

**REMOBILISATION OF NITROGEN BY
TWO HEATH SPECIES:
VACCINIUM MYRTILLUS (DECIDUOUS) AND
V. VITIS-IDAEA (EVERGREEN) COMPARED**

By

Gwen-Aëlle A. Grelet

A Thesis submitted to the

UNIVERSITY OF ABERDEEN, U.K.

And

UNIVERSITÉ BLAISE PASCAL, CLERMONT-F^D II, FRANCE

For the

DEGREE OF DOCTOR OF PHILOSOPHY

And

DIPLÔME DE DOCTORAT EN PHYSIOLOGIE VÉGÉTALE

The Macaulay Land Use Research Institute, Aberdeen, U.K.

U.A. INRA-UBP, P.I.A.F., Clermont-Ferrand, France

Department of Plant and Soil Science, University of Aberdeen

2001

Table of contents

Declaration	
Acknowledgements	
Summary	
Résumé.....	

CHAPTER 1: Literature review

I Implication of leaf longevity for plant growth	2
I.1 Definition of leaf longevity and leaf habit	2
I.2 Adaptive significance of leaf life spans.....	3
I.3 Scaling up from leaf longevity to leaf and plant traits	4
I.4 The advantage of being evergreen in low nitrogen environments	6
II The internal cycling of nitrogen	15
II.1 Definitions.....	15
II.2 Ecological significance	17
II.3 Assessing the contribution of internal cycling of nitrogen to plant nutrient requirement	18
II.4 Characteristics of the internal cycling of N in relation with leaf habit	29
II.5 Feedback between the internal cycling of N and plant growth, as related to leaf habit	32
III The ecophysiology of <i>Vaccinium myrtillus</i> and <i>Vaccinium vitis-idaea</i>	36
III.1 Ecology	36
III.2 Growth pattern: morphology and phenology.....	38
III.3 N nutrition and N internal cycling	44
IV Aims of this thesis.....	47

Chapter 2: Leaf habit influences nitrogen remobilisation in *Vaccinium* species

I Introduction.....	48
II Materials and Methods	50
II.1 Experimental design and plant material.....	50
II.2 Plant harvesting and partitioning	51
II.3 Samples analyses and data calculation.....	52
II.4 Data standardisation	53
II.5 Statistical analysis	54

III Results	56
III.1 Growth in relation to N supply	56
III.2 N remobilisation and N uptake	61
IV Discussion	68
IV.1 Species growth response to N supply	68
IV.2 Long-term and short-term response to N supply	70
IV.3 Sites of N storage.....	73
IV.4 The ecophysiological significance of leaf habit for plant growth in N-poor environments	74

CHAPTER 3: Interspecific variations in growth response to external versus internal N availability

I Introduction.....	75
II Materials and methods.....	76
II.1 Experimental design and plant material.....	76
II.2 Plant harvesting and sample analyses	77
II.3 Statistical analysis	78
III Results	80
III.1 Biomass content and allocation	80
III.2 Morphology of aboveground new growth	87
III.3 N content and remobilisation.....	89
IV Discussion	94
IV.1 Species growth response to N supply	94
IV.2 The effect of N supply on N internal cycling and consequences for growth	96
IV.3 Does storage rely on N uptake in the previous year or over several years? .	99

CHAPTER 4: Source-sink relationships in the context of N remobilisation

I Introduction.....	102
I.1 Movement of N within the plant: analogy with C circulation.....	102
I.2 Factors driving N remobilisation.....	103
I.3 Sink potential.....	104
I.4 Are N stores and sink potential built simultaneously?	105
I.5 Indirect effect of bud removal: compensatory growth	107
I.6 Questions addressed in this experiment	107
II Materials and methods.....	108
II.1 Experimental design and plant material.....	108
II.2 Plant harvesting and analysis of sample.....	110
II.3 Statistical analysis	111
III Results	113

III.1 Species growth response to bud removal.....	113
III.2 N remobilisation	119
IV Discussion.....	129
IV.1 Experimental constraints	129
IV.2 Species growth response to bud removal	130
IV.3 N remobilisation: a source or sink driven process?.....	133
IV.4 Is N stored solely during the previous year or over several years?	136
IV.5 Coupling between N storage and the setting of sink potential.....	139

CHAPTER 5: The effect of N supply on N storage: origin and relationship with sink potential

I Introduction.....	140
II Data calculation and analyses.....	141
II.1 N remobilisation in relation with plant initial N content	141
II.2 Estimation of the relative proportions of remobilised N derived from uptake in year 1 and in years (1-n)	143
II.3 Relationship between the sink potential and the size of N stores	145
III Results and discussion	146
III.1 The proportion of plant N content allocated to storage and subsequently remobilised.....	146
III.2 Remobilisation utilises N taken up over several growing seasons, depending of N availability and on the species	149
III.3 Relationship between N storage and sink potential	153
IV Conclusions.....	155
IV.1 Short-term response	155
IV.2 Long-term response	157
IV.3 Do leaf habits define functional types?	160
References.....	161

