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Diurnal and Seasonal Courses of Photosynthesis, Transpiration and Water Use Efficiency of Japanese Cypress and Japanese Red Pine Seedlings in Different Soil Water Conditions

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異なる土壌水分条件下で育てたヒノキとアカマツ苗木の 光合成・蒸散・水利用効率の日変化及び季節変化

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Summary

Net photosynthesis and transpiration of 3-year old seedlings of Japanese cypress (Chamaecyparis obtusa Endl.) and Japanese red pine (Pinus densiflora Sieb. et Zucc.) were measured as diurnal courses and seasonal fluctuation from May to November in 1994. Three levels of soil moisture were achieved by controlling the irrigated amount of water. Net photosynthesis of both species peaked in the morning, transpiration reached its peak later than net photosynthesis. Net photosynthesis and transpiration decreased in lower water conditions as well as stomatal conductance. However, no distinct differences in water use efficiency was observed among all three treatments. Integrated daily CO₂ uptake peaked in July, for Japanese cypress; and in August, for Japanese red pine. Integrated daily H₂O release had similar patterns to integrated daily CO₂ uptake in most treatments except pF 2.7 of Japanese red pine, whereas it peaked in October. Daily water use efficiency was higher in early summer and late autumn than in mid summer, for Japanese cypress; but was relatively steady, for Japanese red pine. Integrated daily CO2 uptake and H2O release of both species decreased in lower water conditions. However, there was no significant difference among all three treatments in daily water use efficiency. Net photosynthesis of Japanese red pine was higher than that of Japanese cypress under the same water stress conditions. Japanese red pine is more drought-tolerant than Japanese cypress.

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Key words: Japanese cypress, Japanese red pine, photosynthesis, stomatal conductance, water use efficiency, water

キーワード:ヒノキ,アカマツ,光合成,気孔コンダクタンス,水利用効率,水ストレス

1. Introduction

The effect of soil water status on photosynthesis or transpiration of Japanese cypress and Japanese red pine, which are the main two forest tree species in Japan, has been well studied separately. Satoo (1956) reported qualitatively that Japanese red pine is more drought-tolerant than Japanese cypress by measuring transpiration of detached twigs. NEGISI (1966) came to the conclusion that photosynthesis of Japanese red pine responds more sensitively to soil water than that of Japanese cypress. The critical soil moisture at which the transpiration of a Japanese cypress stand began to decline had been estimated at pF 2.45 using the micrometeorological approach (HATTORI *et al.*, 1993).

The gas exchange of carbon dioxide (CO₂) and water vapor between plants and the atmosphere passes through the same stomata (Larcher, 1965). Regulation of gas exchange is important for plant performance, to maintain growth without desiccation in the atmosphere (Schulze, 1986). In recent years, it has been possible to measure the gas exchange of carbon dioxide and water vapor at the same time, and extensive studies on the effect of stomatal conductance on gas exchange have been completed (Farquhar and Sharkey, 1982; Schulze, 1986). The comparative studies on the effect of soil water status on photosynthesis and transpiration between Japanese cypress and Japanese red pine is still lacking. The stomatal regulation effect on gas exchange of these two species is not fully understood yet.

Studying diurnal patterns of water relations, photosynthesis and related parameters can provide fundamental information on plant responses and adaptations to natural environments (SCHULZE and HALL, 1982). In this paper, we examined the effect of soil water status on the 3-year old seedlings of Japanese cypress and Japanese red pine under three levels of soil moisture. Our specific objectives were to: 1) measure diurnal and seasonal courses of gas exchange and stomatal conductance under three steady soil water conditions; 2) find the relationship between stomatal conductance and gas exchange; 3) try to find the optimum soil water conditions for these species.

2. Materials and Methods

2.1 Materials

Three year old seedlings of Japanese cypress (*Chamaecyparis obtusa* Endl.) and Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) were transplanted from a nursery to pots, and have been growing in greenhouse conditions since February, 1994. The general characteristics of the materials are shown in Table 1. Pots were watered according to the following methods and fertilized every 2 weeks with Hyponex solution (N:P:K=5:10:5) during the growing season.

