



Change of evapotranspiration components due to the succession from Japanese red pine to evergreen oak

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Abstract

Extensive measurements of water balance components in a forest under the succession from Japanese red pine (*Pinus densiflora*) to evergreen oak (*Quercus myrsinaefolia*) were carried out. Significant decreases of transpiration from the red pines and forest interception loss were found based on the observational results in 1984/1985 and 2001/2002. The former was the pre-succession period and the latter was the middle succession period in the study forest. Although the forest had a main canopy of the red pines in 1984/1985, the multi-layered canopies were observed in 2001/2002, which were consisted of the upper canopy layer of the red pines and of the lower canopy layer of the evergreen oaks. On the other hand, no significant difference in the amount of total evapotranspiration between the two periods was observed, because the decrease of transpiration from the red pines was compensated by the increase of transpiration from the lower canopy layer, which was about three times larger than that of the red pines. Three factors were identified to produce the large amount of transpiration from the lower canopy layer: (i) increased net radiation over the lower canopy due to the increased gaps in the canopy of red pine, (ii) a relatively small difference of total sapwood area between the red pine and the lower canopies and (iii) larger sap flux densities of main species in the lower canopy which were around two times larger than that of the red pine canopy.

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1. Introduction

The role of the forest in the hydrologic cycle has been studied in the past by paired-catchment experiments focusing on runoff change by alteration of vegetation cover (e.g. Bosch and Hewlett, 1982). Specifically, paired-catchment studies have often been used to assess the potential changes in water yield due to land use

changes and forest disturbances including insect infestations (Bethlahmy, 1974; Love, 1955), forest fire (Helvey, 1980), afforestation (Ayer, 1968; Smith, 1992), vegetation type conversion (Pitman, 1978; Swank and Miner, 1968; Swank and Douglass, 1974), selective shrubs harvesting (Johnson and Kovner, 1956), riparian vegetation conversion (Rich and Gottfried, 1976), partial cutting (Lynch and Sopper, 1970) and selective forest harvesting (Troendle and King, 1985). Although the previous paired-catchment experiments have investigated the effects of

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deforestation and afforestation on the hydrologic cycle, little attention has been paid to changes in hydrologic regime induced by natural succession of a forest.

In warm-temperate regions, natural succession from sun trees to shade trees, which constitute the vegetation climax, is commonly observed (e.g. Yamashita and Hayashi, 1987). During such succession, forests usually have multi-layered canopies consisting of lower layers with shade trees and upper layers with sun trees. Any change of canopy structure may cause alterations of stemflow generation and of the sources of transpiration. It has been reported that the amount of stemflow from the lower layer is equal to or larger than that from the upper layer (Lloyd and Marques, 1988; Manfroi et al., 2004; Murai, 1970; Suzuki et al., 1979). Iida et al. (2005) observed an increase of the amount of stemflow and a decrease of interception loss during a succession from Japanese red pine (*Pinus densiflora*) to evergreen oak (*Quercus myrsinaefolia*). It has also been observed that transpiration from the understory vegetation occupies a significant proportion of evapotranspiration, sometimes being as large as 20–30% (Black et al., 1996; Blanken et al., 2001) or more than 50% (Kelliher and Black, 1986; Kelliher et al., 1997; 1998; Roberts et al., 1980; Tan et al., 1978). Thus, it is likely that a progressing succession will result in increasing stemflow and transpiration from the lower layer.

Since the potential natural vegetation is determined mainly by the air temperature in a warm-temperate region with sufficient soil water availability like Japan, Ishigami et al. (2003) predicted the change in distribution pattern of the potential natural vegetation under four scenarios of global warming, and pointed out that the area of evergreen broadleaved (mainly evergreen oak) forest will expand to the northern part of Japan. To predict possible changes in forest water balance due to the global warming, it is necessary to clarify how the succession affects the water balance.

The competition for light, water and nutrients between the pioneer species and the successors during a succession has already been clarified in the literature. For example, Oren et al. (1987) found that the leaf area index (LAI) of *Pinus ponderosa* decreased as a result of the growth of the understory vegetation. Similarly, Kume et al. (2003) showed that the understory vegetation growing up during secondary succession has a negative physiological effect on

an overstory of Japanese red pine needles through competition for water and nutrient uptakes by the root system. Very few studies, however, have dealt with the succession from the viewpoint of the forest water balance. To shed some light on this issue, in this paper, the changes in the water balance during a succession are studied with emphasis on the sources of the transpiration of the changing vegetation. This is done by making a comparison between two sets of observations conducted at the beginning and at the end of a 17-year period.

2. Materials and methods

2.1. Study site

The study area of 0.017 km² is generally flat and located at 36°07'N and 140°06'E at an altitude of 27 m adjacent to the Terrestrial Environment Research Center (TERC), University of Tsukuba, Japan (Fig. 1). The annual rainfall ranges from 900 to 1600 mm with an average of 1207 mm for the period from 1982 to 2001. The annual mean air temperature for the corresponding period is 14.1 °C.

In this region, the vegetation climax is evergreen oak (*Q. myrsinaefolia*), which is classified as a shade tree. However, this region has become covered by Japanese red pine (*P. densiflora*), a typical sun tree, since the nineteenth century through natural fires and the continuous use of pine trees and understory shrubs for general construction works and as firewood (Horiuchi, 1978). The time of origin of the pine trees in the study area was estimated to be about 1950. The red pine forest was managed until the 1980s for the objectives mentioned above. After that, the management was gradually discontinued due to the introduction of gas and electricity as well as other newer construction materials (Iwaki and Koshizuka, 1981). As a result, shade trees (mainly *Q. myrsinaefolia*) penetrated into the pine forest and the secondary succession started to take place (Yamashita and Hayashi, 1987).

