Ann. For. Sci. 57 (2000) 9–16

Original article

Effects of water supply on gas exchange in *Pinus pinaster* Ait. provenances during their first growing season

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(Received 26 March 1999; accepted 16 July 1999)

Abstract – Gas exchange parameters were monitored during the first growing season on *Pinus pinaster* young seedlings belonging to six provenances and submitted to two water supply regimes in the open air under cover. Significant differences were found between water supply regimes and measurement dates; sometimes also between provenances. Gas exchange rate responses to needle water potential were similar for all the provenances, and rate changes were only detected as water potential went down to less than –1.3 MPa. The Iberian provenances, in contrast to the Landes, showed a tendency to save water at the end of Spring, which indicates an adaptation to locations with Summer drought. The growth differences between provenances were not expressed in terms of differences in the instantaneous net photosynthetic rate, since this will depend on other factors, such as seedling water status and the time that the measurement was made. However, provenance growth differences may be partially explained by the differences in water use efficiency and nitrogen productivity.

maritime pine / early selection / gas exchange parameters

Résumé – **Effets de l'alimentation en eau sur les échanges gazeux des provenances de *Pinus pinaster* Ait. au cours de leur première saison de végétation.** Les échanges gazeux ont été étudiés au cours de la première saison de végétation de jeunes semis de *Pinus pinaster* appartenant à six provenances et soumis à deux régimes d'alimentation en eau sous couvert en plein air. Des différences significatives ont été trouvées entre les régimes d'alimentation en eau et les dates de mesures, parfois aussi entre les provenances. Les réponses des taux d'échanges gazeux au potentiel hydrique des aiguilles étaient similaires entre toutes les provenances, et les changements de taux ne furent seulement détectés que lorsque le potentiel hydrique devint inférieur à –1,3 MPa. Les provenances ibériques, contrairement à celles des Landes, montrèrent une tendance à économiser l'eau à la fin du printemps, ce qui indique une adaptation à la situation de sécheresse estivale. Les différences de croissance entre provenances ne se sont pas exprimées en terme de différences de taux nets instantanés de photosynthèse, car cela dépend aussi d'autres facteurs comme le statut hydrique des semis et de l'époque où les mesures ont été effectuées. Cependant, les différences d'accroissements entre provenances peuvent être partiellement expliquées par des différences dans l'efficience d'utilisation de l'eau et de l'azote.

pin maritime / sélection précoce / échanges gazeux

1. INTRODUCTION

The tendencies in the variation of ecophysiological parameters (gas exchange, water relations and some others) can be useful in explaining plant growth responses in different water availability situations [39, 52, 53, 60]. Forest tree species show differences in stomatal and photosynthetic responses to water stress, a

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fact which has sometimes been linked to drought tolerance and preferences for a particular habitat [4, 37, 51], as well as to differences within the same species [13]. Although sometimes these differences are only expressed within a given rank of plant water potential [3, 9]. Significant differences between provenances were found concerning physiological adaptations to water stress in maritime pine young seedlings [16, 27, 41, 42, 43, 50]. So, the need for a deeper basic knowledge on water stress adaptation of *Pinus pinaster* [36] in those situations is strengthened by its applicability to selection programmes. In this sense, photosynthesis measurements at early age were proposed as growth predictors for forest tree species [34]. However, experimental work has proved that results are satisfactory in some cases [26] but not always [29, 32, 40, 51]. Thus, other factors such as respiration [24] or, even, needle morphology [10], for instance, would have to be taken into account. In any case, since plant biomass comes from the CO_2 fixation, it is not surprising that this would be the first candidate for evaluation and early selection [19].

