

Where will the wood come from? Plantation forests and the role of biotechnology

Trevor M. Fenning and Jonathan Gershenzon

Wood is almost as important to humanity as food, and the natural forests from which most of it is harvested from are of enormous environmental value. However, these slow-growing forests are unable to meet current demand, resulting in the loss and degradation of forest. Plantation forests have the potential to supply the bulk of humanity's wood needs on a long-term basis, and so reduce to acceptable limits the harvest pressures on natural forests. However, if they are to be successful, plantation forests must have a far higher yield of timber than their natural counterparts, on much shorter rotation times. To achieve this in reasonable time, biotechnology must be applied to the tree-improvement process, for which large increases in public and private capital investment are needed. However, additional obstacles exist in the form of opposition to plantations, some forest ecocertification schemes, and concerns about aspects of forest biotechnology, especially genetic engineering. It is the intention of this article to explain, in detail, why plantation forests are needed to sustainably meet the world's demand for wood, why they are not being developed fast enough, and why the application of biotechnology to tree improvement is essential to speeding up this process.

DOI: 10.1016/S0167-7799(02)01983-2

Wood has remarkable physical and structural properties, which have made it immensely valuable to humanity since the earliest prehistoric times, and for which there is, as yet, no environmentally acceptable large-scale alternative [1]. Wood is vital to the world economy and human communities everywhere, but the pressures of human development and the growing demand for wood are contributing to the degradation of natural forests worldwide, creating a dilemma over future supplies [2–5].

Unfortunately, there is considerable uncertainty and confusion in the literature about the forest degradation and wood consumption data, which has contributed to a lack of consensus about how to conserve the remaining natural forest areas. For example, the world's forest area has been variously estimated at between 3.2 and 3.9 billion hectares (or about 30% of the Earth's land area), depending upon the definitions used (FAO, Box 1). There is even more uncertainty about the global wood harvest, and what harvest the world's forest can sustain. Perhaps as

much as 80% of the total forest area is already affected by human activity, with more than a third of the remainder under immediate threat (World Resources Institute, Box 2). Furthermore, it is surprisingly hard to gain reliable answers to the vital question of how much timber is being used worldwide, because all the available data represent crude estimates with large discrepancies readily apparent.

At the global level, the amount of wood produced by industrial mills exceeds that officially supplied to them by ~20%, suggesting significant under-reporting of harvest volumes, or other major accounting errors (Wink Sutton, pers. commun.; IIASA, Box 1) [1]. Also, although small compared to the scale of domestic wood use, nearly 60 million m³ more wood was officially imported by all countries in 2000 than was exported (FAOSTAT, Box 1).

In addition, the amount of personally harvested or informally traded wood is very hard to gauge, although this probably accounts for most of the world's wood use. The FAO has conservatively estimated that 1.8 billion m³ of wood was burned as fuel in 2000, but even this is thought to be insufficient for the billions of people who utilize it (FAO and EU documents, Box 1). Together with the 1.6 billion m³ industrial harvest, this adds up to 3.4 billion m³ of wood consumed in the year 2000, or nearly 1 m³ per hectare of the total forest area (FAO, Box 1), whereas the real harvest could easily have been 50–100% higher.

Global demand for wood is also growing at 1.7% annually, and harvest pressures are very uneven, with 50% of forests either nominally protected or too remote to harvest (FAO, Box 1) [3]. With the maximum sustainable rate of timber extraction from natural forests possibly being as low as 2 m³ ha⁻¹ yr⁻¹ [2,3], the current level of demand is probably exceeding what they can supply, and this is clearly a major factor in their degradation.

The alternative is to farm trees in plantations composed of fast-growing, elite genotypes [1,4]. Such an alternative supply of timber could greatly reduce the harvest pressures on wild forests, and so their development is vital to global sustainability [1,6,7]. But in spite of increasing productivity, plantations only supply ~12% of the total amount of wood consumed (FAO, Box 1), so much remains to be done.

It is the intention of this article to discuss the constraints and obstacles to the development and use of plantations in general, why genetically improved trees are needed, and why biotechnology is essential to this endeavour. The details of what forest biotechnology is capable of have been amply reviewed elsewhere (see, for example, Refs [6,8–12] and Box 3) and so will only be covered briefly.