2.2. Observation periods and changes of forest characteristics

Over the 17-year period under consideration, two experiments were conducted. The first set of

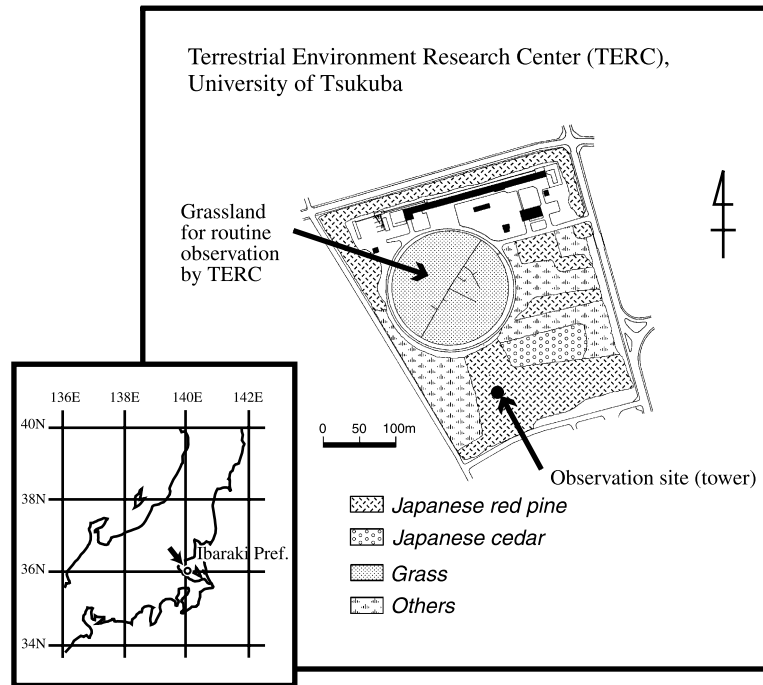


Fig. 1. Location of the Terrestrial Environment Research Center (TERC), University of Tsukuba, and the observation site.

measurements took place from September 1984 to August 1985 (hereafter referred to as 1984/1985) (Sugita, 1987) and the second one from August 2001 to July 2002 (2001/2002). The period of 1984/1985 corresponds to the pre-succession stage and 2001/2002 to the middle stage of the succession process. The relevant statistics for the forest structure in both 1984/1985 and 2001/2002 are listed in Table 1. The main changes can be found in a drastic decrease of the

stand density and the leaf area index (*LAI*) and in an increase of the diameter at breast height (*DBH*) of the pine trees. Although the heights of almost all trees of *Q. myrsinaefolia* were smaller than 4 m in 1984/1985 (Yamashita and Hayashi, 1987), this species constituted the lower canopy layer in 2001/2002 (Fig. 2). In this study, the lower canopy layer is defined as the range of the heights from 4 to 11 m, and the range from 0 to 4 m is defined as the herbaceous layer as

Table 1
Summaries of forest structure in 1984/1985 and 2001/2002

	LAI		Mean diameter at breast height (cm)				Stand density (trees/100 m ²)		Mean tree height (m)		
	All forest	Red pines	Lower canopy trees	Red pines	Lower canopy trees		Red pines	Lower canopy trees	Red pines	Lower canopy trees	
					<i>Q. myrsinaefolia</i>	<i>E. japonica</i>				<i>Q. myrsinaefolia</i>	<i>E. japonica</i>
1984/1985	–	4.0	–	12.4	–	–	27.0	50.5 ^a	10.0 ^a	0.54 ^a	–
2001/2002	5.0 (±0.3)	2.7 (±0.4)	2.3 (±0.4)	18.4	4.9	4.5	6.8	39.0	15.0	6.7	5.2

^a These data are cited from Yamashita and Hayashi (1987) conducted at the same forest in 1985.

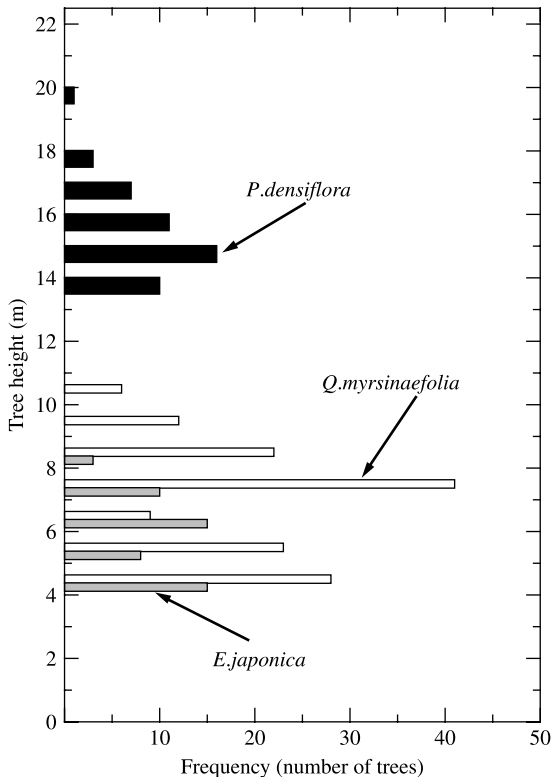


Fig. 2. Histogram of tree height of Japanese red pine (*P. densiflora*), *Q. myrsinaefolia* and *E. japonica* in 2001/2002.

shown in Fig. 3. Among the species of the lower canopy layer, evergreen oak (*Q. myrsinaefolia*), evergreen theaceous tree (*Eurya japonica*) and deciduous rhus tree (*Rhus trichocarpa*) occupied 55.8, 27.5 and 8.7%, respectively, of the total number of trees (Iida et al., 2003).

2.3. Instrumentation for the measurements

In the situation of 1984/1985, the evapotranspiration (ET) from the forest consists of the following components.

$$ET = TR_P + I + ET_F \quad (1)$$

where TR_P and I are the transpiration from the canopy of Japanese red pine and the forest interception loss, respectively. ET_F is the evapotranspiration above the forest floor including two sub-components: (i) the transpiration from the herbaceous layer and (ii) the evaporation from the forest floor.

In 2001/2002, the evapotranspiration comprises the following components.

$$ET = TR_P + TR_L + I + ET_F \quad (2)$$

Where TR_L is the transpiration from the lower canopy layer. The forest water balance was estimated in a circular plot area with a radius of 15 m and with its center at the observation tower (Fig. 1). This plot size was decided upon by taking into account the need for a precise observation of the interception loss (Iida et al., 2005).

2.3.1. Evapotranspiration and meteorological factors

In both periods, meteorological factors were observed on the tower in the forest to evaluate mainly the forest energy balance. Measured factors include the dry- and wet-bulb temperatures, the wind speed (u) above the forest canopy, the net radiation (R_n), the soil heat flux (G), and the sensible heat flux (H). The photosynthetically active radiation (PAR) was measured at the heights of 8.9 and 18.2 m in

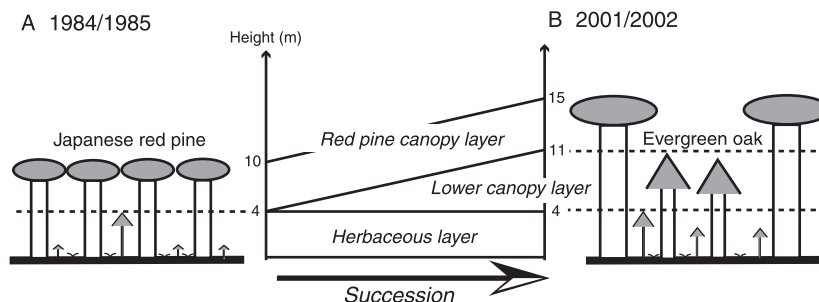


Fig. 3. Schematic diagram of forest structure in (A) 1984/1985 and (B) 2001/2002.