Water stress reduces photosynthesis due to its efect on stomatal aperture and chloroplast dehydration [7, 23, 44]. Therefore, under water shortage, transpiration rate (E) or the ratio photosynthetic rate to transpiration rate (instantaneous water use efficiency, A/E) are important factors to consider. The ratio A/E has been used as a distinguishing criterion for drought tolerance, both between species [6, 21] and intraspecifically [39, 49, 56]. Nevertheless A/E does not give an integrated value through time and some contradictory results have been found [30], since A/E based selection depends on competence and intensity and duration of water stress period [8, 11, 45]. Moreover, it can be presumed that water use efficiency increases in response to leaf nitrogen content by the increase of mesophyl conductance, without stomatal conductance increase. This is the case sometimes [15, 25], but not always [38]; even the response can depend on water availability conditions [17].

In the present paper responses to water stress of some ecologically distant *Pinus pinaster* provenances are analyzed in terms of gas exchange parameters. Seedlings were subjected to two water supply regimes in the nursery, under cover, in order to establish criteria for early selection and suitability for afforestation on drought-prone sites.

2. MATERIAL AND METHODS

In April 1994, seeds from five Iberian provenances (Oria -Or-, Arenas de San Pedro -Ar-, Oña -Oñ-, San Leonardo de Yagüe -SL-, y Boniches -Bo-) and two open pollinated families of Landes (France) provenance (*table I*) were collected and germinated. After germination, seedlings were taken to open air under a translucid cover and sown in containers filled with 230 ml of a sand:black peat mixture (2:1 v/v). Air temperatures were recorded [16]. Seedlings were carefully watered twice a week for two months. After that, two water supply regimes were applied: once a week ($R1$) and every two weeks ($R2$), both up to field capacity. The experimental design consisted of twelve completely randomized blocks with fifteen plants per block, provenance and water supply regime, altogether 2160 seedlings.

Gas exchange and needle water potential (Ψ_n) were measured five times during the growing season (the second week in June, third week in July, second week in September, October and November) on 5–6 seedlings per provenance and water supply just before watering, between 12:00 and 14:00 h. Predawn water potential (Ψ_p) was recorded as well. Measurements were done in two consecutive days, selecting randomly half of the seedlings each day. On these 5-6 seedlings and another five, needles, stem and root dry weight were measured after 48 hours at 70 ºC, and nitrogen content was also analyzed by the Kjeldahl semi-micro system (Kjeltec System 1026, Tecator. Höganäs, Sweden). Projected

Table I. Ecological characteristics of *Pinus pinaster* provenance regions. T = annual mean temperature; P = annual mean precipitation; Phytoclimate regions [1].

	Altitude (m)	T (ºC)	P (mm)	Latitude	Longitude	Phytoclimate regions
Or	1150	15.8	357	37º30'N	2º20'W	IV_1
Ar	750	13.4	1190	40º07'N	4º17'W	$VI(IV)_2$ / IV_4
Oñ	700	10.8	685	42º43'N	3º24'W	$VI(IV)_1$ / $VI(IV)_2$
SL	1200	8.7	641	41º43'N	2º27'W	$VI(IV)_1$ / $VI(IV)_2$
Bo	1120	10.8	663	39º59'N	1º27'W	$VI(IV)_1$ / $VI(IV)_2$
Ld	40	12.0	833	44º00'N	1º00'W	VI(V)

needle area (PNA) was also measured with a leaf area meter (Delta T Devices, Cambridge, England). Net photosynthetic rate (*A*), net transpiration rate (*E*), stomatal conductance to water vapour (g_{wv}) and intercellular to air CO_2 ratio (C_i/C_a) were measured with a portable infrared gas analyser (LCA-4, ADC. Hoddesdon, England). Calculus of parameters was made according to Von Caemmerer and Farquhar (1981) and expressed on a projected needle area basis. Water potentials (Ψ_p, Ψ_n) were measured with a pressure chamber (PMS Instruments Co. Corvallis, OR, USA).

Variance analysis using a BMDP2V statistic package (BMDP Statistical Software Inc. Cork, Ireland) was applied to the data in order to discriminate between provenances, watering treatments and measurement dates. The block effect was not statistically significant for any parameter, so it was excluded from the statistical analysis. The Tukey HSD (Honest Significant Difference) for means comparison was applied whenever differences were significant ($P < 0.05$). It was checked in advance that all the parameters comply with normal distribution and variance equality. No data transformation was carried out.

