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Pine Growth and Nutrient Status as Related to Pine/Alder Ratio in Mixed Stands

Miguel A. Lopez-Lopez, R.M. Reich, C. Aguirre-Bravo and A. Velázquez-Martinez
Km 36.5 Carretera, México-Texcoco, 56230 Montecillo, Texcoco Estado de México

Abstract: The relationships between varying pine/alder ratios and pine growth and nutrient status were experimentally examined in three Regeneration Areas (RA) in the Mexican State of Hidalgo. A randomized complete block design with five pine/alder ratios as pseudo-treatments was established at each of the RAs. Pine density, which varied among plots, was blocked to control its effects on pine growth. The results indicate that the effects of alder on pine growth largely depend on pine density, which affects light availability to alders. Growth variables showed saturation curves with respect to increasing alder densities in the 1987 and 1994 RAs. Pine growth was maximum for pine/alder ratios of 2666/20 and 711/267 in the 1987 and 1994 RAs, respectively. For the 1989 RA, maximum pine growth was not reached since alder densities were low. When alders were in the understory, light limitations probably impaired N-fixation, bringing about competition effects for N between alder clumps and pine trees. Management techniques that promote sunlight reduction to alders may switch alder function from beneficial to detrimental. When alder was fully exposed to sunlight, it gave up all N required by pines. Availability of P and K to pine trees was increased by alders exposed to full sunlight. When sunlight limited alder performance, P and K concentrated within pine needles due to reductions in pine growth resulting from N deficiency.

Key words: *Pinus montezumae*, *Alnus arguta*, vector analysis, growth response, nutrient status

INTRODUCTION

Alders (*Alnus* sp.) are medium-sized (8-10 m high) trees that grow naturally in most temperate forests. Trees of this species live in river beds in non-disturbed areas; however, they usually invade forest sites when wildfires, logging, or any other disturbances take place (Puettmann and Hibbs, 1996). The capacity of these trees to invade disturbed sites may be due to their ability to thrive in N-poor soils (Puettmann and Hibbs, 1996) and to their high sunlight requirements as well. Both conditions are usually met after disturbances occur, so that alders get higher competitive advantages to grow in such sites compared with other plant species. It is the alder's invasive aggressiveness that makes these species to be considered as a weed in most forest areas in Central Mexico. This is why significant financial resources are periodically devoted to eliminate alders from most forests in the region of Tulancingo, Hidalgo, Mexico (Aldrete *et al.*, 1992), even though this species may add N to the ecosystem (Binkley and Menyailo, 2005; Yowhan *et al.*, 2007) and improve site productivity.

How effective alder management is to improve stand productivity remains however poorly understood in Mexico, since too few studies regarding management of pine-alder stands have been developed in this country.

Furthermore, the studies available from other countries (Binkley, 1983; Yowhan *et al.*, 2007) show contrasting results suggesting the existence of unknown details about the interactions occurring in such systems.

The effects of alders on conifer growth and site fertility, for example, were contrasting depending on initial site fertility in southwestern Canada and the State of Washington, United State. In an infertile site (Binkley, 1983), the presence of alder increased nitrogen and carbon content in the soil, Douglas-fir foliar nitrogen and above ground net primary productivity (alder plus fir). In a fertile site, however, alder's effects on soil nitrogen and carbon content were much more subtle, foliar nitrogen of Douglas-fir was unaffected, and total (alder plus fir) aboveground net primary productivity was decreased (Binkley, 1983). Similar results were obtained by Binkley *et al.* (1992b) while studying adjacent conifer and alder-conifer stands in Southeastern Washington.

Alder cover is another factor influencing alder's effect on associated-conifer growth rates. Brockley and Sanborn (2003) found no negative effects of alder on ponderosa pine growth when alder cover was low or moderate. However, when alder cover exceeded 45%, pine diameter and height increments were reduced by 10 and 12%, respectively, relative to no-alder treatments.

The horizontal and vertical distribution of alder in the stand also is a factor determining the effect of alder on stand fertility. Dawson *et al.* (1983) determined that single rows of alder bounded by adjacent rows of hybrid poplar had the greatest increase and concentration of soil nitrogen, contrasting with plantation schemes where an alder row was bounded by an alder row and a poplar one. Lavery *et al.* (2004) found that the optimal arrangement for alder-conifer mixtures would be alder patches or strips at least 10 m wide and about 20 m apart oriented north to south. Regarding the vertical distribution of species within the forest canopy, Heilman and Stettler (1985) found that nitrogen fixation by red alder in mixtures with black cottonwood decreased when alders were outgrown by the *Populus* probably because shading impaired the nitrogen fixation process by alder. Similar results were found by Lopez-Lopez *et al.* (2006) for one out of two areas of regeneration, while studying the interactions between *Alnus arguta* and *Pinus montezumae*.

Because of the growth-induced dilution or concentration of foliar nutrients, the effects of the interactions occurring within conifer-alder stands on the status of foliar nutrients other than nitrogen within the conifer, might be even more complex than those exerted on growth. Phosphorus availability has been found to increase with the presence of nitrogen fixers in some instances (Binkley *et al.*, 1992b; Giardina *et al.*, 1995; Shainsky and Radosevich, 1992; Shainsky and Rose,

1995; Zou *et al.*, 1995), while in other situations, the nitrogen fixers seem to reduce the availability of this nutrient for the associated species (Binkley, 1983; Kaye *et al.*, 2000).

In the case of the conifer forests in Central Mexico, several species of the genus *Alnus* are very common and research on the management of conifer-alder stands is incipient. Accordingly, the objectives of this study are: 1) to determine how growth of *Pinus montezumae* Lamb. is affected by varying pine/alder ratios in three different Regeneration Areas (RAs), 2) to determine the pine/alder ratio for each of the regeneration areas at which maximum pine growth occurs and 3) to study the effects of varying pine/alder ratios on the N, P and K status of Montezuma pine.

