

## Fertilization increases *Hylobius abietis* L. damage in *Pinus pinaster* Ait. seedlings

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### Abstract

Maritime pine (*Pinus pinaster* Ait.) is the most important forest tree species in Galicia (NW Spain), and the pine weevil (*Hylobius abietis* L.) can be a serious problem to its regeneration. Fertilization is a commonly recommended silvicultural tool for *P. pinaster*, especially in second rotation reforestations where large amounts of nutrients may be extracted through harvesting. But increased nutrient availability could promote undesired side-effect on host resistance and pest damage. We studied the effect of fertilization on pine growth and weevil damage during two growth periods after planting in a *P. pinaster* progeny × fertilization trial with nine fertilization treatments. Both factors, fertilization and family, had a strong and significant effect on growth and pine weevil damage. The damage by the pine weevil was greater in fertilized plants (debarked area score up to 2.9-fold greater) than in the unfertilized control, inducing a 3.7-fold greater leader loss in the former. The damage was lower when calcium phosphate was absent than when it was present, averaging about 2- and 2.7-fold above the unfertilized control, respectively. In spite of the attack, 1 year after planting, fertilization significantly increased diameter and height in plants that were able to maintain the leaders alive, averaging about 1.2-fold above the control. But when the height of the whole plantation was considered (actual height), fertilized plants did not differ from unfertilized ones. Moreover, the attack of *H. abietis* during the first growing period affected subsequent growth, resulting in no significant effect of fertilization on growth at the end of the second growing period. Attack by *H. abietis* caused the loss of the growth benefits promoted by the fertilization input.

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### 1. Introduction

The pine weevil (*Hylobius abietis* L.) is a major pest of conifers in Europe. Adults feed on the bark of young seedlings during the first years after cutting a conifer stand, causing important growth losses, stem deformation and high mortality (Orlander and Nordlander, 2003; Petersson and Orlander, 2003). Damage of pine weevil is the most serious problem to regeneration in northern Europe, where seedling mortality of *Pinus sylvestris* L. and *Picea abies* (L.) Karst often reaches 60–80% if no protection measures are applied (Orlander and Nordlander, 2003). Several silvicultural methods have been

used to minimize the pine weevil damage, including delayed planting, soil scarification, shelterwood, feeding barriers, and insecticide applications (Petersson and Orlander, 2003; Sydow, 1997).

In southern Europe, the pine weevil is also an important handicap for regeneration of old maritime pine (*Pinus pinaster* Ait.) stands (Frayse and Saintonge, 1996), but information about the relation between *H. abietis* and this pine species is scarce. Maritime pine is the most important forest tree species in Galicia (NW Spain) where it occupies nearly 400,000 ha (27% of the Galician wooded area) with an annual volume increment estimated around  $3 \times 10^6 \text{ m}^3 \text{ year}^{-1}$  (Xunta-de-Galicia, 2001). Soil fertility in Galicia varies in a broad range, and site index for several forest tree species has been shown to be highly influenced by nutrient availability (Merino et al., 2003; Sánchez-Rodríguez et al., 2002; Zas, 2003a,b; Zas and Serrada, 2003). Conifer plantations in Galicia commonly suffer

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important nutrient deficiencies that can be effectively corrected by adequate fertilization (Solla-Gullón et al., 2004; Zas, 2003a; Zas et al., 2004). Important benefits of fertilization are also expected in *P. pinaster*, especially in second rotation reforestations where large amounts of nutrients may be extracted through harvesting (Dambrine et al., 2000; Ouro et al., 2001).