2.2 Soil moisture control

The soil in each pot was Kanuma tsuchi (volcanic soil). Seedlings were planted in Wagner pots (1/2000a) with the equal amount of air-dried Kanuma tsuchi.

The pF-soil moisture curve (Fig. 1) was measured using the centrifuging method to control soil moisture levels.

The resistance to an extreme depression in soil moisture content is considered to be intermediate, for

 Table 1
 General characteristics of sample seedlings

Species	Treatment	Height (cm)	Diameter at ground surface (cm)	Top and root fresh weight (g)
Japanese cypress	pF 2.2	80.4	0.71	107.2
Japanese cypress	pF 2.7	79.8	0.95	134.1
Japanese cypress	pF 3.2	82.8	0.75	128.0
Japanese red pine	pF 2.7	72.8	1.09	68.9
Japanese red pine	pF 3.2	70.0	0.98	62.0
Japanese red pine	pF 4.0	64.8	0.87	62.6

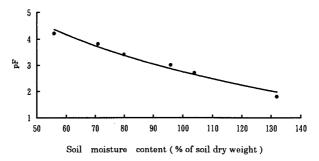


Fig. 1 pF-soil moisture curve.

Japanese cypress, high for Japanese red pine in comparison with Japanese cedar (*Cryptomeria japonica* D. Don), which is considered to be low (NEGISI, 1966). We set the soil moisture on three levels about pF 2.2~(-0.02~MPa, 118% moisture content expressed as percentage of soil dry weight), pF 2.7~(-0.05~MPa, 99%), and pF 3.2~(-0.16~MPa, 82%), for Japanese cypress; pF 2.7, pF 3.2, and pF 4.0~(-0.98~MPa, 63%), for Japanese red pine.

In each treatment, one heat probe sensor (IDL-1600, North Hightech Co. LTD.) was set to measure the soil moisture every 30 minutes. We collected the soil moisture content every day from the data logger and calculated the water loss amount caused by evapotranspiration, and then watered the pot to keep the soil moisture at the required levels.

2.3 Physiological measurement

Diurnal changes of net photosynthesis rate (Ph_n) and transpiration rate (Tr) were measured using the same newly sprouted leaves from May to November, between 0600 and 1800 at 1 hour intervals. As needles of Japanese red pine were still sprouting in May and June, measurements were started from July. Measurements were made on a clear day using simultaneously operated porometer systems (CQP-130, Walz Co.) (Schulze *et al.*, 1982; Lange *et al.*, 1984). The porometer system also recorded PAR (photosynthetically active radiation), air and leaf temperature, ambient relative humidity, ALVPD (air to leaf vapor pressure deficit), stomatal conductance to CO_2 and H_2O , and intercellular CO_2 concentration.

The measured leaves of Japanese red pine were detached and leaf areas were measured using the Delta -T Image Analysis System (DIAS, DELTA-T DEVICES LTD.) after measuring in November. DIAS uses a PC computer to analyze video images. The leaf images were recorded by the computer using a video camera (JVC TK-S310U). DIAS can measure length and width also. In the case of Japanese cypress, leaf areas were measured by recording the leaf images directly using the above method every month after the measurement of diurnal changes.

From the diurnal curves of Ph_n and Tr, the diurnal curves of water use efficiency (WUE) were estimated. In addition, daily CO_2 uptake (IDCU) and H_2O release (IDHR) were estimated per unit leaf area by measuring the area beneath diurnal curves of Ph_n and Tr respectively (WAYNE and BAZZAZ, 1993). The seasonal fluctuation of Ph_n , Tr and WUE were estimated by using the integrated IDCU, IDHR and IDCU/IDHR ratios during each month, respectively.

3. Results

3.1 Soil water control

Soil water conditions are illustrated in Fig. 2. The points showing a dramatic increase are the times at which irrigation took place. This figure shows only five days' data in the middle of August while the soil moisture of each treatment was kept at steady levels respectively during this study. Soil moisture contents have been measured by oven-drying method to verify whether or not heat probe sensor can measure and control soil moisture correctly. The results are shown in Fig. 3. From the strong coefficient of determination of 0.92, it can be considered that the heat probe sensor can efficiently control soil water.

