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Root functional change achieves water source separation under vegetation succession

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Abstract

Water source separation can be one of strategies for different plant species to coexist in a community. This study first demonstrates mechanisms of water source separation during vegetation succession. An isotope-incorporated mechanistic model was employed to simulate the xylem water isotopic composition and the root water uptake profile for a *Pinus densiflora*–*Quercus myrsinaefolia* mixed stand undergoing secondary succession and a pure *P. densiflora* stand before succession. In the mixed stand, the model successfully simulated the xylem water isotopic composition on the assumption that the root surface resistance per unit length of root (r_{rs}^*) decreases with increasing depth for *P. densiflora* but is constant for *Q. myrsinaefolia*. Uptake fraction for *P. densiflora* was greater in deeper zones but in shallower for *Q. myrsinaefolia*. In contrast, in the pure stand, a constant r_{rs}^* for *P. densiflora* gave good reproducibility in isotope simulation and shallow water uptake dominated. These findings highlight root functional change as a mechanism of water source separation; preexisting *P. densiflora* trees decrease their deep-root r_{rs}^* to compensate for an increase in shallow-root r_{rs}^* . This mechanism was caused by competition against invading *Q. myrsinaefolia* trees.

1 INTRODUCTION

The question of how competing plant species manage to stably coexist is an important topic in community ecology (Silvertown, Dodd, Gowing, & Mountford, 1999; Silvertown 2004). It has been suggested that competition for limited resources such as water may be reduced by partitioning of resource utilization (Walter, 1971; Tilman, 1982). Although partitioning of root water uptake among different species has been difficult to observe directly, development of an isotopic approach has enabled the characterization of water source separation among different species within a community (Dawson, Mambelli, Plamboeck, Templer, & Tu, 2002).

In desert scrubland (Ehleringer, Phillips, Schuster, & Sandquist, 1991), semiarid rangeland (Schwinning, Davis, Richardson, & Ehleringer, 2002; Darrouzet-Nardi, D'Antonio, & Dawson, 2006), savanna woodland (Weltzin & McPherson, 1997) and a Sahelian agroforestry system (Smith, Jarvis, & Odongo, 1997), woody plants generally tend to take up water from deeper soils than co-occurring herbaceous plants (Walter, 1971). In semiarid woodland, some shrub or low tree species utilize deeper water-sources than co-occurring tall tree species (Flanagan, Ehleringer, & Marshall, 1992; Williams & Ehleringer, 2000). In communities under relatively humid climates, the partitioning of water uptake is somewhat irregular. It has been reported that in Mediterranean scrubland (Valentini, Mugnozza, & Ehleringer, 1992) and temperate savanna (Jackson et al., 1999), most deciduous species tend to use deeper water sources than co-occurring evergreen species. In contrast, in seasonally dry tropical forests, the opposite was found (Jackson, Cavelier, Goldstein, Meinzer, & Holbrook, 1995) or no significant correlation was observed between the uptake zone and vegetation type (Meinzer et al., 1999). Pinyon pine (*Pinus edulis*) took up water from shallower zones than co-occurring deciduous oak in semiarid woodlands (Williams & Ehleringer, 2000), whereas Japanese red pine (*Pinus densiflora*) utilized deeper water sources than co-occurring evergreen oak in a temperate secondary forest (Yamanaka, Iizuka, & Tanaka, 2006). The pattern of the water source separation was observed to change in accordance with environmental conditions such as water table depth (Smith, Jarvis, & Odongo, 1997) or amount of summer rainfall (Williams & Ehleringer 2000).

Regardless of the presence or absence of competitors, some plant species rely on shallow water sources, whereas others utilize deep sources, depending on their own rooting strategies to cope with stochastic water availability (Rodriguez-Iturbe, Porporato, Laio, & Ridolfi, 2001; Collins & Bras, 2007) and allocation trade-off (Schwinning & Ehleringer, 2001). One possible interpretation for the water source separation is simply the combination of the intrinsic water-use patterns specific to each species. Another interpretation is that one (or some) of the competing species alter their uptake zone to avoid or lessen interspecific competition for water, thus achieving the water source separation. The mechanisms of water source separation are not currently well understood. If one compares water-use patterns between different stages of vegetation succession, it will be possible to clarify the role or effect of competitors in water source separation.

This study tested a hypothesis that the invasion of competitors alters the water uptake zone of

preexisting species and examined its mechanisms from the viewpoint of water flow through the soil–plant–atmosphere continuum (SPAC; Philip, 1966). For this purpose, we compared the root water uptake profile (RWUP) between a mixed stand during secondary succession and a pure stand before the succession in a temperate humid climate. In most previous studies using the isotopic approach, water source separation has been qualitatively discussed based on comparison of the isotopic signatures of xylem water between different species (Ehleringer, Phillips, Schuster, & Sandquist, 1991; Flanagan, Ehleringer, & Marshall, 1992) or quantitative evaluation using isotope mixing models (e.g., shallow versus deep water sources; Dawson, Mambelli, Plamboeck, Templer, & Tu, 2002). However, Ogle, Wolpert, & Reynolds (2004) developed a more comprehensive algorithm that reconstructs RWUP with an inverse estimation technique. In the present study, we employed an isotope-incorporated mechanistic model (Yamanaka, Kimura, Sun, Kato, & Onda, 2017) for reconstructing not only RWUP but also water balance and root zone hydrology.

2 MATERIALS AND METHODS

2.1 Study sites

The two study stands are located in Tsukuba (36.12°N, 140.09°E, 27 m a.m.s.l.), central Japan. In this region, *Pinus densiflora* (Japanese red pine) forest is most common and widespread, although the vegetation climax is *Quercus myrsinaefolia* (Japanese white oak). The forest has been fragmented into a number of small stands during urbanization; some of which are still managed and maintained as pure pine stands, and others are unmanaged and are undergoing secondary succession from shade-intolerant pine forest to shade-tolerant oak forest.

