIEOUT module). When a single tree is in the upper tree layer, then mortality is a function of tree longevity and becomes independent of light.

DECOMPOSE module

This module simulates the input, decomposition, and storage of C in detritus. The functions contained in this module calculate the total amount of detritus input from the various layers and parts, the effect of substrate quality on decomposition, the rate of decomposition, change in detritus stores,

the transfer to a “stable” soil pool, and total detritus and soil stores. All detritus pools are named after the corresponding live plant parts with the prefix “dead” added. Six pools of detritus C are considered: (i) dead foliage, (ii) dead fine roots, (iii) dead branches, (iv) dead sapwood, (v) dead heartwood, and (vi) dead coarse roots. In addition to these detritus pools, the model simulates the dynamics of a stable soil pool that potentially receives inputs from all six detritus pools.

Inputs of material to the detritus pools comes from four potential sources: (i) litterfall, pruning, and mortality; (ii) the dying out of the upper tree layer; (iii) thinning and harvesting; and (iv) fire-killed plants. For any given year, the input can come from several of these sources. Each year the inputs from litterfall and mortality and upper tree die out are calculated first, and then additional inputs from harvesting or burning are added. The total input to a pool is the sum of all the inputs from all the layers in a cell.

The decomposition rate of each pool is dependent on the substrate quality of the inputs to that pool and the current substrate quality of the pool, that is the overall decomposition rate is a weighted average of the input and current stores. The overall decomposition rate is calculated from the substrate effect and the effects of the abiotic factors, temperature, solar radiation, and moisture as calculated in the CLIMATE module. The balance for each detritus pool is the inputs minus the losses from decomposition, consumption by fire, and transfers to the stable soil pool.

In addition to following the dynamics of detritus pools, STANDCARB accounts for changes in a stable soil pool. Mass is transferred from each detritus pool to the stable soil pool as a constant proportion of each detritus pool; climatic influences on these transfers are not modeled explicitly but are included in the calibration stage. In our simulations, inputs to the stable soil pool were from the dead foliage, dead fine root, and dead coarse root pools. As with the detritus pools, the decay rate of stable soil is a function of the substrate and abiotic effects. The former is an average rate for all forms of stable soil material at 10°C and without moisture limitations and is independent of the species or life forms occupying a cell (based on the assumption that extensive decomposition has reduced these differences). The latter represents the combined effects of temperature and moisture calculated by the CLIMATE module.

SOIL TEXTURE module

The maximum amount of water storage in a soil is based upon the soil texture, depth, and fraction of soil free of coarse particles. The fraction of the soil volume that can store water between field capacity and the wilting point is based on soil texture and the fraction of the soil profile with soil particles <2 mm diameter. The depth of soil that can store water is calculated by multiplying the soil depth by the fraction of the soil that can hold water.

CLIMATE module

The CLIMATE module estimates the effect of temperature, precipitation, and solar radiation on the establishment of tree species, growth of plants, and decomposition of detritus. Mean monthly daytime temperature and growing degree-days (with a base temperature 4.4°C) are calculated

once at the start of each simulation and used for all the cells in a stand. Interception, evapotranspiration, water stores, and the effects of climate on decomposition and growth are calculated each month on each cell.

To estimate the amount of water available for plant growth and decomposition, the interception of the canopy, woody detritus, and forest floor is calculated. Canopy interception increases linearly with increasing foliage mass. Monthly canopy interception is calculated by multiplying this proportion by the monthly precipitation.

Once canopy interception is accounted for, the interception by dead sapwood, dead heartwood, dead branches, and stumps is calculated as a function of their mass, current water store, and the maximum moisture content of the woody material. If the moisture content is below the maximum then interception is calculated as the product of the projected area of a detritus pool and the canopy throughfall. If the moisture content of the dead wood pool exceeds the maximum for a dead wood pool, then interception by these pools does not occur. The amount added to the forest floor each month as log “throughfall” (i.e., the water leaving dead wood) is the sum of all the woody detritus interception values subtracted from the monthly canopy throughfall. The amount of interception by the dead foliage pool as a function of the mass, current water store, and the maximum moisture content is calculated in a manner similar to the dead wood pools.

Monthly total potential evapotranspiration of the site is calculated using a modification of the Priestly–Taylor method (Bonan 1989; Jensen 1973; Campbell 1977). Total potential evapotranspiration for a month is assumed to be proportional to the estimated solar irradiance, the monthly mean air temperature, and number of days in a month. The constants used to solve the Priestly–Taylor method are empirically derived after Jensen and Haise (1963) and Jensen (1973) from elevation and the mean minimum and mean maximum daily temperatures for the warmest month of the year.

To estimate the potential amount of transpiration by plants, the total potential evapotranspiration is reduced by a constant fraction each month to account for the evaporation portion of the water loss. This yields a monthly potential transpiration loss assuming that leaf mass and soil water stores are at a maximum. The actual transpiration losses each month are controlled by the soil water stores and the foliage mass. The effect of foliage mass is linear and determined by the ratio of actual foliage mass divided by the maximum foliage mass possible in a cell. The effect of soil moisture on transpiration is calculated from a modification of the relationship developed by Emmingham and Waring (1977). We assume that when soil water potential (WaterPot) is below -0.3 MPa, the transpiration rate decreases exponentially. Volumetric moisture content is converted to water potential using a reciprocal function similar to Running and Coughlan (1988)

The moisture content of six detritus pools and the mineral soil is calculated monthly and represents the balance of inputs through precipitation and outputs via evapotranspiration. For the mineral soil the monthly input is whatever water has not been intercepted by the canopy, dead wood, and the dead foliage pools. The loss of water from the mineral soil is controlled solely by the transpiration from plants,

this assumes that evaporative losses from the mineral soil are minimal. The rate that water is lost from detritus pools is calculated from the monthly evaporative demand (a function of radiation received and temperature) multiplied by a pool-specific drying constant. To calculate the effect of water stores in these detritus layers on decomposition, the values of water depth have to be converted to moisture content based on mass.

