Research requirements to develop complete nutrient budgets for indigenous forests: a case study from hard beech forest, North-West Nelson

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Abstract

The sustainable management of indigenous forests for timber production requires adequate knowledge about the degree of nutrient removal that occurs with harvesting and the impact of this removal on nutrient cycling. However, there is only limited information available with which to draw conclusions about the possible consequences of nutrient removals for long-term productivity of indigenous forests that are managed for timber production. We compare nutrient removals for small coupe and near-natural management scenarios, with and without removal of debris for pest control, for a hard beech forest on an infertile soil in North-West Nelson and consider implications for the sustainable management of beech forests. A simple nutrient-budget approach is used to identify future research required to better understand the impacts of timber removal from indigenous forests.

Introduction

The area of indigenous forest managed under the 1993 provisions of the Forest Act 1949 for the sustainable production of timber is steadily increasing in New Zealand. Currently plans and permits are being processed for 40 000 ha in addition to those already issued for approximately 100 000 ha out of a total area of 1.477 million hectares of privately owned forest (MAF unpubl. data). Areas of forest harvested may range from small, selected groups of trees to small coupes (0.05 ha) such as occur for beech forest on the West Coast. Different harvesting systems will result in disturbances that have varying impacts on the forest environment. These impacts need to be quantified and understood, since sustainable forest management not only requires that production of timber be sustainable in the economic sense, but also that both the soil's productive capacity and environmental quality are maintained (Nambiar 1996). This is also a requirement under most product-certification schemes.

Harvesting and nutrient loss from indigenous forests

Harvesting results in the removal of organic matter and nutrients in stemwood and it is axiomatic that the impacts of this will be greater on poorer soils (Dyck et al. 1991). The impact of nutrient removals in logs extracted from indigenous forest is not well known (James & Norton 2002; Hart et al. 2003). In particular there are few data on the quantity of nutrients contained in the various ecosystem pools (e.g. tree stems) within indigenous forests, and available data are representative of only a few species from selected locations, e.g. hard beech (*N. truncata*) (Miller 1963), mountain beech (*N. solandri* var. *cliffortioides*) (Nordmeyer 1980; Allen et al. 1997; Clinton et al. 2002) and kauri (*Agathis australis*) (Silvester & Orchard 1999; Silvester 2000).

Recently Hart et al. (2003) produced a comprehensive picture (Table 1) of nutrient distribution for a hard beech forest growing on infertile, highly weathered Moutere greywacke gravels in the Donald Creek area, Nelson. Relative to the amounts of nutrients available for plant growth that are found in the soil, considerable quantities of some nutrients are contained in the biomass and detrital pools (forest floor and coarse woody debris (CWD)). When only harvestable tree stem biomass is considered, the amounts of N, P, K, Mg and Ca in this pool are 4, 10, 19, 9, and 26% respectively of the total pools[1] of these nutrients in the ecosystem (Table 1). The magnitude of these removals clearly has important implications for the long-term sustainability of nutrient supply because harvesting circumvents the entry of nutrients contained in logs into the detrital pool and subsequent transfers to the soil and forest regrowth.

Does harvesting technique alter nutrient removal?

Harvesting of indigenous forests is likely to continue under a number of possible management regimes and it is therefore important to consider the consequences of nutrient removals under the differing regimes. On a per hectare basis near natural harvest systems, where small numbers of trees are removed, clearly remove smaller amounts of nutrients than coupe systems (Table 2). However it is unlikely that nutrient removals using near natural systems will differ greatly from those removed by coupe logging regimes if the quantity of nutrients removed is based on a ground area estimate that is in proportion to the amount of stand basal area removed. The actual area affected by the harvest will need to be determined and only

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[1] *Soil pool components are total N and P and exchangeable K, Ca and Mg*

Table 1. Distribution of major nutrients (kg/ha) in a hard beech forest, North-West Nelson, New Zealand. Values are from Hart et al. (2003). The forest floor L and FH layers are included in the pool detritus of all species.

