論　文

日緑工誌
J. Jap. Soc.
Reveget. Tech.
21 (2), 114～123

Diurnal and Seasonal Courses of Photosynthesis, Transpiration and Water Use Efficiency of Apple and Black Locust Seedlings in Different Soil Water Conditions

異なる土壌水分条件下で育てたリンゴとニセアカシア苗木の光合成・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 apple (*Malus pumila* Mill. var. dulcissima Koidz.) and black locust (*Robinia pseudoacacia* L.) were measured as diurnal courses and seasonal fluctuation from May to October in 1994. The soil moisture of apple and black locust was set on three levels by controlling the irrigated amount of water. Both species showed reductions of net photosynthesis during most measurements in low water conditions. Black locust reduced its transpiration at noon during most measurements in low water conditions. Distinct seasonal fluctuations of integrated daily CO_2 uptake and H_2O release were measured in both species, and yield a seasonal fluctuation of daily water use efficiency also. Integrated daily CO_2 uptake and H_2O release of both species decreased in low water conditions, but yielded a low daily water use efficiency in apple and a high value in black locust as the degree of reduction of integrated daily CO_2 uptake and H_2O release were different. The productivity of apple was higher than that of black locust with a very high water consumption during the same water stress conditions. Therefore we can conclude that black locust is more drought-tolerant than apple.

1. Introduction

The Loess Plateau is a severe soil-eroded region in China. 60 million people live off agriculture, forestry, and livestock there. Although the Loess Plateau area is huge, suitable land for agriculture is scarce. Therefore it is important to optimize the proportion of land area used by agriculture, forestry and livestock, so they measure land on small watershed units of 3～50 km² to provide sufficient food, further more to improve the living standards by developing the economy in fruit production and processing, at the same time, disasters from wind and rain can be avoided as well as soil-erosion and water-loss. This principle has been in place in China since the opening policy of the country in 1976 (ENDO, 1991).

Key words: Apple, Black locust, Photosynthesis, Transpiration, Water use efficiency, water stress
キーワード：リンゴ，ニセアカシア，光合成，蒸散，水利用効率，水ストレス

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Although forestry has been known as a very important component in the Loess Plateau region, drought limits the survival rate of afforestation and plant growth (The middle reach bureau of the Yellow River, 1993). Many studies have been made on site classification, right tree on right site, micro-catchment systems and agro-forestry technology to improve soil water conditions (WANG, 1994). Numbers of drought-tolerant tree species have been known qualitatively, however, quantitative evidence of the onset and intensity of water stress is still lacking.

Many studies have been made on the effect of water stress on photosynthesis, transpiration and plant growth (SATOO, 1956; LARCHER, 1965; NEGISI, 1966; PURITCH, 1973; TOBIESSEN and KANA, 1974; FEDERER and GEE, 1976; DOUGHERTY and HINCKLEY, 1981; TAKAHASHI, 1982; MARUYAMA and TOYAMA, 1987; YAMAMOTO *et al.*, 1993). However, almost all of studied materials were divided into well watered and water stress periods. Study of keeping the material under steady water stress conditions for a growing season, is still lacking because of the restriction of soil moisture measurement systems.

From the beginning of 1994, we studied the effect of water stress on the 3-year old seedlings of apple (*Malus pumila* Mill. var. dulcissima Koidz.) and black locust (*Robinia pseudoacacia* L.). We will discuss the diurnal courses and seasonal fluctuation of net photosynthesis (Ph_n), transpiration (Tr) and water use efficiency (WUE) of the above two species under different degrees of water stress, we managed these conditions by controlling the irrigated water amount.

2. Materials and Methods

2.1 Materials

Black locust (*Robinia pseudoacacia* L.) is a common tree species throughout the Loess Plateau. It is considered a drought-tolerant pioneer of afforestation. It grows well in nutritionally poor soils and low moisture conditions. In contrast, apple (*Malus pumila* Mill. var. dulcissima Koidz.) is more drought-intolerant than black locust. It is the main fruit tree species in the Loess Plateau that provides economic income. Its seedlings grow best in rich, moistured soils. Both species are not shade-tolerant (WU *et al.*, 1989; SATO *et al.*, 1991).

As study species, 3-year old seedlings of apple and black lacust were transplanted from a nursery to pots individually, and have been growing in the greenhouse of Shizuoka university since February, 1994. 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 same weight of air-dried Kanuma tsuchi, therefore we can consider that the soil physical properties in each pot were the same.

