

Testing the Unintended Consequences of Lignin Reduction in Genetically Modified Trees on Trophic Interactions

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Executive Summary:

Genetically modified trees with reduced lignin composition have been proposed as a geoengineering scheme that could potentially reduce environmental impact from chemically harsh pulping practices within the paper industry. Lignin is the complex chemical compound that gives trees their protection against climate, disease, and animal activity. However, the presence of lignin in wood demands the use of toxic chemicals in pulping and paper mills, which constitute a health hazard to mill workers as well as the natural environment. Decreasing the amounts of lignin in trees raised specifically for the paper industry should result in increased productivity in paper-making and lessen the need for harsh chemicals. Although lignin reduction is a potential method to maximize efficiency and minimize the environmental footprint of the paper industry, it may have unintended consequences upon the environment. Potential side effects associated with lignin reduction include decreased fitness of the transformed trees, transgene escape, and changes in herbivorous insect populations. These are significant because they may endanger the wellbeing of other species and the entire ecosystem.

The proposed experiment calls for a long-term field trial that will study and quantify the effect of lignin reduction on trophic interactions in the surrounding environment. Specifically, the field trial will genetically transform *Populus tremuloides*, or trembling aspen, a species that is commonly used for papermaking, and observe the populations of associated insect herbivores and non-herbivores. The anticipated results of this field trial are that there will be little to no effect on trophic interactions. Although the experiment will not capture the impact of lignin reduction on an entire ecosystem, the results of the field trial should deepen our understanding of how the effects of such a genetic modification permeate through different trophic levels.

Lignin and Toxic Pulping Waste

Ever since the Chinese developed the first papermaking process in the 2nd century CE, paper has been one of the largest and most widespread commodities across the globe. The eventual mechanized production of paper through the printing press in the early 19th century drove up the demand for newsprint and books since paper became relatively cheap and easy to produce. The increase in international demand for paper has consequently led to the chemical pollution of aquatic environments by paper mills as well as deforestation.

Before wood is made into paper, it undergoes the pulping process. The breakdown of lignin, the complex chemical compound that gives trees their protection against climate, pathogens, and other pests, often requires harsh chemicals. Use of these chemicals results in potential runoff from paper mills that may accumulate in the surrounding environment and have detrimental effects upon the ecosystem and its inhabitants (Sponza, 2003). Runoff from paper mills located near bodies of water contaminates the marine environment, thus negatively impacting resident species. Studies have shown that fish populations exposed to the effluents of the pulp and paper making processes experience a decline in their rate of reproduction. Development of eggs was depressed and the lifespan of the fish decreased. A male-biased sex ratio was observed as well in the fish population (Larsson and Förlin, 2002). Lastly, the accretion of toxic and mutagenic chemicals in the lakes proved harmful to microorganisms and phytoplankton, resulting in the disruption of the natural food chain (Munkittrick *et al.*, 1997; Sibley *et al.*, 1997; Soimasuo *et al.*, 1998).

Not only do pulping chemicals prove dangerous to the natural environment, they pose a serious health risk to paper mill workers. Working directly with these chemicals for extended periods of time leads to long term diseases. Various studies performed on the well-being of mill workers revealed a direct correlation between the toxicity of the pulping process and the workers' poor health (Lee *et al.*, 2002). In all cases, the observed number of deaths was greater

than the expected number in a range of illnesses, including diabetes, mental disorders, and various forms of cancer (See Table 1). These results reveal that the amount of dangerous chemicals used in the paper industry must be reduced in order to preserve our environment and minimize health risks to humans.

Table 1. Observed and expected deaths of paper mill workers in New Hampshire.

Cause of Death	Observed	Expected
Cancer of buccal cavity & pharynx	10	5
Cancer of digestive organs	79	61
Cancer of stomach	15	8
Cancer of rectum	11	5
Cancer of larynx	6	2
Leukemia and aleukemia	12	7
Diabetes mellitus	22	15
Mental and psychoneurotic disorders	12	6

The observed number of deaths exceeds the expected number in a variety of diseases mill workers developed from working in close proximity to pulping chemicals. Adapted from Schwartz (1988).