	N	P	K	Mg	Ca
Non harvestable above-ground beech biomass	310	71	339	47	636
Harvestable beech stem biomass	140	69	215	30	494
Beech root biomass	106	56	189	36	206
Other species above- and below-ground biomass	69	24	94	14	171
Detritus of all species	249	23	74	35	238
Dead roots of all species	53	32	13	10	71
Total soil N (0-60cm), available P and exchangeable cations (0-60cm)	2400	440	178	147	107
Total nutrient pools	3327	715	1102	319	1923

when the area affected by the individual groups of selected trees harvested is greater than that estimated in proportion to basal area will the impact of such a harvesting regime be reduced. The quantity of major nutrients removed can be reduced by 38-46% respectively, however, if branches and non-merchantable stemwood are not removed from the site (Table 2). Retaining this material on site will need to be balanced with the risk of pest build-up.

These observations highlight the need for investigation

Table 2. Estimated ecosystem nutrient removals* from harvest (kg/ha) for various management scenarios for hard beech forest, North-West Nelson.

	N	P	K	Mg	Ca
Clearfelling or small coupe	140	69	215	30	494
Clearfelling or small coupe cleaned[1]	260	110	394	48	883
Near natural (15 stems/ha)[2]	12	4	17	2	41
Near natural (15 stems/ha) cleaned[1]	21	7	31	4	71

* *Nutrient masses calculated using relationships of Hart et al. (2003).*
[1] *Branches and non-merchantable stemwood also removed along with stem with small branches and leaves left behind.*
[2] *15 stems/ha removed once.*

of the effects of nutrient removal through harvest on subsequent regrowth and the need for development of appropriate pest control measures so that the impact of harvesting slash removal can be reduced. Methods for measuring the area affected by natural harvesting also need to be developed so that nutrient removals can be properly quantified on an area basis. As well as the area affected by natural harvesting nutrient removals, the spatial arrangement of harvested areas will also need to be considered so that the mosaic of such areas that develop over time can be appropriately managed using fertiliser if required.

Can nutrient inputs from natural processes balance nutrient loss from harvesting?

In undisturbed forests, nutrient losses from natural processes such as leaching, erosion, volatilisation, denitrification, gaseous loss of N and animal transfer can be balanced by gains in nutrients that can occur through wet and dry deposition, rock weathering, and nitrogen fixation. The available data for the hard beech stand described earlier will be used to explore the extent to which gains from mineral rock weathering may be an important source of nutrients other than N.

A widely used approach to estimate weathering rates is one based on the mass balance of catchment nutrient budgets (Zabowski 1990), where nutrients that arrive in the catchment from wet and dry deposition are considered inputs and those discharged in stream flow from the catchment are considered outputs. This approach is represented in the following mass balance equation:
Change in storage = inputs (atmospheric deposition + weathering) - outputs (leaching)   (equation 1)

This equation can be rearranged as:
Weathering = leaching - atmospheric deposition + change in storage   (equation 1a)

In a steady-state biotic system where change in storage is considered to be zero, this equation becomes:
weathering = leaching – atmospheric deposition
                                                      (equation 2)

Where forest is not in a steady state, i.e. is accumulating or losing nutrients, nutrient uptake (or loss) in vegetation is considered to be the change in storage, and equation 1a becomes:
Weathering = leaching - atmospheric inputs + net biotic uptake   (equation 3)

Net biotic uptake on an annual basis can be calculated as the difference between total nutrient uptake and the contribution from nutrient cycling:
Net biotic uptake = total nutrient uptake - contribution from nutrient cycling   (equation 4)

However, the equations above assume no change in soil storage on an annual basis as this is particularly

difficult to measure, but it is important to note that this may not hold over very long periods of time (e.g. Walker & Syers 1976).

Estimates of weathering can be made using both equations 2 and 3 as detailed information is available on levels of annual productivity and plant nutrient status for our example from the studies of Benecke & Evans (1987) and Hart et al. (2003)[2]. However, when using equation 3 there are a number of assumptions to do with the contribution of nutrient cycling to net biotic uptake and the extent of total nutrient uptake that have to be made. The basis for these assumptions will be discussed in the next section.

