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Genetic control of stem form in *Pinus pinaster* Ait. seedlings exposed to lateral light

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Abstract In order to compare family differences in stem form determination, seedlings of eight half-sib progenies of *Pinus pinaster* were exposed to three different light treatments: fixed lateral light (T1), alternate lateral light (T2), and direct sunlight (T3). From spatial coordinates of several points along the stem we computed four variables: global leaning (GL), apical leaning (APL), flexuosity index (FL) and length of the stem (LEN). Based on comparisons of the four variables, the phototropic stimulus caused different responses in stem form at the familial level. Treatment had an important effect on stem form, although the familial response to treatments was quite variable. Heritability values (h^2) of the four analyzed variables showed a different pattern of variation for the three treatments, being very stable for LEN and FL, whereas h^2 of APL was much greater based on T1 and T2 compared to T3, and h^2 of GL based on T2 was much greater compared to T3 and T1. Differences in stem form were due not only to photomorphogenetic response to different light stimuli, but also to the straightening processes such as compression wood formation. The results suggest that lateral light treatments may be useful in revealing differences in efficiency of the mechanisms involved in stem form determination.

Key words *Pinus pinaster* · Stem form · Phototropic response · Early selection

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Introduction

The function and economic gain obtained from the product “wood” depends not only on volume, but also on quality. The yield in raw material and the quality of the final product are partially determined by the external shape of the stem. Stem flexuosity affects costs and methods of transport, processing and the technological properties of the final piece of wood. Importance of stem flexuosity varies with the species and the use of wood (Aldhous 1986; Bailleres 1991; Kellog and Warren 1984; Larguia 1967). Therefore, the stem form is a relevant character to consider in the management and genetic improvement of forest tree species.

Reports on the genetic control of the stem straightness show great variability. Zobel (1971) showed that inheritance of tree bole straightness in *Pinus elliottii* is so strong in the first breeding generation that further improvement of this trait is not a concern in the second breeding generation. High heritabilities in characters related to stem straightness have been reported by Magini (1969), computing a familial heritability of 0.9 in 13-year-old *P. pinaster* based on an index of tree form described by $Lc/Hc+k$ (Lc : basal curvature length, Hc : height reached by basal curvature, k : constant). Williams and Lambeth (1989) obtained a familial heritability of 0.7–0.8 in 8-year-old *P. taeda* based on stem straightness with a subjective scale from 1 to 6. The same authors reported a familial heritability of 0.59–0.64 based on maximum deflection in the lower portion of the bole.

In contrast, very low heritabilities have been calculated by other authors: Conche (1978) calculated $h^2 = 0.19$ based on deviation from the vertical at 1.5 m high, in 10-year-old *P. pinaster*. Cotterill et al. (1987) evaluated stem straightness on a subjective scale from 1 to 8 and found $h^2 = 0.03 \pm 0.02$ in *P. radiata* and $h^2 = 0.15 \pm 0.09$ in 8.5-year-old *P. elliottii*. Intermediate values have also been reported (e.g. Mauge et al. 1973; Shelbourne et al. 1972).

Comparisons of different results are difficult due to the variability of methods used to evaluate stem straightness,

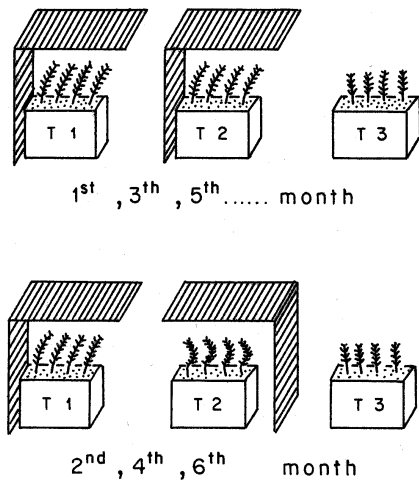


Fig. 1 Diagram of the experiment, showing the position of the shadow sheet in each treatment. Treatment 1: fixed lateral light; treatment 2: alternate lateral light (monthly rotation of light incidence angle 180°); treatment 3: direct sunlight. T1, T2, T3: Treatments 1, 2 and 3 respectively

compounded with variation in testing environments, species, age at the time of evaluation and the inbreeding level of the studied population. Particularly problematic are evaluation methods based on subjective scales which may involve a global concept of the stem form, including straightness, leaning, taper, branches, knots, etc. Each of these characters may be controlled by different genes and their management as a pool may lead to confusing results about genetic control. In this paper, we will use "stem form" to refer to the longitudinal shape of the tree bole, characterized by its straightness and leaning.