Table 2
List of meteorological instruments in 1984/1985 and 2001/2002

Item	Height of sensor (m)	1984/1985	Height of sensor (m)	2001/2002
Dry- and wet-bulb temperature	11.0	Ventilated psychrometer	15.9	Ventilated psychrometer
Wind speed	11.0	3-Cup anemometer	16.2	3-Cup anemometer
Net radiation	13.5	Net radiometer (Eko Instruments Co., Ltd, type CN-11)	8.9, 19.1	Net radiometer (Radiation and Energy Balance System Inc., type Q*7.1)
Photosynthetically active radiation (PAR)	–	–	8.9, 18.2	PAR radiometer (Prede Co., Ltd, type PAR-02)
Soil heat flux	–0.01	Soil heat flux plate (Eko Instruments Co., Ltd, type CN-9)	–0.01	Soil heat flux plate (Hukseflux Thermal Sensors, type HFP-01)
Sensible heat flux	13.5	One-dimensional sonic anemometer (Kaijyo Denki Co., Ltd, type DAT-100)	17.5	One-dimensional sonic anemometer (Kaijyo Denki Co., Ltd, type DA-600-1T)
Soil water content	–0.1 to –1.4	Gravimetric method (0.1-m interval)	–0.1, –0.2, –0.3 –0.5, –0.7, –1.0	Time domain reflectometry (Soil moisture equipment Co., Ltd, type 6050X1 with multiplexer type 6020B05)

2001/2002. The instruments used in this study are listed in Table 2. The air pressure was obtained from the TERC routine observation data. The evapotranspiration was calculated as the residual term of the energy balance equation, as follows

$$ET = \frac{Rn - (H + G)}{\rho_w l} \quad (3)$$

where ρ_w is the density of water, l the latent heat of vaporization. The potential evaporation (PE) was calculated by the following Penman type equation (Monteith, 1965):

$$PE = \frac{\Delta}{\rho_w l (\Delta + \gamma)} (Rn - G) + \frac{\rho_a C_p VPD}{\rho_w l (\Delta + \gamma)} \frac{1}{r_a} \quad (4)$$

The symbols in Eq. (4) are as follows; Δ is the slope of saturation vapor pressure curve at the air temperature, γ the psychrometric constant, ρ_a the air density, C_p the specific heat of air at constant pressure, VPD the vapor pressure deficit and r_a the aerodynamic resistance.

In order to apply Eq. (4) for the calculation of PE , r_a must be known. This was derived by inverting Eq. (4) (e.g. Teklehaimanot et al., 1991). Just after rainfall, when the canopy is still completely wet, it can be assumed that ET obtained from Eq. (3) is equal to PE . In this case, r_a can be calculated from Eq. (4)

using the observed values of Rn , G , and VPD . The following relationships between r_a and wind speed (u ; m/s) were then obtained by regression analysis (Iida et al., 2005),

$$r_a = \frac{59.7}{u}, \quad R^2 = 0.42 \quad (1984/1985) \quad (5)$$

$$r_a = \frac{21.0}{u}, \quad R^2 = 0.59 \quad (2001/2002) \quad (6)$$

and these were used in the subsequent analysis.

The soil water content (θ) was measured monthly by a gravimetric method in 1984/1985; for this purpose, soil cores were sampled between the depths of 0.1 and 1.4 at 0.1-m intervals and θ was evaluated as the gravimetric difference between the moist sampled core and the same completely oven-dried core (Table 2). In 2001/2002, θ was observed hourly by the time domain reflectometry (TDR) method (Table 2). We dug a trench into the forest floor and installed TDR sensors at depths of 0.1, 0.2, 0.3, 0.5, 0.7 and 1.0 m (Table 2). The relative extractable soil water (REW) within the soil column that contains the root system was calculated by

the following equation,

$$REW = \frac{\theta - \theta_{WP}}{\theta_{FC} - \theta_{WP}} \quad (7)$$

where the subscripts WP and FC indicate the permanent wilting point and the field capacity, respectively. The root zone was mainly found between the depths from 0 to 0.8 m in 1984/1985 (Sugita, 1987) and from 0 to 0.7 m in 2001/2002 (Iida et al., 2003).

2.3.2. Interception loss

The amount of interception loss was estimated by the water balance equation for the forest canopy (Iida et al., 2005):

$$I = P - (TF + SF) \quad (8)$$

where I , P , TF and SF are the interception loss, gross rainfall, throughfall and stemflow, respectively. Gross rainfall was observed as part of the TERC routine observation system in the grassland field adjacent to the study site with a 0.5-mm tipping-bucket rainfall gauge.

Throughfall was determined as an average of measurements of 50 and 29 pot-type rain gauges in 1984/1985 and 2001/2002, respectively. There is no significant difference in observational error for throughfall measurements between both periods (Iida et al., 2005). Stemflow was collected using plastic collars fixed by silicon sealant around the stem at a height of 1.2 m. Stemflow was measured for 8 trees of the Japanese red pine in 1984/1985, and six red pine trees, five trees of *Q. myrsinaefolia*, four trees of *E. japonica* and eight trees of the other lower canopy species in 2001/2002 (Iida et al., 2005). The volumes of throughfall and stemflow were measured manually after each rainfall event.

2.3.3. Measurement of sap flux density in 2001/2002

In 2001/2002, due to the progress of the succession, the forest constituted a multi-layer canopy, namely the red pine canopy and the lower canopy layers (Fig. 3). To separate the transpiration from the upper canopy and from the lower canopy layers, their sap flux densities were measured on the north side of the stem at a height of 1 m using the Granier (1985) method. This method is suitable for

long-term and continuous observations because it makes use of a small and constant heat (0.2 W, sensor length 20 mm at 2 mm diameter) as a tracer which causes less damage on the conducting tissues. The apparent temperature difference between the heater and the stem tissue 15 cm below the heater (ΔT) was measured by Cu-Constantan thermocouples (UP GmbH, No. 12600). The sensors were covered with a radiation shield to avoid radiative thermal load on the sensors. Sap flux density (v ; m/s) was calculated from the following regression equation given by Granier (1985),

$$v = 1.19 \times 10^{-4} \left(\frac{\Delta T_0 - \Delta T}{\Delta T} \right)^{1.231}, \quad (9)$$

$$R^2 = 0.96$$

where ΔT_0 is ΔT when $v=0$.