Brief Overview of Geoengineering

The growing awareness of human impact upon the natural environment has led to innovation in solutions for our environmental woes. While some have proposed simply scaling back polluting activities, human ingenuity has also suggested geoengineering as a viable scheme. The concept of geoengineering entails the large-scale manipulation of the environment in order to combat or counteract the negative effects of human activity. Although the concept of geoengineering was first explored with political intent in the context of the Cold War, emerging environmental concerns in the subsequent decade brought about its examination as a legitimate means of resolving environmental problems (Keith, 2000). Two key parameters that guide the use of geoengineering are scale, which must be global, and intent, where environmental change must be the main goal. For example, mowing grass reflects intent without scale because while

suiting human desires, it does not actually impact the environment on a global level. On the other hand, the previous manufacture of chlorofluorocarbons (CFCs) is an example of scale without intent since the depletion of the ozone layer was an unintended side effect.

Geoengineering seeks to reconcile scale and intent. It is important to note that while most geoengineering schemes focus on counteracting the effects of increased anthropogenic gases in the atmosphere, geoengineering is still applicable to other environmental issues.

The focus on geoengineering has produced many proposals varying in concept and execution. Most geoengineering schemes can be grouped according to intent, as in whether they aim to regulate energy balance, the net thermal energy input, or energy transport, the distribution of the energy in the climate system (See Figure 1).

An example of a geoengineering scheme that targets reduction of atmospheric carbon dioxide, hence energy balance, is iron fertilization of the oceans. The concept behind iron fertilization is intentionally introducing iron to the ocean, thus encouraging growth of phytoplankton blooms. Because iron is a limiting factor for phytoplankton in the open ocean, its addition greatly enhances the oceanic carbon sink. Net primary productivity of the oceans should increase and sequester greater amounts of carbon dioxide from the atmosphere. Iron fertilization has worked well in terms of enhancing carbon uptake of the oceans both in lab models and small test patches in the Atlantic (Boyd *et al.*, 2000; Buesseler *et al.*, 2004). However, if iron fertilization of aquatic environments were to cease after being implemented on a long-term basis, the phytoplankton communities would collapse. In other words, the trophic pyramid in the ocean would “bottom out”, the repercussions of which are disastrous. Further research is necessary in order to gain a more thorough understanding of how iron fertilization influences the benthic food web. In addition, there is no conclusive evidence that iron fertilization has a sustained impact upon carbon concentrations in the atmosphere (Bala, 2009; Cooper *et al.*, 1996).

As aforementioned, not all geoengineering schemes aim to counteract global warming. Some are developed as means of manipulating energy transport, such as spreading chemical monolayers on the ocean surface to mitigate hurricanes. In this weather and climate control scheme, a thin film of biodegradable chemicals is spread over the oceans in order to prevent evaporation of water into the air. Because hurricanes form due to heat energy transferred through evaporation, scientists believe that this may lessen the number of annual hurricanes and the destruction of cities and coastlines (Mallinger and Mickelson, 1973). Drawbacks of chemical monolayers include unknown ecological effects upon the marine biome and the film's ability to resist displacement by hurricane-force winds and other inclement weather. Though research has been conducted in reservoirs, it is difficult to assume that chemical monolayers will be viable across the open ocean.

Although most geoengineering projects can be classified in the taxonomy shown in Figure 1, geoengineering is a pertinent solution to other types of environmental problems that do not involve energy manipulation. The topic of this proposal, which is the application of genetic engineering in trees to reduce chemical pollution of aquatic environments located near pulping mills, is an example of such a scheme.

Geoengineering Strategies

Energy Balance	Energy Transport
Ocean fertilization	Chemical or physical control of evaporation
Terrestrial ecosystem carbon capture	Hydrological engineering
Geochemical sequestration	Weather control
Ecosystem productivity by genetic modification	Iceberg transport

Figure 1. Taxonomy separating geoengineering schemes targeted towards reducing greenhouse gases into the categories of energy balance and energy transport. Adapted from Keith (2000).

History and Application of Genetically Engineered Trees

This proposal aims to examine the concept and global application of genetically engineered trees to the paper industry, specifically in lignin reduction. Unlike other geoengineering schemes, transgenic trees are not developed for only one specific means. Instead, the scheme has potential in a diverse set of applications due to the wide variety of modifiable traits in trees. These can be grouped under three general themes, which are silviculture, adaptability, and wood quality traits (See Table 2). Silviculture refers to traits that affect growth, health, and quality of a tree; adaptability encompasses a tree's ability to tolerate certain environmental stresses, like a cold climate; wood quality traits includes characteristics of the tree which affect how easily it can be made into paper.

