Age specific rhizome dynamics of *Phragmites australis* and their effects on nutrient cycling.

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ABSTRACT: Characteristics of rhizome resource storage of common reed, *Phragmites australis* (Cav.) Trin. ex Steudel, were investigated associated with the aboveground biomass in terms of rhizome age category. Age-specific rhizome biomass and total nonstructural carbohydrate (TNC), and standing stock of aboveground biomass were observed monthly. The biomass of one- or two-year old rhizomes did not reduce during the growing season, while a large reduction was observed with older rhizomes. TNC concentration declines twice a year, first in May before the recovery in late spring and second after August, followed by recovery in November. The amount of remobilized TNC is negatively correlated to rhizome age during spring growth and autumnal translocation, except for one year old rhizomes. Analyses of carbon budgets implies that the spring decline is caused by the remobilization of TNC for the aboveground biomass growth and rhizome respiration, and that of autumn is mainly due to respiration, while translocation of dead shoots contributes to the subsequent recovery of rhizome biomass. The nitrogen contents substantially decrease during the second summer, however, phosphorous contents reduce gradually during the whole year.

Key Words: *Phragmites australis*, Resource dynamics, TNC

Introduction

Common reed, *Phragmites australis* (Cav.) Trin. ex Steudel, is a perennial macrophyte distributed across many aquatic environments in the world. In addition to the seasonal dynamics of production of *P. australis* under different field and experimental conditions, much attention has been paid on the rhizome dynamics in previous studies of rhizomatous species. However, studies of reed rhizomes are complicated by the fact that the rhizomes live for several years and most of rhizome characteristics such as respiration (Cizkova & Bauer 1998), starch and sugar accumulation (Cizkova et al. 1996, Kubin & Melzer 1996, Fiala 1976), etc. depend much on their age, and the age specific structures, probably related to the survival strategy of *P.australis*. Yet, the age of the *P.australis* rhizomes has received much less attention than they deserve because of difficulties in the approach for age specific rhizome analyses except for few studies (Cizkova & Lukavska 1999, Klimes et al. 1999, Cizkova & Bauer 1998, Fiala 1976). This paper presents the results of

an extensive study on the age specific aspects of resource translocation between the aboveground organs and rhizomes, conducted in a swampy section of a wetland area, with the objective of understanding their structure to apply for the quantification or modeling of *P. australis* lifecycle.

Materials and Methods

The study was conducted in a swampy section of the Akigase Park, N35°51'10", E139°35'48", located on the flood plain of Arakawa River in the central part of Japan. The study site was dominated by a homogeneous monospecific stand of natural *P.australis* of more than 1000 m², being more than 20 years old without any catastrophic damages during this period.

The investigation was conducted from April to December 2001, following preliminary studies done in the same site (Karunaratne et al, 2002). During the investigation, the site was waterlogged as -70 cm deep in August and +40 cm in October because of the drought and storm events respectively, however, in other periods the water table was about 20 cm below the ground surface. The topography of the site was uniform and the substrate was soft brown organic loam up to 40 cm below the ground surface with underlying hard clay, resulting in more than 95% of the rhizome system contained within the top 40 cm of the substrate.

Three replicates of 25 cm x 50 cm wide and 50 cm thick undisturbed soil blocks were excavated by a spade at visually homogeneous and monospecific spots of uniform shoot density and age, and were transported to the laboratory in large plastic bags. The soil blocks were then flushed off of sediments with a pressurized water spray and a 4 mm sieve, taking care not to disturb the interconnected rhizome branches. The sieve was used to collect the root materials. The washed rhizome mat was carefully separated into clusters of interconnected branches. Rhizome age categories were identified based on the combined criteria proposed by Cizkova & Lukavska (1999): the branching hierarchy and condition of the stems attached to vertical rhizomes, started with one year old vertical rhizome attached to a green shoot; the condition of the nodal sheaths such as intact and tightly sheaths indicating a newly formed rhizome, loosely attached or partly disintegrated sheaths being one or two years old rhizomes and no sheath being more than three year old rhizomes; and the rhizome color which became darker with age. Rhizome age could be identified until six-year-old category.