The first study site is a pine-oak mixed stand under succession with an area of 17,000 m². Stand density was 0.068 trees m⁻² for *P. densiflora* and 0.218 trees m⁻² for *Q. myrsinaefolia*; mean tree height (diameter at breast height; DBH) was 15.0 m (18.4 cm) for *P. densiflora* and 6.7 m (4.9 cm) for *Q. myrsinaefolia* (Iida, Tanaka, & Sugita, 2005). Understories were composed of *Pleioblastus chino*, *Hosta sieboldiana*, and *Rhus trichocarpa*. According to Iida, Tanaka, & Sugita (2005), stand density for *P. densiflora* decreased to some one-fourth of the initial value during 1985–2002. Vertical profiles of root length density could be approximated by exponential curves for both *P. densiflora* and *Q. myrsinaefolia*. Vertical gradient of root length density at shallow zone was steeper for *Q. myrsinaefolia* than for *P. densiflora* (Yamanaka et al. 2005; Figure 1).

The second site is a pure pine stand with an area of 2,400 m², approximately 650 m north of the mixed stand. In 2005, stand density for *P. densiflora* was 0.03 trees m⁻² and mean tree height and DBH were 12 m and 28 cm, respectively. Understories (mainly *P. chino*) were cleared several times every year, so they can be expected to have a minimal effect on the rooting or water-uptake strategies of *P. densiflora*. The root density profile was not substantially different from that for *P. densiflora* in the mixed stand.

For both sites, climatic values of annual mean temperature and annual total precipitation are 13.5°C and 1159.1 mm, respectively. Monthly precipitation is greater (120–180 mm) in the warm

(15–26°C) period from June to October and smaller (<50 mm) in the cold (3–6°C) period from December to February. The vegetation occurs on a loamy, volcanic ash soil (*Andosol*), 1.8–2.0 m thick, overlying a clay layer. The water table depth usually ranges from 1.3 to 1.5 m below the ground.

2.2 Isotopic surveys

Isotopic survey at the mixed stand was carried out in June to October 2003 and was reported by Yamanaka, Iizuka, & Tanaka (2006). Stem core or twig samples were taken from three individuals for each of *P. densiflora* and *Q. myrsinaefolia*. Soil water samples were collected from four depths (10, 20, 40, and 80 cm) using suction lysimeters (DIK-8390, DAIKI, Saitama, Japan). The maximum suction level of this equipment is approximately 80 kPa, and Iizuka, Yamanaka, & Tanaka (2004) confirmed that no isotopic fractionation occurred during the soil water extraction. Precipitation samples were also collected every week or month.

Isotopic survey at the pure stand was carried out in June to October 2005. Stem core or twig samples were taken from five *P. densiflora* individuals. Soil water samples were collected from four depths (10, 20, 40, and 80 cm) by the same method as in the mixed stand. Although precipitation samples were not collected, precipitation isotope data measured by Yabusaki & Tase (2007) are available.

Xylem water was extracted from the stem or twig samples by cryogenic vacuum distillation (Iizuka, Yamanaka, & Tanaka, 2004). For all water samples, the oxygen isotope ratio ($^{18}\text{O}/^{16}\text{O}$) was measured by mass spectrometry using a stable isotope ratio mass spectrometer (Finnigan MAT252, Thermo Fisher Scientific Inc., Waltham, MA, USA). The CO_2 gas equilibration method (Epstein & Mayeda, 1953) was used for sample preparation. Measured results are expressed using the δ -notation in parts per thousand (‰), relative to the Vienna Standard Mean Ocean Water (V-SMOW). The accuracy of the isotopic measurement is approximately $\pm 0.1\text{‰}$. From a series of preliminary pot-experiments, we confirmed that the error potentially introduced in the cryogenic vacuum distillation procedure was no more than 0.2‰ (Iizuka, Yamanaka, & Tanaka, 2004). Because these experiments showed that hydrogen isotope ratio ($^2\text{H}/^1\text{H}$) cannot be accurately measured, probably owing to isotopic exchange with organic matter, only $\delta^{18}\text{O}$ data were employed in the present study.

2.3 Model and data

We used the isotope-incorporated mechanistic model isoRHEA, developed by Yamanaka, Kimura, Sun, Kato, & Onda (2017). The original model (Figure 2a) computes energy and water budgets and precipitation interception for a 3-layer canopy (i.e., tree canopy, understory, and ground layers) and then estimates water and isotope transport (including uptake by roots) within a multi-layered soil (see Supplement of Yamanaka, Kimura, Sun, Kato, & Onda (2017) for full information). Transpiration and evaporation of intercepted water from the tree canopy and the understory, and evaporation from the forest floor soil are computed separately. This model was applied to the pure stand, but negligibly small leaf area index (LAI; 0.001) was assigned for the understory layer because of mowing.

For the mixed stand, the model was modified to allow consideration of the below-ground

competition between *P. densiflora* and *Q. myrsinaefolia* (Figure 2b). In this case, the tree canopy layer corresponds to *P. densiflora*, the understory layer corresponds to *Q. myrsinaefolia*, and the ground layer corresponds to both undergrowth vegetation and the soil. However, the *P. densiflora* canopy does not always overlap that of *Q. myrsinaefolia* because stand density is not very high. Therefore, radiation fluxes were divided horizontally into two tree layers (i.e., *P. densiflora* and *Q. myrsinaefolia*) by considering fractional LAI, and the interaction between the ground layer and each of the two tree-layers was computed as follows:

$$S_P^* = \frac{LAI_P}{LAI_P + LAI_Q} [f_P - \alpha_P + f_P(1 - f_P)\alpha_G] S, \quad (1)$$

$$S_Q^* = \frac{LAI_Q}{LAI_P + LAI_Q} [f_Q - \alpha_Q + f_Q(1 - f_Q)\alpha_G] S, \quad (2)$$

$$S_G^* = \frac{LAI_P(1 - f_C) + LAI_Q(1 - f_U)}{LAI_P + LAI_Q} (1 - \alpha_G) S, \quad (3)$$

