

# Opportunities and Constraints for Forest Climate Mitigation

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*Reversing forest losses through restoration, improvement, and conservation is a critical goal for greenhouse gas mitigation. Here, we examine some ecological, demographic, and economic opportunities and constraints on forest-loss mitigation activities. Reduced deforestation and forest degradation could cut global deforestation rates in half by 2030, preserving 1.5 billion to 3 billion metric tons of carbon dioxide–equivalent (tCO<sub>2</sub>e) emissions yearly. Our new economic modeling for the United States suggests that greenhouse gas payments of up to \$50 per tCO<sub>2</sub>e could reduce greenhouse gas emissions by more than 700 million tCO<sub>2</sub>e per year through afforestation, forest management, and bioelectricity generation. However, simulated carbon payments also imply the reduction of agricultural land area in the United States by 10% or more, decreasing agricultural exports and raising commodity food prices, imports, and leakage. Using novel transgenic eucalypts as our example, we predict selective breeding and genetic engineering can improve productivity per area, but maximizing productivity and biomass could make maintaining water supply, biodiversity, and other ecosystem services a challenge in a carbon-constrained world.*

*Keywords: carbon storage and sequestration, climate change and leakage, invasions and water use, REDD, transgenic Eucalyptus hybrid*

**D**eforestation and other land-use changes have released approximately 150 billion metric tons (1 billion metric tons = 1 gigaton = 1 petagram) of carbon to the atmosphere since 1850, roughly one-fifth of the current atmospheric total (Houghton 2003). Most of this carbon loss from plants and soils occurred as a result of the conversion of forests to croplands and pasture. Reversing or halting this loss, as has occurred in parts of the United States and Europe that are recovering from earlier cycles of deforestation, is a critical policy goal for greenhouse gas mitigation today. We have abundant opportunities to restore and protect forests around the world.

At the same time that climate change policy is creating incentives to preserve and restore forests, population growth and rising per capita consumption are increasing demands for food and fiber around the world. Global food demand is projected to grow 59% to 99% from 2000 to 2050, depending on actual population and economic growth rates (Southgate et al. 2007). Greater consumption of meat and grain is raising commodity prices and concerns about deforestation (Trostle 2008). National policies supporting bioenergy expansion further amplify deforestation concerns. For instance, recent studies suggest that direct and indirect land-use changes for bioenergy expansion produce net carbon losses from ecosystems, not net gains (Fargione et al. 2008, Gibbs et al. 2008, Searchinger et al. 2008, Piñeiro et al. 2009). Despite existing policies and increased agricultural yields per area, deforestation is still occurring in the tropics and elsewhere.

The challenge we face today is how to use forests proactively—to save and restore forests and manage forests for the benefit of climate—while delivering more food and fiber and preserving biodiversity and other ecosystem services. That challenge is the heart of this Special Section examining the role of forests as a climate change mitigation tool. Given the real potential of forests for carbon mitigation in the coming decades, we were asked to examine the opportunity that forests present, along with some of the constraints on that opportunity—ecological, biophysical, demographic, and economic. Specifically, we examine three questions for forest mitigation activities: (1) Where can forests help slow the buildup of greenhouse gases in the atmosphere? (2) To what extent can future management, including genetic engineering, extend productivity beyond what native and managed forests provide today? (3) How many extra resources, including water and nutrients, will be needed to achieve this productivity, and what will be the consequences for other ecosystem services?

These questions might be expressed as a single goal: to increase forest productivity globally while maintaining as many other ecosystem services as possible. We approach that goal using the questions above as an outline for the article. We first examine opportunities and conflicting demands on lands globally, using an economic model to explore competition for land use through climate policy levers in the United States. After considering the opportunities for, and constraints on, increased land area for forestry, we then

examine the opportunities for greater forest productivity per acre, focusing briefly on the opportunities for genetic engineering to improve yields. Because Jansson and colleagues (2010) cover genetic engineering in detail in this Special Section, we instead explore the effects that increased productivity and carbon management may have on ecosystems, using the ideas of Odum (1969) as a foundation. These topics include potential invasions, water provisioning, risk of fires, and gene transfer. Forests that are unmanaged or managed for multiple purposes are likely to be very different in structure and species composition than forests managed or engineered solely for maximum carbon uptake.

### Land demands and policy levers

Preserving today's forests and increasing forest regrowth and productivity are critical goals for greenhouse gas mitigation. To accomplish the policy targets of greater forest protection, restoration, and productivity, economic incentives must alter the market pressures driving land-use trends, particularly as the human population continues to grow. The human population, projected to surge beyond 9 billion by 2050 (Southgate 2009), will inevitably place new pressures on tropical forests and on the urban-rural fringe in countries such as the United States.

Given the projected demands for food, fiber, and energy over the next 50 years, policy incentives are needed if forest carbon sinks are to be increased. Such incentives include payments for avoided deforestation, improved carbon storage through forest management, afforestation on lands currently put to other uses, and the use of forest biomass for bioenergy production. In a climate change context, these incentives should compensate landowners for net carbon gained above business-as-usual scenarios. As a specific example, reducing emissions from deforestation and degradation (REDD) pays countries or landowners for carbon retained in trees that would otherwise have been lost through land clearing. For bioenergy, a price for greenhouse gas emissions boosts the demand for fossil-fuel substitutes, creating a new market for logging residues and for short-rotation woody crops grown specifically for cellulosic ethanol production or cofired bioelectricity generation.

### Reducing deforestation and increasing forest stocks

Deforestation is a significant driver of anthropogenic greenhouse gas emissions, accounting for at least 12% of global carbon dioxide (CO<sub>2</sub>) emissions and comparable in size to the emissions from the global transportation sector (e.g., Van der Werf 2009). Deforestation accounts for an overwhelming portion of total emissions of Brazil and Indonesia, the world's third- and fourth-largest emitters by volume (Gullison et al. 2007). Reducing deforestation rates and improving sustainable forest management may be difficult in a time of continuing population growth and agricultural expansion (Walker and Salt 2006, Ryan et al. 2010). Nevertheless, financial incentives and policy levers can help in this important task.

REDD is a policy incentive that pays countries or landowners to preserve forests (Miles and Kapos 2008, Olander et al. 2008). Several recent studies have evaluated REDD incentives by comparing baseline land-use trajectories to trajectories in which carbon payments compensate landowners for keeping forests intact. Recent modeling efforts suggest that approximately 1.8 billion tons of CO<sub>2</sub> equivalent (tCO<sub>2</sub>e) of global emissions per year, approximately one-third of the amount attributable to deforestation, can be eliminated for approximately \$10 per tCO<sub>2</sub>e. At \$20 and \$30 per tCO<sub>2</sub>e, mitigation estimates rise to 2.5 billion and 2.9 billion tCO<sub>2</sub>e per year, respectively (Gullison et al. 2007, Kindermann et al. 2008). These greenhouse gas benefits from REDD activities would be accompanied by a halving of global deforestation rates by 2030 (Kindermann et al. 2008).