Following Granier et al. (1996), test trees for measuring the sap flux density were selected based on the data of histograms of DBH and sapwood area (SA) shown in Fig. 4. The sapwood depth was identified by the difference in color between the sapwood and the heartwood on the wood cores sampled by an increment borer. In those cases when the color difference was not clear, the sapwood depth was confirmed by using a dye (Acid fuchsin). For the three major species, regression equations were established to predict SA from DBH ($x=DBH$ (cm), $y=SA$ (cm²)). For *P. densiflora*, the results of the regression analysis were $y=3.520x^{1.302}$, $R^2=0.84$, $n=25$; for *Q. myrsinaefolia* the results were $y=0.741x^{1.987}$, $R^2=1.0$, $n=20$ and for *E. japonica* the results were $y=0.501x^{2.198}$, $R^2=1.0$, $n=20$. Note that *Q. myrsinaefolia* and *E. japonica* had no heartwood area. The sapwood area of the remaining minor species, for which the number of trees was smaller than 10, was measured for all trees in each species. Four red pine trees, three trees of *Q. myrsinaefolia*, two trees of *E. japonica* were selected from representative trees with average tree crown size and exposed to average light conditions in each class of DBH shown in Fig. 4. The test trees used in the sap flux density observations are listed in Table 3.

The transpiration from a j th tree of species i (tr_{ij}) (refer to Fig. 4) was calculated as a product of the sapwood area (SA_{ij}) and the mean value of sap flux

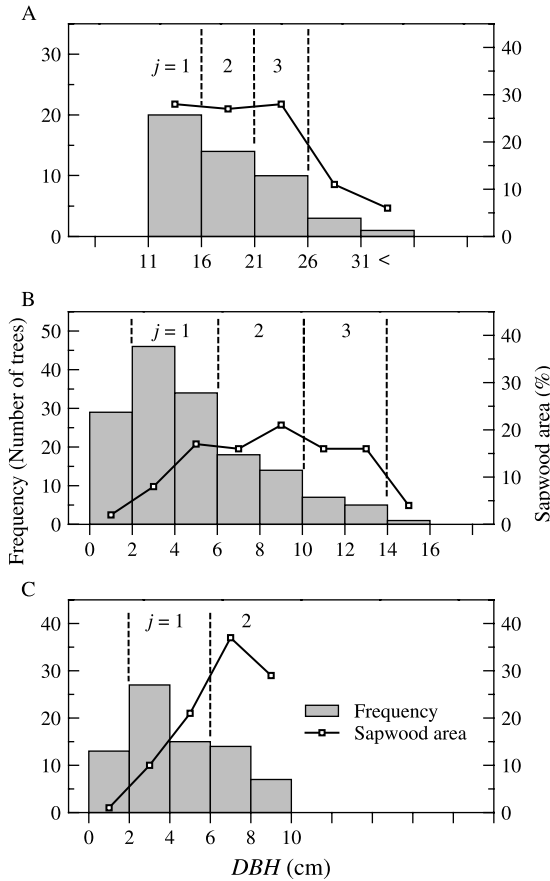


Fig. 4. Histograms of diameter at breast height (*DBH*) and proportion of sapwood area in each class relative to total sapwood area in 2001/2002 for (A) Japanese red pine (*P. densiflora*), (B) *Q. myrsinaefolia* and (C) *E. japonica*.

density over the sapwood area (\bar{v}_{ij}), or

$$tr_{ij} = SA_{ij} \times \bar{v}_{ij} \quad (10)$$

Because Eq. (10) can be applied to all the test trees of the red pines, *Q. myrsinaefolia* and *E. japonica*, the subscript of *i* is replaced by P, Q and E, respectively. To estimate \bar{v}_{ij} correctly, it is necessary to consider the radial gradient of the sap flux density of the stand. For the red pine, Kobayashi and Tanaka (1996) determined this value, and for *Q. myrsinaefolia* and *E. japonica*, this value was observed in the present study. These results show that the sap flux density decreased

Table 3

List of test trees for sap flux density observation in 2001/2002

Tree ID	Tree species	Tree height (m)	<i>DBH</i> ^a (cm)	<i>CPA</i> ^b (m ²)	<i>SA</i> ^c (cm ²)
P1	<i>P. densiflora</i>	14.9	14.5	9.3	119
P2a	(Japanese red	13.0	16.3	3.5	154
P2b	pine)	16.6	18.6	6.6	168
P3		17.0	21.3	12.1	194
Q1	<i>Q. myrsinaefo-</i>	5.7	4.0	3.7	11
Q2	<i>lia</i> (Evergreen	9.8	8.4	9.7	48
Q3	oak)	9.9	12.5	15.5	113
E1	<i>E. japonica</i>	4.9	4.0	2.1	11
E2	(Evergreen	9.1	8.1	6.9	45
	theaceous tree)				

^a Diameter at breast height.

^b Crown projection area.

^c Sapwood area.

from the cambium toward the pith for all species. Therefore, values of \bar{v}_{ij} were calculated by considering the relationships between this negative trend and the relative depth of the sensor within the sapwood area.

The total transpiration for species *i* ($\sum tr_i$) was calculated as the sum of the sub-total amount of transpiration in each class of *DBH*, which is the product of number of trees (n_{ij}) and transpiration from each tree in that class (tr_{ij}) (refer to Fig. 4);

$$\sum tr_i = \sum_j n_{ij} tr_{ij} \quad (11)$$

Thus, the transpiration from the red pines (TR_P), *Q. myrsinaefolia* (TR_Q) and *E. japonica* (TR_E) can be obtained by dividing $\sum tr_i$ by the plot area (*PA*), that is

$$TR_i = \frac{\sum tr_i}{PA} \quad (12)$$

2.3.4. Estimation of ET_F , TR_P and TR_L

Because the canopy structure had changed during the succession from 1984/1985 to 2001/2002 (Fig. 3), evapotranspiration components to be evaluated were also different for both periods (refer to Eqs. (1) and (2)). The procedure for estimation of ET_F , TR_P and TR_L is as follows for both periods.

