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Age-specific seasonal storage dynamics of *Phragmites australis* rhizomes: a preliminary study

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Abstract

Age-specific seasonal rhizome storage dynamics of a wetland stand of *Phragmites australis* (Cav.) Trin. ex Steud. in Japan, were investigated from April to October 2000. For each sampling date, above- and below-ground biomass and age-specific rhizome bulk density, ρ_{rhiz} were measured. Seven rhizome age classes were recognized, from <1 year to six years old, based on their position within the branching hierarchy as main criteria and rhizome color, condition of nodal sheaths and condition of the shoots attached to vertical rhizomes as secondary criteria. *P. australis* stand was moderately productive, having a net aerial and below-ground production of 1980 and 1240 g m^{-2}, respectively, and a maximum mean shoot height of 2.33 ± 0.12 m. In spring, shoot growth started at the expense of rhizome reserves, decreasing the rhizome biomass as well as ρ_{rhiz}. Both parameters reached the seasonal minimum in May followed by a subsequent increase, indicating a translocation of reserves to rhizomes from shoots after they become self supporting. For each sampling date, ρ_{rhiz} increased with rhizome age. Given that the quantity of reserves remobilized by the rhizomes for spring shoot growth, as assessed by the drop in bulk density from April to May, were positively correlated ($r = 0.97$, $P < 0.05$) with rhizome age, it is proposed that for spring shoot formation older rhizomes remobilize stored reserves more actively than younger ones. Given that the accumulation of rhizome reserves (rise in bulk density) from May to August, May to September or May to November was negatively correlated ($r = 0.97$, 0.92 and 0.87, respectively, $P < 0.05$) with rhizome age, it seemed possible that younger rhizomes were 'recharged' at a higher rate than older ones. These resource allocation mechanisms pertaining seasonal rhizome storage dynamics are of paramount importance in formulating management and conservation strategies of wetlands and aquatic habitats. Our results indicate that a harvest of above-ground biomass from May to June would be more effective in reducing the growth than a harvest in July to August or later, when rhizome reserves have already been replenished. However, the latter may remove a larger shoot bound nutrient stock, still preserving a healthy stand for the subsequent years.

Introduction

Phragmites australis (Cav.) Trin. ex Steud. is one of the most widely distributed and studied reed species, mainly due to its invasive or dominating presence in many aquatic habitats around the world. Remobilization/accumulation dynamics of these clonal plants are one of the neglected topics in population ecology, despite its importance for the survival of these species. The spring growth of these plants depends strongly on the reserves stored in the forms of sugars (sucrose, glucose and fructose), starch or fructosans (Ho 1988), which are deposited in, specialized tissues of rhizomes and roots,

accumulated during the previous growing seasons (Klimes et al. 1993, 1999; Kubin and Melzer 1996). Seasonal changes in rhizome biomass can be caused by translocation of constituents to or from other parts of the plant, mortality and metabolism of non-structural carbohydrate reserves (Chapin et al. 1990).

Production and growth dynamics studies concerning the above-ground stand components of *P. australis* (Dykyjova 1971; Dykyjova and Hradecka 1976; Hara et al. 1993; Clevering 1998; Asaeda and Karunaratne 2000; Karunaratne and Asaeda 2000, 2002) are more plentiful than those concerning the below-ground stand components (Graneli et al. 1992; Cizkova and Bauer 1998; Cizkova and Lukavska 1999; Klimes et al. 1999), given the difficulty in sampling *P. australis* rhizomes, which penetrate to a considerable depth.