Estimating the contribution of nutrient cycling processes to net biotic uptake

A major component of the cycling of nutrients is the turnover and retranslocation of nutrients in leaves and fine roots. We have assumed leaf litterfall mass is equal to annual foliage production and estimated the quantity of nutrients returned in annual litterfall as the product of litter mass and

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[2] The study reported by both Benecke & Evans (1987) and Hart et al. (2003) was part of a larger project undertaken by the Forest Research Institute to compare carbon assimilation and nutrient cycling and water use by adjacent stands of hard beech and radiata pine growing in the Donald Creek hydrological research Catchment area in Big Bush State Forest, North West Nelson. The study consisted of detailed plant productivity studies reported by Benecke and Evans (1987) and detailed biomass and nutrient distribution studies reported by Hart et al. (2003).

litter nutrient concentrations. We assume that the balance of nutrients in the foliage not shed in litterfall (i.e. foliage nutrient content – nutrients in litterfall) is retranslocated into new foliage in the same year. Turnover of litterfall nutrients is also assumed to occur in the same year. We have not included nutrient transfer to the forest floor as a result of canopy leaching in our estimates of nutrient cycling. We have assumed that there is no nutrient retranslocation from fine roots (Nambiar 1987). Considerable quantities of nutrients are sequestered into the annual increment of branches, bark, wood, and larger roots (Table 3). These nutrients are removed from the biological nutrient cycle for an indefinite period of time.

Our estimate of nutrient cycling (Table 3) is likely to be low, as apart from leaf litterfall, we do not consider release of nutrients from all sources of organic matter present, e.g. CWD and dead roots, as data for these processes are unavailable. As the decomposition and release of nutrients from dead wood and large branches is very slow (Harmon et al. 1994; Hart 1999; Krankina et al. 1999), this flux and that from dead roots is unlikely to contribute greatly to overall nutrient supply.

We have not included any contribution from nitrogen fixation or made any allowance for loss of N through denitrification in our estimates of nutrient cycling but these fluxes are likely to be very small in relation to the total amount of N cycling on an annual basis. Overall, approximately 95, 10, 51, 13 and 65 kg/ha of N, P, K, Mg and Ca, respectively, are cycling on annual basis (Table 3).

Based on the detailed data for above- and below-ground productivity annual total tree uptake is in the order of 109,

Table 3. Estimated annual nutrient cycling, total plant uptake, and net biotic uptake (kg/ha) for a hard beech forest, Donald Creek, North-West Nelson.

		N	P	K	Mg	Ca
Nutrient cycling (Tc)	Annual litter fall (l)	35.8	3.2	5.1	5.1	35.8
	Retranslocation from foliage (r)	44.2	3.8	40.3	3.8	12.2
	Roots < 2 mm turnover (frt)	14.6	2.9	5.7	3.8	16.6
	Roots < 2 mm retranslocation (frrt)	0	0	0	0	0
	Total cycling (Tc) = (l + r + frt+frrt)	94.6	9.9	51.1	12.7	64.6
Tree uptake (Tu)	Foliage (f)	80	7	45.4	9	48
	Branches including bark (b)	5.6	2.2	8.5	1.4	15.1
	Stem including bark (sb)	2.8	1.7	4.2	0.6	9.7
	Fine roots < 2 mm (fr)	14.6	2.9	5.7	3.8	16.6
	Coarse roots > 2 mm (cr)	5.8	2.2	4.6	1.9	11.4
	Total uptake (Tu) = (f + b + s + fr + cr)	108.7	16.0	68.4	16.6	100.8
Net biotic uptake (Nbu)	Nbu = Tu - Tc	14.2	6.1	17.3	3.9	36.1

16, 68, 17 and 101 kg/ha of N, P, K, Mg and Ca, respectively (Table 3). These amounts do not include any nutrients that may be required by understorey species.

Net biotic uptake, estimated as the difference between total plant uptake and nutrient cycling is the order of 14, 6, 17, 4 and 36 kg/ha for N, P, K, Mg and Ca respectively (Table 3).

Calculation of weathering rates

Annual rates of nutrient weathering at a catchment scale (equation 2) would be in the order of 0.1, 2.5, 2.4 and 6.8 kg/ha for P, K, Mg and Ca, respectively. In contrast, much greater annual weathering rates of 6.2, 19.8, 6.3 and 42.9 kg/ha for P, K, Mg and Ca respectively are estimated using equation 3.

