

Juvenile–mature genetic correlations in *Pinus radiata* D. Don. under different nutrient × water regimes in Spain

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Abstract Individual and family heritabilities and juvenile–mature genetic correlations were estimated for growth and biomass traits recorded in treatment with optimal and limiting water and/or nutrient availability to study how the different growth environments affected genetic parameter estimates. Thirty open-pollinated families, randomly selected among the 58 families used in field progeny tests in Galicia, were cultivated for 30 weeks in a climatic chamber under controlled conditions. Two water regimes (high and low water supply) combined with two nutrient regimes (high and low nutrient supply) were applied by subirrigation. Several growth, branching and dry mass traits were assessed 30 weeks after sowing and compared with field performance (height, diameter and volume) of 4-year-old progeny tests established at three different sites in Galicia (NW Spain). Both the irrigation and the fertilization treatments had a strong effect in all the assessed traits except irrigation for the number of branches. Heritabilities for growth and biomass traits were moderate to high (0.13–0.77) in individual treatments. However, when analyzing all treatments together, the impact of the

family × treatment interactions led to a reduction (0.20–0.35) in the heritability estimates. The results indicated that the genotype × water and genotype × nutrient interactions may be important and could not be ignored in the Galician radiata pine breeding program. Climatic chamber–field correlations were different between different traits measured at climatic chamber experiments and the three field tests. The correlations were larger with the well-watered treatments, suggesting that further development of early testing methods for radiata pine in Galicia should include treatments with no limiting water availability.

Keywords Early selection · Radiata pine · Drought · Nutrient availability · Retrospective studies · Climatic chamber–field correlations

Introduction

Radiata pine (*Pinus radiata* D. Don) was introduced in Galicia (northern Spain) in the middle of the last century and was intensively used in forestation due to its fast growth of approximately 18–36 m³/ha/year depending on the altitude above sea level (Dans del Valle et al. 1999) and its reduced rotation age between 25 and 35 years. Improvement in radiata pine in Galicia started in 1992 and has included phenotypic mass selection in local mature plantations based on growth, stem form, and branching habit. A grafted clonal seed orchard and first-generation progeny tests of the phenotypic selections were established to select genetically superior families for the establishment of seed orchards and for further breeding purposes (Codesido and Merlo 2001). As in other tree breeding programmes, a reliable early selection method is highly desirable to increase the genetic gain per unit of time

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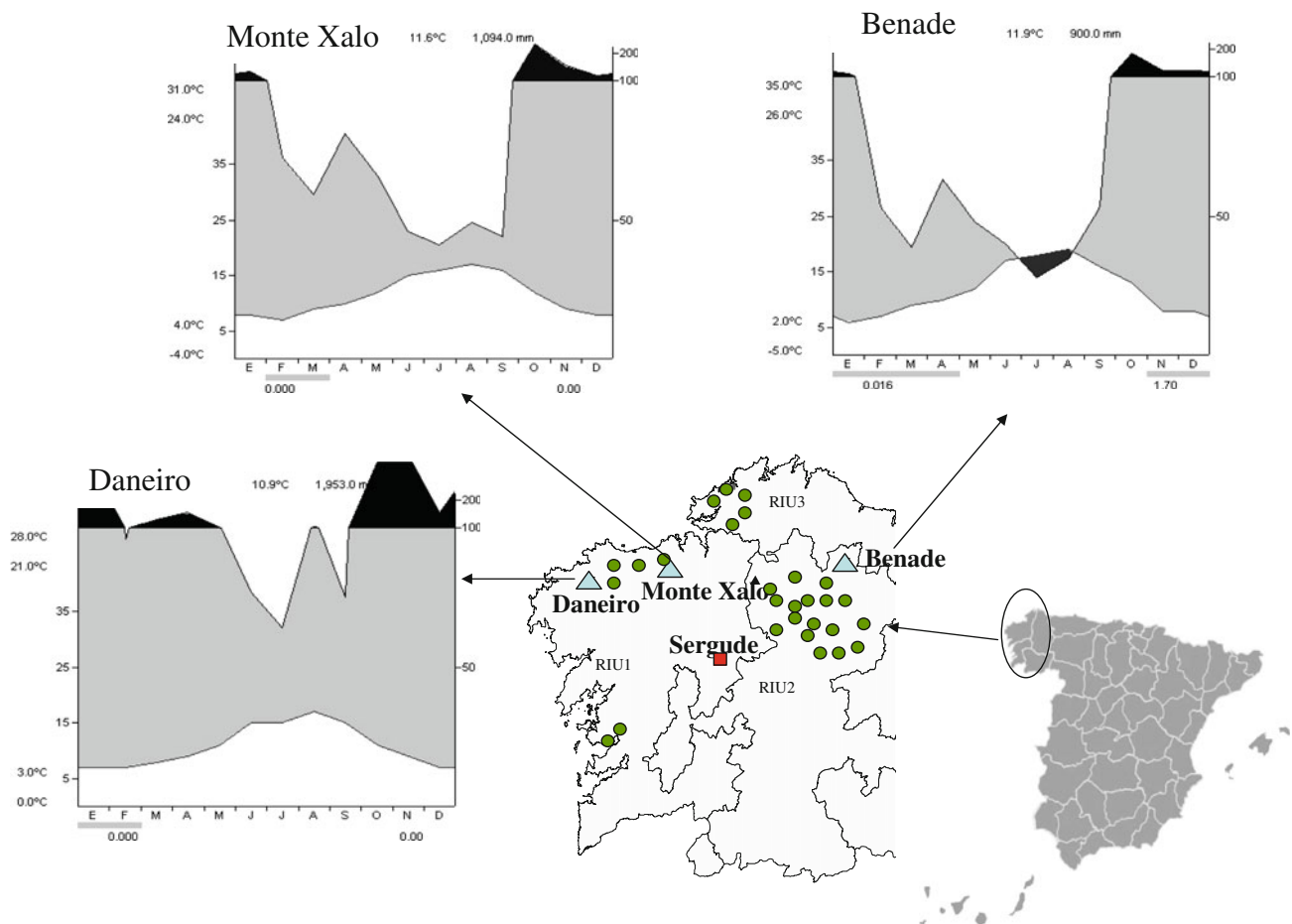


