EFFECTS OF WHOLE-TREE HARVESTING ON THE AMOUNT OF SOIL CARBON: MODEL RESULTS

JAN BENGTSSON and FREDRIK WIKSTRÖM

Department of Ecology & Environmental Research, Swedish University of Agricultural Sciences, Box 7072, S-750 07 Uppsala, Sweden

(Received for publication 30 May 1992; revision 19 September 1994)

ABSTRACT

Using a model of a spruce forest ecosystem, comparisons of soil carbon were made after conventional (stem only) harvesting, harvesting of stems and branches, whole-tree (above ground) harvesting, and no biomass removal at clearfelling. Parameter values in the simulations corresponded to conditions and regulations in Swedish forestry.

As could be expected, soil carbon was less after intensive harvesting than after conventional harvesting, but the differences were rather small. With no removal of biomass, soil carbon increased substantially over the 300 simulation-years, but it decreased over time under all harvesting alternatives. Productivity (measured as harvested stem biomass) decreased with increasing harvesting intensity, whereas total harvested biomass increased with increased harvesting intensity in more productive stands. The results were similar to earlier model studies, and indicate that the major effects on soil carbon in forests come from conventional harvesting, and that increased utilisation of branches and needles for energy purposes is likely to have a relatively small additional impact.

Most simplifications of the model are such that the effects of intensified harvest on soil carbon in the field are likely to be smaller than the model suggests. We conclude that the fears that whole-tree harvesting will lead to substantial decreases in the amount of soil organic matter probably have been exaggerated. Given that the additional harvested biomass is used to replace fossil fuels, intensified harvesting for energy purposes in managed forests probably has only small effects on atmospheric carbon dioxide levels.

Keywords: bioenergy; modelling; soil carbon storage; Sweden; whole-tree harvesting.

INTRODUCTION

The growing concern with global warming due to increased levels of atmospheric carbon dioxide has led to increased attention to the magnitude of carbon storage and fluxes in terrestrial ecosystems (e.g., Houghton *et al.* 1983; Harmon *et al.* 1990; Mooney *et al.* 1991; Anderson 1991; Ojima *et al.* 1991). In managed forests, harvesting necessarily leads to decreased inputs to the soil organic matter pool compared to natural forests not subject to fire, which may result in decreased carbon storage (e.g., Spies *et al.* 1988; Harmon *et al.* 1990). Nonetheless, Eriksson (1991), calculating a carbon budget for Sweden, suggested that because of fire prevention, among other things, soil carbon appeared to have remained fairly stable or increased slightly in Swedish managed forests during the last century. In unburnt

New Zealand Journal of Forestry Science 23(3): 380-389 (1993)

areas of unmanaged boreal forests, soil organic matter has been shown to accumulate (e.g., Bradshaw & Zackrisson 1990).

Intensified harvesting, such as whole-tree harvesting (here defined as removal of branches and needles as well as stems), will lead to even greater decreases in inputs to soil organic matter compared to conventional (stem only) harvesting. Eriksson (1991) estimated that in average Swedish forests, the potential for stemwood harvest at clearfelling is about 20% of the total primary production, and if tops, needles, and branches from thinnings and clearfelling are utilised as well an additional 10% of the production can be removed. Apart from the direct effects of greater biomass removal on the organic material in the soil, some concern has arisen as to whether intensified harvesting may also lead to decreases in soil carbon through decreased forest productivity (e.g., Lundmark 1988; Harmon *et al.* 1990). Forest growth may decrease more than expected from biomass removal because of the removal of large quantities of nitrogen and other nutrients when needles are utilised, and because of the lower water-holding capacity of the soil with thinner forest floor and humus layers (e.g., Lundmark 1988).