Avoided deforestation is therefore a feasible, relatively cheap alternative for greenhouse gas mitigation that could produce many ecological benefits, including biodiversity conservation and additional net cooling from water recycling and biophysical effects (Fearnside 2005, Jackson et al. 2008, Keith et al. 2009). For these and other reasons, countries such as Brazil are increasingly interested in reducing deforestation under the rubric of REDD. The challenges of implementing REDD protocols include the method for distributing payments, uncertainties in land ownership and control, the means of establishing a proper deforestation baseline, and, as discussed below, leakage—shifts in the location of deforestation to places that are not currently monitored.

In addition to REDD and forest conservation in general, afforestation and forest restoration provide additional pathways for greenhouse gas mitigation. Afforestation is defined as the planting of forests in areas that have been without trees for at least 50 years (or some other arbitrary length of time). In the United States, afforestation has the potential to sequester approximately 370 million tCO<sub>2</sub>e per year, depending on the price of carbon (Jackson and Schlesinger 2004, USEPA 2005, SOCCR 2007). Similarly, forest regrowth in the United States since 1940 has recovered about a third of US carbon lost to the atmosphere through deforestation and harvesting between the start of the Industrial Revolution and 1930.

Globally, the combination of reforestation and afforestation activities could reduce atmospheric CO<sub>2</sub> concentrations by as much as 30 parts per million (ppm) this century (House et al. 2002). However, this potential mitigation is limited by many factors. One is the vulnerability of forests to increased disturbances, including those caused by pathogens, droughts, fires, and storms (Galik and Jackson 2009). For example, the mountain pine beetle is projected to convert 374,000 square kilometers (km<sup>2</sup>) of pine forest from a small net carbon sink to a large carbon source in Alberta alone, liberating 1 billion tCO<sub>2</sub>e to the atmosphere (Kurz et al. 2008). Climate change is another factor that could limit the potential for carbon sequestration in forests. The mountain pine beetle in Alberta is thriving in part because of warmer minimum temperatures in the winter

and warmer and drier summers. A third potential limitation is landowner behavior in private-sector forestry, including decisions on what species to plant and how intensely to manage forests. Private forestry competes economically with agriculture, urban development, and other land uses. Landowner decisions will therefore dictate the success of some climate policy efforts, a topic we explore next.

### Competition between forestry and other land uses

Economic factors and human behavior, coupled with biological and physical factors, will help determine the role that forestry plays in greenhouse gas policy. Economic modeling is one approach for projecting how incentives can build the global forest carbon stock. Such models capture market behavior, land-use competition, and comprehensive greenhouse accounting, with different land-use types competing in a full economic system. Economic modeling is particularly helpful in mitigation analyses because it explicitly accounts for land-use competition between alternative uses. In the real world, afforestation and other forest practices must compete with food and biofuel production as well as with other possible uses of the same land; large mitigation “potentials” based solely on total land area will inevitably overestimate what is attainable in the marketplace.

To illustrate the effects of such competition for land, we use the US forest and agricultural sector optimization model with greenhouse gases (FASOMGHG) to simulate land-use trajectories and forest-based potential for mitigation scenarios. This model is a partial-equilibrium economic model of the US agricultural and forestry sectors. For our use, it simulates market responses to carbon price signals, including incentives for bioenergy and management practices that improve carbon sequestration or reduce greenhouse gas emissions. The model has been used in many previous studies of renewable energy and greenhouse gas mitigation policy (e.g., McCarl and Schneider 2001, Jackson et al. 2005, Murray et al. 2005, Baker et al. 2010).

The recently updated FASOMGHG includes a broader range of land-use categories to depict competition between privately owned cropland, forest, pasture, conservation lands, and development (Baker et al. 2010). The model also now contains more than 20 alternative biofuel feedstocks for producing starch- or sugar-based ethanol, cellulosic ethanol, and biodiesel. In addition, biomass from a variety of agricultural and forestry sources can be used for bioelectricity production. Commodity demand, energy market, and input-cost growth assumptions have also been updated to accurately represent current and future technology and market conditions.

Forest productivity in the FASOMGHG is characterized by a number of physical and economic factors, including region, species, land suitability class, management intensity class, and age cohort. Forest carbon is tracked in soils, the forest floor, understory, and trees (including final products) using a methodology similar to the forest carbon model used by the US Forest Service (Birdsey 1996) that varies with the aforementioned factors. This formulation allows the model to

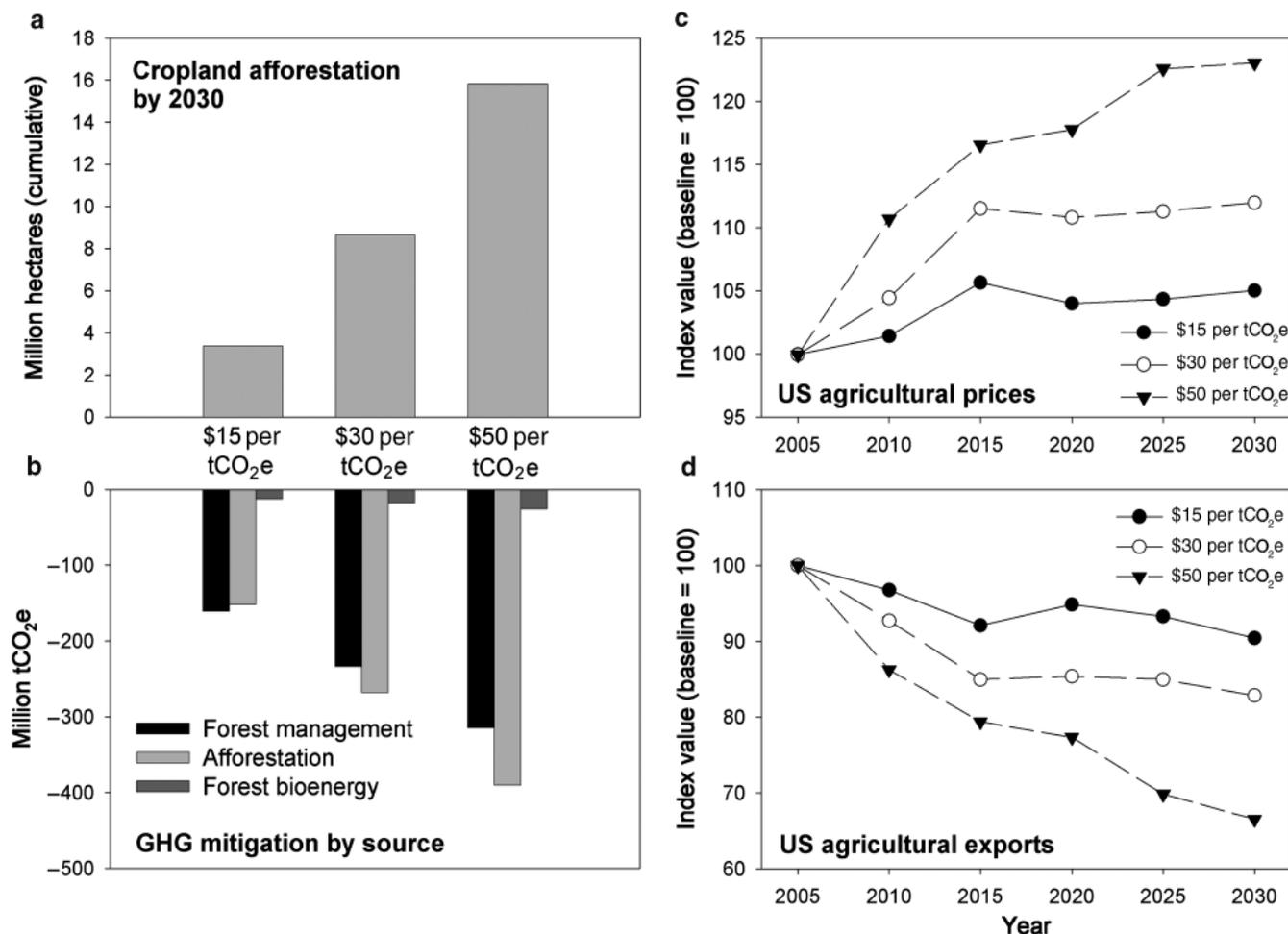
simulate management responses to carbon price signals that, for instance, boost forest carbon stocks.

