

Effect of Pure and Mixed Plantations of *Populus deltoides* with *Alnus subcordata* on Growth, Nutrition and Soil Properties

SEYED ABDOLLAH MOUSAVI KOUPAR^{1,*}, SEYED MOHSEN HOSSEINI¹, ALIREZA MODIRRAHMATI², MASOUD TABARI¹, AHMAD GOLCHIN³ and FARZAM HOSSEINZADEH RAD⁴

¹Forestry Department, Tarbiat Modares University, Noor, Iran
²Research Institute of Forests and Rangelands, Tehran, Iran
³Soil Science Department, Zanjan University, Zanjan, Iran.
⁴Guilan Research Center of Agriculture and Natural Resources, Rasht, Iran

*Corresponding author: E-mail: abdy_mo@yahoo.com

(Received: 11 August 2009;	Accepted: 25 October 2010)	AJC-9211

Plantation and application of fast-growing species such as *Populus deltoides* are increasingly in the north of Iran.Concerns about decline in soil fertility and long-term productivity of fast-growing plantations have promoted interest in using nitrogen-fixing trees in mixed species plantations. *Populus deltoides* and *Alnus subcordata* were planted in five proportions (100P, 70P:30A, 50P:50A, 30P:70A, 100A) in Astaneh, Iran. After 12 years, the effects of species interactions on tree growth and nutrient concentration in live and senescent leaves and soil properties were assessed. Diameter at breast height and total height of individual *Populus deltoides* trees were positively affected by the presence of *Alnus*. Nitrogen concentrations in fully expanded and senescent leaves of *Populus deltoides* were higher in mixed plantations than monoculture plantations. The results of nutrition and nutrient return and growth indicated that mixed plantations of these two species were more productive and sustainable than their monoculture plantations. Within the framework of this experiment, it appeared that production was maximized when these two species were grown together in the relative proportions of 30 % *Populus deltoides* and 70 % *Alnus subcordata*.

Key Words: Nitrogen fixing trees, Growth, Mixed plantations, Populus deltoides, Alnus subcordata.

INTRODUCTION

Poplars (Populus L. spp.) are preferred plantation species, because of their fast growth expected to meet the extensive demands of wood for poles, pulp and fuel¹⁻³. Productivity of plantations depends strongly on soil nutrient supply and it may be malleable under the influence of management practices and species⁴. Almost all the industrial plantations are monocultures, and questions are being raised about the sustainability of their growth and their effects on the site⁵. Repeated harvesting of fast growing trees such as poplar plantations on short rotations may deplete site nutrients. Nitrogen losses are likely to be very important for future growth. It is, therefore, appropriate to explore new systems of plantation management in which N may be added *via* fixation⁵. Mixed plantation systems seem to be the most appropriate for providing a broader range of options, such as production, protection, biodiversity conservation and restoration⁶⁻⁸. Mixed plantations yield more diverse forest products than monospecific stands, helping to diminish farmer's risks in unstable markets. If planned with consideration for each species' response to mixed conditions, mixed designs can be more productive than monospecific systems. In addition, a mixture of species, each with different nutrient requirements and different nutrient cycling properties, may be overall less demanding on site nutrient than monoculture stands⁹. Mixed plantations can produce more biomass per unit area because competition among individuals is reduced and the site is used integrally⁶. The roots of different species may occupy different soil strata allowing more complete utilization of soil and water resources¹⁰. More solar energy can be captured because different species have different light requirements and crowns are broadly distributed in the vertical plane⁶. However, the success of the establishment of mixed forest plantations depends on plantation design and an appropriate definition of the species to be used, taking into consideration ecological and silvicultural aspects¹¹.

Concerns about decline in soil fertility and long-term productivity of fast-growing plantations have promoted interest in using nitrogen- fixing trees in mixed species plantations¹². Nitrogen-fixing trees, mainly leguminous species, have been widely proclaimed for their soil-improving characteristics related to their production of nitrogen-rich, often rapidly decomposing leaf litter⁸. Although there have been some documented cases of increased productivity in mixed-species plantations in both temperate and tropical regions, the collective results of such studies have been inconclusive and show that accurate species/site matching and choice of complementary species strongly influence mixed-species plantation productivity¹³. Experiments in some parts of world such as North America have shown enhanced growth of *Populus* spp. when grown as an intercrop with *Alnus* L. spp.¹³⁻¹⁶. The present study was undertaken to assess the influence of *Alnus subcordata* C.A.Mey and *Populus deltoids* Marsh. plantations on soil fertility parameters, the influence of *Alnus subcordata* on *Populus deltoides* growth and nutrient concentration of fully expanded and senescent leaves in monocultures and mixed plantations.

