overlapping reflections was very clear. For the powder pattern of $(Mg_{0.81}Fe_{0.19})SiO_3$ tetragonal garnet, on the other hand, line splitting was not clear except for the (400)-(004) doublet and the (240)-(402)-(204) triplet; other overlapping reflections were diffused and looked like one broad peak.

Under the optical microscope, sections of the tetragonal garnet phase exhibited low birefringence. In one of the runs on a starting material of $(Mg_{0.8}Fe_{0.2})SiO_3$ composition, an isotropic phase was optically detected; however, the x-ray diffraction pattern resembled that of tetragonal garnet that was synthesized from the same starting material, showing small splitting of some peaks. An electron microprobe analysis indicated that the chemical composition of this optically isotropic phase was also $x = 0.19(1)$ [where $x = Fe/(Fe + Mg)$], $Al_2O_3 \leq 0.1\%$ by weight, with no other contaminants present. The lattice parameters determined by the WPPD method are $a = 11.5323(3)$ Å and $c = 11.4541(4)$ Å, with $R_{wp} = 3.6\%$, which are essentially the values of isochemical tetragonal garnet. In conclusion, this "isotropic" phase is identified as tetragonal garnet. It may appear "isotropic" on account of the fineness of the crystal grain size. The microcrystallinity (<2 μm) is a remarkable microscopic feature of the tetragonal garnets synthesized in the present study.

Kato (9) reported in the conclusion of his experimental studies of the $MgSiO_3$-$FeSiO_3$ system that the cubic garnet phase with a normal garnet structure (majorite) is stable in the range of composition $0.2 < x < 0.4$ at 20 GPa and 2000°C, whereas the tetragonal garnet phase is stable for $x < 0.2$. We carried out a series of experiments with a starting composition of $x = 0.3$ as well but could not observe cubic garnet; we observed only a small amount of optically anisotropic tetragonal phase in insufficient proportions for x-ray diffraction analysis. The major proportion of the sample product was an assemblage of spinel and stishovite when experimental temperature was somewhat low and quench crystals from liquid when it was somewhat high. (The experiments were performed several times at temperatures around 2000°C.) Our present observations thus do not suggest the existence of the cubic garnet phase. It is possible that Kato (9) might have misidentified "isotropic" tetragonal garnet as "cubic" garnet.

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Effects on Carbon Storage of Conversion of Old-Growth Forests to Young Forests

Mark E. Harmon, William K. Ferrell, Jerry F. Franklin

Simulations of carbon storage suggest that conversion of old-growth forests to young fast-growing forests will not decrease atmospheric carbon dioxide (CO_2) in general, as has been suggested recently. During simulated timber harvest, on-site carbon storage is reduced considerably and does not approach old-growth storage capacity for at least 200 years. Even when sequestration of carbon in wooden buildings is included in the models, timber harvest results in a net flux of CO_2 to the atmosphere. To offset this effect, the production of lumber and other long-term wood products, as well as the life-span of buildings, would have to increase markedly. Mass balance calculations indicate that the conversion of 5×10^6 hectares of old-growth forests to younger plantations in western Oregon and Washington in the last 100 years has added 1.5×10^9 to 1.8×10^9 megagrams of carbon to the atmosphere.

DEFORESTATION HAS BEEN A source of increasing C in the atmosphere in the last century (1–9). However, it has recently been suggested that the CO_2 content of the atmosphere could be reduced if slowly growing, "decadent," old-growth forests were converted to faster growing, younger, intensively managed forests (10). Such suggestions may seem reasonable at first glance in that young forests have higher net primary productivity than old-growth forests (11). But such reasoning disregards the critical factor, which is the amount of C stored within a forest, not the annual rate of C uptake.

In this report, we explore the effects that conversion of old-growth to younger forests has on atmospheric CO_2 and terrestrial C budgets. We use three lines of evidence: the current disposition of C resulting from cutting old-growth timber, a model of C dynamics in old-growth and second-growth forests, and a comparison of C storage in an old-growth and a young forest by means of simulation.

Approximately 42% of the timber currently harvested in the Pacific Northwest enters long-term storage (products with a life-span of >5 years) in forms such as structural components of buildings (Fig. 1). This level is significantly higher than the historical level, which was as low as 20% in the 1950s (12). The long-term average is considerably lower than the current value because 75% of the timber harvested in the last 100 years in Oregon and Washington was cut before 1960 (13).