Résumé

Plusieurs études ont montré que les espèces sempervirentes dominent les communautés végétales habitant les sols à faible valeur nutritive, typiquement pauvres en azote. De nombreuses études ont tenté d'identifier les mécanismes physiologiques associés au maintien des feuilles persistantes et facilitant l'adaptation à une croissance en condition d'azote limitante. Ces études sont passées en revue dans la première partie de cette thèse, soulignant le rôle primordial que pourrait jouer le cycle interne de l'azote dans cette adaptation. La deuxième partie de cette thèse présente trois études expérimentales comparant certains aspects du cycle interne de l'azote de deux espèces natives de milieux pauvres en azote : *Vaccinium myrtillus* L. (feuilles caduques) et *V. vitis-idaea* L. (feuilles persistantes). L'isotope stable ^{15}N a été utilisé pour différencier l'azote provenant des réserves de celui provenant directement de l'absorption racinaire. Les résultats de ces études montrent que *V. myrtillus* était plus capable de tirer avantage d'une forte disponibilité en azote que *V. vitis-idaea*. A l'opposé, la croissance de *V. vitis-idaea* était plus forte que celle de *V. myrtillus* lorsque la disponibilité en azote était faible. Cette différence entre les deux espèces n'était pas attribuée à une différence dans l'utilisation des réserves azotées mais à une différente dynamique de remobilisation de ces réserves vers les nouvelles pousses. Chez *V. myrtillus*, la remobilisation était rapide et courte, tandis que chez *V. vitis-idaea* elle était lente et longue. D'autre part, les contraintes morphogénétiques imposées sur la réponse de croissance à l'azote étaient plus sévères chez *V. vitis-idaea* que chez *V. myrtillus*. Les résultats suggèrent aussi que la part des réserves, formées à partir d'azote absorbé pendant la saison précédente, différait entre les deux espèces et dépendait de la relative disponibilité en azote pendant la saison précédente et antérieurement. Finalement, la force de puits exercée par les nouvelles pousses sur les flux d'azote provenant de la remobilisation des réserves a été altérée par débourgeonnement partiel. Les résultats de cette manipulation suggèrent que les flux d'azote sont dépendants de la taille des réserves, plutôt que de la force de puits, pourvu qu'il y ait un puits.

Mots clés : écophysiologie, cycle interne de l'azote, espèces caduques et persistantes, *Vaccinium*, écosystèmes limités en azote.

Abstract

Survey studies have established a correlation between nutrient- poor environments, i.e. mostly nitrogen or phosphorus limited, and the distribution of evergreen plants. Consequently, it has been hypothesised that species with long-lived leaves are better adapted to infertile environments than species with short-lived leaves. Research has then tried to explain which plant traits associated with leaf longevity facilitate such adaptation. In this thesis, the current knowledge on this topic was reviewed, focusing on nitrogen as the limiting nutrient. The need to search for adaptive traits involved in the internal cycling of N and to compare species within the same growth form was highlighted. The two wild species, *Vaccinium myrtillus* L. (deciduous) and *V. vitis-idaea* L. (evergreen), are native of low N environments such as heathlands. They share the same growth form but differ in their leaf habit. Three experiments were run to compare their growth response to nitrogen supply and specific features of their internal cycling of N. ^{15}N -labelling techniques were used to distinguish N derived from remobilisation of internal pools of N (stored N), from N taken up by the roots. Results suggested that *V. vitis-idaea* outperformed *V. myrtillus* when N availability was low, while *V. myrtillus* was better adapted to take advantage of events of high N availability. Although both species utilised stored N to the same extent to support new growth, there were some differences in the dynamics of remobilisation of N from storage: remobilisation was faster in *V. myrtillus*, but lasted longer in *V. vitis-idaea*. Results also suggested that plant architecture imposed a more severe constraint on the plant potential to respond to N supply in the evergreen compared to the deciduous species. Comparisons across experiments indicated that the recycling of N pools of different age differed between the two species and depended on the relative availability of N in the last year and in the years before last. Further attention was given to the interactions between morphological constraints and N storage in each species, and their ecological significance.

References

- Abuarghub, S. M. and Read, D. J. (1988) The biology of mycorrhiza in the Ericaceae .12. Quantitative analysis of individual free amino-acids in relation to time and depth in the soil-profile. *New Phytologist* **108**(4): 433-441.
- Aerts, R. (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia* **84**(3): 391-397.
- Aerts, R. (1995) The advantages of being evergreen. *Trends in Ecology & Evolution* **10**(10): 402-407.
- Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* **84**(4): 597-608.
- Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* **50**(330): 29-37.
- Aerts, R. and Berendse, F. (1989) Above-ground nutrient turnover and net primary production of an evergreen and a deciduous species in a heathland ecosystem. *Journal of Ecology* **77**(2): 343-356.
- Aerts, R., Berendse, F., deCaluwe, H. and Schmitz, M. (1990) Competition in heathland along an experimental gradient of nutrient availability. *Oikos* **57**(3): 310-318.
- Aerts, R., Berendse, F., Klerk, N.M. and Bakker, C. (1989) Root production and root turnover in 2 dominant species of wet heathlands. *Oecologia* **81**(3): 374-378.
- Aerts, R., Boot, R.G.A. and Vandraart, P.J.M. (1991) The relation between aboveground and belowground biomass allocation patterns and competitive ability. *Oecologia* **87**(4): 551-559.
- Aerts, R. and Chapin, F. S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**: 1-67.
- Aerts, R. and van der Peijl, M.J.. (1993) A simple model to explain dominance of low-productive perennials in nutrient-poor habitats. *Oikos* **66**: 144-147.
- Bajwa, R. and Read, D. J. (1985) The biology of mycorrhiza in the Ericaceae .9. Peptides as nitrogen-sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. *New Phytologist* **101**(3): 459-467.
- Bajwa, R. and Read, D.J. (1986) Utilisation of mineral and amino-N sources by the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* and by mycorrhizal and non mycorrhizal seedlings of *Vaccinium*. *Transactions of the British Mycological Society* **87**: 269-277.
- Barker, W.G. and Collins, W.B. (1963) Growth and development of the lowbush blueberry: apical abortion. *Canadian Journal of Botany* **41**: 1319-1324.
- Beadle, N.C.W. (1954) Soil phosphate and the delimitation of plant communities in Eastern Australia. *Ecology* **35**: 370-375.
- Bell, K.L. and Bliss, L.C. (1977) Overwinter phenology of plants in a polar semi-desert. *Arctic* **30**: 118-121.