The economics of forestry

Although wood is a highly prized commodity, the economics of its production have always been problematic. Unlike conventional agriculture, it is

Trevor M. Fenning*
Jonathan Gershenzon
Max Planck Institute for
Chemical Ecology,
Winzerlaer Str. 10,
D-07745 Jena, Germany.
*e-mail:
fenning@ice.mpg.de

Box 1. Relevant scientific and forestry data web sites

- State of the World's Forests (1999) Report of the Food and Agriculture Organization (FAO) of the United Nations, Viale delle Terme di Caracalla, 00100 Rome, Italy. See: <http://www.fao.org/forestry/FO/SOFO/SOFO99/sofo99-e.stm>
- State of the World's Forests (2001) FAO report update. See: <http://www.fao.org/forestry/fo/sofo/SOFO2001/sofo2001-e.stm>
- The Global Forest Resources Assessment 2000, FAO report (2001). See: http://www.fao.org/docrep/meeting/003/X9835e/X9835e00.htm#P469_24024
- Brown, C. (2000) The global outlook for future wood supply from forest plantations. FAO Report. See under *Forest products outlook study* at: http://www.fao.org/forestry/foris/index.jsp?lang_id=1&geo_id=42&start_id=2711
- Zhu, S. *et al.* (1999) Global forest products consumption, production, trade and prices: global forest products model projections to 2010. FAO Report. See under *Forest products outlook study* at: http://www.fao.org/forestry/foris/index.jsp?lang_id=1&geo_id=42&start_id=2711
- The FAOSTAT Database for World Agriculture and Forestry. See: <http://apps.fao.org/>
- Valentini, R. *et al.* (2000) Accounting for carbon sinks in the biosphere, European perspective. CarboEurope scientific note to articles 3.3, 3.4 and 12 of the Kyoto Protocol. See: <http://www.bgc-jena.mpg.de/public/carboeur/>
- Hancock, J.F. and Hokanson, K.E. (2001) Invasiveness of transgenics versus exotic plant species: How useful is the analogy? *Proceedings of the First (IUFRO) Symposium on Ecological and Societal Aspects of Transgenic Plantations* (Strauss, S.H. and Bradshaw, H.D., eds), College of Forestry, Oregon State University pp. 187–192. See: http://www.fsl.orst.edu/tgerc/iufro2001/eprcd_29.pdf
- Nilsson, S. (2001) Forest policy, criteria and indicators, and certification. Interim Report IR-01-024. *International Institute for Applied Systems Analysis (IIASA)*, Schlossplatz 1, A-2361 Laxenburg, Austria. See: www.iiasa.ac.at
- Nilsson, S. (2001) Future challenges to ensure sustainable forest management. Interim Report IR-01-039. *International Institute for Applied Systems Analysis (IIASA)*, Schlossplatz 1, A-2361 Laxenburg, Austria. See: www.iiasa.ac.at
- Europe and the Forest (vol. 3) (1997) Publication of the European Parliament. See: http://www.europarl.eu.int/workingpapers/forest/eurfo74_en.htm
- Europe and the Forest (memento) (1998) Publication of the European Parliament. See: http://www.europarl.eu.int/workingpapers/agri/default_en.htm#e3

usually cheaper to harvest trees from the wild than to plant for harvest, and this is often accomplished by clear cutting with little regard for the success of regeneration and other environmental consequences. Most of the world's wood is still harvested this way (FAO, Box 1) [2,3,5,6,13,14].

Thus, although specific forests have value in terms of the wood they contain, historically there was little incentive to maintain them, as long as other forests were available. However, owing to increasing human population and the increasing global demand for wood, consumption is exceeding the natural rate of regeneration in many areas [3,6], resulting in forest loss and degradation.

An alternative that has been variously pursued is plantation forestry, but this has not happened on the scale needed because of the long timescales and heavy capital outlays involved. Large areas of land need to be dedicated to what amounts to a single crop, which

only realizes its value once every few decades and can be lost to storms, diseases or fire at any time [13]. To try and overcome these problems, governments have often undertaken planting schemes themselves, or encouraged others to do so with subsidies and tax breaks (FAO, Box 1) [15], but the scale of planting is still inadequate.