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

In general, pF 4.2 (−1.6 MPa) is considered to be the permanent wilting point, pF 2.7～3.0 (−0.05～−

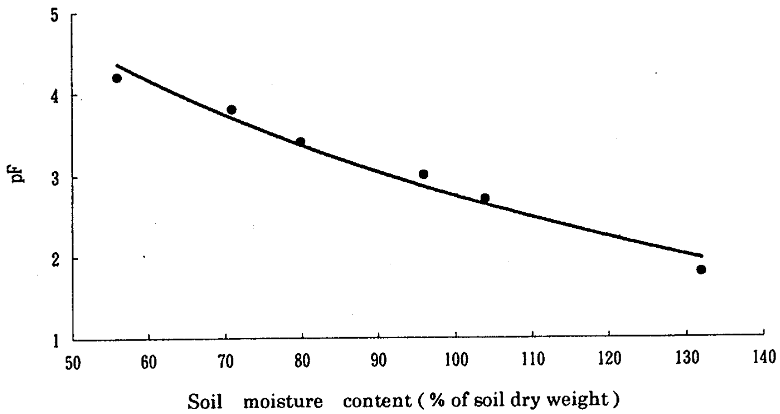

Fig. 1 pF-soil moisture curve.

0.10 MPa) known as moisture of rupture of capillary bond, and pF 1.8 (−0.01 MPa) to be field capacity, respectively. The drought tolerance of apple is considered to be intermediate, therefore, its soil moisture was set 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%) depending on the above pF-soil moisture curve. On the other hand, the soil moisture of black locust was established at pF 2.7, pF 3.2, and pF 4.0 (−0.98 MPa, 63%), respectively, because its drought tolerance is considered to be high (Wu *et al.*, 1989).

In each treatment, one heat probe sensor (IDL-1600, North Hightech Co. LTD) was set to measure 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 (HAN and KAKUBARI, 1994).

2.3 Physiological measurements

Diurnal changes of Ph_n and Tr were measured in leaves which had relatively the same position on the same shoot 1 time per month from May to October, between 0600 and 1800 at 1 hour intervals. 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), and stomatal conductance to CO_2 and H_2O.

The measured leaves of both species were detached and leaf areas were measured using the Delta-T Image Analysis System (DIAS, DELTA-T DEVICES LTD.) after measuring in October. 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.

Depended on the experiments of LARCHER (1965), woody plants are able to utilize water more rationally when soil moisture is rather low in comparison to high soil moisture conditions. It is shown by directly calculating the Ph_n/Tr ratio and it is called wateh use efficiency (WUE). From the above diurnal curves of Ph_n and Tr, the diurnal curves of WUE were estimated by integrating diurnal Ph_n/Tr ratios. In addition, integrated daily CO_2 uptake (IDCU) and H_2O release (IDHR) were estimated per unit leaf area by integrating 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.

To more precisely evaluate the effect of the changes in soil water status on the magnitude of assimilation and transpiration of these species, the peaks of Ph_n and Tr values in each diurnal curve were selected monthly.

3. Results and discussion

3.1 Diurnal courses of photosynthesis, transpiration and water use efficiency

The diurnal courses of Ph_n, Tr and WUE for apple from May to October are illustrated in Fig. 2, and Fig. 3 shows that of black locust in the same period. Soil water conditions are illustrated in Fig. 4, the points showing a drastic increase are the times at which irrigation took place. This figure shows only three days data in the middle of August while the soil moisture of each treatment was kept at steady levels respectively during this study.

Both apple and black locust had peaks of Ph_n in the morning during most measurements whereas Tr peaked at noon, later than its Ph_n, Black locust showed a distinct reduction of Ph_n during most measurements in pF 3.2 and pF 4.0 compared with that of pF 2.7 except the measurement in September. Black locust decreased its Tr remarkably at noon during most measurements in pF 3.2 and pF 4.0 compared with that of pF 2.7. Apple decreased its Ph_n in pF 2.7 and pF 3.2 in comparison to pF 2.2 during most measurements. However, no distinctive reduction of Tr was observed from apple during this study. Transpiration and CO_2 acquisition by a plant are linked by the stomata, through which both water vapor and CO_2 are diffused. The rates of diffusion of the two substances, however, are not identical. The chief problem associated with gas exchanges is that of "tacking adroitly between thirst and starvation". Some plants can do this better than others and are thus more successful competitors in dry habitats (LARCHER, 1975). As an example, the stomatal conductance to H_2O for black locust