Fig. 1 Location of the *Pinus radiata* plus trees (dots), clonal seed orchard (square) and progeny tests (triangles) over the bioclimatic regions of Galicia. The ombrothermic Gaussen diagrams of three

representative climatic stations are also included. The shadow area of the climatic diagrams denotes the summer drought intensity

(Wu 1999) or to reduce the size and cost of the field tests by early culling of the worse families (Wu 1998). Selection of individuals in tree breeding programmes normally takes place when the trees are younger than the age at commercial felling. Moreover, the efficiency of early selection depends on the juvenile–mature genetic correlation (JM), the heritability for the juvenile trait, and the selection intensity. If these values are high, the potential for efficient early selection is increased, especially if the heritability and/or the selection intensity for the mature trait is low (Sonesson et al. 2002).

The hypothesis that the JM correlations can be improved by mimicking the field environment in the early test environments has been supported by several studies but not in others. In the study by Cannell et al. (1978), the strongest family-mean correlations between nursery performance and field volume at 8 year of *Pinus taeda* families were obtained when the nursery conditions resembled the field conditions. Tan et al. (1995) studied 2-year-old *Picea mariana* seedlings and found significant correlation

between the drought-stressed nursery environment and a field trial at a dry site. From considerations of the literature, it would be particularly interesting to test the hypothesis that genetic correlations between characters assessed at early age and performance in the field would be considerably improved if the environmental conditions were similar in both cases (Eriksson et al. 1993).

The environmental factors that would be of major interest to mimic in the early test environment are the growth-limiting ones. Due to the different kinds of climate within the radiata pine plantation area in Galicia (Fig. 1), the most growth-limiting factors are water and nutrient availability. Climate in the coastal area of Galicia is typically Atlantic with high annual precipitation and lack of summer drought, whereas in the interior area, the summer drought increases, resulting in a more Mediterranean climate (Martínez et al. 1999). The availability of water in summer is clearly the main limiting factor for tree growth in this area.

Additionally, Galicia is a region with acid and sandy soils, of little depth, and with important problems for

