Responses of Tree Seedling (*Abies sachalinensis* Mast. and *Picea glehnii* Mast.) to Water Stress

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Responses of plants to water stress are composed of two components as proposed by Levitt[1]. One is related to the ability to postpone dehydration (drought avoidance), and the other is related to the ability to survive dehydration (drought tolerance). Drought resistance of plants is caused by various combinations between different kinds of avoidance and tolerance, and a wide variety of adaptations to drought has arisen.

Todo-fir (*Abies sachalinensis* Mast.) and Akaezo-spruce (*Picea glehnii* Mast.) are most important tree species of afforestations in Hokkaido. Immediately after transplanting their seedlings, damage is sometimes caused by serious drought from spring to summer. Todo-fir is usually rated as a more drought-resistant tree than Akaezo-spruce, but we do not have sufficient evidences as to which of these two tree species is more drought-resistant. The present paper describes both drought avoidance and drought tolerance of these two tree species and the total drought resistance is compared between the two species.

Outlines of this study and experimental methods

Fig. 1 shows the framework of this study[3]. Drought avoidance was based on the xylem pressure potential at stomatal closure, the dehydration rate of seedlings, the transpiration coefficient, and the decreasing rate of photosynthesis during droughts. Drought

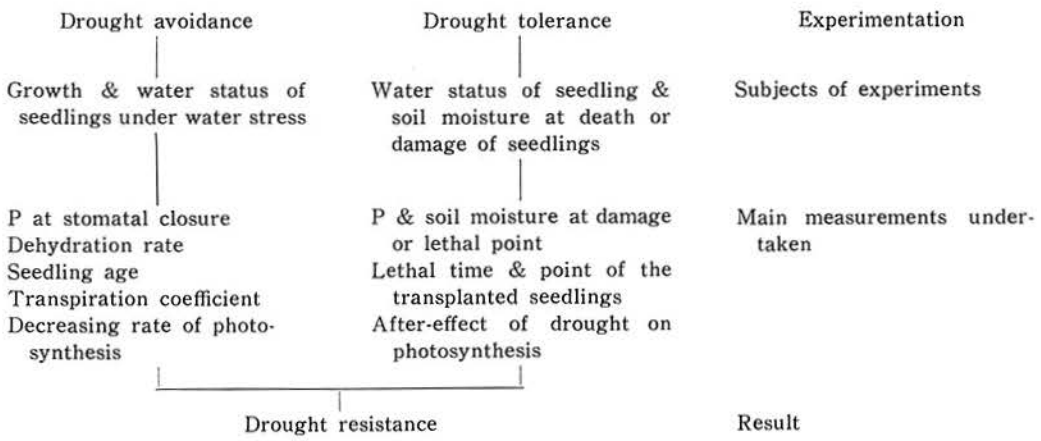

Fig. 1. Framework of this study

Table 1. Effect of soil moisture on growth and water consumption in the open

Species	Soil* moisture	Number of samples	Transpiration coefficient	Growth/ leaf amount	Transpiration/ leaf amount	T–R ratio
Todo-fire	W	9	362 (510–311)	1.37 (1.85–0.92)	490 (600–301)	2.10 (2.33–1.75)
	M	11	346 (442–278)	1.78 (2.73–1.05)	603 (884–395)	1.91 (2.60–1.70)
	D	10	309 (393–219)	1.47 (2.75–0.82)	427 (601–306)	1.74 (2.02–1.11)
Akaezospruce	W	8	442 (545–349)	0.95 (1.29–0.75)	413 (487–367)	2.49 (3.00–2.08)
	M	10	506 (637–410)	0.84 (1.20–0.62)	417 (527–296)	2.52 (3.19–1.74)
	D	7	556 (782–386)	0.56 (0.79–0.32)	292 (382–224)	2.33 (2.66–1.99)

* W: 85–75% on a dry weight basis, M: 60–50%, D: 35–25%

tolerance was based on the xylem pressure potential and the soil moisture content at which death or visible damage was observed, and the aftereffect of drought on photosynthesis. The water status of the seedlings was determined by measuring the xylem pressure potential (P) of the shoots, the relative water content (RWC) and the water content (WC) of the needles. P above −40 atm was measured with a pressure chamber, and the osmotic pressure potential of the shoots was substituted for P below −40 atm. The osmotic pressure potential of the shoots was measured by the cryoscopic method using a copper-constantan thermocouple after the shoots were killed by freezing. RWC was measured after floating the needles in distilled water for 24 hr at 20°C in the dark. The apparent photosynthesis of the seedlings was measured by an infrared gas analyzer at a temperature of 20°C in the assimilation chamber under the light intensity above the seedlings of 30 klux. The age of Todo-fir seedlings which were used in this study was mainly 4-year old to 6-year old and that of Akaezo-spruce was mainly 4-year old to 7-year old.