The need for biotechnology

However, the prospects for tree improvement are good, as most of the trees used even in plantations are essentially wild, coming from simple seed collections [1,2]. The process of domesticating trees to human needs has only just begun, and similar improvements in yield to that seen with agricultural crops are possible [1,6,13,14]. However, this will not happen by itself. Forest research and tree-improvement schemes are time consuming and expensive, and are poorly funded even in comparison to other fields of plant

Box 2. Web sites and information from environmental non governmental organizations

- World Rainforest Movement, Maldonado 1858–11200, Montevideo, Uruguay. WRM Special Bulletin Jan 2001. See: <http://www.wrm.org.uy/bulletin/44.html>
- The Forest Stewardship Council A.C., Avenida Hidalgo 502, 68000 Oaxaca, Mexico. See: <http://www.fscoax.org/principal.htm>
- Owusu, R.A. (1999) GM technology in the forest sector. Report of the World Wildlife Fund International (WWF), Avenue du Mont-Blanc, 1196 Gland, Switzerland. See: <http://www.panda.org/resources/publications/forest/gm/>
- The Forest Industry in the 21st Century. Lobbying and document from the World Wildlife Fund International, with information about current trends in timber usage. See: <http://www.panda.org/forestandtrade/index.html>
- UK must reduce its forest footprint (March 2001) News item from the World Wildlife Fund, UK web site. See: <http://www.wwf.org.uk/news/news2001.asp>
- WWF Position Statement (2001) Pan-European forest certification system. Criticism of rival timber certification schemes to the FSC, by the World Wildlife Fund International. See: <http://www.panda.org/forests4life/news/PEFCposition.pdf>
- Out of the woods – reducing wood consumption to save the world's forests. Briefing sheet by Friends of the Earth, 56–58 Alma Street, Luton, UK LU1 2PH. See: <http://www.foe.co.uk/pubsinfo/briefings/html/19971215150023.html>
- Re-source, market alternatives to ancient forest destruction (1999) Lobbying document from Greenpeace International, Keizersgracht 176, 1016 DW Amsterdam, The Netherlands. See under *documents* at: <http://www.greenpeace.org/-forests/index.html>
- The Soil Association, Bristol House, 40–56 Victoria Street, Bristol, UK BS1 6BY. See: <http://www.soilassociation.org/SA/SAWeb.nsf/!Open>
- Scrase, H. *et al.* (1999) Certification of forest products for small businesses: Improving access – issues and options. Report on the burdens and costs of ecocertification for the UK Dept for International Development (DFID document FZ0083), The Forest Stewardship Council, and the Soil Association. See: http://www.proforest.net/small_enterprises_pub.htm
- World Resources Institute, 10 G Street, NE (Suite 800), Washington, DC 20002, USA. See: <http://www.wri.org/> for press release of 3rd April 2002, and reports under *Earth Trends* for analysis of current rates of forest loss and degradation.

Box 3. What is 'forest biotechnology'?

The phrase 'forest biotechnology' could encompass almost any basic biological manipulation of forest organisms (principally for human use) and not only trees. However, for the purposes of this article a narrower definition has been adapted from the FAO's statement on biotechnology: "A range of different molecular technologies, such as gene manipulation and gene transfer, DNA typing and cloning of forest trees."

Thus, conventional tree breeding and provenance trials would not be included in this definition, but advanced programs routinely make use of biotechnological innovations in their work. For example, molecular markers have been used for many years, originally in the form of isozymes and nowadays with DNA sequences.

These are most commonly randomly generated to saturate the genome under study, but for more complex multigenic traits, functional markers are needed – where the interacting role(s) of the genes (and alleles) affecting the trait of interest have been determined. This formidable task is only just beginning. These and other forms of DNA and biochemical typing are also used for studying forest biodiversity, and potentially for determining the susceptibility of the trees within a particular region to environmental stresses, such as might occur with global warming.