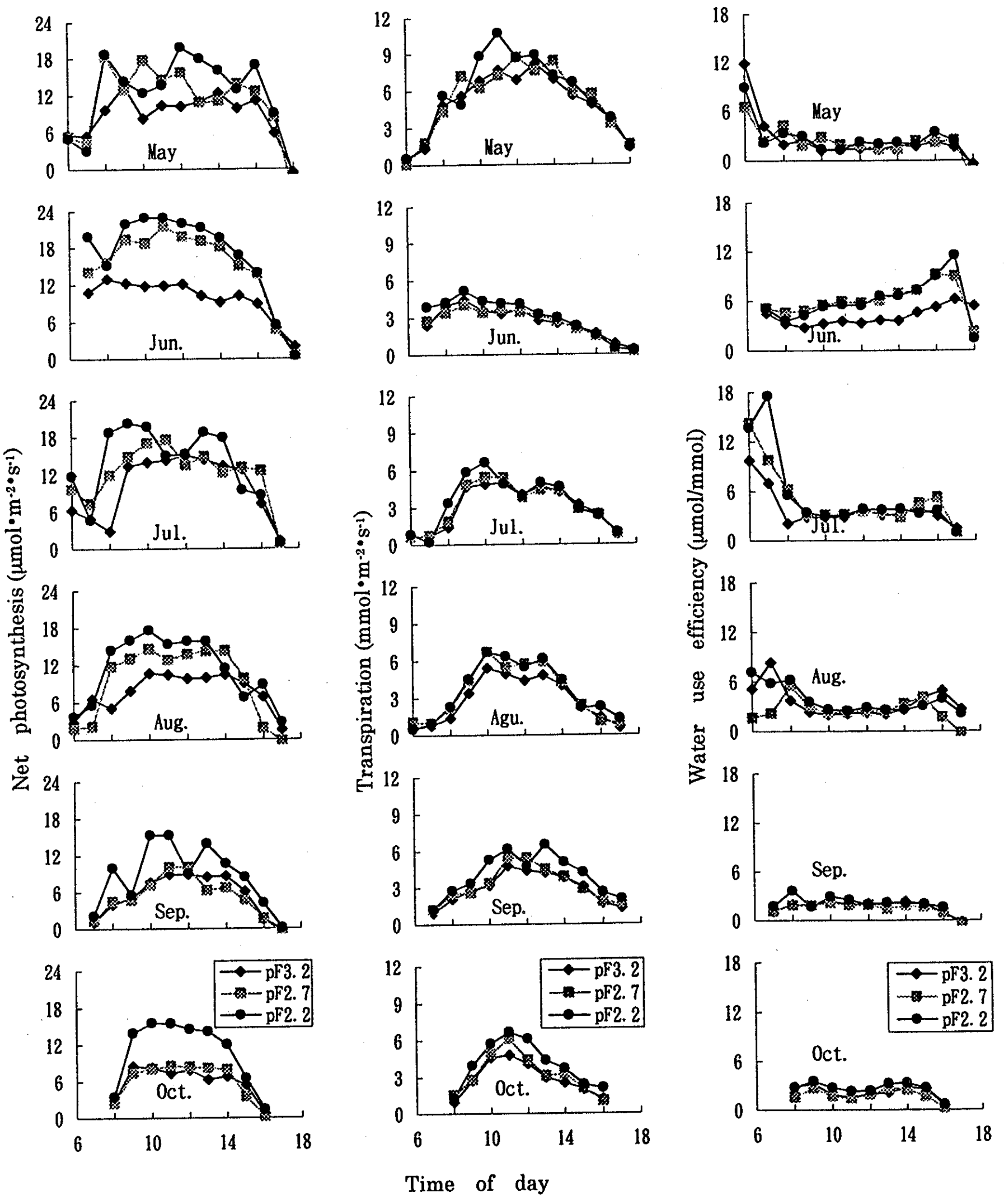

Fig. 2 The diurnal courses of net photosynthesis, transpiration and water use efficiency for apple (*Malus pumila* Mill. var. dulcissima Koidz.).

and apple are illustrated in Fig. 5, which were measured on 17 Aug., 18 Aug. 1994, respectively, because it is the warmest season and the most susceptible period to water stress. The following percentages were calculated with the corresponding values of each treatment measured at the same time. Apple decreases it stomatal conductance to H_2O, compared with pF 2.2, to 68%~95% in pF 2.7, 58%~83% in pF 3.2 to adapt to water stress conditions. But stomatal conductance to H_2O for black locust in pF 3.2 decreased to 41%~91% of pF 2.7, it fell to 20%~49% in pF 4.0. Further more, stomatal conductance to H_2O of black locust decreased more markablely than that of apple from pF 2.7 to pF 3.2. In addition, the relationship between net photosynthesis and stomatal conductance to CO_2 is illustrated in Fig. 6 for both species. Data measured from all treatments from May to October were used in this figure. It is evident that black locust often had a higher net photosynthetic rate than apple at the same stomatal conductance when it was lower than 150 mmol・m^{-2}・s^{-1}. This means black locust is more adroit than apple in controlling the gas exchanges.