MATERIALS AND METHODS

Study site: The study was carried out at Southeastern Hidalgo, Mexico in the Regeneration Areas (RAs) 1987, 1989 and 1994, between the years 2000 and 2004. The first two RAs belong to the Ejido Los Romeros, Santiago Tulantepec, Hidalgo, Mexico, while the other is part of a private forest located close to the Ejido (Fig. 1). Topography of the study sites is fairly flat (mean slope ~ 10%), except in the 1989 RA, where slopes may reach values as high as 50%. Mean annual temperature is around 15°C and annual precipitation varies from 600 to 1000 mm (Aldrete *et al.*, 1992). The dominant tree species

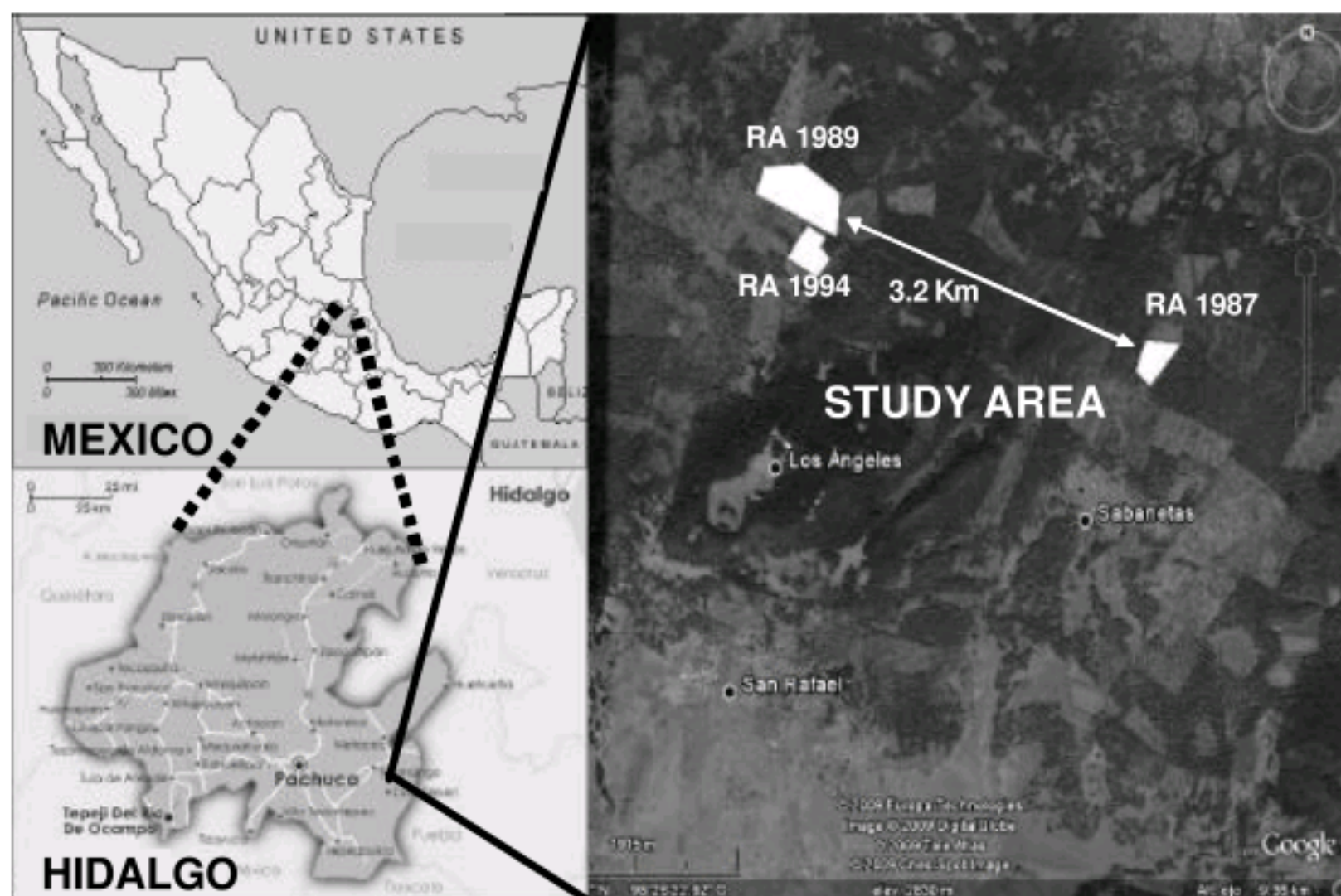


Fig. 1: Location of the study area. RA: Regeneration area

Table 1: Characteristics of the areas of regeneration studied

Area of regeneration	Tree age (year)	Slope (%)	Pine density (Stems plot ⁻¹)	Alder density (Clumps plot ⁻¹)
1987	17	10	57	17
1989	15	30	31	13
1994	10	10	16*	31

*3x3 m spacing pine plantation after clear cutting in 1994

is *Pinus montezumae*, but several other tree species are present in the sites at very low densities. These include *Pinus patula* Schiede and Deppe, *P. leiophylla* Schl. et Cham., *P. teocote* Schl. et Cham., *Quercus rugosa* Née, *Quercus laurina* Humb. et Bonpl. and *Alnus arguta* (Schelechtendal) Spach.. *A. arguta* (alder) is by far the most widely distributed species following *P. montezumae* regionwide.

During the stands lifespan, management strategies have been directed mainly to *P. montezumae* and *A. arguta* in the naturally regenerated 1987 and 1989 RAs. Management activities in these RAs have basically included pine density control and pruning and bi-annual alder elimination. Such activities have not been done in the 1994 RA, where pine plantation and alder elimination were carried out for the only time following clearcut.

Experimental approach: Three parallel pseudo-experiments in each of the RAs were carried out. Each pseudo-experiment was established as a randomized complete block design. The experimental unit was a 15x15 m plot. Five pine/alder ratios or pseudo-treatments were established. Blocks corresponded to pine density levels. Pseudo-treatments were replicated 6, 5 and 4 times in the RAs 1987, 1989 and 1994, respectively.