Studies of reed rhizomes are further complicated by the fact that the rhizomes live for several years (Fiala 1976; Hara et al. 1993) and their age affects numerous rhizome characteristics, such as respiration (Cizkova and Bauer 1998) or starch and sugar accumulation (Fiala 1976; Kubin et al. 1994; Cizkova et al. 1992, 1996; Kubin and Melzer 1996). With few exceptions (Fiala 1976; Cizkova and Bauer 1998; Cizkova and Lukavska 1999; Klimes et al. 1999), most of the previous studies done on carbohydrate storage, nutrient contents and rhizome bulk density (ρ_{rhiz}) of *P. australis* rhizomes, have not taken into account the differences among age categories. However, even those prior studies, which have considered the age-dependency issue, have lacked the added component of seasonal dynamics, which is of paramount importance in understanding the stability and survival of *P. australis* stands under different habitats and conditions of environmental stress, and to formulate management and conservation strategies of wetlands and aquatic habitats.

Rhizome bulk density (ρ_{rhiz}) and chemical characterization of rhizome carbohydrates are often utilized as indicators of storage reserve level of rhizomes of *P. australis* and other similar species (Midorikawa 1959; Mutoh et al. 1968; Fiala 1976; Graneli et al. 1992; Kubin et al. 1994; Klimes et al. 1999). Midorikawa (1959) and Mutoh et al. (1968) successfully applied the bulk density measurements to evaluate the growth and production of several herbaceous and grass species, including *Miscanthus sacchariflorus*, *Aconitum japonicum*, *Rodgersia podophylla* and *Angelica edulis*. Also, increases and decreases in ρ_{rhiz} are correlated with rhizome total non-structural carbohydrates (TNC), starch, fructosan, sucrose, glucose and fructose content (Fiala 1976; Graneli et al. 1992). Consequently, ρ_{rhiz} can serve as a fairly representative indicator of rhizome storage content. Therefore, more easily and rapidly assessed parameter of age-specific ρ_{rhiz} accompanied by rhizome biomass was chosen to examine the seasonal storage dynamics in this preliminary study.

The results published in this paper represent a portion of the work the authors have done on the ecology of a *P. australis* stand in a swampy section of a wetland, which is representative of many Japanese shallow water areas. The present study investigates the seasonal storage dynamics of different age categories of *P. australis* rhizomes and addresses the following questions: (i) how does rhizome age affects the ρ_{rhiz} and the seasonal storage pattern of *P. australis* rhizomes? and (ii) do remobilization and translocation rates differ among the different rhizome age categories?

Methods

Site description

The study was conducted from April to October in 2000 over an area of about 0.1 ha dominated by a monospecific and more-or-less homogeneous (shoot height and stem distribution) wetland stand of *P. australis* located in Akigase Park in central Japan (35°51″N, 139°39″E). The park, located on the flood plain of the Arakawa River, is a nature reserve covering some 500 ha adjacent to the river and comprised of many such wetland areas. The *P. australis* stand being more than 10 years old appeared to be in dynamic equilibrium having a closed canopy.

The topography of the study area was uniform (slope $< 5\%$) and the substrate was soft brown organic loam ($\approx$0.4 m), overlying hard clay, thus more than 95% of the rhizome system was contained within the top 0.4 m. During the investigation in 2000, water depth at sampling varied between 0.5 m below and 0.2 m above the soil surface. At each sampling date, depth of standing

water was measured using a steel measuring tape while the shallow water table was measured at the excavated sample pits no earlier than 3 h after finishing the work. Above- and below-ground plant samples were harvested on April 3 (onset of spring shoot growth) and 19, May 10, June 4, July 4, August 1, September 9 and October 24, 2000. On April 19, July 4 and September 9, only the above-ground biomass was sampled. Further on April 28, July 18 and September 18 below-ground biomass was sampled only for ρ_{rhiz} measurements due to elevated water levels caused by the heavy seasonal rains.

Above-ground sampling

Three replicate samples of the above-ground standing crop within a 0.125 m^2 (0.25 $\times$ 0.5 m^2) frame were cut with hedge clippers at substrate level and harvested. Sampling was always performed within a visually homogeneous, monospecific area of uniform shoot density and age.