Various tissue-culture techniques have also been routinely used for many years to clonally propagate elite trees for breeding purposes and for immediate use in plantations, but genetic engineering is currently limited to experimental studies.

research. Because of the clear importance of forests to us all and the rising pressures that they face, a huge boost in funding is urgently needed [10], because the penalty for failure will be severe.

The long generation times, self-incompatibility mechanisms and space requirements of trees make them more difficult to work with than other plants [16]. For example, although apple (*Malus domestica*) is not a forest species, it is probably the tree most domesticated to human needs. In spite of abundant knowledge about its agronomy, silviculture and genetics (plus a relatively short juvenile period), producing a single new variety costs UK£250 000 (€400 000) and takes 15–20 years of work at the UK's premier apple-breeding institute (Horticulture Research International, East Malling; Ken Tobutt, pers. commun.). Marker assisted breeding and some tissue culture procedures are already used in this process (Box 3), the development of which has been an extra cost.

Forest trees present additional problems, because of the need to assess the wood and disease-resistance characteristics of mature trees. For the long rotation species grown for timber, many genotypes are required to minimize the risk of mass disease outbreaks within a plantation [17]. Easier than directed breeding is collecting seeds from phenotypically superior trees, but the potential gains are limited [18].

Consequently, only a handful of forest tree species are likely to be subject to major improvement. Just as 70% of the world's food today comes from only nine plant and three animal species, a similar phenomenon is likely to occur with the supply of wood for human needs [1,13]. Those species groups that are currently most amenable to improvement are likely to remain so in future [1], including Douglas fir (*Pseudotsuga menziesii*) [19], *Eucalyptus* spp. [20], loblolly pine (*Pinus taeda*) [21], Monterey pine (*P. radiata*) [13], poplars (*Populus* spp.) [12,22], and the spruces (*Picea* spp.) [1,9,13]. It is

unrealistic and probably undesirable for the 1000 or so tree species currently used for industrial wood production [1,13], to be subject to more than minor harvesting in future.

The role of biotechnology

There are many objectives for domesticating forest trees to human needs, but two of the most important are the need to understand wood formation, and the desire to shorten the length of the juvenile phase. To modify these complex traits in trees by conventional breeding is impractical, however, unless the precise role(s) of the underlying genes are known (Box 3). It is essential to apply biotechnology if we are to gain this knowledge.

Although good progress has been made in breeding trees for altered xylem-fibre lengths and lignin content, which is valuable to the paper and pulp industries (FAO, Box 1) [20,22], much less progress has been made in improving timber quality, precisely because wood formation is so poorly understood [16,23,24]. It is probably one of the most complex phenomena facing plant biologists today, with perhaps 40 000 genes being involved [25], so without biotechnological tools to gain a better understanding of the process, markers for wood-quality traits will remain a distant prospect.

Faster progress has been made in understanding the genetics of flowering in trees, however [26–28], with precociously flowering poplar and citrus plants having been produced with genetic engineering [29,30]. This opens up the valuable prospect of being able to breed trees in much less time than was previously needed, either directly with genetic engineering, or by some other treatment made possible by the knowledge gained.

Genetic engineering has the potential to boost global wood production in many ways [1,8,13,14]. Applications currently under consideration for plantation forests include resistance to biodegradable herbicides, altered lignin properties for reduced downstream processing costs or improved burning, resistance to selected pests, altered reproductive mechanisms for faster breeding or genetic containment, phytoremediation of polluted sites, and the production of novel chemicals or pharmaceuticals (for recent reviews see [8–12,14,16,23]). It might also be possible to manipulate wood-quality traits, photosynthetic efficiency, and tolerance to abiotic stresses such as drought.

Although there are, as yet, too many unanswered environmental concerns to deploy genetically modified (GM) forest trees outside closely monitored field trials [31], genetic engineering is undoubtedly an essential tool in helping to unravel those complex phenomena that make trees such interesting and valuable subjects. However, even experimental GM trees sometimes need to be field trialed to be fully assessed [8,9,32], so total bans, press scare stories and other forms of opposition (legal and illegal)

(e.g. [33–35]) are inhibiting a technology that has much to offer on the road to a globally sustainable wood supply.