$$L_P^* = \frac{LAI_P}{LAI_P + LAI_Q} f_P [L + \sigma T_G^4 - 2\sigma T_P^4], \quad (4)$$

$$L_Q^* = \frac{LAI_Q}{LAI_P + LAI_Q} f_Q [L + \sigma T_G^4 - 2\sigma T_Q^4], \quad (5)$$

$$L_G^* = \frac{[LAI_P(1 - f_Q) + LAI_Q(1 - f_P)]L + LAI_P f_P \sigma T_P^4 + LAI_Q f_Q \sigma T_Q^4}{LAI_P + LAI_Q} - \sigma T_G^4, \quad (6)$$

where S^* (W m^{-2}) is the net absorbed short-wave radiation, LAI ($\text{m}^2 \text{m}^{-2}$) is the LAI, f the fractional interception of radiation fluxes, α is the albedo, S (W m^{-2}) is the downward short-wave radiation above the canopy, L^* (W m^{-2}) is the net absorbed long-wave radiation, L (W m^{-2}) is the downward long-wave radiation above the canopy, σ ($\text{W m}^{-2} \text{K}^{-4}$) is the Stefan–Boltzmann constant, T (K) is the temperature, and subscripts P , Q , and G denote the *P. densiflora* tree layer, the *Q. myrsinaefolia* tree layer, and the ground layer, respectively.

In addition to the above modification, no isotopic fractionation due to forest floor evaporation was assumed for the mixed stand because the ground surface in the stand was densely covered by undergrowth. In contrast, in the pure stand, *Q. myrsinaefolia* and undergrowth were not apparent. Therefore, we considered isotopic fractionation due to soil evaporation on the basis of the Craig–Gordon model (Craig & Gordon, 1965; Yamanaka, Kimura, Sun, Kato, & Onda, 2017).

As input to the model, we used meteorological data from the Japan Meteorological Agency for Tsukuba (station ID = 40336; air temperature, relative humidity, precipitation, wind speed, air pressure, and sunshine duration; 7 km south from the study sites). Downward shortwave and longwave radiation fluxes above the canopy were estimated using these observed values by the method of Allen, Pereira, Raes, & Smith (1998).

Analogous to Ohm's law, the root water uptake by trees for each species is given as:

$$U_r = \frac{\psi_{rc} - \psi}{r_{tot}} = \frac{\psi_{rc} - \psi}{r_{sm} + r_{rs} + r_{rx}}, \quad (7)$$

$$\psi_{rc} = \frac{\left(\sum_{i=1}^n \frac{\psi}{r_{tot}} \right) - T_r}{\sum_{i=1}^n \frac{1}{r_{tot}}}, \quad (8)$$

where U_r ($\text{kg m}^{-2} \text{s}^{-1}$) is the root water uptake from each soil layer for each species, ψ_{rc} (J kg^{-1}) is the plant water potential at the root crown, ψ (J kg^{-1}) is the water potential in a soil layer, r_{tot} ($\text{m}^4 \text{s}^{-1} \text{kg}^{-1}$) is the total resistance, r_{sm} ($\text{m}^4 \text{s}^{-1} \text{kg}^{-1}$) is the soil matrix resistance, r_{rs} ($\text{m}^4 \text{s}^{-1} \text{kg}^{-1}$) is the root surface resistance, r_{rx} ($\text{m}^4 \text{s}^{-1} \text{kg}^{-1}$) is the root xylem resistance, i is the layer number, and n is the total number of the soil layers, and T_r ($\text{kg m}^{-2} \text{s}^{-1}$) is the transpiration rate for each species. The three resistances can be given as (modified from Yamanaka, Kimura, Sun, Kato, & Onda, 2017):

$$r_{sm} = \frac{1}{4\pi K_\psi L_r \Delta_z}, \quad (9)$$

$$r_{rs} = \frac{\theta_{sat} r_{rs}^*}{\theta L_r \Delta_z}, \quad (10)$$

$$r_{rx} = \frac{r_{rx}^* z}{\tau_r L_r}, \quad (11)$$

where K_ψ (kg s m^{-3}) is the unsaturated hydraulic conductivity, L_r (m m^{-3}) is the root length density, Δ_z (m) is the thickness of each soil layer, θ_{sat} ($\text{m}^3 \text{m}^{-3}$) is the saturated soil water content, r_{rs}^* ($\text{m}^3 \text{s}^{-1} \text{kg}^{-1}$) is the root surface resistance per unit length of root, θ ($\text{m}^3 \text{m}^{-3}$) is the soil water content, r_{rx}^* ($\text{m s}^{-1} \text{kg}^{-1}$) is the root xylem resistance per unit length of root, z (m) is the depth, and τ_r is the root tortuosity parameter. Consequently, RWUP is determined by the difference in water potential and resistance to the water flow within the root–soil system like a parallel circuit, as schematically illustrated in Figure 2. An output of xylem water isotope ratio is expected to be sensitive to the reconstructed RWUP, and thus comparison between modelled and observed values helps to validate the model.

LAI and soil parameters used in the model are summarized in Table 1. The other parameter values

were the same as those described in Yamanaka, Kimura, Sun, Kato, & Onda (2017) except for the below. The r_{rs}^* was assumed to be constant in the original isoRHEA. In this study, however, it was given as a constant or an exponential function of the depth as follows:

$$r_{rs}^* = a \exp(bz) \quad (12)$$

where a and b are experimental constants. Although a large number of experimental cases have been attempted, we show below the results of two cases (Case A and Case B) for each of the two stands, as described in Table 2. The value of b was selected considering reproducibility of xylem water isotope ratio because it is sensitive to b . The value of a has little effect on xylem water isotope ratio and RWUP, although ψ_{rc} depends on a . Kobayashi (1999) reported that ψ_{rc} of *P. densiflora* at the mixed stand was from -5000 to -7000 kPa at the lowest in summer. Therefore, we selected the value of a to cause the minimum water potential to lie within such a range.