EXPERIMENTAL

Site characteristics: The study area is located at the Safrabasteh experiment station, in Guilan province, on the northern parts of Iran (37°19'N, 49°57'E). Experimental plots were located at an altitude of 15 m above sea level and with low slope (0-3 %). Annual rainfall averages 1186 mm, with wetter months occurring between September and February and a dry season from April to August monthly rainfall usually averages < 40 mm for 4 months. Average daily temperatures range from 11.7 °C in February to 29.5 °C in August. The soils are well-drained and have a silty loam texture with a pH 7.4-8.2. Previously (*ca.* 50 years ago) this area was dominated by natural forests containing native tree species such as *Quercus castaneifolia* C.A. Meyer., *Gleditschia caspica* Desp., *Carpinus betulus* L., *etc.* The surrounding area is dominated by agricultural fields and commercial building.

Experimental design: Experimental plantations were established in 1996 using a randomized complete block design (Fig. 1) that included four replicate 40 m × 40 m plots of each of the following treatments: (i) 70 % *P. deltoides* + 30 % *A. subcordata* (67P:33A), (ii) 50 % *P. deltoides* + 50 % *A. subcordata* (50P:50A), (iii) 30 % *P. deltoides* + 70 % *A. subcordata* (30P:70A), (iv) *Populus deltoides* (100P), (v) *Alnus subcordata* (100A). Tree spacing within plantations was 4 m × 4 m and tow species were systematicly mixed within rows.

V	III	v
IV	I	III
III	II	IV
II	V	I
I	IV	II
Block 1	Block 2	Block 3

Fig. 1. Experimental plot layout. Plot treatment codes: (i) 70 % Populus deltoides + 30 % Alnus subcordata, (ii) 50 % Populus deltoides + 50 % Alnus subcordata, (iii) 30 % Populus deltoides + 70 % Alnus subcordata, (iv) 100 % Populus deltoides, (v) 100 % Alnus subcordata

Site preparation and planting of seedlings: Site preparation for all plantations and control plots consisted of disk harrowing to a depth of 10-15 cm. Containerized seedlings,

50-100 cm in height, were used for planting in April 1996. Seedlings of both species were planted simultaneously in monocultures and mixed plantations.

Tree survival and growth measurements: Diameters of trees at 1.3 m height (DBH), crown diameter, tree volume and tree heights were measured in the central 20 m \times 20 m area (subplot) of each plot, excluding the outer two tree rows, in July 2008.

Nutrition and nutrient return by the leaves: Foliage samples were collected from the stands in September 2008. Leaves were collected from the bottom one-third of the tree by clipping two small twigs located on opposite sides of the crown. Six representative trees (two near the center of subplot and one in each corner of it) of each species were sampled for fully expanded leaves. In addition, senescent leaves were collected from each species in each sub-plot. The Samples were dried at 70 °C. Nitrogen was determind using the Kjeldhal, P using spectrophotometer (by the Olsen method) and K, Ca and Mg (by ammonium acetate extraction at pH 9) was determined using atomic absorption spectrophotometer¹⁷.

Soils: Soils were sampled to a depth of 60 cm in all plantations and control plots in August using a 7.6 cm diameter core sampler (n = 3 cores/plot) taken at two 15 cm and a 30 cm interval. After air drying, soils were passed through a 2.0 mm (20 mesh) sieve to remove roots prior to chemical analyses. Soil pH was determined using an Orion Ionalyzer Model 901 pH meter in a 1:2.5, soil: water solution. Electrical conductivity (EC) was determined using an Orion Ionalyzer Model 901 EC meter in a 1:2.5, soil: water solution. Soil organic matter was determined using the Walkley-Black method. Total N was determined using the Kjeldhal method¹⁸. Available P wasdetermined with spectrophotometer by using Olsen method¹⁹. Available K, Ca and Mg (by ammonium acetate extraction at pH 9) were determined with atomic absorption spectrophotometer¹⁷.