Currently, 225 field trials of genetically modified trees exist across 16 countries, all in various stages of research and development. In the United Kingdom and France, long-term field trials have been conducted on the quality of pulp produced by transgenic poplars. Brazil has also instituted large-scale experiments on modified *Eucalyptus* in order to preserve its natural forests (Sedjo, 2004; Snow *et al.*, 2005). Testing of trees in the United States makes up the majority of global field trials with a diverse set of applications, from pulping to restoration of American tree species. Although most countries have kept genetically engineered trees in the research and development stage, China has moved into commercial development of transgenic trees and has planted over one million trees throughout the nation.

Genetically modifying trees is particularly useful in the restoration of endangered species. The American elm (*Ulmus americana* L.) was once commonly found in northeastern United States and southeastern Canada and used in lining city streets. Unfortunately, the tree population was decimated by the fungal Dutch-elm disease in the 1930s. While remediation efforts and pesticides targeted at the host insect have been implemented, there has been much interest in producing a disease-resistant tree through genetic engineering. Recent research has

shown that the American elm may be making a comeback as DNA-transformed young saplings with mycorrhizal resistance are released into the wild (Newhouse *et al.*, 2007). A similar conclusion can be drawn for the European and American chestnut population, both of which were ravaged by ink disease and chestnut blight (Adams *et al.*, 2002; Andrade and Merkle, 2005; Corredoira *et al.*, 2008). Improving the adaptability of a species by imbuing plant cells with selected genotypes like antifungal or antimicrobial genes will have large implications upon the species of trees that will populate the Earth in the coming years.

Whereas the use of transgenic trees to bring back endangered species is useful on a regional scale, genetically modified trees are applicable on a global scale in the paper industry. As global demand for timber and timber products grows at an annual rate of 1.7% from 5-7 billion m³ of forest, lignin engineering must be examined as a viable option to decrease the chemical pollution of paper mills (Szabó, 2009; Walter, 2004). Transgenic trees with a lower lignin content can be achieved through genetic engineering. Several studies have been performed on the lignin biosynthesis pathway, leading to the transformation of the genes encoding enzymes involved in the creation of lignin within the plant as well as the use of RNA interference to “silence” gene expression (Baucher *et al.*, 2003; Li *et al.*, 2008).

Results on the pulping of wood with modified lignin content in the laboratory have proven that genetic alterations have a profound impact on pulping quality and efficiency. Some alterations work better than others in terms of increasing pulp output and decreasing chemical consumption. Research conducted on tobacco with modified lignin concentrations found that more lignin could be removed through alkali extraction without sacrificing paper pulp quality (O'Connell *et al.*, 2002). In fact, the pulp was comparable to that produced from wild-type tobacco. Similar results were found for transgenic poplars (Pilates *et al.*, 2002). A closer examination of the structure and biosynthesis of lignin as well as general pulping practices

should yield a better understanding of the breakdown of the compound.

Table 2. Traits of Interest in Genetically Modified Trees

Silviculture	Adaptability	Wood Quality Traits
Growth rate	Drought tolerance	Wood density
Nutrient uptake	Cold tolerance	Lignin reduction
Flowering control	Fungal resistance	Lignin extraction
Herbicide tolerance	Insect resistance	Fiber quality

Commonly modified traits in transgenic trees grouped according to purpose (Sedjo, 2004.)

Lignin and Specific Pulping Processes

Lignin is one of the most abundant biopolymers in the world. As a major component of wood cell walls, its purpose is to protect the insides of the tree from outside damage. Because of its toughness, it also represents a major obstacle to pulping, forage digestibility, and biofuel production. The lignin polymer is characterized by ether and carbon-carbon bonds, which are extremely resistant to chemical degradation. Alterations in the lignin synthesis pathway can lead to a modified form that is much more susceptible to breakage. For example, suppression of the final step in the pathway, cinnamyl alcohol dehydrogenase (CAD), results in lignin that is much more easily extracted, thus improving pulping efficiency (Baucher *et al.*, 2003).

Pulping is the process by which lignin is removed from raw wood, thus producing wood pulp. The two primary pulping methods are mechanical and chemical. In 2000, world pulp production surpassed 185 million metric tons, 70% of which was derived from chemical pulping (Pilates *et al.*, 2002). Because most of the pulp, and subsequently paper, is produced by chemical means, the main focus will be on improving the yield of current chemical practices.