3. RESULTS

Tables II and III show mean values and significance levels of gas exchange parameters. *Table IV* shows the values of dry weight and projected needle area. Total, shoot and root dry weight were positively correlated ($r^2 > 0.90$, $p < 0.01$). Shoot/root ratio did not show significant differences between provenances ($p > 0.23$), its mean values were 1.95 ± 0.05 in the *R*1 treatment and 2.24 ± 0.06 in the *R*2 at the end of the experiment.

No significant differences in net photosynthetic rate ($p = 0.097$) were found between provenances as a whole. However, for *R*1 water supply regime in the October measurement, Oria provenance showed a rate (17.2 ± 1.2 µmol CO_2 m^{-2} s^{-1}) significantly higher (40% to 100%) than the other provenances. A similar behaviour was found for stomatal conductance (g_{wv}).

The provenance factor resulted significant for transpiration. It was only due to the values obtained for the *R*1 treatment in June, as the transpiration rate of Boniches provenance (3.6 ± 0.3 mmol H_2O m^{-2} s^{-1}) was significantly different from Oria, Arenas and the Landes, whose rates were respectively 2.0, 2.0 and 1.9 mmol H_2O m^{-2} s^{-1}. In July these values decreased up to 80% for all the Iberian provenances. In contrast to them, for the Landes families, these parameters showed an increase of up to 9%, from June to July. In September, photosynthetic rate and stomatal conductance were significantly different in Or, Ar and Ld provenances (5.8 to 6.6 µmol CO_2 m^{-2} s^{-1} and 74 to 96 mmol H_2O m^{-2} s^{-1}, respectively) than in Oñ, SL and Bo (5.0–5.4 and 53–61, respectively), however there were no significant differences between provenances in the transpiration rate. On the other hand, for *R*1 treatment in June, Or, Ar and Ld provenances tended to be more efficient in water use than Oñ, SL and Bo, since they showed similar photosynthetic rates but up to 30 to 40% lower transpiration and stomatal conductance values.

Table II. Leaf temperature range in each measurement date (T_{leaf}, ºC) and mean values of net photosynthetic rate (*A*, µmol CO^2 m^{-2} s^{-1}), net transpiration rate (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance to water vapour (g_{wv}, mmol H_2O m^{-2} s^{-1}) and intercellular to ambient CO_2 ratio (C_i/C_a). Means with the same letter do not differ significantly (Tukey's HSD test, $P = 0.05$). Vapour pressure deficit (VPD) was: 2.1 KPa in June, 4.5 KPa in July, 2.0 KPa in September, 1.2 KPa in October and 0.9 KPa in November.

	A	*E*	g_{wv}	C_i/C_a	T_{leaf}
Provenance					
Or	6.96 a	1.57 a	93 a	0.694 a	
Ar	6.22 a	1.67 ab	89 a	0.700 a	
Oñ	6.32 a	1.78 ab	77 a	0.676 a	
SL	5.95 a	1.77 ab	80 a	0.664 a	
Bo	6.67 a	1.90 b	87 a	0.677 a	
Ld	6.41 a	1.67 ab	84 a	0.671 a	
Water treatment					
*R*1	8.96 b	2.37 b	134 b	0.879 b	
*R*2	3.88 a	1.08 a	36 a	0.482 a	
Date					
June	6.47 b	1.95 c	71 b	0.672 bc	28.2 – 31.0
July	3.15 a	1.06 a	37 a	0.826 d	38.1 – 39.7
September	5.63 b	1.75 c	71 b	0.540 a	30.0 – 32.6
October	9.37 d	2.45 d	149 d	0.632 b	25.4 – 28.1
November	7.50 c	1.44 b	97 c	0.731 c	19.9 – 21.2

Water potential was not significantly different among provenances. For the *R*1 treatment, predawn water potential averaged –0.49 to –0.62 MPa, and midday water potential (Ψ_n) –0.89 to –1.05 MPa. For the *R*2 treatment, predawn water potential dropped up to –2.5 MPa for the provenances as a whole in July. The relationship between gas exchange parameters and water potential is showed in *figure 1*.