Statistical analyses: One-way analyses of variance (ANOVA) were used to compare tree growth, soil properties and leaf nutrients data among experimental treatments. Tukey-HSD and Duncan tests were used to separate the means of dependent variables which were significantly affected by treatment.

RESULTS AND DISCUSSION

Tree survival and growth: The survival of *Populus deltoides* was generally unaffected by the presence of *Alnus subcordata* with the exception of higher *Populus deltoides* survival when the two species were grown in equal proportion (70P:30A) than 30P:70A (p < 0.05, Duncan) (Fig. 2a).

Alnus subcordata survival, in contrast, was unaffected by the presence of *Populus deltoides* in any proportion (p < 0.08, Duncan). Mixed plantations had a positive effect on the DBH of *Populus deltoides* when compared with the trees growing in monoculture. *Populus deltoides* in the 30P:70A treatment had the highest DBH. The DBH of *Alnus subcordata* was reduced when this species was grown in combination with *Populus deltoides* as compared with monocultures but the relative proportion of *Populus deltoides* did not further affect this result (p < 0.01, Tukey-HSD) (Fig. 2b).



Fig. 2. (a) Survival, b) DBH, c) Basal area, d) Height and e) Crown diameter of both tree species were separately compared. The letters on different column indicate a different comparison. Mean values with the same letter within a tree species do not differ significantly with each other

Total volume of both species was not affected by relative proportions of the two species (p < 0.08, Duncan) (Fig. 2c). Within the 30P:70A treatment Populus deltoides accounted for significantly more of the total volume than did Alnus subcordata. Height growth of Populus deltoides was affected by the presence of Alnus subcordata (Fig. 2d). In the 30P:70A and 50P:50A as well as 70P:30A treatments Populus deltoides height was higher than in the treatment 100P (p < 0.01, Tukey-HSD). The height growth of Alnus subcordata however, was unaffected by the presence of *Populus deltoides* (p < 0.08, Duncan). Similarly the crown diameter of Populus deltoides was positively affect by the presence of Alnus subcordata (p < 0.01, Tukey-HSD) but the crown diameter of Alnus subcordata was unaffected by the presence of *Populus deltoides* (p < 0.08, Duncan) (Fig. 2e). When the two monocultures were compared, Alnus subcordata had a larger crown diameter than Populus deltoides.

Soil properties: Soil pH, ranging from 5.78 to 7.12 and Carbon: nitrogen ratio, ranging from 7.56 to 18.09, did not show any significant difference between the treatments. Soil EC in 0-15 cm depth of monoculture Alnus subcordata and control treatments was different and no significant differences were found in deeper soil layers (p < 0.08, Duncan) (Table-1). Organic matter was different between 0-15 cm depth of monoculture Populus deltoides and 50P:50A treatments whereas no significant differences were found in deeper soil layers (p < 0.08, Duncan) (Table-1). Total nitrogen had some differences between the treatments in 0-15 cm and 15-30 cm soil layers. The differences in 15-30 cm depth were stronger than 0-15 cm depth (p < 0.05, Duncan). It seems that the treatments that had more proportion of Alnus subcordata had lower C:N ratio than others (Table-1). Available P in 0-15 cm depth of monoculture Alnus subcordata was different (p < 0.08, Duncan) with monoculture Populus deltoides, 70P:30A and 30P:70A treatments whereas no significant differences were found in deeper soil layers (Table-1). Available K, ranging from 22.5 to 61.25 mg kg⁻¹ and available Mg, ranging from 10.00 to 16.25 mg kg⁻¹, did not show any significant difference between the treatments.

Nutrition and nutrient return by the leaves: The presence of Alnus subcordata as N-fixing tree had strong influence on nitrogen cycling of Populus deltoides. Populus deltoides leaves (fully expanded and senescent) had significantly higher N concentration when grown in mixtures than in monocultures (p < 0.05, Duncan). Nitrogen return by senescent leaves of Alnus subcordata in monoculture plantations was significantly lower than the ones that grown in mixed plantations (p < .05, Duncan) (Table-2). Phosphorus concentrations in fully expanded and senescent leaves of *Populus deltoides* and *Alnus* subcordata did not show any significant differences (p < 0.08, Duncan). Potassium concentrations in fully expanded (ranging from 1.07 to 1.67 %) and senescent (1.51 to 1.91 %) leaves of Populus deltoides and fully expanded (0.66 to 1.07 %) and senescent (1.27 to 1.34 %) leaves of Alnus subcordata did not show any significant differences among treatments (p < 0.08, Duncan). Magnesium concentrations followed similar trends among treatments: branging from 1.46 to 2.67 % and 1.03 to 1.24 % orderly in fully expanded leaves of Populus deltoides

