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To cite this version:

Denis Loustau, F. El Hadj Moussa. Variability of stomatal conductance in the crown of a maritime pine (Pinus pinaster Ait.). International symposium Forest Tree Physiology, Sep 1988, Nancy, France. hal-02856142

HAL Id: hal-02856142

https://hal.inrae.fr/hal-02856142v1

Submitted on 8 Jun 2020

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Ann. Sci. For. (1989) 46 suppl., 426s-428s
Forest Tree Physiology, E. Dreyer *et al.*, eds.
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Variability of stomatal conductance in the crown of a maritime pine (*Pinus pinaster* Ait.)

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Introduction

Stomatal response of conifers to environmental variables, such as air water vapor deficit, has been reported by many authors (Whitehead *et al.*, 1984; Sandford and Jarvis, 1986). Variations of stomatal conductance (g_s) related to needle age and situation in the canopy have also been described (Leverenz *et al.*, 1982; Tan *et al.*, 1977).

In order to estimate a general pattern of stomatal conductance (g_s) in the crown of a maritime pine, the effects of each of these sources of variability have been assessed.

Materials and Methods

All measurements were made in the crown of a single standard tree from an 18 yr old stand of maritime pine (mean height = 12 m; mean circumference at B.H. = 61 cm). A sample of shoots was stratified with respect to whorl height (8 levels), branch orientation (9 levels) and needle age (3 levels).

For each of the 30 shoots, measurements were made on a pair of needles of a single fascicle of the shoot. Measurements of the whole sample were made on 5 d, from 07:00 to 19:00 (U.T.), between June 2, and August 30, 1988. An automatic steady state porometer (LICOR 1600) was used with a chamber of 63 cc internal volume. g_s was expressed in cm/s, on a total leaf area basis.

During the experiment, hourly means of temperature, relative humidity, wind speed and irradiance were calculated from micrometeorological measurements made 2 m above the canopy. Hourly means of canopy transpiration were also computed from sap flow measurements (Granier, 1985) on a sample of 10 pines (including the sample tree).

Results

Seasonal pattern

In the course of the experiment, a dry period began on July 20. Fig. 1 shows the diurnal pattern of g_s mean ± SD before this period (June 2) and 40 d after it began (August 30).

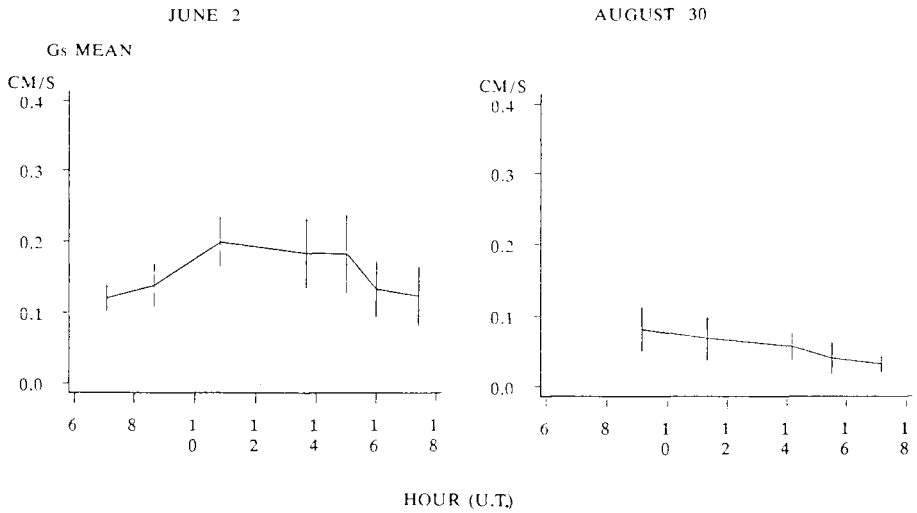

Fig. 1. Diurnal pattern of the mean ± SD (vertical bars) of stomatal conductance (g_s cm/s) on June 2, and August 30, 1988.

As had been noticed during previous years, the ratio of canopy transpiration to potential evapotranspiration (PET) (Penman-Monteith) dropped from 0.75 in June to 0.44 in late summer.

Linear regression of g_s on air water vapor deficit D (Pa) and irradiance Ir ($W \cdot m^{-2}$) for spring and late summer resulted in the following equation: spring (all data before the beginning of the dry period):

$g_s = 0.15 - (0.95 \times 10^{-4} \times D) + (1.6 \times 10^{-4} \times Ir)$ ($N = 542$; $r^2 = 0.52$).

Late summer (data after the beginning of the dry period):

$g_s = 0.08 - (0.34 \times 10^{-4} \times D) + (0.38 \times 10^{-4} \times Ir)$ ($N = 111$; $r^2 = 0.33$).

Variations related to needle features

Spring

Because of the diurnal pattern of the variance of g_s, all subsequent analyses were conducted on data divided into 3 time periods (before 09:00, 09:00–16:00, and after 16:00 h).

Effects of whorl position, branch orientation, age of needle and interactions were tested using ANOVA. When significant effects were detected, means at each level were compared with Duncan's test.

No significant difference in g_s was found between morning and evening. But between 9:00 and 16:00, significant effects (< 0.05) were shown for each of the 3 selected features (Table I).

Late summer

There was a significant decrease of g_s during the day, but no significant differences in g_s in terms of whorl position, branch orientation or needle age could be detected.

Discussion and Conclusions

Variations in g_s over a growing season show a seasonal pattern with 2 contrasted periods, before and after the beginning of the dry period.

Table I. Mean values of g_s measured between 9:00 and 16:00 for each level of selected features.

g_s *mean (cm/s)*	*Whorl no.*	g_s *mean (cm/s)*	*Branch orientation*	g_s *mean (cm/s)*	*Needle age (yr)*
0.17 ab	1	0.18 ab	NNE	0.09 a	0
0.18 a	2	0.20 a	ENE	0.18 b	1
0.18 a	3	0.17 b	ESE	0.15 c	2
0.13 c	4	(–)	SSE		
0.15 b	5	0.16 b	SSW		
0.17 ab	6	0.17 b	WSW		
0.14 bc	7	0.16 b	WNW		
		0.11 c	NNW		

Means with the same letter are not significantly different.

In the pre-drought period, the stomatal response to air water vapor deficit and irradiance explains 52% of the total g_s variation; g_s decreases as D increases, and increases with Ir, as observed by many authors (Sandford and Jarvis, 1986; Tan *et al.*, 1977; Running, 1979).

In midday, when g_s variance and mean are high, the general pattern of stomatal conductance of a pine shows significant differences related to needle age, whorl position and branch orientation. Position effects probably reflect a micrometeorological stratification within the crown, and age effects could be related to the physiological development of the needle. Cumulated effects of environmental variables and needle features explained 75% of the total variation of g_s.

During the drought period, the mean and variance of g_s were much lower and showed only a slight decrease during the course of the day. Variation in vapor deficit and irradiance explained only 33% of the variation of g_s. No stratification could be shown in the crown at any time of the day.

Soil water deficit is assumed to be the main limiting factor for needle transpiration. Stomatal closure could be general throughout the crown and would explain the absence of any stratification.

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