The estimates of annual net biotic uptake are much greater than the annual nutrient inputs in rainfall (Table 4; M.R. Davis unpubl. data) so either rates of weathering are greater than those estimated using equation 2 and shown in Table 4, or the assumption that annual changes in soil storage are small, and therefore do not need to be considered in the nutrient balance approach of equation 3, is not a valid assumption to make. In addition to the nutrient inputs shown in Table 4, there is also a loss of nutrients in stream water leaving the catchment, suggesting that rates of weathering may be greater than stream losses if the changes in the vegetation pool are not in equilibrium with the soil pool.

Table 4. Estimates of annual nutrient inputs from precipitation, outputs in streamflow, net biotic uptake and potential weathering rates (assuming soil is at a steady state) (kg/ha) for a hard beech forest, Donald Creek, North-West Nelson.

	N	P	K	Mg	Ca
Input (rainfall) (I)	2.1	0.1	2	0.8	2.5
Output (Stream flow) (O)[1]	1.1	0.2	4.5	3.2	9.3
Catchment level weathering (equation 2)	-1.0	0.1	2.5	2.4	6.8
Net biotic uptake (Nu)	14.2	6.1	17.3	3.9	36.1
Weathering* (Nu + O - I) (equation 3)	13.1	6.2	19.8	6.3	42.9

*For N this quantity comes from N fixation or additional N mineralisation of forest floor and other detrital pools.

[1] Data from Fahey and Jackson (1997).

Comparisons to other studies

There are few New Zealand studies of weathering or rates of weathering that are not based on catchment studies or soil change alone (e.g. Walker & Syers 1976; Zabowski et al. 1994; McIntosh 1997). Making direct comparisons to our estimates, for which we have assumed that the soil is at a steady state, is therefore difficult. In making all the assumptions that we have, we may have over-estimated rates of nutrient weathering but it has been a very useful approach for the purposes of identifying areas where we need to increase our levels of understanding.

Our estimates of mineral weathering for Ca, K and Mg (Table 4), for which we have assumed there is no change in soil storage (including forest floor layers) on an annual basis are, however, within the range for international estimates of weathering rates for forest ecosystems (Homann et al. 1992). This supports the assumptions we have made in estimating plant uptake and nutrient cycling. If our assumed turnover rates of litter and fine roots are too fast, then more nutrients would need to be supplied from mineral weathering, or alternatively from the decomposition of other ecosystem pools to meet changes in plant storage. Based on the limited studies in the literature (e.g. Krankina et al. 1999), it is unlikely that rates of nutrient release from CWD would be sufficient to meet plant uptake demand to any great extent. This further supports our case for significant release of nutrients from soil minerals. Natural mortality of trees would also lead to greater nutrient storage in CWD resulting in another change in plant and soil storage, suggesting higher weathering rates.

Our estimate of annual P weathering (6.2 kg/ha) is, however, much larger than such estimates for other ecosystems (Newman 1995). Estimates of annual rates of P weathering from rock determined over long periods of time are in the order of 0.5–1.0 kg P per hectare (Walker & Syers 1976). There are few studies of weathering of P that do not rely on long term changes in soil P storage to estimate rates of weathering and it is unclear if weathering rates remain constant, or increase as soil particles become more weathered. Further work is required to test if it is valid to make the assumption that there is no change in soil P storage (eg. adsorbed and organic P, including the forest floor) on an annual basis. However, in cases where most ecosystem P is in organic matter pools, as is the case for hard beech stands on highly weathered Moutere gravels, management of the organic matter pools will be of critical importance in supplying P and sustaining wood production as inputs of P in rainfall are generally low (e.g. McColl 1978; Neary et al. 1978).

In the case of N, our estimate of annual biotic uptake of 14.2 kg/ha is greater than likely levels of N fixation based on estimates for other ecosystems (e.g. Silvester et al. 1982; Wei & Kimmins 1998). This suggests that, as above, the assumption of no change in forest floor and soil pools may not be appropriate. Alternatively, it may be that although inputs of N from decaying logs and dead roots are considered to be too small to make a significant contribution to N cycling in northern coniferous forests (Laiho & Prescott 2004), they may be an important N source in N budgets for southern temperate beech forests. Further research is required to test this assumption so as to establish rates of N fixation and N mineralisation in CWD and forest floor, given that the mass of CWD and forest floor can be quite large in some ecosystems (eg Stewart & Burrows 1994; Davis et al. 2003; Silvester & Orchard 1999).

