



Land use strategies to mitigate climate change in carbon dense temperate forests

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Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but ecosystem process-based integration of climate change, enhanced CO₂, disturbance from fire, and management actions at regional scales are extremely limited. Here, we examine the relative merits of afforestation, reforestation, management changes, and harvest residue bioenergy use in the Pacific Northwest. This region represents some of the highest carbon density forests in the world, which can store carbon in trees for 800 y or more. Oregon's net ecosystem carbon balance (NECB) was equivalent to 72% of total emissions in 2011–2015. By 2100, simulations show increased net carbon uptake with little change in wildfires. Reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increase NECB 56% by 2100, with the latter two actions contributing the most. Resultant cobenefits included water availability and biodiversity, primarily from increased forest area, age, and species diversity. Converting 127,000 ha of irrigated grass crops to native forests could decrease irrigation demand by 233 billion m³·y⁻¹. Utilizing harvest residues for bioenergy production instead of leaving them in forests to decompose increased emissions in the short-term (50 y), reducing mitigation effectiveness. Increasing forest carbon on public lands reduced emissions compared with storage in wood products because the residence time is more than twice that of wood products. Hence, temperate forests with high carbon densities and lower vulnerability to mortality have substantial potential for reducing forest sector emissions. Our analysis framework provides a template for assessments in other temperate regions.

forests | carbon balance | greenhouse gas emissions | climate mitigation

Strategies to mitigate carbon dioxide emissions through forestry activities have been proposed, but regional assessments to determine feasibility, timeliness, and effectiveness are limited and rarely account for the interactive effects of future climate, atmospheric CO₂ enrichment, nitrogen deposition, disturbance from wildfires, and management actions on forest processes. We examine the net effect of all of these factors and a suite of mitigation strategies at fine resolution (4-km grid). Proven strategies immediately available to mitigate carbon emissions from forest activities include the following: (i) reforestation (growing forests where they recently existed), (ii) afforestation (growing forests where they did not recently exist), (iii) increasing carbon density of existing forests, and (iv) reducing emissions from deforestation and degradation (1). Other proposed strategies include wood bioenergy production (2–4), bioenergy combined with carbon capture and storage (BECCS), and increasing wood product use in buildings. However, examples of commercial-scale BECCS are still scarce, and sustainability of wood sources remains controversial because of forgone ecosystem carbon storage and low environmental cobenefits (5, 6). Carbon stored in buildings generally outlives its usefulness or is replaced within decades (7) rather than the centuries possible in forests, and the factors influencing product substitution have yet to be fully explored (8). Our analysis of mitigation strategies focuses on the first four strategies, as well as bioenergy production, utilizing harvest residues only and without carbon capture and storage.

The appropriateness and effectiveness of mitigation strategies within regions vary depending on the current forest sink, competition with land-use and watershed protection, and environmental conditions affecting forest sustainability and resilience. Few process-based regional studies have quantified strategies that could actually be implemented, are low-risk, and do not depend on developing technologies. Our previous studies focused on regional modeling of the effects of forest thinning on net ecosystem carbon balance (NECB) and net emissions, as well as improving modeled drought sensitivity (9, 10), while this study focuses mainly on strategies to enhance forest carbon.

Our study region is Oregon in the Pacific Northwest, where coastal and montane forests have high biomass and carbon sequestration potential. They represent coastal forests from northern California to southeast Alaska, where trees live 800 y or more and biomass can exceed that of tropical forests (11) (Fig. S1). The semiarid ecoregions consist of woodlands that experience frequent fires (12). Land-use history is a major determinant of forest carbon balance. Harvest was the dominant cause of tree mortality (2003–2012) and accounted for fivefold as much mortality as that from fire and beetles combined (13). Forest land ownership is predominantly public (64%), and 76% of the biomass harvested is on private lands.

