

Morphology and Water Relations of Leaves of *Eucalyptus globulus* Sprouts

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Morphology and Water Relations of Leaves of *Eucalyptus globulus* Sprouts*

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Abstract

Characteristics of leaf morphology and water relations were examined and compared for the leaves of *Eucalyptus globulus* which shows continuous changes of leaf form from oval in the current sprouts to lanceolate in the normally grown shoots. With the changes of leaf form, several anatomical features were observed to change continuously. The normal leaves had long petioles and showed some 'sun leaf' characteristics, i. e., three or four layers of mesophyll palisade cells, small specific leaf area, dense venation, and low air space ratio. On the other hand, the current sprout leaves showed the 'shade leaf' characteristics. On the abaxial surface of the current sprout leaves, smaller stomata in high frequency compared to those of normal leaves were observed. No stomata was observed on the adaxial surface of the sprouts leaves although there was about a frequency of 60% of abaxial stomata in the normal leaves. Water relation parameters obtained by the pressure-volume curve technique suggested that the sprout leaves were inferior in maintaining cell turgor against water loss compared to the normal leaves. Under field conditions, transpiration rates and stomatal conductances were higher in the sprout leaves, while leaf water potentials were almost the same in both the sprout and the normal leaves. The leaf specific conductance of tree bole supporting unit leaf area, calculated from the relationship between leaf water potentials and transpiration rates, was higher in sprouts. It was concluded that the sprout leaves, which have a lower-light efficient morphology and a smaller content of osmotic water, maintain the high stomatal conductance supported by a high leaf specific conductance.

1. Introduction

Many hardwood species sprout when the tree bole is injured or cut down. It has been reported that sprouts grow faster than seedlings (Blake, 1980)(Ito et al. 1989) and have

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been utilized in the practical management of fuel wood forests over a long period. It is also known that sprout leaves in many species have some juvenile morphology and we can expect a physiological difference among those leaves varying morphologically. Blake(1980) reported that coppice leaves of *Eucalyptus camaldulensis* following decapitation of stem showed a higher transpiration rate and lower stomatal resistance in relation to increased stomatal frequency and length. Ito and Suzaki(1989) obtained similar results in experiments carried out with sprouts and seedlings established after a clear-cut of *Pasania edulis* forests. While the higher leaf conductance of sprout leaves may explain the faster growth of sprouts, it is important to evaluate the mechanism which maintains this higher leaf conductance in order to discuss the superiority of sprouts from the view point of water relations.

In this paper we have investigated the morphological changes of leaves induced by sprouting in relation to the water relations characteristics in *Eucalyptus globulus* which is known for conspicuous changes of leaf form.

2. Materials and methods

2.1. Plant material

Materials were taken at a height of 6m from the sunny crown of *Eucalyptus globulus* (12m in height, 56cm in diameter at breast height) grown under field conditions at the nursery of Kyushu University, located in southwestern Japan. Measurements were made for three categories of shoots; current sprouts, 1-year-aged sprouts and normally grown shoots (Fig.1).

2.2. Leaf morphology

To analyze the change of leaf form, blade length, blade width, length of a petiole, leaf area and leaf dry weight (85°C, 48hr) were measured for fully expanded leaves sampled from three or more shoots of each category. Stomatal frequency and dimension were also examined for both abaxial and adaxial leaf surfaces using transparent replicas. Measurements of stomatal frequency and dimension were made on a projection microscope at 100 magnification for three locations; adjacent to the midrib, midway between the midrib and leaf margin, and near the leaf margin, from six or more leaves from each category. For anatomical investigations, three or four transverse leaf sections (10 micrometer) were taken from the above three shoot categories, and numbers of layers of the mesophyll palisade cells were counted. The air space ratio was determined from the ratio occupied by the air space on photographs taken at 20 magnification. Photographs of vein patterns were taken directly at 9 magnification by permeating the light through the leaves mounted on the stage of a microscope. The vein ratio was determined from the ratio of the area occupied by venation on the photographs for 8 leaves of each category of shoots.