In this study, we examined the effects of various intensities of harvesting at clearfelling on the amount of carbon in the soil, using a model of a spruce forest ecosystem (Rolff 1988; C.Rolff & G.I.Ågren, unpubl.) based on the theories by Ågren (1983, 1985), Ågren & Bosatta (1987), and Bosatta & Ågren (1985, 1991). Carbon and nitrogen dynamics of managed stands with different productivities were modelled over a time-span of 300 years and comparisons were made between soil carbon after conventional stem-only harvesting, whole-tree (above ground) harvesting, and a simulated clearfell or windthrow with no harvesting of biomass (hereafter called "no biomass removal"). The aim of the study was to evaluate some plausible alternatives to increase biomass harvesting in Swedish forestry. Harvesting regimes and parameter values in the model were chosen to generally correspond to Swedish conditions.

THE MODEL Model Structure

A brief discussion of the model used has been given by Rolff (1988) and, as full details will be presented elsewhere (C.Rolff & G.I.Ågren unpubl.), only a short description will be given here.

The model simulates the effects of various harvesting practices on productivity and other aspects of the spruce forest ecosystem over 300 years, with a time-step of 1 year. It is derived from a theory of carbon and nitrogen dynamics in terrestrial ecosystems (Ågren 1983, 1985; Ågren & Bosatta 1987; Bosatta & Ågren 1985, 1991), and based on a general understanding of ecosystem processes. Hence, it is not site-specific or empirical in the sense of Yarie (1990). Although it is in principle possible to parameterise the model for particular sites and draw quantitative conclusions, this is not recommended. It is best to use the model for qualitative predictions, where the conclusions may apply to different management practices in larger regions rather than specific stands (for a balanced critique of this type of modelling, *see*, e.g., Yarie 1990).

The nitrogen productivity concept (Ågren 1983, 1985) is used to model tree growth, i.e., growth is controlled by the amount of mineralised nitrogen available to the plant. Since the

value for nitrogen productivity used in the model is calculated from field data, it includes other factors influencing plant use of nitrogen in the field, e.g., intra-specific competition, insect consumption, and water.

At the end of each year, three components of fresh litter, i.e., needles, branches, and fine roots, are added to the soil and subsequently decomposed (Ågren & Bosatta 1987; Rolff & Ågren unpubl.). Coarse roots and stems are added after thinnings and clearfellings only, because self-thinning is negligible in managed Swedish forests. The soil is defined as the forest floor *and* the mineral soil. The model is not concerned about where the organic matter is situated in the soil, but only distinguishes between different qualities of organic matter. During decomposition the organic components mineralise carbon and may either immobilise or mineralise nitrogen according to the quality of the substrate. Quality is a function of the N:C ratio of the substrate, and is defined as the accessibility of the substrate to microbes, i.e., needles have a higher quality than branches, etc. The mineralisation rates of carbon and nitrogen are tuned to empirical data, mainly from the work of Berg & Ågren (1984).

The capacity of trees to utilise mineralised nitrogen is a function of fine-root biomass, and ground vegetation uses nitrogen up to a maximum biomass limit. Any remaining mineral nitrogen is considered to be lost from the system by leaching. In the present version of the model, ground vegetation is simplified to annual "grass".

In many parts of Europe, e.g., southern Scandinavia, nitrogen deposited from the atmosphere may contribute substantially to forest nitrogen dynamics (e.g., Nihlgård 1985; Bartnicki & Alcamo 1989). This is included in the model as a yearly input of nitrogen which can be varied (*see below*).

Parameter Values and Harvesting Regimes

As the main part of the model, including parameter values for growth and decomposition, will be described elsewhere (Rolff & Ågren unpubl.), only values pertinent to this particular study will be discussed here. As in several examples in the work by Rolff & Ågren (unpubl.), the input file for soil organic matter, which creates the soil at year 0, assumes that during the 300 years before the simulation, organic matter has been added at constant rates from the respective biomass fractions. Although this is clearly unrealistic, it has been done to avoid the results being dependent on stand history and harvesting before the time period of the simulation.

For the present study, stands with three different productivities were modelled. They corresponded roughly to the Swedish site indices (height at 100 years) G20, G24, and G32, and had been managed according to Swedish recommendations (Anon. 1982). The growth curves and yields of the modelled stands corresponded fairly well to natural ones, but no attempt was made to maximise the fit between model and observed stands (cf. above). Such exercises depend on the availability of better data on decomposition, nitrogen mineralisation, growth, and allocation.