Environmental considerations

To reduce the level of deforestation worldwide, it is necessary to bring wood consumption into line with the level of sustainable supply. This can be achieved by either increasing production, or by reducing consumption – or both. However, given the scale of global wood use, the implications of trying to reduce it need to be considered carefully, as this might result in substitution with nonrenewable materials and an overall negative environmental impact.

For example, plastics, steel, concrete, bricks and kerosene release 9–30 times more CO₂ than if wood were used for the same purpose [1,13], while the carbon needed for trees to grow is absorbed from the atmosphere. Even the rise of the ‘paperless office’ has been bought at the cost of more electricity use. That wood consumption has been growing at less than the rate for the world economy for many years, suggests that substitution might indeed be occurring (FAO, Box 1). However, the precise extent is unclear, owing to increased recycling, falls in the amount of wood needed to manufacture some products (notably paper and fibreboard), better use of nonforest sources of wood and less wastage at the more advanced wood mills (FAO, Box 1; WWF Box 2) [36].

Annual plants, such as hemp, could also be used to meet some of the global demand for fibre currently supplied by trees, but such crops offer few if any environmental advantages, and their uses are limited [37–39]. Overall though, there seems little scope for reducing wood use in the developed world, and any that is achieved will probably be more than offset by the rapidly rising demand in developing economies (FAO, Box 1) [1,2,13].

If globally sustainable plantation forests can be established, however, it should be possible to expand the use of wood to replace other energy-intensive or polluting materials [1]. But for plantations to meet this demand, they must be much more productive than natural forest, if only because the amount of land needed otherwise would not be available without using existing forest areas.

Advances in tree breeding and management practices are indeed making the necessary gains. For example, wood formation rates in excess of 40 m³ ha⁻¹ y⁻¹ have been achieved in New Zealand with *P. radiata*, although the average is still nearer 20 m³ ha⁻¹ y⁻¹ on a rotation time of 25–35 years [13]. Even more impressive, the Aracruz Forestal company of Brazil has recorded yields >70 m³ ha⁻¹ yr⁻¹ with *Eucalyptus* hybrids grown under optimal conditions for the pulp and paper industry (FAO, Box 1; Andréa Leite, Aracruz Celulose S.A., pers. commun.) and 100 m³ ha⁻¹ y⁻¹ could be within reach.

If these results can be extended beyond the current trial plots, and similar progress can be

made with structural and fuelwood species, then 200 Mha (million hectares) of plantation forests could supply 10 billion people with 2.5 m³ of wood per person per year indefinitely. At lower levels of productivity, however, either more plantations would be needed and/or timber extraction would need to continue from natural forests. There are compelling reasons why this latter alternative should be minimized, however.

The harvesting process disturbs the flora and fauna of the forest, especially the tree species being cut, and numerous service roads and transport links are needed to collect the timber. Lastly, recent work has shown that undisturbed forests are major sinks of CO₂, not so much for the wood they contain, but because of the sequestering abilities of forest soils. This carbon is released when forests are even modestly disturbed (CarboEurope note, Box 1) [40,41].

Although forest plantations are far from being the monocultures that agricultural plantations are, harbouring considerable amounts of wildlife, sometimes including endangered species (FAO, Box 1) [42,43], they are undoubtedly ecologically impoverished compared with most natural forests. Consequently, effort is needed to minimize their impact. For example, plot sizes can be adjusted to suit local wildlife needs, more than one tree species can be planted within the plots or between them, and key areas for the survival of locally valuable wildlife avoided. To fulfil their purpose, forest plantations must always be production orientated, but with a few precautions they need not be biological deserts.

The negative effects of forest plantations upon their surrounding environment should also be considered. For instance, tree species with numerous weedy characteristics can invade neighbouring areas (IUFRO proceedings, Box 1), and the pollen from plantation species that can hybridize with indigenous trees might genetically swamp neighbouring populations [8,44–46]. It might be possible to minimize these effects by using trees that are unable to produce viable pollen or seeds, perhaps produced by genetic engineering [8,12,45]. Used imaginatively in this way, GM trees have the potential not only to boost the productivity of the plantation forests, but also to lower their impact.