Fertilization and plant genotype are known to modify the potential damage caused by other forest pests (e.g. Mutikainen et al., 2000; vanAkker et al., 2004) and also by *H. abietis* (Selander and Immonen, 1992). Resource availability for the plant (namely soil fertility, water and light regime) could modify the allocation of carbon resources in both induced and constitutive defenses, leading to altered herbivore resistance and plant growth (Lombardero et al., 2000). Several hypotheses have been proposed: carbon nutrient balance (Bryant et al., 1983), growth differentiation balance (Loomis, 1932; Lorio, 1986; Herms and Mattson, 1992), optimal allocation (Tuomi et al., 1991), substrate/enzyme imbalance (Waterman and Mole, 1989) and plant stress hypothesis (Mattson and Haack, 1987; White, 1984). Some of these models predict that responses of plants to increased fertilization involve a decrease in carbon based secondary compounds and plants become less defended against herbivores. Furthermore, alteration of plant defensive mechanisms to herbivory due to diverse nutrient availability could be interacting with direct effects of fertilization on plant growth and plant tissue quality, which are expected to modify the insect preferences and performance (Ayres et al., 2000; Reeve et al., 1995). Common forest management practices such as fertilization after cutting may subsequently modify plant resistance. The effect of fertilization on plant health should be studied before any general fertilization recommendation is made.

In 2003, several progeny × fertilization trials were established in Galicia to test the plasticity of a subset of the actual *P. pinaster* breeding population in relation to soil fertility. The massive attack of *H. abietis* in one of these trials gave us the opportunity to test how the genotype and the fertilization affected the pine weevil damage. The effect of the pine genotype on pine weevil damage has been extensively attended in a companion paper (Zas et al., 2005). In the present study we analyze the effect of different fertilization treatments on both pine growth and pine weevil damage through two growth periods. We hypothesize that fertilization of second rotation *P. pinaster* seedlings may increase pine weevil damage.

## 2. Material and methods

### 2.1. Location and site description

The study was carried out in a progeny × fertilization trial located nearby the Atlantic coast of Galicia (Rianxo, NW Spain, 42°36'N, 8°46'W, altitude 90 m). The soil, derived from granite parent material, has a sandy texture, acidic pH, high levels of organic matter and low levels of nutrients. The previous *P. pinaster* mature forest was clear-cut harvested in January 2002, and 6-month-old containerized seedlings were planted at 3 × 2 m spacing in March 2003. The study material consisted of open-pollinated progenies from 28 maternal plus trees randomly selected in a first generation seed orchard (Sergude, 42°49'N, 8°27'W) which provides high genetic quality seed for reforestation in the Atlantic coast of Galicia. First damage symptoms were observed at the end of summer 2003. All the experimental surface area was surrounded by mature maritime pine stands.

### 2.2. Experimental design

The experimental layout consisted in a progeny × fertilization trial arranged following a randomized split plot design replicated in 10 blocks, with nine fertilization treatments acting as whole plots and 28 families as split plots. The total number of seedlings was 10 × 9 × 28 = 2520 plants occupying around 1.5 ha. The fertilization treatments (control and eight treatments built upon combinations of four commercial fertilizers, Table 1) were randomly assigned to the whole plots within each block. Whole plots were around 12 × 18 m in size. Fertilizers were applied immediately after planting, and were manually distributed around the seedlings (30 cm in diameter). The fertilizers were combined to allow testing the effect of the combinations of single fertilizers (phosphorus (P), potassium (K) and magnesium (Mg)) with nitrogen (N).

### 2.3. Assessment of plant growth and weevil damage

Plant growth, survival and weevil damage were assessed in January and November 2004, i.e. after one and two growing periods from planting. To minimize subjectivity, the damage caused by *H. abietis* feeding was assessed by dividing the pine stem in 10 parts (five parts in the second assessment), and recording the weevil damage in each part. The intensity of wounding was evaluated by estimating the relative debarked

Table 1  
Codes and composition of the fertilization treatments

Nutrient	Fertilizer	Dose	Treatment code								
			Control	F1	F2	F3	F4	F5	F6	F7	F8
N	Ammonium nitrate	5 g N plant <sup>-1</sup>	–	+	–	+	+	+	–	–	–
P–Ca	Calcium phosphate	10 g P plant <sup>-1</sup>	–	+	+	–	+	+	–	+	+
K	Potassium sulphate	15 g K plant <sup>-1</sup>	–	+	+	+	–	+	+	–	+
Mg	Magnesium sulphate	5 g Mg plant <sup>-1</sup>	–	+	+	+	+	–	+	+	–

Presence and absence of a given compound in the fertilizer mixture is indicated by + and –, respectively.