In Sweden, stands with high productivity occur mainly in the south. The reasons are primarily climatic, but there is also a gradient in atmospheric deposition of nitrogen that declines from the south-west to the north (e.g., Bartnicki & Alcamo 1989). For this reason, we allowed the yearly external nitrogen input (EXTNIT) to vary from 2 kg N/ha in the G20-stand to 10 kg N/ha in the most productive G32-stand (Table 1). For similar reasons, soil

nitrogen at year 0 (NSCALE) also increased with productivity in our simulations (Table 1). The values were chosen to correspond to empirical regional trends, and to produce model stands with similar yields to the natural stands they represent.

The management of the model stands with respect to rotation lengths and thinnings is given in Table 1 and Fig. 1. Rotations were 100 or 150 years rather than the slightly shorter

	Site index		
	G20	G24	G32
EXTNIT (kg N/(ha·year)*	2.0	5.0	10.0
NSCALE†	0.8	1.0	1.5
Rotation length (years)	150	100	100
No. conventional thinnings	2	2	4

TABLE 1-Values for certain parameters and harvesting regimes specific to this study.

* EXTNIT = External nitrogen input (atmospheric deposition and nitrogen-fixation)

† NSCALE = Proportionality factor for the amount of nitrogen in the soil at year 0, used to create stands with different productivity.

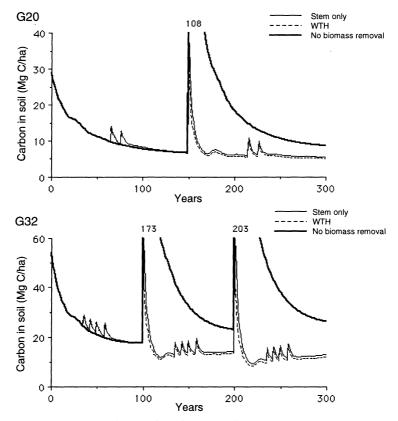


FIG. 1–Total amount of carbon in the soil during simulations at the lowest (G20) and highest (G32) site indices modelled. Stem only = conventional harvesting of stems; WTH = whole-tree harvesting (above ground); no biomass removal = all trees cut down at the end of the rotation and left on the site (*see* Table 2 for further details).

ones recommended (Anon. 1982). This was done to finish all simulations at the end of a rotation, and hence make the results comparable. In thinnings, stem biomass only was removed from the site. At clearfelling, the following harvesting intensities were modelled:

- Stem only, i.e., conventional harvesting of stems with 100% utilisation (removal from site). Branches and needles were left on the site.
- Harvesting of stems and branches, i.e., 100% stem utilisation plus 90% utilisation of branches, the rest of the branches and all needles left on the site.
- Whole-tree harvesting (WTH), i.e., as for "stems and branches" plus 90% utilisation of needles.
- We also simulated stands with clearfelling or windthrow but without removal from the site (called "no biomass removal"). These stands were not thinned, and after clearfelling at the end of the rotation all biomass was left on the site to decompose. This treatment can be regarded as corresponding to natural unmanaged forests not affected by fire. At least in the southern parts of Sweden, the natural disturbance regime in unmanaged forests has been dominated by small-scale disturbances such as gap regeneration (Nilsson 1992). Hence, this treatment is not wholly unrealistic, although few forests correspond to it today.

RESULTS

Comparisons of soil carbon under different harvesting regimes are shown in Table 2, and the results from model runs at the lowest and highest productivities simulated are given in Fig. 1. With the present parameter values, clearfelling or windthrow but no biomass removal led to increased soil carbon over time, while all harvesting alternatives produced less carbon in the soil at the end of the last rotation period than at the end of the first (Table 2a). Whole-tree harvesting decreased soil carbon after 300 years less than 10% compared to conventional harvesting (Table 2b), but the decreases in comparison to the no biomass removal treatment were of the order of 50% at the two higher site indices and about 40% in the low-productivity stand (Table 2c).