Moisture controls decomposition in two ways. The first is through matric potential, which makes water unavailable for decomposers once the fiber saturation point is reached. The second effect is caused by low oxygen diffusion when the moisture content is too high a significant limitation for coarse woody detritus (Harmon et al. 1986). We model the matric potential and diffusion limitation portions separately from the minimum and maximum moisture contents that decomposition occurs for a given detritus pool. The overall effect of moisture is calculated by multiplying these two indices.

The effect of temperature on the detritus pools also has two components. The first part is an increase in respiration rate with temperature following a Q_{10} curve, and the second part simulates the effect of a lethal temperature limit that arrests decomposer activity. These functions are calculated from the Q_{10} rate and the monthly optimum temperature for decomposition. The combined effects of moisture and temperature on decomposition are calculated by multiplying the two indices.

HARVEST, BURNKILL, AND SITEPREP modules

The HARVEST, BURNKILL, and SITEPREP modules determine if a cell is to be disturbed by silvicultural treatments, timber harvest, or fire and the degree to which these disturbances reallocate the C in the living and dead pools.

If a harvest activity occurs on a cell in a given simulation year, then the HARVEST module determines which type and spatial pattern of activity is to occur. Possible activities include: precommercial thinning, commercial thinning, and clear-cut harvest. These activities may be performed on the upper or lower tree layer separately or together on all the cells or a subset of cells. Once the type and timing of a harvest treatment has been determined, the HARVEST module calculates the amount of bole mass removed, the mass of bole left in tops and stumps, and the mass of other detritus or slash created by the harvest.

The BURNKILL module determines the timing and amount of live vegetation killed by natural- or management-caused fire reducing the amount of live C in the GROWTH module and transferring some to the DECOMPOSE module as fire-killed detritus inputs. Not all the live vegetation killed by fire is necessarily transferred to detritus; some is consumed by the fire itself. The fraction of plant material that is killed and consumed by fire also increases with fire severity. Above- and below-ground plant parts are consumed by fire to different degrees, with below-ground parts having less material consumed for a given fire severity.

When a natural- or management-caused fire occurs the SITEPREP module determines the degree that detritus in the DECOMPOSE module is reduced. The degree that the detritus pools are reduced is determined by the user; in this version we have assumed that as fire severity increases from

Table 1. Model predictions of steady-state C stores of each of the two species as well as the mixed forest used in the simulations.

| Species | Live | Dead | Total |
|-----------------|---------------------------|-------------|--------------|
| Western hemlock | 589.8 (17.5) ^a | 267.1 (3.5) | 859.9 (17.1) |
| Douglas-fir | 702.9 (33.8) | 208.0 (2.6) | 911.0 (31.5) |
| Mixed forest | 595.5 (24.9) | 265.5 (4.0) | 861.1 (24.8) |

^aValues are means with SEs given in parentheses ($N = 5$).

low to high the fraction of each of the aboveground detritus pools removed by fire increases. It is assumed that the dead coarse roots and the stable soil pools do not decrease when there is a fire.

Model calibration

Given that the purpose of our simulation experiments was to predict the relative effects of various treatments on potential C stores, we calibrated STANDCARB to represent a common mixed species forest in the Pacific Northwest. Therefore, we make no claims that the absolute levels of C stores are being predicted a priori. The stands simulated represent a mixture of two species, each with different potentials to store C (Table 1). The parameters of these species (Appendix A) are based on values estimated for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with the latter storing approximately 6% less than the former (Table 1). Therefore, a species with high potential is eventually replaced by one with lower C stores potential.

The climate and radiation data used to drive the simulations was from the H.J. Andrews Experimental Forest, a typical Oregon Cascade site. The soil used was a loam, with no coarse fragments >2 mm in diameter and a depth of 1 m. Live biomass accumulation rates of the species were calibrated to match those predicted from yield tables (McArdle and Meyer 1930; Barnes 1962) for highly productive sites (Fig. 3). Stores in detritus and soils were calibrated to published data (Grier and Logan 1977) but also match those of other more recent studies of forests that had been disturbed catastrophically by fire 400–500 years ago (Harmon et al. 1998; Smithwick et al. 2002) (Fig. 4).

Forest products stores

Although our primary purpose in these simulation experiments is to examine the potential effect of various practices on C stores of forests, some C is stored in forest products following timber harvest. Therefore, comparisons of natural disturbances versus harvest systems are more valuable if forest products as well as ecosystem level C stores are considered (Houghton et al. 1983). This approach also allows one to track all the C produced by the forest and obeys the law of conservation of mass. We used the FORPROD model (Harmon et al. 1996b) to estimate the fraction of harvested boles that is initially stored as forest products and to estimate the average annual rate of release to the atmosphere. Based on current log uses (pulp-, saw-, and veneer-logs), manufacturing efficiencies, as well as product and waste lifetimes, we estimated that 48% of the harvested logs are

initially stored and the rate-constant of release to the atmosphere is 0.0085 year^{-1} (based on semi-logarithmic regression of stores predicted by FORPROD, $r^2 = 0.99$, $N = 10$). These parameters were used to convert the mass of harvested C to forest products and to estimate decreases as this material is incinerated and decomposed. In the case of multiple harvests in a simulation run, we added the new harvests at the appropriate time and calculated subsequent losses. We assumed that manufacturing efficiencies would not change in the future and that product uses and longevity would not change. While these parameters are likely to change in the future, this is unlikely to change the ranking of results.

Simulation of managed forests

A series of simulation experiments was conducted to test the effects of initial conditions, tree regeneration rate, slash burning, harvest rotation length, and partial harvest. Each of these simulation experiments is named after the main effect being examined as described below; however, we often considered other factors in these simulation experiments to test for possible interactions. In each experiment, simulations were started from bare ground, with only the stable soil C fraction present. The model then was allowed to run 500 years to approach a quasi-steady state before the experimental treatments were imposed. Five simulations, each with a different random number seed, were run for each experimental treatment. The processes involving random numbers include planting of layers and mortality of upper trees. Each simulation consisted of 100 cells that were allowed to interact through shading, and the border was assumed to be the same age as the stand mean.