Pinus pinaster Ait. has a remarkable tendency for flexuosity. Its theoretical architectural pattern is described as a main stem, growing straight and vertical, dominant over the lateral branches. Different external factors may affect the main stem, inducing curvatures. For instance, damage in the apex of the leader by frost, wind or herbivores usually induces lateral branch dominance. The reorientation of a lateral branch to the vertical position is a typical origin of curvatures in the bole (Loup 1990). The effect of wind in causing basal curvature of the bole has also been reported (Polge and Illy 1967; Radi and Castera 1992).

Another external factor affecting stem form is the lateral incidence of light. Phototropism may play a relevant role in the determination of the stem form. The main direction of the incident light on a tree may be lateral for many years, or may change repeatedly during its life (e.g. because of the development or disappearance of neighboring trees, or because of seasonal growth of herbaceous plants or shrubs in the early stages of its life).

Differences in stem form may be due to different sensitivities to the external deforming factor and different abilities to straighten following a deviation from the vertical line. This ability of reorientation is directly related to the differentiation of compression wood. An initial curva-

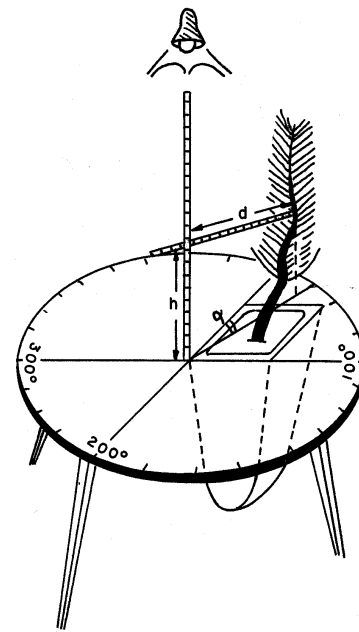


Fig. 2 Device to obtain spatial coordinates on the stem

ture formed in an early given year due to a phototropic response, for instance, may persist for years, more or less reduced by compression wood.

The aim of this work is to evaluate *P. pinaster* familial level responses in stem form to three phototropic stimuli. We also discuss the value of phototropic response as an early selection index for stem form.

Materials and methods

In spring 1990, seeds from 100 open pollinated *P. pinaster* trees from Sierra de Gredos provenance (mountains in central Spain) were collected in distant natural stands to establish an improvement population (Sierra-de-Grado and Alía 1993). Average age of mother trees was 62 years. Eight of those seed-lots were sown in a greenhouse in December 1990, originating eight half-sibs families genetically independent one from each other. In March 1991, seedlings had reached a medium height of 12 cm and were established in the INIA nursery in Madrid. Seedlings were exposed to the following treatments:

Treatment 1 (T1): Fixed lateral light.

Treatment 2 (T2): Alternate lateral light (monthly rotation of light incidence angle 180°).

Treatment 3 (T3): Direct sunlight.

The lateral incidence of the light was created covering the seedlings with an 80% black shadow sheet. In treatment 1, the shadow sheet was always in the same position; in treatment 2, it was changed to the opposite position monthly (Fig. 1). The experimental unit consists of six seedlings of the same family, with three repetitions by treatment (total 432 plants). Mortality reduced the total number of seedlings to 425.