- Berendse, F. and Aerts, R. (1987) Nitrogen-use-efficiency: a biologically meaningful definition? *Functional Ecology* **1**: 293-296
- Birk, E.M. and Vitousek, P.M. (1986) Nitrogen availability and nitrogen use efficiency in loblolly- pine stands. *Ecology* **67**(1): 69-79.
- Birkhold, K.T. and Darnell, R.L. (1993) Contribution of storage and currently assimilated nitrogen to vegetative and reproductive growth of rabbiteye blueberry. *Journal of the American Society of Horticultural Science* **118**(1): 101-108.
- Brown, C.L. and Sommer, H.E. (1992) Shoot growth and histogenesis of trees possessing diverse patterns of shoot development. *American Journal of Botany* **79**(3): 335-346.
- Brzeziecki, B. and Kienast, F. (1994) Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management* **69**(1-3): 167-187.
- Camm, E. (1993) Photosynthetic response in developing year-old Douglas-Fir needles during new shoot development. *Trees* **8**: 61-66.
- Chabot, B.F. and Hicks, D.J. (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**: 229-259.
- Chapin, F.S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233-260.
- Chapin, F.S. and Kedrowski, R.A. (1983) Seasonal-changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* **64**(2): 376-391.
- Chapin, F.S., Schulze, E.D. and Mooney, H.A. (1990) The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**: 423-447.
- Chapin, F.S. and Shaver, G.R. (1985) Individualistic growth-response of tundra plant-species to environmental manipulations in the field. *Ecology* **66**(2): 564-576.
- Chapin, F.S. and Shaver, G.R. (1989) Differences in growth and nutrient use among arctic plant- growth forms. *Functional Ecology* **3**(1): 73-80.
- Chapin, F.S. and Shaver, G.R. (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* **77** (3): 822-840.
- Chen J.L., Reynolds J.F., Harley P.C. and Tenhunen J.D. (1993) Coordination theory of leaf nitrogen distribution in a canopy. *Oecologia* **93**: 63-69.
- Chester, A.L. and McGraw, J.B. (1983) Effects of nitrogen addition of the growth of *Vaccinium vitis-idaea* and *Vaccinium uliginosum*. *Oecologia* **69**: 121-125.
- Clapham, A.R., Tutin, T.G. and Warburg, E.F. (1962) *Flora of the British Isles. 2nd Edition*. The syndics of the Cambridge University press, London, Publisher.
- Coleman, G.D., Englert, J.M. Chen, T.H.H. and Fuchigami, L.H. (1993) Physiological and environmental requirements for poplar (*Populus-deltoides*) bark storage protein-degradation. *Plant Physiology* **102**(1): 53-59.

- Cornelissen, J.H.C., Diez, P.C. and Carnelli, A.L. (1998) Variation in relative growth rate among woody species. In: Lambers H, Poorter H and van Vuuren MMI, eds. *Inherent variation in plant growth, physiological mechanisms and ecological consequences*. The Netherlands, Leiden: Backhuys Publishers. pp 363-392.
- Cornelissen, J.H.C., Diez, P.C. and Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* **84**(5): 755-765.
- Cornelissen, J.H.C., Werger, M.J.A., CastroDiez, P., vanRheenen, J.W.A. and Rowland, A.P. (1997) Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia* **111**(4): 460-469.
- Coutts, M.P. and Philipson, J.J. (1976) The influence of mineral nutrition on the root development of trees. *Journal of Experimental Botany* **27**(100): 1102-1111.
- Davidson, C.G. and Remphrey, W.R. (1994) Shoot neof ormation in clones of *Fraxinus pennsylvanica* in relation to genotype, site and pruning treatments. *Trees* **8**: 205-212.
- deAldana, B.R.V. and Berendse, F. (1997) Nitrogen-use efficiency in six perennial grasses from contrasting habitats. *Functional Ecology* **11**(5): 619-626.
- Deng, X., Weinbaum, S.A., DeJong, T.M. and Muraoka, T.T. (1989) Utilization of nitrogen from storage and current-year uptake in walnut spurs during the spring flush of growth. *Physiologia Plantarum* **75**(4): 492-498.
- Dirr, M.A., Barker, A.V. and Maynard, D.N. (1973) Extraction of nitrate reductase from leaves of Ericaceae. *Phytochemistry* **12**: 1261-1264.
- Eckstein, R.L. and Karlsson, P.S. (1997) Above-ground growth and nutrient use by plants in a subarctic environment: effects of habitat, life-form and species. *Oikos* **79**(2): 311-324.
- Eckstein, R.L., Karlsson, P.S. and Weih, M. (1998) The significance of resorption of leaf resources for shoot growth in evergreen and deciduous woody plants from a subarctic environment. *Oikos* **81**(3): 567-575.
- Eckstein, R.L., Karlsson, P.S. and Weih, M. (1999) Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist* **143**(1): 177-189.
- Ferrier, R.C. and Alexander, I.J. (1991) Internal redistribution of N in sitka spruce seedlings with partly droughted root systems. *Forest Science* **37**(3): 860-870.
- Field C. (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**: 341-347.
- Flower-Ellis, J.G.K. (1971) Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.) *Research notes of the royal College of Forestry, Stockholm* **9**, 108p.
- Fogel, R. and Hunt, G. (1983) Contribution of mycorrhizae and soil fungi to nutrient cycling in a douglas-fir ecosystem. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* **13**(2): 219-232.