area caused by feeding in each part of the stem using a four-level scale (0 = undamaged, 1 = some wounds, 2 = many wounds, and 3 = death due to girdling). The sum of these values by plant was considered as the damage trait “wounds” ( $WND_1$  (0–30 score) and  $WND_2$  (0–15 score)). Additionally, the leader loss ( $LL_1$  and  $LL_2$ ) due to stem girdling by the pine weevil was also recorded in both dates as a binomial variable (leader alive:  $LL = 0$ , leader death:  $LL = 1$ ). When the pine weevil attack led to stem girdling, “actual height” was defined as the height of the live stem, i.e. up to the girdling. We used “potential height” – the total height in plants with living leaders– and groundline diameter ( $D_1$  and  $D_2$ ) as indicators of plant growth.

#### 2.4. Spatial analysis

Geostatistics were used to test whether the weevil damage was homogeneously distributed in the study area or whether there was a spatial pattern not explained by the block design. The absence of an explicit spatial pattern in the weevil damage is an essential assumption for analyzing this variable with the split plot design. The spatial distribution of the trait  $WND_1$  and of the residuals of the model defined in Eq. (2) for this trait were plotted. We calculated a semivariogram for these two variables. A semivariogram plots the average semivariance found in comparisons of plants taken at increasing distance from one another, evaluating the resemblance between neighbors as a function of spatial separation distance (Cressie, 1993). The semivariance  $\gamma(h)$  was calculated as:

$$\gamma(h) = \frac{1}{2n} \sum_{i=1}^n [z(s_i) - z(s_{i+h})]^2 \quad (1)$$

where  $n$  is the number of observation pairs separated by distance  $h$ ,  $z(s_i)$ , the value of the variable of interest at location  $s_i$ , and  $z(s_{i+h})$  is its value in a tree separate  $h$  from  $s_i$ . The two variables were previously standardized to a  $N(0, 1)$  in order to attain an equivalent scale. For randomly distributed data there is little change in the semivariance encountered with increasing distance and the semivariogram is essentially flat. When spatial dependence is present at the scale sampled, semivariance will be lower at short distances, increasing for intermediate distances, and typically reach an asymptote for long distances. The distance at which the asymptote is reached signifies the range or patch sizes of heterogeneity beyond which data are stochastically independent (see Ettema and Wardle, 2002). By common convention, the analysis is restricted to distances of half the dimension of the study area (Gallardo, 2003).

#### 2.5. Statistical analysis

Analyses of variance (ANOVA) were performed on pine growth and weevil damage data using the MIXED procedure of the SAS System (SAS-Institute, 1999) and the following model:

$$Y_{ijk} = \mu + F_i + G_j + B_k + FG_{ij} + FB_{ik} + \varepsilon_{ijk} \quad (2)$$

where  $\mu$  is the general mean,  $F_i$  is the effect of the fertilization treatments,  $G_j$  is the effect of the open-pollinated families,  $B_k$  is the effect of the blocks,  $FG_{ij}$  is the interaction between fertilization and family,  $FB_{ik}$  is the interaction between fertilization and blocks and  $\varepsilon_{ijk}$  is the random error. All factors except  $FB_{ik}$  were considered fixed. The  $FB_{ik}$  interaction was considered random in order to use the correct error term for testing the whole plot factor, i.e. the fertilization effect.

Binomial variables ( $LL_1$ ,  $LL_2$  and survival) were analyzed on a whole plot mean basis. Whole plot means were previously transformed (arsin(square root)) and then analyzed assuming a randomized complete block design, and using the following model:

$$Y_{ik} = \mu + F_i + B_k + \varepsilon_{ik} \quad (3)$$

where  $Y_{ik}$  is the transformed whole plot mean.

When main effects were significant, differences among treatment means were tested for significance using the LSMEAN statement of the MIXED procedure (SAS-Institute, 1999). Data are shown as mean  $\pm$  S.E.

Pearson correlation was used to explore the relationships between weevil damage and pine growth at the two assessment dates. These correlations were carried out on a treatment mean ( $n = 9$ ), family mean ( $n = 28$ ) and whole plot mean ( $n = 90$ ) basis.