nutrient assimilation, especially P, K, Ca, and Mg (Fernández et al. 1996). Many radiata pine plantations in the area suffer important deficiencies in these nutrients, whereas N seems to be well supplied or even in excess (Sánchez-Rodríguez et al. 2002; Romanyà and Vallejo 2004). Knowledge of the genotype \times nutrition and genotype \times water interactions and inclusion of the nutrient and water use efficiency and/or the ability to respond to fertilizer applications as selection factors could be an interesting complement in breeding programmes of rapid growth species in regions where the soils are not fertile like in Galicia. Following the results obtained by Jahromi et al. (1976), the genetic improvement for growth following a genetic selection based on nutritional aspects was 30% higher than the improvement in growth following a conventional genetic selection. Matheson et al. (1995) found significant family differences in response to different combinations of water, N, and P in *Pinus radiata*. They conclude that family \times water and family \times nutrient interactions in climatic chamber could be very similar to family \times environment interaction in field trials. When such interactions are strong, tree breeders must decide whether to select for the stability of performance and accept a slower rate of improvement or to develop populations specifically adapted to each environment in view to maximize gain (Namkoong et al. 1988). Regionalized populations can only be advocated if there is firm evidence that family \times site interactions among the candidate families were so large that potential gains would be reduced to a degree regarded as practically disadvantageous if alternative breeding population structures were adopted. Even where regionalization is not required, knowledge of the patterns of interaction can be crucial for efficient screening of selection candidates (Johnson and Burdon 1990).

The objectives of this study were (i) to determine the genetic variation in seedling growth traits and biomass characteristics of radiata pine open-pollinated families grown under two water regimes and two nutrient conditions and the significance and practical importance of the genotype \times water and genotype \times nutrient availability interactions in Galicia and (ii) to explore the relationships between growth and biomass traits measures in the climatic chamber and 4-year field performance in order to find out a reliable procedure for a pre-selection at the nursery.

Materials and methods

Material

The material used in this study consisted in 30 radiata pine open-pollinated families, three of them from seed recollected from plus trees selected in the Basque Country

(north of Spain) used as controls and 27 families from seed recollected from Galician (northwest of Spain) plus trees: 17 in Lugo, 8 in A Coruña and 2 in Pontevedra. Those families were randomly selected between the 58 families used in field progeny tests in Galicia.

Climatic chamber experiment

As previously established by Zas and Fernández-López (2005) for *Pinus pinaster*, seeds from the 30 open-pollinated families were cultivated in the climatic chamber for one growth period (30 weeks) under different water and nutrient regimes. We followed exactly the same experimental design, culture protocols, and treatment definition as in Zas and Fernández-López (2005). The seeds were sown in 2001 in $7 \times 7 \times 8$ cm pots filled with perlite and covered with a thin layer of sand. Seven weeks after sowing, the successfully germinated pots were placed following a design with four blocks, divided into 4 randomly distributed sub-blocks (one sub-block per treatment). Within each sub-block, there were five randomly distributed repetitions of the 30 families. The total number of seedlings was 5 repetitions \times 30 families \times 4 treatments \times 4 blocks = 2,400 seedlings (Zas and Fernández-López 2005).

As described previously by Zas and Fernández-López (2005), two fertilization treatments crossed with two irrigation regimes were applied together by subirrigation during 23 weeks. The two different irrigation regimes were the well-watered treatment (water high, w:H) with watering to field capacity everyday, and the drought treatment (water low, w:L) with a periodical drought. Drought was regulated by measuring the loss of water content of ten randomly selected seedlings per treatment–block combination, a procedure similar to that described by Sonesson and Eriksson (2000) and Sonesson et al. (2002). These control seedlings were weighed every day or every second day to estimate the water content. The drought treatment seedlings were watered to field capacity that is the maximum amount of water that a particular soil can hold, when the water weight was reduced to 40–20% of the field capacity weight, increasing the drought intensity with time. The control seedlings were weighed again after irrigation.

Within each irrigation regime, two different nutrient solutions were used: the free access treatment (nutrient high, n:H) and the deficiency treatment (nutrient low, n:L). The n:H treatment consisted of a complete nutrient solution (macroelement proportions by weight 100 N:20P:70 K:7Ca:9 Mg:9S and micronutrients) containing 100 mg N Kg⁻¹. The low nutrient availability treatment (n:L) was a 10 times dilution of the n:H solution.

Seedlings were harvested 23 weeks after treatments have started. Total height (H), root collar diameter (D), and dry

weights (80°C, 24 h) of shoots (SDW) and roots (RDW) were measured. The total dry weight (TDW = SDW + RDW), the volume index ($V = H \times D^2$), the root/shoot ratio (RSR = RDW/SDW), and the height/diameter ratio (HDR = H/D) were also calculated.

Analysis

Two types of analysis were carried out, a separate analysis for each treatment and a joint analyses of the four treatments together.