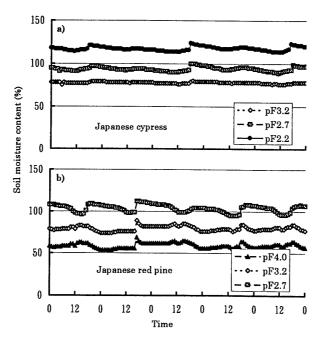


Fig. 2 Soil water conditions of Japanese cypress (*Chamaecyparis obtusa* Endl.) and Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) from 10 Aug. to 14 Aug. 1994.

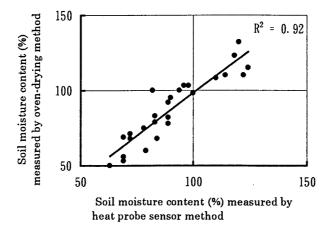


Fig. 3 A comparison of heat probe sensor method to oven-drying method in measurement of soil moisture content.

3.2 Diurnal courses of photosynthesis, transpiration, water use efficiency and stomatal conductance The diurnal courses of Ph_n, Tr and WUE for Japanese cypress and Japanese red pine are illustrated in Fig. 4 from May to November, and in Fig. 5 from July to November, respectively.

 Ph_n of Japanese cypress and Japanese red pine peaked in the morning in most measurements. Midday depression of Ph_n was observed in both species in most measurements. Both species showed decreases of Ph_n in lower soil water potential treatments compared with that in higher soil water potential treatments. Tr of both species reached its peak later than Ph_n in most measurements. Tr decreased in lower soil water potential treatments.

As shown in Table 2, the maximum daily Ph_n and Tr of Japanese cypress changed to $83\% \sim 93\%$ and $62\% \sim 102\%$ in pF 2.7, $55\% \sim 94\%$ and $38\% \sim 76\%$ in pF 3.2, respectively, in comparison to levels in pF 2.2. On the other hand, Japanese red pine changed Ph_n and Tr to $71\% \sim 94\%$ and $72\% \sim 109\%$ in pF 3.2, 70%

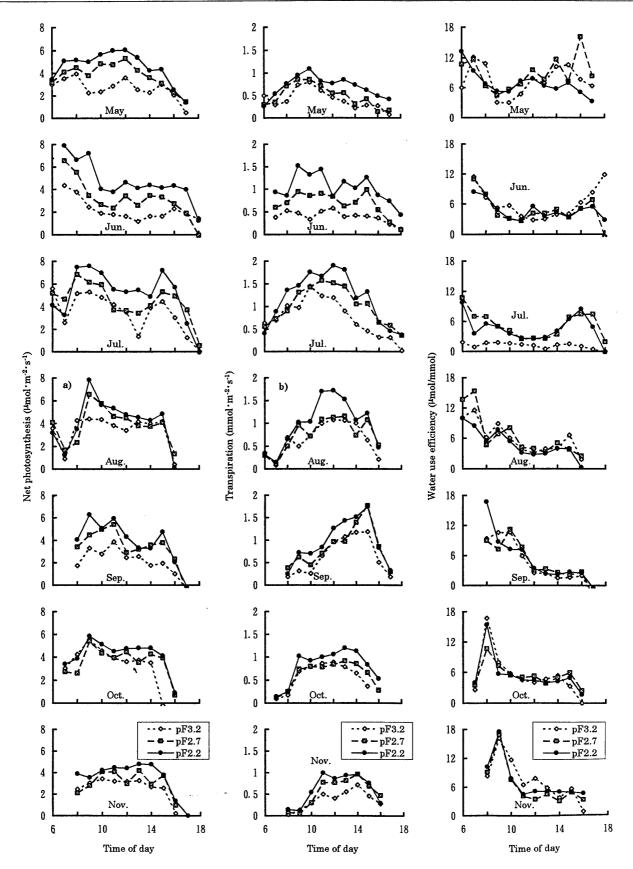


Fig. 4 The diurnal courses of net photosynthesis, transpiration and water use efficiency for Japanese cypress (*Chamaecyparis obtusa* Endl.). a) and b) marks will be used in 4.1 Increasing water deficits and leaf gas exchange.