GM trees are costly, so even when environmental concerns are resolved, they are unlikely to be planted at high densities, except in the most pressing cases. However, in experiments with mixed populations of insect-resistant GM and susceptible non-GM trees, the entire stand benefited [47]. Such strategies might help reduce the selection pressure on pests to overcome any introduced resistance mechanisms in the GM trees, and minimize the risk of mass disease outbreaks [17]. Nevertheless, such deployments must only take place as the necessary biosafety information is obtained.

Consideration of environmentalists

Many cultures have a powerful attachment to forests, and concern over their destruction has driven much of the growth of environmental groups. Their activities have done much to highlight the problems of deforestation worldwide, but the solutions they offer for stabilizing the world's wood supply have sometimes been less than helpful.

Logging bans for instance usually transfer harvest pressure onto neighbouring areas (FAO, Box 1), and so achieve nothing at the global level. Environmental groups also frequently exhort the people of the developed nations to use less wood and paper (Box 2), in spite of the problems that substitution is likely to cause [1], or try to stop the export of wood from those regions worst affected by deforestation.

Although stopping exports from these regions is a laudable aim, the principal mechanism which is currently being pursued, namely third-party ecocertification of sustainably harvested timber, might well be having the opposite effect to that intended. Of many schemes in existence (see IIASA documents, Box 1) [44], the one most widely supported by environmental pressure groups is operated by the Forest Stewardship Council (FSC), which includes among its backers the Friends of the Earth, Greenpeace, the Soil Association (an 'organic' farming group in the UK), the World Wildlife Fund, and inevitably the World Bank (Box 2)

For a forest enterprise to be certified by the FSC, it must manage its forest according to a stringent set of conservation and social guidelines, which exclude even limited scientific trials of GM trees [8,32,35,44]. The logic of this approach is that if consumers and suppliers (especially in the developed world) preferentially choose such products, then trade in unsustainably harvested timber will be suppressed. However, this ignores the fact that the problem is fundamentally one of inadequate supply that cannot be addressed by conservation measures alone.

Although some plantations have recently been approved by the FSC, they are strongly discouraged by the certification criteria, which barely mention production goals, but do require a plan for turning them into more natural forest. Indeed, 75% of the 24 Mha of forests currently certified by the FSC are natural or seminatural, of intentionally low timber output.

This entire approach is fundamentally flawed because it simultaneously encourages the harvesting of wood from natural forests, whilst suppressing the development of plantations. Furthermore, it is likely to increase the cost of timber to the consumer, which is presumably the attraction of the scheme to some forest enterprises, in spite of the burden that certification imposes (DFID document, Box 2). If this occurs, it will stimulate further substitution of wood for other materials in the world's markets, with all the problems that is likely to cause.

If the FSC's scheme continues in its current format, the most likely result will be that the investment that the forestry sector so desperately needs will be inhibited (IIASA, Box 1) [10], forest plantations might never reach their potential, the current high rate of natural forest loss will continue or even accelerate, and the use of energy intensive substitutes will increase (FAO Box 1; WRI Box 2) [1,6,10]. Far from being an environmental boon, this approach to forest certification will be a disaster of the environmental pressure groups own making (for a more detailed commentary, see IIASA documents Box 1, and [48]).

The misunderstandings that have led to this situation might stem from a widespread belief that the world's natural forests are easily capable of meeting demand, if only they were managed properly (e.g. in Box 2). This is demonstrably false. For reasons that are unclear, even the official wood consumption levels have been consistently understated in documents produced by well known environmental groups, including the Friends of the Earth, Greenpeace and the World Wildlife Fund, even though the correct numbers are readily available (e.g. FAO documents, Box 1, and [1,13]). In particular, the figure for the industrial roundwood harvest is repeatedly treated as if it represented the total harvest.

Correctly understanding and interpreting global wood consumption data is definitely not a straightforward undertaking, but it is shockingly careless for high-profile organizations to be making errors of this magnitude, lobbying for their preferred solutions drafted on the basis of this faulty analysis, and obstructing the development of alternatives. Just as some environmentalist groups have called for politicians, business leaders and scientists to be held to account for the consequences of their actions, so too must they. Good intentions alone are not enough.