Initial conditions

The amount of C uptake and release is a function of the difference between the starting point and the ending point. While seemingly obvious, much potential confusion exists in the literature because the ending point is often emphasized more than the starting point. These simulation experiments were designed to examine the effect of initial conditions (i.e., the starting point) on changes in C stores. We examined several common situations: (i) conversion of bare ground to an old-growth forest (here defined as a forest greater than 200 years in age), (ii) conversion of bare ground to plantations with a 60-year rotation (i.e., the interval between harvest), (iii) conversion of old-growth to plantations with a 60-year rotation, (iv) elimination of low severity wildfires, and (v) elimination of moderate severity wildfires. The latter two simulation experiments represented stands that were burned once every 40 years with low-severity fire killing 10% of the upper tree layer mass and moderate-severity fires killing 20% of the upper tree layer mass. The amount of detritus removed by these types of fires was calculated (Table 2). The plantation treatment represented high bole utilization (i.e., 100% cut and 95% removed) and a high-severity slash burning fire (Table 2).

Tree regeneration rate

Although rapid tree regeneration is often assumed in C stores assessments (e.g., Harmon et al. 1990), a considerable lag between disturbance and the establishment of tree regen-

Fig. 3. Comparison of calibrated model run to yield table for Douglas-fir forest with a site index of 51 m at 100 years (McArdle and Meyer 1930).

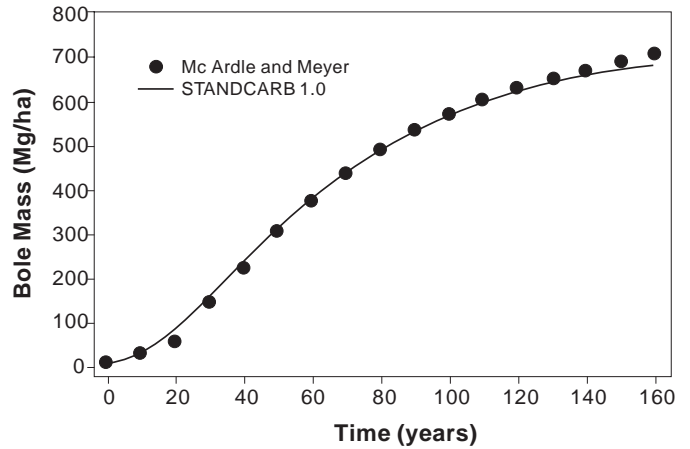
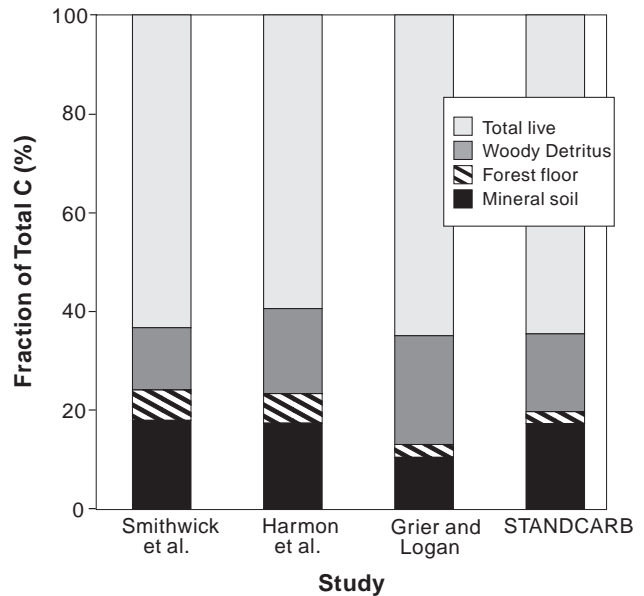


Fig. 4. Comparison of model predictions of distribution of C in Douglas-fir – western hemlock forest to that from field studies (Grier and Logan 1977; Harmon et al. 1998; Smithwick et al. 2002).



eration can occur (Cohen et al. 1996). This regeneration lag can reduce C accumulation in live C (Turner and Long 1975), as well as reduce stores in woody detritus (Harmon et al. 1986). We, therefore, examined the effect of repeatedly halving the upper tree establishment rate constant from 0.6 to 0.3 to 0.15 to 0.075 to 0.0375 year^{-1} . This series of rates would correspond to 5, 10, 20, 40, and 80 years for 95% of the simulation cells to have upper trees established in them. For each of these tree establishment rates, two sets of initial conditions were examined: (i) bare soil with only stable soil stores and (ii) a windthrown old-growth forest, 500 years of age with no removal of boles. These represented the range of initial conditions regarding detritus amount and they were selected to examine the interaction between tree regenera-

Table 2. Fraction of detritus pools remaining after fire used in various simulation experiments.

| Detritus pool ^a | Burn severity | | |
|----------------------------|---------------|----------|------|
| | Low | Moderate | High |
| Dead foliage | 75 | 50 | 0 |
| Dead fine roots | 100 | 75 | 0 |
| Dead sapwood | 95 | 75 | 50 |
| Dead heartwood | 100 | 90 | 50 |
| Dead branches | 75 | 50 | 5 |
| Dead coarse roots | 100 | 100 | 50 |

^aThe stable soil pool is assumed to lose no C during a burn.

tion rate and the initial amount of detritus. These 10 combinations were then examined for three disturbance intervals (150, 300, and 600 years) to examine if there was an interaction between regeneration rate and disturbance interval.

Utilization level: slash burning

The type of timber harvest and preparation of the site for planting can potentially have major impacts on the amount of C stored in a forest. The fraction of trees cut and proportion of boles removed during harvest has varied dramatically over the last century (Harmon et al. 1996a). Likewise the type of slash burning has varied from virtually none to hot broadcast burns that removed virtually all the fine and much of the coarse fuels. We examined four combinations of utilization and slash burning: (i) low utilization, no fire, (ii) high utilization, no fire, (iii) low utilization, followed by a high-severity slash-burning fire, and (iv) high utilization, followed by a high-severity slash-burning fire. Low utilization was defined as cutting 80% of the tree mass and removing 80% of the felled bole mass, whereas high utilization was defined as cutting 100% of the tree mass and removing 100% of the bole mass. The no-fire scenario left all detritus on the site and did not kill any of the vegetation remaining following the cutting. The high-severity fire scenario killed all the vegetation surviving the cutting and consumed a large fraction of the aboveground detritus (Table 2, see high-severity fire).