We began our analysis with a baseline trajectory of agricultural and forest production and land use that includes the bioenergy mandates imposed by the US Energy Independence and Security Act of 2007. To simulate the effects of greenhouse gas mitigation efforts, we imposed CO<sub>2</sub>-equivalent prices on all emission sources and sinks from agricultural and forestry activities. We then compared the results from policy incentives for greenhouse gas mitigation with the baseline scenario.

Economic incentives, such as greenhouse gas offset payments to landowners, could substantially alter the balance of forestry in the United States. Across mitigation price scenarios of \$15, \$30, and \$50 per tCO<sub>2</sub>e, privately owned timberland in the United States in 2030 is projected to increase between 11.2 million and 23.5 million hectares above a baseline that declines over time because of development pressures. The forest expansion is caused by cropland and pasture afforestation, avoided deforestation, and longer rotation times. For our three carbon-price scenarios, approximately 3.4 million, 8.7 million, and 15.8 million hectares, respectively, are projected to convert from cropland to forestry by 2030 under the influence of carbon sequestration payments (figure 1a), although there are uncertainties in such estimates. For the \$50-per-tCO<sub>2</sub>e scenario, potential afforestation by 2030 represents approximately 10% of the total US cropland stock currently in production. Such a shift in land resources would store substantial amounts of carbon in the next few decades. Additional mitigation options for forest management include lengthening rotation times, changing the species grown, reducing management intensity, and stand thinning.

For bioenergy production, we imposed the requirements of the renewable fuels standard (from the Energy Independence and Security Act of 2007) on the use of forest biomass for cellulosic ethanol. Bioelectricity production from forest biomass, however, is then allowed to respond to a given carbon price signal. The FASOMGHG can produce bioelectricity from logging and pulp-and-paper residues, as well as from dedicated short-rotation woody crops such as hybrid poplar and willow. Recent analyses suggest that use of forest biomass for electricity production should not be treated as carbon neutral as a result of land-use change emissions unless the biomass harvested for energy had sequestered “additional” carbon while growing (e.g., Searchinger 2009). Our analysis addresses this concern by imposing a carbon price on land-use change emissions above baseline levels, thus internalizing the cost of clearing land solely for bioenergy production.

Overall, we find significant net mitigation potential for the United States that ranges from 325 million to 730 million tCO<sub>2</sub>e per year on an annuity basis, including activities that improve carbon sequestration in forests (160 million to 315 million tCO<sub>2</sub>e), afforest dedicated agricultural lands (152 million to 390 million tCO<sub>2</sub>e), or promote bioelectricity from forest biomass (13 million to 26 million tCO<sub>2</sub>e; figure 1b).



**Figure 1.** Forest mitigation potential and commodity prices in the United States for three carbon price scenarios (\$15, \$30, and \$50 per ton of carbon dioxide equivalent; tCO<sub>2</sub>e). (a) Estimated cumulative afforestation potential in 2030 across mitigation scenarios in million hectares. (b) Greenhouse gas (GHG) mitigation potential in the United States for afforestation, forest management, and bioelectricity from forest products; values represent annualized deviations from the baseline, with net present value of emissions beyond 2010 converted to an annuity using a 4% discount rate for 70 years. (c) US agricultural commodity price index values across mitigation scenarios. (d) Index values for US agricultural exports across mitigation scenarios.

Some activities, such as afforestation, need to be maintained for long time horizons, presenting a number of institutional complications and potentially leading to some adverse market impacts that we discuss below.

### Uncertainties and barriers to forest mitigation

Reduced deforestation rates, forest regrowth, improved forest productivity, and afforestation are all possible options for increasing the global forest carbon stock. Implementing policies that promote these practices can be difficult, however. Given the promise of forest mitigation for climate policy, what are some of the barriers or impediments to such efforts?

Recent work has described numerous potential barriers to forest policy improvements. One is the extent to which reducing agricultural land area—10% or more in our simulations for the United States—would increase commodity

prices nationally and globally (figure 1c, 1d). Another barrier to forest credits is the transaction cost, including aggregating, verifying, and enforcing greenhouse gas offset activities (Galik et al. 2009). A third barrier is the issue of additionality, the notion that greenhouse gas savings must be “additional” to what would have happened without a policy incentive. Finally, a lack of permanence—the loss of forest carbon back to the atmosphere within a given time period—may also reduce the effectiveness of some forest activities (e.g., Canadell and Raupach 2008, Galik and Jackson 2009). In fact, some authors have proposed that temporary carbon “rentals,” rather than permanent credits, are a better model for greenhouse gas mitigation activities, perhaps as an extension of the Conservation Reserve Program for forests (e.g., Marland et al. 2001).

One particular barrier that we highlight here for more detailed discussion is the potential for leakage. To what extent

will forest mitigation activities drive agricultural development elsewhere, particularly into tropical forests and marginal agricultural lands? The global marketplace connects such effects in an increasingly direct way, as recent biofuels analyses have suggested (Fargione et al. 2008, Searchinger et al. 2008).

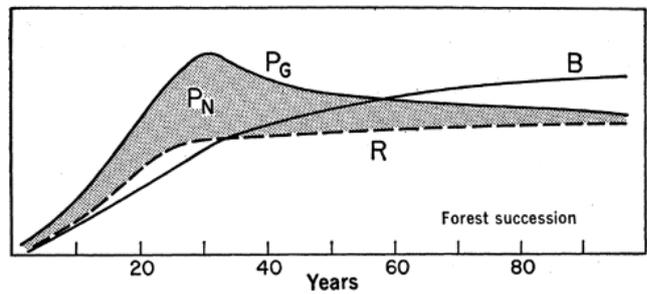
Characterizing leakage requires that a marginal increase in land-clearing activities in one region can be at least partly attributed to a market price response brought on by production decisions in another. Hence, by allocating land in one area away from conventional commodity production and toward bioenergy production or carbon sequestration, altered market conditions may induce land-use change in another region. In a worst-case scenario, the resulting emissions from land clearing can be large enough to offset the carbon benefits of the original mitigation activity.