The height of each shoot was measured by taking the distance from the clipped base to the tip of the uppermost leaf, or to the tip of the panicle if the latter was present. Shoot material was then sorted into stems with leaf sheaths, leaves and panicles, when present. The individual types of above-ground plant materials from each quadrat were cut into 2–3 cm long pieces and individually dried at 85 °C to a constant weight ($\approx$24 h).

Below-ground sampling

Three replicate samples of rhizomes and roots were taken by excavating soil under a surface area of 0.125 m^2, to a minimum depth of 0.6 m using a garden spade. Every effort was made to excavate the soil monoliths as deep as possible to obtain larger undamaged interconnected rhizomes branches.

Plant materials were cleaned of soil with a pressurized water spray, over a 4 mm sieve, which served to retain root material. When cleaning the rhizome mat, care was taken to preserve the interconnected rhizome branches. The washed rhizome mat was then carefully separated into clusters of interconnected rhizome branches and sorted into roots and rhizomes, and separated as live or dead. After dating, rhizome material of individual age classes excluding those used for ρ_{rhiz} measurements were cut into 2–3 cm long pieces and individually dried in the oven at 85 °C to a constant weight.

Rhizome dating

Rhizome clusters with interconnected rhizome branches were blotted and the branches were tentatively dated using a method modified from Cizkova and Lukavska (1999) and Klimes et al. (1999). Identification of rhizome age categories (<1 to six years) was based on (i) their position within branching hierarchy; (ii) condition of the shoots attached to vertical rhizomes: live green shoots are attached to one-year-old rhizomes, dead shoots are attached to older rhizome material; (iii) condition of the nodal sheaths: intact and tightly covered in newly formed rhizomes, loosely attached or partly disintegrated in one- to two-year-old rhizomes and absent in rhizomes over three years old; and (iv) color (which becomes darker with age), but not necessarily in this order. The detailed dating procedure is as follows:

1. *New rhizomes* (younger than one year): Rhizomes bearing a terminal bud formed in the current year, tightly covered with scale leaves, present only after June sampling.
2. *One-year-old rhizomes* (formed in the previous year): Rhizomes bearing a green shoot in the terminal position, with preserved scale leaves, roots missing during the early growing season and with sparse roots during the late season.
3. *Two-year-old rhizomes*: Rhizomes bearing a light brown dead culm in the terminal position, usually attached to a new or one-year-old rhizome, sometimes with scale leaves, generally with adventitious roots. Such rhizomes had rusty colored spots, which were removable upon washing with water while rubbing.
4. *Three-year-old rhizomes*: Rhizomes generally bearing a dark brown or almost black dead culm in the terminal position, usually attached to a new, one- or two-year-old rhizome, generally with adventitious roots.
5. *Four-year-old rhizomes*: Rhizomes generally bearing a black or rotted dead basal part of a culm in the terminal position, usually attached to a new, two- or three-year-old rhizomes, generally with large roots.

6. *Five-year-old rhizomes*: Rhizomes more frequently attached to three- or four-year-old rhizomes than two-year-old rhizomes, some times with large attached roots.
7. *Six-year-old rhizomes*: Rhizomes generally attached to four- or five-year-old rhizomes, often with longest nodal lengths, usually with sparsely or no attached roots.

Rhizome bulk density determination

At each harvest date, ρ_{rhiz} of rhizome segments of different age class was measured. Using a sharp knife to prevent undue damage, rhizome segments bearing two undamaged nodes at either extremity of an internode were excised from undamaged rhizome branches. On each sampling date, ρ_{rhiz} of some 35–40 intact internodes from each age category was measured. Incomplete or damaged internodes were discarded, though they were included in biomass. However, the number of new rhizome internodes at the early stage of new rhizome formation and six-year-old rhizome internodes, especially after May, were limited to 15–25, due to the low relative biomass of these age categories. Volume of a rhizome internode in ml (V) was measured by water displacement when a fresh intact rhizome internode was completely immersed in the water with the aid of a needle. Dry mass of the rhizome internodes in mg (W) was obtained after drying them to a constant mass at 85 °C. ρ_{rhiz} of a rhizome internode was then defined as dry mass per unit volume of fresh rhizome [W/V (mg DW mm^{-3})].