3 RESULTS AND DISCUSSION

3.1 Isotopic variability and RWUP at the mixed stand

Observed soil water $\delta^{18}\text{O}$ at shallow (<10 – 20 cm depth) zones drastically decreased in mid-August in response to a large storm event associated with low $\delta^{18}\text{O}$ in precipitation, and then recovered gradually (Figure 3). Temporal variation pattern of observed xylem water $\delta^{18}\text{O}$ of *Q. myrsinaefolia* was similar to that of shallow soil water $\delta^{18}\text{O}$, whereas xylem water $\delta^{18}\text{O}$ of *P. densiflora* was close to soil water $\delta^{18}\text{O}$ at 80-cm depth.

Assuming constant r_{rs}^* (Case A), the mechanistic model successfully reproduced xylem water $\delta^{18}\text{O}$ of *Q. myrsinaefolia* but failed for *P. densiflora* (Figure 3a). When we assumed that r_{rs}^* for *P. densiflora* decreases with increasing depth (Case B), the reproducibility of xylem water $\delta^{18}\text{O}$ remarkably improved; in this case, *P. densiflora* trees took up more water from deeper zones (Figure 3b).

In both cases, temporal variations of reproduced soil water $\delta^{18}\text{O}$ at four depths generally agreed with observation. Although the amplitude and phase of those variations were different between the model and observations, such deviations are attributable to horizontal heterogeneity in precipitation and soil water fluxes. Minor deviations in the estimated xylem water $\delta^{18}\text{O}$ from the observations was related to both horizontal heterogeneity of observed soil water $\delta^{18}\text{O}$ and incompleteness of reproduced soil water $\delta^{18}\text{O}$.

Consequently, it is most likely that *Q. myrsinaefolia* trees rely mainly on shallow soil water, whereas *P. densiflora* trees utilize more water from deeper zones. This result is consistent with the estimation by Yamanaka, Iizuka, & Tanaka (2006) from isotopic data alone. However, uptake zone for *P. densiflora* was suggested to be broader in the present study than they expected.

3.2 Isotopic variability and RWUP at the pure stand

Observed soil water $\delta^{18}\text{O}$ and its temporal variation range were greater in shallow zones than in deep

zones (Figure 4). Observed xylem water $\delta^{18}\text{O}$ of *P. densiflora* was similar to soil water $\delta^{18}\text{O}$ at the intermediate (20–40-cm depth) zone.

In contrast to the mixed stand, Case A was a good approximation for reproducing xylem water $\delta^{18}\text{O}$ of *P. densiflora*, and the uptake fraction was greater in shallower zones (Figure 4a). In contrast, in Case B, xylem water $\delta^{18}\text{O}$ was greatly overestimated (Figure 4b).

The reproducibility of soil water $\delta^{18}\text{O}$ in shallow zones was not substantially different between the two cases. However, $\delta^{18}\text{O}$ at 40-cm and 80-cm depths were considerably underestimated in Case B. This was due to strong the deep-water uptake, which enhanced the downward propagation of isotopic signals more than in reality.

Thus, it is a reasonable interpretation that *P. densiflora* trees in the pure stand utilize more water from shallow zones. This must be an intrinsic water-use-pattern for *P. densiflora* without competitors. In addition, it is likely that *P. densiflora* trees in the mixed stand altered their water source in response to invasion of competitors. As noted in Section 2.1, stand density of *Q. myrsinaefolia* trees was three times greater than that of *P. densiflora* trees. It is likely that invasion of *Q. myrsinaefolia* trees have increased competition for water.

It should be noted that stand density of *P. densiflora* trees was lower in the pure stand than in the mixed stand. One may expect that intraspecific competition can alter the RWUP of *P. densiflora* trees. However, xylem water $\delta^{18}\text{O}$ of all sample trees of *P. densiflora* in the pure stand indicated shallow water use, regardless of the fact that local tree density (or tree spacing) for some sample trees was similar to that in the mixed stand. Therefore, it is likely that alteration of RWUP was induced by interspecific competition rather than intraspecific competition.

3.3 Validity of water flux estimations and reproduced RWUP

The performance of water flux estimation by the isoRHEA model has been validated for a *Chamaecyparis obtusa* stand (Yamanaka, Kimura, Sun, Kato, & Onda, 2017), whereas it was not validated for the other stands. Uncertainties in assigned parameter values (e.g., stomatal resistance) may introduce errors to the flux estimation. However, model outputs of annual water balance in this study were nearly the same as those previously reported for the same study stands (Table 3). However, there are some minor biases (e.g., overestimation of transpiration from *P. densiflora* in the pure stand, and underestimation of forest floor evaporation in both stands), which are likely to be caused in part by interannual variation of precipitation conditions.

It should be noted that, in the current version of the isoRHEA model, the dependence of leaf stomatal resistance on soil water conditions is not assumed; thus, the rate of transpiration from *P. densiflora* trees is independent of the r_{rs}^* profiles (i.e., Cases A or B) and cannot be related to the reproduced RWUP. This assumption may be inappropriate in some drought cases. In terms of transpiration suppression, the soil moisture deficit can be evaluated by the relative extractable water (REW) defined as follows (Iida, Tanaka, & Sugita, 2006):

$$\text{REW} = \frac{\theta - \theta_{WP}}{\theta_{FC} - \theta_{WP}} \quad (13)$$

where θ is the volumetric water content, and subscripts WP and FC indicate wilting point ($\psi = -1553.2$ kPa = pF4.2) and field capacity ($\psi = -6.18$ kPa = pF1.8), respectively. According to Iida, Tanaka, & Sugita (2006), transpiration suppression due to the soil moisture deficit in the mixed stand does not occur when $\text{REW} > 0.4$. Sugita (1987) also reported that this fact holds true for the pure stand when $\text{REW} > 0.6$. In the present study, REW exceeded 0.7 for both stands. Therefore, the above assumption cannot introduce serious errors in reproduced RWUP.