Plot selection: For selecting the experimental plots, pine-alder clusters were identified within each RA. From these clusters, we selected 60, 60 and 45 plots 15x15 m in size in the RAs 1987, 1989 and 1994, respectively. All plots selected were evaluated in terms of pine and alder densities (number of individuals of each species), which were variable since both pines and alders were regenerated naturally, except in the area of regeneration 1994, where pine trees were planted after clear cutting. Plots with extreme numbers of pine trees were discarded to reduce pine density variability among plots. After this process, only 30, 30 and 25 plots were left in the RAs 1987, 1989 and 1994, respectively. Thereafter, the proportions between pine and alder stems were estimated for each plot. By using pre-built mathematical models, the Leaf Area (LA) per plot was estimated for both species and so was the leaf-area-based pine/alder ratio for each plot. The sets of plots for a RA were arranged in ascending order according to the Pine/Alder Ratio (PAR) and the pine/alder levels (A0-A4, i.e., the pseudo-treatments) for each RA were defined.

The models used to estimate leaf area for the involved species were:

$$PLA = 0.0073963NDW - 0.00014055, R^2 = 0.9685, RMSE = 3.1562, N = 10$$

Where:

PLA = Pine leaf area (m²)

NDW = Needle dry weight (g)

- $NDW = 0.0088DBH^{2.0809}, R^2 = 0.8172, RMSE = 0.2775, N = 9$, for the RAs 1987 and 1989
- $NDW = 0.1882RCD^{3.9449}, R^2 = 0.9275, RMSE = 0.2130, N = 8$, for the RA 1994

Where:

DBH = Diameter at breast height (cm)

RCD = Root Collar Diameter (cm)

- $ALA = 0.19113SD^{1.5392536}, R^2 = 0.9168, RMSE = 0.2748, N = 33$

Where:

ALA = Alder Leaf Area (m²)

SD = Sprout collar diameter (cm)

Response variables: The variables evaluated were: pine height, diameter at breast height, tree age, stem biomass, pine height and diameter increments, biomass of a fixed number of needles, foliar nitrogen, phosphorus and potassium.

Pine height and Diameter at Breast Height (DBH) were measured by using a telescopic ruler and diameter tape, respectively. Pine age was estimated from the number of whorls. Stem biomass was estimated by using the following pre-built model:

$$SB = 1.7759 e^{0.1497DBH}, R^2 = 0.8696, RMSE = 0.1569, N = 9$$

Where:

SB = Stem biomass (kg)

DBH = Diameter at Breast Height (cm)

Height and DBH increments were estimated from tree height, DBH and tree age. Since *P. montezumae* is a pre-formed-growth species (Lopez-Lopez *et al.*, 2006), annual height growth corresponded to inter-whorl lengths, which were directly measured from dominant pine trees within each plot. Pine needle nitrogen, phosphorus and potassium were determined for the RAs 1987 and 1994. Chemical analyses were carried out in the Soil Fertility Laboratory at Colegio de Postgraduados, Mexico. Nitrogen was determined by the micro-kjeldahl procedure.

P was determined colorimetrically by the vanadomolybdophosphoric yellow color method as described by Kalra and Maynard (1991) and K was determined by flame spectrophotometry. Biomass of 150 or 300 needles was also determined for the RAs 1987 and 1994. Statistical analyses of growth variables included analysis of variance and orthogonal contrasts. Analysis of variance was used to identify pseudo-treatment effects. Orthogonal contrasts were used to compare groups of pseudo-treatments. Statistical analyses were carried out using the Statistical Analysis System version 8 (Universidad Complutense de Madrid, 2004). The low-alder plus high-alder pseudo-treatments were contrasted against the intermediate-alder ones (Fig. 2). Pine nutrient status was evaluated by using the vector analysis technique (Timmer and Stone, 1978).

RESULTS

Growth responses to varying pine/alder ratios: In the 1987 (Fig. 2a-e) and 1994 (Fig. 2k-o) regeneration areas, most variables show increasing values as the proportion of alders in the plots goes up [decreasing pine/alder ratios (PARs)]. In the 1989 RA (Fig. 2f-j), even though a higher variation was found as compared with the other regeneration areas, it appears that there exists a trend showing increased values for all growth variables with increasing the amount of alders.

On the other hand, the trends of the curves in the 1987 and 1994 RAs show a quadratic shape, which seems to be better defined in the 1987 RA. That is, pine growth increases with increasing the amount of alders within the plot and after reaching a peak, a reduction in growth