Using instantaneous rates of demand and supply as estimated in this study may not be appropriate to represent long term trends in nutrient supply. However, our results indicate mineral weathering may be greater than expected for P, Ca and Mg or alternatively deadwood may be a more important source of nutrients than currently thought. Therefore, removing fallen or standing dead trees or altering rates of deadwood formation may reduce long term nutrient supply. Of great importance to the discussion about the impacts of nutrient removals through harvest and how inputs will offset them is the length of time considered to balance the removal. Estimates of the long-term inputs in rainfall (Davis unpubl. data), simple catchment-level estimates of weathering and assuming some inputs from dry deposition and N fixation, suggests that these sources of nutrient inputs, with the major exception of P, would be adequate to replace removals following any type of harvesting.

Future research directions

Our nutrient-budgeting approach has helped us identify several areas that require further investigation so as to provide a robust basis for understanding the impacts of harvesting on sustainability of harvesting indigenous forests. Additional areas where research is required are outlined below.

Species and fertility effects on nutrient pools

Hart *et al.* (2003) provide very good estimates of the nutrient pools in hard beech forest on nutrient-poor soil, but there are few other reports detailing the contents of major nutrients for important indigenous timber species e.g. rimu, totara, tawa. It would be useful to collect these data for key harvested species across gradients of soil fertility. It is possible that this might be collected in conjunction with studies designed to obtain information on the carbon content of our native forests.

Nutrient removal by harvesting

The effects of near-natural harvesting systems in terms of the size of the area affected and the impacts of nutrient removal on subsequent regrowth need to be studied. Methods for measuring the area affected by harvesting need to be developed so that the effects of harvesting systems on nutrient removals can be evaluated on an area basis. This would require the study of gradients of nutrient availability or soil moisture, soil temperature and photosynthetically active radiation within coupes in relation to seedling growth. Tree crowns contain large quantities of nutrients that are, in the case of the foliage nutrients, relatively available. The consequences of how the harvesting slash is arranged within coupes needs to be considered so that nutrients are not leached from large piles of slash and regeneration is not restricted due to the presence of piles of slash. Regeneration around stumps of harvested trees may be limited due to nutrient immobilisation during the decay of stumps and buttress roots. In this case, suitable fertiliser strategies may need to be considered to allow for rapid regeneration of desired species.

CWD dynamics following harvesting

Conclusions from recent studies of the local effects of logs on soil development (Klinka *et al.* 1995), and on the diversity of forest floor properties and invertebrate communities (Evans *et al.* 2003; Spears *et al.* 2003), suggest that further work is also required to fully understand the possible consequences of alteration of CWD dynamics following stem harvesting. It is also necessary to highlight any differences between harvested areas and areas of natural tree throw so that the consequences for the forest ecosystems can be assessed and appropriate actions can be suggested to managers.

There is certainly a lack of data and understanding on the decomposition of CWD and factors controlling nutrient release (Clinton *et al.* 2002) and how any alteration to the CWD pool may impact on ecosystem function. While some information is available for beech species, there is an urgent need to consider the role of CWD of other species. The role of N fixation in decaying logs of indigenous species warrants study. Published rates of N fixation in other forest types are equal to atmospheric inputs (e.g. Brunner & Kimmins 2003; Hicks *et al.* 2003). This type of input could be important over long time frames given the large size of logs and accumulated mass of CWD and the very long length of time that logs are present on the forest floor. In some cases the contribution of N fixation by free living heterotrophs in decaying litter to ecosystem N storage may be quite large over long periods of time, e.g. Silvester (2000).

Importance of mineral weathering

This study has highlighted that our knowledge of ecosystem nutrient fluxes is limited. In particular the catchment balance method (equation 2) we used to determine weathering assumes no change in nutrient storage on an annual basis, which is unlikely to be true. Our estimates for weathering rates therefore need to be verified, preferably along environmental gradients with an independent method, for example by using Sr isotope ratios for soil cations (e.g. Miller *et al.* 1993). Similarly, studies of P weathering from rocks are required perhaps using loss of Si in streamwater as described by Gardner (1990).