Rotation length

Increasing the rotation length has often been suggested as a way to increase the live and dead C stores of forests. We examined the effect of increasing the time between harvests from 40 to 120 years in 20-year increments. These ages bracket the planned rotation times on industrial and Federal forest lands in the Pacific Northwest, respectively. Two combinations of timber utilization and slash burning were examined in this set of simulation experiments: (i) high utilization, followed by a hot slash-burning fire and (ii) low utilization without a slash-burning fire. Utilization levels and high severity fire effects were the same as those used in the utilization level – slash burning simulation experiments described above.

Presentation of results

As our presentation of simulation results differs from many past papers, an explanation is warranted. In most cases, changes in C stores have been presented over time for individual stands (e.g., Harmon et al. 1990; Dewar 1991;

Row 1996). While there is nothing inherently wrong with this approach, it does make comparison of treatments difficult, especially when the timing of events is not similar. To make the comparisons as independent of time as possible, we have calculated the mean C store over the last rotation or disturbance interval being examined (Parks et al. 1997). This eliminates short-term fluctuations but also has the advantage of representing C stores of a theoretical landscape with a uniform age-class distribution (Harmon et al. 1990; Krankina and Harmon 1994; Harmon 2001). The maximum age-class of this theoretical landscape is the rotation age or disturbance interval. This makes it possible to compare the effect of treatments on a landscape-level steady-state basis, rather than at particular times. Shifting from a silvicultural system that stores more to one that stores less on the landscape level would result, therefore, in a net loss of C to the atmosphere (and visa versa).

In addition to comparing the amount stored in landscapes with different treatments, it is important to understand the approximate time required to reach new steady-state levels of C stores when a change is introduced. To estimate the time required for a theoretical landscape to adjust to treatments, we calculated a moving average over time, with the length of the window used equal to the rotation or disturbance interval of the experimental treatment. For example, if one is moving from an old-growth system to a 40-year harvest rotation, the window used to calculate the average is 40 years. If the rotation length was 60 years, the window would be 60 years, etc. The advantage of this approach is that by the time the end of the first rotation of the new treatment is reached, the entire theoretical landscape has been converted to the new system, and the new uniform age-class distribution has been imposed. Although the age structure of the new landscape is in steady state at this point, the C stores may not. We, therefore, calculated the time difference between the time the age structure and C stores steady state was reached.

Finally, the forests we have simulated admittedly represent a particular case and the absolute levels of C stores predicted will differ from other cases. To eliminate differences in productivity levels and other factors, we have presented the results in relative terms scaled to the maximum landscape stores the model simulated. This maximum from the model was $875 \pm 5.8 \text{ Mg}\cdot\text{ha}^{-1}$ (mean \pm SE; $N = 10$) for a landscape consisting of entirely 400- to 500-year-old forests and is near the Pacific Northwest mean of $773 \text{ Mg}\cdot\text{ha}^{-1}$ estimated by Smithwick et al. (2002). The lower value for Smithwick et al. (2002) is caused by the fact that their study included forests east of the Cascades, and these have far lower C stores than those west of this mountain range. Although it is unlikely this landscape could be maintained over time because of natural disturbances, it represented a logical theoretical upper bound of C stores. Therefore, it was assigned a value of 100%, and all other landscape capacities were standardized by dividing by 8.75.

Results

Initial conditions

The potential for a landscape to store C was primarily a function of frequency and severity of disturbance. The landscape with the minimum C store (15% of maximum) was an

Table 3. Effect of treatments on C stores in a landscape with a uniform age distribution.

| Treatment | Fraction of maximum C stores (%) ^a |
|--------------------------------------|---|
| Agricultural row crop | 15.0 (0.2) ^b |
| Old growth to plantation | 30.8 (0.1) |
| Agriculture to plantation | 30.7 (0.1) |
| Agriculture to old growth | 82.8 (0.6) |
| Low-severity burn | 87.7 (0.4) |
| Low-severity burn to protection | 92.9 (1.8) |
| Moderate-severity burn | 71.8 (0.8) |
| Moderate-severity burn to protection | 91.8 (1.2) |

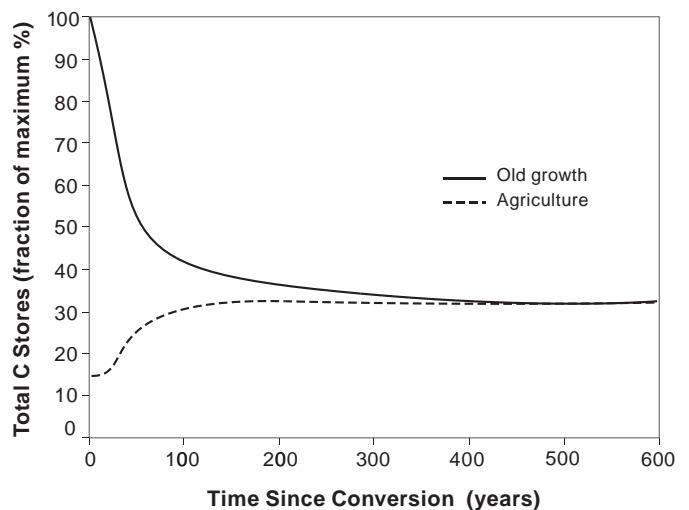
^aThe maximum was set at 875 Mg C·ha⁻¹.

^bValues are means with SEs given in parentheses ($N = 5$).

agricultural row crop system that consisted mostly of stable soil stores and minimal live vegetation (Table 3). The highest C store was for burned forest protected from either low- or moderate-severity fire; these landscapes stored between 91.8 and 92.9% of the maximum. Given sufficient time the differences of initial conditions on landscape C stores decreased. This is most evident for the plantation system, which stored similar amounts of C at the landscape scale regardless of starting from an agricultural system or old growth (Fig. 5).