### 3. Results

#### 3.1. Growth of pine seedlings

Average actual height and groundline diameter were  $45.9 \pm 0.43$  cm and  $9.6 \pm 0.05$  mm 1 year after plantation, and  $84.2 \pm 0.50$  and  $20.9 \pm 0.15$  mm 2 years after. In the first growing period, all the fertilization treatments significantly increased diameter and potential height (as defined in Section 2.3) of *P. pinaster* seedlings in comparison to the unfertilized control (Table 2 and Fig. 1) indicating that nutrient availability is limiting to some extent pine growth in the experimental field. Among the different fertilization treatments, the absence of calcium–phosphate (treatments F3 and F6, Table 1) produced lower growth responses (Fig. 1). In the second growth period, the significant effect of fertilization on growth disappeared (Table 2), probably due to the interferences of the pine weevil damage during the previous year (see later).

Significant differences among families were observed for all the growth variables in the 2 years (Table 2). Fertilization  $\times$  family (Fer  $\times$  Fam) interaction was not significant in the first growth period (Table 2), indicating that, initially, all families showed similar responses to fertilization. However, Fer  $\times$  Fam interaction became significant in the second growth period for both diameter and height, suggesting that the consequences of the pine weevil damage on the subsequent growth differed among families.

#### 3.2. Damage by the pine weevil

Attack of pine weevil was extensive and 94% and 96% of all plants were damaged at the end of the first and second growth

Table 2  
Results of the mixed model for growth of *P. pinaster* seedlings and damage by the pine weevil *H. abietis*

Effect	DF	Growth of pine seedlings		Damage by the pine weevil			
		Diameter	Potential height <sup>a</sup>	Wounds	Leader loss <sup>b</sup>	Survival <sup>b</sup>	Actual height <sup>c</sup>
<b>First growth period</b>							
Fertilization <sup>d</sup> (Fer)	8	4.81 <sup>***</sup>	7.76 <sup>***</sup>	18.05 <sup>***</sup>	12.14 <sup>***</sup>	3.35 <sup>**</sup>	1.29
Block <sup>d</sup> (B)	9	5.27 <sup>***</sup>	3.60 <sup>**</sup>	4.59 <sup>***</sup>	3.97 <sup>***</sup>	1.35	5.27 <sup>***</sup>
Family (Fam)	27	3.96 <sup>***</sup>	5.42 <sup>***</sup>	7.03 <sup>***</sup>			4.49 <sup>***</sup>
Fer × Fam	216	1.17	1.07	1.33 <sup>**</sup>			1.22 <sup>*</sup>
B × Fam	243	0.76	0.90	1.09			1.07
<b>Second growth period</b>							
Fertilization <sup>d</sup>	8	1.90	0.48	4.13 <sup>***</sup>	6.55 <sup>***</sup>	4.06	0.92
Block <sup>d</sup>	9	3.80 <sup>***</sup>	2.30 <sup>*</sup>	4.88 <sup>***</sup>	4.80 <sup>***</sup>	2.64	2.52 <sup>*</sup>
Family	27	2.23 <sup>***</sup>	5.26 <sup>***</sup>	2.72 <sup>***</sup>			6.17 <sup>***</sup>
Fer × Fam	216	1.33 <sup>**</sup>	1.21 <sup>*</sup>	1.09			1.29 <sup>**</sup>
B × Fam	243	1.02	1.03	1.01			1.07

*F* values and probability levels for fixed effects.

<sup>a</sup> Plants with leader loss were dropped from the analysis.

<sup>b</sup> Leader loss and survival were assessed as binary variables. Analysis were performed on transformed (arsin(sqrt)) whole plot mean values.

<sup>c</sup> Height of the live part of the stem, all plants considered.

<sup>d</sup> Fertilization × Block as error term.

\* Significance levels:  $P < 0.05$ .

\*\* Significance levels:  $P < 0.01$ .