Another approach may be that of Ranger & Nys (1994) who have studied mass loss of a range of minerals in bags *in situ* over time to determine weathering rates. Additionally, the importance of poorly understood processes such as mycorrhizal weathering of rock needs further investigation (Thompson *et al.* 2001: Blum *et al.* 2002; Watmough & Dillon 2003: Hoffland *et al.* 2004). Long-term monitoring of soil nutrient pools, including forest floor pools over soil fertility gradients is required to determine how these change in response to harvest operations (Zabowski *et al.* 1994).

Other consequences of harvesting and log removal in natural forests

Soil mixing by tree throw following events such as wind storms and earthquakes may be an important process in natural forest systems (e.g. Allen *et al.* 1999). Such mixing may be potentially reduced when forests are harvested (Norton 1989; Schaetzl *et al.* 1989; Schaetzl & Follmer 1990).

Windthrow can result in large amounts of earth being deposited on the soil surface. Any reduction in tree uprooting will have consequences such as reducing the variability in soil properties (Beatty & Stone 1986), and changing soil development (Campbell & Mew 1986). This issue needs further consideration in relation to issues of long-term nutrient balances of forest stands under near-natural forest management regimes that may lead to reductions in windthrow. Reduced windthrow along with salvaging of logs from the forest may also reduce inputs of N from N fixation occurring in decaying logs. This may also occur following coupe clearing of large pieces of woody debris. Losses of nutrients from harvested areas also need to be considered, as do possible mechanisms for nutrient retention such as rapid occupation of harvested areas by weeds and regenerating seedlings (Wiser 2001). Finally, there is very little information about the decay of dead roots in soils and the contribution that this process may play in nutrient budgets.

Conclusions

Without increasing our knowledge in the areas identified we will not improve our certainty about input-output budgets and implications of harvesting, thereby making it harder to achieve sustainable management of our indigenous timber species. In terms of setting research priorities it is important to increase our knowledge of soil fertility effects on nutrient pools for a range of species so that we can use this knowledge to determine the quantities of nutrients removed through harvesting. This will require the development of methods to assess the actual impacts of this removal on harvested areas.

Of equal importance is the need to understand weathering rates of mineral particles in soil, rates of N fixation, denitrification, gaseous loss, and rates of turnover of soil organic matter and detrital pools (including CWD) to determine the extent to which removals may be balanced by additions from natural processes. Longer term studies are required to understand the effects of harvesting on processes such as windthrow and soil mixing although this issue along with N fixation in CWD could be investigated outside the realms of harvesting natural forests.

Acknowledgments

References

Allen, R.B.; Clinton, P.W.; Davis, M.R. 1997: Cation storage and availability along a *Nothofagus* forest development sequence in New Zealand. *Canadian Journal of Forest Research 27*: 323-330.

Allen, R.B.; Bellingham, P.J.; Wiser S.K. 1999: Immediate damage by an earthquake to a temperate montane forest. *Ecology 80*: 708-714.

Beatty, S.W.; Stone, E.L. 1986: The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research 16*: 539-548.

Benecke, U.; Evans, G. 1987: Growth and water use in *Nothofagus truncata* (hard beech) in temperate hill country, Nelson, New Zealand. Pp.131-140 in Yang, H.; Wang, Z.; Jeffers, J.N.R.; Ward, P.A. (Eds) "The Temperate Forest Ecosystem". Symposium No. 20, Institute of Terrestrial Ecology, Cumbria, UK.

Blum, J.D.; Klaue, A.; Nezat, C.A.; Driscoll, C.T.; Johnson, C.E.; Siccama, T.G.; Eager, C.; Fahey, T.J.; Likens, G.E. 2002: Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. *Nature 417*: 729-731.

Brunner, A.; Kimmins, J.P. 2003: Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga heterophylla* forests on northern Vancouver Island. *Canadian Journal of Forest Research 33*: 1670-1682.

Campbell, I.B.; Mew, G. 1986: Soils under beech forest in an experimental catchment area near Nelson, New Zealand. *Journal of the Royal Society of New Zealand 16*: 193-223.

Clinton, P.W.; Allen, R.B.; Davis, M.R. 2002: Nitrogen storage and availability during stand development in a New Zealand *Nothofagus* forest. *Canadian Journal of Forest Research 32*: 344-352.

Davis, M.R.; Allen, R.B.; Clinton, P.W. 2003: Carbon storage along a stand development sequence in a New Zealand *Nothofagus* forest. *Forest Ecology and Management 177*: 313-321.