Differences between landscapes indicate conversion from old-growth to an agricultural landscape will release the greatest amount of C, whereas conversion of a fire-protected landscape to a frequent, low-severity fire regime would release the least. The latter transition is unlikely to be smooth, and an intermediate period of much lower stores at the landscape level would be expected. Although plantations converge on a common landscape steady state regardless of origin, this does not mean initial conditions are not important. Plantations on former agricultural landscapes had double the stores of an agricultural system. In contrast, conversion from an old growth dominated system to a plantation system decreased stores by approximately two-thirds, depending on the origin of the old-growth stand. The maximum gain in C stores at the landscape level would come from converting an agricultural to an old growth dominated landscape, which results in a fivefold increase. This is compared to a twofold increase for establishing plantations on agricultural land.

With the exception of agricultural clearing, the rate of transitions between landscape states appears to be a function of the difference in C stores between landscapes. The landscape transition with the fastest timing is probably the conversion of forests (either old growth or plantations) to agricultural use. Although we did not model this change over time, it might occur in as little as a decade for a reasonably large landscape. The modeled transition from an agricultural to a plantation landscape was quite rapid, with the ecosystem and total C stores (i.e., including products) being reached in one and three rotations of 60 years, respectively. The slowest rate of change was for the transition between the agricultural system and an old-growth system, which took 300 or more years. Conversion from old growth to plantations took at least four rotations of 60 years required for the ecosystem to reach a C steady state. The inclusion of

Fig. 5. Effect of initial conditions on total C stores after conversion to a 60-year, high-utilization tree plantation: (i) conversion from old-growth forest and (ii) conversion from agricultural row crops.

forest products extends this differential even further to eight rotations (480 years).

Tree regeneration rate

There was a small but steady decrease in the landscape C stores as tree regeneration rate (defined as the time for 95% of the cells to be occupied by trees) increased (Fig. 6). The decrease, however, is not as dramatic as expected with about a 5% decrease for a disturbance interval of 600 years as the time of tree establishment increases from 5 to 80 years. Disturbance interval had a larger influence than tree regeneration rate on landscape C stores. Halving the disturbance interval to 300 years decreased landscape stores by ~10%. A further halving of the disturbance interval to 150 years resulted in an additional decrease of ~20%. As expected, landscapes starting with a higher amount of detritus (i.e., windthrow) stored more C than those with less (i.e., bare soil).

Utilization level and slash burning

Slash burning had a greater effect on landscape C stores than the fraction of boles harvested and removed (Fig. 7). The lowest stores were predicted for systems incorporating a high-severity slash-burning fire. The obvious reason is that this type of fire removes a great deal of detritus, but less obvious is the effect on plant survival. This is most evident in the low-utilization – high-severity slash fire case where 20% of the trees were left after cutting but were then killed by the subsequent fire.

Rotation length

Increasing the rotation length or the interval between harvests increased the total amount of C a landscape stored (Fig. 8). In the case of the high utilization, severe slash-burning harvest system, increasing the rotation length from 40 to 120 years increased landscape stores more than 2.5-fold. The increase in stores associated with increasing rotation for the low-utilization – no-fire harvest system was less dramatic, with only a 16% increase as rotation length was

Fig. 6. Effect of rate of tree establishment, expressed as time for 95% of the cells to be established, on C stores, expressed as a fraction of the landscape maximum. Values in the key are disturbance intervals in years. WT, windthrow; OF, old field.

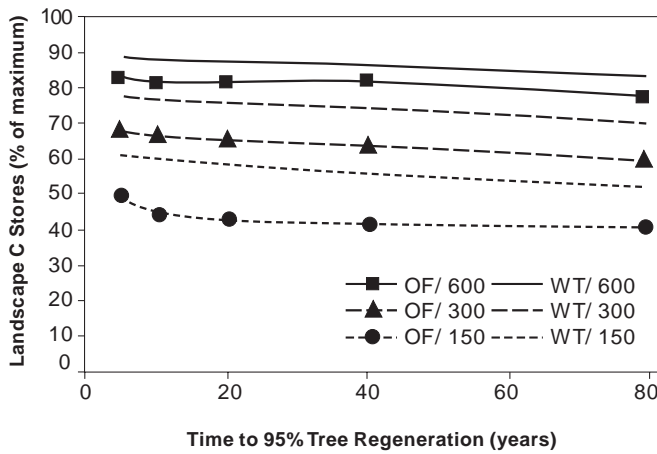
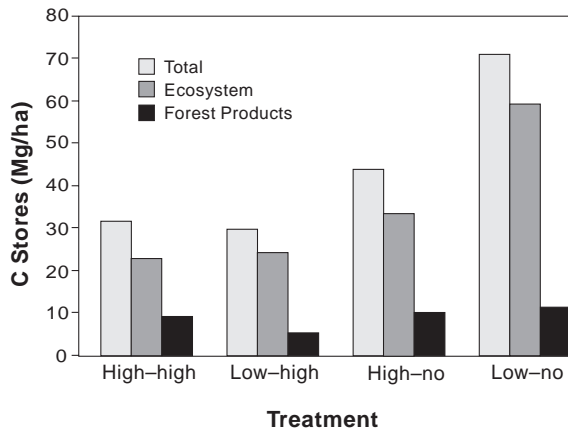


Fig. 7. Effect of tree-utilization and slash-burning system on C stores, expressed as a fraction of the landscape maximum. High-high, high utilization – high-severity fire; high-no, high utilization – no fire; low-high, low utilization – high-severity fire; low-no, low utilization – no fire.



varied from 40 to 120 years. In both harvest systems, increasing rotation length beyond a certain point marginally increased C stores.