Leakage is often thought of in a biofuels context (e.g., Searchinger et al. 2008), but pure climate change mitigation activities can also lead to indirect land-use changes. Several studies have evaluated leakage from forest conservation, altered forest management practices, and afforestation efforts (Murray et al. 2004, Gan and McCarl 2007, Sun and Sohngen 2009); upward pressure on commodity markets from forest carbon sequestration can shift timber production elsewhere, leading to diminished greenhouse gas gains for the mitigation effort. This effect can vary tremendously, with leakage estimated to range from less than 10% to more than 90% of total mitigation, depending on the region and activity undertaken (Murray et al. 2004).

Although the FASOMGHG is not a global timber supply model and does not represent agricultural production and land use outside the United States, our results reveal important information about domestic forest offsets, bioenergy, and potential international leakage. For instance, as soon as the greenhouse gas mitigation policy is put into effect in 2010, simulated agricultural prices and imports rise for a given CO<sub>2</sub>e price (figure 1c). More broadly, US agricultural exports decline substantially, as well (figure 1d). Reduced US agricultural exports can lead to international leakage as production expands elsewhere to satisfy global demand for food and fiber. Hence, by afforesting US cropland, boosting bioenergy production, and decreasing transfers of land into agriculture, a lower food and fiber supply induces higher commodity prices and lower agricultural exports. Note, however, that a number of factors contribute to this shift in commodity prices, including additional production of dedicated bioenergy on productive agricultural lands, and shifts in livestock management patterns. Further research on the topic of leakage is desperately needed to encourage policy that maximizes terrestrial greenhouse gas mitigation potential while reducing emissions from land-clearing activities outside the United States.

### Resource demands and potential trade-offs for intensively managed forests

Now that we have examined issues surrounding the additional land area needed for forest mitigation, we turn to the



**Figure 2. Carbon fluxes and biomass as a function of time since planting or disturbance (in years). For this ecosystem, maximum ecosystem productivity occurs at about 30 years (Odum 1969). Abbreviations: B, biomass;  $P_G$ , gross photosynthesis;  $P_N$ , net photosynthesis; R, respiration.**

consequences of the second mitigation opportunity: greater productivity *per* area. Jansson and colleagues (2010; this issue) describe the potential for increased forest productivity through genetic engineering and improvement; we instead focus on the demands that the intensification of forestry will place on ecosystems. We use Gene Odum's framework to begin examining this issue.

In a seminal paper in ecology, Odum (1969) characterized the opportunities and trade-offs that accompany attempts to maximize net primary productivity. Describing the bioenergetics of ecosystem development, he defined the goal of intensive forestry and agriculture as achieving "high rates of production of readily harvestable products with little standing crop left to accumulate on the landscape." Often in land management, these high rates of productivity are obtained by managing for early successional species in monocultures. For the ecosystem pictured in figure 2, maximum productivity (and potential harvest) occurs after about 30 years.

Odum also recognized that managing lands for maximum productivity sometimes reduced the amount or quality of other services that ecosystems provide. His list of trade-offs included invasions (as a subset of biodiversity loss), clean water, and climate feedbacks (Odum 1969). We examine Odum's trade-offs for the intensification of forestry, including increased invasion and fire risk, water use, and transgene spread.

We do not discuss in detail—but do acknowledge—the loss of biodiversity that occurs when native ecosystems are replaced with monocultures. A diverse native forest and a monoculture plantation may have the same carbon storage but differ substantially in other services that people value. This trade-off was apparent to Odum and others many decades ago. In reality, many managed systems have lower productivity than their natural counterparts and require fertilizers and other high-intensity inputs to boost growth. If croplands and forest ecosystems are fertilized, some of the applied nitrogen is inevitably lost as nitrous oxide and other greenhouse gases, offsetting at least some of the ecosystem gains from carbon sequestration (e.g., Magill et al. 1997).

Odum's classic perspective bears a fresh look for carbon mitigation policy today.

### Risks of invasion

The United States alone has more than 50,000 invasive species that cost, collectively, about \$100 billion each year (though the figure is hard to estimate accurately). These invaders are also the primary threat to 42% of threatened and endangered species in the United States (Pimentel et al. 2005). Although tree species increasingly suffer the effects of invasive insects and pathogens (Chornesky et al. 2005), forestry species themselves invade native landscapes throughout the world (Thompson et al. 2009).

Of the more than 110 pine species found worldwide, only one, *Pinus merkusii*, is native to the Southern Hemisphere. Nevertheless, pines have become a mainstay of forestry in much of South America, Africa, Australia, and New Zealand (Richardson and Petit 2006). At least 18 pine species in the Southern Hemisphere are currently invasive in four or more countries per species, including *Pinus pinaster*, *Pinus elliottii*, *Pinus patula*, *Pinus taeda*, *Pinus halepensis*, and *Pinus radiata* (Richardson and Petit 2006). In South Africa, where 80 or more pine species have been planted, *P. pinaster* has invaded thousands of square kilometers of native fynbos, a biodiversity hot spot, with *P. radiata* and *P. patula* also expanding in area (Richardson et al. 1994, Rouget et al. 2004). Pines have similarly invaded native eucalypt forests in Australia (e.g., Williams MC and Wardle 2005).

High-productivity eucalypts can also be invasive. Based on their history in California, two eucalypt species, *Eucalyptus globulus* (Tasmanian blue gum) and *Eucalyptus camaldulensis* (red gum), are already classified as invasive in California (Bossard et al. 2000, Cal-IPC 2006). Data from eucalypts also illustrate a more general result in invasion biology: The more often a species is planted, the more likely it is to become invasive. In southern Africa, the number of records of spontaneous occurrences of 57 *Eucalyptus* species correlates strongly with the number of plantations on which each species is grown (Rejmánek 2000). An increase in the plantings of exotic plantation species worldwide will almost certainly increase invasions into native habitats.

Predicting the potential ranges of invasive species is difficult because hybridization and adaptation to novel environments can expand species' ranges beyond the conditions in which they were originally found (Bossdorf et al. 2005). *Rhododendron ponticum*, native to the Mediterranean and Black Sea regions, is one of the most problematic invasive plants in the British Isles, where landowners have spent millions of dollars to control it (Dehnen-Schmutz et al. 2004). Analyses of chloroplast and nuclear ribosomal DNA suggest that the invasive individuals of *R. ponticum* came from the relatively warm Iberian Peninsula (Milne and Abbott 2000). Molecular data also suggest that hybridization of invasive *R. ponticum* with *Rhododendron catawbiense*, a horticultural species from the Appalachian

Mountains, most likely provided the cold tolerance that allows *R. ponticum* to survive in Scotland and other habitats that are colder than its native range (Milne and Abbott 2000). This potential for hybridization and adaptation shows that invasive species will not always stay within their predicted climate envelope after they establish.