Table V shows foliar nitrogen concentration ($\%N_{needles}$) and photosynthetic nitrogen use efficiency ($A_{N needles,}$ µmol CO_2 $molN^{-1}$ s^{-1}), as well as the significance levels. As comparing needle nitrogen concentration in *R*1 and *R*2 treatments, Ld and SL were the most

Table III. Significant level (p) from ANOVA. n.s.: not significant ($p > 0.05$); *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Parameter	Provenance (P)	Water Treatment (WT)	Date (D)	P × WT	P × D	WT × D	P × WT × D
A	n.s.	***	***	**	**	***	***
E	*	***	***	*	*	***	**
g_{wv}	n.s.	***	***	**	***	***	***
C_i/C_a	n.s.	***	***	n.s.	n.s.	***	n.s.

Table IV. Total dry weight increment from June to November (ΔTDW, g), projected needle area increment from June to November (ΔPNA, cm^2) and mean specific leaf area ($PNA/DW_{needles}$, $cm^2_{needles}/g_{needles} \times 10^4$) from June to November. Means with the same letter do not differ significantly (Tukey's HSD test, $P = 0.05$). n.s.: not significant ($p > 0.05$); *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

	ΔTDW	ΔPNA	$PNA/DW_{needles}$
Provenance			
Or	0.364 b	12.3 b	7.26 a
Ar	0.366 b	13.5 b	7.73 ab
Oñ	0.246 a	9.6 a	8.29 b
SL	0.260 a	9.4 a	8.25 b
Bo	0.280 a	10.1 ab	8.28 b
Ld	0.333 ab	13.0 b	8.94 c
Water treatment			
$R1$	0.346 b	14.3 b	8.44 b
$R2$	0.277 a	8.8 a	7.86 a
p-value			
provenance (P)	***	***	***
water treatment (WT)	***	***	**
P × WT	*	*	n.s.

unfavoured provenances by water shortage. The average reduction was 0.4 units for these provenances, significantly different from the 0.2 units for Or, Ar and Bo. Oña provenance showed an intermediate behaviour with 0.3 units.

Seed dry weights (withuot seed coat) of Ld, Or and Ar (27.6, 26.4 and 24.8 g/1000 seeds, respectively) were significantly different from those of SL, Bo and Oñ (21.8, 18.8 and 18.6 g/1000 seeds respectively). Seed nitrogen concentration (%N_{seeds}) was not significantly different between provenances, mean values were from 5.5 to 5.7%. Seed dry weight (SDDW) was positively correlated to total plant dry weight (TDW, $r^2 = 0.70$, $p = 0.03$) and total plant nitrogen content ($N_{seedling}$, mg; $r^2 = 0.72$, $p = 0.03$), but not to plant nitrogen concentration ($r^2 = 0.27$, $p = 0.31$). Seed nitrogen content (N_{seeds}, mg) was well correlated to SDDW ($r^2 = 0.94$, $p = 0.02$) but not to seed nitrogen concentration.

Average values for photosynthetic nitrogen use efficiency in $R2$ treatment were similar for all the provenances. However for $R1$ treatment, Ld (58.7 ± 1.7 μmol CO_2 $molN^{-1}$ s^{-1}) became significantly different to Oñ and SL (46.8 ± 2.4 y 41.5 ± 2.4 μmol CO_2 $molN^{-1}$ s^{-1}, respectively). Average values for Or, Ar and Bo for the $R1$ were 51.2, 51.0 and 53.0 μmol CO_2 mol N^{-1} s^{-1}, respectively. $A_{Nneedles}$ and A/E ratio were positively correlated ($A/E = 0.9601\ A_{Nneedles}^{0.3703}$; $r^2 = 0.53$), considering all the provenances, water treatments and dates.