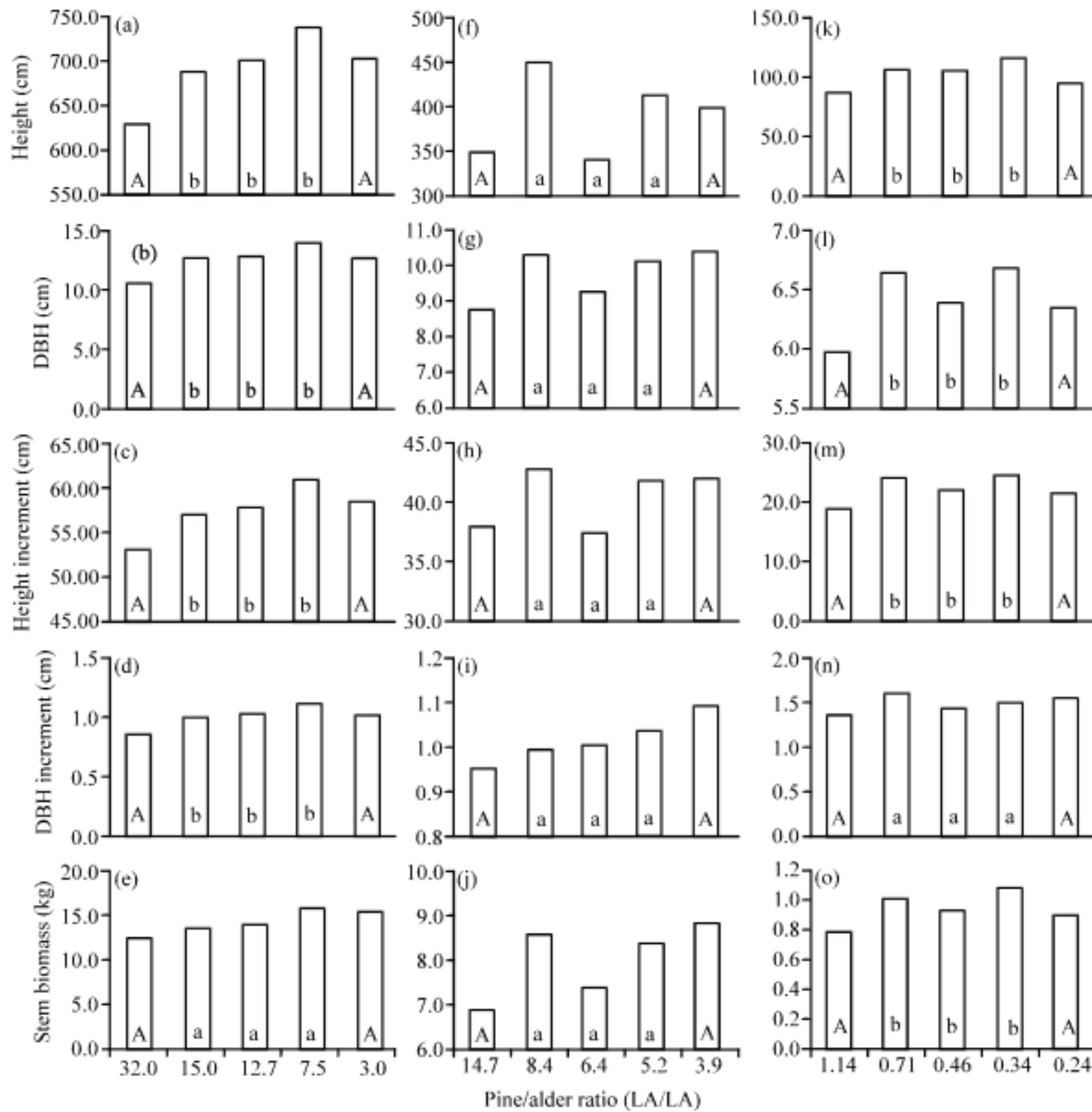


Fig. 2: Pine growth patterns with varying pine/alder ratios (LA/LA), from the 1987 AR (left column), 1989 AR (central column) and 1994 AR (right column). A bar represents the average of six (1987 AR), five (1989 RA) and four plots (1994 RA). Different-case letters were statistically confronted for a variable within a RA. Different letters between the case-groups compared indicate groups are statistically different ($\alpha = 0.05$)

Table 2: Pine/alder ratios (PAR, LA/LA) effects on growth variables and optimum PARs in the 1987 and 1994 RAs

Area	Model/parameter	R ²	RMSE	Optimum PAR
1987	H = -0.192 PAR ² + 4.3285 PAR + 687.39	0.97	8.6732	11.27
1994	H = -71.373 PAR ² + 86.005 PAR + 79.442	0.567	10.0083	0.60
1987	DBH = -0.0054 PAR ² + 0.1177 PAR + 12.103	0.8895	0.5076	10.90
1994	RCD = -1.9799 PAR ² + 2.2579 PAR + 5.968	0.7606	0.2028	0.57
1987	HI = -0.0138 PAR ² + 0.2994 PAR + 57.616	0.9839	0.4746	10.85
1994	HI = -15.778 PAR ² + 18.351 PAR + 18.457	0.7055	1.7775	0.58
1987	DBHI = -0.0004 PAR ² + 0.0093 PAR + 1.0108	0.8287	0.0524	11.63
1994	RCDI = -0.46449 PAR ² + 0.4816 PAR + 1.3831	0.4663	0.1113	0.52
1987				
1994	*SB = -0.6466 PAR ² + 0.7236 PAR + 0.8082	0.5883	0.103	0.56
1987	Average			11.16
1994	Average			0.57

H: Pine height (cm), DBH: Diameter at breast height (cm), RCD: Root Collar Diameter (cm), HI: Height increment (cm), DBHI: Diameter at breast height increment (cm), RCDI: Root Collar Diameter Increment (cm), SB: Stem biomass (Kg), *No quadratic curve

Table 3: Growth variable mean values for the PAR groups contrasted in all regeneration areas

Variable	PAR group	RA		
		1987	1989	1994
Height (cm)	A0+A4	666.300	373.338	87.355
	A1+A2+A3	707.800	398.556	105.152
Diameter (cm)	A0+A4	11.300	9.579	6.152
	A1+A2+A3	12.700	9.875	6.679
Height Increment (cm year ⁻¹)	A0+A4	55.850	39.924	20.167
	A1+A2+A3	58.970	40.675	23.508
Diameter increment (cm year ⁻¹)	A0+A4	0.942	1.027	1.422
	A1+A2+A3	1.061	1.014	1.483
Stem biomass (kg)	A0+A4	14.104	7.935	0.845
	A1+A2+A3	14.741	8.195	1.01

A0-A4: Pine/alder ratio levels 0 through 4

takes place when the proportion of alders is too high for a given condition. The positive effect of low-to-intermediate alder densities on conifer growth are in agreement with results reported by Binkley (1983) Binkley *et al.* (1992) and Dawson *et al.* (1983) and are supported on the N that the N-fixer introduces into the N deficient system. The values for the PAR that maximize pine growth vary among the RAs. In the 1987 RA, such PAR (LA/LA) is around 11.16 (Table 2) for all growth variables (considering 60 pine trees per plot with 20 cm DBH, this ratio equals 2,666 pine stems ha⁻¹/20 alder trees ha⁻¹), while in the 1994 RA it is around 0.57 (considering an average of 16 pine trees per plot with a root collar diameter of 9 cm, this ratio equals 711 pine trees ha⁻¹ / 267 alders ha⁻¹).