To more closely evaluate the effect of the changes of soil water status on the magnitude of assimilation and

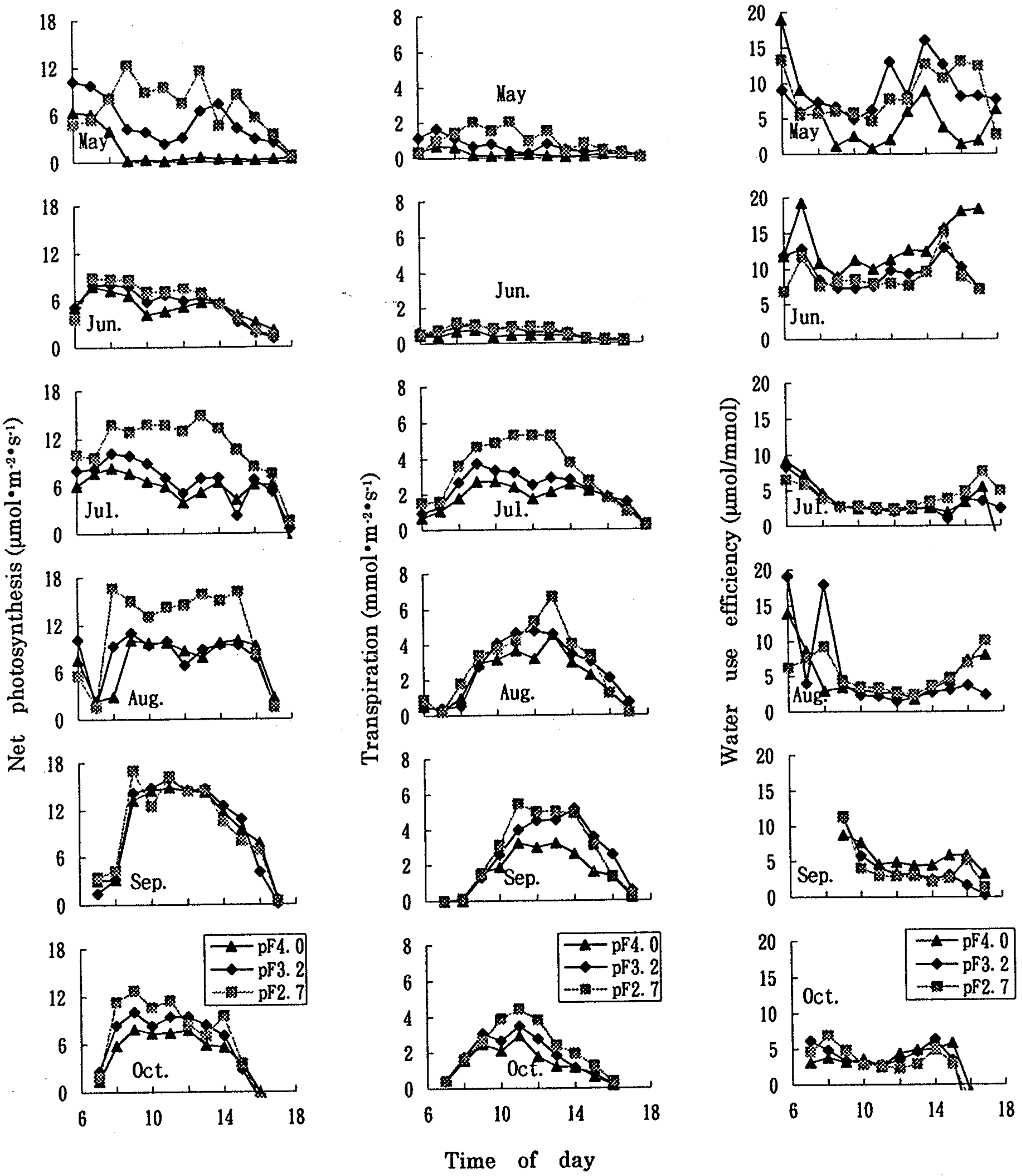

Fig. 3 The diurnal courses of net photosynthesis, transpiration and water use efficiency for black locust (*Robinia pseudoacacia* L.).

transpiration, the maximum daily Ph_n and Tr of apple and black locust are shown in Table 1 and Table 2, respectively.