In this series of simulation experiments, the largest effect on C stores was associated with the harvest system used. For example, a 40-year rotation, low-utilization – no-burn system stored 3.4 times more than the same rotation using high-utilization standards and high-severity slash-burning fires. The difference between systems was less at longer rotations, but even for a 120-year rotation the difference between harvest systems is as large or larger than the difference for increasing rotation length. In part these differences are caused by increases in live and detritus stores associated with the low-utilization system. Rather than being burned within a few years of harvest, detritus is allowed to decompose slowly in place. Moreover, live trees remain in the low-utilization system, many of which continue to grow.

Fig. 8. Effect of rotation length on ecosystem C stores, expressed as a fraction of the landscape maximum. High-high, high utilization – high-severity fire; low-no, low utilization – no fire.

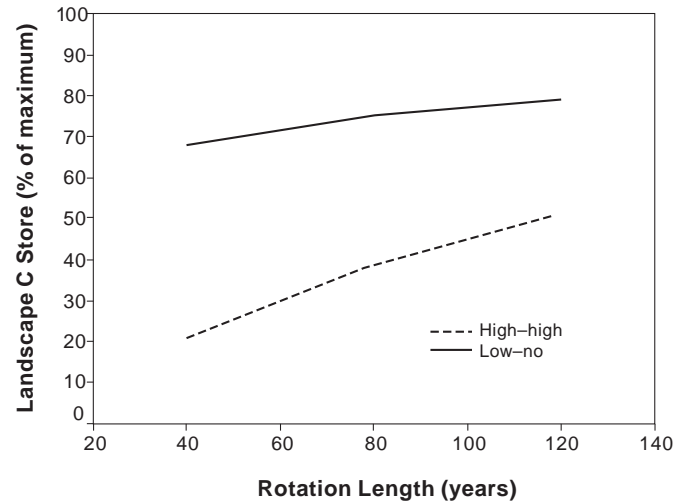
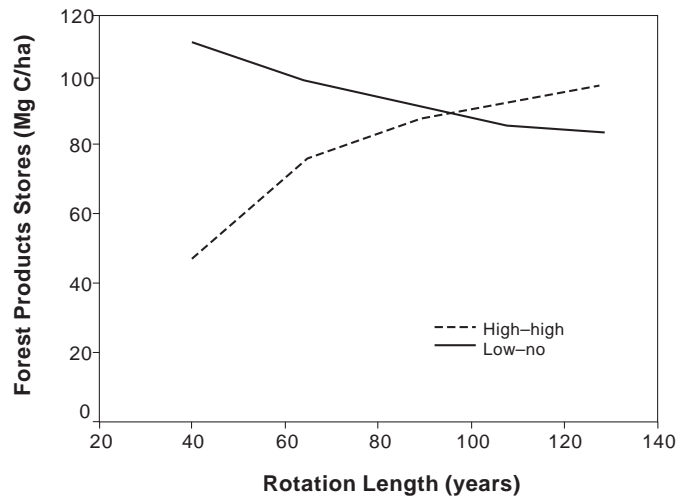


Fig. 9. Effect of rotation length on forest products stores. High-high, high utilization – high-severity fire; low-no, low utilization – no fire.



Despite the fact the lower utilization system removed a smaller fraction of the bole mass, for shorter rotations this system resulted in more forest products than the high-utilization system (Fig. 9). The amount of forest products stores decreased with rotation length for the low-utilization system; however, it did not fall below the high-utilization system until a rotation length of approximately 90 years. For the high-utilization harvest system, the amount stored in forest products increased as rotation age increased but leveled out as rotation length approached 100–120 years. These results have important implications for the supply of forest products, which is usually assumed to decrease if utilization standards (fraction cut and removed) decrease. Ironically, these simulations indicate it may be possible to store more in the ecosystem and in forest products if utilization standards are decreased, not increased.

In this set of simulation experiments, an old-growth landscape was converted to a plantation system. The relationship between rotation length and the time required to create the new landscape-level C steady state increased with decreasing rotation length. This is best seen by comparing the 40-year rotation, which took almost 10 rotation lengths to reach a C steady state to the 120-year rotation, which took two rotation lengths to reach a C steady state. Even in absolute years, the shorter rotation system took longer than the longer rotation system (400 vs. 300 years).

Discussion

The lack of attention to initial conditions in various assessments has led to considerable confusion in the literature about the effects of various silvicultural and management treatments. As our simulation experiments show, it is not so much the effect of the treatment per se that is important but how it relates to the initial conditions. Thus, one would expect that establishing short-rotation plantations on a degraded old field will increase C stores and result in a net uptake of C from the atmosphere (Row 1996). Establishing the same system by converting older forests, will, however, have the opposite effect (Harmon et al. 1990). The issue of intensity of management also is not particularly relevant. Kurz et al. (1996) indicated that not all management activities lead to a decrease in C stores making their case by contrasting the results of converting old-growth to short-rotation plantations (Harmon et al. 1990) versus the effects of fire suppression. Our analysis indicates both conclusions are valid and can be predicted from change from initial conditions but not necessarily the intensity of management.

Our simulation experiments also shed light on another area of potential confusion, specifically the effect of detritus on C stores and flux. Several past modeling studies (e.g., Birdsey 1992) have indicated that NEP (net ecosystem production) is always positive regardless of the amount of detritus left after disturbances. We found no support for this conclusion in our own simulation experiments or field studies (Janisch and Harmon 2002). Rather, the pattern of NEP following disturbance is strongly controlled by the amount of detritus left following disturbance. Although we examined the most extreme conditions (bare soil and windthrow), we can estimate the amount of detritus required to have decomposition offset the positive portion of NEP caused by plant production. The simulations starting from bare soil in the tree regeneration simulation experiments indicate the maximum possible NEP at various times. The overall detritus decomposition rate constant of 0.05 year^{-1} can then be used to calculate the initial mass of detritus required to offset this positive NEP. The maximum possible NEP at 10 and 20 years for example would be approximately 1 and 2 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, respectively. The initial amounts of detritus required to offset these rates of positive NEP are 35 $\text{Mg C}\cdot\text{ha}^{-1}$ to offset the first decade and 100 $\text{Mg C}\cdot\text{ha}^{-1}$ to offset the second decade of positive NEP. These amounts of detritus are surprisingly small (4 and 11% of the maximum potential C stores) and could easily be accounted for by not harvesting the branches or roots or by leaving only a portion of the preharvest detritus in place. Thus, it seems highly unlikely that commonly used harvest systems could remove

enough C to avoid a period of negative NEP of at least a decade.