- Fouldrin, K. and Limami, A. (1993) The influence of nitrogen ($^{15}\text{NO}_3$) supply to chicory (*Cichorium intybus* L.) plants during forcing on the uptake and remobilization of N reserves for chicon growth. *Journal of Experimental Botany* **44**(265): 1313-1319.
- Genstat, 5 Committee (1993) Genstat 5 Release 3 Reference manual. Oxford: Clarendon Press.
- Gimingham, C.H. (1982) Ecology of heathlands. Chapman and Hall, London Publishers.
- Gray, J.T. (1983) Nutrient use by evergreen and deciduous shrubs in southern California. 1. Community nutrient cycling and nutrient use efficiency. *Journal of Ecology* **71**: 21-41.
- Gray, J.T. and Schlesinger, W.H. (1983) Nutrient use by evergreen and deciduous shrubs in southern California. 2. Experimental investigations of the relationship between growth, nitrogen uptake and nitrogen availability. *Journal of Ecology* **71**: 43-56.
- Grayston, S. J., Vaughan, D. and Jones, D. (1997) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Applied Soil Ecology* **5**(1): 29-56.
- Grime J.P., Hodgson J.G. and Hunt R. 1988. Comparative plant ecology: a functional approach to common British species. London: Unwin Hyman Ltd.
- Hawkins, B.T. and Henry, G. (1999) Nutrition and bud removal affect biomass and nutrient allocation in Douglas-Fir and western red cedar. *Tree Physiology* **19**: 197-203.
- Hawkins, B.J., Henry, G. and Kiiskila, S.B.R. (1999) Biomass and nutrient allocation in douglas fir and amabilis fir: influence of growth rate and nutrition. *Tree Physiology* **19**: 59-63.
- Heath, G.H. and Luckwill, L.C. (1938) The rooting systems of heath plants. *Journal of Ecology* **26**: 331-339
- Heilmeyer H., Freund M., Steinlein T., Schulze E.-D. and Monson R.K. (1994) The influence of nitrogen availability on carbon and nitrogen storage in the biennial *Cirsium vulgare* (Savi) Ten. I. Storage capacity in relation to resource acquisition, allocation and recycling. *Plant, Cell and Environment* **17**: 1125-1131.
- Helmisaari, H. S. (1995) Nutrient cycling in *Pinus-sylvestris* stands in eastern Finland. *Plant and Soil* **169**: 327-336.
- Hocking, P.J. and Steer, B.T. (1995) Effects of timing and supply of nitrogen on nitrogen remobilization from vegetative organs and redistribution to developing seeds of sunflower. *Plant and Soil* **170**: 359-370.
- Holmes, R.S. (1960) Effect of phosphorus and pH on iron chlorosis of the blueberry in water culture. *Soil Science* **90**: 374-379.
- Honkanen, T., Haukioja, T. and Kitunen, V. (1999) Responses of *Pinus sylvestris* branches to simulated herbivory are modified by tree sink/source dynamics and by external resources. *Functional Ecology* **13**(1): 126-140.
- Honkanen T., Haukioja T. and Suomela J. (1994) Effects of simulated defoliation and debudding on needle and shoot growth in Scots pine (*Pinus sylvestris*): implications of plant source/sink relationships for plant herbivore studies. *Functional Ecology* **8**(5): 631-639.