Significance

Regional quantification of feasibility and effectiveness of forest strategies to mitigate climate change should integrate observations and mechanistic ecosystem process models with future climate, CO₂, disturbances from fire, and management. Here, we demonstrate this approach in a high biomass region, and found that reforestation, afforestation, lengthened harvest cycles on private lands, and restricting harvest on public lands increased net ecosystem carbon balance by 56% by 2100, with the latter two actions contributing the most. Forest sector emissions tracked with our life cycle assessment model decreased by 17%, partially meeting emissions reduction goals. Harvest residue bioenergy use did not reduce short-term emissions. Cobenefits include increased water availability and biodiversity of forest species. Our improved analysis framework can be used in other temperate regions.

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Data deposition: The CLM4.5 model data are available at Oregon State University (terraweb.forestry.oregonstate.edu/FMEC). Data from the >200 intensive plots on forest carbon are available at Oak Ridge National Laboratory (https://daac.ornl.gov/NACP/guides/NACP_TERRA-PNW.html), and FIA data are available at the USDA Forest Service (<https://www.fia.fs.fed.us/tools-data/>).

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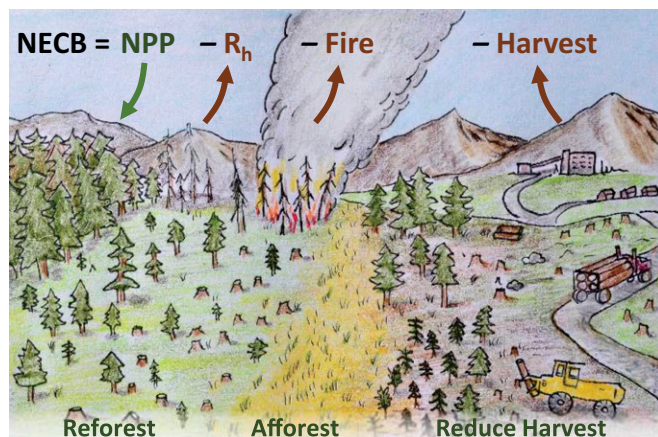


Fig. 1. Approach to assessing effects of mitigation strategies on forest carbon and forest sector emissions. NECB is productivity (NPP) minus R_h and losses from fire and harvest (red arrows). Harvest emissions include those associated with wood products and bioenergy.

Many US states, including Oregon (14), plan to reduce their greenhouse gas (GHG) emissions in accordance with the Paris Agreement. We evaluated strategies to address this question: How much carbon can the region's forests realistically remove from the atmosphere in the future, and which forest carbon strategies can reduce regional emissions by 2025, 2050, and 2100? We propose an integrated approach that combines observations with models and a life cycle assessment (LCA) to evaluate current and future effects of mitigation actions on forest carbon and forest sector emissions in temperate regions (Fig. 1). We estimated the recent carbon budget of Oregon's forests, and simulated the potential to increase the forest sink and decrease forest sector emissions under current and future climate conditions. We provide recommendations for regional assessments of mitigation strategies.

Results

Carbon stocks and fluxes are summarized for the observation cycles of 2001–2005, 2006–2010, and 2011–2015 (Table 1 and Tables S1 and S2). In 2011–2015, state-level forest carbon stocks totaled 3,036 Tg C (3 billion metric tons), with the coastal and montane ecoregions accounting for 57% of the live tree carbon (Tables S1 and S2). Net ecosystem production [NEP; net primary production (NPP) minus heterotrophic respiration (R_h)] averaged 28 teragrams carbon per year (Tg C y^{-1}) over all three periods. Fire emissions were unusually high at 8.69 million metric tons carbon dioxide equivalent ($\text{tCO}_2\text{e y}^{-1}$, i.e., 2.37 Tg C y^{-1}) in 2001–2005 due to the historic Biscuit Fire, but decreased to 3.56 million $\text{tCO}_2\text{e y}^{-1}$ (0.97 Tg C y^{-1}) in 2011–2015 (Table S4). Note that 1 million tCO_2e equals 3.667 Tg C.