All samples were dried for 48 hours at 85°C to obtain the dry weight, then were ground into less than 0.425 mm to analyze carbohydrates, nitrogen and phosphorus contents. Nonstructural carbohydrates were extracted by diluted sulfuric acid (Smith et al. 1964) and were measured by phenol-sulfuric acid colorimetric method (Dubois et al. 1956) as was followed by Graneli et al. (1992). Carbon contents were analyzed by CHN-Coder (YANACO, MT-5).

Without significant difference in the annual temperature in 5 years (p=0.7507, Kurskal-Wallis test), the annual transition of the aboveground biomass underwent within 16% of difference in the last three years (p=0.3178, 0.3189 and 0.7515 in July, August and October respectively, Kurskal-Wallis test). The stand therefore, was tentatively assumed to be in a steady state as per the local meteorological conditions so as to understand the lifecycle behavior of the rhizomes, although three years may not be long enough to conclude it firmly.



Fig. 1. Seasonal variation of standing biomass (\blacklozenge), carbon stocks (\square), and total nonstructural carbohydrate that converted to carbon weight (O) of living rhizomes of each age categories and carbon contents in rhizomes (\triangle).

Results

Seasonal variation of aboveground biomass and rhizome biomass

Figure 1 shows the seasonal variation of standing biomass, carbon stocks, and total nonstructural carbohydrate that converted to carbon weight of living rhizomes of each age categories, and Fig.2 shows the total standing stocks of total living and dead rhizome and shoot biomass. Primarily emerged shoot biomass markedly increased until the end of



Fig. 2. Ssonal variation of total standing stocks of living (\blacksquare) and dead (\triangle) rhizome and total (\diamondsuit), living (\diamondsuit) and dead (\times) shoot biomass.

June, reaching 1086 g/m² in the beginning of August. From August the dead biomass increased associated with decreasing living biomass, and all shoots died off before the middle of November. Although new shoots formed secondarily especially after August, their total biomass was only 4% of that of the primarily emerged shoots. The total living rhizomes decreased by 25% (225 g/m²) from April to May, simultaneously with the shoot formation of 441 g/m², while, dead rhizomes increased by 236 g/m² from April to June. The total rhizome biomass increased from June to October, especially until the end of August, by 55% of the original quantity, and then reduced onwards to the level of April. The synchronized behavior of the aboveground and belowground biomass followed the typical patterns often reported previously (Fiala 1976, Schierup 1978, Hocking 1989).

Translocated photosynthates from well- developed shoots, biomass of all age categories increased substantially in late spring to summer, which however commenced earlier with younger ones. One year old rhizomes started to increase their biomass markedly from April, compared with only from June for the cases of four to five year old rhizomes. New rhizomes, after first appearing in June, started to grow from June (Graneli et al. 1992). The present results imply that the beginning of recovery is not uniform with all age categories but depends on the age category.

The decline of biomass is evident in autumn to winter for all age categories. By contrast to the increasing phase, younger rhizomes maintained the biomass longer than the older ones; newborn and one year old categories started to decline from December and continued to reduce during winter, while the older categories decreased from late autumn to early winter and remained almost constant values during winter except for some fluctuation just before spring.

Therefore, longer period of increasing phase than the decreasing phase gradually maximized the biomass of rhizomes younger than three year old, while the opposite tendency of phase length minimized rhizomes older than five years. Five year old category substantially decreased in autumn.

Assuming the dynamic steady condition of this population, spring growth was 52, -37, -162, -121, -43, 13 g/m², while winter loss of age specific rhizome biomass were obtained as 170.5, 109.2, -105.2, -22.5, 5.9 g/m^2 , and essentially zero, respectively for the new-born to 6-year old ones.