Statistics

The effects of rhizome age and sampling date (factors) on the age-specific rhizome biomass and ρ_{rhiz} (class variables) were analyzed using two-factor analysis of variance (ANOVA) with Tukey's multiple comparison as a post test. Differences in ρ_{rhiz} among the age classes during a sampling date were analyzed using one-way ANOVA. An unpaired *t*-test was used to evaluate the differences between two independent means. The differences between the single values were assessed using 95% confidence intervals for means (Zar 1999).

Results

Primary shoot emergence was observed in the first week of April at which time most of the buds remained still at the ground level while about 10% shoots had grown to 0.2–0.6 m above the soil level. The total live above-ground biomass and percentage ratio of leaf biomass amounted to 6 g m^{-2} and 0.2%, respectively. Primary shoot emergence (≈95%) was completed by June. Only a few late emerging shoots were observed. In June, some of the shoots in the stand were attacked by reed bug (a local term to cover all caterpillars living in reed stems and large enough to cause harm). This probably brought about a decrease in stand density followed by few shoot branching and regeneration of several secondary shoots in August. However, no increase in rhizome branching level was observed.

The increase in shoot height was relatively slow from early April to mid April but rapid thereafter until July, after which growth slowed and leveled off (Figure 1a). The pattern of the increase in shoot dry weight was very similar to that of shoot height (Figure 1b). Shoot biomass peaked in August (1290 ± 170 g m^{-2}) whereas leaf biomass and hence LAI peaked in July, a month before. Panicles appeared in early August, and were in full bloom by October.

The first below-ground biomass sampling was carried out in April, just before the shoots began their active growth. The mean live rhizome biomass decreased significantly (38%, $P \leq 0.05$) from 2200 ± 10 g m^{-2} in early April to 1360 ± 50 g m^{-2} in early May, probably as a result of rhizomes remobilizing stored reserves for the rapid spring growth of shoots, respiration and mortality (Figure 1c). There was a significant variation of total live rhizome biomass during the investigation period ($P \leq 0.05$) where as the mean dead rhizome biomass did not show a significant pattern of variation over the same period ($P > 0.05$). From May onwards, the live rhizome biomass increased steadily and by August reached 2100 ± 110 g m^{-2}, only 5% less than the initial rhizome biomass ($P \leq 0.05$). New rhizomes began forming as early as June, but through August, their biomass remained below the threshold of significance. Therefore, by early June the shoots should have become self-supporting and capable of translocating some of

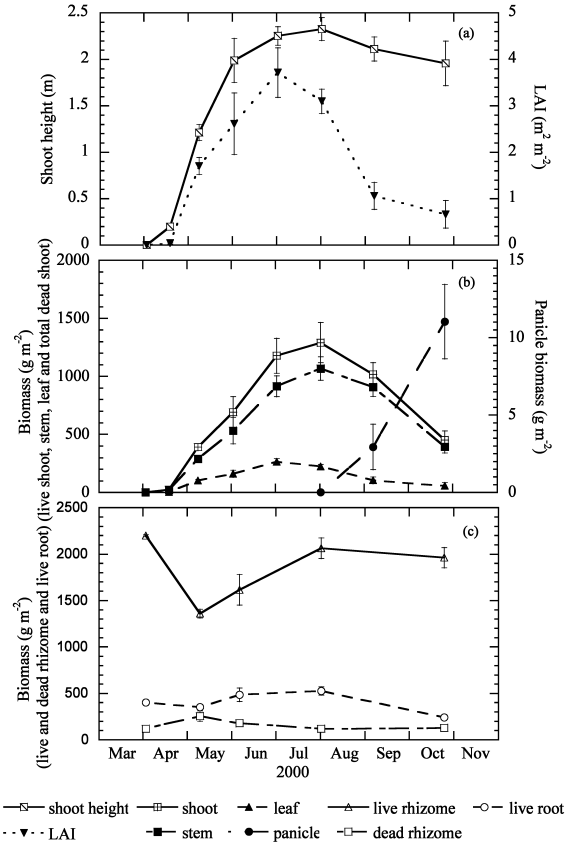

Figure 1. Seasonal variation of (a) shoot height and LAI (b) above- and (c) below-ground biomass of *P. australis*. Bars indicate standard error for means.