The type of paper product determines what kind of pulping process is used. The Kraft process is the most popular method, using sodium hydroxide and sodium sulfide to remove lignin. Sulfur reacts with the lignin to form thioglignins, which are more easily removed. Because lignin and other cellulose fibers are removed, the yield is around 45-55% of the original

biomass. The amount of residual lignin determines the Kappa number, which indicates the bleachability of wood pulp. Therefore, a lower Kappa number is desirable for trees raised specifically for the papermaking industry. Another approach is bleaching, most used for the production of high-quality paper, such as printer paper and card stock. In order to produce paper that is bright, the pulp must be bleached with chlorine dioxide, sodium hydroxide, and hydrogen peroxide. Because the purpose of bleaching is to remove residual lignin, the lower the lignin content, the brighter the pulp will be. Sodium hydroxide and hydrogen peroxide are extremely basic in nature while chlorine dioxide is a very strong acid.

Accrued runoff of either sodium hydroxide or bleach could lead to a drastic change in pH in lake and pond ecosystems that would exterminate life. Neutralization and dilution of these chemicals also exude dangerous fumes that are hazardous to the health of mill workers. Therefore, lignin reduction is desirable in the respect that there will be less chemical and energy expenditure as well as improved environmental well-being.

Unintended Consequences of Reduced Lignin Composition

Although there are many economic and health benefits to humans from reduced lignin content in trees, there are some serious ecological risks associated with genetically engineered trees. If transgenic trees are to be implemented worldwide, they must be able to withstand diversity in growing conditions and not cause inadvertent harm to the surrounding environment.

The effects of reduced lignin content upon the biotic and abiotic components of an ecosystem demand attention. Trees often play host to a number of fungal, microbial, and insect communities. Figure 3 shows an array of interactions trees have with the environment. Insect larvae that feed on tree leaves may react positively to changes in lignin composition. Lowering lignin content would increase the digestability of leaves, thus providing the possibility that lignin reduction in transgenic trees would impact feeding patterns and population growth rates of leaf defoliators (James *et al.*, 1997). However, it is impossible to generalize that this is true for all

insect species, some of which may be more selective than others regarding diet.

On the other hand, transgenes may inadvertently harm the trees themselves, whether directly or indirectly. For example, because lignin safeguard trees against the elements, it follows that the transgenic trees would be less fit in their environment since they cannot protect themselves from cold climate and pests (Pedersen *et al.*, 2005). Tests carried out with transgenic silver birch where fungal resistance was added revealed unexpectedly that the modified trees suffered more leaf damage due to increased aphid population even though the expression of the transgene successfully warded off fungal infections (Vihervuori *et al.*, 2008). Because the insertion of transgenes may result in unintended consequences on other aspects of tree health, future studies must direct their focus towards minimizing such effects.

Lignin alteration can also influence the rate of soil carbon formation. Comparisons between low-lignin and wildtype trees show that lower lignin content decreases the plant's ability to form roots and create new soil carbon (Hancock *et al.* 2006). In contrast, other studies show this is not true across different species and soil types (Bradley *et al.*, 2007). For example, while lignin modification in poplars did not show any significant effects on three different types of soil, tobacco with reduced lignin negatively impacted the fungal community in clay soil. Therefore, before genetically modified trees are released into commercial development, they must be tested with a variety of soils to ensure compatibility.

In addition, there is the possibility of transgene "escape". The decomposition of transgenic trees makes the altered DNA available for incorporation into bacteria living in the ground. Rapid reproduction rate could lead to a large amount of bacteria with the modified genes in the natural environment, the consequences of which are unknown. Studies performed on the persistence of DNA in decomposing leaves show that while initial degradation of the DNA occurs rapidly, fragments can remain in the soil for up to four months (Hay *et al.*, 2002).

Because the lifetime of a tree can last many decades to over a century, it is difficult to

observe and evaluate through field trials all the possible risks. Therefore, any application of lignin reduction and genetically engineered trees must be approached with caution and regard towards any unintended consequences.

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Figure 3. Displays the interactions between tree and other populations in the environment as well as the community of organisms that a tree plays host to. (Halpin et al., 2007)

Hypothesis

The proposed experiment tests thoroughly the effect of trees with reduced lignin content upon the natural environment. I hypothesize that reducing the lignin content of trees will have minimal detrimental effects on insect herbivory and trophic interactions within the ecosystem.

The impact of low lignin composition in genetically modified trees upon insect feeding and insect communities should be little to none. Studies reveal that insects do not show preference for leaves from either transgenic or wildtype trees (Pilate *et al.*, 2002). Other research indicates that survival of forest tent caterpillars and gypsy moth larvae was not linked to lignin reduction (Brodeur-Campbell *et al.* 2006; Robison and Raffa, 1994; Tiimonen *et al.*, 2005.) Similarly, Vihervuori *et al.* (2008) notes that while transgenic trees suffered from more leaf damage, no decrease in insect population was detected.