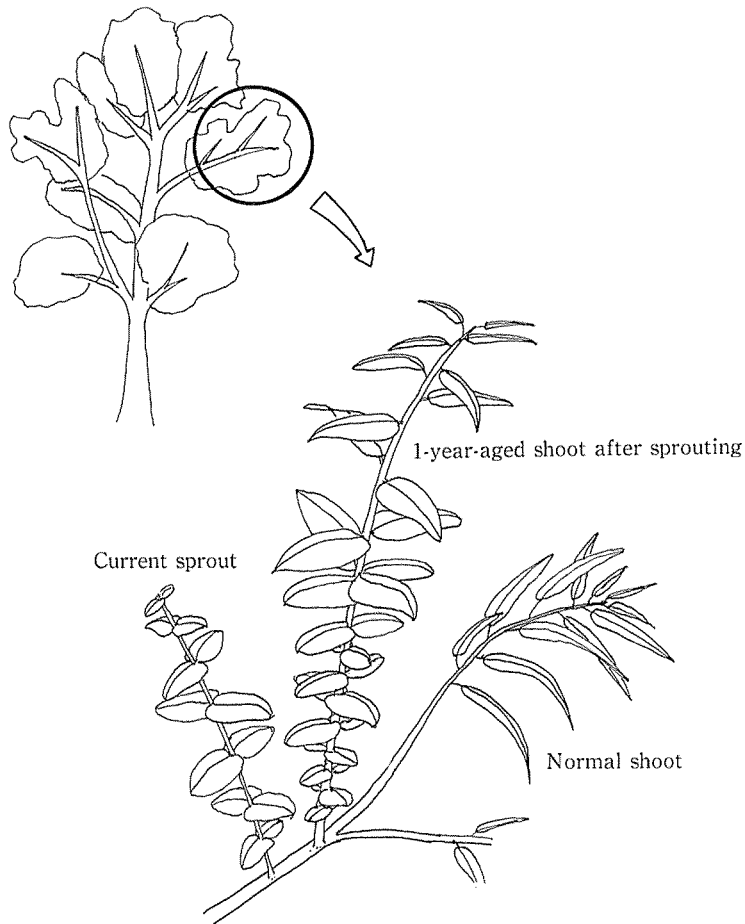


Fig.1 Schematic drawings of the sample tree used in this study.

2.3. Water relation characteristics of leaves

Water relation parameters were measured by a pressure chamber (Daiki CoLtd.) for fully expanded leaves of the current sprouts and the normal shoots in June in 1989 by using the pressure-volume curve technique (Scholander et al., 1965) (Tyree and Hammel, 1972). Parameters measured were as follows; osmotic potential at water saturation ($\Psi_{o,sat}$), pressure potential at the turgor loss point ($\Psi_{1,tip}$), relative water content at the turgor loss point (Rwc_{tip}), water content at water saturation (Ws), symplastic water content at water saturation (Vo), maximum elastic modulus (ϵ_{max}) (Cheung et al., 1975).

2.4. Diurnal changes of leaf water potential, transpiration rate and stomatal conductance

Diurnal changes of transpiration rates, stomatal conductances and leaf water

potentials of leaves were measured at the sunny crown on October 10 in 1989. Measurements were made from 05:00 to 20:00 at 1 or 3 hours interval. Transpiration rates and stomatal conductances were measured on the abaxial surface using a steady-state porometer (Li-Cor, Li-1600). There were four replications for each shoot category in each measurement. Transpiration rates per unit leaf area were calculated by total leaf conductances and the vapor pressure difference. Total leaf conductances were estimated by the relationship between the conductance of abaxial and adaxial surfaces, where following equations (1) and (2) were fitted by using the least square method for 1-year-aged sprout and normal leaves, respectively (statistically significant at 0.1% level) :

$$g_{ad} = 1.113g_{ab}^{0.885} \quad (r=0.990), \quad (1)$$

$$g_{ad} = 0.683g_{ab}^{0.611} \quad (r=0.951), \quad (2)$$

where g_{ab} and g_{ad} are the conductance of abaxial and adaxial surface, respectively.

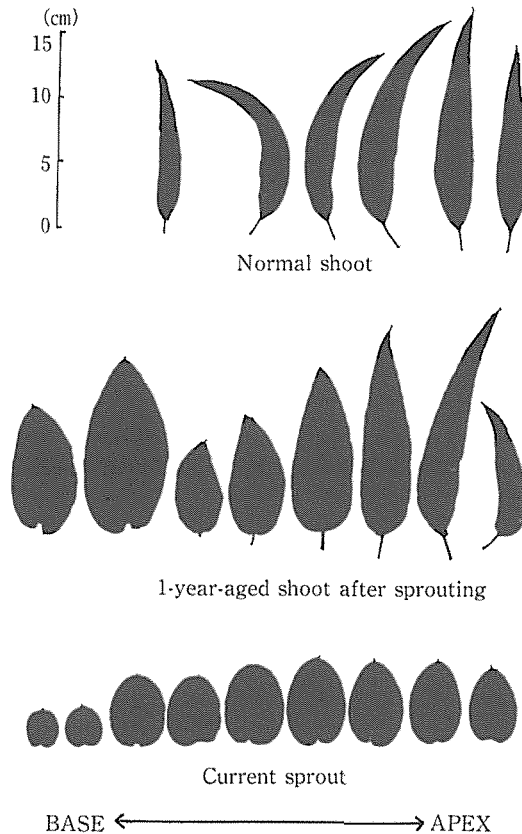


Fig.2 Schematic drawings showing the change of leaf form induced by sprouting in *Eucalyptus globulus*.

The adaxial conductance of current sprout leaves was assumed to be constant (unpublished data). Leaf water potentials were measured for one or two leaves in each measurement using a pressure chamber (Daiki CoLtd.). Diurnal changes of photosynthetic photon flux density (PPFD), air temperature and relative humidity were also measured.