The effects of harvesting on long-term productivity of stem biomass are summarised in Table 3. The no biomass removal and conventional harvesting treatments did not seem to result in any decreases in productivity, while utilisation of branches and needles in addition to stems could have negative effects on long-term productivity.

The total amount of biomass harvested during 300 years under the different harvesting regimes increased with harvesting intensity at the two higher productivities (Fig. 2). At the lowest productivity, however, utilisation of needles did not result in increased total biomass harvest. At all three productivities, the harvest of stemwood decreased with increased harvesting intensity, indicating that site productivity may be negatively influenced by whole-tree harvesting.

DISCUSSION

Limitations of the Model

In the model, soil nitrogen is the main driving variable which, through the nitrogen productivity concept, is linked to tree growth and decomposition rates, and in this way the amount of soil carbon is determined by nitrogen mineralisation and availability. This means Bengtsson & Wikström—Effects of harvesting on soil carbon

TABLE 2-Relative differences in total soil carbon in model spruce stands, after different harvesting				
intensities and with different productivities. Relative differences were calculated as $(y-x)$				
x, where y is the value of soil carbon resulting from different harvesting intensities, and x				
is the value it is compared with, i.e., (a) at the end of the first rotation, (b) after conventional				
harvesting, and (c) after the no biomass removal treatment.				

	Productivity/site index							
	G20	G24	G32					
(a) Differences in soil carbon between the end of the first and the end of the last rotation (%)								
No biomass removal*	+30	+52	+49					
Stem only (conventional)	-18	-26	-26					
Stems and branches	-22	-31	-30					
WTH	-24	-33	-32					
(b) Differences in soil carbon between more intensive harvesting practices and conventional harvesting, after 300 years (%)								
Stem only (conventional)	0	0	0					
Stems and branches	-5.0	-6.4	-4.8					
WTH	-7.3	-9.7	-7.6					
(c) Differences in soil carbon between the three harvesting practices and no biomass removal treatment, after 300 years (%)								
No biomass removal	0	0	0					
Stem only (conventional)	-35	-50	-50					
Stems and branches	-39	-53	-53					
WTH	-40	-55	-54					
Stem only= conventional haStems and branches= As for stem only	y, plus 90% utilisat	vith 100% utilisation of branches.	l left on the site. n (removal from site). us 90% utilisation of bran	nches				

and needles.

TABLE 3-Long-term productivity—(a) effects of different harvesting practices, measured as relative differences in stem biomass between the end of the first and the end of the last rotation (%);
(b) comparisons of productivity (stem biomass) at 300 years, between conventional harvesting (stem only) on the one hand, and stems and branches or WTH on the other.

		Site index		
	G20	G24	G32	
(a) Relative differences in stem biomass betw period (%)	een the end of the	first and the end	l of the last rotation	
No biomass removal	+28	+39	+28	
Stem only (conventional)	+3.8	+7.4	+3.5	
Stems and branches	-3.9	-1.5	-1.7	
WTH	-7.6	-6.4	-4.9	
(b) Comparisons of productivity (stem biomas	ss) at 300 years			
Stems and branches v . stem only	-7.5	-8.3	-5.1	
WTH v . stem only	-11	-13	-8.2	

that our results are not pertinent if factors other than nitrogen are limiting tree growth—for example, water or other nutrients such as phosphorus or potassium. If harvesting is intense, such elements may become growth-limiting (cf. Lundmark 1988; Hornbeck 1990) and soil carbon will decrease more rapidly than anticipated from the model.

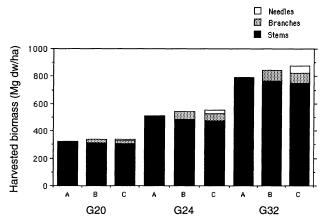


FIG. 2-Harvested biomass in stem, branch, and needle fractions at different harvesting intensities and productivities during the 300-year term of the model. A = stem only, B = stems and branches, C = WTH (see Table 2 for details).