- Hunt, R. and Cornelissen, J.H.C. (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* **135**(3): 395-417.
- Ingestad, T. (1973) Mineral nutrient requirements of *Vaccinium vitis-idaea* L. and *V. myrtillus* L. *Physiologia Plantarum* **29**: 239-246.
- Jaeger, C.H. and Monson, R.K. (1992) Adaptive significance of nitrogen storage in *Bistorta bistortoides*, an alpine herb. *Oecologia* **92**: 578-585.
- Karlsson, P.S. (1982) Ecology of a deciduous and an evergreen dwarf shrub: *Vaccinium uliginosum* and *Vaccinium vitis-idaea* in subarctic Fennoscandia. Ph.D. Thesis, University of Lund, Sweden.
- Karlsson, P. S. (1985) Effects of water and mineral nutrient supply on a deciduous and an evergreen dwarf shrub – *Vaccinium uliginosum* L. and *V. vitis-idaea* L. *Holarctic Ecology* **8**(1): 1-8.
- Karlsson, P.S. (1987) Micro-site performance of evergreen and deciduous dwarf shrubs in a subarctic heath in relation to nitrogen status. *Holarctic Ecology* **20**: 114-119.
- Karlsson, P. S. (1992) Leaf longevity in evergreen shrubs - variation within and among european species. *Oecologia* **91**(3): 346-349.
- Karlsson, P. S. (1994) Photosynthetic capacity and photosynthetic nutrient-use efficiency of *Rhododendron lapponicum* leaves as related to leaf nutrient status, leaf age and branch reproductive status. *Functional Ecology* **8**(6): 694-700.
- Kato, T., Yamagata, M. and Tsukahara, S. (1984) Storage forms and reservoirs of nitrogen used for new shoot development in satsuma mandarin tree. *Journal of Japan Society of Horticultural Science* **52**(4): 393-398.
- Kielland, K. (1994) Amino-acid-absorption by arctic plants - implications for plant nutrition and nitrogen cycling. *Ecology* **75**(8): 2373-2383.
- Killingbeck, K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* **77**: 1716-1727.
- Kim, T.H., Ourry, A. and Boucaud, J. (1993) Partitioning of nitrogen derived from N₂ fixation and reserves in nodulated *Medicago sativa* L. during regrowth. *Journal of Experimental Botany* **44**: 555-562.
- Kramer, P.J. and Kozlowski, T.T. (1979) *Physiology of woody plants*. Academic press, New-York, Publishers.
- Kummerow, J. and Russell, M. (1980) Seasonal root growth in the arctic tussock tundra. *Oecologia* **47**: 196-199
- Lacointe, A. (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Annals of Forest Science* **57**(5-6): 521-533.
- Lähdesmäki, P., Pakonen, T., Saari, E., Laine, K., Tasanen, L. and Havas, P. (1990) Changes in total nitrogen, protein, amino-acids and NH₄⁺ in tissues of bilberry, *Vaccinium-myrtillus*, during the growing- season. *Holarctic Ecology* **13**(1): 31-38.

- Leake, J.R. and Read, D.J. (1990) Proteinase activity in mycorrhizal fungi .2. the effects of mineral and organic nitrogen-sources on induction of extracellular proteinase in *Hymenoscyphus ericae* (Read) Korf and Kernan. *New Phytologist* **116**(1): 123-128.
- Lehtilä K., Tuomi J. and Sulkinoja, M. (1994) Bud demography of the mountain birch. *Betula pubescens* ssp. *tortuosa* near tree line. *Ecology* **75**(4): 945-955.
- Lipson D.A., Bowman W.D. and Monson R.K. (1996) Luxury uptake and storage of nitrogen in the rhizomatous alpine herb, *Bistorta bistortoides*. *Ecology* **77**(4): 1277-1285.
- Livingston, N.J., Whitehead, D., Kelliher, F.M., Wang, Y.P., Grace, J.C., Walcroft, A.S., Byers, J.N., McSeveny, T.M. and Millard, P. (1998) Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young *Pinus radiata* D. Don tree. *Plant Cell and Environment* **21**(8): 795-803.
- Mäkipää, R. (1999) Response patterns of *Vaccinium myrtillus* and *V. vitis-idaea* along nutrient gradients in boreal forest. *Journal of Vegetation Science* **10**(1): 17-26.
- Mariotti, A. (1983) Atmospheric nitrogen is a reliable standard for natural N-15 abundance measurements. *Nature* **303**: 685-687.
- Marmann, P., Wendler, R., Millard, P. and Heilmeyer, H. (1997) Nitrogen storage and remobilization in ash (*Fraxinus excelsior*) under field and laboratory conditions. *Trees-Structure and Function* **11**(5): 298-305.
- Marriott, C.A. and Haystead, A. (1990) The effect of defoliation on the nitrogen economy of white clover – regrowth and the remobilisation of plant organic nitrogen. *Annals of Botany* **66**: 465-414.
- Martinoia, E., Thume, E., Vogt, E., Rentsch, D. and Dietz, K.J. (1991) Transport of arginine and aspartic acid into isolated barley mesophyll vacuoles. *Plant physiology* **97**: 644-650.
- Marschner, H. and Dell, B. (1994) Nutrient-uptake in mycorrhizal symbiosis. *Plant and Soil* **159**(1): 89-102.
- Meier, C.E., Grier, C.C. and Cole, D.W. (1985) Belowground and above-ground N and P use by *Abies-amabilis* stands. *Ecology* **66**(6): 1928-1942.
- Millard, P. (1988) The accumulation and storage of nitrogen by herbaceous plants. *Plant Cell and Environment* **11**(1): 1-8.
- Millard, P. (1994) Measurement of the remobilization of nitrogen for spring leaf growth of trees under field conditions. *Tree Physiology* **14**(7-9): 1049-1054.
- Millard, P. (1996) Ecophysiology of the internal cycling of nitrogen for tree growth. *Zeitschrift fur Pflanzenernahrung und Bodenkunde* **159**(1): 1-10.
- Millard P., Hester A., Wendler R. and Baillie G. (2001) Interspecific defoliation responses of trees depend on sites of winter N storage. *Functional Ecology* (In press)
- Millard, P. and Neilsen, G.H. (1989) The influence of nitrogen supply on the uptake and remobilization of stored N for the seasonal growth of apple- trees. *Annals of Botany* **63**(3): 301-309.