As shown in Table 1, maximum daily Ph_n and Tr of apple, compared with that of pF 2.2, decreased to 55%～94% and 78%～100% in pF 2.7, 55%～74% and 72%～86% in pF 3.2, respectively. The reduced maximum daily Ph_n of apple was much lower than its Tr. On the other hand, black locust reduced these value, compared with that of pF 2.7, to 66～95% and 70%～95% in pF 3.2, 51%～88% and 33%～68% in pF 4.0, respectively (Table 2). The reduced maximum Ph_n of black locust was less lower than its Tr. For the management of afforestation, where the target is the greatest possible productivity, it is important to know the relationship between water consumption and productivity. We will discuss this in the following WUE section.

Ph_n and Tr under the same soil water conditions were discussed further as follows. Apple decreased its Ph_n remarkably in September and October (Fig. 2, Table 1), the data from May to August will be used in the following discussion. From pF 2.7 to pF 3.2, Ph_n decreased by 15～40%, for apple; 5～34%, for black locust, respectively (Tables 1 and 2). Tr decreased by 6-20%, for apple except in June; 5-30%, for black locust, respectively (Tables 1 and 2). Ph_n decreased more in apple than in black locust, but Tr showed a contrasted result. This appears that

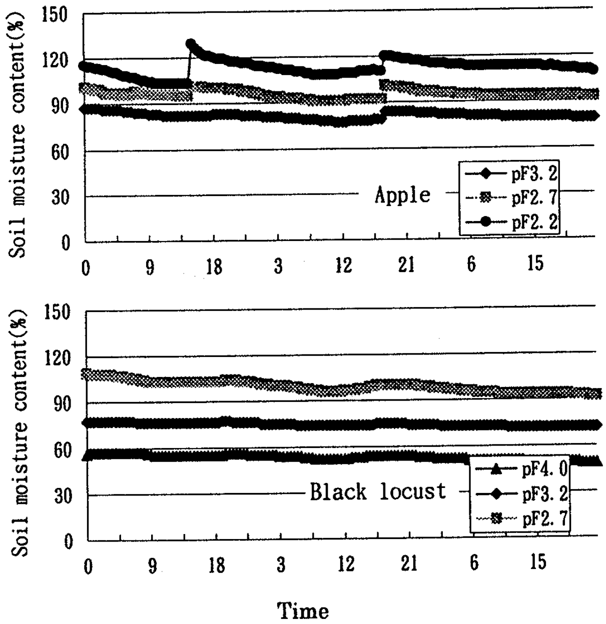

Fig. 4 Soil water conditions for apple (*Malus pumila* Mill. var. dulcissima Koidz.) and black locust (*Robinia pseudoacacia* L.) from 10 Aug. to 12 Aug. 1994.

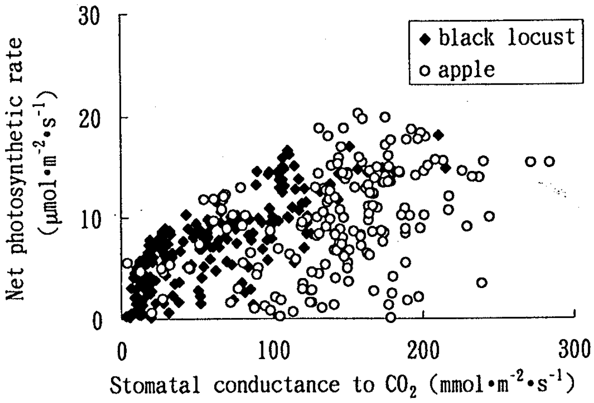

Fig. 6 The relationship between stomatal conductance to CO_2 and net photosynthesis for apple (*Malus pumila* Mill. var. dulcissima Koidz.) and black locust (*Robinia pseudoacacia* L.).