Our LCA showed that in 2001–2005, Oregon's net wood product emissions were 32.61 million tCO_2e (Table S3), and 3.7-fold wildfire emissions in the period that included the record fire year (15) (Fig. 2). In 2011–2015, net wood product emissions were 34.45 million tCO_2e and almost 10-fold fire emissions, mostly due to lower fire emissions. The net wood product emissions are higher than fire emissions despite carbon benefits of storage in wood products and substitution for more fossil fuel-intensive products. Hence, combining fire and net wood product emissions, the forest sector emissions averaged 40 million $\text{tCO}_2\text{e y}^{-1}$ and accounted for about 39% of total emissions across all sectors (Fig. 2 and Table S4). NECB was calculated from NEP minus losses from fire emissions and harvest (Fig. 1). State NECB was equivalent to 60% and 70% of total emissions for 2001–2005 and 2011–2015, respectively (Fig. 2, Table 1, and Table S4). Fire emissions were only between 4% and 8% of total emissions from

all sources (2011–2015 and 2001–2004, respectively). Oregon's forests play a larger role in meeting its GHG targets than US forests have in meeting the nation's targets (16, 17).

Historical disturbance regimes were simulated using stand age and disturbance history from remote sensing products. Comparisons of Community Land Model (CLM4.5) output with Forest Inventory and Analysis (FIA) aboveground tree biomass (>6,000 plots) were within 1 SD of the ecoregion means (Fig. S2). CLM4.5 estimates of cumulative burn area and emissions from 1990 to 2014 were 14% and 25% less than observed, respectively. The discrepancy was mostly due to the model missing an anomalously large fire in 2002 (Fig. S3A). When excluded, modeled versus observed fire emissions were in good agreement ($r^2 = 0.62$; Fig. S3B). A sensitivity test of a 14% underestimate of burn area did not affect our final results because predicted emissions would increase almost equally for business as usual (BAU) management and our scenarios, resulting in no proportional change in NECB. However, the ratio of harvest to fire emissions would be lower.

Projections show that under future climate, atmospheric carbon dioxide, and BAU management, an increase in net carbon uptake due to CO_2 fertilization and climate in the mesic ecoregions far outweighs losses from fire and drought in the semiarid ecoregions. There was not an increasing trend in fire. Carbon stocks increased by 2% and 7% and NEP increased by 12% and 40% by 2050 and 2100, respectively.

We evaluated emission reduction strategies in the forest sector: protecting existing forest carbon, lengthening harvest cycles, reforestation, afforestation, and bioenergy production with product substitution. The largest potential increase in forest carbon is in the mesic Coast Range and West Cascade ecoregions. These forests are buffered by the ocean, have high soil water-holding capacity, low risk of wildfire [fire intervals average 260–400 y (18)], long carbon residence time, and potential for high carbon density. They can attain biomass up to 520 Mg C ha^{-1} (12). Although Oregon has several protected areas, they account for only 9–15% of the total forest area, so we expect it may be feasible to add carbon-protected lands with cobenefits of water protection and biodiversity.

Reforestation of recently forested areas include those areas impacted by fire and beetles. Our simulations to 2100 assume regrowth of the same species and incorporate future fire responses to climate and cyclical beetle outbreaks [70–80 y (13)]. Reforestation has the potential to increase stocks by 315 Tg C by 2100, reducing forest sector net emissions by 5% by 2100 relative to BAU management (Fig. 3). The East and West Cascades ecoregions had the highest reforestation potential, accounting for 90% of the increase (Table S5).

Afforestation of old fields within forest boundaries and non-food/nonforage grass crops, hereafter referred to as “grass crops,” had to meet minimum conditions for tree growth, and crop grid cells had to be partially forested (SI Methods and Table S6). These crops are not grazed or used for animal feed. Competing land uses may decrease the actual amount of area that can be afforested. We calculated the amount of irrigated grass crops (127,000 ha) that could be converted to forest, assuming success of carbon offset programs (19). By 2100, afforestation increased stocks by

Table 1. Forest carbon budget components used to compute NECB

Flux, Tg C y^{-1}	2001–2005	2006–2010	2011–2015	2001–2015
NPP	73.64	73.57	73.57	73.58
R_h	45.67	45.38	45.19	45.41
NEP	27.97	28.19	28.39	28.18
Harvest removals	8.58	7.77	8.61	8.32
Fire emissions	2.37	1.79	0.97	1.71
NECB	17.02	18.63	18.81	18.15

Average annual values for each period, including uncertainty (95% confidence interval) in Tg C y^{-1} (multiply by 3.667 to get million tCO_2e).

and mitigation into a common framework, melding biophysical with social components (22). We developed a framework to examine a suite of mitigation actions to increase forest carbon sequestration and reduce forest sector emissions under current and future environmental conditions.