Responses of seedlings to soil drought

1) Efficiency of water utilization[2)]

Effects of three levels of soil moisture (85–75%, 60–50% and 35–25% on a dry weight basis) on the transpiration and the dry matter production of these two species were studied during the growing seasons for three years. The permanent wilting percentage of the used soil was 21.8%. The transpiration coefficient of Todo-fir was 611–337 in the shaded condition with a light intensity of 75% that in the open, and 511–219 in the open. That of Akaezo-spruce was 1042–345 in the shaded condition and 782–349 in the open. The effects of the three levels of soil moisture on the transpiration coefficient of both species were not statistically significant, but in the open the transpiration coefficient of Todo-fir decreased with decreasing soil moisture while that of Akaezo-spruce increased with the decrease in soil moisture as shown in Table 1. With the decrease in soil moisture, the dry matter production and the transpiration of Akaezo-sprude decreased in both shade and open, but the dry matter production of Todo-fir in the open almost never decreased with the decreasing soil moisture. In the open the dry matter production per gram of oven-dry weight of Todo-fir needles was nearly three times as much as that of Akaezo-spruce under dry soil conditions. The transpiration coefficient of Todo-fir showed a higher drought avoidance than Akaezo-spruce in dry soil conditions.

2) Changes of water status and visible damage of seedlings

The seedlings of these two species under soil moisture stress were placed in a growth cabinet with the temperature at 20°C and a light intensity of 45 klux with a day length of 14 hr. A rapid decrease of P began when the soil moisture content dropped below 25%

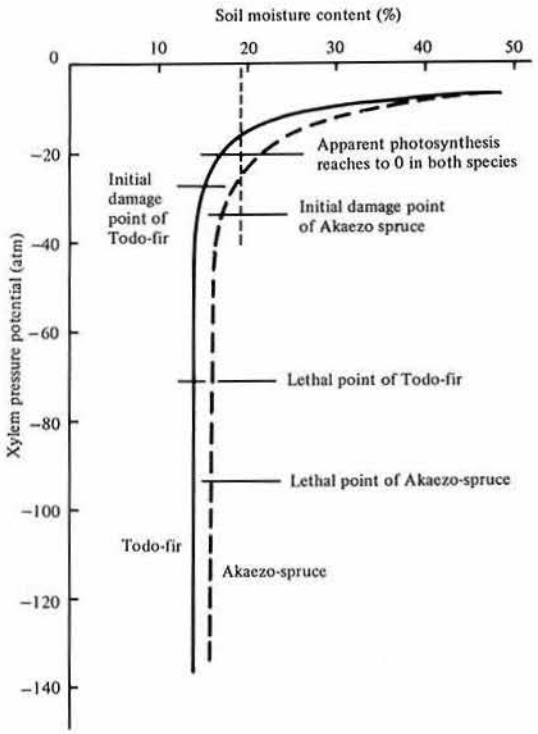

Fig. 2. Typical relationship between xylem pressure potential and soil moisture.

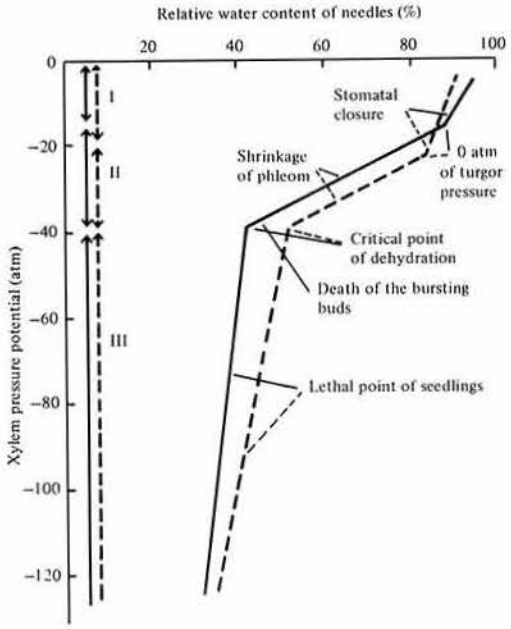

Fig. 3. Typical water status of seedlings in Todo-fir (solid line) and Akaezo-spruce (broken line) under water stress.
I: Usual water stress
II: Damage symptoms occur in some seedlings and death occurs in bursting buds and transplanted seedlings after drought
III: Damage symptoms occur in all seedlings and below around −80 atm all seedlings are killed