3.4 Root surface resistance as a key for water source separation

Judging from isotopic reproducibility, it was found that r_{rs}^* was constant for *P. densiflora* in the pure stand and *Q. myrsinaefolia* in the mixed stand. In these cases, shallower water uptake was more dominant (reflecting root density profile). In contrast, only for *P. densiflora* in the mixed stand, r_{rs}^* decreased with increasing depth, and RWUP was relatively flat but with more uptake from deeper zones.

Unfortunately, there are no available data on the measured r_{rs}^* values for tree species. Bristow, Campbell, & Calissendorf (1984) reported that the r_{rs}^* value for sunflower was $2.5 \times 10^{10} \text{ m}^3 \text{ kg}^{-1} \text{ s}^{-1}$. The r_{rs}^* values for *P. densiflora* and *Q. myrsinaefolia* estimated in the present study are comparable to the value for sunflower.

Shallow-root r_{rs}^* of *P. densiflora* was greater in the mixed stand Case B than in the pure stand Case A (Figure 5). The lowering of metabolic activity of roots is known to have a potential to increase r_{rs}^* (Hillel, 1980). Interspecific competition for water (and nutrients) may negatively impact the metabolic activity of the shallow roots. Kume et al. (2003) reported that leaves of *P. densiflora* in western Japan suffer negative physiological effects (i.e., reduction of net photosynthesis, stomatal conductance, and nitrogen content in leaves) from co-occurring understory species through the competition for water and nutrients. Griscom & Ashton (2003) showed that root competition for water in the presence of bamboo tends to reduce tree growth and/or survival in a bamboo-dominated forest. These findings suggest that competition for water can alter r_{rs}^* through change in metabolic activity of the shallow roots of *P. densiflora*.

As opposed to that of shallow roots, the deep-root r_{rs}^* of *P. densiflora* was smaller in the mixed stand than in the pure stand. This may be a compensation (Rubio & Lynch, 2007) for the increase in shallow root resistance during competition. For instance, an increase in the number of root hairs can reduce deep-root r_{rs}^* .

Change in root resistance of *P. densiflora* enables a reduction of its competition for shallow soil water with *Q. myrsinaefolia*. Indeed, in the mixed stand, minimum soil water potential at the top layer was 1.3 kPa higher in Case B than in Case A. Although the difference in soil water potential is small, it can be enlarged in severe drought periods. Thus, the water source separation in the mixed stand is likely to be an adaptation strategy for *P. densiflora*.

3.5 Implications from the viewpoint of vegetation succession

Even though the water source separation is an adaptation strategy to cope with invasion of competitors, it is debatable whether it assures stable coexistence. As noted in Section 2.1, stand density for *P. densiflora* in the mixed stand decreased to one-fourth of initial state during 1985–2002. This is because *P. densiflora* is a shade-intolerant tree species and its seedlings cannot grow under low light conditions (Yamashita & Hayashi, 1987). Therefore, although water source separation can be an important strategy at a transient state in vegetation succession, it is not always effective for stable coexistence over generations. However, water source separation may support stable coexistence unless there is competition for the other resources.

A remaining debatable issue is why *P. densiflora* trees rather than *Q. myrsinaefolia* trees changed their root resistance. The *Q. myrsinaefolia* trees are younger than *P. densiflora* trees and their transpiration rates were nearly double those of *P. densiflora*. These facts indicate higher assimilation and metabolism, and thus higher competitive power of *Q. myrsinaefolia*. In such cases, shallow roots of *Q. myrsinaefolia* suffered few negative impacts and would not have to reduce their root resistance in deep zones. According to relative strength of competitors, different patterns of water source separation may be achieved.

4 CONCLUSIONS

Intrinsically *P. densiflora* trees under humid temperate climate utilize shallow water sources. However, during progression of secondary succession, they came to use a deeper water source as a part of their adaptation strategy to cope with invasion of *Q. myrsinaefolia* trees. Increase of competition for water negatively impacted on the metabolic activity of the shallow roots of *P. densiflora* trees and increased their root surface resistance. To compensate for this, root surface resistance of their deep roots was decreased, probably by increase in the number of root hairs.

In conclusion, interspecies competition under vegetation succession alters the water uptake profile of weak competitors through a change in root surface resistance, and thus water source separation is achieved. This mechanism could be key to improving our understanding of the diverse patterns of differential water uptake. Future research involving direct observation of root resistance and the relationship between stomatal resistance and RWUP are valuable for further validation of simulation results and mechanisms of root resistance change.

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Table 1 Leaf area index (LAI) and soil parameters in isoRHEA model

Parameter	Unit	Value	
		Mixed stand	Pure stand
LAI for <i>P. densiflora</i>	m ² m ⁻²	1.5*	2.85*
LAI for <i>Q. myrsinaefolia</i>	m ² m ⁻²	1.6*	N/A
Saturated soil water content	m ³ m ⁻³	0.756 [†]	
Saturated hydraulic conductivity	kg s m ⁻³	2.29×10 ^{-4†}	
Air entry potential	J kg ⁻¹	-2.65 [†]	
<i>b</i> value for moisture retention curve	-	16.704 [†]	

* Modified from Iida, Tanaka, & Sugita (2005) considering seasonal variation and Iida (personal communication, Oct. 3, 2017)

[†] Measured

Table 2 Root surface resistance per unit length of root (r_{rs}^* , $\text{m}^3 \text{s}^{-1} \text{kg}^{-1}$) in two experimental cases for each of the two stands, where z is the depth (m).

	<i>P. densiflora</i>	<i>Q. myrsinaefolia</i>
<u>Mixed stand</u>		
<i>Case A</i>	4.0×10^9	1.5×10^9
<i>Case B</i>	$2.5 \times 10^{10} \exp(-3z)$	1.5×10^9
<u>Pure stand</u>		
<i>Case A</i>	1.3×10^{10}	N/A
<i>Case B</i>	$7.5 \times 10^{10} \exp(-3z)$	N/A

Table 3 Comparison of annual water flux components between observation and model.