3. Results

3.1. Leaf morphology

As shown in Fig.2, leaf forms of current sprout leaves were oval and those of normal

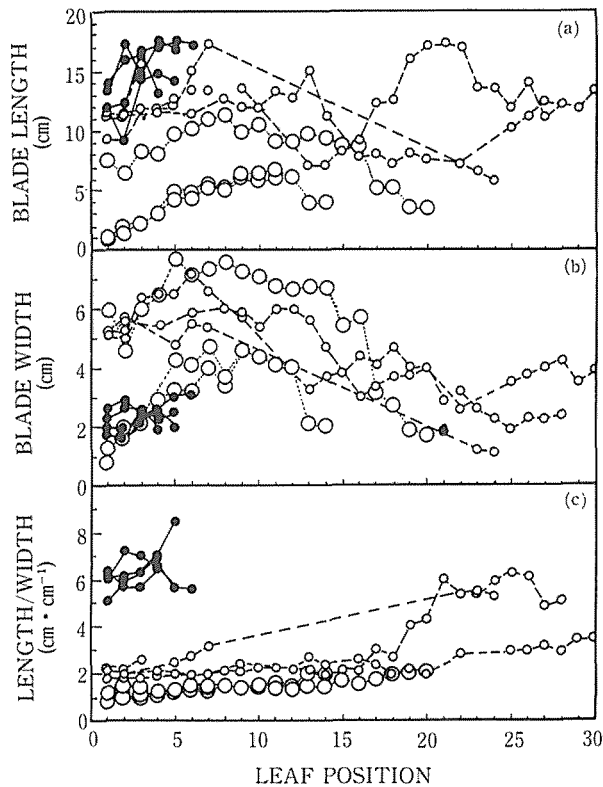


Fig.3.(a)-(c). Changes of leaf dimensions along the leaf insertion induced by sprouting in *Eucalyptus globulus*. a) blade length, b) blade width, and c) blade length per blade width. Large open circles and dotted lines, current sprouts ; small open circles and dashed lines, 1-year aged sprouts ; closed circles and solid lines, normal shoots. The circles linked by a line indicate the leaves on the same shoot. Positions without circles in the figure were decided by leaf scars.

leaves were lanceolate (Some of them can be described as 'falcate', but in this paper we only use the term 'lanceolate'). In the 1-year-aged sprouts leaf showed a continuous change of leaf form from ovate to lanceolate along the acropetal leaf insertion. It is, therefore, necessary to recognize the ontogenetic change of leaf form from current sprouts to normal shoots. The changes in leaf dimensions along the leaf insertion are shown in Fig.3. Length (Fig.3 (a)) and width (Fig.3 (b)) of leaf blade fluctuated widely and showed no significant difference in the shoot categories. However a leaf form index, i.e., a ratio of blade length to blade width (Fig.3 (c)) showed a certain trend to increase in the range of 1 to 2 in the current sprouts and 2 to 6 in the 1-year-aged sprouts, respectively, and ranged from 5 to 8 in the normal shoots. As this simple index of leaf form may indicate the change of leaf form from the current sprouts to the normal shoots, we have shown the leaf morphology and anatomy along the axis of this index.

Petiole length of leaves was shorter in the current sprouts compared to the normal leaves and tended to increase with the change of leaf form (Fig.4 (a)). Specific leaf area

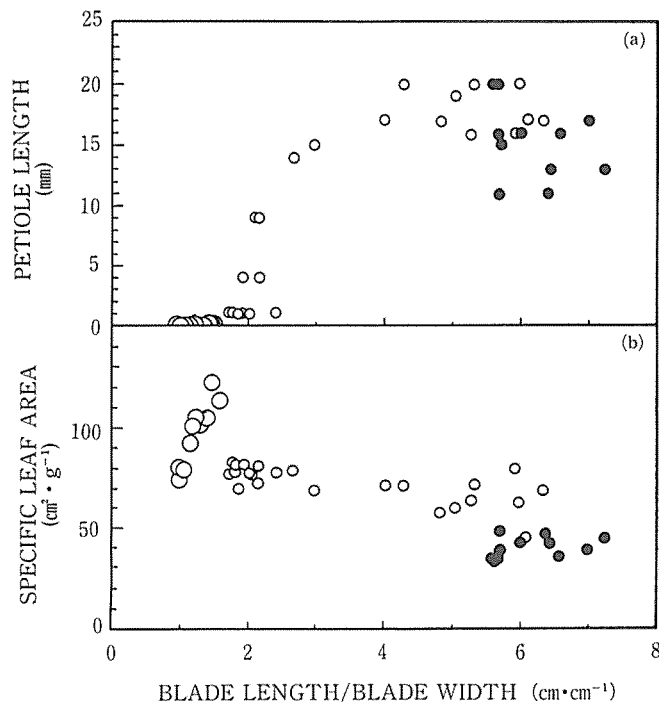


Fig.4.(a)-(b). Changes of leaf petiole length(a) and specific leaf area(b) with the change of the leaf form induced by sprouting in *Eucalyptus globulus*. Symbols are the same as in Fig.3.