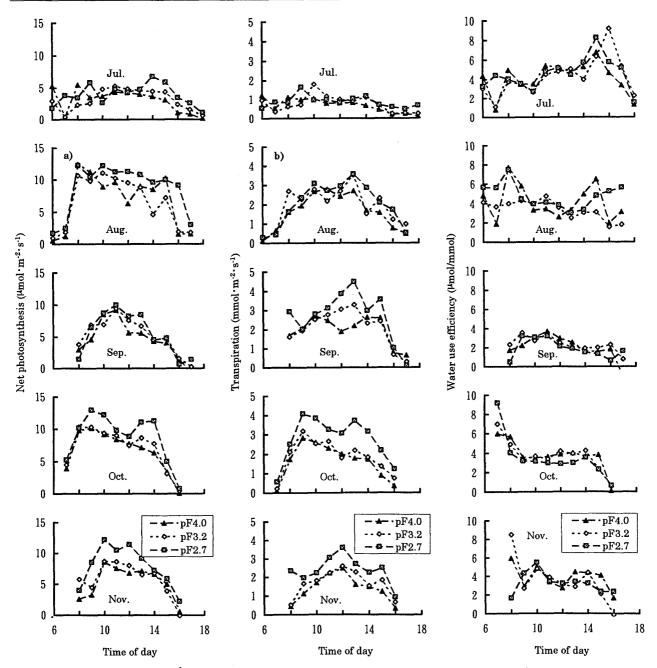


Fig. 5 The diurnal courses of net photosynthesis, transpiration and water use efficiency for Japanese red pine (*Pinus densiflora* Sieb. et Zucc.). a) and b) marks will be used in 4.1 Increasing water deficits and leaf gas exchange.

 \sim 102% and 61% \sim 78% in pF 4.0, respectively, in comparison to levels in pF 2.7 (Table 3).

Under the same soil water conditions of pF 2.7, the maximum daily Ph_n and Tr were 6.834 μ mol·m⁻²·s⁻¹, 1.767 mmol·m⁻²·s⁻¹, respectively, for Japanese cypress (Table 2); 12.971 μ mol·m⁻²·s⁻¹, 4.488 mmol·m⁻²·s⁻¹, respectively, for Japanese red pine (Table 3). In pF 3.2 treatment, the maximum daily Ph_n and Tr were 5.583 μ mol·m⁻²·s⁻¹, 1.447 mmol·m⁻²·s⁻¹, respectively, for Japanese cypress (Table 2); 11.079 μ mol·m⁻²·s⁻¹, 3.528 mmol·m⁻²·s⁻¹, respectively, for Japanese red pine (Table 3). Japanese red pine had higher Ph_n and Tr than Japanese cypress under the same soil water conditions.

WUE reached its peak twice a day (Fig. 4, Fig. 5): in the morning and the afternoon in most measurements of both species. In the morning at fairly low leaf temperatures and ALVPD (Fig. 6), Ph_n was intense and Tr was only moderate, yielding a high level of WUE. At midday, Tr increased

Table 2 The maximum daily net photosynthesis (Ph_n, μmol·m⁻²·s⁻¹) and transpiration (Tr, mmol·m⁻²·s⁻¹) for Japanese cypress.

Month	pF 2.2 treatment		pF 2.7 treatment		pF 3.2 treatment	
	Ph_n	Tr	Ph_n	Tr	Ph_n	Tr
May	6.042	1.091	5.294(88)	0.853(78)	3.941(65)	0.794(73)
Jun.	7.885	1.514	6.547(83)	0.938(62)	4.346(55)	0.578(38)
Jul.	7.578	1.899	6.834(90)	1.572(83)	5.583(74)	1.447(76)
Aug.	7.813	1.716	6.537(84)	1.153(67)	4.394(56)	1.072(62)
Sep.	6.262	1.739	5.390(86)	1.767(102)	3.851(61)	1.192(69)
Oct.	5.822	1.196	5.396(93)	0.911(76)	5.498(94)	0.886(74)
Nov.	4.782	0.993	4.088(85)	0.964(97)	3.427(72)	0.717(72)

Note: Numbers in parenthesis represent decreases of Ph_n or Tr expressed as a percentage of maximum daily Ph_n or Tr in pF 2.2 respectively.