Orthogonal contrast analysis indicated that the PAR groups compared (lowest + highest alder versus the sum of the intermediate alder levels) were significantly different for all variables (except stem biomass) in the 1987 RA (Fig. 2a-e), being the values from intermediate PARs always higher than those from extreme PARs (p=0.0431, p = 0.0138, p = 0.0410, p = 0.0242, p = 0.7095 for height, diameter, height increment, diameter increment and stem biomass, respectively; Table 3). In the 1994 RA, intermediate PAR levels also significantly increased pine height (p = 0.0023), diameter (p = 0.0168), height increment

(p = 0.0098) and stem biomass (p = 0.0160) with respect to extreme PARs (Fig. 2k-o, Table 3).

Figure 3 shows that the effects of alder density on pine growth (height) vary throughout time. That is especially true for the 1987 RA, where higher alder densities increased pine height (p = 0.025) only when pines were 3-6 years of age. As pine trees became older, the effect of alder on pine height disappeared. In the 1989 RA, on the other hand, the effect of alder has been significant and positive during all stand development stages. This behavior also occurred in the 1994 RA. However, in this case such effects are not significant (Fig. 3g-i).

Pine nutrient status responses to varying pine/alder ratios: Figure 4a shows that all alder levels in the 1987 RA induced a decrease in needle dry weight and nitrogen content and, with the exception of alder level 3 (A3), all of them also decreased nitrogen concentration. According to the criteria defined by Valentine and Allen (1990) for the interpretation of Timmer's nomograms, the trends followed by most vectors in this graph would be interpreted as antagonistic relationships between alder and nitrogen status of pine trees.

Contrarily, most alder densities induced increasing concentrations of phosphorus and potassium within pine needles in the same RA (Fig. 4b, c) but they still exerted negative effects on needle dry weight and nutrient content. Based on the criteria defined by Imo and Timmer (1997), the status for phosphorus and potassium should be interpreted as excess.

In the 1994 RA (Fig. 4d-f), uptake of at least nitrogen and potassium increased as a result of the increased alder levels according to the criteria proposed by Valentine and Allen (op. cit.), such that even luxury consumption happened to occur (Fig. 4f, vector A4, Imo and Timmer, 1997). All alder density levels induced a sufficiency level of pine needle phosphorus (Valentine and Allen, 1990; Imo and Timmer, 1997; Salifu and Timmer, 2001).

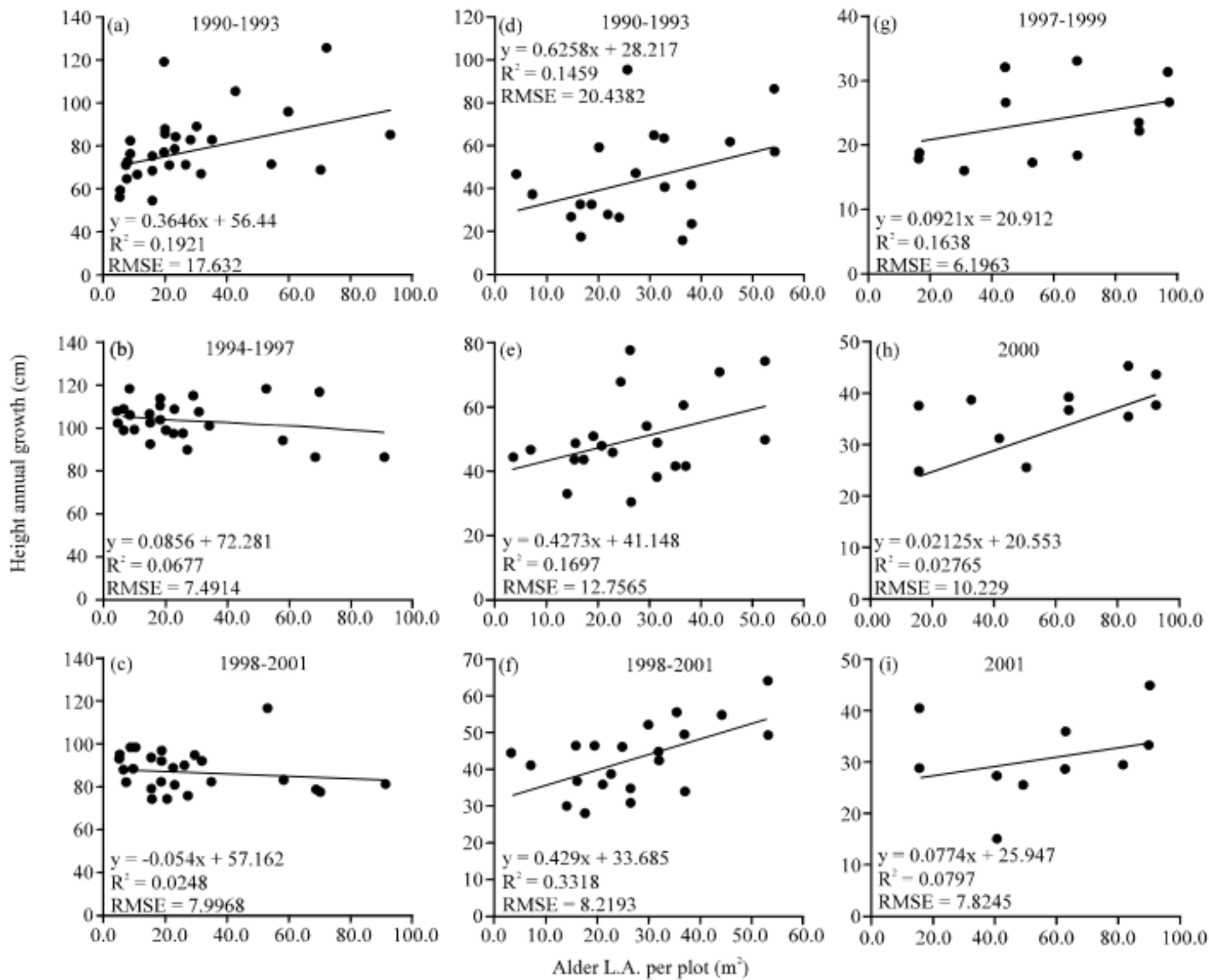


Fig. 3: Behavior of mean height periodic growth with varying alder leaf area in the (a-c) 1987, (d-f) 1989 and (g-i) 1994 RAs