SOIL PROPERTIES IN PLANTATIONS IN DIFFERENT SOIL LAYERSA WITH THEIR STANDARD DEVIATIONS (BELOW)							
Soil properties	Depth	100P	70P:30A	50P:50A	30P:70A	100A	ANOVA ^b
EC (ds/cm)	0-15	0.08ab (0.05)	0.11ab (0.05)	0.08ab (0.02)	0.12ab (0.05)	0.25a (0.04)	*
Total N (%)	0-15	0.29ab (0.03)	0.24b (0.01)	0.25ab (0.02)	0.26ab (0.09)	0.32ab (0.04)	**
	15-30	0.14abc (0.04)	0.10bc (0.02)	0.11c (0.01)	0.16ab (0.04)	0.17a (0.05)	**
	30-60	0.08a (0.03)	0.06a (0.01)	0.06a (0.02)	0.07a (0.02)	0.08a (0.02)	ns
Organic matter (%)	0-15	4.77a (0.05)	4.27ab (0.48)	4.13b (0.38)	4.17ab (1.30)	4.42ab (0.57)	*
P available (mg/kg)	0-15	22.83b (4.42)	20.89b (3.31)	20.27ab (4.31)	16.38b (7.96)	24.26a (10.22)	*
Ca available (mg/kg)	0-15	18.77b (7.50)	13.69b (8.54)	20.12ab (7.07)	17.48ab (8.66)	23.78ab (10.31)	*
a) Based on three composited 7.6 cm diameter core samples per plot: b) ANOVA results: $n_s = treatment effect not significant *n < 0.08 **n <$							

0.05, Duncan; Mean values with the same letter within the soil layer do not differ significantly with each other.

TABLE-2 NITROGEN CONCENTRATIONS IN FULLY EXPANDED AND SENESCENT LEAVES WITH THEIR STANDARD ERROR IN THE PARENTHESIS

Tractmont	Populus	deltoids	Alnus subcordata		
N (%)	Fully expanded	Senescent	Fully expanded	Senescent	
100P	1.51b	1.01b			
	(0.04)	(0.07)			
70P:30A	1.88a	1.23a	2.75a	2.63a	
	(0.10)	(0.08)	(0.12)	(0.15)	
50P:50A	1.94a	1.32a	2.76a	2.57a	
	(0.15)	(0.01)	(0.1)	(0.26)	
30P:70A	1.86a	1.24a	2.76a	2.54a	
	(0.10)	(0.13)	(0.05)	(0.15)	
100A			2.63a	2.19b	
			(0.03)	(0.13)	
ANOVA	**	**	ns	ns	
ANOVA and the second offer the state of the second state of the se					

ANOVA results: ns = treatment effect not significant; **p < 0.05Duncan; Mean values with the same letter within each column do not differ significantly with each other.

and *Alnus subcordata* and 1.48 to 2.10 % and 0.96 to 1.27 % orderly in senescent leaves of *Populus deltoides* and *Alnus subcordata* (p < 0.08, Duncan). Calcium concentrations of fully expanded leaves of *Populus deltoides* (2.67 to 3.80 %) in 70P:30A treatment was different (p < 0.05, Duncan) with those of 50P:50A treatment and did not show any significant differences from *Alnus subcordata* (0.96 to 1.36 %). Calcium concentration in senescent leaves of *Alnus subcordata* (0.73 to 1.32 %) in monoculture treatments was significantly (p < 0.08, Duncan) lower than those in mixtures whereas it did not show any significant differences from *Populus deltoides* (1.48 to 2.10 %).