While the aforementioned studies are optimistic about the effects of lignin reduction on the natural environment, there is a general lack of knowledge on how modified lignin content

affects a variety of herbivorous insect populations. The response of herbivorous insects to the transgenes is especially significant since they are the primary consumers in the forest trophic pyramid and eat the leaves of the modified trees. Without rigorous testing, we cannot assume that low lignin composition in trees will affect all insect species in the same way.

Field Trial Design

I propose using the species *Populus tremuloides* as my test subject due to the ease of DNA transformation. The small genome size of poplars, around 450-550 Mbp, has led the species to become the first woody plant that will have its entire genome sequenced (Taylor, 2002). In addition, the ability of the species *Populus* to propagate vegetatively is extremely beneficial since this method of asexual reproduction makes the large-scale production of clones for the experiment very simple. Previous studies, like the one conducted by Pilate *et al.* (2002), do not specify what kind of poplars were tested. Because *Populus tremuloides*, or trembling aspen, is most commonly used for pulping, it is sensible to utilize only the species relevant to the pulping industry for testing of lignin reduction. The modified poplars will express transgenes suppressing the lignin biosynthesis gene cinnamyl alcohol dehydrogenase (CAD), thus producing a modified form of lignin that leads to improved pulping efficiency (O'Connell *et al.*, 2002).

Whereas previous research has focused mostly on how transgenic trees affect only one aspect of the environment, the goal of this experiment is to observe how lignin reduction affects trophic interactions, specifically between herbivorous and non-herbivorous insects. Trembling aspen has several associated insect herbivores including the larvae of many moth families. For the purposes of this experiment, we will use the larvae of species *Bucculatrix staintonella* as the insect herbivores because they feed only on trembling aspens. Monophagy in the herbivorous insects is important since using polyphagous insects such as forest tent caterpillars in this particular field trial may not yield results that reflect changes in trophic interactions. In addition to

the moth larvae, a population of ground beetles will also be introduced. As non-herbivorous insects, their main function is to prey on the insect herbivores. Their interactions with the moth larvae will be important in determining the impact of altered lignin content upon trophic dynamics.

It is logical to locate the test site in Canada since *Populus tremuloides* is native to that region and results from the transgenic trees can be compared with the wildtype grown there (Taylor, 2002). For this experiment, field trials will last ten years. Although studies conducted before lasted typically from around four to six years due to constraints in funding, such as the ones conducted by Vihervuori *et al.* (2008), long-term field trials are necessary in order to fully evaluate the effects of genetically modified trees with reduced lignin content. While it is hardly realistic to conduct a field trial for the entire lifetime of a poplar, which is around seventy to a hundred years, experiment time must be sufficiently long enough to detect a consistent trend and account for unique circumstances year to year, such as a decrease in insect population. It is also desirable to see if there are any changes as the tree develops and matures. Since poplars have a relatively short life span compared to other species, a longer field trial will be able to observe different stages in the life time of the transgenic trees. To this end, the experiment will use young poplar trees that will mature and become middle-aged within the time span of the trial.

A total of 40 trees will be used in the experiment, 20 of which will be transgenic poplars, and the remaining 20, wildtype. The poplars will be planted in 5 rows and 8 columns, with a gap of 1 meter between each tree. The experiment will take place indoors in a greenhouse in order to keep out rabbits and other unwanted animals as well as to prevent the emigration and immigration of insect populations. Both herbivorous and nonherbivorous insects will be introduced to the transgenics and wildtype poplars.

During the field trial, patterns in insect populations and tree health will be observed.

Measurements of population densities of herbivorous and nonherbivorous insects will only be taken in the warm seasons of the year since they go into diapause, or hibernation, for the fall and winter. Survival rates of the both species' larvae should be recorded in the spring and population densities in the summer. General health assessments of the trees should be conducted annually at the end of the growing season by both a color assay and size measurement of the leaves. According to Hoch *et al.* (2001), color indicates how much stress the tree is under. On a scale from 1 to 4, green leaf color corresponds to 1, mixed green and yellow with 2, mixed yellow and red with 3, and mostly red with 4. Another useful way to quantify tree health is through the leaf area index (LAI), which is defined as the ratio of total leaf surface area of the trees divided by the area of the plot. The growth of the trees will also be monitored by recording tree height and basal diameter. At the conclusion of the experiment, all data collected on insect populations and tree health through the duration of the field trial should be aggregated for evaluation.