The linear model for the single-treatment analysis was:

$$Y_{ilm} = \mu + F_i + B_l + sb_m(B_l) + \varepsilon_{ilm}$$

where Y_{ilm} is the value of single observation, μ is the overall mean, F_i is the random effect of the family i , B_l is the fixed effect of the block l , $sb_m(B_l)$ is the fixed effect of the sub-block m within the block l and ε_{ilm} is the random error term.

The linear model for the joint treatment analysis was:

$$Y_{ijklm} = \mu + F_i + N_j + W_k + NW_{jk} + B_l + sb_m(NWB_{jkl}) + FN_{ij} + FW_{ik} + FNWI_{ijkl} + \varepsilon_{ijklm}$$

where Y_{ijklm} is the value of single observation, N_j , W_k , and NW_{jk} are the fixed effects of the j th fertilization, the k th irrigation treatments, and their interaction, respectively, $sb_m(NWB_{jkl})$ is the fixed effect of the sub-block m within the fertilization–irrigation–block combination, FN_{ij} , FW_{ik} , and $FNWI_{ijkl}$ are the random interactions between the family i and the j th fertilization treatment, the k th irrigation regime, and the interaction of both treatments, respectively.

Variance components, standard errors, and significance levels were estimated using the restricted maximum likelihood (REML) method of the MIXED procedure in the SAS software (SAS 1989). The data were previously transformed to equal additive genetic variance (Sonesson and Eriksson 2000; Sonesson et al. 2002) to reduce the scale effects resulting from the strong differences among treatments. For each trait and treatment, the original assessed values were multiplied by the scaling factor $k = \sigma_{An}/\sigma_A$, where σ_{An} and σ_A are the additive genetic standard deviation for the w:H-n:H treatment and the given treatment, respectively.

Genetic parameters

Individual heritabilities were calculated as:

$$h_i^2 = \frac{\sigma_A^2}{\sigma_F^2 + \sigma_{FN}^2 + \sigma_{FW}^2 + \sigma_{FNW}^2 + \sigma_e^2}$$

where σ_A^2 is the additive genetic variance estimated as $4\sigma_F^2$, σ_F^2 is the family variance component, σ_{FN}^2 , σ_{FW}^2 , and σ_{FNW}^2 are the variance components for the family \times nutrient,

family \times water and family \times nutrient \times water interactions, respectively, and σ_e^2 is the error variance component.

Approximate standard errors of individual and family heritabilities were calculated as described by Wright (1976).

Field trials

The selected 27 half-sib families are represented in 3 progeny tests established in 2001–2002 in Daneiro (site A), Monte Xalo (site B), and Benade (site C) in Galicia (NW Spain). Site characteristics were presented elsewhere (Codesido 2006; Codesido and Fernández-López 2009). Daneiro and Monte Xalo have Atlantic climate characterized by relative high annual precipitation (mean annual precipitation: 1,776 and 1,200 mm for Daneiro and Monte Xalo, respectively) and low summer drought. Benade show a slight Mediterranean influence with lower annual (900 mm) and summer precipitation (Fig. 1). All sites have acid soils, relatively high levels of total nitrogen, and very low levels of phosphorus.

The sites were within RIUs (region of identification and utilization of forest reproductive material, García del Barrio et al. 2000) number 1 and 2, which constitute, a priori, the breeding area for the selected material (Fig. 1). All sites previously supported radiata pine plantations. Site preparation involved clearing, plowing, and ridging before planting. The design was a randomized complete block design with 25 replicates of single-tree plots with 3×3 m spacing. Tree height (H) and diameter (D) were measured in all trees at age 4 from plantation. A stem volume index was calculated for each tree as $V = H \times D^2$.

Correlations

The significance of the correlations between the early traits in the climatic chamber and the traits measured in field was estimated by Pearson correlation between family means using the SAS corr procedure (SAS 1989).

The type B genetic correlation between traits measured in the climatic chamber and traits measured in the field were estimated as (Burdon 1977):

$$r_{G_{xy}} = \frac{r_{xy}}{\sqrt{h_x^2 h_y^2}}$$

where r_{xy} is the Pearson correlation of family means and h_x^2 and h_y^2 are the family heritabilities of the climatic chamber and field trait, respectively. Heritabilities were calculated on a single-treatment (or single-site) basis. Family heritabilities for the field traits were reported by Codesido and Fernández-López (2008).