Because the survival of both species (*Populus* and *Alnus*) did not show in most cases any differences between monocultures and mixed plantations. It can be concluded that there was little competition between the two species, as a result of their planting spacing. Parrotta⁸ found more survival in monoculture plantations of *Eucalyptus robusta* than mixtures with *Casuarina* and *Leucacna*. The differences between present results and those obtained by Parrotta⁸ were probably due to differences in planting space. The other reason might be the difference in growth rate and crown diameter of his target and associated species in comparison with present species. Present results were, however, similar to those obtained by Khanna⁵ about *Eucalyptus glabulus* and *Acacia mearnsii* in monocultures and mixed plantations. Higher *Populus deltoides* diameter growth was observed in treatments with less proportion of Populus deltoides. This could be due to a decrease in light competition, as the most important competition factor²⁰. Results of present work correspond with that of Khanna's work⁵ on monocultures and mixed plantations of Eucalyptus and Acacia. It was also found⁵ that N-fixation by Acacia in mixed plantations resulted in increased diameter growth of *Populus deltoides*. Rapid diameter growth was also found⁹ to be due to domination of the target species. No influence of nitrogen fixing trees on diameter growth on non nitrogen fixing tree was observed by Parrotta⁸ but Binkley²¹ found contrary results with Alnus rubra having a positive effect on the diameter growth of Pesudotsuga menziesii in poor sites. Basal area of both Populus deltoides and Alnus subcordata did not show any significant differences in monocultures compared to mixed plantations in present study. In contrast, Parrotta⁸, Khanna⁵ and Montagnini⁹ found bigger basal area for target species in mixed plantations compared to monocultures. Increased light competition in mixed plantations containing a grater proportion of Populus deltoides may explain the greater height growth of this species in these plots. Alnus subcordata did not show any differences in height growth between the monocultures and mixtures. Present results are similar to those obtained by Parrotta⁸ and Khanna⁵, in monocultures and mixed plantations of Eucalyptus and Acacia and Hansen and Dawson¹⁵ in monocultures and mixed plantations of poplar species and Alnus glotinosa. The crown diameter of Populus deltoides was significantly smaller in monoculture plantations in comparison with that in the 50P:50A and 30P:70A treatments. It might be the result of decreasing light competition in mixed plantations with less proportion of Populus deltoides. Water and light competition in mixed plantations result in decreasing crown diameter²². These results have strong correlation with other results such as increasing diameter in the treatment with high Alnus subcordata proportions and increasing height in treatment with low Alnus subcordata proportions. No statistically significant differences were observed in soil pH between the treatments, whereas significant reductions in soil pH have been found in half of the studies about the effect of nitrogen fixing trees (NFT) on soil²². Montagnini⁹ and Gia rdina et al.²³ reached the same result as we, whereas Rhoades and Binkley¹² and Parrotta⁸ found lower soil pH in mixed plantations. Higher planting density and low age of our plantations might be the main reasons for no significant difference in soil pH. No significant differences were observed in soil organic matter content in 15-30 cm and 30-60 cm soil layers between the treatments. The main reason for the reduction of soil organic matter in 0-15 cm depth

in the 50P:50A treatment compared to that in the monoculture of Populus deltoides might be the result of increasing biological activities in the soil. Parrotta⁸ came to the same conclusion. In contrast with our results Garcia-Montiel and Binkley²⁴ found that organic matter content in 0-20 cm depth of soil under NFT Albizia was higher than in soil under Eucalyptus. It is obvious that Alnus subcordata increased soil nitrogen in 15-30 cm depth in comparsion with 70P:30A and 50P: 50A treatments. In 0-15 cm depth, soil nitrogen was highest in the control plot, which we can relate to grasses. The decrease in soil nitrogen of mixed plantations with high proportions of Populus deltoides might be the result of invading *Populus deltoides* roots to nodules of *Alnus subcordata*²⁰. Binkley⁴ and Garcia-Montiel and Binkley²⁴ found that Albizia increased soil nitrogen more than *Eucalyptus*. Parrotta⁸ and to some extent Montagnini⁹ did not observe any significant differences in soil nitrogen between monocultures and mixed plantations. Whereas Hansen and Dawson¹⁵ observed that mixed plantations of Populus deltoides and Alnus glutinosa resulted in increasing soil nitrogen in comparison with their monoculture plantations¹³. No significant differences were observed in the C:N ratio. The main reason might be the low percentage in the mixtures. Parrotta⁸ reached the same result with us in monocultures and mixed plantations of Eucalyptus and two NFTs. Few significant differences were observed between the treatments in concentrations of available Mg, K, Ca and P in soil. We can relate these differences to previous soils condition such as what Parrotta⁸ did. Montagnini⁹ came to the same results in monocultures and mixed plantations as we did. Nitrogen concentrations in fully expanded and senescent leaves of Populus deltoides were higher in the mixed plantations than those in the monocultures of Populus deltoides. This is a good reason for the influence of mixed plantations with Alnus subcordata as an N-fixing tree on nutrition and nutrient return of our target species. The other result is less N of Alnus subcordata senescent leaves in monoculture plantations than mixed ones that shows more nitrogen return in mixed plantations. Parrotta⁸ reached to the same results and found that litterfall (leaves) of NFT and target species in mixed plantations had more N than in monocultures. In contrast to present studies Khanna⁵ did not observe any significant differences in fully expanded and senescent leaves of Acacia between monocultures and mixed plantations. The higher concentration of calcium in senescent leaves of Alnus subcordata in mixed plantations