The fluctuation of the total carbon concentration has the apparent opposite phase with the rhizome biomass until three-year old rhizomes. This is supposed to be due to the high consumption of carbon for rapid growth of young rhizome to compensate the insufficient translocation of the photosynthates.

The growth of young rhizome segments decelerated after October, while the increasing mortality of shoots translocated the materials mainly to the young rhizome segments. Then, the supplied carbon was stocked more in the form of TNC for the energy source during winter rather than the structural materials.

With its easily translocatable characteristics, TNC concentration showed a lager seasonal fluctuation than TC between 50 to 400 mg/g.d.w., comparable to the value reported by Graneli et al. (1992). Regardless of age categories, marked reduction was noted twice a year, in spring and in autumn. The spring reduction corresponds to the decline of rhizome biomass apparently indicating the translocation of stocks for shoot formation. The magnitude of reduction was gradually minimized with age (r=0.574, p=0.234). After the spring reduction, TNC recovers markedly, reaching the highest value in the year by the intensive translocation of photosynthates. The autumnal reduction was also synchronized with the shoot formation in autumn. Differently from the spring reduction, however, there were no evident apparent age specific trends (r=0.277, p=0.548). Compared with the recovery in spring, the autumnal recovery was milder and weaker, supported by the translocation from senescent aboveground organs. The autumnal recovery also decreased with rhizomes older than four year old.

Age-specific seasonal variation of nitrogen and phosphorous contents

Figure 3 presents the age-specific nitrogen and phosphorus contents in each age categories. Both nitrogen and phosphorous have higher contents in new segments, however they decrease afterwards until the level of old ones, showing the same fluctuating patterns of biomass. The concentration of nitrogen decreases rapidly during first winter, while it takes a whole year for phosphorus concentration to reach the



Fig. 3. Seasonal variation of nitrogen (\blacklozenge) and phosphorus (\Box) contents in each age categories.

old rhizome levels.

Discussion

Seasonal variation of age specific total carbon stock shows typical age-specific characteristics: although new-formed to three-year old segments increased constantly from April until the end of the year, while the old ones only increased after the aboveground foliage have almost established. Young segments markedly reduced during winter, while old rhizomes reduced before the end of the year. Together with the previously reported respiration rate and photosynthesis rate (Cizkova & Bauer 1998, Asaeda & Karunaratne 2000) the carbon budgets were estimated.

From April to May, out of totally reduced biomass, 61 gC/m² and 11 gC/m² were lost by respiration and mortality respectively and 70 gC/m² of old segments was translocated to the aboveground. From May to August, downward translocation rate was about 700 gC/m², which was partially lost by 240 gC/m² and 40 gC/m² for respiration and mortality, respectively. Although age-specific allocation was evident until June, materials were evenly allocated after the foliage was fully established.

In the senescence stage from August to October, about 100 to 200 gC/m² of tranlocated material from the aboveground was consumed mainly by respiration, resulting in slight reduction in the total amount. However, compared to the slight decrease in old segments, mostly by respiration, the increase in the young segments implies the downward translocation has mainly allocated matter to the young segments. The reduction of old segments substantially decreased from October to December, although young segments still increased. With small amount of downward translocation, 20 gC/m², and 150 gC/m² of respiration loss, 110g C/m² was reduced in total.

Winter respiration and mortality loss was evident with young segments, 70 gC/m², 51 gC/m², and 15 gC/m² for new-born, one and two-year old categories, which were well estimated by the high respiration loss of young segments and buds and mortality.

The reduction of old segments from August to December was considerable compared to the slight increase in young segments. Although there was formation of secondary shoots during the season, it alone cannot account for this large reduction. Winter respiration loss was substantial with young rhizomes, therefore it seems that old segments fuel young segments beforehand as young ones can survive and produce buds during winter.

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