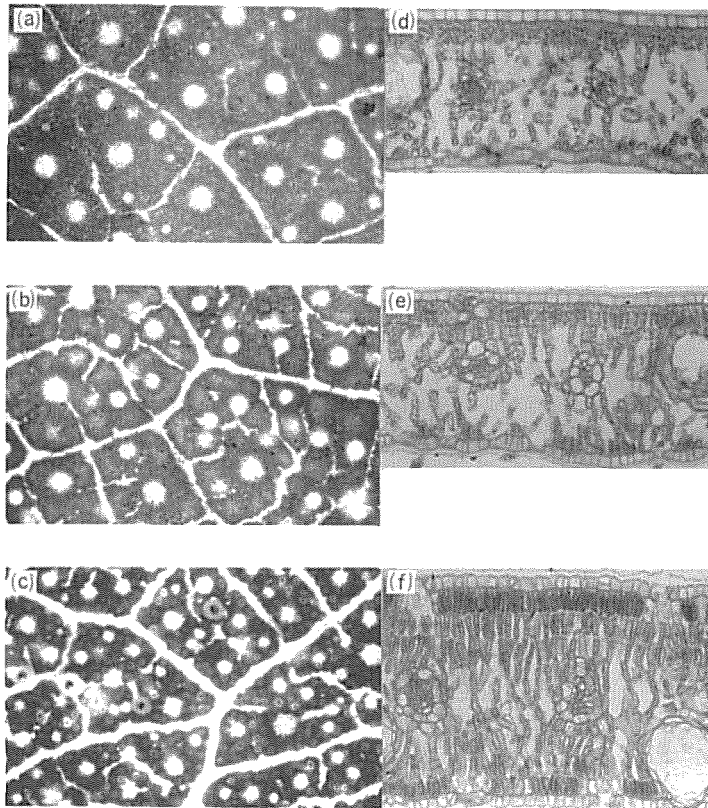


Fig.5.(a)-(f). Leaf surface views and leaf transverse sections of the current sprouts(a, d), 1-year-aged sprouts(b, e) and normal shoots(c, f) of *Eucalyptus globulus*.

was larger in the current sprout leaves than in the normal shoots.

Fig.5 (a)-(c) shows some examples of the venation patterns of each category. The vein ratio showed lower values in the current sprout leaves and a tendency to increase to the normal leaves (Fig.6). Fig.5 (d)-(f) shows examples of leaf transverse sections. Mesophyll palisade cells were observed in one layer in the current sprout leaves, one to two layers in the 1-year-aged sprout leaves and three to four layers in the normal leaves, respectively. The air space ratio showed a tendency to decrease from the current sprouts to the normal shoots (Fig.6 (b)). Fig.7 and Fig.8 show stomatal frequency and guard cell length, respectively. On the adaxial surface stomatal frequency was higher in the normal leaves, but no stomata was observed in the current sprout leaves. In the 1-year-aged sprout leaves, a few stomata were observed only adjacent to the midrib, and stomatal frequency showed a tendency to decrease when leaf forms resembled those of the current sprouts. Guard cell length obtained here, which were

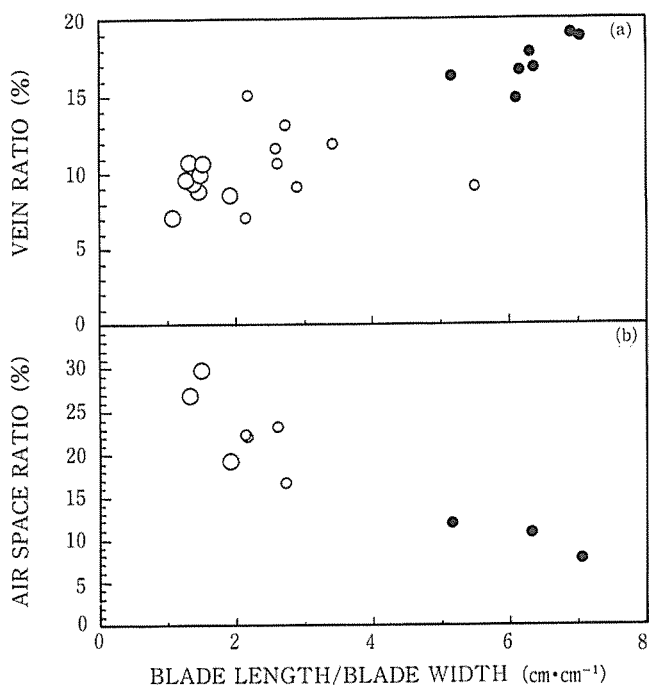


Fig.6.(a)-(b). Changes of the vein ratio(a) and the air space ratio(b) with the change of leaf form induced by sprouting in *Eucalyptus globulus*. Symbols are the same as in Fig.3.

somewhat shorter than those of same species reported by Pereira and Kozłowski(1976) and Ridge et al.(1980), were greater in the normal shoots than in the current sprouts on both abaxial and adaxial surfaces. Blake(1980) showed that both stomatal frequency and guard cell length were greater in coppice shoots than in normal seedlings on both surfaces of the leaves of *E. camaldulensis*. We also observed the similar trends as in Blake(1980) in several *Eucalyptus* spp.(data not shown). However, the comparison of the stomatal frequency and dimension between the sprouts and the normal shoots of *E. globulus* in this study indicated quite abnormal trends, i.e., smaller stomata on the abaxial surface and smaller stomata in low frequency on the adaxial surface of the sprouts leaves. Nevertheless, Pereira and Kozłowski(1976) reported that seedlings of *E. globulus* have no stomata on the adaxial surface. Their observations suggest that changes of stomatal frequency on the adaxial surface induced by sprouting observed in this study indicate 'rejuvenated leaf' characteristics of the sprout leaves in spite of the peculiarity of response to sprouting in *E. globulus* compared to the other *Eucalyptus* spp.