Dyck, W.J.; Hodgkiss, P.D.; Oliver, G.R.; Mees, C.A. 1991: Harvesting sand-dune forests: impacts on second rotation productivity. Pp. 163-176 in Dyck, W.J.; Mees, C.A. (Eds) "Long-term Field Trials to Assess Environmental Impacts of Harvesting". IEA/BE T6/A6 Report No. 5. *FRI Bulletin 161*.

Evans, A.M.; Clinton, P.W.; Allen, R.B. 2003: The influence of logs on the spatial distribution of litter-dwelling invertebrates and forst floor processes in New Zealand forests. *Forest Ecology and Management 184*: 251-262.

Fahey, B.D.; Jackson, R.J. 1997: Environmental effects of forestry at Big Bush forest, South Island, New Zealand: (I) Changes in Water chemistry. *Journal of Hydrology (NZ) 36*: 43-71.

Gardner, L.R. 1990: The role of rock weathering in the phosphorus budget of terrestrial watersheds. *Biogeochemistry 11*: 97-110.

Harmon, M.E.; Sexton, J.; Caldwell, B.A; Carpenter, S.E. 1994: Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. *Canadian Journal of Forest Research 24*: 1883-1893.

Hart, P.B.S.; Clinton, P.W.; Allen, R.B.; Nordmeyer, A.H.; Evans, G. 2003: Biomass and macro-nutrients (above-and below-ground) in a New Zealand beech (*Nothofagus*) forest ecosystem: implications for carbon storage and sustainable forest management. *Forest Ecology and Management 174*: 281-294.

Hart, S.C. 1999: Nitrogen transformations in fallen tree boles and mineral soil of an old-growth forest. *Ecology*

80: 1385-1394.

Hicks, W.T.; Harmon, M.E.; Myrold, D.D. 2003: Substrate controls on nitrogen fixation and respiration in woody debris from the Pacific North West, USA. *Forest Ecology and Management 176*: 25-35.

Hoffland, E.; Kuyper, T.W.; Wallander, H.; Plassard, C.; Corbushina, A.A.; Haselwandter, K.; Holmstrom, S.; Landeweert, R.; Lundstrom, U.S.; Rosling, A.; Sen, R.; Smits, M.M.; van Hees, P.A.W.; van Breemen, N. 2004: The role of fungi in weathering. *Frontiers of Ecology and the Environment 2*: 258-264.

Homann, P.S.; VanMiegroet, H.; Cole, D.W.; Wolfe, G.V. 1992: Cation distribution, cycling, and removal from mineral soil in Douglas-fir and red alder forests. *Biogeochemistry 16*: 121-150.

James, I.L.; Norton, D.A. 2002: Helicopter-based natural forest management for New Zealand's rimu (*Dacrydium cupressinium*, Podocarpaceae) forests. *Forest Ecology and Management 155*: 337-346.

Klinka, K.; Lavkulich, L.M.; Wang, Q.; Feller, M.C. 1995: Influence of decaying wood on chemical properties of forest floors and surface mineral soils: a pilot study. *Annales des Sciences Forestieres 52*: 523-533.

Krankina, O.N.; Harmon, M.E.; Griazkin, A.V. 1999: Nutrient stores and dynamics of woody detritus in a boreal forest: modelling potential implications at the stand level. *Canadian Journal of Forest Research 29*: 20-32.

Laiho, R.; Prescott, C.E. 2004: Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Canadian Journal of Forestry Research 34*: 763-777.

McColl, R.H.S. 1978: Chemical runoff from pasture: the influence of fertilizer and riparian zones. *New Zealand Journal of Marine and Freshwater Research 12*: 371-380.

McIntosh, P.D. 1997: Nutrient changes in tussock grasslands, South Island, New Zealand. *Ambio 26*: 147-151.

Miller, E.K.; Blum, J.D.; Friedland, A.J. 1993: Determination of soil exchangeable-cation loss and weathering rates using Sr isotopes. *Nature 362*: 438-441.

Miller, R.B. 1963: Plant nutrients in hard beech. I. The immobilisation of nutrients. *New Zealand Journal of Science 6*: 365-377.

Nambiar, E.K.S. 1987: Do nutrients retranslocate from fine roots? *Canadian Journal of Forest Research 17*: 913-918.