Harvest-related emissions had a large impact on recent forest NECB, reducing it by an average of 34% from 2001 to 2015. By comparison, fire emissions were relatively small and reduced NECB by 12% in the Biscuit Fire year, but only reduced NECB 5–9% from 2006 to 2015. Thus, altered forest management has the potential to enhance the forest carbon balance and reduce emissions.

Future NEP increased because enhancement from atmospheric carbon dioxide outweighed the losses from fire. Lengthened harvest cycles on private lands to 80 y and restricting harvest to 50% of current rates on public lands increased NECB the most by 2100, accounting for 90% of total emissions reduction (Fig. 3 and Tables S5 and S6). Reduced harvest led to NECB increasing earlier than the other strategies (by 2050), suggesting this could be a priority for implementation.

Our afforestation estimates may be too conservative by limiting them to nonforest areas within current forest boundaries and 127,000 ha of irrigated grass cropland. There was a net loss of 367,000 ha of forest area in Oregon and Washington combined from 2001 to 2006 (23), and less than 1% of native habitat remains in the Willamette Valley due to urbanization and agriculture (24). Perhaps more of this area could be afforested.

The spatial variation in the potential for each mitigation option to improve carbon stocks and fluxes shows that the reforestation potential is highest in the Cascade Mountains, where fire and insects occur (Fig. 4). The potential to reduce harvest on public land is highest in the Cascade Mountains, and that to lengthen harvest cycles on private lands is highest in the Coast Range.

Although western Oregon is mesic with little expected change in precipitation, the afforestation cobenefits of increased water availability will be important. Urban demand for water is projected to increase, but agricultural irrigation will continue to consume much more water than urban use (25). Converting 127,000 ha of irrigated grass crops to native forests appears to be a win–win strategy, returning some of the area to forest land, providing habitat and connectivity for forest species, and easing irrigation demand. Because the afforested grass crop represents only 11% of the available grass cropland (1.18 million ha), it is not likely to result in leakage or indirect land use change. The two forest strategies combined are likely to be important contributors to water security.

Cobenefits with biodiversity were not assessed in our study. However, a recent study showed that in the mesic forests, cobenefits with biodiversity of forest species are largest on lands with harvest cycles longer than 80 y, and thus would be most pronounced on private lands (26). We selected 80 y for the harvest cycle mitigation strategy because productivity peaks at 80–125 y in this region, which coincides with the point at which cobenefits with wildlife habitat are substantial.

Habitat loss and climate change are the two greatest threats to biodiversity. Afforestation of areas that are currently grass crops would likely improve the habitat of forest species (27), as about 90% of the forests in these areas were replaced by agriculture. About 45 mammal species are at risk because of range contraction (28). Forests are more efficient at dissipating heat than grass and crop lands, and forest cover gains lead to net surface cooling in all regions south of about 45° latitude in North American and Europe (29). The cooler conditions can buffer climate-sensitive bird populations from approaching their thermal limits and provide more food and nest sites (30). Thus, the mitigation strategies of afforestation, protecting forests on public lands and lengthening harvest cycles to 80–125 y, would likely benefit forest-dependent species.