For each plant, spatial coordinates of the points where the stem changed its direction were recorded. The device used to obtain spatial coordinates consisted of a graduated vertical axis, a graduated needle to measure distances (mm) in the horizontal plane, and a zenithal light projecting the needle shadow on a circular protractor placed at the base of the seedling, to measure azimuths (Fig. 2). The accuracy of

Table 1 Mean values and standard deviations of global leaning (GL, grades), apical leaning (APL, grades), flexuosity index (FI) and length (LEN, cm) in July measurements (T: treatment, F: family)

T	F	GL	STGL	APL	STAPL	FI	STFI	LEN	STLEN
1	1	16.28	8.73	20.00	7.85	0.02	0.01	16.65	3.89
1	2	14.56	10.61	24.72	15.01	0.06	0.05	13.19	2.58
1	3	16.61	8.75	19.67	7.41	0.05	0.11	16.88	3.47
1	4	10.89	6.94	19.89	11.69	0.02	0.02	13.20	2.72
1	5	19.17	12.88	29.89	13.61	0.06	0.04	13.57	3.42
1	6	18.33	12.67	12.44	23.38	0.04	0.06	15.66	4.02
1	7	23.06	14.52	28.61	7.86	0.07	0.08	11.21	1.58
1	8	11.89	14.74	10.33	7.38	0.03	0.05	14.59	2.92
1		16.35	11.87	20.69	14.16	0.04	0.06	14.37	3.59
2	1	22.67	13.11	39.61	17.42	0.07	0.11	14.39	4.91
2	2	12.39	8.96	23.61	11.61	0.06	0.07	11.67	2.02
2	3	23.28	13.12	25.72	12.10	0.08	0.08	13.14	3.12
2	4	8.50	7.87	14.78	6.53	0.01	0.01	12.17	3.28
2	5	15.44	7.35	16.17	22.90	0.05	0.05	11.67	2.09
2	6	17.83	11.37	20.33	9.24	0.03	0.04	12.92	2.88
2	7	15.28	9.55	23.94	12.28	0.04	0.05	9.06	1.88
2	8	14.11	8.92	16.11	9.25	0.03	0.03	16.14	3.37
2		16.19	11.04	22.53	15.23	0.05	0.06	12.64	3.59
3	1	5.31	6.01	9.44	6.94	0.02	0.01	7.78	1.21
3	2	7.94	12.34	7.88	5.35	0.03	0.03	6.15	2.11
3	3	5.06	6.57	11.78	9.90	0.01	0.01	7.42	1.62
3	4	3.13	4.27	9.69	8.62	0.01	0.01	7.36	1.34
3	5	5.94	6.53	11.38	6.04	0.04	0.03	6.19	0.72
3	6	7.11	9.12	12.44	7.85	0.02	0.02	8.24	1.33
3	7	1.78	4.17	12.56	12.55	0.02	0.02	5.08	0.96
3	8	9.00	4.59	11.06	9.38	0.03	0.06	8.57	1.66
3		5.68	7.38	10.82	8.60	0.02	0.03	7.11	1.80

measurements was 1 mm in vertical distances, 5 mm in horizontal distances and 5 grades in azimuths.

Measurements of the 425 were taken in July, when the seedlings were 8 months old. In October 1990 and March 1991 measurements were repeated on a subset of 35 plants exposed to the fixed lateral light treatment and of 20 plants in the alternate lateral light treatment to observe changes over time. Comparisons among the three dates of measurement have been made based on the same 35 plants in T1 and the same 20 plants in T2.

Analysis

The original data are the spatial coordinates of a set of points M_i , $i = 1 \dots N$, representing the central line of the stem. The principal axes of inertia of this set of points have been calculated through the diagonalization of the inertia matrix, initially expressed as the inertia matrix respective to the coordinates' axes translated to the center of inertia of the set of points (Mouliu et al. 1994). It can also be seen as a Principal Component Analysis (PCA), but done on a covariance matrix to maintain the proper scale (Sinoquet et al. 1991). The longitudinal shape of the central line has been characterized by four morphometric variables which have been defined as follows:

GL: Global leaning; angle between first major axis and the vertical axis (grades). It represents the overall mean direction of the stem.

APL: Leaning of the apical segment of the stem, i.e. angle between segment $M_N M_{N-1}$ and the vertical axis (grades). It represents the direction of longitudinal growth in relation to the vertical.

FI: Flexuosity index (dimensionless), defined as $FI = 1 - (PL/LEN)$, where:

PL: Length of the projection of the set of N points on the first major axis,

LEN: Length of the line joining the N points (cm).

If $PL = LEN$ ($FI = 0$), then the set of points are on a straight line. The closer FI is to 1, the greater the stem flexuosity.