The present formulation of the model does not explicitly consider changes in plant allocation to roots and shoots in response to changes in nitrogen availability (e.g., Tilman 1988; Ingestad & Ågren 1991). As nitrogen availability decreases, which may be one effect of whole-tree harvesting, the trees may allocate relatively more carbon to roots. Hence, in real stands, a larger contribution of roots to soil carbon may partly compensate for increases in above-ground biomass removal.

The amount of soil carbon produced by the model, usually between 10 and 40 Mg C/ha (Fig. 1), is low compared to carbon pools in natural boreal and temperate coniferous forest soils. In part, this is due to the model considering mainly nitrogen. While nitrogen can be leached out of the system, i.e., down the soil profile, carbon cannot in the present version of the model. Hence, estimates of carbon pools in the entire soil profile, such as 150–200 Mg C/ha (Houghton *et al.* 1983; Anderson 1991), are not comparable with those in the model. In a whole-tree harvesting experiment on a site in south Sweden, S865 at Tönnersjöheden, with approximately the same site index as the productive stand in Fig. 1, soil carbon down to 10 cm in the mineral soil was about 50–60 Mg·C/ha (J.Bengtsson, H.Lundkvist & B.Olsson, unpubl. data). This is still higher than the values obtained in the model, but of similar magnitude. Since the model includes only soil carbon produced during the last 300 simulation-years, the low values in the model are explicable (cf. below). If, as is likely, the model estimates of soil organic matter are too low compared to natural soils because of the low age of the carbon in the model, this means that the model probably over-estimates the relative decreases in soil carbon with increasing harvesting intensity (Fig. 1 and Table 2).

Related to the above is that all carbon is mineralised in the model. In coniferous forest soils, there is a stabilised carbon fraction that mineralises extremely slowly or not at all (e.g., Anderson 1991). This property of the model probably leads to over-estimation of carbon losses from the soil.

Thus, several facts (no increased allocation to roots with increased nitrogen limitation, no soil carbon older than 300 years, and all carbon being mineralised) suggest that the model

Bengtsson & Wikström-Effects of harvesting on soil carbon

estimates of soil carbon decreases with whole-tree harvesting probably are too high rather than too low. On the other hand, if elements other than nitrogen become growth-limiting, then the model estimates of soil carbon may be lower than in real stands. However, most temperate and boreal forests still seem to be nitrogen-limited (e.g., Binkley 1986). The effect of nitrogen being the driving variable on the accuracy of the model predictions has not been assessed.

The present formulation of the model does not allow predictions of long-term changes due to increased atmospheric carbon dioxide-levels and global warming. The summary effects of these factors on vegetation, forest production, and decomposition may be complex and difficult to predict (e.g., Strain 1985; Anderson 1991; Mooney *et al.* 1991; Esser 1992).

Effects of Harvesting on Soil Carbon

Although removal of biomass during more intensive harvesting inevitably results in lower carbon inputs to the soil, the simulations suggest that this effect is likely to be small. The decrease in soil carbon estimated in the model (5-10%) is probably larger than in real forest stands (cf. above). Thus, it is unlikely that the drastic effects of whole-tree harvesting on soil organic matter anticipated by, for example, Lundmark (1988) will be found, at least in nitrogen-limited forests. Small negative effects may often be difficult to reveal, since they may be hidden by the natural variability due to topography, soil characteristics, or even pure chance. This suggestion is supported by results from the whole-tree harvesting experiment S865 at Tönnersjöheden in south-west Sweden, where we found no significant decreases in soil carbon even after repeated whole-tree removals (J.Bengtsson, H.Lundkvist & B.Olsson, unpubl. data).

On a larger scale a small decrease in soil carbon could still be considered an important carbon-flux to the atmosphere. However, the extra biomass utilised in whole-tree harvesting, i.e., branches and needles, will be used mainly for bioenergy, and hence replace fossil fuels. The major part of these biomass fractions would have decomposed to carbon dioxide quite rapidly, anyway. Therefore, this contribution of forest bioenergy to global warming is likely to be negligible (cf. Vitousek 1991). Given that fossil energy is indeed *replaced* with bioenergy, the long-term effect of increased biomass utilisation in forestry may be to slow the increase in atmospheric carbon dioxide-levels rather than the reverse.