Table 3 The maximum daily net photosynthesis (Ph_n , μ mol·m⁻²·s⁻¹) and transpiration (Tr, mmol·m⁻²·s⁻¹) for Japanese red pine.

Month	pF 2.7 treatment		pF 3.2 treatment		pF 4.0 treatment	
	Ph_n	Tr	Ph_n	Tr	Ph_n	Tr
Jul.	6.783	1.647	5.275(78)	1.791(109)	5.492(81)	1.220(74)
Aug.	12.273	3.573	11.079(90)	3.528 (99)	12.476(102)	2.794(78)
Sep.	10.031	4.488	9.450(94)	3.284(73)	9.219(92)	2.717(61)
Oct.	12.971	4.081	10.320(80)	3.183(78)	10.176(78)	2.839(70)
Nov.	12.190	3.591	8.698(71)	2.578(72)	8.581(70)	2.476(69)

Note: Numbers in parenthesis represent decreases of Ph_n or Tr expressed as a percentage of maximum daily Ph_n or Tr in pF 2.7 respectively.

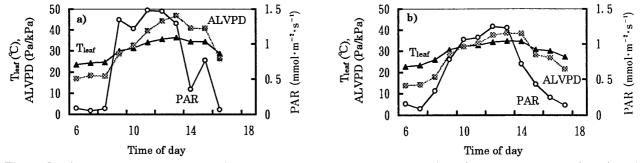


Fig. 6 Leaf microclimate conditions of photosynthetically active radiation (PAR), leaf temperature (T_{leaf}) and air to leaf vapor pressure deficit (ALVPD) for a) Japanese cypress (*Chamaecyparis obtusa* Endl.) measured on Aug. 19; b) Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) measured on Aug. 23, 1994.

Table 4 The daily average water use efficiency (μ mol/mmol) for Japanese cypress.

Month	pF 2.2 treatment	pF 2.7 treatment	pF 3.2 treatment
May	$6.887\!\pm\!2.545$	8.861 ± 3.271	7.453±3.035
Jun.	4.702 ± 1.875	4.672 ± 2.908	6.090 ± 3.088
Jul.	4.540 ± 2.630	5.283 ± 2.673	$1.158 \pm 0.581*$
Aug.	4.911 ± 2.849	6.500 ± 4.260	6.004 ± 3.072
Sep.	5.227 ± 4.930	4.608 ± 4.063	4.426 ± 4.463
Oct.	5.446 ± 3.660	5.457 ± 2.280	6.129 ± 4.249
Nov.	7.200 ± 4.305	6.304 ± 4.470	7.374 ± 4.461

^{*}Significant difference at $p \le 0.01$ by t test. Data are the means and SDs.

			•
Month	pF 2.7 treatment	pF 3.2 treatment	pF 4.0 treatment
Jul.	4.549 ± 1.659	4.286±2.049	4.166 ± 1.669
A 110	4.772 ± 1.250	3.360 ± 0.990	A 132+1 850

Table 5 The daily average water use efficiency (μmol/mmol) for Japanese red pine.

Month	pF 2.7 treatment	pF 3.2 treatment	pF 4.0 treatment
Jul.	4.549±1.659	4.286 ± 2.049	4.166±1.669
Aug.	4.772 ± 1.250	3.360 ± 0.990	4.132 ± 1.850
Sep.	$1.913\!\pm\!1.007$	2.356 ± 0.787	$2.018\!\pm\!1.335$
Oct.	$3.495\!\pm\!2.204$	3.744 ± 1.674	3.796 ± 1.578
Nov.	3.270 ± 1.136	3.584 ± 2.352	3.840 ± 1.305

^{*}No significant difference at $p \le 0.05$ by t test. Data are the means and SDs.

significantly while Ph_n remained at the same level or even dropped as a result of increasing respiration and water stress. Therefore the WUE was low. In the afternoon, Tr declined more rapidly than Ph_n and recorded a high level of WUE. There was no significant differences in WUE between different treatments of each specimen for both species (Table 4, Table 5). Japanese cypress had relatively higher WUE than Japanese red pine under the same soil water conditions.