Concluding remarks

For the world to be supplied with the wood it needs on a long-term sustainable basis, it needs to invest much more in the development of high-yielding, short-rotation plantation forests. Biotechnology is essential to achieving this goal. The alternative is that the world's remaining natural forests will continue to be degraded, probably at an accelerating rate, and/or pollution from wood substitutes will increase. Those who oppose plantation forests either in any form, or the application of biotechnology to their development, need to be clear what the choices really are, rather than what they might like them to be.

The logic of plantation forests is so strong that they will undoubtedly play a major role in achieving global sustainability. The only real question is how much more damage will be done to Earth's natural forests before the essential contribution of plantation forests is fully recognized.

Acknowledgements

The authors thank Adrian Whiteman and Felice Padovani of the FAO Forests and Forestry section, for their help with interpreting some of the FAO data, and Kenneth Elmgren of the European Commission Enterprise DG Forest-based industries unit for his help with interpreting EU timber trade data. We are also particularly grateful to Wink Sutton of Plantation Focus Limited, Rotorua, New Zealand, Kevan Gartland of the University of Abertay, Dundee, Scotland, and Armand Séguin of the Canadian Forest Service, Quebec City, for their many useful discussions, and help in revising this article.

References

- 1 Sutton, W.R.J. (1999) Does the World need planted forests? *New Zealand J. Forest.* 44, 24–29
- 2 Victor, D.G. and Ausubel, J.H. (2000) Restoring the forests. *Foreign Aff.* 79, 127–144
- 3 South, D.B. (1999) How can we feign sustainability with an increasing population? *New Forest.* 17, 193–212
- 4 Boyle, J.R. (1999) Planted forests: views and viewpoints. *New Forest.* 17, 5–9
- 5 Libby, W.J. (2001) Some thoughts on plantations and global cooling. *Unasylva* 52, 28–32
- 6 Sedjo, R.A. (2001) The role of forest plantations in the world's future timber supply. *Forest. Chron.* 77, 221–225
- 7 Sedjo, R.A. (1999) The potential of high-yield plantation forestry for meeting timber needs. *New Forest.* 17, 339–359
- 8 Strauss, S.H. *et al.* (1999) Forest biotechnology makes its position known. *Nat. Biotechnol.* 17, 1145
- 9 Pe?a, L. and Séguin, A. (2001) Recent advances in the genetic transformation of trees. *Trends Biotechnol.* 19, 500–506
- 10 Bradshaw, A.H. and Strauss, S.H. (2001) Plotting a course for GM forestry. *Nat. Biotechnol.* 19, 1103–1104
- 11 Yanchuck, A.D. (2001) The role and implications of biotechnological tools in forestry. *Unasylva* 52, 53–59
- 12 Strauss, S.H. *et al.* (2001) Genetically modified poplars in context. *Forest. Chron.* 77, 271–279
- 13 Sutton, W.R.J. (1999) The need for planted forests and the example of radiata pine. *New Forest.* 17, 95–109
- 14 Sedjo, R.A. (2001) From foraging to cropping : the transition to plantation forestry, and implications for wood supply and demand. *Unasylva* 52, 24–27
- 15 Alig, R.J. *et al.* (1999) Private forest investment and long-run sustainable harvest volumes. *New Forest.* 17, 307–327
- 16 Lev-Yadun, S. and Sederoff, R. (2000) Pines as model gymnosperms to study evolution, wood formation and perennial growth. *J. Plant Growth Regul.* 19, 290–305
- 17 Raffa, K.F. (1989) Genetic engineering of trees to enhance resistance to insects. *Bioscience* 39, 524–534
- 18 Kingswell, G. (1998) Wild cherry (*Prunus avium* L.) – the benefits and costs of planting genetically improved stock. In: *Tree Biotechnology, Towards the Millennium* (Davey, M.R. *et al.*, eds). pp. 23–29, Nottingham University Press, UK