DISCUSSION

Positive effects of increasing alder densities on the growth of crop forest species have frequently been reported in the literature (Binkley, 1983; Dawson *et al.*, 1983; Binkley *et al.*, 1992a; Rothe and Binkley, 2001; Yowhan *et al.*, 2007). Most research work on this field, however, has been carried out in the United States of America, so that those results should be verified for the alder-conifer associations in other parts of the world. Our finding regarding the positive effects of alders on pine growth when alder densities go from low to intermediate (Fig. 2) is in agreement with the results reported by the mentioned authors (Binkley, 1983; Dawson *et al.*, 1983; Binkley *et al.*, 1992a; Rothe and Binkley, 2001) and is a result of the increased N availability brought about by the N-fixer in N-deficient soils.

The quadratic shape that most of our growth response curves presented, especially in the 1987 and

1994 RAs, as judged by the orthogonal contrast analyses, implies that there exists a PAR that optimizes pine growth and more detailed studies should be conducted on a local and temporal basis in order to precisely determine such PARs, since the optimum PAR greatly varies depending on pine stand age and density and probably soil fertility among other characteristics (Binkley, 1983).

Calculations of the optimum PARs for our RAs (in terms of number of alders per hectare) resulted in very divergent values for optimum alder densities between the 1987 and 1994 RAs (20 Vs. 267 alders ha⁻¹ for the 1987 and 1994 RAs, respectively). In some sense, the low optimum alder density in the 1987 RA may be a reflection of the role alders are playing in that system. Figure 3 indicates that alders in this RA have behaved as rather weed shrubs since 1993. In turn, this negative effect of alders in this area may be due to the high pine density in this site, coupled with the mechanical control of alder growth, which probably has lead pine trees to overtop

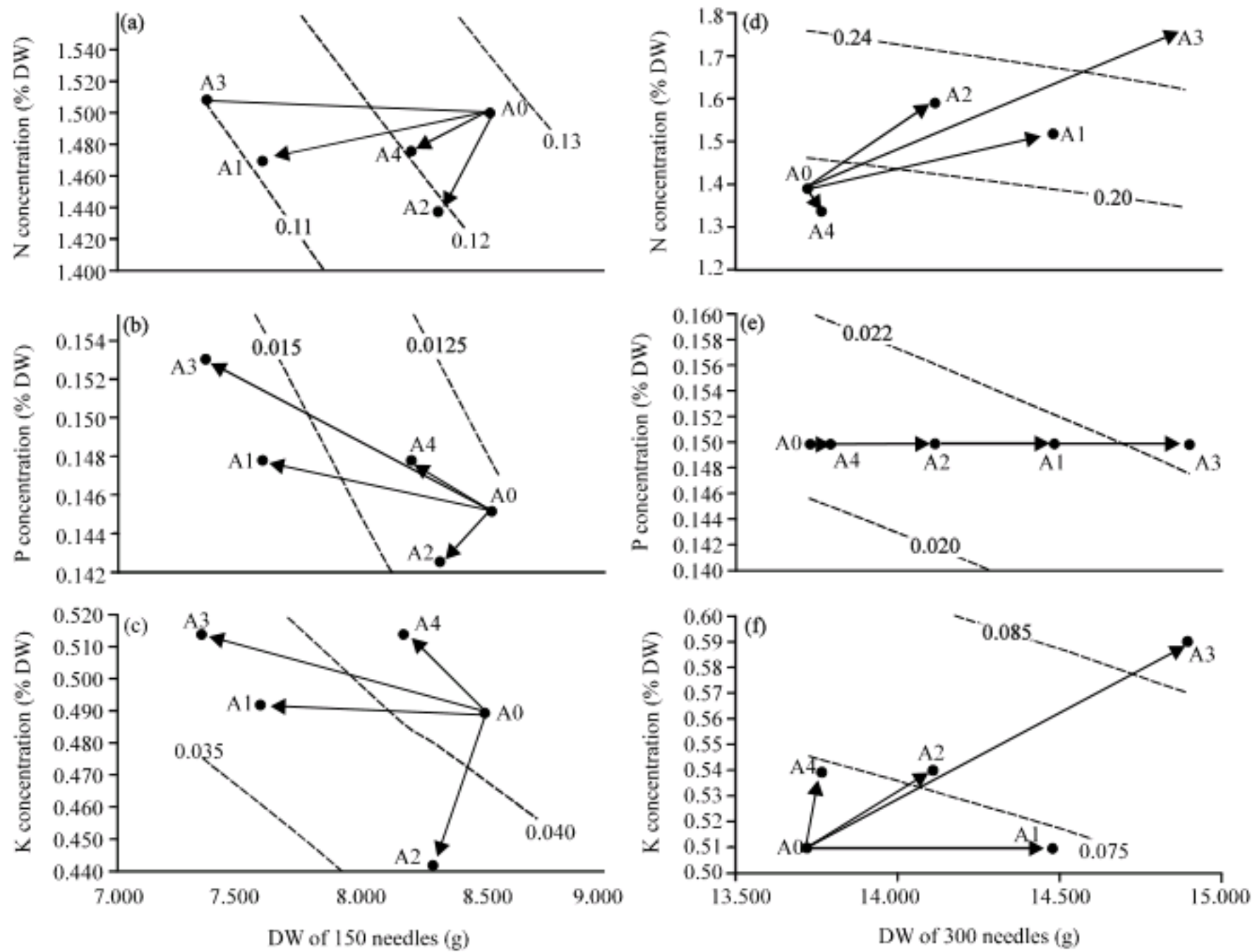


Fig. 4: Effects of varying pine/alder levels (A0-A4) on needle dry weight and needle nutrient concentration and content in the (a-c) 1987 and (d-f) 1994 RAs. Diagonal dashed curves are nutrient content isolines (values in grams of nutrient). PARs (LA/LA) for the RA 1987 are: A0: 31.98, A1: 15.90, A2: 12.13, A3: 7.18 and A4: 2.96. PARs (LA/LA) for the RA 1994 are: A0: 1.14, A1: 0.71, A2: 0.46, A3: 0.34 and A4: 0.24