As shown in Table 1, where morphological characteristics of leaves were summarized for three categories, the morphology of leaves of sprouts was characterized by

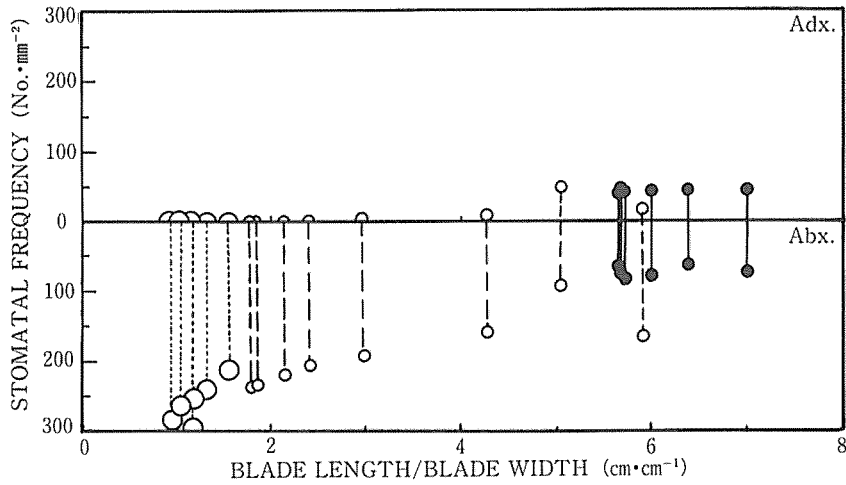


Fig.7 Changes of stomatal frequency on the abaxial and adaxial surfaces with the change of the leaf form induced by sprouting in *Eucalyptus globulus*. Symbols and lines are the same as in Fig.3.

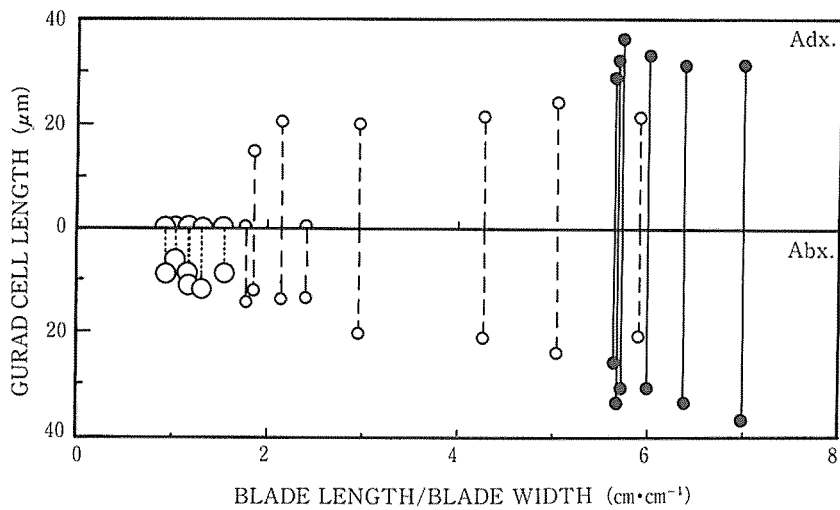


Fig.8 Changes of guard cell length on the abaxial and adaxial surfaces with the change of the leaf form induced by sprouting in *Eucalyptus globulus*. Symbols and lines are the same as in Fig.3.

that of 'shade leaf', i.e., higher specific leaf area and the vein ratio, fewer layers of mesophyll palisade cells and a higher air space ratio (Fitter and Hay, 1981)(Eschrich et al., 1989).

3.2. Water relation characteristics of leaves

Water relation parameters of leaves of current sprouts and normal shoots are

Table 1 Morphological characteristics of the leaves of normal shoots and sprouts in *Eucalyptus globulus*.

	L/W ¹⁾ (mm/mm)	Lp (mm)	SLA (m ² /kg)	Vein ratio (%)	Air space ratio (%)	Frequency of stomata (per mm ²)		Length of guard cell (μ M)	
						abaxial	adaxial	abaxial	adaxial
Normal shoot	6.32 ²⁾ 0.74	15.3 3.0	3.96 0.72	17.39 1.40	10.16 1.79	72.71 7.20	44.13 2.90	26.83 12.31	17.39 12.18
1-year-aged shoot after sprouting	2.97 1.31	10.0 7.8	7.24 0.93	10.96 2.37	21.13 2.61	184.64 43.99	10.03 14.98	18.07 4.25	15.90 8.82
Current sprout	1.41 0.27	0.0 0.0	9.74 1.47	9.29 1.11	25.28 4.43	257.87 27.24	0.00 0.00	9.25 1.91	*

¹⁾ L, W, Lp indicate length, width of the leaf blade and length of the petiole, respectively.

²⁾ Upper and lower values indicate means and standard deviations, respectively.

Table 2 Water relation parameters of leaves of normal shoots and sprouts in *Eucalyptus globulus*.