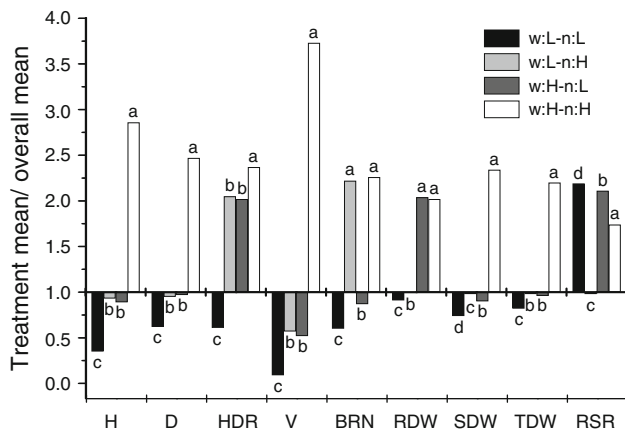


Fig. 2 Effect of treatments on the measured and derived traits. Relative values to overall trait mean are presented. Different letters within the same trait denote significant (Tukey’s test, $P < 0.05$) differences among treatments. Treatments: w:L-n:L = low water and nutrient supply. w:H-n:L = high water and low nutrient supply. w:L-n:H = low water and high nutrient supply. and w:H-n:H = high water and nutrient supply

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{\sigma_m^2}{m}}$$

where m is the harmonic mean number of seedlings per family.

Results

The overall means for all traits were calculated as the average of all trait means measured under each treatment (Fig. 2). Differences between treatments were observed for almost all traits. The highest values for growth and biomass traits were recorded in the treatment that combined high fertilization and irrigation (w:H-n:H), whereas the lowest values were achieved in the drought and poor fertilized treatment (w:L-n:L). Differences between these two extreme treatments were as high as 5, 2.5, and 2 times

higher for height, diameter, and shoot dry weight, respectively. The intermediate treatments (w:L-n:H and w:H-n:L) gave similar intermediate results for all the growth and biomass traits, except for the number of branches (BRN) where best and similar values were for those treatments with high fertilization. The fertilization caused also a significant increase in all the traits measured except in root dry weight. Water stress generally reduced biomass of all components at all nutrient levels. The root/shoot ratio (RSR) was higher in the two low fertilized treatments.

All traits showed significant ($P < 0.05$) family variance in all treatments. Heritabilities estimates were moderate to high for all traits and all treatments (Table 1). For growth traits (H, D, V), the heritabilities were generally higher under low level of nutrients. For almost all traits, the higher heritabilities were observed in the well-watered treatments. Heritabilities for shoot weight were generally higher than for root weight within the same treatment. The w:H-n:L treatment showed the highest heritabilities for all the traits studied.

In the joint analysis, significant family variances were obtained for all the traits (Table 2). Significant interactions with nutrient and water treatments were observed for almost all traits. There was no significant $F \times W \times N$ interaction for HDR and $F \times W$ for BRN. All interactions showed very similar percentage of variance. The ratio $(\sigma_{fw}^2 + \sigma_{fn}^2 + \sigma_{fwn}^2) / \sigma_f^2$, which can be interpreted as the relative importance of the three interactions together in relation to the family variance, was high in all cases. The higher values of the ratio were for volume (V) and for root/shoot ratio (RSR), whereas the lower ones were for HDR and RDW. Significant interactions in the joint analysis produced a reduction in the values of across-site heritabilities in comparison with within-site heritabilities.

The overall means for the juvenile field trials ranged from 157.2 (Benade) to 313.7 cm (Daneiro) for height, from 3.2 (Benade) to 5.8 cm (Daneiro) for diameter, and from 1967.1 (Benade) to 3731.3 dm³ (Daneiro) for volume.

Table 1 Estimates of individual and family heritabilities and their standard errors for single analysis of individual treatments