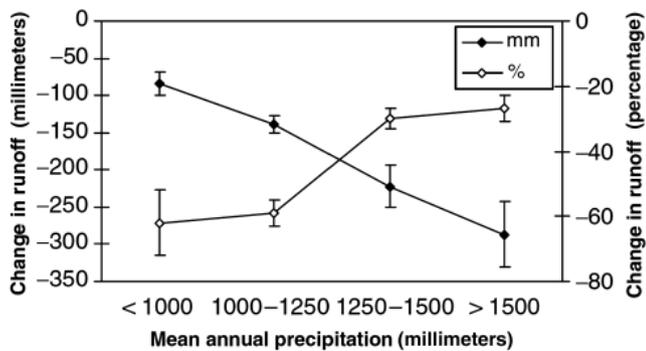
Invasive trees are problematic not just for their effects on native species but for the water and other resources they consume. Versfeld and colleagues (1998) found that about 10.1 million hectares (ha), or 6.8% of South Africa, had been invaded by woody aliens. These alien plants consume approximately 6.7% of the country's runoff and would cost \$860 million to clear over 20 years (Le Maitre et al. 2000). Studies in four South African catchments show that partial invasion by pines, eucalypts, acacias, and other woody species have reduced annual stream flow by 7% to 22%; if invasives were allowed to reach 100% of canopy cover in the catchments, the estimated decreases in stream flow would be 22% to 96% (Le Maitre et al. 2002). In response to this problem, South Africa launched the Working for Water program, which has cleared invasives from more than a million hectares of land since 1995.

### Water trade-offs

From the pioneering work of Arnold Engler (1919) and Charles Hursch (e.g., Hursch and Brater 1941), research has clearly shown that trees consume more water—sometimes much more water—than do grasslands, croplands, and shrublands (Holmes and Sinclair 1986, Vertessy 1999, Jackson et al. 2005, 2009). Forests and tree plantations tend to have greater leaf surface areas and greater transpiration than other ecosystems (e.g., Calder 1986). They also typically have more extensive root systems, allowing water uptake from deeper underground, and their canopies intercept more water, keeping precipitation from reaching the soil (Schenk and Jackson 2002).

How extensive are these reductions in stream flow caused by plantations, and where may problems be the greatest? A global analysis of more than 500 years of catchment data showed that plantations reduced total annual stream flow by 180 millimeters (mm), or 38% on average, compared with native grasslands and shrublands; 10- to 20-year-old stands showed the largest losses of 227 mm, or 52% (Jackson et al. 2005). Stream flow losses are also positively related to the net primary production (NPP) of the planted stands, with eucalypts increasing evapotranspiration more than most other trees because of their early rapid growth and canopy closure (Dye 1996). One trade-off highlighted by Odum (1969) is that maximizing forest productivity will inevitably increase water use.

If plantation forestry is pushed into marginal, drier habitats by competition with other land uses (see above), relative water losses are likely to be even greater (Farley et al. 2005). Although absolute losses in stream flow were larger for plantations at wetter sites (> 1500 mm annual precipitation), relative losses were greater at drier sites



**Figure 3.** Mean change in runoff globally ( $\pm$  standard error) following afforestation as a function of mean annual precipitation for sites that were originally grasslands. For millimeters,  $p < 0.01$ . For percentage,  $p < 0.001$ . Adapted from Farley and colleagues (2005).

(< 1000 mm mean annual precipitation), with annual stream flow declining by two-thirds (figure 3). Relative losses in low or base flow were even bigger than losses in annual flow. Dry-season losses may therefore be even more severe, leading to shifts from perennial to intermittent flow in some cases.

One way to reduce losses in water yield is to increase forest life spans and plantation rotation times. Catchment data from two sites in South Africa with *P. radiata* and *Eucalyptus grandis* show that 20 to 25 years after planting, losses in water yield dropped by half (Scott and Prinsloo 2008). At the Tierkloof catchment, where 36% of the catchment was planted in *P. radiata*, the loss in annual stream flow for the plantation decreased from approximately 50% to 20% compared with native fynbos (Scott and Prinsloo 2008). Thus, land managers could decrease rotation times and maintain older forests to reduce water losses; however, such a strategy is sometimes incompatible with the goal of maximizing productivity on the landscape (figure 2).

What else can be done to lessen carbon and water trade-offs? Planting only part of a catchment with trees would reduce the likelihood of complete stream loss, particularly in drier areas. Using deciduous instead of evergreen species can reduce water losses in some cases and help to maintain a productive understory for livestock and wildlife. Breeding and genetic engineering for drought tolerance may also increase water-use efficiency for commercial trees in the coming decades. All of the approaches mentioned here reduce the amount of extra water needed but are likely to decrease the maximum storage that forests can provide per area. If maximizing forest net primary productivity remains the goal, then growing more wood will require more water.

### Transgene flow

At least a half dozen important forestry genera are currently targets of genetic engineering, including *Populus*, *Pinus*, and *Eucalyptus*. These efforts can substantially improve productivity per acre, insect resistance, and heavy metal and

freezing tolerances, while also reducing lignin content and increasing cellulose concentrations where desirable (e.g., Grace et al. 2005, Grattapaglia and Kirst 2008, Nelson and Johnsen 2008). Decreasing lignin content by as much as 30% (e.g., Kawaoka et al. 2006) can reduce bleaching costs for the pulp and paper industry, whereas increased cellulose concentrations can improve ethanol yields for biofuel production. In Europe, the first field trial of genetically modified trees was a planting of herbicide-resistant poplars in Belgium in 1988; at least six more European countries have had additional trials. In China, genetically modified poplars have been commercially available since 2002.

Because Jansson and colleagues (2010, this issue) discuss the potential for genetically engineered trees to increase primary productivity and to be useful as fuel sources, we examine some of the associated risks. One potential risk of plantation crops and trees, particularly transgenic ones, is gene flow or “contamination” to surrounding individuals, species, and areas. Examples include invasion of the species outside of the planted area, transgene flow to compatible wild species, and potential transgene introgression. Such establishments and gene flow have been documented in transgenic crop and forage species. For instance, glyphosate-resistant creeping bentgrass, *Agrostis stolonifera*, has established and persisted in abundance beyond where it was originally planted; gene flow to surrounding plants of the same and different *Agrostis* species from windborne pollen has also been clearly documented (Watrud et al. 2004, Zapiola et al. 2008).

For trees, the risks of transgene flow depend on many factors, including the distance and direction pollen and seeds travel, synchronies in the timing of flowering and pollination, and various reproductive barriers (e.g., Williams CG et al. 2006, Barbour et al. 2008). Because trees are taller than grasses, wind-dispersed tree pollen will likely travel farther—many miles downwind from its site of origin (e.g., Williams CG 2008). The potential for transgene flow in trees may also be greater than in crops because most crops have been isolated by selective breeding for hundreds or thousands of years, whereas selective breeding in forestry is more recent. On the other hand, genetic engineering of sterility can reduce the likelihood of transgene flow in all species (Richardson and Petit 2006), although complete sterility in any large population is unlikely (Strauss et al. 2004, Van Frankenhuyzen and Beardmore 2004).