	$\Psi_{o,sat}$ ¹⁾ (MPa)	$\Psi_{l,tip}$ (MPa)	Rwc _{t,tip} (%)	Ws/Dw (%)	Vo/Ws (%)	Vo/La (kg/m ²)	ϵ_{max} (MPa)
Normal shoot	-1.22(0.067) ²⁾	-1.44(0.065)	0.872(0.015)	1.80(0.204)	0.851(0.040)	0.388(0.063)	11.54(1.179)
Current sprout	-1.19(0.118)	-1.38(0.095)	0.920(0.007)	2.18(0.417)	0.596(0.112)	0.133(0.031)	15.48(5.478)
Significance level ³⁾	N.S.	N.S.	0.5%	N.S.	1%	0.2%	N.S.

¹⁾ $\Psi_{o,sat}$, osmotic potential at water saturation ; $\Psi_{l,tip}$, leaf water potential at the turgor loss point ; Rwc_{t,tip}, relative water content at the turgor loss point ; Ws, water content at water saturation ; Vo, symplastic water content at water saturation ; La, leaf area ; ϵ_{max} , maximum elastic modulus. Vo/La (kg/m²) were calculated by using mean values of specific leaf area of each shoot (Table 1).

²⁾ Values in parentheses show standard deviations.

³⁾ Results of t-test. N.S. means no significance at 5% level.

shown in Table 2. Although both $\Psi_{o,sat}$ and $\Psi_{l,tip}$ were relatively higher in both shoots than those reported in other hardwood species (Hinckley et al., 1978), these parameters of the current sprout leaves were slightly higher (not significant) than those of normal leaves. Rwc_{t,tip} and Ws/Dw were greater in the current sprouts leaves than in the normal leaves, and the relative content of symplastic water (Vo/Ws) was greater in the normal leaves. Symplastic water content per unit leaf area (Vo/La), calculated from the parameters in Table 2 and mean SLA, was far greater in the normal leaves. ϵ_{max} was slightly larger in the current sprouts leaves, but fluctuated widely in both leaves.

From these results, it is suggested that sprout leaves were inferior to normal leaves in maintaining cell turgor against the water loss of leaves. These characteristics of sprout leaves were consistent with the results of Ito and Suzaki (1989) who made a comparison between leaves of mature trees and sprouts of *Pasania edulis* established after clear-cutting.

3.3. Diurnal changes of leaf water potential, transpiration rate and stomatal conductance

Fig.9 shows the diurnal changes of transpiration rates, stomatal conductances of abaxial surface, leaf water potentials and meteorological factors. Leaf water potentials showed similar trends in all shoots early in the morning, and slightly lower values in the sprouts from 10:00 to 16:00. Transpiration rates were generally highest in the current sprouts leaves and lowest in the normal leaves from 05:00 to 15:00, but from 16:00 they fluctuated largely because of self-shading by other branches. Similar changes were measured in stomatal conductances. In current sprout leaves, an early abrupt

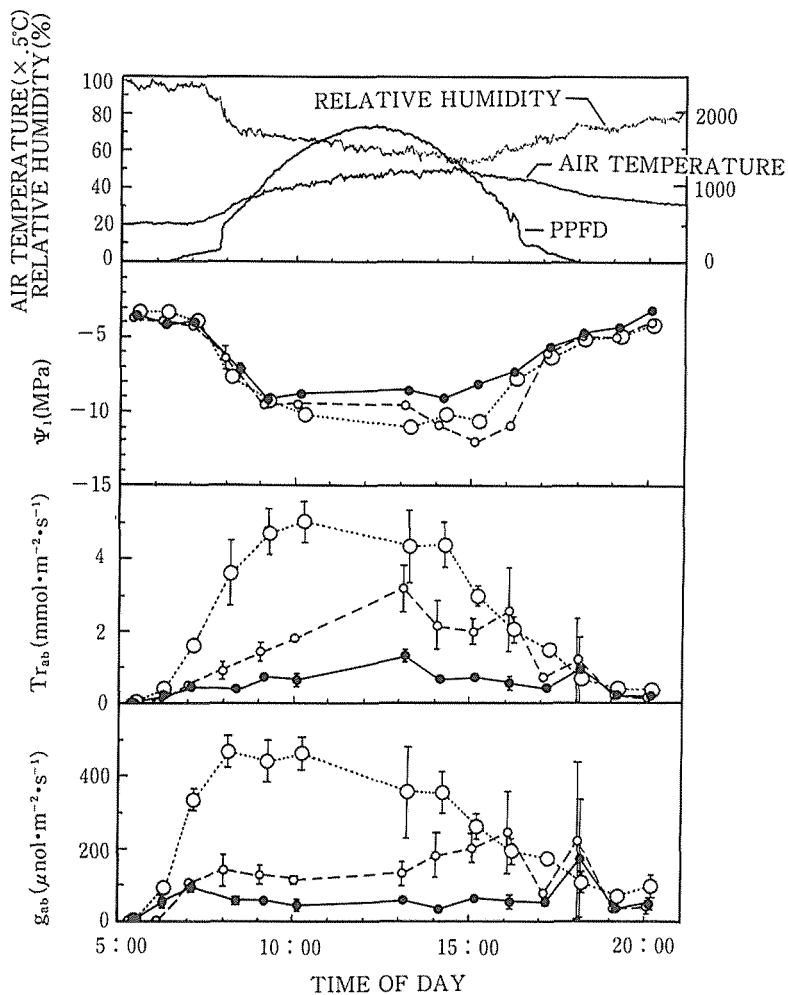


Fig.9 Diurnal changes of leaf water potentials(Ψ_l), transpiration rates(Tr_{ab}) and stomatal conductances(g_{ab}) in current sprouts, 1-year-aged sprouts and normal shoots of *Eucalyptus globulus*. Symbols and lines are the same as in Fig. 3. Bars indicate standard deviations.