For the July measurements we first applied a mixed model of ANOVA to study treatment response and familial effect. The main effects analyzed were family, treatment, repetition within treatment and interaction of treatment by family. Secondly, we estimated heritability of indices GL, APL, FI and LEN based on the separate treatments. Heritability, in a narrow sense, has been calculated as:

$$h^2 = 4V_f/V_e + V_f$$

with V_f the familial variance and V_e the variance of error (Falconer 1986).

Results

The mean values and standard deviations of analyzed variables by family and treatment for the July measurements are shown in Table 1. Table 2 summarizes the ANOVAS for each variable. The factors are highly significant for all the variables analyzed, except the treatment*family interaction for FI.

Treatment is the most significant factor for all the variables. The analysis of this main factor in the population as a whole indicates that interaction has no effect in the ranking of treatments. Plants of lateral light treatments (T1 and T2) reached higher longitudinal growth than control plants (T3). This higher growth can be explained both by photomorphogenetic enlargement and better conditions of temperature and humidity under the shadow sheet. As a result, plants of treatments 1 and 2 had longer internodes than plants with direct sunlight treatment (T3). Seedlings of

Table 2 Summary of analysis of variance for GL, APL, FI and LEN in July measurements

Source of variation	DF	GL		APL		FI		LEN	
		MS	PR > F	MS	PR > F	MS	PR > F	MS	PR > F
TREATMENT	2	5202.26	0.0001	5511.12	0.0001	0.02347	0.0003	2002.58	0.0001
REP(TREAT)	6	290.96	0.0059	436.52	0.0050	0.00679	0.0269	10.33	0.2032
FAMILY	7	317.51	0.0017	683.63	0.0001	0.00936	0.0019	137.93	0.0001
TREAT*FAM	14	250.14	0.0011	688.38	0.0001	0.00456	0.0719	16.28	0.0061
RESIDUAL	395	94.64		138.51		0.00282		7.25	

Table 3 Multiple range analysis (Tukey) for treatment factor (T) in July measurements. Means with the same letter do not significantly differ at $P = 0.05$

Treatment	GL	Treatment	APL	Treatment	FI	Treatment	LEN
3	5.65 A	3	10.77 A	3	0.023 A	3	7.09 A
2	16.18 B	1	20.69 B	1	0.043 B	2	12.64 B
1	16.34 B	2	20.53 B	2	0.047 B	1	14.36 C

fixed lateral light treatment were significantly longer (13%) than plants of alternate lateral light treatment.

The variables GL, APL and FI did not show statistically significant differences between treatments 1 and 2 (Table 3). Treatment 3 greatly differed from treatments 1 and 2 for all the analyzed variables. It is notable that means of GL,

APL and FI in direct sunlight treatment are significantly different from 0.

Family effect is highly significant for all the analyzed variables. As shown in Table 1, the mean length (LEN) of the stem is higher in fixed lateral light treatment than in alternate lateral light. This is true for plants in each family, except for family 8, in which plants reached a higher length in treatment 2 (Fig. 3).

The familial response to treatments is quite variable (Fig. 3), which is expressed through the interactions of treatment by family (Table 2). Global leaning (GL) in direct sunlight treatment (T3) was always lower than in treatments 1 and 2, but some families (1, 3 and 8) show lower GL under fixed lateral light treatment than under alternate lateral light, while the other families tend to have greater

Fig. 3 Means of global leaning, apical leaning, flexuosity index and length by family and by treatment. *GL*: global leaning, *APL*: apical leaning, *FI*: flexuosity index; *LEN*: length