in Akaezo-spruce and 20% in Todo-fir in the autumn as shown in Fig. 2. The P and RWC at the permanent wilting point of soil moisture (19.5%) were −15 atm to −20 atm and 90% to 80%, respectively in Todo-fir and −20 atm to −25 atm and 85% to 75%, respectively in Akaezo-spruce. The soil moisture content at which the visibl damage was observed was around 19% in both species, but the soil moisture, RWC, and WC at which the death of seedlings of Todo-fir occurred were lower than those of Akaezo-spruce. The P at stomatal closure was concluded to be below −12 atm in Todo-fir and below −15 atm in Akaezo-spruce by the measurement of the evapotranspiration from a pot with a seedling. The phloem of shoots or of needles in both species was observed under a microscope to shrink severely before visible damage occurred. The P-RWC curves of both species had two inflection points which were around −20 atm and around −40 atm as shown in Fig. 3. It was considered that the turgor pressure of the shoots reached nearly 0 atm at the former point and the dehydration of the seedlings reached the critical point at the latter point. The apparent photosynthesis of both species declined with the decreasing soil moisture. But the apparent photosynthesis of Todo-fir did not decline so much as that of Akaezo-spruce at the soil moisture content just before permanent wilting point.

Responses of seedlings to dehydration

1) Apparent photosynthesis of seedlings during drought and after watering

Seedlings with roots wrapped in gauze were fixed in empty plastic pots covered with foam polystyrene. The depression of the apparent photosynthesis of Todo-fir occurred more slowly than that of Akaezo-spruce. The apparent photosynthesis of Akaezo-spruce declined to 20% of its maximum value 10 hr faster than that of Todo-fir. The seedlings of the two species were watered when P decreased to around −20 atm. The relative value of the apparent photosynthesis increased to 60% in Todo-fir and 30% in Akaezo-spruce 20 hr after watering, indicating that Todo-fir recovered the apparent photosynthesis twice as fast as Akaezo-spruce. In both species the apparent photosynthesis after watering was smaller than that before watering at the same P. Todo-fir was more drought-tolerant than Akaezo-spruce, because Todo-fir showed a smaller after-effect of drought than Akaezo-spruce as shown in Fig. 4.

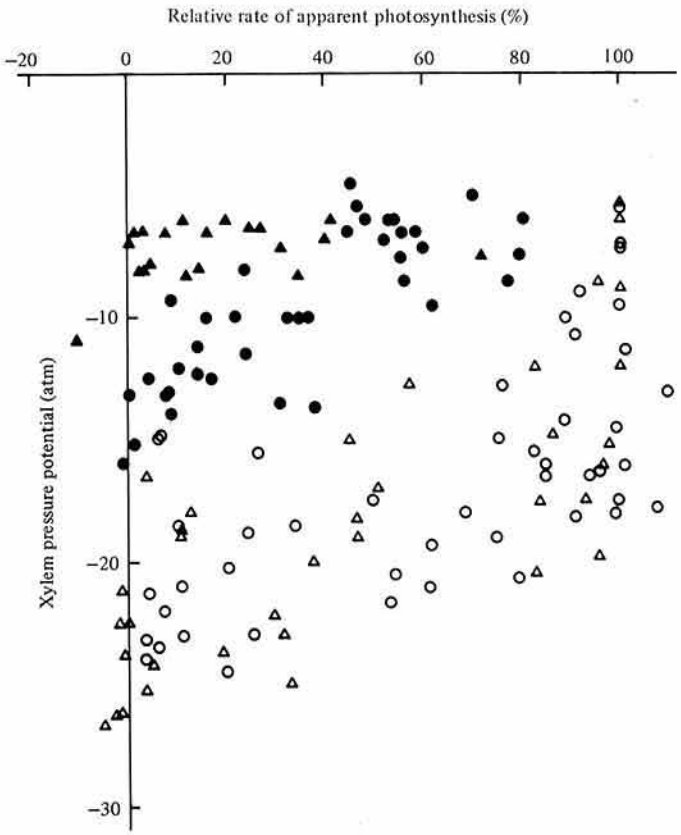

Fig. 4. Photosynthetic response of Todo-fir (○) and Akaezo-spruce (△) to drought and watering.
○△ : Before watering
●▲ : After watering