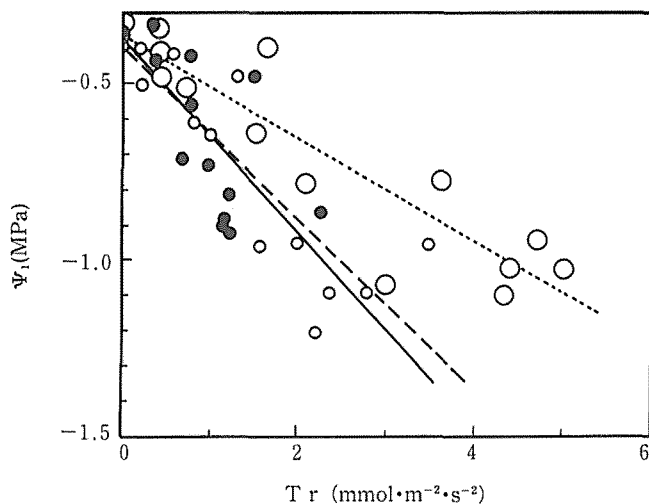


Fig.10 Relationships of the leaf water potentials(Ψ_1) and the transpiration rates(Tr) in current sprouts, 1-year-aged sprouts and normal shoots of *Eucalyptus globulus*. Symbols and lines are the same as in Fig.3.

Table 3 Leaf specific conductance from the soil to the leaf of normal and coppice shoots in *Eucalyptus globulus*.

	leaf specific conductance ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$)
Normal shoot	0.366
1-year-aged shoot after sprouting	0.412
Current sprout	0.690

increase of the stomatal conductance was observed in the morning.

Assuming that water loss from leaves and the inflow to leaves balanced each other when measurements were made, we can calculate the leaf specific resistance of the plant parts supporting the unit leaf area from transpiration rates and leaf water potentials. Fig.10 shows the relationship between the transpiration rates and leaf water potentials of each shoot category. The intercepts of lines are considered to indicate base points of leaf water potentials, and those of each shoot category showed almost the same values around -0.38 MPa. The leaf specific resistance are given as the slopes of lines. Leaf specific conductance(LSC'), the inverse value of the leaf specific resistance, of each shoot category is shown in Table 3. LSC' was higher in the sprouts than in the normal shoots.

Discussion

Leaf morphology affects photosynthesis in four main ways; light interception, temperature regulation, water balance and CO₂ diffusion (Fitter and Hay, 1981). We investigated the morphology and water relations of sprouts and normal shoots of *E. grobulus* in order to clear the mechanism to maintain high stomatal conductance in sprout leaves, and observed great differences between them.

Our results suggested that the normal leaves are inefficient in the diffusion of CO₂ because of the low air space ratio (Fitter and Hay, 1981), but photosynthetically more efficient at high light intensity because of the thick palisade tissue (Terashima and Saeki, 1983). Moreover, the high vein ratio suggests an advantage in supplying water to mesophyll cells. On the other hand, sprout leaves were supposed to be efficient at low light intensity and inefficient in the supply of water to mesophyll cells. Generally under natural conditions, epicormic branches flushed from a tree bole are considered to be located at the lower position, i.e., lower light intensity, than the original crown top. Thus, the sprout leaves which have efficient morphology at lower light intensity would adjust to such a light-stressed environment.

From the view point of water relations, these leaf morphology of sprouts may affect the water relation parameters which influence the water balance and productivity of the plant. The sprout leaves which have low V_o/L_a may be less effective as a buffer and apt to reduce stomatal conductance with transpirational water loss, despite their high relative water content (Table 2) because of the following reasons.

The water balance of leaves should be determined by the relationship between the rate of transpirational water loss and inflow rates into leaves. In recent studies, the delayed sap flow at the beginning of transpiration in leaves has been observed and discussed as a capacitance or buffering function of transpirational water loss (e.g., Schulze et al., 1985)(Kitano and Eguchi, 1989)(Milne, 1989). The delay of sap flow may be caused by both the resistance and the capacitance of the water passway (Yahata, 1987). Because, it is assumed that organs showing large capacitance, which have a less changeable xylem pressure potential with the change of water content due to high plasticity, might be able to maintain the xylem water potential against water loss. Besides, the delay of sap flow might occur at a position where sap flow at the same level of xylem pressure potential gradient is slower, namely where resistance is greater. Among the parts of a tree, leaves have a higher plasticity, and therefore their water potentials might be less changeable with the change of water content. Thus leaves may play a role of a capacitance as reported in sugi (*Cryptomeria japonica* D. Don) by Yahata(1987). However, sprout leaves have low V_o/L_a and are considered to be less effective as a capacitance.