- Millard, P. and Proe, M.F. (1991) Leaf demography and the seasonal internal cycling of nitrogen in sycamore (*Acer-pseudoplatanus* L.) seedlings in relation to nitrogen supply. *New Phytologist* **117**(4): 587-596.
- Millard, P. and Proe, M.F. (1992) Storage and internal cycling of nitrogen in relation to seasonal growth of sitka spruce. *Tree Physiology* **10**(1): 33-43.
- Millard, P. and Proe, M.F. (1993) Nitrogen uptake, partitioning and internal cycling in *Picea- sitchensis* (Bong) Carr as influenced by nitrogen supply. *New Phytologist* **125**(1): 113-119.
- Millard, P. and Thomson, C.M. (1989) The effect of the autumn senescence of leaves on the internal cycling of nitrogen for the spring growth of apple-trees. *Journal of Experimental Botany* **40**(220): 1285-1289.
- Millard, P., Wendler, R., Hepburn, A. and Smith, A. (1998) Variations in the amino acid composition of xylem sap of *Betula pendula* Roth. trees due to remobilization of stored N in the spring. *Plant Cell and Environment* **21**(7): 715-722.
- Miller H.G. (1984) Nutrient cycles in birchwoods. *Proceedings of the Royal Society of Edinburgh* **85**(B): 83-96.
- Miller H.G. (1986) Carbon x nutrient interactions – the limitations to productivity. *Tree Physiology* **2**: 373-385.
- Monk C.D. (1966) An ecological significance of evergreenness. *Ecology* **47**: 504-505.
- Morecroft M.D., Marrs R.H. and Woodward F.I. (1992) Altitudinal and seasonal trends in soil nitrogen mineralisation rates in the Scottish Highlands. *Journal of Ecology* **80**, 49-56.
- Münch, E. (1927) Versche uber den Saftkneislauf. *Deut. Bot. Gesell.* **45**: 340-356.
- Muñoz, N., Guerri, J., Legaz, F. and Primo-Millo, E. (1993) Seasonal uptake of ¹⁵N-nitrate and distribution of absorbed nitrogen in peach trees. *Plant and Soil* **150**: 263-269.
- Myers, M. D. and Leake, J. R. (1996) Phosphodiesteres as mycorrhizal P sources .2. Ericoid mycorrhiza and the utilization of nuclei as a phosphorus and nitrogen source by *Vaccinium macrocarpon*. *New Phytologist* **132**(3): 445-451.
- Nambiar, E.K.S. and Fife, D.N. (1987) Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. *Annals of Botany* **60**: 147-156.
- Nambiar, E.K.S. and Fife, D.N. (1991) Nutrient retranslocation in temperate conifers. *Tree Physiology* **9**: 185-207.
- Näsholm, T. (1991) *Aspects of nitrogen metabolism in Scots pine, Norway spruce and birch as influenced by the availability of nitrogen in pedosphere and atmosphere*. Akademisk abhandling för vinnande av filosofie doktorsexamen. Editor P. Nissen. The Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Umeå, Publisher. 514p.
- Näsholm, T., Edfast, A.B., Ericsson, A. and Norden, L.G. (1994) Accumulation of amino-acids in some boreal forest plants in response to increased nitrogen availability. *New Phytologist* **126**(1): 137-143.
- Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M. and Hogberg, P. (1998) Boreal forest plants take up organic nitrogen. *Nature* **392**(6679): 914-916.

- Neilsen, D., Millard, P., Neilsen, G.H. and Hogue, E.J. (1997) Sources of N for leaf growth in a high-density apple (*Malus domestica*) orchard irrigated with ammonium nitrate solution. *Tree Physiology* **17**(11): 733-739.
- Nordin, A. and Näsholm, T. (1997) Nitrogen storage forms in nine boreal understory plant species. *Oecologia* **110**(4): 487-492.
- Oertli, J.J. (1963) Effect of form of nitrogen and pH on growth of blueberry plants. *Agronomy Journal* **55**:305-307.
- Ohlson, M., Nordin, A. and Näsholm, T. (1995) Accumulation of amino-acids in forest plants in relation to ecological amplitude and nitrogen supply. *Functional Ecology* **9**(4): 596-605.
- Ourry, A., Kim, T.H. and Boucaud, J. (1994) Nitrogen reserve mobilization during regrowth of *Medicago sativa* L. - relationships between availability and regrowth yield. *Plant Physiology* **105**(3): 831-837.
- Parsons, A.N., Welker, J.M., Wookey, P.A., Press, M.C., Callaghan, T.V. and Lee, J.A. (1994) Growth-responses of 4 sub-arctic dwarf shrubs to simulated environmental-change. *Journal of Ecology* **82**(2): 307-318.
- Penning de Vries, F.W.T. (1975) The cost of maintenance processes in plant cells. *Annals of Botany* **39**: 77-92.
- Poorter H., Remkes, C. and Lambers, H. (1990) Carbon and nitrogen economy of 24 wild-species differing in relative growth-rate. *Plant Physiology* **94**(2): 621-627.
- Poorter H. and Remkes, C. (1990) Leaf-area ratio and net assimilation rate of 24 wild-species differing in relative growth-rate. *Oecologia* **83** (4): 553-559.
- Proe, M.F., Midwood, A.J. and Craig, J. (2000) Use of stable isotopes to quantify nitrogen, potassium and magnesium dynamics in young scots pine (*Pinus sylvestris*) *New Phytologist* **146**(3): 461-469.
- Raven, J.A. (1986) The role of vacuoles. *New Phytologist* **106**: 351-422.
- Read, D.J. and Stribley, D.P. (1973) Effect of mycorrhizal infection on nitrogen and phosphorus nutrition of ericaceous plants. *Nature, New Biology* **244**: 81-82
- Reich, P.B., Walters, M.B. and Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730-13734.
- Remphrey, W.R. and Davidson, C.G. (1994) Shoot preformation in clones of *Fraxinus pennsylvanica* in relation to site and year of bud formation. *Trees* **8**: 126-131.
- Remphrey, W.R. and Steeves, T.A. (1984a) Shoot ontogeny in *Arctostaphylos uva-ursi* (baerberry): the annual cycle of apical activity. *Canadian Journal of Botany* **63**: 1925-1932.
- Remphrey, W.R. and Steeves, T.A. (1984b) Shoot ontogeny in *Arctostaphylos uva-ursi* (baerberry): origin and early development of lateral vegetative and floral buds. *Canadian Journal of Botany* **62**: 1933-1939.
- Ritchie, J.C. (1955) Biological flora of the British Isles: *Vaccinium vitis-idaea* L. *Journal of Ecology* **43**: 701-708