Japanese cypress and Japanese red pine had similar diurnal patterns of stomatal coductance to CO2 (g_s) (Fig. 7). In most measurements, g_s reached peaks in the morning, and recovered a little in the afternoon. g_s decreased at lower soil water potential treatment for both species. Japanese red pine had higher g_s than Japanese cypress under the same soil water conditions of pF 2.7 and pF 3.2 except the measurement in July, where difference in gs between two species was not significant as needles of Japanese red pine had just stopped expansion and not developed their full photosynthetic capacity (Table 6).

3.3 Seasonal fluctuation of daily amount of photosynthesis, transpiration and water use efficiency In order to understand the difference of productivity of the two species, further more to find the best water condition to yield high productivity with the least water consumption, it is necessary to know the daily amount of Ph_n, Tr, and WUE.

We integrated daily CO2 uptake (IDCU) and H2O release (IDHR), and divided IDCU by IDHR to get daily WUE (Fig. 8).

IDCU of Japanese cypress peaked in July. IDHR had similar patterns of seasonal fluctuation to IDCU, but the shape was more convex than the IDCU. Therefore daily WUE was higher in early summer and late autumn than in mid-summer. IDCU of Japanese red pine showed two peaks with the low value in September caused by short period of cloud. IDHR of Japanese red pine peaked in August in pF 3.2 and pF 4.0 treatments, however, IDHR showed peak value in October in pF 2.7 treatment. Noticeable seasonal fluctuation in daily WUE was not present in Japanese red pine, the decrease in September could be for the same reason as mentioned above.

IDCU and IDHR of Japanese cypress decreased significantly in low soil water potential treatments in comparison with high soil water potential treatments. However, there was no significant difference in daily WUE between different treatments (Fig. 8, Table 7). IDCU of Japanese red pine in pF 3.2 and pF 4.0 treatments were at the same level (Fig. 8, Table 7) and significantly lower than in pF 2.7 treatment. IDHR of Japanese red pine in low soil water potential treatments decreased significantly in comparison to high soil water potential treatments. Daily WUE was not different among all three treatments (Fig. 8, Table 7).

Under the same soil water conditions of pF 2.7, IDCU and IDHR of Japanese red pine were 1.8 and 2.9 times higher than that of Japanese cypress, respectively. Daily WUE was 36% lower in Japanese red pine than in Japanese cypress. A similar result was observed in pF 3.2 (Table 7).

4. Discussion

4.1 Increasing water deficits and leaf gas exchange

Increased water deficits may alter leaf gas exchange in at least three ways. First, localized, transitory