Treatments	w:H-n:H		w:H-n:L		w:L-n:H		w:L-n:L	
Traits	$h_i^2 \pm \sigma_{h_i}$	$h_f^2 \pm \sigma_{h_i}$	$h_i^2 \pm \sigma_{h_i}$	$h_f^2 \pm \sigma_{h_i}$	$h_i^2 \pm \sigma_{h_i}$	$h_f^2 \pm \sigma_{h_i}$	$h_i^2 \pm \sigma_{h_i}$	$h_f^2 \pm \sigma_{h_i}$
H	0.42 ± 0.01	0.70 ± 0.06	0.66 ± 0.19	0.80 ± 0.08	0.18 ± 0.10	0.48 ± 0.05	0.34 ± 0.13	0.65 ± 0.06
D	0.34 ± 0.01	0.65 ± 0.05	0.47 ± 0.15	0.72 ± 0.07	0.27 ± 0.12	0.60 ± 0.06	0.36 ± 0.13	0.66 ± 0.07
HDR	0.51 ± 0.02	0.74 ± 0.07	0.72 ± 0.20	0.81 ± 0.08	0.29 ± 0.12	0.61 ± 0.06	0.36 ± 0.13	0.66 ± 0.07
V	0.38 ± 0.01	0.67 ± 0.05	0.47 ± 0.16	0.72 ± 0.07	0.19 ± 0.10	0.50 ± 0.05	0.37 ± 0.14	0.67 ± 0.07
BRN	0.60 ± 0.02	0.77 ± 0.07	0.64 ± 0.19	0.79 ± 0.08	0.42 ± 0.15	0.70 ± 0.07	0.77 ± 0.21	0.83 ± 0.08
RDW	0.22 ± 0.01	0.53 ± 0.05	0.44 ± 0.15	0.71 ± 0.07	0.22 ± 0.09	0.81 ± 0.08	0.13 ± 0.08	0.40 ± 0.04
SDW	0.29 ± 0.01	0.60 ± 0.05	0.45 ± 0.15	0.72 ± 0.07	0.28 ± 0.12	0.60 ± 0.06	0.28 ± 0.12	0.60 ± 0.06
TDW	0.27 ± 0.01	0.59 ± 0.05	0.41 ± 0.14	0.69 ± 0.07	0.38 ± 0.14	0.68 ± 0.07	0.14 ± 0.09	0.43 ± 0.04
RSR	0.31 ± 0.01	0.62 ± 0.05	0.69 ± 0.19	0.80 ± 0.08	0.28 ± 0.12	0.60 ± 0.06	0.57 ± 0.17	0.77 ± 0.08

Table 2 Results from the joint treatments analysis. Percentage of variance components estimates, level of significance, estimates of individual heritabilities and their standard errors, and the ratio of interactions to family variance component ($\sigma_{INT}^2/\sigma_F^2 = (\sigma_{FW}^2 + \sigma_{FN}^2 + \sigma_{FWN}^2)/\sigma_F^2$) for the joint linear model of four treatments

Fixed effects				Variance components						
Trait	N	W	N × W	σ_F^2	σ_{FW}^2	σ_{FN}^2	σ_{FWN}^2	σ_c^2	$h_i^2 \pm \sigma_{h_i}$	$\sigma_{INT}^2/\sigma_F^2$
H	***	***	***	8.65 ^{***}	16.96 ^{**}	14.81 [*]	15.02 [*]	44.56	0.35 ± 0.003	5.41
D	***	***	***	6.87 ^{***}	16.03 ^{**}	15.27 ^{**}	15.27 ^{**}	46.56	0.27 ± 0.003	6.78
V	***	***	ns	5.96 ^{***}	23.57 ^{***}	21.41 ^{***}	20.36 ^{***}	28.68	0.24 ± 0.002	10.96
HDR	***	***	***	7.06 ^{***}	13.84 ^{**}	12.75 ^{**}	6.60 ns	59.73	0.28 ± 0.033	4.70
BRN	***	***	**	5.07 ^{***}	7.23 ns	10.10 ^{**}	9.17 ^{**}	68.43	0.20 ± 0.044	5.23
RDW	***	***	***	8.33 ^{***}	12.19 [*]	17.07 ^{**}	13.62 [*]	48.78	0.33 ± 0.029	5.15
SDW	***	***	***	7.86 ^{***}	20.60 ^{***}	22.43 ^{***}	17.23 ^{**}	31.83	0.31 ± 0.002	7.67
TDW	***	***	***	9.37 ^{***}	21.42 ^{***}	22.76 ^{***}	17.40 ^{**}	37.48	0.35 ± 0.021	6.57
RSR	***	***	***	4.88 ^{***}	17.01 ^{**}	17.01 ^{**}	17.01 ^{**}	40.82	0.20 ± 0.002	10.46

ns No significance, F family, W water, N nutrients

*** Significance at 1%, ** significance at 1%, * significance at 0.1%

Table 3 Type B genetic correlation for vigor traits between controlled conditions and progeny tests