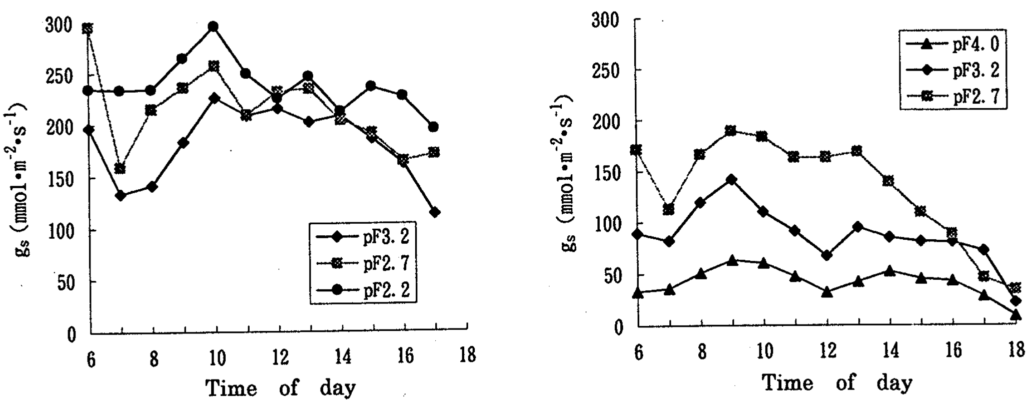

Fig. 5 Stomatal conductance to H_2O (g_s, mmol・m^{-2}・s^{-1}) for black locust (*Robinia pseudoacacia* L.) on 17 Aug. 1994 on the right side and apple (*Malus pumila* Mill. var. dulcissima Koidz.) on 18 Aug. 1994 on the left side.

Table 1 The maximum daily net photosynthesis (Ph_n, μmol・m^{-2}・s^{-1}) and transpiration (Tr, mmol・m^{-2}・s^{-1}) for apple

Month	pF 2.2 treatment		pF 2.7 treatment		pF 3.2 treatment	
	Ph_n	Tr	Ph_n	Tr	Ph_n	Tr
May	19.835	10.711	18.334(92)	8.743(82)	13.434(68)	8.201(77)
Jun.	22.941	5.121	21.504(94)	3.983(78)	12.885(56)	4.389(86)
Jul.	20.239	6.651	17.610(87)	5.462(82)	15.039(74)	5.010(75)
Aug.	17.627	6.693	14.570(83)	6.720(100)	10.672(61)	5.400(81)
Sep.	15.335	6.521	10.130(66)	5.446(84)	8.890(58)	4.772(73)
Oct.	15.525	6.667	8.581(55)	6.107(92)	8.507(55)	4.780(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 treatment respectively.

Table 2 The maximum daily net photosynthesis (Ph_n, $\mu mol \cdot m^{-2} \cdot s^{-1}$) and transpiration (Tr, $mmol \cdot m^{-2} \cdot s^{-1}$) for black locust

Month	pF 2.7 treatment		pF 3.2 treatment		pF 4.0 treatment	
	Ph_n	Tr	Ph_n	Tr	Ph_n	Tr
May	12.268	2.046	10.239(83)	1.651(81)	6.306(51)	0.669(33)
Jun.	8.860	1.158	8.036(91)	1.071(92)	7.779(88)	0.741(64)
Jul.	14.774	5.303	10.154(69)	3.728(70)	8.332(56)	2.739(52)
Aug.	16.589	6.703	10.947(66)	4.753(71)	10.047(61)	4.580(68)
Sep.	16.984	5.459	16.078(95)	5.183(95)	14.868(88)	3.247(59)
Oct.	12.729	4.416	10.082(79)	3.470(79)	7.894(62)	2.933(66)

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.

black locust is more drought-tolerant than apple.

Although both H_2O and CO_2 are diffused by the same stomata, the rates of diffusion of the two substances are not identical (LARCHER, 1975). By analyzing the diurnal changes of WUE, the drought-tolerance of apple and black locust can be understood further. The diurnal changes of WUE are illustrated in Fig. 2 for apple ; Fig. 3 for black locust, respectively. WUE reached its peak twice a day : in the morning and the afternoon during most measurements. In the morning at fairly low temperatures and saturation deficits of air, Ph_n was intense, but the Tr was only moderate, yielding a high WUE ; at noon Tr increased significantly while Ph_n remained at the same level or even dropped as a result of increasing respiration and water stress, at this point the WUE was low ; in the afternoon, Tr declined more rapidly than Ph_n and recorded high WUE. Several minus values of WUE were shown in Fig. 2 and Fig. 3 as respiration, but not photosynthesis, occurred at that time.

In apples, lower water potential treatment showed lower WUE than higher water potential treatment although it was not very distinct. However, no distinct differences of WUE among the three treatments was measured at this time in black locust because Ph_n and Tr increased or reduced simultaneously as a result of stomatal regulation in different water conditions.

At the same soil water conditions of pF 2.7 and pF 3.2 treatments, black locust was higher in WUE than apple from Fig. 2 and Fig. 3. As mentioned above, this means black locust can adjust its water consumption and productivity more rationally than apple, in the other words, it is able to use restricted water more efficiently, therefore, it is more drought-tolerant. This will be further discussed in the following section as unit per day.