2.3.4.1. 1984/1985. The monthly ET_F was estimated by the energy-balance and Bowen ratio ($Bo = H/(\rho_w l ET)$) method, which can be formulated as

$$ET_F = \frac{(Rn_F - G)/(1 + Bo)}{\rho_w l} \quad (13)$$

The Bowen ratio above the forest floor was assumed to be the same as the value observed in 1983 by Sugita (1984) on the basis of the differences of air temperature (ΔT_a) and vapor pressure (Δe) between heights of 0.5 and 2.0 m (i.e. $Bo = \gamma \Delta T_a / \Delta e$). The monthly net radiation above the forest floor (Rn_F) was estimated by the following modified equation proposed originally by Budagovsky et al., 1968,

$$Rn_F = Rn \exp\left(-\frac{\lambda LAI}{\sin \beta}\right) \quad (14)$$

where β is the solar elevation and λ is an empirical coefficient. Values of this coefficient were determined from a data set of Rn_F , Rn , LAI observed at the same forest in 1983 (Sugita, 1984).

Based on the above-mentioned data, monthly TR_P was calculated by rearranging Eq. (1) as follows,

$$TR_P = ET - (I + ET_F) \quad (15)$$

2.3.4.2. 2001/2002. The lower canopy layer was composed of evergreen and deciduous species at this stage of the succession (Iida et al., 2003). During the leafless period of the deciduous trees in the lower canopy (mainly *R. trichocarpa*) from December 2001 to March 2002, the source of TR_L was restricted to the evergreen species. Because the red pine and *Q. myrsinaefolia* and *E. japonica* occupied 98.5% of the total evergreen trees, TR_L can be assumed to be the sum of TR_Q and TR_E (i.e. $TR_L = TR_Q + TR_E$). In the leafless period of *R. trichocarpa*, ET_F is estimated by rearranging Eq. (2) as follows

$$ET_F = ET - \{TR_P + (TR_Q + TR_E) + I\} \quad (16)$$

To estimate the annual amount of ET_F , it is necessary to evaluate the seasonal trend of ET_F . However, the measurement of Rn_F is very difficult because of its high spatial heterogeneity due to the complex canopy structure in 2001/2002 (Fig. 3). Therefore, three possible cases were considered in

this study. Case (i): the proportion of ET_F/ET during the leafless period is assumed to be constant through the whole period. This case will estimate the possible maximum amount of annual ET_F , because ET_F/ET is higher from autumn to spring (e.g. Hattori, 1983). Case (ii): the proportion of ET_F/ET during the foliated period in 2001/2002 is assumed to be same as in 1984/1985, and case (iii): the seasonal trend of Rn_F in 2001/2002 can be estimated using the same value of λ as in 1984/1985 and the seasonal trend of LAI was also as same in 1984/1985. These last two cases were considered to estimate the possible minimum value of annual ET_F .

The transpiration from the lower canopy layer (TR_L) was estimated by the following equation, again obtained from Eq. (2),

$$TR_L = ET - (TR_P + I + ET_F) \quad (17)$$

3. Results

3.1. Annual amount of ET , TR_P , TR_L , ET_F and I

Forest water balances in 1984/1985 and 2001/2002 are shown in Fig. 5. The results of forest floor evapotranspiration (ET_F) estimated by the three cases were confirmed in 2001/2002. The three possible cases described above resulted in an annual amount of ET_F of 110, 82 and 75 mm, respectively. The maximum difference among these annual amounts of ET_F was only 35 mm, so the simplest case (i) is adopted for the following discussion (Fig. 5). In 1984/1985, the annual amount of ET_F was estimated as 88 mm (Fig. 5).

The amounts of ET were almost equal in both periods and the proportions of ET to P were around 50%, which corresponds to the average figure for Japan as a whole (e.g. Tsukamoto, 1992). However, the transpiration from the red pines (TR_P) decreased significantly from 344 to 119 mm (Fig. 5), resulting from the decrease in stand density of these trees during the succession (Table 1). The forest interception loss (I) also decreased largely from 208 to 115 mm. These differences of TR_P and I between both periods are statistically significant by a t -test with significance level of 5% ($p < 0.01$). The decrease of I

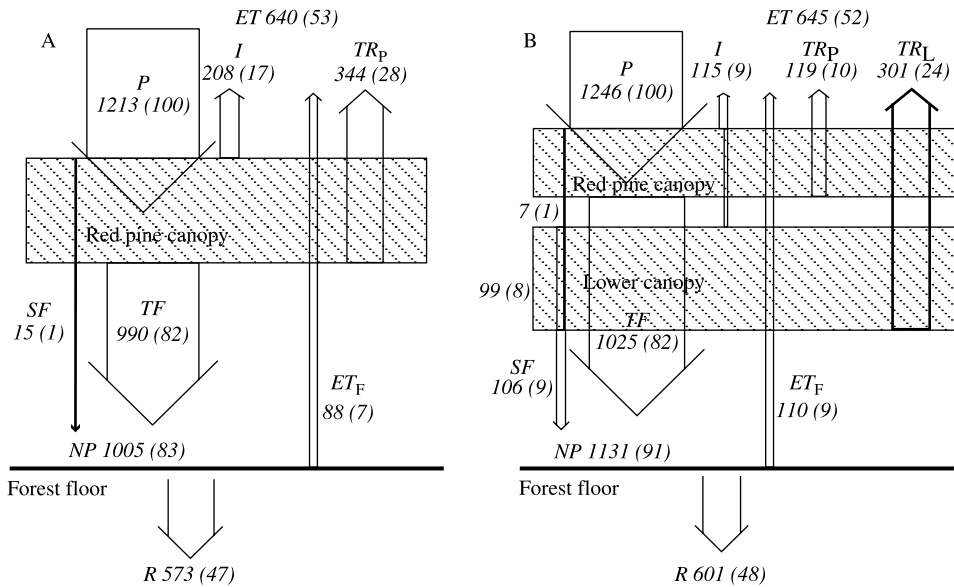


Fig. 5. Summary of the annual water balance in (A) 1984/1985 and (B) 2001/2002. The values have the unit of mm and their magnitude relative to the annual gross rainfall is shown in brackets. *P* is gross rainfall, *TF* throughfall, *SF* stemflow, *NP* net rainfall, *ET* evapotranspiration, *I* interception loss, *TR_p* transpiration from the red pines, *TR_L* transpiration from the lower canopy layer, *ET_F* forest floor evapotranspiration and *R* groundwater recharge.

was caused by the decrease of the rainfall storage on the tree surface, because of tree characteristics facilitating stemflow generation in the lower canopy layer, especially bark smoothness (Iida et al., 2005). The transpiration from the lower canopy layer (*TR_L*) in 2001/2002 was 301 mm and about three times larger than *TR_p* (Fig. 5). Therefore, the small difference between the *ET* values was caused by the large amount of *TR_L*.