4. DISCUSSION

Seasonal variations of temperature and air relative humidity as well as water supply regime highly influenced gas exchange. Within-day gradient of temperature (≤ 3 ºC) did not influence too much. Results reveal a similar pattern and the same order of magnitude values as those given by other authors for several species [12, 22]. However, environmental conditions did not affect all the gas exchange parameters in a similar way and their evolution through time was not the same. Maximum A and E out of phase values have been also reported for three conifer species [20], suggesting a different sensitivity to pressure potential variation by stomata and mesophyll cells.

Provenance did not influence so much gas exchange rates. The lack of statistical differences between provenances or varieties of the same species is not surprising [33, 59]; it has occurred in comparing species [35]. Appreciable differences in the gas exchange rates between trees and limitations of measuring equipments [14] make difficult the detection of provenance differences.

At the end of the growing period, differences in growth did not merely result from the differences found in the photosynthetic rate. It was more important for the total carbon incorporated into the plant the biomass of

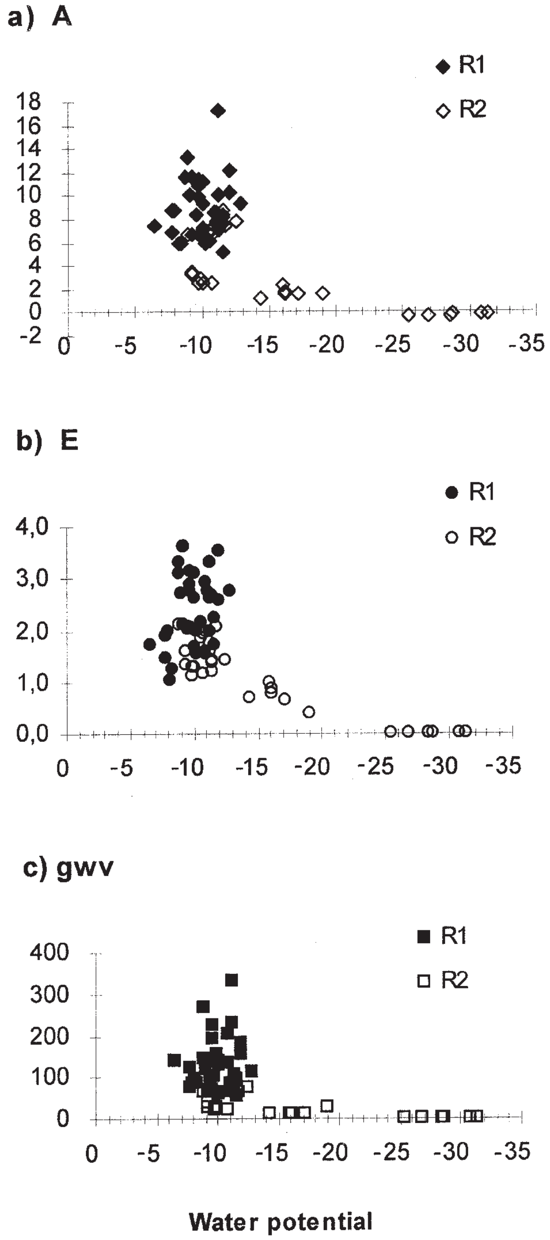

Figure 1. a) Net photosynthetic rate (A, µmol CO_2 m^{-2} s^{-1}), b) net transpiration rate (E, mmol H_2O m^{-2} s^{-1}) and c) stomatal conductance to water vapour (g_{wv}, mmol H_2O m^{-2} s^{-1}) *versus* leaf water potential (Ψ_n, MPa). Each point is the mean value (n = 5 or 6) per provenance, water supply regime and date.

photosynthetic tissue than assimilation rate, as it was already indicated [26, 31]. Seed size and seed nitrogen content influenced plant growth and $N_{seedling}$, at least during the first growing season, but they did not influence plant nitrogen concentration neither $A_{N needles}$.