### Genetically modified eucalypts as a case study

Research is under way in the United States on many genetically modified horticultural and forestry species, including the hybrid of *E. grandis* and *Eucalyptus urophylla* recently approved in May of 2010 for field trials in seven states. The hybrid eucalypt has been engineered with gene constructs that provide three benefits: (1) cold or freezing tolerance, reducing vulnerability to cold temperatures in the southern United States; (2) reduced lignin biosynthesis for improved pulp and paper applications and possibly for biofuels; and (3) reduced tree fertility, making them less likely to be invasive or

to contaminate neighboring plants. The fast-growing hybrid is likely to be released commercially in the United States to be planted in a belt from east Texas to Georgia and Florida.

The opportunity to grow eucalypts in the southeastern United States presents some economic advantages for foresters. Foresters, both public and private, face growing challenges in the region (e.g., Wear and Greis 2002). They compete in an increasingly global marketplace, particularly with tropical forestry that can complete a rotation in half the time with lower labor costs. Southeastern foresters also face economic pressures from urbanization and population growth in the region. The chance to grow high-productivity eucalypts to complement traditional pine forestry in the Southeast could bring important benefits (e.g., Fenning and Gershenzon 2002).

The large-scale planting of genetically modified eucalypts across the southeastern United States also raises some questions about sustainability and risk management. Switching land use from pasture and agriculture to eucalypts will almost certainly decrease local stream flow, as described above, and possibly affect aquatic diversity. Almost half of all animals listed as federally endangered in the United States are aquatic species (e.g., Dobson et al. 1997, Jackson et al. 2001). As described above, eucalypts also have a history of invasion, including in the United States (Bossard et al. 2000, Cal-IPC 2006); in general, the larger an area of planting for an exotic species, the greater the likelihood of invasion (Rejmánek 2000).

The risk of invasion can compound with another attribute of eucalypts—their propensity to burn. Eucalypts are generally well adapted to frequent fires and are more fire prone than most temperate forest species, which poses potential risks that should be minimized through management. In Canberra, Australia, a combination of drought, high winds, and suburban encroachment contributed to the catastrophic eucalypt bushfires in 2003 that burned 500 homes and caused half a billion dollars of economic damage (e.g., Fromm et al. 2006). Eucalypts are also generally high emitters of volatile organic compounds that can lower the flashpoint for fires (e.g., Maleknia et al. 2009, Wilkinson et al. 2009). The propensity of eucalypts to burn and their ability to regenerate quickly after fire suggest a possible risk of postfire invasion into surrounding landscapes. Eucalypts often increase in dominance relative to other less-fire-tolerant species in post-fire environments (e.g., Pekin et al. 2009).

However, invasive transgenic eucalypts planted in the southeastern United States would likely pose a lower risk for gene transfer than would genetically modified pine species such as *P. taeda*. *Pinus taeda* is common in the region, and the potential for hybridization among pine species is fairly high. A eucalypt planted among native eucalypt species in a different region would have a similar potential for hybridization (e.g., Barbour et al. 2008).

Overall, transgenic eucalypts are likely to be commercialized in the United States. Because of this, we believe that the US Department of Agriculture should establish a eucalypt monitoring program for the southern United States

immediately, ideally establishing baseline data before commercial plantings. There would be many advantages to this approach, which would use the species as a study system not just for productivity measurements but for also additional research to quantify the risks described above, including water losses, invasion potential, and transgene flow. For instance, catchment studies should be established now in at least a few sites to provide baseline data on water flow for later comparisons with paired eucalypt stands.

Commercialization will likely help growers compete in an increasingly global marketplace. The fast growth rate of the trees may also help maximize productivity and could potentially offset some fossil-fuel use. However, the risks that accompany eucalypt introductions are difficult to quantify without long-term data, and are hard to correct should they occur. Finally, commercial forestry in the United States has historically been based solely on native species. With the introduction of transgenic eucalypts, that forestry era is about to end.

## Conclusions

At the start of this article we posed three questions for forest climate mitigation. Specifically, we examined some opportunities and constraints associated with forests' ability to maximize climate benefits while maintaining as many other ecosystem services as possible. Reduced emissions from deforestation and degradation is an immediate opportunity that could offset about 10% of current fossil-fuel emissions. Reforestation and afforestation together could reduce atmospheric CO<sub>2</sub> concentrations by as much as 30 ppm this century. However, forestry must compete economically with other land uses, including agriculture, recreation, and urban and suburban development, which will limit the opportunity for forest mitigation without economic incentives. In our simulations, replacing cropland or boosting bioenergy production provides substantial greenhouse gas benefits in the United States but could reduce the food and fiber supply along with agricultural exports, while inducing higher commodity prices and agricultural imports, particularly from Brazil and other tropical countries where deforestation emissions are of paramount concern.

The intensification of forest management brings substantial opportunities to produce more biomass per unit of land, reducing some of the pressures on land conversion globally. Genetic engineering offers the promise of improved yields, resistance to pests, and many other benefits. The intensification of forestry also carries some potential trade-offs, however, including increased water use, fertilizer applications that could raise trace-gas emissions, and a greater likelihood of species invasions.

As Odum (1969) described, "Man has generally been preoccupied with obtaining as much 'production' from the landscape as possible, by developing and maintaining early successional types of ecosystems, usually monocultures. But, of course, man does not live by food and fiber alone; he also needs a balanced CO<sub>2</sub>-O<sub>2</sub> atmosphere, the climatic buffer provided by oceans and masses of vegetation, and clean (that

is, unproductive) water for cultural and industrial uses.... In other words, the landscape is not just a supply depot but is also the *oikos*—the home—in which we must live” (p. 266). Our goal should be to conserve, restore, and improve forest productivity, while preserving the quality of life for people and other species on Earth.