alders by that year, thus reducing alder performance by decreasing the amount of radiation reaching alders. Sanborn *et al.* (2002) found that *Alnus viridis* was able to fix nitrogen even when shrubs grew under 18% sunlight. Nonetheless, it is little likely that the amount of N fixed under such conditions be sufficient to meet shrub needs thus using some recycled N and competing with neighboring trees. Heilman and Stettler (1985) and Shainsky and Rose (1995) encountered similar results to those found in the present study and argued light limitations for N-fixation by alder.

In contrast to the 1987 RA, the relatively high alder density that optimizes pine growth in the 1994 RA indicates that alders have maintained high N-fixation rates and this positive effect outweighs the possible negative effects alders have in the systems as they compete with crop trees for resources other than N (Fisher and Binkley, 2000). This behavior of alders is consistent with our expectation, provided that the biological N-fixation process is very energy-demanding (Binkley *et al.*, 1994)

and alders in this RA are fully exposed to sun. Such behavior is also consistent with the trends of the curves shown in Fig. 3g-i, which reveal that positive effects of alder on pine growth have dominated over the negative ones throughout the stand's life.

The curves for pine growth in the 1989 RA (Fig. 2f-j) are much more irregular than those in the other RAs. Even so, it looks like alders had just positive effects on pine growth (also confirmed by Fig. 3d-f) and that the optimum PARs were not reached in this area even though alder densities are quite similar to those in the 1987 RA (12.9 Vs. 16.6 alders plot⁻¹ for the 1989 and 1987 RAs, respectively).

One of the most remarkable differences between stands 1989 and 1987 deals with pine density (31.4 Vs. 56.8 pine trees plot⁻¹ for the 1989 and 1987 RAs, respectively). This difference may be determining the role of alders (as beneficial or weed shrubs) in each of the RAs since the high pine density (and high pine leaf area) in the 1987 RA may restrict sunlight reception by alder and the

N-fixation process as well, provided that alders are generally very light-demanding (Harrington, 1990; Hibbs, 1996). Similar results were found by Heilman and Stettler (1985) and Shainsky and Rose (1995) who also argue that N-fixation was reduced by limited light. This finding implies that monitoring of radiation reaching understory alders should be incorporated to management strategies as an extra input for both alder and pine density control decisions, if maximum pine growth is to be pursued in pine-alder stands.

Regarding pine nutrient status as affected by the presence of alders, the antagonistic relationship between the pseudo-treatment (alder density) in most alder levels and the nitrogen (N) status in pine trees in the 1987 RA (Fig. 4a), should be interpreted rather as a competition effect between alder clumps and pine trees. In fact, even though compensatory or synergistic relationships (Imo and Timmer, 1999) between N-fixing species and crop species (where either the crop species or both species in the mixture may be benefited) are expected in mixed stands, our pine species in this specific RA was negatively affected in terms of its N status.

Diverse changes in the status of nutrients other than nitrogen have been reported to occur in crop trees when in mixture with N-fixing species (Binkley, 1983; Van Miegroet *et al.*, 1990; Shainsky and Radosevich, 1992; Shainsky and Rose, 1995; Rothe and Binkley, 2001; Binkley, 2005; Lopez-Lopez *et al.*, 2006). However, We know of no case in the literature where N status of crop trees has been negatively influenced by this type of plant species as it did occur in the 1987 RA. Binkley (1983) reported negative effects of red alder on growth of Douglas-fir growing on fertile soils. However, conifer N concentration remained pretty the same as with no alder. The decrease in N concentration and content in pine needles in our study (Fig. 4a) indicates that competition for N between alder shrubs and pine trees took place in virtually all alder levels and this finding is in agreement with the negative effects alders had on pine growth during the last eight years of stand development in this RA (Fig. 3b,c).

As explained before, light limitations for alder are likely to be at work in this RA. Many of the conditions prevailing at this site and some intrinsic alder's characteristics as well, are probably favoring light limitations for alder performance. First, pine density in this RA is pretty high (56.8 pine trees per plot) and so is pine leaf area. Second, pine trees are much taller than alder clumps (alders are in the understory). Third, alder requirements for light are known to be high (Harrington 1990; Binkley *et al.*, 1994; Fisher and Binkley, 2000) and probably unsatisfied in this site.

In agreement with our results, Heilman and Stettler (1985) found that N-fixation by red alder declined in the fourth growing season, presumably due to increasing shading by the taller black cottonwoods. In 1983, the same authors found that partially shaded red alder trees produced just half the nodule biomass of trees fully exposed to sun. Additionally, they encountered that the lower nodule biomass under shade was accompanied by lower acetylene reduction rates.

The excess of phosphorus (P) and potassium (K) found in the 1987 RA may have two sources: 1) a concentration process due to limitation of growth by other factor (i.e., nitrogen), or 2) an increase in the availability of these nutrients by alder. Even though there are several reports on increased P availability by alder or other N-fixing species (Binkley *et al.*, 1992b; Giardina *et al.*, 1995; Shainsky and Radosevich, 1992; Shainsky and Rose, 1995; Zou *et al.*, 1995), in our case it appears that the cause for the increased concentration of P and K was the decreased needle biomass (concentration effect, Koricheva, 1999; Lopez and Estañol, 2007). Otherwise, the content of these nutrients would have increased, especially that of K, since this nutrient is widely known to tend to be absorbed by most plants to luxury consumption when its availability in soil is high (Epstein, 1972; Rodríguez, 2005; Mengel and Kirkby, 2001).