- 19 Hermann, R.K. and Lavender, D.P. (1999) Douglas-fir planted forests. *New Forest.* 17, 53–70
- 20 Turnbull, J.W. (1999) Eucalypt plantations. *New Forest.* 17, 37–52
- 21 Schultz, R.P. (1999) Loblolly – the pine for the twenty-first century. *New Forest.* 17, 71–88
- 22 Heilman, P.E. (1999) Planted forests: poplars. *New Forest.* 17, 89–93
- 23 Sederoff, R. (1999) Building better trees with antisense. *Nat. Biotechnol.* 17, 750–751
- 24 Plomion, C. *et al.* (2001) Wood formation in trees. *Plant Physiol.* 127, 1513–1523
- 25 Lorenz, W.W. and Dean, J.F.D. (2002) SAGE profiling and demonstration of differential gene expression along the axial developmental gradient of lignifying xylem in loblolly pine (*Pinus taeda*). *Tree Physiol.* 22, 301–310
- 26 Rutledge, R.G. *et al.* (1998) Characterization of an AGAMOUS homologue from the conifer black spruce (*Picea mariana*) that produces floral homeotic conversions when expressed in *Arabidopsis*. *Plant J.* 15, 625–634
- 27 Soltis, D.E. *et al.* (2002) Missing links: the genetic architecture of flower and floral diversification. *Trends Plant Sci.* 7, 22–31
- 28 Baum, D.A. *et al.* (2002) Response: Missing links: the genetic architecture of flower and floral diversification. *Trends Plant Sci.* 7, 31–34
- 29 Weigel, D. and Nilsson, O. (1995) A developmental switch sufficient for flower initiation in diverse plants. *Nature* 377, 495–500
- 30 Peña, L. *et al.* (2001) Constitutive expression of *Arabidopsis* LEAFY or APETALA1 genes in citrus reduces their generation time. *Nat. Biotechnol.* 19, 263–267
- 31 Strauss, S.H. *et al.* (2000) Ethics and genetically engineered plantations. *J. Forest.* 98, 48
- 32 Strauss, S.H. *et al.* (2001) Plantation certification & genetic engineering FSC's ban on research is counterproductive. *J. Forest.* 99, 4–7
- 33 Warwick, H. (1999) When the woods get really scary. *BBC Wildlife Magazine* August, 6
- 34 Kaiser, J. (2001) Words (and axes) fly over transgenic trees. *Science* 292, 34–36
- 35 Cauley, H. (2001) Genetic engineering FSC says risks are still to great. *J. Forest.* 99, 4–7
- 36 Sales, C. (2001) Technological innovation in the wood sector. *Unasylva* 52, 63–65
- 37 Horta Nogueira, L.A. *et al.* (1998) Wood fuels for household consumption and industrial energy in relation to global fibre supplies. *Unasylva* 49, 44–50
- 38 Pandey, D. (1998) Non-wood fibre and the global fibre supply. *Unasylva* 49, 44–50
- 39 Pandey, D. and Ball, J. (1998) The role of industrial plantations in the future global fibre supply. *Unasylva* 49, 37–43
- 40 Schulze, E.D. *et al.* (2001) Managing forests after Kyoto. *Science* 289, 2058–2059
- 41 Wolfsy, S.C. (2001) Where has all the carbon gone? *Science* 292, 2261–2263
- 42 Sutton, W.R.J. (1995) Plantation forests protect our biodiversity. *New Zealand Forest* 40, 2–5
- 43 Lindenmayer, D.B. *et al.* (1999) Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* 14, 941–950
- 44 Strauss, S.H. *et al.* (2001) Certification of genetically modified forest plantations. *Int. Forest. Rev.* 3, 85–102
- 45 Strauss, S.H. *et al.* (1995) Genetic engineering of reproductive sterility in forest trees. *Mol. Breed.* 1, 5–26
- 46 James, R.R. *et al.* (1998) Environmental effects of genetically engineered woody biomass crops. *Biomass Bioenerg.* 14, 403–414
- 47 Hu, J.J. *et al.* (2001) Field evaluation of insect-resistant transgenic *Populus nigra* trees. *Euphytica* 121, 123–127
- 48 Freris, N. and Laschefski, K. (2001) Seeing the wood for the trees. *The Ecologist* 31, 40–43