The major effect on soil carbon in the present study is caused by conventional harvesting compared to no biomass removal. Large effects on soil organic matter pools from harvesting have been suggested previously (e.g., Houghton *et al.* 1983; Harmon *et al.* 1990). Logs and other coarse woody debris utilised for lumber, pulp, and fuel can constitute a quite large fraction of the total input of organic matter to the soil in natural forests, from around 25% to more than 60%, and they have slow decomposition rates (Harmon *et al.* 1986). These fractions are likely to be important for the long-term dynamics and accumulation of carbon in forest soils (Ågren & Bosatta 1987), and may also play several other important roles in the forest ecosystem (Harmon *et al.* 1986).

When no biomass is removed from a site, our simulations suggest that soil carbon will increase over time. This has also been observed in unburnt areas in unmanaged boreal forests (e.g., Bradshaw & Zackrisson 1990). Conventional harvesting resulted in sustained productivity (Table 3) but lower amounts of soil carbon (Table 2), suggesting that if the

estimate by Eriksson (1991) that soil organic matter in Swedish forests has remained stable during the last century is true, this is due to increased forest productivity.

To summarise, increased use of branches and needles for energy purposes probably has relatively small effects on soil carbon sequestering in managed forests. We conclude that fears that whole-tree harvesting will lead to large decreases in the amount of soil organic matter have been exaggerated. However, this applies only under the conditions for which the model is applicable, and if nutrients other than nitrogen become limiting, our conclusions may no longer be valid.

ACKNOWLEDGEMENTS

We thank Göran Ågren, Carl Rolff, Heléne Lundkvist, Bengt Olsson, P-O Brandtberg, and Hillevi Eriksson for comments on the manuscript, discussions, and/or access to unpublished data. J.P.Kimmins reviewed the manuscript and gave insightful comments, though he may not agree with all our conclusions. Carl Rolff made a first version of the model. The study is part of a project on the ecological effects of intensive harvesting financed by the National Board for Industrial and Technical Development (NUTEC).

REFERENCES

- ÅGREN, G.I. 1983: Nitrogen productivity of some conifers. *Canadian Journal of Forest Research 13*: 494–500.
- ÅGREN, G.I.; BOSATTA, E. 1987: Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. *Ecology* 68: 1181–9.
- ANDERSON, J.M. 1991: The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications 1*: 326–47.
- ANON. 1982: Praktisk skogshandbok, 10:e upplagan. Sveriges Skogsvårdsförbund, Djursholm. 492 p. [in Swedish].
- BARTNICKI, J.; ALCAMO, J. 1989: Calculating nitrogen deposition in Europe. Water Air and Soil Pollution 47: 101–23.
- BERG, B.; ÅGREN, G.I. 1984: Decomposition of needle litter and its organic chemical components: theory and field experiments. Long-term decomposition in a Scots pine forest. III. Canadian Journal of Botany 62: 2880–8.
- BINKLEY, D. 1986: "Forest Nutrition Management". Wiley, New York. 290 p.
- BOSATTA, E.; ÅGREN, G.I. 1985: Theoretical analysis of decomposition of heterogeneous substrates. Soil Biology and Biochemistry 16: 63–7.
- BRADSHAW, R.H.W.; ZACKRISSON, O. 1990: A two thousand year history of a northern Swedish boreal forest stand. *Journal of Vegetation Science 1*: 519–28.
- ERIKSSON, H. 1991: Sources and sinks of carbon dioxide in Sweden. Ambio 20: 146-50.
- ESSER, G. 1992: Implications of climate change for production and decomposition in grasslands and coniferous forests. *Ecological Applications* 2: 47–54.
- HARMON, M.E.; FERRELL, W.K.; FRANKLIN, J.F. 1990: Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247: 699–702.
- HARMON, M.E.; FRANKLIN, J.F.; SWANSON, F.J.; SOLLINS, P.; GREGORY, S.V.; LATTIN, J.D.; ANDERSON, N.H.; CLINE, S.P.; AUMEN, N.G.; SEDELL, J.R.; LIENKAMPER, G.W.; CROMACK, K. Jr; CUMMINS, K.W. 1986: Ecology of coarse woody debris in temperate forest ecosystems. Advances in Ecological Research 15: 133–302.