At least 15% of the wood fiber in a typical harvest is left behind as broken or defective (14, 15). Some of this material is used for fuel or paper production and is therefore quickly converted to atmospheric CO_2. Of the C removed from the site, 11% is in bark (16), which is either burned or composted to form mulch. Most of the tree volume removed from a stand is used in lumber production (17). When undecayed harvested wood is converted to boards or plywood, at least 35 to 45% is lost to sawdust or scrap during production (15). Some of this waste material is used in particle- and wafer-board production, but most is consumed as fuel or converted to paper. Production of paper, even with recycling, results in a loss of CO_2 to the atmosphere, in that only 46 to 58% of primary paper production is recovered as fiber (15) and the residue serves largely as fuel.

The result of all this activity is that, of the 325 Mg of C per hectare harvested from a typical old-growth forest, 187 Mg of C per hectare may be lost to the atmosphere from paper production, fuel consumption, or de-

M. E. Harmon and W. K. Ferrell, Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR 97331.
J. F. Franklin, U.S. Department of Agriculture Forest Service Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, OR 97331, and College of Forest Resources, University of Washington, Seattle, WA 98195.
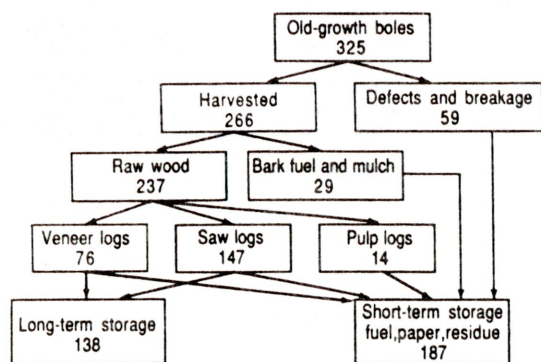
Fig. 1. Flow of C (megagrams per hectare) into long- and short-term storage components after harvest of a 1-ha old-growth forest. Data are from studies on Douglas fir and western hemlock (*14–17*). Boards and plywood are assumed to enter long-term storage (>5 years). Sawdust, scrap, and pulp are assumed to enter short-term storage.

composition (Fig. 1). The proportion of young forests converted to long-term storage is probably even lower than that of old-growth forests because less breakage or defect will be offset by less recovery of boards and plywood (*15*). If we assume that 45% of the boles in a 60-year-old stand is converted to long-term storage, harvest of a 60-year-old forest will still result in a net loss to the atmosphere of 132 Mg of C per hectare. For wood harvested from either old-growth or young-growth forests, the "long-term" storage is perhaps 200 years at most (*18*).

We constructed a computer simulation model to examine the temporal dynamics of C storage in the Douglas fir and hemlock (*Pseudotsuga-Tsuga*) ecosystems common to the Pacific Northwest. This nonlinear difference model with a 1-year time step tracks C storage in the following forest components: foliage, branchwood, boles, coarse roots, fine roots, fine woody debris, forest floor, coarse woody debris, and light and heavy soil C (*19*). Data for the biomass, production, and C turnover of these components were compiled for young and old-growth Douglas fir and hemlock forests growing on the west side of the Oregon and Washington Cascade Mountain Range.

For the purposes of analysis, we adopted several assumptions: that changing climatic conditions and CO_2 concentrations would not affect processing rates; that net production of bole wood and bark for all simulations would peak at 30 years at 8.5 Mg of C per hectare per year (*20, 21*); and that repeated harvesting would not reduce long-term site productivity. The latter assumption is conservative in that repeated harvest may well reduce productivity (*22*) and detrital storage (*23*). In the simulations, we compared and assessed the effect on C storage of (i) a natural disturbance versus timber harvest, (ii) a 50% increase in the decomposition rate after disturbance versus no increase, and (iii) the removal of logging residues versus no removal in repeated harvests on a 60-year rotation.

The simulated biomass accumulation rates matched those for the old-growth condition

closely (+2%) but were 25% higher than actual values for natural stands at 60 years (Table 1), matching more closely the values for plantations (*20*). Harvest of old-growth forests reduced C storage for at least 250 years, and, interestingly, a natural disturbance such as fire or windthrow also reduced storage but much less drastically (Fig. 2). Storage declined with harvest both with and without an assumption of increased decomposition with disturbance, although the decrease was larger with this assumption. The decomposition rate of the forest floor has increased with harvest in other forest ecosystems (*24*) and is expected to increase in the Pacific Northwest because sapwood volume is greater in woody detritus from young trees than from old trees (*25*) and leaf-litter decay is greater early in succession (*26*).