3.2. Seasonal change of *ET*, *TR_p*, *TR_L*, *ET_F*, and *I*

The seasonal change in the proportion of each component of *ET* in 1984/1985 and 2001/2002 is shown in Figs. 6 and 7, respectively. In 1984/1985, the proportion of *ET_F*/*ET* was relatively large from February to May (Fig. 6). In this period, the red pines defoliated partly, and their *LAI* reached its minimum value in May (Sugita, 1987). This decrease of *LAI* caused an increase of *Rn_F*, and the ratio *ET_F*/*ET* was relatively larger than in the other months. Generally, the amount of interception loss depends on the frequency of gross rainfall events (e.g.

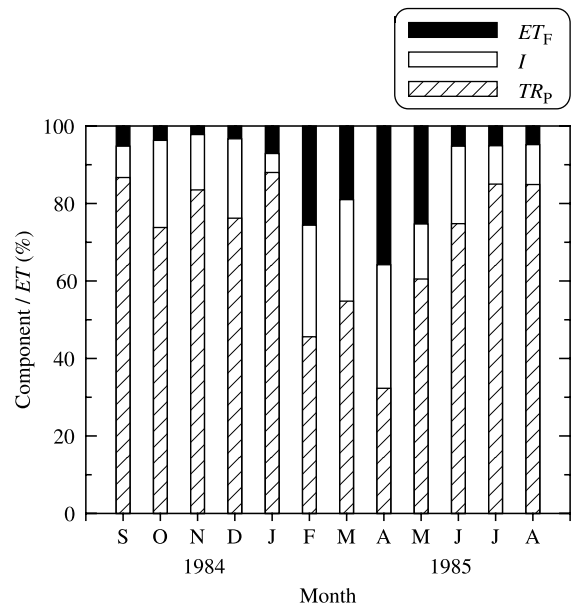


Fig. 6. Seasonal change of the proportion of the different components relative to evapotranspiration in 1984/1985.

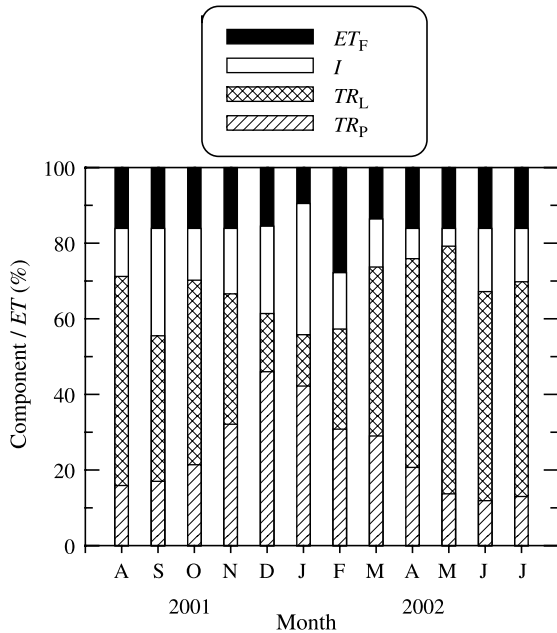


Fig. 7. Same as Fig. 6, but in 2001/2002.

Crockford and Richardson, 2000), and a relatively large difference of the seasonal trends of I/ET was observed in both periods.

The proportion of transpiration to evapotranspiration, TR_P/ET in 1984/1985 and $(TR_P+TR_L)/ET$ in 2001/2002, showed the maximum and the minimum values in summer and winter. In 2001/2002, however, a different trend was found between TR_P/ET and TR_L/ET (Fig. 7). The ratio TR_L/ET had its maximum and minimum value in summer and winter, respectively. However, the ratio TR_P/ET had the completely opposite seasonal trend, i.e. the maximum in winter and the minimum in summer. The largest source of transpiration was the red pine canopy layer in winter of 2001/2002 (Fig. 7). During the winter of 2001/2002, the daily mean values of photosynthetically active radiation (PAR) under the red pine canopy were around $150 \mu\text{mol}/\text{m}^2/\text{s}$. Endo and Oikawa (1985) showed that the net photosynthesis of seedlings of *Q. myrsinaefolia* decreased when PAR was less than $170 \mu\text{mol}/\text{m}^2/\text{s}$. They suggested that the shortage of PAR under the red pine canopy decreased TR_L and thus resulted in $TR_P/ET > TR_L/ET$ in the winter of 2001/2002.

4. Discussion

4.1. Difference of environmental factors affecting ET between both periods

ET , TR_P and I will vary depending not only on change of forest structure but also on environmental factors; i.e. downward shortwave radiation, rainfall characteristics and soil water deficit. It is necessary to investigate the effect of these factors on ET , I and TR_P in both periods.

Saigusa et al. (1996) reported that the evapotranspiration from the plant canopy depends mainly on the downward shortwave radiation (R_s) in an area with sufficient soil water like in Japan. According to the routine data measured at TERC, the average of the annual mean R_s values from 1982 to 2001 was $149 (\pm 8) \text{ W}/\text{m}^2$. On the other hand, the annual mean R_s values were also $149 \text{ W}/\text{m}^2$ in both study periods. In other words, the incoming energy available for evapotranspiration was the same in the two periods.

The amount of gross rainfall (P) and its temporal distribution may affect the amount of interception loss (e.g. Crockford and Richardson, 2000). The annual amount of P was 1213 mm in 1984/1985 and 1246 mm in 2001/2002, and thus the difference was only 33 mm. Iida et al. (2005) reported that the mean rainfall intensity was 1.4 mm/event in 1984/1985 and 1.2 mm/event in 2001/2002, that the mean rainfall duration time was 13.3 h in 1984/1985 and 12.5 h in 2001/2002 and that the mean intermittent time during rainfall event was 3.2 h in 1984/1985 and 3.7 h in 2001/2002. All this shows that there was no significant difference in rainfall amount, intensity, duration and intermittent time between both periods.