- Ritchie, J.C. (1956) Biological Flora of the British Isles: *Vaccinium myrtillus* L. *Journal of Ecology* **44**: 291-299
- Robinson, D. and Van Vuuren, M.M.I. (1998) Responses of wild plants to nutrient patches in relation to growth rate and life-form. In: Lambers, H., Poorter, H., van Vuuren, M.M.I., Eds., *Inherent variations in plant growth, physiological mechanisms and ecological consequences*, Leiden: Backhuys Publishers. pp 237-257.
- Rodwell, J.S. (1991) British plant communities. V.1. Woodlands and scrub. University Press, Cambridge.
- Rook, D.A. (1985) Physiological constraints on yield. Crop physiology of forest trees (Eds PMA Tigrstedt, P. Puttoness, V. Roski) pp 1-19. Helsinki University Press, Helsinki.
- Roos, W., Schulze, R. and Steighardt, J. (1997) Dynamic compartmentation of vacuolar amino acids in *Penicillium cyclopium* – cytosolic adenylates act as a control signal for efflux into the cytosol. *Journal of Biological Chemistry* **272**: 15849-15855.
- Rose, M.A. and Biernacka, B. (1999) Seasonal patterns of nutrient and dry weight accumulation in freeman maple. *HortScience* **34**(1): 91-95.
- Rosecrance, R.C., Weinbaum, S.A. and Brown, P.H. (1998) Alternate bearing affects nitrogen, phosphorus, potassium and starch storage pools in mature pistachio trees. *Annals of Botany* **82**: 463-470.
- Russell, R.S. (1936) The mechanism of leaf-fall in certain New Zealand trees. *Transactions and Proceedings of the Royal Society of New Zealand* **65**: 407-421.
- Sanchez, E.E., Righetti, T.L., Sugar, D. and Lombard, P.B. (1992) Effects of timing of nitrogen application on nitrogen partitioning between vegetative, reproductive, and structural components of mature 'Comice' pears. *Journal of Horticultural Science* **67**(1): 51-58.
- Schimel, J. P. and Chapin, F. S. (1996) Tundra plant uptake of amino acid and NH₄⁺ nitrogen in situ: plants compete well for amino acid N. *Ecology* **77**(7): 2142-2147.
- Shaver, G.R. and Chapin, F.S. (1991) Production - biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs* **61**(1): 1-31.
- Small, E. (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany* **50**: 2227-2233
- Smirnoff, N., Todd, P. and Stewart, G.R. (1984) The occurrence of nitrate reduction in the leaves of woody-plants. *Annals of Botany* **54**(3): 363-374.
- Söderström, B. and Read, D.J. (1987) Respiratory activity of intact and excised ectomycorrhizal mycelial systems growing in unsterilized soil. *Soil Biology & Biochemistry* **19**(3): 231-236.
- Souza, M.S., Puntieri, J.G., Barthelemy, D. and Brion, C. (2000) Bud content and its relation to shoot size and structure in *Nothofagus pumilio* (Pepp. et Endl.) Krasser (Nothofagaceae). *Annals of Botany* **85**(4): 547-555.
- Steinlein T., Heilmeyer H. and Schulze E.-D. (1993) Nitrogen and carbohydrate storage in biennials originating from habitats of different resource availability. *Oecologia* **93**: 374-382.