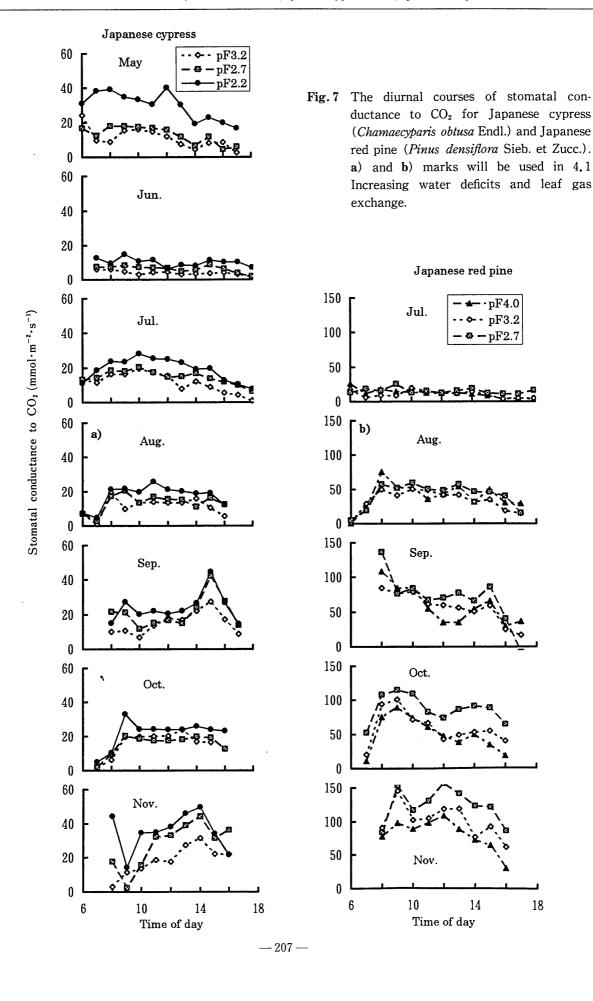


Table 6 Daily average stomatal conductance to CO₂ (mmol·m⁻²·s⁻¹) for Japanese cypress and Japanese red pine.

(1996)

Month	pF 2.7 t	reatment	pF 3.2 treatment		
	Japanese cypress	Japanese red pine	Japanese cypress	Japanese red pine	
Jul.	14.800± 3.826 ^a	15.592± 3.993ª	11.615±5.752 ^b	10.715±5.116 ^b	
Aug.	13.573 ± 5.053	41.475 ± 18.171	11.227 ± 5.118	52.458 ± 24.286	
Sep.	20.980 ± 9.011	69.850 ± 36.522	$15.744 \!\pm\! 6.553$	57.130 ± 21.931	
Oct.	16.211 ± 7.251	59.430 ± 24.855	15.570 ± 5.890	87.510 ± 20.145	
Nov.	28.000 ± 13.391	123.489 ± 26.064	18.600 ± 8.517	$100.711\!\pm\!25.001$	

^{a,b} No significant difference at p \leq 0.05 by t test. Data are the means and SDs.

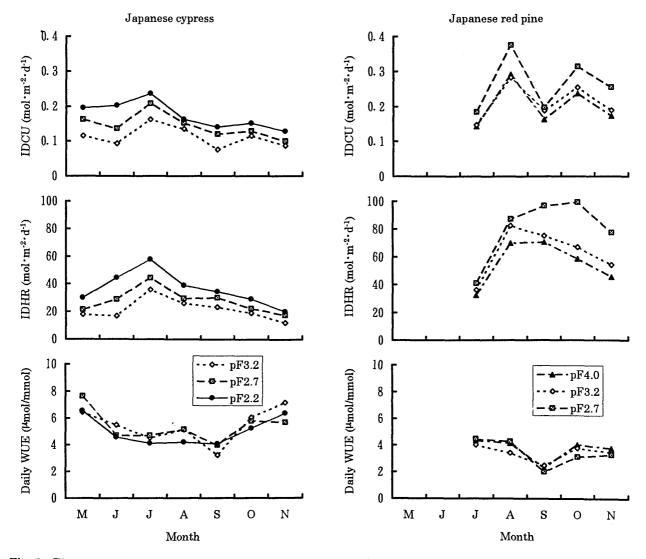


Fig. 8 The seasonal fluctuation of integrated daily CO₂ uptake (IDCU), integrated daily H₂O release (IDHR) and daily water use efficiency (daily WUE) for Japanese cypress (*Chamaecyparis obtusa* Endl.) and Japanese red pine (*Pinus densiflora* Sieb. et Zucc.).

Table 7 Integrated daily CO₂ uptake (IDCU, mol·m⁻²·d⁻¹), H₂O release (IDHR, mol·m⁻²·d⁻¹) and daily water use efficiency (daily WUE) for Japanese cypress and Japanese red pine.

		pF 2.2	pF 2.7	pF 3.2	pF 4.0
	IDCU	0.174 ± 0.036	0.144 ± 0.033	0.112± 0.028	
Japanese cypress	IDHR	36.471 ± 11.340	27.851 ± 8.131	21.667 ± 7.223	
	Daily WUE	4.986± 0.987a	5.358 ± 1.089^{a}	5.416 ± 1.203^{a}	
	IDCU		0.265 ± 0.072	0.212± 0.049 ^b	0.202± 0.055 ^b
Japanese red pine	IDHR		80.520 ± 21.172	63.032 ± 16.348	55.570 ± 14.714
	Daily WUE		3.453 ± 0.882^{c}	3.456 ± 0.525^{c}	3.743 ± 0.743^{c}