Traits	Treatments	Daneiro	Monte Xalo	Benade
H	W:H-n:H	0.59 ^{**}	0.51 ^{**}	ns
	W:H-n:L	0.58 ^{**}	0.57 ^{**}	0.37 ^{**}
	W:L-n:H	ns	ns	ns
	W:L-n:L	ns	ns	ns
D	W:H-n:H	0.52 ^{***}	0.41 ^{***}	ns
	W:H-n:L	0.57 ^{***}	0.50 ^{***}	ns
	W:L-n:H	0.49 ^{**}	0.30 ^{***}	ns
	W:L-n:L	0.47 ^{***}	ns	ns
V	W:H-n:H	0.37 ^{***}	0.32 ^{***}	ns
	W:H-n:L	0.42 ^{++*}	0.45 ^{***}	0.32 ^{***}
	W:L-n:H	ns	ns	ns
	W:L-n:L	ns	ns	ns

ns No significance

*** Significance at 5%, ** significance at 5%, * significance at 0.5%

Individual heritabilities varied from 0.12 (Daneiro) to 0.26 (Monte Xalo) for height, from 0.14 (Daneiro) to 0.29 (Monte Xalo) for diameter, and from 0.13 (Daneiro) to 0.26 (Monte Xalo) for volume (Codesido and Fernández-López 2008).

Genetic correlations between climatic chamber traits and traits measured at field were highly variable (Table 3). Height in Monte Xalo and Daneiro showed high positive genetic correlations with height measured in the well-watered treatments studied at the climatic chamber. Nevertheless, in Benade, there were only low positive correlations with height measured at the w:H-n:L treatment. Genetic correlations with diameter were high between Daneiro and Monte Xalo and juvenile diameter in

each treatment, being highest between w:H-n:L and Daneiro field test. The volume followed the same pattern that height with high positive correlations between treatments and Daneiro and Monte Xalo and no correlations between Benade and almost the four treatments with only moderate positive correlation with w:H-n:L treatment. Coefficients of correlation higher than 0.5 were obtained for H, D, and V between the well-watered treatments and Daneiro and Monte Xalo trials.

Discussion

The differences among treatment means (Fig. 2) reflected the very different growth conditions among treatments. For almost all traits, highest values were obtained for the w:H-n:H, as expected. In the w:H-n:H treatment, the root dry weight biomass is about the 50% of the shoot dry weight biomass (Fig. 2), whereas for the other three treatments, the differences between those biomass traits are not so high. Olykan and Adams (1995) found a shift in biomass production from the roots to the shoots after application of nitrogen fertilizer in radiata pine seedlings. The present work showed that a water stress imposed to roots resulted in a growth reduction of the shoot but not of roots in radiata pine as occurred in *Pinus pinaster* (Harfouche 2003; Zas and Fernández-López 2005). The root/shoot ratio was higher for the w:L-n:L treatment (1.00) than for w:H-n:H treatment (0.61), whereas the intermediate treatments showed similar values (0.93) for RSR, indicating that the absence of water and/or nutrient stimulated the root system development. Under those conditions, the seedlings had higher growth rate of the root than of the shoot as a defense

mechanism of the plant that employs more efforts to find water and nutrients than to its shoot growth.

Otherwise, fertilization increased the number of branches because under water and/or nutrient availability, there was no root growth. Nambiar and Fife (1987) found that application of nitrogen fertilizer to radiata pine increased the number and size of needles, rates of shoot production, stem volume, and tree biomass. The immediate response to fertilization alone in radiata pine was an increase in new foliage production in an experiment carried out in Australia (Snowdon and Benson 1992).

The heritabilities are higher for the growth traits in the climatic chamber experiment than in the field trials reflecting enhanced genetic expression under increased environmental control as occurs for *Populus tremuloides* (Thomas et al. 1997), *Picea abies* (Sonesson et al. 2002), and *Pinus sylvestris* (Sonesson et al. 2001). The strength of the controlled conditions experiments is the possibility to reduce the environmental variance and make genetic variances appear more clearly, so the heritability estimates are normally higher than the heritability estimated in field trials (Sonesson and Eriksson 2000). Heritabilities were high for growth traits under the four treatments. The heritabilities found for biomass traits were, nevertheless, moderate (Table 1). In general, the highest heritabilities were found under the w:H-n:L treatment, except for the number of branches (BRN) that the highest one was found under the w:L-n:L treatment and for the RSR that where the highest value was found under the w:L-n:H treatment. Those data agree with other studies where the highest heritabilities were found under low nutrient availability (Li et al. 1991; Mari et al. 2002). The highest heritability obtained for BRN under the poorest treatment could be due to the high production of branches under nutrient availability that could diminish the family differences for this trait and in consequence diminish also the heritability estimate.