\*\*\* Significance levels:  $P < 0.001$ .

period, respectively. Although mortality was not very high (11 and 15%), pine weevil damage caused leader loss due to stem girdling in 42% of the seedlings in the first year, and in 30% in the second, generating important growth losses. At the end of the first growth period, total height of those plants with no leader loss ('potential height') averaged  $57.0 \pm 0.35$  cm, and doubled that of plants with leader loss ( $26.1 \pm 0.55$  cm). New

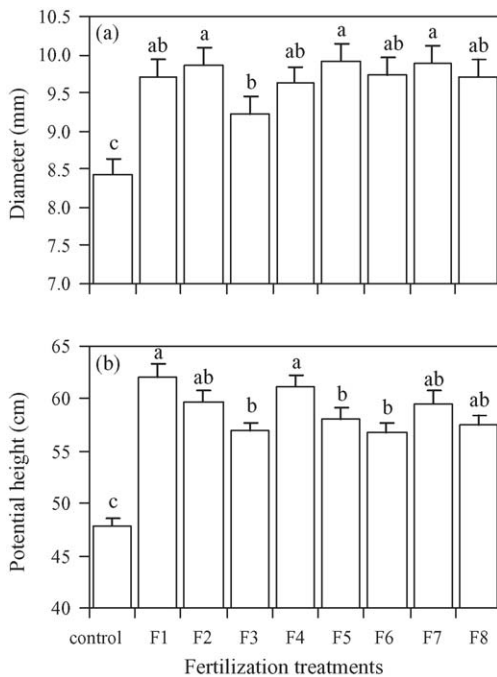


Fig. 1. Effect of the fertilization treatments on the growth (groundline diameter (a) and potential height (b)) of *P. pinaster* seedlings during the first growing period. Data are treatment means  $\pm$  standard errors. Different letters indicate significant differences ( $P < 0.05$ ) among treatments.

leaders, emerging below stem girdling, were observed in many plants, and subsequent stem deformities are expected in those plants where some lateral branches recover apical dominance.

The attack of *H. abietis* was uniformly distributed in all the experimental surface area, as indicated by the random spatial distribution of the residuals of the mixed model (Eq. (2)) applied to the wounds caused by the pine weevil in the first year (WND<sub>1</sub>) (Fig. 2). The constant semivariance for these residuals irrespective of the distance between the trees contrasted with the clear decrease of the semivariance for the original variable WND<sub>1</sub> when distance fall below 20 m (Fig. 3). WND<sub>1</sub> showed, thus, a small-scale heterogeneity with many small and sharply discontinuous patches. The distance at which the asymptote is reached (approximately 20 m, Fig. 3) – which represents the range or patch size – corresponded well with the maximum distance within the whole plots. Taking into account the highly significant effect of fertilization on WND<sub>1</sub> (see below), spatial heterogeneity of the initial attack can be attributed to the experimental treatment distribution.

In the first year, fertilization influenced the pine weevil damage significantly (Table 2). The mean damage score by feeding on the bark in fertilized plants was 2.6-fold greater than in the unfertilized control. Leader loss was 3.7-fold significantly greater in fertilized plants than in the control, too. Judging from the *F* values of the ANOVA, fertilization explained the highest amount of variance for these two traits. Conversely to potential height, no differences between the fertilized plants and the control were detected in actual height (Table 2), suggesting larger height losses due to more severe pine weevil damage in fertilized plants. It seems that all the extra growth due to fertilization was lost by the pine weevil damage. Despite all the fertilization treatments significantly increased both WND<sub>1</sub> and LL<sub>1</sub> in relation to the control, the