Although detrital components store 25 to 30% of the C in Douglas fir and hemlock ecosystems, they can be strongly and negatively affected by management manipulations. Coarse woody debris, for example, virtually disappeared in one simulation of short harvest rotations and intensive utilization (*23*). Soil organic matter, especially the light fraction (*27*), most likely will decrease under intensive management. In simulations of repeated 60-year harvests, the reduction

in C storage was stabilized after two rotations (Fig. 3). Increases in living-tree storage brought about by genetic improvement, nutrient fertilization, and CO_2 fertilization (*28*) may offset some of the losses from detrital pools. However, even if coarse woody debris is the only detrital component reduced (with a reduction of 100 Mg of C per hectare), these improvements will need to nearly double the mean annual increment at rotation age to offset the losses.

In a comparison of total C storage, there was 2.2 to 2.3 times as much storage in a 450-year-old *Pseudotsuga-Tsuga* natural stand as in a 60-year-old *Pseudotsuga* plantation (Table 1). However, over a landscape, managed forests in the full range of age classes store less C than a forest of uniform age. With the assumption of a sustained forest yield, one can calculate the mean C stored in a landscape after conversion from the old-growth condition by averaging over the first t years of the simulation, where t is rotation age. For landscapes with rotations of 50, 75, and 100 years, the C stored would be at most 38, 44, and 51%, respectively, of that stored in the old-growth stand (*29*). As discussed above, these differences are conservative because storage in detrital components would be greatly reduced with repeated harvest.

Conversion of old-growth forests to young plantations invariably reduces C storage, even when structural components in buildings are considered. Comparison of the actual biomass of an old-growth forest and that of a 60-year-old forest of similar site quality indicates that C storage is reduced 350 Mg of C per hectare by conversion, again a conservative estimate because forests continue to lose mass for three decades after disturbance. Model results accounting for this process indicate that C storage is reduced on site by 370 Mg of C per hectare as a result of conversion. However, C stored

Table 1. Carbon (*33*) storage in a 60-year-old *Pseudotsuga* forest and a 450-year-old *Pseudotsuga-Tsuga* forest.

Component	60-year-old forest		450-year-old forest	
	Mg of C per hectare	Reference	Mg of C per hectare	Reference
Foliage	5.5	(*20*)	6.2	(*16*)
			−7.0	(*40*)
Branchwood	7.0	(*20*)	26.3	(*16*)
Boles (wood and bark)	145	(*20*)	323	(*16*)
Coarse roots	29	(*34*)	71	(*16*)
Fine roots	5.6	(*35*)	5.6	(*16*)
Fine woody debris and forest floor	7.1	(*36*)	26	(*16*)
Coarse woody debris	3.8	(*37*)	97	(*25*)
	−19	(*38*)		
Soil carbon	56	(*39*)	56	(*16*)
Total*	259 to 274		611 to 612	

*Range given because of variation in estimates for foliage and coarse woody debris.

off site in buildings offsets some of the reductions in on-site storage. Given a 42% conversion of the boles to structural components in buildings and a 2% annual replacement of the structures, the conversion of old-growth to younger forests reduces storage by 305 Mg of C per hectare in one 60-year rotation. Unless utilization standards greatly increase and structural components in buildings can be made to have greater life expectancy, it is doubtful that repeated harvests can offset the original losses caused by conversion (30).