It is well known that a severe soil water deficit will suppress the amount of ET (e.g. Rutter, 1967). This phenomenon is referred to as water stress on ET . Threshold values for the occurrence of water stress among conifer species were reported in terms of REW as 0.4 for Scots pine (Rutter, 1967), 0.4 for Douglas-fir (Black, 1979) and 0.3 for Douglas-fir (Granier, 1987). In 1984/1985, no water stress could occur, because REW calculated from daily tensiometer data was larger than 0.6 throughout the period (Sugita and Kotoda, 1985). However, a severe soil water deficit was found to have occurred from July to August in 2001. The relationship between REW and the ratio

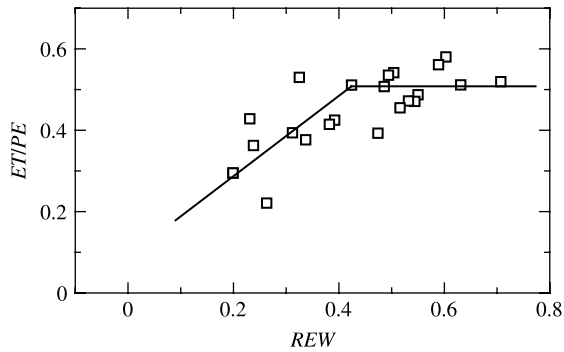


Fig. 8. Comparison between the relative extractable water (REW) and the ratio of evapotranspiration (ET) to potential evaporation (PE) from June to August 2001. The data are plotted for fine weather conditions, in which daytime average net radiation exceeds 400 W/m^2 and there is no rainfall. The lines are drawn by eye.

ET/PE in this period clearly showed that ET/PE decreased markedly for the range of $REW < 0.4$ (Fig. 8). This threshold value of the water stress corresponds to the value of the previous studies mentioned above. Fig. 8 further shows that the ratio ET/PE maintains an almost constant value of 0.5 for the range of $REW > 0.4$, that is, in the absence of water stress. Therefore, the unsuppressed ET was estimated from PE using the simple relationship of $ET/PE = 0.5$. The decrease in ET by the water stress was calculated as 16 mm, which means that it can be neglected for the following discussion.

4.2. Factors determining TR_L

Due to the progress of the succession, the main source of the transpiration changed from the red pines to the lower canopy layer (Fig. 5) since $TR_p/ET = 54\%$ in 1984/1985, and $TR_p/ET = 18\%$ and $TR_L/ET = 47\%$ in 2001/2002. Although this fact that the upper canopy layer is not the primal source of transpiration was also reported by previous studies (Kelliher and Black, 1986; Kelliher et al., 1997; 1998; Roberts et al., 1980; Tan et al., 1978), these studies were conducted in a forest composed of the main canopy trees and the lower vegetation in the herbaceous layer. Our study site consisted mainly of the upper and the lower canopy layers (Fig. 3), and the latter was higher in vegetation height and larger in DBH than the herbaceous layer. Factors responsible for this large amount of TR_L will be discussed below by considering

the available energy for the lower canopy layer, total sapwood area and sap flux density of the lower canopy layer.

4.2.1. Net radiation above the lower canopy layer

Fig. 9 shows the time series of the monthly mean net radiation above the red pine canopy (Rn) and net radiation above the lower canopy layer (Rn_L) in 2001/2002. Both types of net radiation showed a parallel seasonal change, such the ratio Rn_L/Rn remained nearly constant throughout the observation period with an annual mean value of 35%. Because the lower canopy layer did not exist in 1984/1985 (Fig. 3), Rn_F was independent of height within the red pine forest and was comparable with Rn_L observed in 2001/2002. In comparison with $Rn_F/Rn = 8\%$ in 1984/1985, a 27% increase in Rn_L/Rn was found from 1984/1985 to 2001/2002, indicating the decline of the stand density of the red pines during the succession. The increase of Rn_L was one of reasons for the significant amount of TR_L observed in 2001/2002.

4.2.2. Total sapwood area and sap flux density of the lower canopy layer

The transpired water is transported from the root system to the leaves through the sapwood area in the stem, and it can be estimated by multiplying of the sapwood area with the mean sap flux density

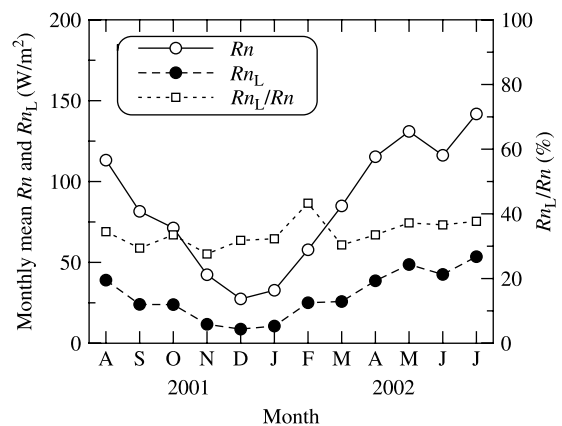


Fig. 9. Time series of monthly mean net radiation above the Japanese red pine (open circles) and above the lower canopy layer (solid circles) with the proportion of the net radiation above the lower canopy layer relative to that above the red pine (open rectangles) in 2001/2002.

Table 4
List of basal area and sapwood area in 2001/2002

Tree species	Basal area (cm ²)	Sapwood area $\sum SA_i$ (cm ²)	Proportion of sapwood area to basal area (%)
Japanese red pine ($i=P$)	14,072	7583	53.9
Lower canopy layer ($i=L$)	8027	6988	87.1
Total	22,099	14,571	
Species of lower canopy			
<i>Q. myrsinaefolia</i> ($i=Q$)	4004	3695	92.3
<i>E. japonica</i> ($i=E$)	1530	1411	92.2
Others	2493	1882	75.5
Sub-total	8027	6988	

(Eq. (10)). For each species, the total sapwood area ($\sum SA_i$) is summarized in Table 4. Although the average *DBH* of the red pines was around four times larger than that of the lower canopy layer (Table 1), the corresponding sapwood area were nearly the same, namely $\sum SA_P = 7583 \text{ cm}^2$ and $\sum SA_L = 6988 \text{ cm}^2$, that is a difference of only 595 cm^2 . This relatively small difference can be attributed to the larger proportion of sapwood area in the stem cross section in the lower canopy layer and to the larger numbers of trees in the lower canopy layer than that of the red pines.

The mean sap flux density over the total sapwood area of species i (V_i) can be calculated for each species by the following equation.

$$V_i = \frac{\sum tr_i}{\sum SA_i} \quad (18)$$

The values of V_Q and V_E were significantly larger than V_P (Fig. 10). The maximum value of the monthly mean of V_Q and V_E was 3.7 and 2.6 times larger than that of V_P , and the annual mean of V_Q and V_E was 2.3 and 1.5 times larger than that of V_P . Thus, the larger amount of transpiration from the lower canopy layer was mostly caused by its larger sap flux densities as compared with the red pines, since $\sum SA_L$ was nearly equal to $\sum SA_P$.