Conclusion and Recommendations

The presence of humans has indelibly shaped the Earth system as we know it. With the advent of agriculture and industrialization in human history, we have only expedited the process by which we exploit and pollute the environment. The burgeoning human population and unbridled growth of developing countries result in our outstripping resources we require in order to sustain our lifestyle faster than they can be replenished. However, the advances in technology combined with human creativity have presented geoengineering, or the large-scale manipulation of the environment to counterbalance negative effects of human activity, as a means of resolving problems like global warming. While geoengineering is hardly a panacea for our environmental concerns, the gravity of the situation demands that we consider it as a viable solution when it comes to preserving the health of our home. Field trials for many proposed geoengineering schemes, such as iron fertilization of the oceans and genetically engineered

trees, have returned promising results in terms of ameliorating the effects of human activity while having negligible negative impact upon the environment. The challenge then is to keep on expanding our knowledge of the intricate workings of the global Earth system so that we can continuously improve and adapt our geoengineering schemes to the world we live in.

In this specific proposal, we examine how we can decrease the amount of toxic chemicals used in pulping process by inserting transgenes expressing reduced lignin content in trees. This is significant on a global level because the bleaching chemicals used in paper mills everywhere are often hazardous to human health and result in runoff that destroy local lake and pond ecosystems. The purpose of this field trial is to shed light on how genetically modified trees with reduced lignin composition impact trophic interactions within the ecosystem. Based on previous research, we anticipate that the effects on trophic interactions due to low lignin content in trees should be little to none. Neither non-herbivorous nor herbivorous insect population should be adversely affected by the transgene. Comparisons between the health of transgene and control trees may find that the transgene trees are more susceptible to cold climate and pests, but this makes sense in that the modified trees do not have as much protection.

Whether or not the results from this field trial affirm that low lignin content negatively affects trophic interactions, future research must continue this focus on trophic dynamics. We recommend that future experiments involve other species of nonherbivorous insects, predators, and parasites in conjunction with herbivorous insects since these combinations may reveal emergent properties of the ecosystem. These properties would not necessarily show themselves in studies testing the effect of transgenic trees on only one species. In other words, the whole is not a sum of its parts. If we want to understand how the reduced lignin transgene affects an ecosystem as a whole, we must simulate the natural environment as accurately as we can and that entails creating a complex web of interactions.

In addition, it is recommended that future studies in the field expand across species due to the global nature of the papermaking industry. It would be remiss to devote research solely to *Populus tremuloides* when other species of birch, maple, and oak are used extensively for pulping as well. Only after consistent recommendations have been made from repeated studies using a variety of organisms can conclusions be reached about the transformation and implementation of a particular species in the natural environment. With a more nuanced understanding of how such changes influence the forest environment, we can avoid inflicting inadvertent ecological damage upon resident species and the habitat as a whole.

In the context of the global paper industry, the results of this field trial are especially significant. If the effect on trophic interactions due to lignin reduction is indeed negligible, then we will be able to move more swiftly towards the implementation of transgenic trees as an environmentally-friendly source of wood and wood products. Not only will we decrease the negative impact that pulping processes have on the immediate environment, we will lessen the need for chemicals which threaten the health of mill workers.

The application of genetic engineering to trees all over the world is but one geoengineering scheme that may counterbalance the deleterious effects of human activity. There exist many other ideas that strive to tackle a variety of global environmental concerns. Regardless of the geoengineering approach, the key to a livable and healthy Earth entails that we act soon if we are to sustain our present lifestyle and undo the ecological damage we have done. That being said, we cannot act wisely if we do not strive to understand our Earth system.

References

- Adams, J. M., Piovesan, G., Strauss, S., & Brown, S. (2002). The case for genetic engineering of native and landscape trees against introduced pests and diseases. *Conservation Biology*, 16(4), 874-879.
- Andrade, G. M., & Merkle, S. A. (2005). Enhancement of american chestnut somatic seedling production. *Plant Cell Reports*, 24(6), 326-334. doi:10.1007/s00299-005-0941-0 ER
- Bala, G. (2009). Problems with geoengineering schemes to combat climate change. *Current Science*, 96(1), 41-48.
- Baucher, M., Halpin, C., Petit-Conil, M., & Boerjan, W. (2003). Lignin: Genetic engineering and impact on pulping. *Critical Reviews in Biochemistry and Molecular Biology*, 38(4), 305-350.
- Boyd, P. W., Watson, A. J., Law, C. S., Abraham, E. R., Trull, T., Murdoch, R., Bakker, D. C. E., Bowie, A. R., Buesseler, K., & Chang, H. (2000). A mesoscale phytoplankton bloom in the polar southern ocean stimulated by iron fertilization. *Nature*, 407(6805), 695-702.
- Bradley, K. L., Hancock, J. E., Giardina, C. P., & Pregitzer, K. S. (2007). Soil microbial community responses to altered lignin biosynthesis in populus tremuloides vary among three distinct soils. *Plant and Soil*, 294(1), 185-201.
- Brodeur-Campbell, S. E., Vucetich, J. A., Richter, D. L., Waite, T. A., Rosemier, J. N., & Tsai, C. J. (2006). Insect herbivory on low-lignin transgenic aspen. *Environmental Entomology*, 35(6), 1696-1701.
- Buesseler, K. O., Andrews, J. E., Pike, S. M., & Charette, M. A. (2004). The effects of iron fertilization on carbon sequestration in the southern ocean. *Science*, 304(5669), 414.