Conversion of old-growth forests in the Pacific Northwest has been a significant source of C in the atmosphere. In western Oregon and Washington there are 10×10^6 ha of commercial forest land (31). If we use as a basis the age-class structure of large, uncut areas, such as those in Mount Rainier and Olympic national parks, we calculate that 7×10^6 ha were probably in an old-growth condition in 1890. Currently, 2×10^6 ha of old growth remain (31); thus 5×10^6 ha have been converted. If C storage has been reduced by ~305 to ~370 Mg of C per hectare by the conversion, 1.5×10^9 to 1.8×10^9 Mg of C has been added to the atmosphere in the last century. In reality, the total flux from this region from changes in land use will have been considerably higher because of the harvest of second-growth forest, widespread fires, and the removal of forest land from production by such processes as road construction and urbanization. Given the small area we are considering, a mere 0.017% of the earth's land surface, old-growth forest con-
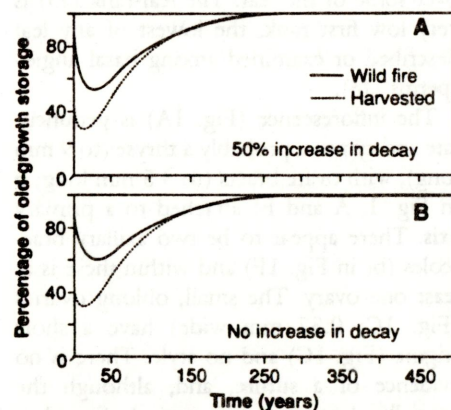
Fig. 2. Carbon storage, expressed as a percentage of old-growth storage, in a simulation of a Douglas fir and hemlock old-growth ecosystem disturbed by fire or timber harvest. The assumptions are that fire used in site preparation will remove 50% of the fine woody debris and forest floor and 25% of the coarse woody debris. The simulation was run with two scenarios: (**A**) disturbance is followed by a 50% increase in the decomposition rate, which decreases 3% annually and reaches old-growth values in 100 years; (**B**) disturbance does not affect decomposition rates.
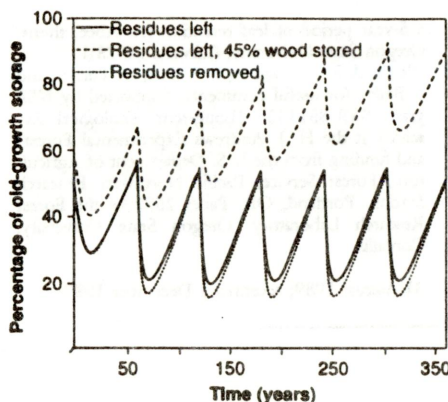
Fig. 3. Carbon storage expressed as a percentage of old-growth storage in a simulation of repeated harvests on a 60-year rotation. The assumptions are that site productivity will not change, that disturbance will initially increase decomposition rates 50%, and that fire used in site preparation will remove 50% of the fine woody debris and forest floor and 25% of the coarse woody debris. Three scenarios were examined: (i) coarse woody debris and residues such as defective boles are left on site; (ii) coarse woody debris is left but other residues are removed; and (iii) all residues are left, but 45% of harvested wood is converted to long-term storage (buildings and other structures) with a 2% annual loss.

version appears to account for a noteworthy 2% of the total C released because of land use changes in the last 100 years (6, 7, 32).

Although reintroducing forests to deforested regions will increase C storage in the biota, conversion of old-growth forests to younger forests under current harvesting and use conditions has added and will continue to add C to the atmosphere. This conclusion is likely to hold in most forests in which the age of harvest is less than the age required to reach the old-growth stage of succession. The amount of C added by conversion will vary among forests, depending on their maximum storage capacity and the difference between the timber rotation age and the age of the old-growth state within the given ecosystem.

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30. A decrease in the replacement rate of wooden structures to 1.5 and 1% per year results in losses of 279 and 237 Mg of C per hectare, respectively, at 360 years, resulting in storage that is 96 and 104% of the original old-growth storage, respectively.
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An Aptian Plant with Attached Leaves and Flowers: Implications for Angiosperm Origin

DAVID WINSHIP TAYLOR AND LEO J. HICKEY

Recent phylogenetic studies and fossil finds support a new view of the ancestral angiosperm. A diminutive fossil angiosperm from the Aptian of Australia has attached leaves, with intermediate pinnate-palmate, low-rank venation, and lateral axes bearing pistillate organs subtended by bracts and bracteoles that are the oldest direct evidence of flowers. A variety of data suggests a similar morphology for the ancestral angiosperm. This hypothesis explains similarities between rhizomatous to herbaceous Magnoliidae and basal monocots, scarcity of early angiosperm wood, and lack of recognition of earlier remains.

THE OLDEST UNEQUIVOCAL ANGIOsperm remains, mostly dispersed organs, are from Lower Cretaceous strata. Fossil pollen is reported from the Hauterivian of England and Barremian of West Africa (1), and leaves from the Barremian to Aptian of eastern North America (2). Unequivocal angiosperm flowers (3) and wood (4) first appear during the Albian. These remains show affinities to taxa with diminutive stature and reproductive organs (2, 5–7) and to taxa with shrub to tree habit and moderate-sized, complex flowers (2, 3). The early and possibly oldest occurrence of the former conflicts with the existing theory that the ancestral angiosperm was a small tree or shrub, with pinnately veined, simple leaves and flowers of moderate to large size with numerous reproductive parts (8), though other views have been proposed (2, 9, 10).