Oregon has a legislated mandate to reduce emissions, and is considering an offsets program that limits use of offsets to 8% of

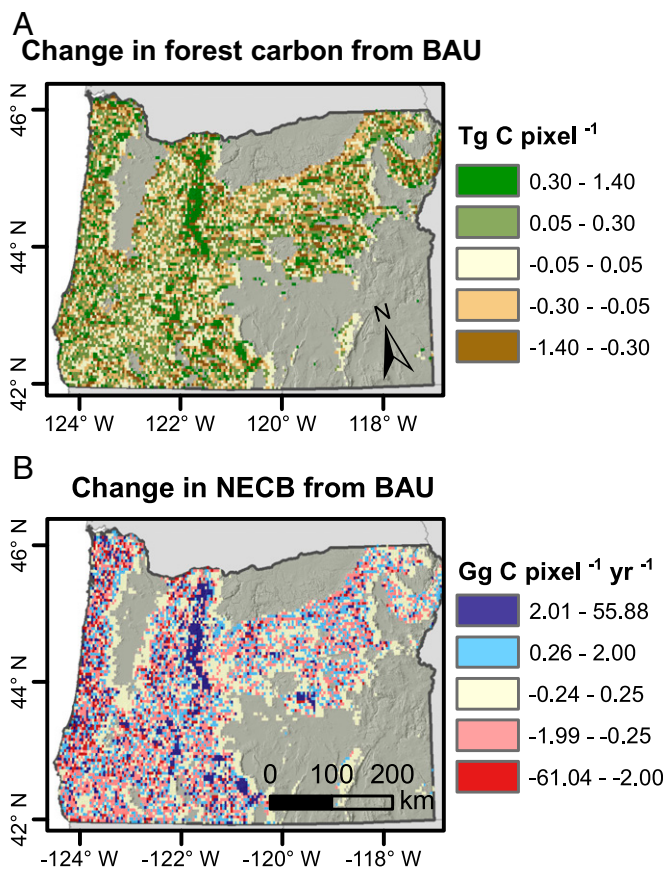


Fig. 4. Spatial patterns of forest carbon stocks and NECB by 2091–2100. The decadal average changes in forest carbon stocks (A) and NECB (B) due to afforestation, reforestation, protected areas, and lengthened harvest cycles relative to continued BAU forest management (red is increase in NECB) are shown.

the total emissions reduction to ensure that regulated entities substantially reduce their own emissions, similar to California's program (19). An offset becomes a net emissions reduction by increasing the forest carbon sink (NECB). If only 8% of the GHG reduction is allowed for forest offsets, the limits for forest offsets would be 2.1 and 8.4 million metric tCO₂e of total emissions by 2025 and 2050, respectively (Table S6). The combination of afforestation, reforestation, and reduced harvest would provide 13 million metric tCO₂e emissions reductions, and any one of the strategies or a portion of each could be applied. Thus, additionality beyond what would happen without the program is possible.

State-level reporting of GHG emissions includes the agriculture sector, but does not appear to include forest sector emissions, except for industrial fuel (i.e., utility fuel in Table S3) and, potentially, fire emissions. Harvest-related emissions should be quantified, as they are much larger than fire emissions in the western United States. Full accounting of forest sector emissions is necessary to meet climate mitigation goals.

Increased long-term storage in buildings and via product substitution has been suggested as a potential climate mitigation option. Pacific temperate forests can store carbon for many hundreds of years, which is much longer than is expected for buildings that are generally assumed to outlive their usefulness or be replaced within several decades (7). By 2035, about 75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends (31, 32). Recent analysis suggests substitution benefits of using wood versus more fossil fuel-intensive materials have been overestimated by at

least an order of magnitude (33). Our LCA accounts for losses in product substitution stores (PSSs) associated with building life span, and thus are considerably lower than when no losses are assumed (4, 34). While product substitution reduces the overall forest sector emissions, it cannot offset the losses incurred by frequent harvest and losses associated with product transportation, manufacturing, use, disposal, and decay. Methods for calculating substitution benefits should be improved in other regional assessments.

Wood bioenergy production is interpreted as being carbon-neutral by assuming that trees regrow to replace those that burned. However, this does not account for reduced forest carbon stocks that took decades to centuries to sequester, degraded productive capacity, emissions from transportation and the production process, and biogenic/direct emissions at the facility (35). Increased harvest through proposed thinning practices in the region has been shown to elevate emissions for decades to centuries regardless of product end use (36). It is therefore unlikely that increased wood bioenergy production in this region would decrease overall forest sector emissions.