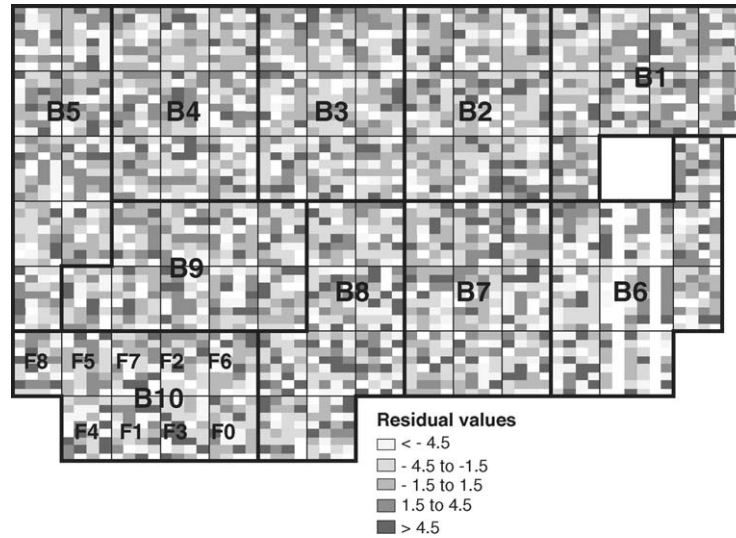


Fig. 2. Spatial distribution of the residuals of the mixed model for the damage caused by *H. abietis* during the first growth period ( $WND_1$ ) in maritime pine seedlings. The 10 blocks of the experimental design are outlined by a thick black line and labeled by B1–B10. The nine whole plots of each block are outlined by fine black lines. Each small gray square represents one seedling. The random distribution of the fertilization treatments through the whole plots is indicated for B10.

lack of calcium–phosphate (F3 and F6) led to significantly lower weevil damage (Fig. 4).

The effect of fertilization on weevil damage (both  $WND_2$  and  $LL_2$ ) was also significant in the second year (Table 2) with a similar pattern of variation among treatments (Fig. 5b). However, comparisons among treatments (not shown) were not as clear as in the first year, probably due to the own noise generated by the initial attack.

Survival was also significantly influenced by fertilization in the 2 years (Table 2). Survival in all fertilized plots except in F6 ( $SUR_2 = 90.0\%$ ) was consistently lower ( $SUR_2 = 76.6–87.5\%$ ) than in the unfertilized control ( $SUR_2 = 93.8\%$ ).

Pine weevil damage through fertilization treatments showed a positive linear relationship with growth in the first growing season measured well as potential height ( $r^2 = 0.80, P < 0.001, n = 9$ ) as diameter ( $r^2 = 0.86, P < 0.001, n = 9$ ; Fig. 5a). Despite this positive relation, interannual diameter growth ( $D_2 - D_1$ ) decreased as the initial damage ( $WND_1$ ) increased

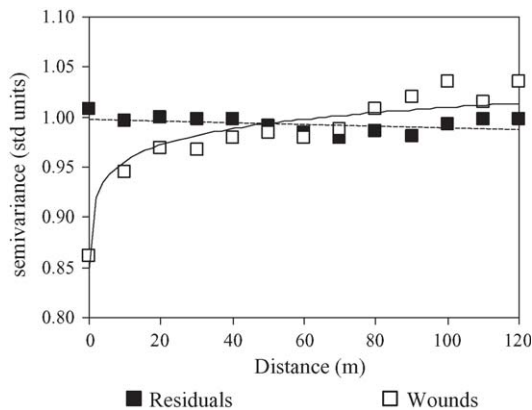


Fig. 3. Semivariogram for the wounds caused by the pine weevil in the first growth period ( $WND_1$ , white squares) and for the residuals of the mixed model (Eq. (2) for  $WND_1$ , black squares). Dots are the semivariance means for 10 m distance intervals.

(Fig. 5c), indicating that weevil damage was affecting the pine growth capacity. All these relations were also significant ( $P < 0.05$ ) on a family basis ( $n = 28$ ) or on a whole plot means basis ( $n = 90$ ).

The family effect was also significant for both variables. Contrary to what occurred with growth,  $Fer \times Fam$  interaction was significant for the three damage variables (Table 2). It seems that genetic resistance is altered with fertilization in different ways, or, in other words, the effect of fertilization on weevil damage varied among families.