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### References cited

- Baker JS, McCarl BA, Murray BC, Rose SK, Alig RJ, Adams DM, Latta G, Beach RH, Daigneault A. 2010. Net-farm income and land use under a US greenhouse gas cap-and-trade. *Policy Issues* (April): 17. (8 September 2010; [www.aaea.org/publications/policy-issues.pdf](http://www.aaea.org/publications/policy-issues.pdf))
- Barbour RC, Otahal Y, Vaillancourt RE, Potts BM. 2008. Assessing the risk of pollen-mediated gene flow from exotic *Eucalyptus globulus* plantations into native eucalypt populations of Australia. *Biological Conservation* 141: 896–907.
- Birdsey RA. 1996. Regional estimates of timber volume and forest carbon for fully stocked timberland, average management after cropland and pasture revision to forest. Pages 309–333 in Hair D, Sampson NR, eds. *Forests and Global Change, vol. 2: Forest Management Opportunities for Mitigating Carbon Emissions*. American Forests.
- Bossard CC, Randall JM, Hoshovsky MC. 2000. *Invasive Plants of California's Wildlands*. University of California Press.
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144: 1–11.
- Calder IR. 1986. Water use of eucalypts: A review with special reference to south India. *Agricultural Water Management* 11: 333–342. [Cal-IPC] California Invasive Plant Inventory. Cal-IPC Publication 2006-02. California Invasive Plant Council.
- Canadell JG, Raupach MR. 2008. Managing forests for climate change mitigation. *Science* 320: 1456–1457.
- Chornesky EA, et al. 2005. Science priorities for reducing the threat of invasive species to sustainable forestry. *BioScience* 55: 335–348.
- Dehnen-Schmutz K, Perrings C, Williamson M. 2004. Controlling *Rhododendron ponticum* in the British Isles: An economic analysis. *Journal of Environmental Management* 70: 323–332.
- Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS. 1997. Geographic distribution of endangered species in the United States. *Science* 275: 550–553.
- Dye PJ. 1996. Climate, forest, and streamflow relationships in South African afforested catchments. *Commonwealth Forestry Review* 75: 31–38.
- Engler A. 1919. Untersuchungen über den Einfluss des Waldes auf den Stand der Gewässer. *Mitteilungen der Schweizerischen Zentralanstalt für das forstliche Versuchswesen* 12: 1–626.
- Fargione J, Hill J, Tilman D, Polasky S, Hawthorne P. 2008. Land clearing and the biofuel carbon debt. *Science* 319: 1235–1238.
- Farley KA, Jobbágy EG, Jackson RB. 2005. Effects of afforestation on water yield: A global synthesis with implications for policy. *Global Change Biology* 11: 1565–1576.
- Fearnside PM. 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conservation Biology* 19: 660–668.
- Fenning TM, Gershenzon J. 2002. Where will the wood come from? Plantation forests and the role of biotechnology. *Trends in Biotechnology* 20: 291–296.
- Fromm M, Tupper A, Rosenfeld D, Servranckx R, McRae R. 2006. Violent pyro-convective storm devastates Australia's capital and pollutes the stratosphere. *Geophysical Research Letters* 33: L05815. doi:10.1029/2005GL025161
- Galik CS, Jackson RB. 2009. Risks to forest carbon offset projects in a changing climate. *Forest Ecology and Management* 257: 2209–2216.
- Galik CS, Baker JS, Grinnell J. 2009. Transaction Costs and Forest Carbon Offset Potential. *Climate Change Policy Partnership*. Duke University. (12 July 2010; [http://nicholas.duke.edu/ccpp/ccpp\\_pdfs/transaction.07.09.pdf](http://nicholas.duke.edu/ccpp/ccpp_pdfs/transaction.07.09.pdf))
- Gan J, McCarl BA. 2007. Measuring transnational leakage of forest conservation. *Ecological Economics* 64: 423–432.
- Gibbs HK, Johnston M, Foley JA, Holloway T, Monfreda C, Ramankutty N, Zaks D. 2008. Carbon payback times for crop-based biofuel expansion in the tropics: The effects of changing yield and technology. *Environmental Research Letters* 3: 034001.
- Grace LJ, Charity JA, Gresham b, Kay N, Walter C. 2005. Insect-resistant transgenic *Pinus radiata*. *Plant Cell Reports* 24: 103–111.
- Grattapaglia D, Kirst M. 2008. Eucalyptus applied genomics: From gene sequences to breeding tools. *New Phytologist* 179: 911–929.
- Gullison RE, et al. 2007. Tropical forests and climate policy. *Science* 316: 985–986.
- Holmes JW, Sinclair JA. 1986. Water yield from some afforested catchments in Victoria. *Hydrology and Water Resources Symposium*. River Basin Management, Griffith University, Brisbane, 25–27 November 1986. Institution of Engineers, Australia.
- Houghton RA. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus* 55: 378–390.
- House JL, Prentice IC, Le Quere C. 2002. Maximum impacts of future reforestation or deforestation on atmospheric CO<sub>2</sub>. *Global Change Biology* 8: 1047–1052.
- Hirsch CR, Brater EF. 1941. Separating storm-hydrographs from small drainage-areas into surface- and subsurface-flow. *Transactions of the American Geophysical Union, Part 3*: 863–871.
- Jackson RB, Schlesinger WH. 2004. Curbing the U.S. carbon deficit. *Proceedings of the National Academy of Sciences* 101: 15827–15829.
- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW. 2001. Water in a changing world. *Ecological Applications* 11: 1027–1045.
- Jackson RB, Jobbágy EG, Avissar R, Baidya Roy S, Barrett DJ, Cook CW, Farley KA, Le Maitre DC, McCarl BA, Murray BC. 2005. Trading water for carbon with biological carbon sequestration. *Science* 310: 1944–1947.
- Jackson RB, et al. 2008. Protecting climate with forests. *Environmental Research Letters* 3: 044006. doi:10.1088/1748-9326/3/4/044006
- Jackson RB, Jobbágy EG, Nosoeto MD. 2009. Ecohydrology in a human-dominated landscape. *Ecohydrology* 2: 383–389.
- Jansson C, Wullschlegel SD, Kalluri UC, Tuskan GA. 2010. Phytosequestration: Carbon biosequestration by plants and the prospects of genetic engineering. *BioScience* 60: 685–696.
- Kawaoka A, Nanto K, Ishii K, Ebinuma H. 2006. Reduction of lignin content by suppression of expression of the LIM domain transcription factor in *Eucalyptus camaldulensis*. *Silvae Genetica* 55: 269–277.
- Keith H, Mackey BG, Lindenmayer DB. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences* 106: 11635–11640.
- Kindermann G, Obersteiner M, Sohngen B, Sathaye J, Andrasko K, Ramesteiner E, Schlamadinger B, Wunder S, Beach R. 2008. Global cost estimates of reducing carbon emissions through avoided deforestation. *Proceedings of the National Academy of Sciences* 105: 10302–10307.
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.
- Le Maitre DC, Versfeld DB, Chapman RA. 2000. The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. *Water SA* 26: 397–408.
- Le Maitre DC, van Wilgen BW, Gelderblom CM, Bailey C, Chapman RA, Nel JA. 2002. Invasive alien trees and water resources in South Africa: Case studies of the costs and benefits of management. *Forest Ecology and Management* 160: 143–159.

- Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Stuedler PA. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. *Ecological Applications* 7: 402–415.
- Maleknia SD, Bell TL, Adams MA. 2009. Eucalypt smoke and wildfires: Temperature dependent emissions of biogenic volatile organic compounds. *International Journal of Mass Spectrometry* 279: 126–133.
- Marland G, Fruit K, Sedjo R. 2001. Accounting for sequestered carbon: The question of permanence. *Environmental Science and Policy* 4: 259–268.
- McCarl BA, Schneider UA. 2001. Greenhouse gas mitigation in U.S. agriculture and forestry. *Science* 294: 2481–2482.
- Miles L, Kapos V. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: Global land-use implications. *Science* 320: 1454–1455.
- Milne RI, Abbott RJ. 2000. Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British isles. *Molecular Ecology* 9: 541–556.
- Murray BC, McCarl BA, Lee HC. 2004. Estimating leakage from forest carbon sequestration programs. *Land Economics* 80: 109–124.
- Murray BC, Sohngen B, Sommer AJ, Depro B, Jones K, McCarl B, Gillig D, DeAngelo B, Andrasko K. 2005. Greenhouse Gas Mitigation Potential in U.S. Forestry and Agriculture. Environmental Protection Agency. EPA 430-R-05-006.
- Nelson CD, Johnsen KH. 2008. Genomic and physiological approaches to advancing forest tree improvement. *Tree Physiology* 28: 1135–1143.
- Odum EP. 1969. The strategy of ecosystem development. *Science* 164: 262–270.
- Olander LP, Gibbs HK, Steininger M, Swenson JJ, Murray BC. 2008. Reference scenarios for deforestation and forest degradation in support of REDD: A review of data and methods. *Environmental Research Letters* 3: 025011.
- Pekin BK, Boer MM, Macfarlane C, Grierson PF. 2009. Impacts of increased fire frequency and aridity on eucalypt forest structure, biomass and composition in southwest Australia. *Forest Ecology and Management* 258: 2136–2142.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.
- Piñeiro G, Jobbágy EG, Baker J, Murray BC, Jackson RB. 2009. Set-asides can be better climate investment than corn ethanol. *Ecological Applications* 19: 277–282.
- Rejmánek M. 2000. Invasive plants: Approaches and predictions. *Austral Ecology* 25: 497–506.
- Richardson DM, Petit RJ. 2006. Pines as invasive aliens: Outlook on transgenic pine plantations in the Southern Hemisphere. Pages 169–188 in Williams CG, ed. *Landscapes, Genomics and Transgenic Conifers*. Springer.
- Richardson DM, Williams PA, Hobbs RJ. 1994. Pine invasions in the Southern Hemisphere; determinants of spread and invadability. *Journal of Biogeography* 21: 511–527.
- Rouget M, Richardson DM, Milton SJ, Polakow D. 2004. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. *Plant Ecology* 152: 79–92.
- Ryan MG, et al. 2010. A Synthesis of the Science on Forests and Carbon for U.S. forests. *Issues in Ecology* 13: 1–16.
- Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water limited ecosystems. *Journal of Ecology* 90: 480–494.
- Scott DF, Prinsloo FW. 2008. Longer-term effects of pine and eucalypt plantations on streamflow. *Water Resources Research* 44: W00A08. doi:10.1029/2007WR006781
- Searchinger T, Heimlich R, Houghton RA, Dong F, Elobeid A, Fabiosa J, Tokgoz S, Hayes D, Yu TH. 2008. Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* 319: 1238–1240.
- Searchinger TD, et al. 2009. Fixing a critical climate accounting error. *Science* 326: 527–528.
- [SOCCR] The First State of Carbon Cycle Report. 2007. The North American Carbon Budget and Implications for the Global Carbon Cycle. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. NOAA, National Climatic Data Center.
- Southgate D. 2009. Population growth, increases in agricultural production and trends in food prices. *Electronic Journal of Sustainable Development* 1: 29–35.
- Southgate DD, Graham D, Tweeten D. 2007. *The World Food Economy*. Wiley.
- Strauss SH, Brunner AM, Busov VB, Ma C, Meilan R. 2004. Ten lessons from 15 years of transgenic *Populus* research. *Forestry* 77: 455–465.
- Sun B, Sohngen B. 2009. Set-asides for carbon sequestration: Implications for permanence and leakage. *Climatic Change* 96: 409–419.
- Thompson I, Mackey B, McNulty S, Mosseler, A. 2009. *Forest Resilience, Biodiversity, and Climate Change*. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43.
- Trostle R. 2008. *Global Agricultural Supply and Demand: Factors Contributing to the Recent Increase in Food Commodity Prices*. US Department of Agriculture Economic Research Service. Report WRS-0801.
- [USEPA] US Environmental Protection Agency. 2005. Greenhouse gas mitigation potential in U.S. Forestry and Agriculture. EPA. EPA 430-R-05-006.
- Van Frankenhuyzen K, Beardmore T. 2004. Current status and environmental impact of transgenic forest trees. *Canadian Journal of Forest Research* 34: 1163–1180.
- Versfeld DB, Le Maitre DC, Chapman RA. 1998. *Alien Invading Plants and Water Resources in South Africa: A Preliminary Assessment*. Water Research Commission. Report TT99/98.
- Vertessy RA. 1999. The impacts of forestry on streamflows: A review. Pages 93–109 in Croke J, Lane P, eds. *Forest Management for Water Quality and Quantity*, Proceedings of the Second Forest Erosion Workshop, May 1999, Warburton, Australia. Report 99/6. Cooperative Research Centre for Catchment Hydrology, CSIRO Land and Water.
- Van der Werf GR, Morton DC, DeFries RS, Olivier JGJ, Kasibhatla PS, Jackson RB, Collatz GJ, Randerson JT. 2009. CO<sub>2</sub> emissions from forest loss. *Nature Geosciences* 2: 737–738.
- Walker B, Salt D. 2006. *Resilience Thinking: Sustaining Ecosystems and People in a Changing World*. Island Press.
- Watrud LS, Lee EH, Fairbrother A, Burdick C, Reichman JR, Bollman M, Storm M, King G, Van de Water PK. 2004. Evidence for landscape-level, pollen-mediated gene flow from genetically modified creeping bentgrass with CP4 EPSPS as a marker. *Proceedings of the National Academy of Sciences* 101: 14533–14538.
- Wear DN, Greis JG. 2002. Southern forest resource assessment: Summary of findings. *Journal of Forestry* 7: 6–14.
- Wilkinson MJ, Monson RK, Trahan N, Lee S, Brown E, Jackson RB, Polley HW, Fay PA, Fall R. 2009. Leaf isoprene emission rate as a function of atmospheric CO<sub>2</sub> concentration. *Global Change Biology* 15: 1189–1200.
- Williams CG. 2008. Aerobiology of *Pinus taeda* pollen clouds. *Canadian Journal of Forest Research* 38: 2177–2188.
- Williams CG, LaDeau SL, Oren R, Katul GG. 2006. Modeling seed dispersal distances: implications for transgenic *Pinus taeda*. *Ecological Applications* 16: 117–124.
- Williams MC, Wardle GM. 2005. The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue Mountains, New South Wales, Australia. *Biological Conservation* 125: 55–64.
- Zapiola ML, Campbell CK, Butler MD, Mallory-Smith CA. 2008. Escape and establishment of transgenic glyphosate-resistant creeping bentgrass *Agrostis stolonifera* in Oregon, USA: A 4-year study. *Journal of Applied Ecology* 45: 486–494.

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