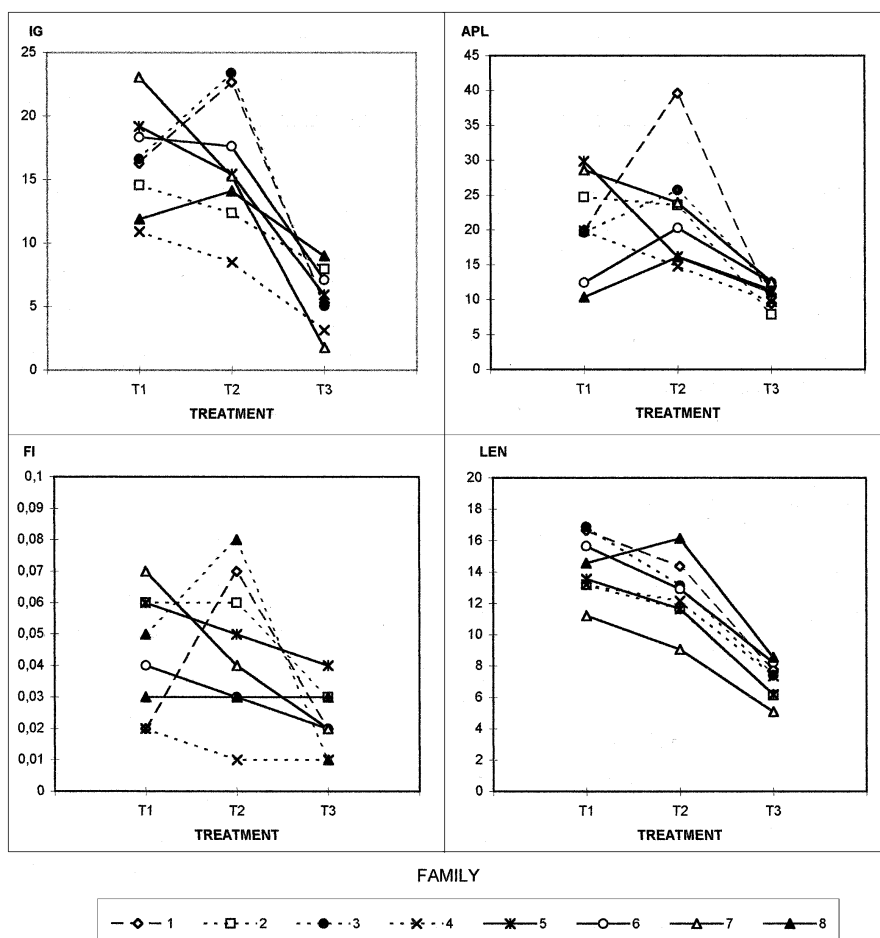


Table 4 Heritabilities of variables GL, APL, FI and LEN for each treatment, based on July measurements

Variable	Direct sunlight (T3)	Fixed lateral light (T1)	Alternate lateral light (T2)
GL	0.17 ± 0.19	0.23 ± 0.23	0.61 ± 0.37
APL	0	0.77 ± 0.22	0.91 ± 0.45
FI	0.27 ± 0.24	0.22 ± 0.22	0.27 ± 0.25
LEN	1.58 ± 0.59	0.98 ± 0.47	1.15 ± 0.51

Table 5 Correlation matrix between GL, APL, FI and LEN in July (425 observations)

	GL	APL	FI	LEN
GL	–	0.48 0.0000	0.51 0.0000	0.36 0.0000
APL		–	0.30 0.0000	0.26 0.0000
FI			–	0.15 0.0020

leaning under fixed lateral light. Familial response to treatments is quite variable for APL and FI, as well.

Heritabilities of indices GL, APL, FI and LEN estimated for each treatment are shown in Table 4. The total length of the stem (LEN) and the flexuosity index (FI) have very stable values in all treatments. Heritability of LEN is always near 1, while heritability of FI is quite low for all three treatments. The variance of the heritability estimate is 22% of the heritability value. We estimated the variance of heritability by computing:

$$V(h^2) = 32 h^2/T$$

with T = the total number of data (Falconer 1986). In our case, as h^2 is calculated separately for each treatment, T = 144.

In contrast, heritability of general leaning (GL) varies from low values in direct sunlight and fixed lateral light treatment to 0.61 in alternate lateral light treatment. The terminal leaning (APL) exhibits a dramatic increment of the heritability value, ranging from 0 in direct sunlight treatment, increasing to 0.77 in fixed lateral light treatment, and reaching a maximum of 0.91 in alternate lateral light treatment.

The correlation matrix of the variables LEN, GL, APL and FI in July measurements (Table 5) shows a positive correlation between them, but correlation coefficients are quite low.