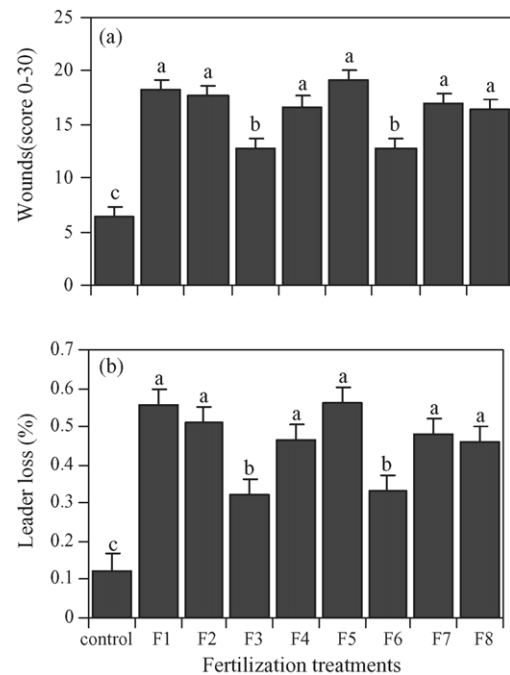


Fig. 4. Effect of the fertilization treatments on the damage (wounds (a) and leader loss (b)) caused by *H. abietis* to *P. pinaster* seedlings in the first growth period. Data are treatment means  $\pm$  standard errors. Different letters indicate significant differences ( $P < 0.05$ ) among treatments.

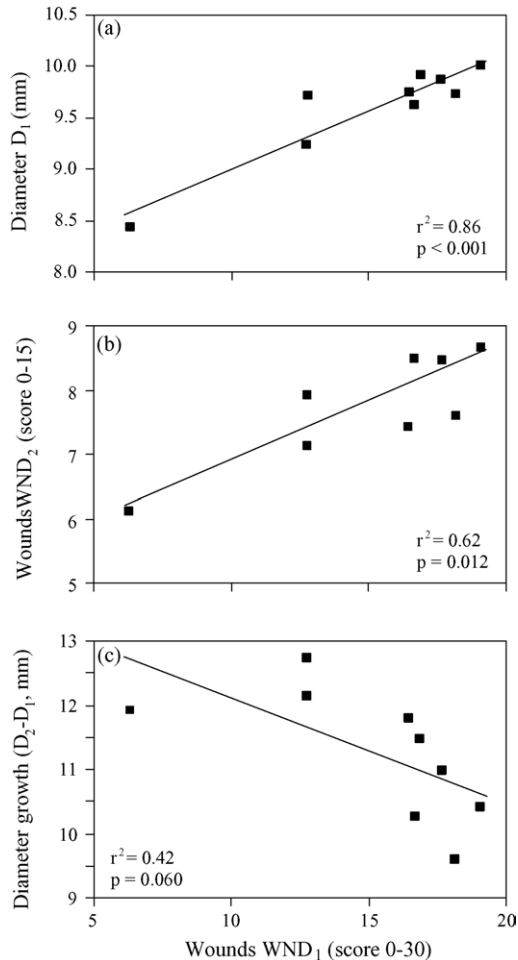


Fig. 5. Relationship between the wounds caused by the pine weevil to *P. pinaster* seedlings in the first growing season ( $WND_1$ ) and a) the diameter in the first year ( $D_1$ ), b) the wounds caused by the pine weevil in the second growing period ( $WND_2$ ), and c) the diameter increment between the two assessment dates ( $D_2 - D_1$ ). Data are shown as mean values of eight fertilization treatments (F1–F8, see Table 1) and the unfertilized control.

#### 4. Discussion

The positive effect of fertilization on growth was expected based on the deficiencies found in forest tree species on the acidic forest soils on granites in Galicia (Merino et al., 2003; Sánchez-Rodríguez et al., 2002; Zas, 2003a,b). For example, in the case of *Pinus radiata* D. Don young plantations, P and Mg are commonly deficient (Zas, 2003b; Zas and Serrada, 2003), and important benefits of an adequate fertilization have been reported (Solla-Gullón et al., 2004; Zas et al., 2004). We have also found great responses to P and Mg fertilization in *P. pinaster* seedlings in a range of site qualities across Galicia (Zas, unpublished data). Important growth increments through P fertilization have also been reported in maritime pine growing in the sandy acidic soils of Landes, France (e.g. Saur, 1990).