^{a,b,c} No significant difference at $p \le 0.05$ by t test. Data are the means and SDs from May to Nov., for Japanese cypress; from Jul. to Nov., for Japanese red pine.

water stress that developed during periods of high transpiration reduced assimilation rate (Sharkey, 1984; Nowak *et al.*, 1988). Second, the longer-term development of water deficits over a period of days or weeks gradually decreased the magnitude of both stomatal conductance and assimilation in a number of species (Bates and Hall, 1982; Ehleringer and Cook, 1984; Gollan *et al.*, 1985; Turner *et al.*, 1985; Nowak *et al.*, 1988). Finally, the functional relationships between gas exchange and environmental parameters can be altered (Bates and Hall, 1982; Gollan *et al.*, 1985; Turner *et al.*, 1985), although this effect has not been a universal response of plants to water stress (Schulze and Küppers, 1979).

For Japanese red pine and Japanese cypress, both the transitory and long-term development of water deficits generally reduced the magnitude of gas exchange. Evidence that high transpiration rates reduced assimilation was present on August 19 (Fig. 4a, Fig. 4b, Fig. 7a), for Japanese cypress; on August 23 (Fig. 5a, Fig. 5b, Fig. 7b), for Japanese red pine: after 10 o'clock, stomatal conductance was relatively constant, transpiration increased greatly, and assimilation rates decreased. During long-term development of drought stress, the magnitude of stomatal conductance and assimilation decreased. The evidence came from the diurnal courses of photosynthesis and stomatal conductance under different soil water conditions, for Japanese cypress (Fig. 4, Fig. 7) and Japanese red pine (Fig. 5, Fig. 7). Finally, the functional relationships between gas exchange and environmental parameters such as temperature, vapor gradient should be further studied under steady environmental conditions.

4.2 The optimum soil water condition

Japanese cypress and Japanese red pine decreased photosynthesis at lower soil water potential conditions (Fig. 4, Fig. 5). This is partially caused by stomatal limitation (Fig. 7). Transpiration was also limited at the same time (Fig. 4, Fig. 5). However, no distinct difference in water use efficiency was observed under different soil water potential conditions based on diurnal courses of WUE (Fig. 4, Fig. 5, Table 4, Table 5) and daily WUE data (Fig. 8, Table 7).

Under the same soil water conditions, Japanese red pine had higher Ph_n than Japanese cypress (Table 2, table 3) as well as IDCU (Table 7). This indicates that the productivity of Japanese red pine is higher than that of Japanese cypress, although the daily WUE of Japanese cypress was higher than that of Japanese red pine (Fig. 8).

Based on our measurements, Japanese cypress is a suitable tree species for afforestation in pF 2.7 or pF 3.2 soil, and Japanese red pine is suitable in pF 3.2 or even in pF 4.0 soil.

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要旨

5月から11月までヒノキ(Chamaecyparis obtusa Endl.)とアカマツ(Pinus densiflora Sieb. et Zucc.)の3年生苗木の光合成・蒸散速度の日変化及び季節変化を測定した。潅水量によって、土壌水分を3段階に設定した。両樹種ともに、午前中に純光合成速度がピークになったが、その時間は蒸散のほうが光合成より遅かった。土壌含水比が低い場合は、純光合成速度、蒸散速度及び気孔コンダクタンスが減少したが、水利用効率に違いは見られなかった。ヒノキの総同化量は7月にピークになったが、アカマツの場合は、8月にピークになった。アカマツのpF2.7の処理区では、総蒸散量は10月に最も多かったが、それ以外の処理区では総同化量と同じような季節変化を示した。ヒノキの水利用効率は5、10、11月に高く、6月から9月まで低かった。一方、

アカマツの水利用効率は季節を通して変化しなかった。土壌含水比が低い場合は,総同化量および総蒸散量が減ったが,水利用効率に違いが見られなかった。ヒノキとアカマツの純光合成速度を同じ土壌水分条件で比べると,アカマツのほうがヒノキより優れていたので,アカマツはヒノキより耐乾性が優れていると思われる。