Although our simulation model predicts stand-level impacts of various treatments, it is extremely useful to present these results on a theoretical landscape basis. This is a non-traditional way to present sequestration results but avoids the problem of mixing short-term trends with longer term trends in NEP (Harmon 2001). For most of our simulation experiments there are periods when each treatment had short-term periods of negative or positive NEP. When the landscape reaches a C stores steady state these short-term changes in NEP offset one another. However, when one type of disturbance regime or management is replaced by another at the landscape scale, there is also a long-term trend in NEP that can be positive or negative depending on the relative difference between the initial condition and the final state. It is the latter trend that is of most interest when interpreting the impact of altering management strategies.

The time required for transitions from one landscape to another appears to be dependent on several factors. Firstly, the magnitude of change from one state to another is important with more time required the greater the change in C stores. Secondly, the difference between establishing a steady-state age structure versus steady-state C stores increases as the ability of the new system to maintain detritus and forest products stores decreases. This is because these two components have the slowest dynamics of the overall system, and if they cannot be maintained, their dynamics dominate the long-term changes of the system. For example, harvesting a hectare of old-growth forest creates 200 Mg C of new forest products, but the steady-state amount of forest products that can be maintained from 1 ha of the plantation forest is 74–100 Mg C . The rate constant of 0.0085 year^{-1} controlling forest products losses indicates >350 years are required for this pool to reach steady state. This second point leads to the final factor controlling the time required to move from one management system to another: the direction of the change. Changing from a system with a minimum of detritus (e.g., agricultural fields) and forest products to one with higher amounts of these two components may be faster than going the opposite direction. The third factor is likely to be modified by the relative difference in stores, with the time required increasing as the relative difference increases. Finally, the landscapes we considered were theoretical. Real landscapes have probably not developed with the uniform age-class structure presented in our results. Examination of actual landscapes and evaluation of realistic rates as one management system is replaced by another would add additional insight into the feasibility of changing management systems.

Forest products stores, while considered in our analysis, were not a major store of C compared with the ecosystem itself comprising 10–25% of the total. Our estimates of product stores are low, in part because they do not include emissions associated with wood waste based fuels. This differs from the approach used by Row and Phelps (1996) who assumed most wood-based fuels offset fossil fuel usage and, thus, should be counted as C stores. We feel, however, there are several issues that need to be addressed before one can assume these wood fuel emissions are C stores. First, one must demonstrate that wood-waste fuels are actually offset-

ting fossil fuels. The answer to this question depends on regional energy sources. For regions with high direct use of fossil fuels for forest products manufacturing or that generate a large fraction of electrical energy that is used in forest products manufacturing, it may be reasonable to assume that burning wood waste offsets use of fossil fuel C. This then could be envisioned as a potential store of C. In regions where hydro power is a major source of energy that could be used in forest products manufacturing, the assumption that fossil fuels are saved by the burning of wood waste is potentially erroneous. Secondly, if one decides to count burning wood waste as a C store, then one should deduct all the fossil fuel costs associated with harvesting, transportation, manufacture, and disposal of forest products. As a detailed energy analysis of the potential sources of manufacturing energy and the fossil fuel costs of handling harvested wood was beyond the scope of this paper, we have opted for the simpler assumption that loss of C by any process (fire, manufacturing, or decomposition) is a loss of C to the atmosphere.

Selecting the optimum management strategy requires that C stores be balanced against the production of forest products. Our simulation experiments indicate that if C stores were the only concern, then conversion to an old-growth dominated landscape would be the best option as this system stores close to 90% of the potential maximum, even with fire or wind disturbance and no timber salvage. This strategy, however, would not supply the wood products needed by society and could lead to higher fossil fuel use in the long run if substitute materials required high energy inputs for manufacture. The best system in terms of balancing C stores against forest products production appears to be either a partial-cutting system or a 80- to 100-year rotation with a low-utilization harvest system in which fire use is minimized. These systems would provide as much or more forest products as the short-rotation – high-utilization system in common use today and would store at least twice the amount of C at the landscape level as short-rotation – high-utilization systems.

The three factors most important in developing an optimum C sequestration system are (i) rotation length, (ii) amount of live mass harvested, and (iii) amount of detritus removed by slash-burning fires. These three factors are not independent but clearly interact. By increasing rotation length the C stored in live and detritus pools increases approaching that of old-growth forests. Although the benefits of increasing rotation length decrease eventually, intervals of up to 100–120 years increase C stores and supply high amounts of forest products. The increase in forest products is associated with the fact that older forests have more C to harvest. Gains associated with increasing rotation length interact with the utilization standards and use of fire, with the largest gains evident in the high-utilization – high-severity fire system. Next to rotation length, the largest gain in C stores would appear to be associated with low tree utilization systems. While counterintuitive, this result makes sense as trees that are not cut continue to grow eventually providing higher C stores and amounts of forest products. This system may not be possible to maintain if the species is short lived or requires high light levels to establish and grow, however, it may be possible for a species such as Douglas-fir, which is

long lived and can establish and grow under high to moderate light levels. Finally, by increasing the amount of detritus one can increase the C stores of a system. This is also a counterintuitive result as the decomposition of this material leads to a net loss from the ecosystem and in some cases can offset plant production causing NEP to be negative. While it is true that decomposition leads to a loss, alternative treatments such as slash-burning fires, use as fuel wood, and even processing into forest products leads to a far more rapid loss to the atmosphere with a 50% loss to the atmosphere in 2 years if this material was put through the latter process. Keeping this material in the ecosystem might be the best option as long as tree regeneration rates are not reduced. There may be additional benefits as well in terms of nutrient availability, although exceedingly high levels of woody detritus may temporarily reduce nutrient availability.