Fertilization increased the incidence of *H. abietis*, increasing the debarked area, the percentage of seedlings that lost their leaders and mortality. *H. abietis* significantly preferred fertilized seedlings to unfertilized controls, and its preference

was significantly lower when calcium phosphate was absent in the fertilization treatment (Fig. 4). Additionally, growth gains due to fertilizer treatments were outweighed by height losses due to weevil attack. Moreover, the effect of fertilization on growth became no significant in the second year (Table 2), although in other identical unattacked trials it remained highly significant through several years (Zas, unpublished data). This can be explained by the effect of the first weevil damage on the seedling growth capability. Fertilized plants grew faster in the first year but were also more attacked by the weevil, and, as a consequence, were those that grew less in the second year (Fig. 5c), resulting in no significant effect of fertilization on growth. A negative effect of pine weevil damage on subsequently growth of Norway spruce seedlings was also reported by Orlander and Nilsson (1999).

*H. abietis* preferences in the first year were maintained in the second growing period with fertilized plants significantly more attacked than unfertilized ones. However, despite there was a correspondence between the effect of different treatments through the 2 years (Fig. 5b), the relevance of the application of calcium–phosphate for the weevil preference was no so clear in the second year. The response of the pine seedlings to the initial attack (e.g. through induced defences or differential resource allocation) can be altering the results of the second year, generating unidentifiable noise that difficulties the interpretation.

Differences in pine weevil damage among families were also highly significant (Table 2). Variation in insect resistance among plant genotypes has been observed for many insect–plant systems (Kiss and Yanchuk, 1991; Mutikainen et al., 2000) and also for resistance of *P. pinaster* to *Dioryctria sylvestrella* Razt. (Kleinhentz et al., 1998). The highly significant family effect on pine weevil damage indicates the possibility to include the resistance to this pest as selection criteria in the maritime pine breeding program of Galicia. However, the Fer  $\times$  Fam interaction was significant for the pine weevil damage (Table 2), indicating that genetic resistance is altered by fertilization, and hindering the possibilities of genetic improvement. The significant Fer  $\times$  Fam interaction for growth traits in the second but not in the first year could be also related to different genetic responses to the initial attack, i.e. families differed in how the pine weevil damage affected the subsequent growth. The family and Fer  $\times$  Fam interaction effects are extensively analyzed in a companion paper (Zas et al., 2005).

As a practical conclusion of the present study, fertilization should be considered as a potential dangerous practice when *H. abietis* risk is high. Although harvesting is known to affect nutrient availability (Dambrine et al., 2000; Ouro et al., 2001), the recommendation to fertilize pine plantations (e.g. Sánchez-Rodríguez et al., 2002; Zas et al., 2004) should be revised for second rotation plantations. Besides, several authors have recommend to combat *H. abietis* by combining several silvicultural measures such as delayed planting, soil scarification, shelterwood, and feeding barriers (Orlander and Nordlander, 2003; Sydow, 1997). The recommendation of no fertilization or delayed fertilization should be also included as one of these prophylactic measures.

The effects of fertilization on the insect preferences have been reported previously for other insect–plant systems, and it has been explained in different ways. Fertilization may increase the nutritional quality of the plant tissues eaten by the insects (Ayres et al., 2000; Waring and Cobb, 1992; White, 1993), and/or the resource availability (e.g. greater leader size or bark thickness in fertilized trees) (vanAkker et al., 2004). Fertilization may also decrease secondary metabolite concentrations in plants, thereby reducing host defenses. The increase in growth through fertilization may result in less C available for the production of C-based secondary defensive metabolites (Bryant et al., 1983; Kytö et al., 1996; Waterman and Mole, 1989). Negative effect of fertilization on plant resistance due to a reduction of the number of resin canals per area, changes in secondary metabolite concentrations, and decreased resin flow rate have been reported for *P. sylvestris* and *P. taeda* (Kytö et al., 1999; Turtola et al., 2002; Warren et al., 1999). Unfortunately, since we have no data available on plant nutrient contents or defensive compounds, we do not know whether the increase in feeding damage reported here was related to better host tissue quality, decreased host resistance, or both, or due to some other unknown factor(s).

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