- Cooper, D., Watson, A., & Nightingale, P. (1996). Large decrease in ocean-surface CO₂ fugacity in response to in situ iron fertilization.
- Corredoira, E., Valladares, S., Vieitez, A. M., & Ballester, A. (2008). Improved germination of somatic embryos and plant recovery of european chestnut. *In Vitro Cellular & Developmental Biology-Plant*, 44(4), 307-315. doi:10.1007/s11627-008-9105-6 ER
- Halpin, C., Thain, S. C., Tilston, E. L., Guiney, E., Lapierre, C., & Hopkins, D. W. (2007). Ecological impacts of trees with modified lignin. *Tree Genetics & Genomes*, 3(2), 101-110.
- Hancock, J. E., Loya, W. M., Giardina, C. P., Li, L., Chiang, V. L., & Pregitzer, K. S. (2007). Plant growth, biomass partitioning and soil carbon formation in response to altered lignin biosynthesis in populus tremuloides. *New Phytologist*, 173(4), 732-742.
- Hay, I., Morency, M., & Seguin, A. (2002). Assessing the persistence of DNA in decomposing leaves of genetically modified poplar trees. *Canadian Journal of Forest Research*, 32(6), 977.
- Hoch, W. A., Zeldin, E. L., & McCown, B. H. (2001). Physiological significance of anthocyanins during autumnal leaf senescence. *Tree Physiology*, 21(1), 1.
- James, R. R., DiFazio, S. P., Brunner, A. M., & Strauss, S. H. (1998). Environmental effects of genetically engineered woody biomass crops. *Biomass and Bioenergy*, 14(4), 403.
- Keith, D. W. (2000). GEOENGINEERING THE CLIMATE: History and prospect 1. *Annual Review of Energy and the Environment*, 25(1), 245-284.
- Larsson, D. G. J., & Förlin, L. (2002). Male-biased sex ratios of fish embryos near a pulp mill: Temporary recovery after a short-term shutdown. *Environmental Health Perspectives*, 110(8), 739.

- Lee, W. J., Teschke, K., Kauppinen, T., Andersen, A., Jäppinen, P., Szadkowska-Stanczyk, I., Pearce, N., Persson, B., Bergeret, A., & Facchini, L. A. (2002). *Environmental Health Perspectives*, 110(10), 991.
- Li, J. Y., Brunner, A. M., Shevchenko, O., Meilan, R., Ma, C., Skinner, J. S., & Strauss, S. H. (2008). Efficient and stable transgene suppression via RNAi in field-grown poplars. *Transgenic Research*, 17(4), 679-694. doi:10.1007/s11248-007-9148-1 ER
- Mallinger, W. D., & Mickelson, T. P. (1973). Experiments with monomolecular films on the surface of the open sea. *Journal of Physical Oceanography*, 3(3), 328-336.
- Munkittrick, K., Servos, M., Carey, J., & Van Der Kraak, G. (1997). Environmental impacts of pulp and paper wastewater: Evidence for a reduction in environmental effects at north american pulp mills since 1992. *FOREST INDUSTRY WASTEWATER 5. SELECTED PROCEEDINGS OF THE 5 TH IAWQ INTERNATIONAL SYMPOSIUM ON FOREST INDUSTRY WASTEWATERS, HELD IN VANCOUVER, BC, CANADA 10-13 JUNE 1996*, , 35(2-3) 329-338.
- Newhouse, A. E., Schrodt, F., Liang, H. Y., Maynard, C. A., & Powell, W. A. (2007). Transgenic american elm shows reduced dutch elm disease symptoms and normal mycorrhizal colonization. *Plant Cell Reports*, 26(7), 977-987. doi:10.1007/s00299-007-0313-z ER
- O'Connell, A., Holt, K., Piquemal, J., Grima-Pettenati, J., Boudet, A., Pollet, B., Lapierre, C., Petit-Conil, M., Schuch, W., & Halpin, C. (2002). Improved paper pulp from plants with suppressed cinnamoyl-CoA reductase or cinnamyl alcohol dehydrogenase. *Transgenic Research*, 11(5), 495-503.
- Pedersen, J., Vogel, K., & Funnell, D. (2005). Impact of reduced lignin on plant fitness. *Crop Science*, 45(3), 812.