Results of the measured variables over time indicate a general correspondence between the four morphometric variables and the occurrence of longitudinal growth. Longitudinal growth occurred in fixed and alternate lateral light treatments between July and October. In this period, GL and APL increased but there is no significant change in FI. Between October and March there was no longitudinal growth due to low temperatures. Mean values of GL, APL and FI are not significantly different in this period (Table 6).

Discussion

In the studied population, the longitudinal shape of the stem differs from a straight and vertical line even in the direct sunlight treatment, showing once more the tendency for flexuosity in *P. pinaster*.

At the familial level the phototropic stimuli elicit different responses in stem form, mainly in GL (global leaning) and APL (leaning of the apical segment). Differences in phototropic sensitivity among progenies of *Pinus sylvestris* have been reported by Bolland (1965). They have also been detected among clones of *Populus* spp. (Lattke 1965; Barner 1954).

However, after 4 months of treatment, the stem form is not only a function of sensitivity to the initial factors inducing curvatures or leaning (phototropism in our case), but also a function of the straightening processes, that is the formation of compression wood, and of the influence of geotropism (Sierra-de-Grado and Alía 1994).

The mean values of GL in fixed and alternate lateral light treatments are not significantly different, which may result from the same initial position of the shadow sheet in both treatments. The reorientation of stems in the alternate lateral light treatment have not been great enough to change the overall direction of the stem. This may be explained by a progressively weaker response to the phototropic stimulus, as is reported by Roussel (1966), or simply because the lag of 1 month between changes in the orientation of the

Table 6 Mean values and 95% confidence intervals of GL, APL, FI and LEN in July, October and March measurements (J: July, O: October, M: March; T: treatment; n: number of seedlings measured)

	T	n	GL		APL		FI		LEN	
			Mean	95% Confidence limits	Mean	95% Confidence limits	Mean	95% Confidence limits	Mean	95% Confidence limits
J	1	35	17.8	14.0–21.6	20.8	14.4–27.3	0.040	0.013–0.067	14.8	12.0–17.5
	2	20	13.6	8.6–18.7	17.4	8.9–25.9	0.036	0.001–0.072	14.2	10.5–17.9
O	1	35	25.7	21.9–29.5	29.5	23.1–35.9	0.052	0.025–0.079	19.1	16.3–21.9
	2	20	19.4	14.4–24.5	31.1	22.6–39.6	0.056	0.020–0.091	21.1	17.4–24.8
M	1	35	29.5	25.7–33.3	32.4	26.0–38.9	0.078	0.052–0.105	20.3	17.5–23.1
	2	20	23.0	17.9–28.0	35.0	26.5–43.5	0.089	0.054–0.125	25.2	21.5–28.9

shadow sheet in treatment 2 is shorter than the time required to recover another position. Loup et al. (1991) describe a 3-year-old *P. pinaster* artificially bent to 45°, which required nearly 2 months to reduce the leaning angle by one-half.

In experiments with *P. pinaster* (Loup et al. 1991; Fournier et al. 1994) and several other conifers (Yoshizawa et al. 1986) with artificially bent stems, gravitropic stimuli for changes in stem form have demonstrated a very rapid reorientation of the apical portion of the stem (scale of hours) and, subsequently, the whole stem slowly straightening to reduce the leaning. In the experiment reported here, with a phototropic stimulus inducing changes in stem form, the apex leads the longitudinal growth direction with an angle from the vertical, ultimately displayed by GL. This GL, instead of decreasing during the growth period as in these cited experiments, increases from July to October, and shows negligible change from October to March.

The difference can be explained in terms of initial treatments. In the cited experiments, plants were grown upright for 3 years and then inclined to 45° producing the artificially bent form. Once inclined, they had to readjust their structure with the altered gravitational condition. In contrast, in the present study, plants were continuously grown under lateral light. Therefore, the leaning of the stem has been a consequence of the interaction between responses to a constant gravitropic condition and the phototropic treatment stimulus applied during the growing period. Simultaneously, this leaning stem has been exposed to a gradual increment of weight (because of growth between July and October), which also contributes to the increment of leaning.

From October to March, the lack of growth results in lack of increment of weight and lack of response to the phototropic stimulus, since only elongating stems can move to the light (Wiesner 1897, cited in Timell 1986). Correspondingly, there are no changes in GL, APL and FI in this period.