Our model included the effects of changing species mixtures and age structures on C stores. It accounted, therefore, for changes in these factors brought about by the simulated treatments. However, as in many C models, the effects of nutrient availability were not considered. As long as the treatments did not alter this status, then our results are probably robust. This assumption is likely to be true for most of the treatments we considered with the exception of those involving severe fires. In this case, complete removal of the litter layer is likely to reduce the productive capacity of the ecosystem (Aber et al. 1979; Kimmins et al. 1990). The net effect of ignoring this process is likely to make the differences predicted by STANDCARB to be conservative. That is the high-utilization – high-severity plantation system resulted in the lowest C store of any treatment except an agricultural one. If nutrient availability is reduced in this extreme treatment, then the C store is likely to be lower than we predicted. Exploration of this hypothesis using a model that includes nutrient limitations (e.g., Kimmins et al. 1999) would be helpful.

Our analysis indicates that some nontraditional systems, such as partial harvest, with minimum use of slash-burning fires, may provide as much timber harvest as traditional systems. They also appear to increase C stores to twice the level that can be maintained in a traditional system. Therefore the issue may not be one trading off C stores versus the supply of wood products as much as it is one of assessing the economic practicality of these nontraditional systems. Given the area occupied by forests in the Pacific Northwest, U.S.A. ($\sim 10^7$ ha), doubling of the current stores in this region could sequester an additional ~ 2.5 Pg of C. This would have an economic value of \$25 to \$50 billion given the range of prices currently being discussed (\$10 to $\$20 \cdot \text{Mg}^{-1}$). Therefore, the change from the current system to one that optimizes C stores may depend more on the timing of the harvest rather than the total amount of harvest or C value provided from a landscape (Sedjo et al. 1997). Another consideration is the silvicultural practicality of these nontraditional systems. Our simulation experiments indicate there are no obvious problems for an ecosystem that provides a major share of the U.S. timber supply. This is despite the potential effects of nontraditional silvicultural systems to shift species composition and increase competition between age-classes of trees. Fortunately, experimental treatments of alternative silvicultural systems are being established in the

Pacific Northwest (Kolm and Franklin 1997) that can be used to test our model projections. Although it will be many decades before their effects on C stores can be fully assessed, some of the underlying assumptions and conclusions from our model concerning tree establishment and competition could be tested in a shorter time period.

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Appendix A

Table A1. Parameter values used in the STANDCARB model for the simulation experiments.

| Parameter (units) | Species | | |
|--|-------------|----------------------------|-----------------|
| | Douglas-fir | Both | Western hemlock |
| Tree establishment | | | |
| Light _{Max} (fraction of full sunlight) | 1.00 | | 0.90 |
| Light _{Min} (fraction of full sunlight) | 0.15 | | 0.05 |
| Degree-day _{Max} (°C) | 3095 | | 3095 |
| Degree-day _{Min} (°C) | 625 | | 625 |
| Tree soil water _{Max} (MPa) | -0.2 | | -0.1 |
| Tree soil water _{Min} (MPa) | -2.0 | | -1.7 |
| Growth | | | |
| Light compensation point (%) | 10 | | 5 |
| Light extinction coefficient (ha·Mg ⁻¹) | 0.15 | | 0.15 |
| Foliage increase rate _{Max} (dimensionless) | 0.5 | | 0.5 |
| Fine root/foliage ratio (dimensionless) | 1.0 | | 1.0 |
| Branch/bole ratio (dimensionless) | 0.25 | | 0.85 |
| Coarse root/bole ratio (dimensionless) | 0.37 | | 0.37 |
| Sapwood alive (% sapwood volume) | 7.4 | | 8.8 |
| Live Q_{10} (dimensionless) | 2.0 | | 2.0 |
| Woody respiration rate (year ⁻¹) | | 0.017 | |
| Rate of heartwood formation (year ⁻¹) | 0.059 | | 0.022 |
| Height _{Max} (m) | 90 | | 85 |
| Canopy interception constant (mass ⁻¹) | | 0.006 | |
| Mortality | | | |
| Tree mortality _{Max} (year ⁻¹) | 0.011 | | 0.013 |
| Branch prune _{Max} (year ⁻¹) | 0.020 | | 0.02 |
| Coarse root prune _{Max} (year ⁻¹) | 0.005 | | 0.005 |
| Tree age _{Max} (years) | 1000 | | 700 |
| Foliage turnover rate (year ⁻¹) | 0.2 | | 0.2 |
| Fine root turnover rate (year ⁻¹) | 0.5 | | 0.5 |
| Decomposition | | | |
| Foliage decay rate ₁₀ (year ⁻¹) ^a | 0.3 | | 0.3 |
| Fine root decay rate ₁₀ (year ⁻¹) | 0.3 | | 0.3 |
| Branch decay rate ₁₀ (year ⁻¹) | 0.15 | | 0.15 |
| Coarse root decay rate ₁₀ (year ⁻¹) | 0.1 | | 0.1 |
| Sapwood decay rate ₁₀ (year ⁻¹) | 0.15 | | 0.15 |
| Heartwood decay rate ₁₀ (year ⁻¹) | 0.1 | | 0.05 |
| Transfer rate to soil (year ⁻¹) | | 0.02 | |
| Soil decay rate ₁₀ (year ⁻¹) | | 0.005 | |
| Decay Q_{10} (dimensionless) | | 2 | |
| Decay temperature optimum (°C) | | 35 | |
| Moist _{Min} (% mass or volume) | | 30 | |
| Moist _{Max} (% mass or volume) | | 175–350 ^b | |
| Drying constant (cm ² ·degrees ⁻¹ ·cal ⁻¹) | | 0.0007–0.0038 ^c | |
| Moist store _{Max} (% mass) | | 200–400 | |

^aDecay rates are for 10°C with no moisture limitations.

^bTwo-parameter values depends on detritus pool, with woody detritus having a lower maximum moisture limit than dead foliage or fine roots.

^cParameter values depends on detritus pool, with coarse woody detritus having a lower drying rate constant than dead branches or dead foliage.