- Pilate, G., Guiney, E., Holt, K., Petit-Conil, M., Lapierre, C., Leplé, J., Pollet, B., Mila, I., Webster, E. A., Marstorp, H. G., Hopkins, D. W., Jouanin, L., Boerjan, W., Schuch, W., & Cornu, D. (2002). Field and pulping performances of transgenic trees with altered lignification. *Nature Biotechnology*, 20(6), 607.
- Pilate, G., Guiney, E., Holt, K., Petit-Conil, M., Lapierre, C., Leplé, J., Pollet, B., Mila, I., Webster, E. A., Marstorp, H. G., Hopkins, D. W., Jouanin, L., Boerjan, W., Schuch, W., Cornu, D., & Halpin, C. Field and pulping performances of transgenic trees with altered lignification. *Nature Biotechnology*, 2002 Jun,
- Robison, D. J., McCOWN, B. H., & Raffa, K. F. (1994). Responses of gypsy moth (Lepidoptera: Lymantriidae) and forest tent caterpillar (Lepidoptera: Lasiocampidae) to transgenic poplar, *Populus* spp., containing a *Bacillus thuringiensis* δ -endotoxin gene. *Environmental Entomology*, 23(4), 1030-1041.
- Schwartz, E. (1988). A proportionate mortality ratio analysis of pulp and paper mill workers in New Hampshire. *British Medical Journal*, 45(4), 234.
- Sedjo, R. A. (2004). *RFF Report, Washington, DC: Resources for the Future*,
- Sibley, P., Legler, J., Dixon, D., & Barton, D. (1997). Environmental health assessment of the benthic habitat adjacent to a pulp mill discharge. I. acute and chronic toxicity of sediments to benthic macroinvertebrates. *Archives of Environmental Contamination and Toxicology*, 32(3), 274-284.
- Snow, A. A., Andow, D. A., Gepts, P., Hallerman, E. M., Power, A., Tiedje, J. M., & Wolfenbarger, L. L. (2005). Genetically engineered organisms and the environment: Current status and recommendations. *Ecological Applications*, 15(2), 377-404.

- Soimasuo, M., Karels, A., Leppänen, H., Santti, R., & Oikari, A. (1998). Biomarker responses in whitefish (*Coregonus lavaretus* L. sl) experimentally exposed in a large lake receiving effluents from pulp and paper industry. *Archives of Environmental Contamination and Toxicology*, 34(1), 69-80.
- Sponza, D. T. (2003). Application of toxicity tests into discharges of the pulp-paper industry in turkey. *Ecotoxicology and Environmental Safety*, 54(1), 74-86.
- Szabó, L., Soria, A., Forsström, J., Keränen, J. T., & Hytönen, E. (2009). A world model of the pulp and paper industry: Demand, energy consumption and emission scenarios to 2030. *Environmental Science & Policy*, 12(3), 257-269. doi:DOI: 10.1016/j.envsci.2009.01.011
- Taylor, G. (2002). Populus: Arabidopsis for forestry. do we need a model tree? *Annals of Botany*, 90(6), 681.
- Tiimonen, H., Aronen, T., Laakso, T., Saranpää, P., Chiang, V., Ylioja, T., Roininen, H., & Häggman, H. (2005). Does lignin modification affect feeding preference or growth performance of insect herbivores in transgenic silver birch (*Betula pendula* Roth)? *Planta*, 222(4), 699-708.
- Vihervuori, L., Pasonen, H., & Lyytikäinen-Saarenmaa, P. (2008). Density and composition of an insect population in a field trial of chitinase transgenic and wild-type silver birch (*Betula pendula*) clones. *Environmental Entomology*, 37(6), 1582-1591.
- Walter, C. (2004). Genetic engineering in conifer forestry: Technical and social considerations. *In Vitro Cellular & Developmental Biology-Plant*, 40(5), 434-441.

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