The comparison of the four studied variables in the three different treatments leads to some points for discussion:

1. The pattern of variation for the four variables and their respective heritabilities differ greatly (Table 4). This pattern, along with the low correlations between variables, suggest that we are evaluating characters responsive to different processes, or in other words, controlled by different genes.
2. The heritabilities of longitudinal growth (LEN) and flexuosity index (FI) scarcely vary with treatment, but treatment greatly affects heritability of GL and APL. Heritability of LEN is possibly overestimated by maternal effects. FI does not seem a very sensitive index, because the geometrical shape of a seedling stem always has a longitudinal predominant direction. The strong effect of treatment on the heritability of GL and APL can be explained by the physiologic response at the familial level to the lateral light stimulus (T1) which is not elicited in direct sunlight treatment (T3) for APL; similarly for GL, there is a familial level physiologic response elicited by alternate lateral light

(T2), which is absent in T1 and T3. A similar case would be tolerance to draught non-manifested in a moist environment. In this sense, T2 would be an environment inducing more stress than T1, and T1 inducing more stress than T3, with respect to the stem form determination.

As noted above, the apical part of the stem reacts more quickly than the whole stem when the stem is bent. Differences in abilities for reorientation of the apical stem, coupled with a strong genetic control of this ability would explain the great differences in the heritability of APL.

For GL, the distinctive process elicited by T2 and absent in T3 and T1 could be related to compression wood formation speed. Following Wilson and Archer's theory (1979), compression wood formation occurs when the stem undergoes a change of orientation in the gravitational field, and consequently, auxin concentration increases in the lower side of the stem and decreases in the upper side.

Differences of stem reorientation speed in response to a change in the light incidence direction, or differences in auxin translocation rate at the familial level could be responsible for the increment of GL heritability in T2 with respect to T1. This hypothesis is supported by the anatomic study undertaken in plants of families 3 and 8 (Sierra-de-Grado 1994). In T2, areas of compression wood in the upper side of the stem were more frequently found in seedlings from family 8 than in family 3, suggesting a higher response speed in family 8. Familial differences were not manifested in T1. References to variability in compression wood formation patterns are found in the literature, although mainly at species level (Fisher and Wassmer 1981; Yoshizawa et al. 1986).

These results confirm the existence of variation of stem form in response to phototropic stimuli at the familial level in *P. pinaster*. However, to what extent can seedling stem form response to phototropic stimuli be used as an early selection criterion for stem form in the adult stage?

Arbez (1979) argues against a possible early selection test based on seedling phototropism in *P. pinaster*, since the mean of hypocotyl leaning at provenance level in germination tests under lateral light did not agree with mean stem straightness at provenance level. However, from our observations, there was no strong correlation between hypocotyl and epicotyl performance. We observed that hypocotyl performance can be quite erratic (unpublished results). Also, the rate of compression wood formation and the rate of weight increment may introduce important modifications that are not present at emergence time. In contrast, Schrock (1958) reported that progenies of *Pinus sylvestris* selected by straightness and yield, generally had scarce phototropic reaction, although there was great variability in some progenies.

Another unfavorable argument might come from Rousset (1966). He observed in 11 of 12 conifer species that trees lose their phototropic sensitivity at 3 or 4 years old, except *Pinus sylvestris*, which can retain a phototropic tendency up to an advanced age, developing flexuous stems. *P. pinaster* was not included in his study, and to

our knowledge there are no detailed studies of phototropic responses in *P. pinaster* at an advanced age.

There are still many unknowns related to the possible juvenile-adult correlation of stem form, and to processes involved in stem form determination. The mechanisms by which plants adapt their form to environmental events are manifested in phototropic reactions. Those mechanisms may be more or less efficient in different progenies. Tests based on reactions to stimuli that produce curvatures or leaning, like phototropism, can be useful in revealing such mechanisms and their efficiency. As we have suggested above, different mechanisms may be involved in stem form determination under different treatments of lateral light and direct sunlight, with familial effects enhanced when the environment is less favorable to formation of straight and vertical stems. Finally, a more detailed knowledge of the evolution of such mechanisms during ontogeny is required to establish more useful indices in early selection of stem form.

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