The resistance, another factor of the water balance, can be discussed as follows by

the term of leaf specific conductance (LSC') measured in this study. Zimmermann (1978) (1983) and Ewers and Zimmermann (1984) measured the leaf specific conductivity (LSC) of several species and showed that LSC was higher at the lower parts and lower at the higher sections of the stem. Particularly low values of LSC were obtained at the junction of branches. Similar results were shown by Ikeda and Suzuki (1984) who measured the relative water conductivity of several hardwood species. Further, Zimmermann (1983) reported that the lowest LSC was observed at the petiole and its junction.

The value of leaf specific conductance (LSC') measured here may correspond to the integrated value of LSC from the soil to the leaf. LSC' and transpiration rates of sprouts were far greater than those of normal shoots flushed from similar position (Fig. 10, Table 3). Conner (1977) showed that water use in young regrowth stands of *E. regnans* was greater than in taller trees of greater age because of the lesser resistance to water flow. On the other hand, Blake (1980) concluded in his results for *E. camaldulensis* that the higher transpiration rate of coppiced seedlings than of intact seedlings was due to changes in stomatal characteristics rather than to a decrease in stem resistance, because coppiced seedlings were as tall as intact seedlings. Changes in stomatal frequency and dimension induced by sprouting were observed in *Pasania edulis* (Ito and Suzuki, 1989) as well as in this study, and these changes may partly explain the high transpiration rates of sprout leaves. However, to maintain the high transpiration rate, plants must have some mechanism to maintain the high stomatal conductance against the water loss, or high water conductivity to compensate for water loss. From the results obtained here, it can be concluded that although sprout leaves of *E. globulus* have water relation characteristics which are inferior in maintaining cell turgor against water loss, they can show high transpiration rates due to high LSC' .

We observed higher LSC' in the sprouts of original tree stumps which have a large and deep root system of original tree than in seedlings of *Pasania edulis* (unpublished data), and it is possible to consider the greater capacity of water absorption of the original root system to be one of the reasons for the high LSC' of sprouts. However, as each shoot used in this study flushed from similar position, the difference in LSC' was assumed to result from the difference in the conductivity from the shoot junction to the leaf. It is of particular interest that petioles which may be the narrowest bottleneck because of their low LSC (Zimmermann, 1983) were shorter in sprouts which showed higher LSC' than normal shoots. In the actual results, several problems such as the relative importance of the conductivity within the branch or through the membrane of the mesophyll cell are yet to be resolved.

As mentioned above, it is thought that changes in the water relations of leaves are closely related to the changes in leaf morphology and anatomy induced by sprouting. In relation to changes of leaf form, some factors influencing water relations and gas

exchange characteristics, such as boundary layer resistance, can be anticipated. However, no data was collected here to account for the significance of changes in leaf form.

E. globulus used in this study showed peculiar changes of stomatal frequency and demension when sprouting. Stomata were absent on the adaxial surface of the sprout leaves. Nevertheless, there is only a little information about the ecological significance of one-sided stomata. Blake and Tschaplinski(1983) reported that a poplar clone in which stomata were absent on the adaxial surface showed the highest water use efficiency of several poplar clones, and suggested that the absence of stomata on the adaxial surface was one of the foliar adaptations which would tend to increase the resistance to water loss. They also referred to the significance of high stomatal frequency as a factor of foliar adaptation. On the other hand, Ceulmans et al.(1989) showed that stomata on the abaxial surface were less responsive to the changes of PPF_D or water loss after leaf excision than those on the adaxial surface in *Populus* sp. Therefore, the morphological changes observed in this study should be discussed in evaluating the differences of the responsiveness between small stomata with high frequency and large stomata with low frequency, and between abaxial and adaxial surfaces.

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ユーカリノキの萌芽葉の形態および水分特性

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要 約

ユーカリノキ (*Eucalyptus globulus*) では当年生萌芽枝の葉は広楕円形であるのに対し、通常枝の普通葉は披針形である。1年生萌芽枝の葉は基部から梢端へ向かって卵形から披針形へと連続的に変化している。これらの葉について、形態および水分生理的特性の比較を行った。葉形の変化にともない葉の内・外部形態は連続的に変化していた。普通葉は長い葉柄を持ち、SLAが小さく、葉脈が密で、細胞間隙が比較的少なく、3~4層の柵状組織を有しており、全体的に強光利用型の特性を示した。これに対して当年生萌芽葉は逆の特性を示し、弱光利用型であると考えられた。萌芽葉の気孔は普通葉と顕著に異なり、背軸側では普通葉より小型の気孔を多数つける傾向がみられたが、向軸側では気孔がほとんど観察されず、萌芽により、片面気孔化する傾向が認められた。また、葉の水分特性をP-V曲線法で求めた結果、萌芽葉は葉の水分損失に対する気孔開度の維持機構が普通葉に比較して劣ることが推察された。自然状態で測定された蒸散速度および気孔コンダクタンスは、萌芽葉で非常に大きな値を示したが、葉の水ポテンシャルの日変化では、両者に大きな差はみられなかった。これらの野外測定データから計算された単位葉面積を支持する器官の水分通導性は、普通枝よりも萌芽枝で高かった。したがって、弱光利用型の形態を持ち、相対シンプラスト水量の少ない萌芽葉では、水分通導性が高く葉への水分供給が容易なことが、高い気孔コンダクタンスを維持する大きな要因となっていると考えられた。