than monocultures showed that more calcium can return to the soil in mixed plantations. Finally, it is concluded that mixed plantations of these two species are more productive and sustainable than monocultures. The introduction of one mixture as the best one is rather difficult but 30P:70A could be the most productive and sustainable.

REFERENCES

- Sh. Kiadaliri, Study of *Populus* Plantations on Different Soils in Western Parts of Mazandaran, M.Sc. Thesis of Tarbiat Modarres University, p. 94 (2003).
- R. Ghasemi, Study of Phenology of Different *Populus* in Karaj and Safrabasteh Gilan, M.Sc. Thesis of Tarbiat Modarres University, p. 171 (2000).
- Z.F. Ziabari, The Importance of *Populus* in Forestry, Proceedings of Forest Restoration and Forestry, Research Institute of Forests and Range Lands Publication, Iran, p. 11 (1993).
- 4. D. Binkley, Forest Ecol. Manag., 91, 229 (1997).
- 5. P.K. Khanna, Forest Ecol. Manag., 94, 105 (1997).
- M.R. Guariguata, R. Rheingans and F. Montagnini, *Restor. Ecol.*, 3, 252 (1995).
- R.J. Keenan, D. Lamb and G. Sexton, *Commonwealth Forestry Rev.*, 74, 315 (1995).
- 8. J.A. Parrotta, Forest Ecol. Manag., 124, 45 (1999).
- 9. F. Montagnini, Forest Ecol. Manag., 134, 257 (2000).
- D. Lamb and P. Lawrence, in eds.: H. Lieth and M. Lohmann, Mixed Species Plantations Using High Value Rainforest Trees in Australia, Restoration of Tropical Forest Ecosystems, Kluwer Academic Publishers, Holanda, pp. 101-108 (1993).
- 11. T.J. Wormald, Mixed and Pure Forest Plantations in the Tropics and Subtropics, FAO No. 103, p. 166 (1992).
- 12. C. Rhoades and D. Binkley, Forest Ecol. Manag., 80, 47 (1996).
- FAO, Mixed and Pure Forest Plantation in the Tropics and Subtropics, FAO Forestry Paper 103, p. 152 (1992).
- 14. B. Coté and C.C. Camiré, Can. J. Forest Res., 17, 516 (1987).
- 15. E.A. Hansen and J.O. Dawson, Forest Sci., 28, 49 (1982).
- 16. M.A. Radwan and D.P. DeBell, Plant Soil, 106, 171 (1988).
- 17. C.A. Bower, R.F. Reitemeier and M. Fireman, Soil Sci., 73, 251 (1952).
- 18. J.M. Bremmer, J. Agric. Sci., 55, 11 (1960).
- C.D. Homer and P.F. Pratt, Methods of Analysis for Soils, Plants and Waters, University of California, Agricultural Sciences Publications, Berkeley, USA, p. 309 (1961).
- D. Binkley, in eds.: M.G.R. Cannel, D.C. Malcom and P.A. Robertson, Mixture of Nitrogen-Fixing and Non-Nitrogen-Fixing Tree Species, The Ecology of Mixed Species Stands of Trees, Blackwell Scientific Publications, Oxford, pp. 99-123 (1992).
- 21. D. Binkley, Forest Ecol. Manag., 5, 215 (1983).
- R. Fisher and D. Binkley, Ecology and Management of Forest Soil, John Wiley & Sons, Inc., edn. 3, p. 489 (1999).
- 23. C.P. Giardina, S. Huffman, D. Binkley and B.A. Caldwell, *Can. J. Forest Res.*, **25**, 1652 (1995).
- 24. D.C. Garsia-Montiel and D. Binkley, Oecologia, 113, 547 (1998).