2) Changes of water status and visible damage of seedlings

Seedlings with roots covered by polyetylene bags and aluminum foil were desiccated in the growth cabinets at 20°C under natural light or artificial light conditions, because the experimental periods must be shortened in the bud-bursting season. The visible damage to both buds and needles was observed at the same value of P which was −26 atm in Todo-fir and −34 atm in Akaezo-spruce in the bud-bursting season. Those values were the same as the values of P at which the damage to needles occurred in the autumn. The lethal P of the seedlings was assumed to be around −80 atm in both species. Needles were more drought-tolerant than buds in the bud-bursting season. The RWC and WC in the bud-bursting season was higher than those in the autumn. The P-RWC curves of Todo-fir had two inflection points, similar to those in the autumn, but the curves of Akaezo-spruce did not show even a single inflection point because of increase of RWC.

The younger seedlings of both species were dehydrated more rapidly than the older ones, and in younger seedlings the WC of the tops was smaller than that of the roots covered with polyetylene bags. It was easy for younger seedlings to lose water from the top in comparison with the older seedlings. The dehydration rate of both species was limited to −40 atm and was kept at a constant rate about 40%. Akaezo-spruce showed a lower P than Todo-fir at the same rate of dehydration, and the difference of P between the two species became large below the dehydration rate around 30%.

3) Lethal point and lethal time of the seedlings transplanted after drought

The seedlings of about the same weight of both species were desiccated in the growth cabinet at 20°C under natural light conditions for 19, 25, 42, and 50 hr starting from May 28th, and also for 48, 73, 116, and 169 hr from July 3rd. In September, after the seedlings were transplanted in the nursery of Hokkaido branch of the Institute the drought damage of the seedlings was observed. The P at which one-half of the seedlings were damaged was about −20 atm in Todo-fir. The P and dehydration rate at which all the seedlings were killed were −30 atm and 35% in Todo-fir and −20 atm and 30% in Akaezo-spruce, respectively, but if the roots of the seedlings reaching around −20 atm were immersed in water for 24 hr, the seedlings of both species were hardly damaged. The lethal time of Todo-fir was 42 hr and that of Akaezo-spruce was 19 hr. The difference of the lethal time between the two species may be caused by the drought tolerance of the roots. The results of this study are arranged as shown in Fig. 2 and 3.

Table 2. Components of drought resistance of seedlings

Components	Todo-fir	Akaezo-spruce
P at which initial damage occurred by soil moisture stress (T)	−28.5 atm	−34.5 atm
Lethal point by soil moisture stress (T)	−72 atm	−95 atm
Soil moisture at lethal point (D, T)	17%	19%
P at which initial damage occurred by dehydration of seedlings (T)	−26 atm	−34 atm
Lethal point by dehydration of seedlings (T)*	−80 atm	−80 atm
Lethal point after transplanting (T)	−30 atm	−20 atm
Time to death after transplanting (D, T)	42 hr	19 hr
P at stomatal closure (A)	−12 atm	−15 atm
Transpiration coefficient in dry soil moisture (A)	309	556
Decreasing rate of photosynthesis under water stress (A)	slow	fast
After-effect of drought on photosynthesis (T)	small	large

T: Drought tolerance, A: Drought avoidance, D: Drought resistance
* Estimated value

Total drought resistance

Table 2 shows the different components of drought resistance. The P value at which the damage or the death of seedlings occurred indicates a drought tolerance, but did not show drought resistance because P of both species showed different values from each other under the same stress of soil moisture or the same rate of dehydration. Both drought avoidance (the P at stomatal closure, the transpiration coefficient in dry soil, and the decreasing rate of apparent photosynthesis) and drought tolerance or drought resistance (the soil moisture at lethal point, the lethal point and the time to death after transplanting, and the after-effect of drought on photosynthesis) show that Todo-fir is more drought-resistant than Akaezo-spruce.

References

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