Nambiar E.K.S. 1996: Sustained productivity of forests is a continuing challenge to soil science. *Soil Science Society of America Journal 60*: 1629-1642.

Neary, D.G.; Pearce, A.J.; O'Loughlin, C.L.; Rowe, L.K. 1978: Management impacts of nutrient fluxes in beech-podocarp-hardwood forests. *New Zealand Journal of Ecology 1*: 19-26.

Newman, E.I. 1995: Phosphorus inputs to terrestrial ecosystems. *Journal of Ecology 83*: 713-726.

Nordmeyer, A.H. 1980: Tree nutrient concentations near timberline, Craigieburn Range, New Zealand. Pp. 111-124 in Beneke, U.; Davis, M.R. (Eds) "Mountain Environments and Subalpine Tree Growth". *New Zealand Forestry Research Institute Technical Paper 70*.

Norton, D.A. 1989: Tree windthrow and forest soil turnover. *Canadian Journal of Forest Research 19*: 386-389.

Ranger, J.; Nys, C. 1994: The effect of spruce (*Picea abies* Karst.) on soil development: an analytical and experimental approach. *European Journal of Soil Science 45*: 193-204.

Schaetzl, R.J.; Follmer, L.R. 1990: Longevity of tree throw microtopography: implications for mass wasting. *Geomorphology 3*: 113-123.

Schaetzl, R.J.; Johnson, D.L.; Burns, S.F.; Small, T.W. 1989: Tree uprooting; review of terminology, process, and environmental implications. *Canadian Journal of Forest Research 19*: 1-11.

Silvester, W.B. 2000: The biology of kauri (*Agathis australis*) in New Zealand II. Nitrogen cycling in four kauri forest remnants. *New Zealand Journal of Botany 38*: 205-220.

Silvester, W.B., Orchard, T.A. 1999: The biology of kauri (*Agathis australis*) in New Zealand I. Production, biomass, carbon storage, and litter fall in four forest remnants. *New Zealand Journal of Botany 37*: 553-571.

Silvester, W.B.; Sollins, P.; Verhoeven, T.; Cline, S.P. 1982: Nitrogen fixation and acetylene reduction in decaying coniferous boles: Effects of incubation time, accretion and moisture content. *Canadian Journal of Forestry Research 12*: 646-652.

Spears, J.D.H.; Holub, M.E.; Harmon, M.E.; Lajtha, K. 2003: The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, USA. *Canadian Journal of Forest Research 33*: 2193-2201.

Stewart G. H.; Burrows, L.E. 1994. Coarse woody debris in old-growth temperate beech (Nothofagus) forests of New Zealand. Canadian Journal of Forest Research 24: 1989-1996.

Thompson, R.M.; Craw, D.; Frew, R.; Riley, R. 2001: (Further) links from rocks to plants. *Trends in Ecology and Evolution 16*: 543.

Walker, T.W.; Syers, J.K. 1976: The fate of phosphorus during pedogenesis. *Geoderma 15*: 1-9.

Watmough, S.A.; Dillon, P.J. 2003: Ecology – Mycorrhizal weathering in base-poor forests. *Nature 423*: 823-824.

Wei, W.; Kimmins, J.P. 1998: Asymbiotic nitrogen fixation in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. *Forest Ecology and Management 109*: 343-353.

Wiser, S.K. 2001. Exotic plants in Nothofagus forests managed sustainably for timber production in New Zealand. Pp. 88-95 in Stewart, G.H.; Benecke, U.; Hickey, J. (Eds) "Sustainable Management of Indigenous Forest". Proceedings of a Symposium held at Southern Connections Congress III, Lincoln University, 17-22 January 2000. Wickliffe Press Ltd, Christchurch.

Zabowski, D. 1990: Role of mineral weathering in long-term site productivity. Pp. 55-71 in Dyck, W.J.; Mees, C.A. (Eds) "Impact of Intensive Harvesting on Forest Site Productivity". IEA/BE/A6 Report No. 2. *FRI Bulletin 159*.

Zabowski, D.; Skinner, M.F.; Rygiewicz, P.T. 1994. Timber harvesting and longterm productivity: weathering processes and soil disturbance *Forest Ecology and Management 66*, 55-68.