Conclusions

GHG reduction must happen quickly to avoid surpassing a 2 °C increase in temperature since preindustrial times. Alterations in forest management can contribute to increasing the land sink and decreasing emissions by keeping carbon in high biomass forests, extending harvest cycles, reforestation, and afforestation. Forests are carbon-ready and do not require new technologies or infrastructure for immediate mitigation of climate change. Growing forests for bioenergy production competes with forest carbon sequestration and does not reduce emissions in the next decades (10). BECCS requires new technology, and few locations have sufficient geological storage for CO₂ at power facilities with high-productivity forests nearby. Accurate accounting of forest carbon in trees and soils, NECB, and historic harvest rates, combined with transparent quantification of emissions from the wood product process, can ensure realistic reductions in forest sector emissions.

As states and regions take a larger role in implementing climate mitigation steps, robust forest sector assessments are urgently needed. Our integrated approach of combining observations, an LCA, and high-resolution process modeling (4-km grid vs. typical 200-km grid) of a suite of potential mitigation actions and their effects on forest carbon sequestration and emissions under changing climate and CO₂ provides an analysis framework that can be applied in other temperate regions.

Materials and Methods

Current Stocks and Fluxes. We quantified recent forest carbon stocks and fluxes using a combination of observations from FIA; Landsat products on forest type, land cover, and fire risk; 200 intensive plots in Oregon (37); and a wood decomposition database. Tree biomass was calculated from species-specific allometric equations and ecoregion-specific wood density. We estimated ecosystem carbon stocks, NEP (photosynthesis minus respiration), and NECB (NEP minus losses due to fire or harvest) using a mass-balance approach (36, 38) (Table 1 and *SI Materials and Methods*). Fire emissions were computed from the Monitoring Trends in Burn Severity database, biomass data, and region-specific combustion factors (15, 39) (*SI Materials and Methods*).

Future Projections and Model Description. Carbon stocks and NEP were quantified to the years 2025, 2050, and 2100 using CLM4.5 with physiological parameters for 10 major forest species, initial forest biomass (36), and future climate and atmospheric carbon dioxide as input (Institut Pierre Simon Laplace climate system model downscaled to 4 km × 4 km, representative concentration pathway 8.5). CLM4.5 uses 3-h climate data, ecophysiological characteristics, site physical characteristics, and site history to estimate the daily fluxes of carbon, nitrogen, and water between the atmosphere, plant state variables, and litter and soil state variables. Model components are biogeophysics, hydrological cycle, and biogeochemistry. This model version does not include a dynamic vegetation model to simulate resilience and

establishment following disturbance. However, the effect of regeneration lags on forest carbon is not particularly strong for the long disturbance intervals in this study (40). Our plant functional type (PFT) parameterization for 10 major forest species rather than one significantly improves carbon modeling in the region (41).

Forest Management and Land Use Change Scenarios. Harvest cycles, reforestation, and afforestation were simulated to the year 2100. Carbon stocks and NEP were predicted for the current harvest cycle of 45 y compared with simulations extending it to 80 y. Reforestation potential was simulated over areas that recently suffered mortality from harvest, fire, and 12 species of beetles (13). We assumed the same vegetation regrow to the maximum potential, which is expected with the combination of natural regeneration and planting that commonly occurs after these events. Future BAU harvest files were constructed using current harvest rates, where county-specific average harvest and the actual amounts per ownership were used to guide grid cell selection. This resulted in the majority of harvest occurring on private land (70%) and in the mesic ecoregions. Beetle outbreaks were implemented using a modified mortality rate of the lodgepole pine PFT with 0.1% y⁻¹ biomass mortality by 2100.

For afforestation potential, we identified areas that are within forest boundaries that are not currently forest and areas that are currently grass crops. We assumed no competition with conversion of irrigated grass crops to urban growth, given Oregon's land use laws for developing within urban growth boundaries. A separate study suggested that, on average, about 17% of all irrigated agricultural crops in the Willamette Valley could be converted to urban area under future climate; however, because 20% of total cropland is grass seed, it suggests little competition with urban growth (25).