	Component / P (%)					Reference
	T_{rPd}	T_{rQm}	I_c	E_f	ET	
<u>Mixed stand</u>						
Observation	10	24	9	9	52	Iida, Tanaka, & Sugita (2006)
Model	13	18	16	2	48	This study
<u>Pure stand</u>						
Observation	28	N/A	17	7	53	Sugita (1987) Iida, Tanaka, & Sugita (2006)
Model	43	N/A	18	3	64	This study

P , precipitation; T_{rPd} , transpiration for *Pinus densiflora*; T_{rQm} , transpiration for *Quercus myrsinaefolia*; I_c , interception; E_f , forest floor evaporation; ET , total evapotranspiration

Figures

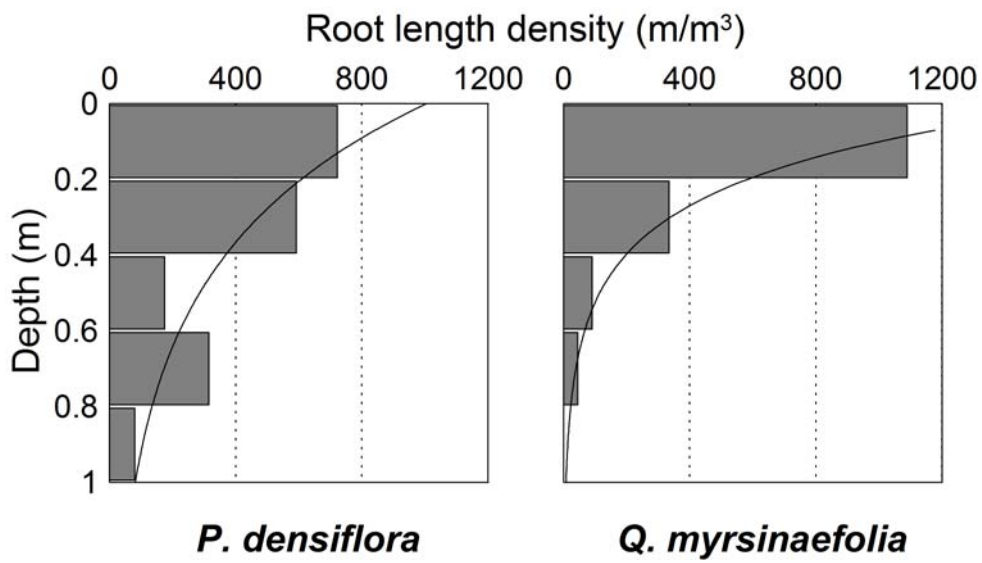


Figure 1 Depth-profile of root length density at the mixed stand (Yamanaka et al., 2005). Exponential functions from regression analysis were also shown.

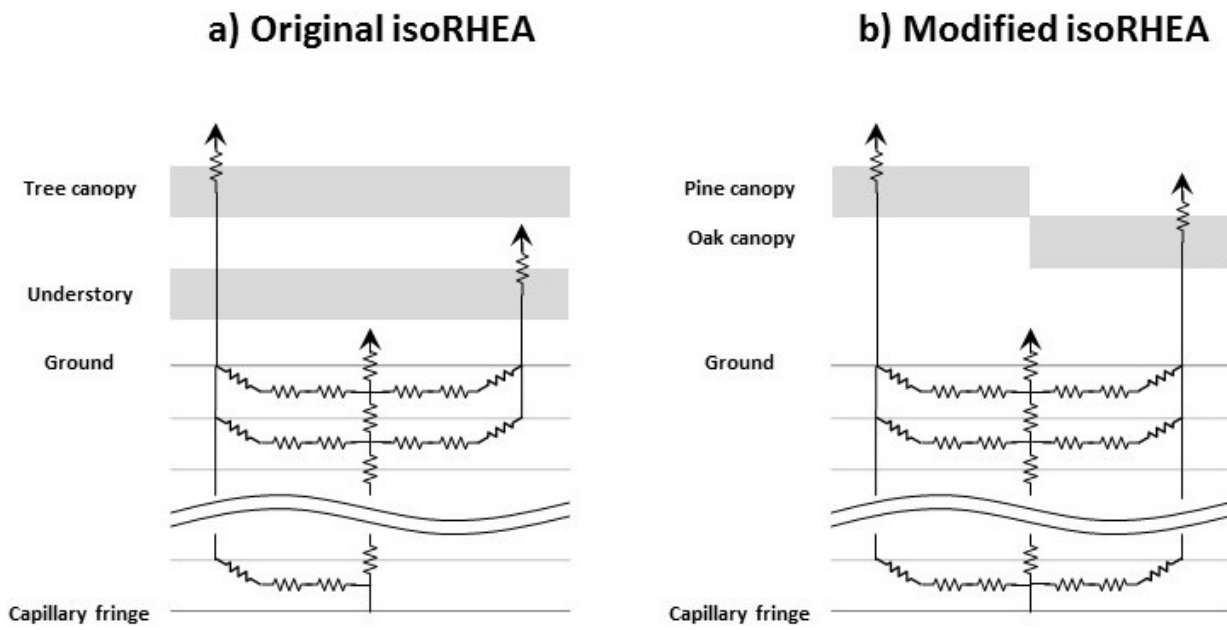
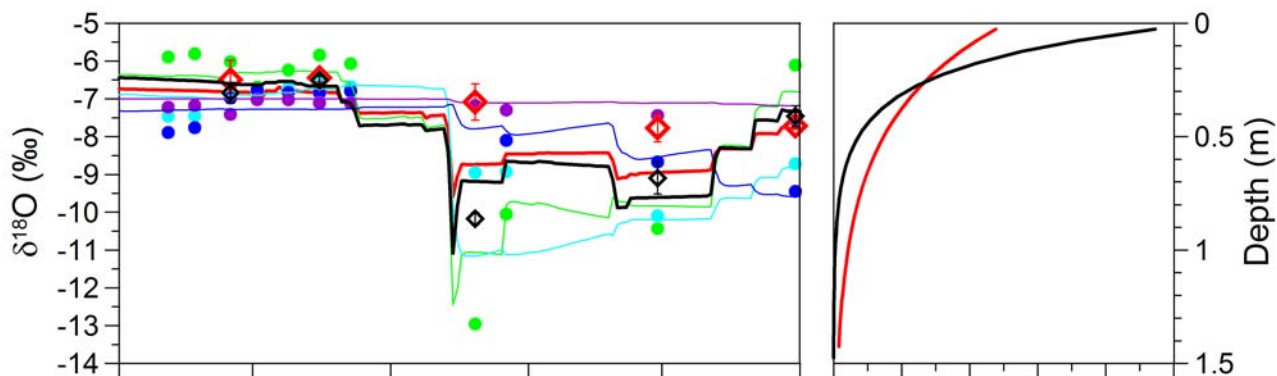