Because $\sum SA_i$ and $\sum tr_i$ are key factors for estimating V_i as well as forest transpiration, it is necessary to confirm the estimation errors in these factors. SA was obtained for test trees in each species as the difference between the total cross section area of a stem and the sum of bark and heartwood areas. $\sum SA_i$ was estimated by a regression equation between *DBH* and SA for each species, which was derived from observations with 25 *P. densiflora* trees,

20 *Q. myrsinaefolia* trees and 20 *E. japonica* trees. The estimation errors in $\sum SA_Q$ and $\sum SA_E$ should be small since there was no heartwood area found in *Q. myrsinaefolia* and *E. japonica*, and thus, the estimation could be made solely from the measurement of *DBH* and width of bark. On the other hand, Japanese red pine had the heartwood area. It is necessary for estimating SA for this species that *DBH* and widths of bark and sapwood must be measured. Therefore, it is expected that the estimation error in $\sum SA_P$ may be larger than in $\sum SA_Q$ and $\sum SA_E$. Kumagai et al. (2005) showed for two conifer species that the coefficient of variation in total sapwood area of a stand is quite stable provided that the sample size

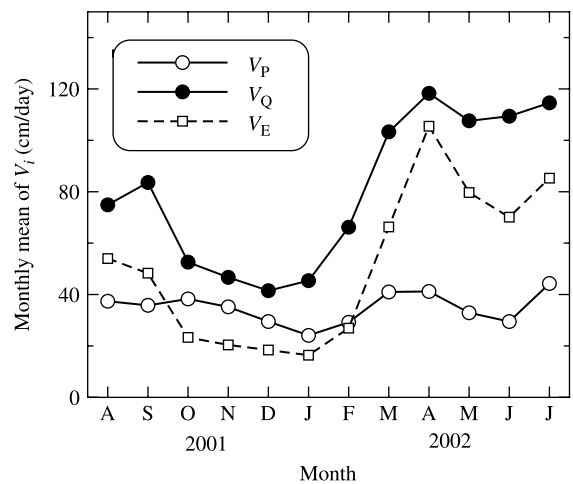


Fig. 10. Time series of monthly mean sap flux densities in 2001/2002. The open circles, solid circles and open rectangles show the sap flux density of Japanese red pine (*P. densiflora*), *Q. myrsinaefolia* and *E. japonica*, respectively.

exceeds 20. Therefore, it is safe to conclude that the sample size of 25 for Japanese red pine yielded a precise estimate of $\sum SA_P$. It is possible that the estimation of $\sum tr_i$ produced relatively larger error than that of $\sum SA_i$ in Eq. (18) due to the relatively small sample size of sap flux density observations. However, since the selected test trees for sap flux density measurement were quite representative, being exposed to average light conditions and having mean tree crown size in each class of *DBH*, it seems that the final results of V_i should probably be reasonable.

According to previous studies (Bi and Jurskis, 1996; Cienciala et al., 1997; Cornish and Vertessy, 2001; Langford, 1976; Roberts et al., 2001; Vertessy et al., 2001; West and Mattay, 1993), the amount of transpiration reaches a maximum at the mature stage of the forest, only to decrease after that with increasing age. Generally, the stand sapwood area per unit ground area tends to be smaller for older stands due to an increase of heartwood area and a decrease of stand density (e.g. Haydon et al., 1996; Mencuccini and Grace, 1996; Roberts et al., 2001; Vertessy et al., 2001). It has also been observed that the stand sapwood area and *LAI* decrease with the age and that this decrease is the main reason for the depletion of transpiration with the age for eucalypts (Roberts et al., 2001; Vertessy et al., 2001). Although the age of red pines was around 50 years in 2001/2002, the trees in the lower canopy layer were at most 20 years old and were still in their developmental stage in the succession. This explains how the nearly identical values of $\sum SA_L$ with $\sum SA_P$ but values of V_Q and V_E , which were larger than V_P , resulted from the difference in tree species and in the growth stages between the red pines and the lower canopy layer.

5. Conclusions

To elucidate the changes of the evapotranspiration components during the succession from Japanese red pine (*P. densiflora*) to evergreen oak (*Q. myrsinaefolia*), two intensive observations were conducted in 1984/1985 in the pre-succession stage and in 2001/2002 in the middle-stage of the succession. Although the forest had a main canopy of the red pines in 1984/1985, the multi-layered canopies were observed in 2001/2002, which were consisted of the

upper canopy layer of the red pines and of the lower canopy layer. The main species in the lower canopy layer were evergreen oak and evergreen theaceous tree (*E. japonica*). Based on the comparison between two results, the following conclusions can be drawn.

The observed large decrease in transpiration from the red pines from 344 mm in 1984/1985 to 119 mm in 2001/2002 and that in forest interception from 208 mm in 1984/1985 to 115 mm in 2001/2002 was largely due to the decrease in the stand density of the red pines by the succession. The amount of transpiration from the lower canopy layer was about three times larger than that from the red pine canopy, and constituted around 50% of the total evapotranspiration in 2001/2002. As a result, there was no difference in total evapotranspiration between both periods.

Three factors causing the large amount of transpiration from the lower canopy were identified:

- (i) The net radiation over the lower canopy increased with the increase in gaps in the red pine canopy.
- (ii) The total sapwood area of the lower canopy layer was nearly equal to that of the red pine canopy layer. This is because the trees in the lower canopy layer had larger proportion of the sapwood area and larger number of trees than that of the red pines.
- (iii) Sap flux densities of main species in the lower canopy (*Q. myrsinaefolia* and *E. japonica*) were around two times larger than that of the red pines.

These factors were induced by the decline of stand density of the red pines and the difference in tree age between the red pines and the lower canopy layer.

It became clear that the succession changes the evapotranspiration components, especially the transpiration and the interception loss, although there is no significant difference in the forest water balance ($P=ET+R$) between both periods. Thus, further observations are needed to clarify the relative contributions of the different evapotranspiration components to the total evapotranspiration at various stages of the succession. Moreover, global warming, when or if it occurs, is likely to affect the climax and may cause a new succession. To predict the effect of

possible global warming scenarios on the forest hydrologic cycle, it will be necessary first to gain a better understanding of the role of the likely successions resulting from climate change in the forest water transport processes.

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