- Stribley, D.P. and Read, D.J. (1974) The biology of mycorrhiza in the Ericaceae. V. The effects of mycorrhizal infection on uptake of ¹⁵N from labelled soil by *Vaccinium macrocarpon* Ait. *New Phytologist* **73**: 1149-1155.
- Stribley, D.P. and Read, D.J. (1976) The biology of mycorrhiza in the Ericaceae. VI. The effects of mycorrhizal infection and concentration of ammonium nitrogen on growth of cranberry (*Vaccinium macrocarpon* Ait.) in sand culture. *New phytologist* **77**: 63-72.
- Stribley, D.P. and Read, D.J. (1980) The biology of mycorrhiza in the Ericaceae. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. *New phytologist* **86**: 365-371
- Tagliavini, M., Millard, P., Quartieri, M. and Marangoni, B. (1999) Timing of nitrogen uptake affects winter storage and spring remobilisation of nitrogen in nectarine (*Prunus persica* var. nectarina) trees. *Plant and Soil* **211**(2): 149-153.
- Tagliavini, M., Quartieri, M. and Millard, P. (1997) Remobilised nitrogen and root uptake of nitrate for spring leaf growth, flowers and developing fruits of pear (*Pyrus communis* L.) trees. *Plant and Soil* **195**(1): 137-142.
- Thornton, B. and Millard, P. (1993) The effects of nitrogen supply and defoliation on the seasonal internal cycling of nitrogen in *Molinia caerulea*. *Journal of Experimental Botany* **44**(260): 531-536.
- Thornton, B., Millard, P. and Duff, E.I. (1994) Effects of nitrogen supply on the source of nitrogen used for regrowth of laminae after defoliation of 4 grass species. *New Phytologist* **128**(4): 615-620.
- Thornton, B., Millard, P., Duff, E.I. and Buckland, S.T. (1993) The relative contribution of remobilization and root uptake in supplying nitrogen after defoliation for regrowth of laminae in 4 grass species. *New Phytologist* **124**(4): 689-694.
- Thornton, B., Millard, P. and Tyler, M.R. (1995) Effects of nitrogen supply on the seasonal re-mobilization of nitrogen in *Ulex-europaeus*. *New Phytologist* **130**(4): 557-563.
- Thume, E. and Dietz K.J. (1991) Reconstruction of the tonoplast amino-acid carrier into liposomes – evidence for an ATP-regulated carrier in different species. *Planta* **185**: 569-575.
- Tolvanen, A. (1995) Aboveground growth habits of 2 *Vaccinium* species in relation to habitat. *Canadian Journal of Botany* **73**(3): 465-473.
- Tolvanen, A. (1997) Recovery of the bilberry (*Vaccinium myrtillus* L.) from artificial spring and summer frost. *Plant Ecology* **130**(1): 35-39.
- Tolvanen, A. and Laine, K. (1997) Effects of reproduction and artificial herbivory on vegetative growth and resource levels in deciduous and evergreen dwarf shrubs. *Canadian Journal of Botany* **75**(4): 656-666.
- Tolvanen, A., Laine, K., Pakonen, T., Sääri, E. and Havas, P. (1992) Compensatory responses of a deciduous dwarf shrub, the bilberry (*Vaccinium myrtillus* L.) to simulated herbivory - some comparisons with the evergreen lingonberry (*Vaccinium vitis-idaea* L.) *Acta Oecologica-International Journal of Ecology* **13**(5): 607-615.

- Tolvanen, A., Laine, K., Pakonen, T., Saari, E. and Havas, P. (1993) Effect of habitat and time of clipping on the recovery of the bilberry (*Vaccinium myrtillus* L.) *Annales Botanici Fennici* **30**(1): 15-20.
- Townsend, L.R. and Blatt, C.R. (1966) Lowbush blueberry: evidence for the absence of a nitrate reducing system. *Plant and Soil* **25**: 456-460.
- Troelstra, S. R., Wagenaar, R. and Deboer, W. (1990) Nitrification in dutch heathland soils . 1. General soil characteristics and nitrification in undisturbed soil cores. *Plant and Soil* **127**(2): 179-192.
- Vitousek, P. (1982) Nutrient cycling and nutrient use efficiency. *The American Naturalist* **119**: 553-572.
- Weih, M. (2000) Delayed growth response of mountain birch seedlings to a decrease in fertilisation and temperature. *Functional Ecology* **14**: 566-572.
- Weiland, R.T. and Ta, T.C. (1992) Allocation and retranslocation of ¹⁵N by maize (*Zea Mays* L.) hybrids under field conditions of low and high N fertility. *Australian Journal of Plant Physiology* **19**: 77-88.
- Weinbaum, S.A., Klein, I., Broadbent, F.E., Micke, W.C. and Muraoka, T.T. (1984) Effects of time of nitrogen application and soil texture on the availability of isotopically labeled fertilizer nitrogen to reproductive and vegetative tissue of mature almond trees. *Journal of the American Society for Horticultural Science* **109**(3): 339-343.
- Weinbaum, S.A., Klein, I. and Muraoka, T.T. (1987) Use of nitrogen isotopes and a light-textured soil to assess annual contributions of nitrogen from soil and storage pools in mature almond trees. *Journal of the American Society for Horticultural Science* **112**(3): 526-529.
- Welch, D., Scott, D., Moss, R. and Bayfield, N.G. (1994) Ecology of blaeberry and its management in British moorlands. Institute of Terrestrial Ecology, Banchory, Publisher. 39p.
- Wendler, R., Carvalho, P. O., Pereira, J. S. and Millard, P. (1995) Role of nitrogen remobilization from old leaves for new leaf growth of *Eucalyptus globulus* seedlings. *Tree Physiology* **15**(10): 679-683.
- White, J. (1979) The plant as metapopulation. *Annual Review of Ecology and Systematics* **10**: 109-145.
- Williams, B.L. (1992) Nitrogen dynamics in humus and soil beneath Sitka spruce (*Picea sitchensis* (Bong.) Carr.) planted in pure stands and in mixture with Scots pine (*Pinus sylvestris* L.) *Plant and Soil* **144**: 77-84.
- Wilson, B.F. (1992) Compensatory growth in shoot populations of young white pine trees. *Trees* **6**: 204-209.
- Woodward, F.I. (1986). Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia* **70**: 580-586.
- Wookey, P.A., Parsons, A.N., Weller, J.M., Potter, J.A., Callaghan, T.V., Lee, J.A. and Press, M.C. (1993). Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos* **67**: 490-507.
- Zamski, E. (1996) Anatomical and Physiological characteristics of sink cells pp 283-310. In: Photoassimilates distribution in plants and crops: source-sink relationships. Eds Zamski E. and Schaffen A.A. Pbs Mandel Dekker, inc. (New York)