Landsat observations (12,500 scenes) were processed to map changes in land cover from 1984 to 2012. Land cover types were separated with an unsupervised K-means clustering approach. Land cover classes were assigned to an existing forest type map (42). The CropScape Cropland Data Layer (CDL 2015, <https://nassgeodata.gmu.edu/CropScape/>) was used to distinguish nonirrigated grass crops from other grasses. For afforestation, we selected grass cropland with a minimum soil water-holding capacity of 150 mm and minimum precipitation of 500 mm that can support trees (43).

Afforestation Cobenefits. Modeled irrigation demand of grass seed crops under future climate conditions was previously conducted with hydrology and agricultural models, where ET is a function of climate, crop type, crop growth state, and soil-holding capacity (20) (Table S7). The simulations produced total land area, ET, and irrigation demand for each cover type. Current grass seed crop irrigation in the Willamette Valley is 413 billion m³·y⁻¹ for 238,679 ha and is projected to be 412 and 405 billion m³ in 2050 and 2100 (20) (Table S7). We used annual output from the simulations to estimate irrigation demand per unit area of grass seed crops (1.73, 1.75, and 1.84 million m³·ha⁻¹ in 2015, 2050, and 2100, respectively), and applied it to the mapped irrigated crop area that met conditions necessary to support forests (Table S7).

LCA. Decomposition of wood through the product cycle was computed using an LCA (8, 10). Carbon emissions to the atmosphere from harvest were calculated annually over the time frame of the analysis (2001–2015). The net carbon emissions equal NECB plus total harvest minus wood lost during manufacturing and wood decomposed over time from product use. Wood industry fossil fuel emissions were computed for harvest, transportation, and manufacturing processes. Carbon credit was calculated for wood product storage, substitution, and internal mill recycling of wood losses for bioenergy.

Products were divided into sawtimber, pulpwood, and wood and paper products using published coefficients (44). Long-term and short-term products were assumed to decay at 2% and 10% per year, respectively (45). For product substitution, we focused on manufacturing for long-term structures (building life span >30 y). Because it is not clear when product substitution started in the Pacific Northwest, we evaluated it starting in 1970 since use of concrete and steel for housing was uncommon before 1965. The displacement value for product substitution was assumed to be 2.1 Mg fossil C/Mg C wood use in long-term structures (46), and although it likely fluctuates over time, we assumed it was constant. We accounted for losses in product substitution associated with building replacement (33) using a loss rate of 2% per year (33), but ignored leakage related to fossil C use by other sectors, which may result in more substitution benefit than will actually occur.

The general assumption for modern buildings, including cross-laminate timber, is they will outlive their usefulness and be replaced in about 30 y (7). By 2035, ~75% of buildings in the United States will be replaced or renovated, based on new construction, demolition, and renovation trends, resulting in threefold as many buildings as there are now [2005 baseline (31, 32)]. The loss of

the PSS is therefore PSS multiplied by the proportion of buildings lost per year (2% per year).

To compare the NECB equivalence to emissions, we calculated forest sector and energy sector emissions separately. Energy sector emissions ["in-boundary" state-quantified emissions by the Oregon Global Warming Commission (14)] include those from transportation, residential and commercial buildings, industry, and agriculture. The forest sector emissions are cradle-to-grave annual carbon emissions from harvest and product emissions, transportation, and utility fuels (Table S3). Forest sector utility fuels were subtracted from energy sector emissions to avoid double counting.

Uncertainty Estimates. For the observation-based analysis, Monte Carlo simulations were used to conduct an uncertainty analysis with the mean and SDs for NPP and Rh calculated using several approaches (36) (*SI Materials and Methods*). Uncertainty in NECB was calculated as the combined uncertainty of NEP, fire emissions (10%), harvest emissions (7%), and land cover estimates

(10%) using the propagation of error approach. Uncertainty in CLM4.5 model simulations and LCA were quantified by combining the uncertainty in the observations used to evaluate the model, the uncertainty in input datasets (e.g., remote sensing), and the uncertainty in the LCA coefficients (41).

Model input data for physiological parameters and model evaluation data on stocks and fluxes are available online (37).

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