We recently recognized the angiospermous affinities of a plant described by Drinnan and Chambers as a fern ("Marsileales ? indet?") (11) from the Aptian Korumburra Group of the Gippsland Basin at Koonwarra, Victoria, Australia (11–13). This fossil has leaves and attached female inflorescences (Fig. 1A), which are the oldest unequivocal angiosperm reproductive struc-

tures. The only angiospermous pollen reported from Koonwarra, *Clavatipollenites hughesii* (12), is of a type having the earliest range of any flowering plant. Taken together, the fossil evidence and recent phylogenetic analyses of extant plants (10, 14) are compatible with a new hypothesis for the ancestral angiosperm.

The fossil has two leaves attached to the axis, which bends sharply to the right at the upper node, and two axillary inflorescences (Fig. 1A). Attachment of the proximal leaf and distal inflorescence is shown by their orientation and similarity to the other clearly attached organs. The inflorescences are masses of overlapping bracts, bracteoloes, and ovaries; distinct bracts are noticeable at the apex of the lower inflorescence and along the right side of the upper, where they overlap the distal petiole.

The axis is thin (1.4 mm wide) and exhibits longitudinal ridges, which may be the remains of vascular bundles. Apparent fragility, an apparently dissected stele, and co-occurrence of fully expanded, diminutive leaves with well-developed axillary inflorescences suggest a herbaceous habit. Widely spaced yellow-brown, translucent, discoidal impressions (0.03 to 0.04 mm; Fig. 1G) occurring throughout the fossil may be the remains of ethereal oil cells.

The leaves are alternately arranged (Fig. 1A). The lower (Fig. 1E) has a long petiole that clasps the axis, and a lamina that is apparently folded over distally (Figs. 1E and 2A). Evidence for folding derives from two major veins that extend to the margin and abruptly reverse at the fold; complex, anomalously dense higher venation apparently resulting from superimposition of two levels of veins; and lack of a carbonaceous thickening along the folded margin. The leaf is simple, unlobed, slightly asymmetrical at the base, and broadly ovate, to 10.1 mm wide. The lower laminar margin is darkly stained, suggesting a thickening, and has an inferred incipient sinus (at indentation on left; Fig. 1E). The overfolded upper portion appears to be dissected into three deeply incised dentations. Evidence for dentations, rather than tears, is the symmetry of their outline and vein convergence toward their apices.

A five-stranded vascular trunk emerges into the leaf blade (Figs. 1E and 2A) with the medial strand composed of two bundles. The vein pattern qualifies equally as very loosely and irregularly palinactinodromous or weakly pinnate with three to four pairs of secondary veins. The basal two pairs are crowded proximally and arise as lateral bundles directly from the petiole at an acute angle. The festooned brochidodromous distal secondaries have irregular spacing and angles of origin, branch dichotomously to form loose and irregular loops in at least two series, and are poorly differentiated from the primary and tertiary venation.

Tertiary and higher (to fifth) order veins (Figs. 1E and 2A) form a random reticulum in which vein orders cannot be consistently determined, and the angle of tertiary vein origin is irregular but mostly acute. A fimbrial vein appears to be present. Areolation is apparently incomplete or possibly lacking over some of the leaf. The leaf-rank (15) is very low first rank, the lowest of any leaf described or examined among basal angiosperms (16).

The inflorescence (Fig. 1A) is pedunculate and cymose, probably a thryse (to 9 mm long), with ovate bracts (to 3.5 mm long; b in Fig. 1, A and F) attached to a primary axis. There appear to be two axillary bracteoles (br in Fig. 1F) and within these is at least one ovary. The small, oblong ovaries (Fig. 1C; 0.57 mm wide) have a short stigma (Fig. 1C) and no style. There is no evidence of a suture, and, although the specially placed stigma is typical of ascidate carpels, the ovary could be syncarpous.

Leaf characters alone reveal the angiospermous affinities of the fossil. Random-reticulate venation with anastomoses at several vein orders, a multistrand splaying out into the laminar base forming an indeterminate actinodromous-brochidodromous venation, and incomplete areoles occur in combination only in angiosperms (5, 16). In addition, the morphology of the reproductive

D. W. Taylor, Department of Biology, Yale University, P.O. Box 6666, New Haven, CT 06520.
L. J. Hickey, Department of Geology and Geophysics, Yale University, New Haven, CT 06520.