Figure 2 Schematic illustrations of original (for the pure stand) and modified (for the mixed stand) isoRHEA models.

a) Case A



b) Case B

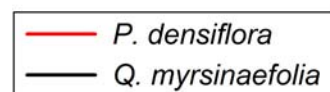
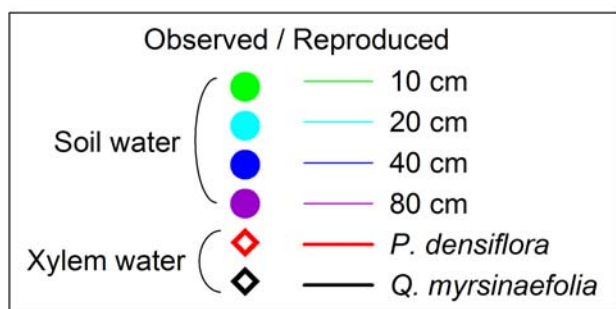
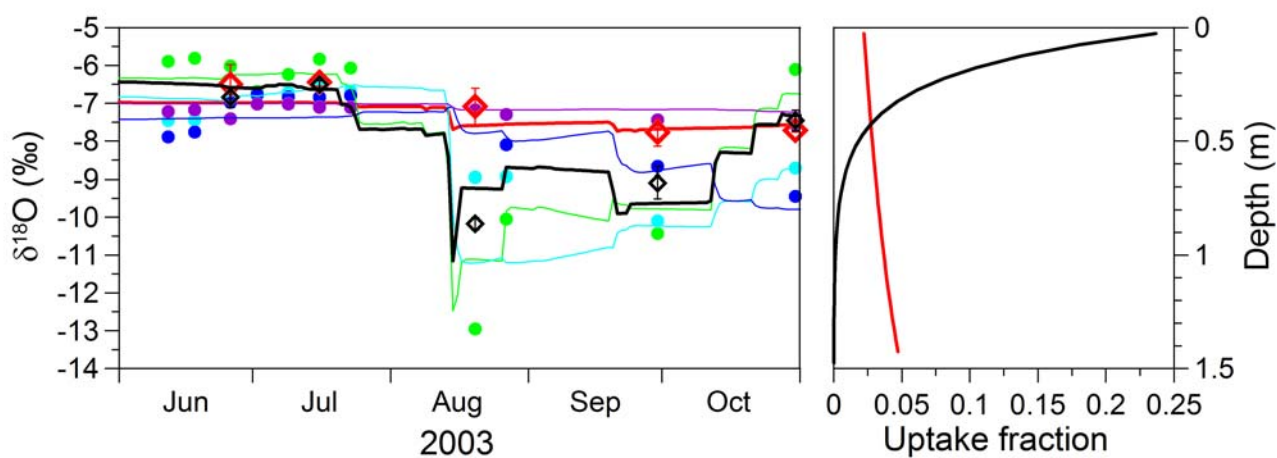
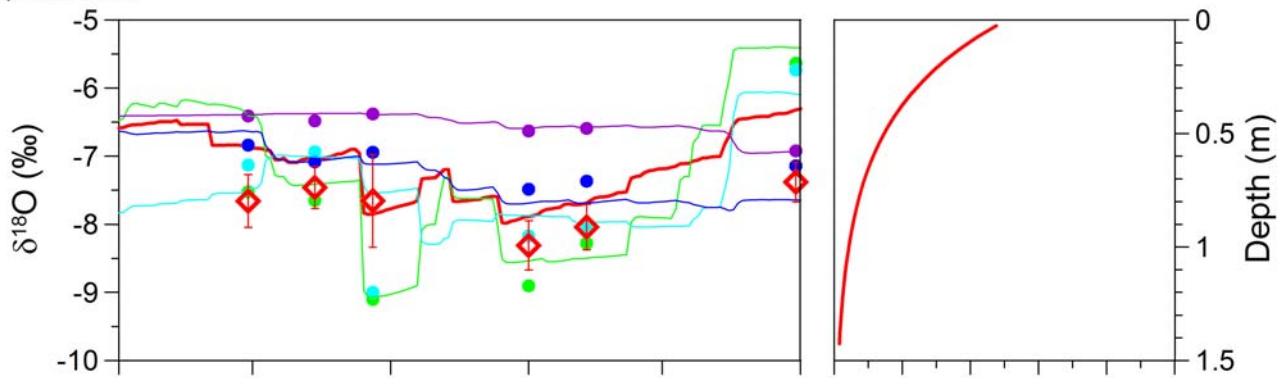


Figure 3 Results in the mixed stand on (left) temporal variation of observed and reproduced $\delta^{18}\text{O}$ of soil/xylem waters and (right) reproduced depth-profile of uptake fraction per 5-cm depth intervals for (a) Case A and (b) Case B.