In the combined analysis (Table 2), the heritabilities were lower than for the individual analysis due to the family \times water ($F \times W$) and the family \times nutrients ($F \times N$) interactions. These interactions were significant and very similar in magnitude for almost all of the studied traits. Progeny tests under controlled conditions for other species like *Pinus pinaster* (Zas et al. 2004), *Pinus sylvestris* (Sonesson and Eriksson 2003), *Picea abies* (Sonesson et al. 2002), and *Pseudotsuga menziesii* Mirb. Franco (Joly et al. 1989) showed important $F \times N$ interactions but the $F \times W$ interaction had very little importance. Several authors found significant $F \times N$ interaction for other species like *Pinus sylvestris* (Jonsson et al. 1997), *Picea abies* (L.) Karst. (Mari et al. 2002), and *Picea mariana* (Mill.) B.S.P. (Mullin 1985). The sum of the three interaction variances was high in relation to the family variance as occurred in an identical experiment carried out

with *Pinus pinaster* families from the breeding program of this species in Galicia (Zas et al. 2004), indicating that the $F \times W$ and $F \times N$ interactions should not be ignored in the Galician radiata pine breeding program.

One of the main goals of this study was to find out the best traits and the best environmental conditions to use in a reliable early selection strategy. Growth traits, especially diameter, appeared as a better early trait than dry masses. Similar conclusion was obtained by Matheson et al. (1995) for *Pinus radiata*, Sonesson et al. (2001) for *Pinus sylvestris*, and Zas et al. (2004) for *Pinus pinaster*. The heritabilities for this trait under each treatment and also in the combined analysis were from moderate to high as well as the correlations with diameter measured at field (Table 3).

Optimal environments and appropriate juvenile–mature correlations were investigated to improve the heritability at early ages and to increase the juvenile–mature correlations to reinforce the effectiveness of early selection (Harfouche 2003). We obtained significant JM correlations for height between water high treatments and Daneiro and Monte Xalo trials but there were no correlations with water low treatments (Table 3). This could be because the low availability treatments did not mimic trial conditions. The JM correlations found for diameter were higher than for height. There were no correlations between Benade trial and all the four treatments, as well as between Monte Xalo trial and the w:L-n:L treatment. In Galicia, the soils are normally well watered but there is low concentration of nutrients. Then, mimicking those conditions when early testing could be a way to optimize early selection in Galician radiata pine breeding program. The treatment w:H-n:L, which is the treatment most similar to Galician conditions, increased greatly the heritability estimated for all traits studied. Average juvenile–mature family-mean correlations between climatic chamber traits and 4-year-old growth traits in the field trials were generally also higher for the treatment w:H-n:L. Intermediate water and nutrient conditions should be tested to find out the best environmental conditions for early testing in the Galician *Pinus radiata* breeding program. In loblolly pine, strongest family-mean correlations were found when the nursery conditions were comparable to field environments (Cannell et al. 1978); on the other hand, shoot/root biomass ratio of well-watered seedlings was the better predictor of later performance than other traits of seedlings disregarding the water regime (Waxler and van Buijtenen 1981). In lodgepole pine, 2-year seedling traits in the climatic chamber were correlated with 9-year tree height on the only site (among four) whose growth conditions were closer to those in climatic chamber (Wu et al. 1997). In Scots pine, growth chamber data were found to be more genetically correlated with older field data for the higher fertilization regime in one study (Eriksson et al. 1993), whereas several strong

juvenile–mature correlations between low nitrogen treatment and northern field sites (where *N* was more limiting) were obtained in another one (Abraitis et al. 1998). In Norway spruce, it was found that heritabilities for biomass and height of 2-year-old plants were moderate to high in the well-watered treatment and weaker in the drought treatment; on average, juvenile–mature (24-year-old growth traits in the field) correlations were stronger in the drought treatment than in the well-watered treatment (Sonesson et al. 2002).

It could be concluded from this work that candidate traits for early selection for adult growth in radiata pine could be found at a very juvenile age. The heritability estimates should provide a baseline for direct comparisons with future trials. The most questionable thing is whether mimicking field conditions in growth chamber should really improve the efficiency of retrospective tests in this species. Field conditions are a complex of interlinked factors, and genotype \times site interaction in field trials is also a major factor for the lack of juvenile–mature correlations in forest trees. Otherwise, field trials are still too young so further investigations at mature age must be carried out as well as refinement on the field and at the growth chamber to find adequate experimental conditions as well as appropriate juvenile traits in radiata pine in Galicia.

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