3.2 Seasonal fluctuation of daily 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 a high productivity with little water consumption, it is necessary to know the daily Ph_n, Tr, and WUE.

We integrated daily CO_2 uptake (IDCU) and H_2O release (IDHR), respectively, and divided IDCU by IDHR to get daily WUE (Fig. 7).

The seasonal fluctuations of IDCU of apple in pF 2.2 and pF 2.7 treatments were in the same shape as illustrated in Fig. 7. It hit a peak in June, then fell quickly from July. However, in pF 3.2, it showed a relatively high value from May to July, then fell from August.

Compared with its IDCU, IDHR in three treatments showed a similar trend, it fell drastically in June, then increased slowly and fell again. The seasonal fluctuation of daily WUE kept this similar shape as its IDCU in all three treatments.

On the other hand, the IDCU of black locust in pF 2.7 treatment increased from May, then hit its peak in July and August, and fell from September, however, in pF 3.2 and pF 4.0, the peak was late in September.

IDHR of black locust increased from May, then hit a peak in July, and fell from August in pF 2.7 treatment. However, in pF 3.2 and pF 4.0, the peak was late in August. The seasonal fluctuations of daily WUE were high in May and June, and fell lower from July.

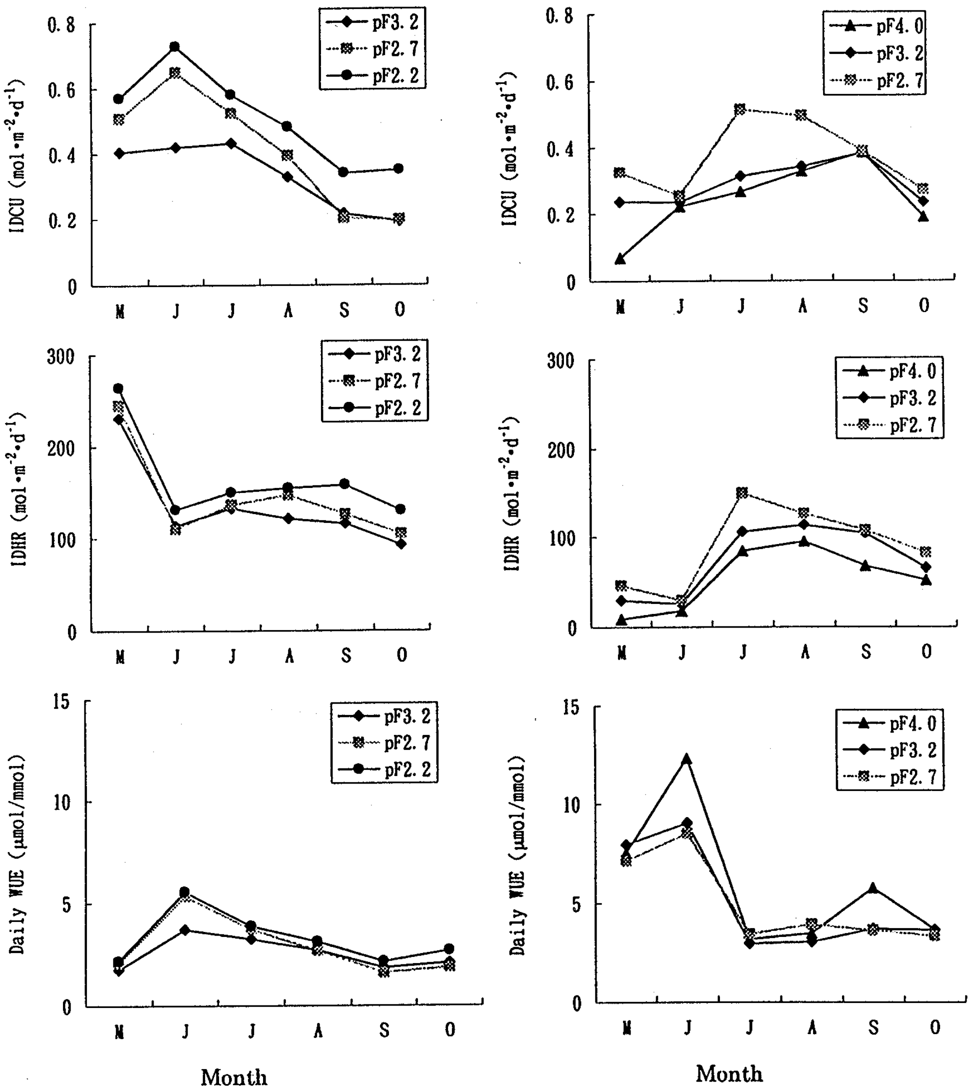

Fig. 7 The seasonal fluctuation of integrated daily CO_2 uptake (IDCU, mol・m^{-2}・d^{-1}), integrated daily H_2O release (IDHR, mol・m^{-2}・d^{-1}) and daily water use efficiency (daily WUE, μmol/mmol) for apple (*Malus pumila* Mill. var. dulcissima Koidz.) on the left side and black locust (*Robinia pseudoacacia* L.) on the right side.

IDCU of apple, compared with that of pF 2.2, fell to 56%～88% in pF 2.7, 54%～72% in pF 3.2. IDHR decreased to 80%～94% in pF 2.7 and 72%～88% in pF 3.2. At the same water stress conditions (pF 2.7 or pF 3.2 treatments). IDCU fell lower than IDHR, therefore daily WUE in pF 2.7 and pF 3.2 were lower than in pF 2.2, fell to 67～99% of pF 2.2 (Fig. 7). This means that the suitable soil water condition for apple is about pF 2.2, because apple is a tree species with high water consumption.