It can occur that the highest growth rates take place because stomatal conductance and photosyntethic rate maintain high values at the end of the growing season, whatever those were in the hottest days in Summer [2]. In some way, Oria, Arenas and Landes provenances show this behaviour.

Gas exchange parameters show independence of needle water potential values up to about –1.3 MPa and then gas exchange rates decrease shiftly. No differences between provenances have been found, as reported by Cregg (1993) for several *Pinus ponderosa* origins, in contrast to the results by Sands et al. (1984) as comparing three *Pinus radiata* D. Don families.

The transpiration rate evolution from June to July and the high water availability (water regime supply $R1$) make evident that Iberian provenances adopt a “water saving strategy” to face up to the Summer dryness conditions they live in, in contrast to the Landes families which are shown as water consumers in such situation. On the other hand, under water shortage conditions ($R2$), the decrease of osmotic potential, bulk elasticity modulus and turgor to dry weight ratio previously reported [16] and the increase of intrinsic water use efficiency (A/g_{wv}) indicate strategies of acclimation to water stress, as it has been shown in some conifers [3, 24, 48, 59].

The range of needle nitrogen concentration is in agreement with the values found for maritime pine and other conifers elsewhere [18, 28, 46, 58]. In addition to stomatal limitations, water stress ($R2$) provokes non-stomatal limitations to CO_2 assimilation by reducing $\%N_{needles}$ and $A_{N needles}$. The relationship between A/E and $A_{N needles}$ indicates a positive effect of nitrogen on water conservation. Arenas, in spite of being the provenance with the lowest nitrogen concentration, showed higher growth than Oñ, SL and Bo, which means a higher nitrogen productivity. It can suggest that the latter provenances should make an “over-investment” of nitrogen in the photosynthetic machinery or even in other components not directly related to photosynthesis [31, 54, 55]. Survival in impredictible environments demands from species a high potential of adaptation, which involves large variability among individuals in relation to nitrogen use [47, 57]. It makes difficult to select genotypes which reach a high production and, at the same time, show wide adaptations. Arenas provenance may be in this sense a sound candidate. It can be concluded that water use efficiency in Summer days, photosynthetic nitrogen use efficiency and gas exchange rates in Autumn and late Spring might be taken into account together with growth and water relations parameters in early selection programs.

Table V. Mean values of leaf nitrogen concentration ($\%N_{\text{needles}}$, % of dry weight) and photosynthetic nitrogen use efficiency ($A_{N\text{needles}}$, μmol CO_2 mol N^{-1} s^{-1}). Means with the same letter do not differ significantly (Tukey's HSD test, $P = 0.05$). n.s.: not significant ($p > 0.05$); *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

	$\%N_{\text{needles}}$	$A_{N\text{needles}}$
Provenance		
Or	1.44 a	36.5 abc
Ar	1.30 a	37.7 bc
Oñ	1.55 b	35.5 ab
SL	1.52 b	33.5 a
Bo	1.49 ab	37.9 bc
Ld	1.49 ab	40.1 c
Water treatment		
*R*1	1.61 b	50.4 b
*R*2	1.32 a	23.4 a
Date		
June	1.67 c	35.9 b
July	1.47 b	19.5 a
September	1.53 b	31.6 b
October	1.33 a	51.7 d
November	1.33 a	45.6 c

factor and interactions	*p*-value	
	$\%N_{\text{needles}}$	$A_{N\text{needles}}$
Provenance (P)	***	*
Water Treatment (WT)	***	***
Date	***	***
P × WT	*	***
P × D	n.s.	n.s
WT × D	***	***
P × WT × D	*	**

Acknowledgments: We thank Irena Trnkova Farrel for checking of the English version. This research was supported by CEC-DG 12 Forest Project Contract MA2b-CT91-0040 and the *Ministerio de Educación y Ciencia* of Spain.

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