Bengtsson & Wikström-Effects of harvesting on soil carbon

- HORNBECK, J.W. 1990: Cumulative effects of intensive harvest, atmospheric deposition and other land use activities. Pp. 147–54 in Dyck, W.J.; Mees, C.A. (Ed.). "Impact of Intensive Harvesting on Forest Site Productivity". Proceedings, IEA/BE A3 Workshop, South Island, New Zealand, March 1989. IEA/BE T6/A6 Report No 2. New Zealand Forest Research Institute, FRI Bulletin No.159.
- HOUGHTON, R.A.; HOBBIE, J.E.; MELILLO, J.M.; MOORE, B.; PETERSON, B.J.; SHAVER, G.R.; WOODWELL, G.M. 1983: Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO₂ to the atmosphere. *Ecological Monographs* 53: 235–62.
- INGESTAD, T.; ÅGREN, G.I. 1991: The influence of plant nutrition on biomass allocation. *Ecological Applications 1*: 168–74.
- LUNDMARK, J.-E. 1988: Skogsmarkens Ekologi: Ståndortsanpassat Skogsbruk. Del 2 Tillämpning. Skogsstyrelsen, Jönköping. 319 p. [Forest Soil Ecology. In Swedish].
- MOONEY, H.A.; DRAKE, B.G.; LUXMORE, R.J.; OECHEL, W.C.; PITELKA, L.F. 1991: Predicting ecosystem responses to elevated CO₂ concentrations. *BioScience* 41: 96–104.
- NIHLGÅRD, B. 1985: The ammonium hypothesis—An additional explanation to the forest dieback in Europe. *Ambio* 14: 2–8.
- NILSSON, S.G. 1992: Forests in the temperate-boreal transition—Natural and man-made features. Pp. 373–93 in Hansson, L. (Ed.) "Nature Conservation by Ecological Principles". Elsevier, UK.
- OJIMA, D.S.; KITTEL, T.G.F.; ROSSWALL, T.; WALKER, B.H. 1991: Critical issues for understanding global change effects on terrestrial ecosystems. *Ecological Applications 1*: 316– 25.
- ROLFF, C. 1988: Some model aspects on whole tree harvesting and site classification. Pp. 121–9 in Williams, T.M.; Gresham, C.A. (Ed.). "Predicting Consequences of Intensive Forest Harvesting on Long-term Productivity by Site Classification". IEA/BE Project A3, Report No. 6. Baruch Forest Science Institute of Clemson University, Georgetown, S.C.
- SPIES, T.A.; FRANKLIN, J.F.; THOMAS, T.B. 1988: Coarse woody debris in Douglas-fir forests of Western Oregon and Washington. *Ecology* 69: 1689–702.
- STRAIN, B.R. 1985: Physiological and ecological controls on carbon sequestering in terrestrial ecosystems. *Biogeochemistry 1*: 219–32.
- TILMAN, D. 1988: "Plant Strategies and the Dynamics and Structure of Plant Communities". Princeton University Press, Princeton, N.J. 360 p.
- VITOUSEK, P.M. 1991: Can planted forests counteract increasing atmospheric carbon dioxide? Journal of Environmental Quality 20: 348-54.
- YARIE, J. 1990: Role of computer models in predicting the consequences of management on forest productivity. Pp. 3–18 in Dyck, W.J.; Mees, C.A. (Ed.). "Impact of Intensive Harvesting on Forest Site Productivity". Proceedings, IEA/BE A3 Workshop, South Island, New Zealand, March 1989. IEA/BE T6/A6 Report No 2. New Zealand Forest Research Institute, FRI Bulletin No.159.