During the growing season, IDCU of black locust fell to 72%～98% in pF 3.2 and 20%～96% in pF 4.0 treatments in comparison to pF 2.7 treatment. However, IDHR reduced to 64%～96% in pF 3.2 and 20%～72% in pF 4.0. In the high growing period of July and August, the daily WUE of pF 3.2 and pF 4.0 fell to 80%～90% of pF 2.7 as IDCU fell lower than IDHR respectively; but in contrast, the values in the other periods were higher, they increased to 105%～150% of pF 2.7 (Fig. 7). This means that black locust is drought-tolerant and it is suitable in pF 3.2 and even in more dry conditions.

At the same soil water condition of pF 2.7, IDCU, IDHR, and daily WUE during the growing season were 0.197～0.648 mol・m^{-2}・d^{-1}, 104.843～244.862 mol・m^{-2}・d^{-1}, 1.593～5.868 μmol/mmol, respectively, for apple; 0.254～0.495 mol・m^{-2}・d^{-1}, 29.884～150.098 mol・m^{-2}・d^{-1}, 2.945～9.045 μmol/mmol, respectively, for black locust. In addition to pF 3.2 treatment, the values were 0.193～0.432 $mol \cdot m^{-2} \cdot d^{-1}$, 92.398～230.382 $mol \cdot m^{-2} \cdot d^{-1}$, 1.848～3.700 $\mu mol/mmol$, respectively, for apple; 0.235～0.383 $mol \cdot m^{-2} \cdot d^{-1}$, 25.956～113.551 $mol \cdot m^{-2} \cdot d^{-1}$, 3.322～8.513 $\mu mol/mmol$, respectively, for black locust. The IDCU of apple in pF 2.7 and pF 3.2 treatments was higher than that of black locust, respectively, and its IDHR was much higher than that of black locust, therefore the daily WUE was lower. This indicates that black locust can use water more efficiently than apple under the same water stress conditions, and it is more drought-tolerant.

Acknowledgments

The authors would like to thank the students of the silvicultural laboratory who helped to do the transplantation work and measurement assistance. They also thanks Michael E Jackson of the same laboratory for his English correction.

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* These English titles are tentative translations by the authors of this paper from the original Japanese.

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(Received September 5, 1995)

要　旨

5月から10月までリンゴ（*Malus pumila* Mill. var. dulcissima Koidz.）とニセアカシア（*Robinia pseudoacacia* L.）苗木の光合成・蒸散の日変化及び季節変化を測定した。潅水量によって，りんごとニセアカシアの土壌水分を3段階に設定した。ニセアカシアとリンゴの純光合成は土壌含水比が低い場合，低い値を示したことが多かった。土壌水分が低い場合，ニセアカシアの蒸散が日中低い値を示したことは多かった。1日の総同化量・蒸散量及び水利用効率は顕著な季節変化を示した。2樹種とも，土壌含水比が低い場合は総同化量および蒸散量は減ったが，リンゴの場合は低い日水利用効率を示して，ニセアカシアの場合は高い日水利用効率を示した。これは樹種によって1日の総同化量と蒸散量の減少の割合が異なるためである。同じ土壌水分条件で2樹種の耐乾性を比べると，ニセアカシアのほうがリンゴよりすぐれていることがわかった。