The decreased concentration of N within pine needles when alder clumps were present in the 1987 regeneration area indicates that alders are currently not fixing N. N status in this RA is in agreement with the reduction in growth of pine trees occurring during the last years of stand development (Fig. 3a-c). Moreover, the integration of these facts suggests that alders competed with pine trees for N. Although, somewhat intriguing (being alder a N-fixing species), this possibility is highly probable provided that alders are high-N-demanding species as judged by their high foliar N concentrations and in this case, they were unable to reduce their own N due to light limitations.

The accumulation of N and K in pine needles from plots with alder levels other than zero in the 1994 RA indicates that the availability of these nutrients was increased by alder. In the case of N, this effect seems pretty reasonable since appropriate conditions for high N-fixation rates to take place were present in this site. In fact, alder density was quite high in this location (31.2 alder clumps per plot) and alders were as tall as or even taller than pine trees, so that they were fully exposed to sunlight.

The accumulation of K, however, is harder to understand, especially if N-fixation rates were high. In fact, literature reports that high N-fixation rates may promote nitrification; a microbiological process through

which, H⁺ ions are released into the soil solution (Schlesinger, 1997). H⁺ ions may displace basic cations (such as Ca⁺⁺, Mg⁺⁺ or K⁺) from soil adsorption sites, making them vulnerable to loss to deeper soil horizons (Van Miegroet *et al.*, 1990). We did not measure nitrification in our site; however, if this process occurred in this RA, K losses would have also taken place and this would contradict the results from our data.

Nonetheless, there are reports indicating that broad leaved species may increase organic matter decomposition rates and nutrient turnover and availability (Van Miegroet, 1990; Binkley *et al.*, 1992b; Prescott *et al.*, 2000). For example, phosphorus availability has been found to increase in some cases when N-fixing species are mixed with crop trees (Binkley *et al.*, 1992b; Giardina *et al.*, 1995; Shainsky and Rose, 1995; Zou *et al.*, 1995). Decomposition and turnover of nutrient rich organic matter such as that of alders from the 1994 RA may explain the increased K availability.

On the other hand, the accumulation of N and K also indicates that there exists some other factor that is limiting pine growth in this RA. Otherwise, these nutrients would dilute within a greater pine biomass. Figure 4e shows that P status corresponds to the so called steady state (Imo and Timmer, 1997; Quoreshi and Timmer, 2000; Salifu and Timmer, 2001) That is, P availability is just sufficient to keep pace with the increase in needle weight (Imo and Timmer, 1997). However, vectors with this direction correspond to the Macy's concept of "minimum percentage" level for internal nutrient concentration and are on the boundary between the dilution zone and the deficiency zone. Accordingly, in this RA (1994), P was more probably the nutrient that limited pine growth, thus causing N and K to concentrate within pine needles.

It is worth noticing that pine growth was a reflection of P availability in this RA if P was the nutrient limiting pine growth. Therefore, it may be deduced that P availability described a quadratic-curve trend as growth variables did in the 1994 RA (Fig. 2k-o). In turn, this means that P availability was increased by alder levels as reported by several authors for various N-fixing species (Binkley *et al.*, 1992b; Giardina *et al.*, 1995; Shainsky and Rose, 1995; Zou *et al.*, 1995).

Integration of our findings suggest that management strategies for pine-alder stands in Central Mexico should include: 1) to assure that the area is N-limited; if not, alders are unlikely to improve site quality, 2) to monitor and control alder density to avoid interference with pine establishment and competition with pine for nutrients other than N, 3) to avoid pine trees to overtop alder clumps and limit the N-fixation process and 4) to monitor and control pine P and K status.

CONCLUSIONS

The shape of the curves describing pine growth variables as a function of PAR levels (Fig. 2) corresponds to a quadratic function, indicating that the beneficial effects of alder outweighed the competition effects in alder levels lower than optimum. On the other hand, competition effects from alder became dominant over beneficial ones when the proportion of alder was higher than optimum.

The PARs (LA/LA) that optimize pine growth are 11.16 and 0.57 (number of pine trees per ha/number of alder trees per ha = 2,666/20 and 711/267) for the 1987 and 1994 RAs, respectively. Maximum pine growth was not reached with the alder densities currently occurring in the 1989 RA.

The effects of alder on pine growth in pine-alder ecosystems may go from beneficial to detrimental. Our results suggest that the alder's beneficial effects on pine growth occurred during the first six or seven years following the regeneration treatment in the 1987 RA. Since that time, alders exerted just negative effects on pine growth as they became weeds.

Light limitations for the N-fixation process by alder are likely to be responsible for the change of alder's effects from beneficial to detrimental. We suggest that more precise studies at this respect be carried out to determine the limiting factor for the N-fixation process by alder.

The presence of even low alder densities may have negative effects on pine growth as it occurred in the 1987 RA. However, maybe the most remote expectation in pine-alder mixtures is to register negative effects of alder on pine growth through a competition effect for nitrogen, since alder is a nitrogen fixer. Nonetheless, our results indicate that the decrease in pine growth was associated with a reduction in the availability of N with the presence of alder clumps in the plots.

Under appropriate conditions for the N-fixation process to take place, alders can give up amounts of N sufficient to satisfy and even surpass N requirements of montezuma pine trees, as it occurred in the 1994 RA.

K availability increased when alder was present in the 1994 stand, where light availability was sufficient (full sunlight) for the N-fixation process to occur. In the 1987 RA, where light limitations for the alder growth occurred, K also concentrated within pine needles. However, in this case, it appears that such effect was a result of the reduced pine growth in turn due to N limitations and not to an increased K availability.

Phosphorus availability was improved by alder in the 1994 RA and such increased availability determined the extent to which pine growth took place.

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