a) Case A



b) Case B

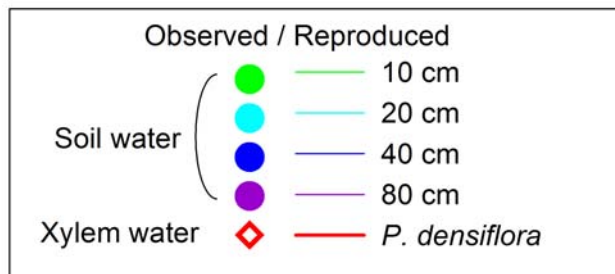
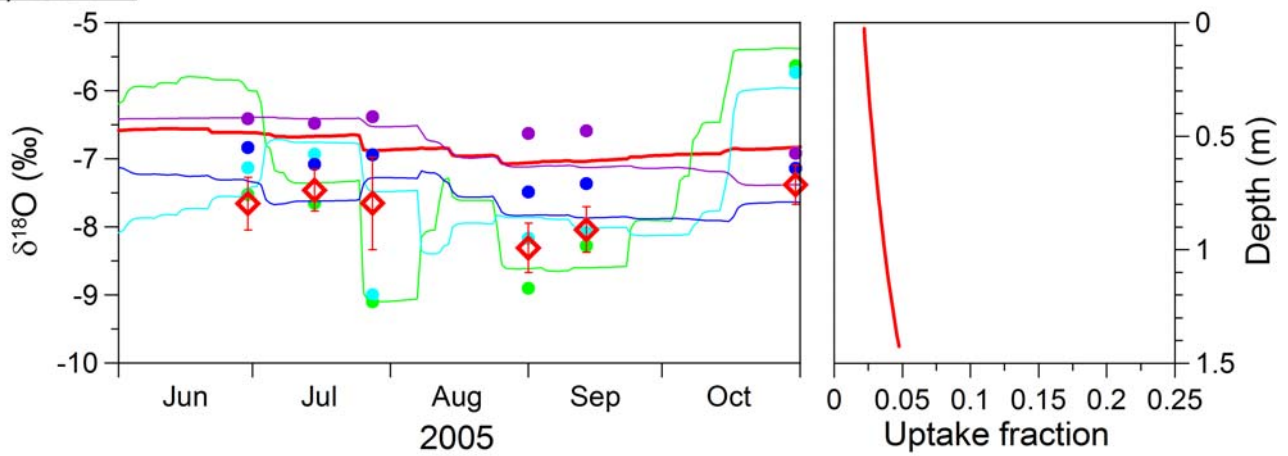


Figure 4 Same as Fig. 3 but in the pure stand.

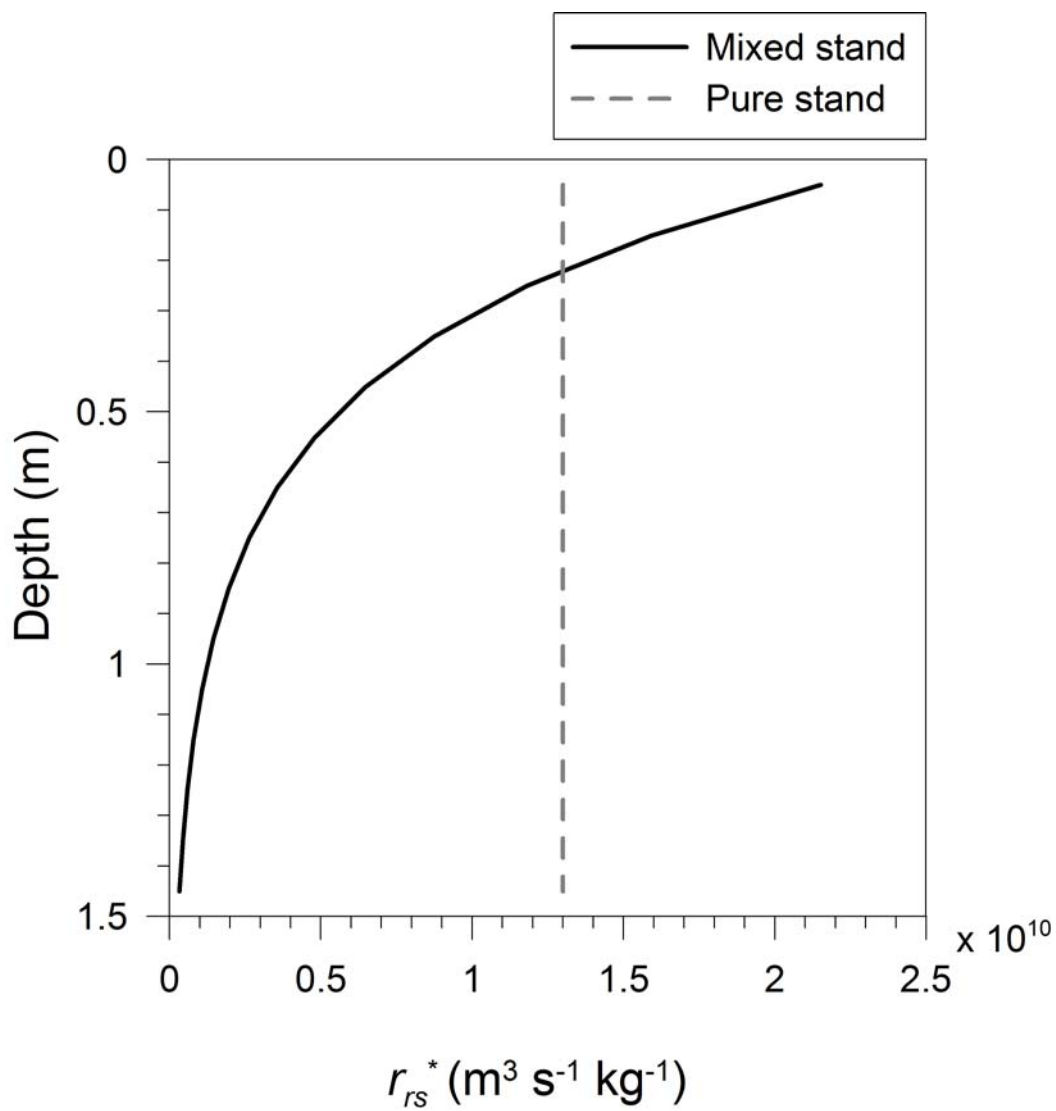


Figure 5 Vertical profiles of the root surface resistance per unit length of roots (r_{rs}^*) in the two study stands.