their reserves (most probably photosynthetic production) to increase rhizome reserves and also to form new rhizomes. Unlike the rhizome biomass, the root biomass remained relatively stable throughout the growing season ($P > 0.05$). Live root biomass accounted for 15%, 21%, 23% and 20%, respectively, of the total live below-ground biomass from April to August. Dead root biomass was insignificant compared to dead rhizome biomass and therefore not shown.

Seasonal pattern of remobilization and accumulation of age-specific rhizome ρ_{rhiz} and biomass corresponded closely to that of total live rhizome biomass (Figure 2). Significant changes in age-specific rhizome biomass (two-factor ANOVA excluding newly formed rhizome age category; df = 5; $F = 10130$; $P < 0.0001$) were observed during the investigation period (two-factor ANOVA; df = 4; $F = 1783$; $P < 0.0001$). Rhizome biomass (Figure 2a) of three-, four- and five-year-old age categories collectively comprised more than 60% of the total live rhizome biomass at all samplings while six-year-old rhizome biomass contributed only 3–10% of the total live rhizome biomass. Therefore, the average lifespan of the *P. australis* stand in consideration can be estimated as five to six years. One to six-year-old rhizome biomass underwent 19%, 35%, 40%, 44%, 39% and 45% reductions from April to May. Biomass of all the age categories except six-year-olds started increasing steadily from June onward. Biomass increment can be considered as an indication of accumulation of storage reserves, increase in structural biomass or a combination of both. However, the six-year-old rhizomes, the oldest age category continued to decrease, most probably due to structural death.

Significant changes in age-specific rhizome ρ_{rhiz} (two-factor ANOVA excluding newly formed rhizome category; df = 5; $F = 481.3$; $P < 0.0001$) were observed during the investigation period (two-factor ANOVA; df = 6; $F = 795.8$; $P < 0.0001$). Age-specific ρ_{rhiz} from new to six-year-old rhizomes, measured at roughly monthly intervals are as shown in Figure 2b. During spring growth in late April, six-year-old rhizomes showed the highest ρ_{rhiz} (0.1946 mg mm^{-3}) and the one-year-old rhizomes, the lowest (0.1150 mg mm^{-3}). All age categories showed their seasonal minimum ρ_{rhiz} in May, 0.0930 mg mm^{-3} for one-year-old rhizomes and 0.1364 mg mm^{-3} for six-year-old rhizomes, showing 19%, 20%, 25%, 23%, 25% and 30% reductions with respect to April values for one- to six-year-old segments, respectively ($P \leq 0.05$). Across all age categories, the drop in ρ_{rhiz} was 23% during the corresponding period. Though the percentage reductions are slightly lower, these changes in ρ_{rhiz} paralleled those of age-specific rhizome biomass. After attaining a seasonal minimum in May, ρ_{rhiz} of one- to five-year-old rhizomes began to increase. However, the six-year-old rhizomes showed a reduced accumulation capacity, lagging behind five-year-old and even three-year-old rhizomes ($P \leq 0.05$). However, during all sampling dates, ρ_{rhiz} increased significantly ($P \leq 0.05$) from new/one-year-old rhizomes through five/six-year-old rhizome categories.

The rate of reduction in ρ_{rhiz} of different age categories of rhizomes plotted against rhizome age showed that the rate of ρ_{rhiz} reduction during

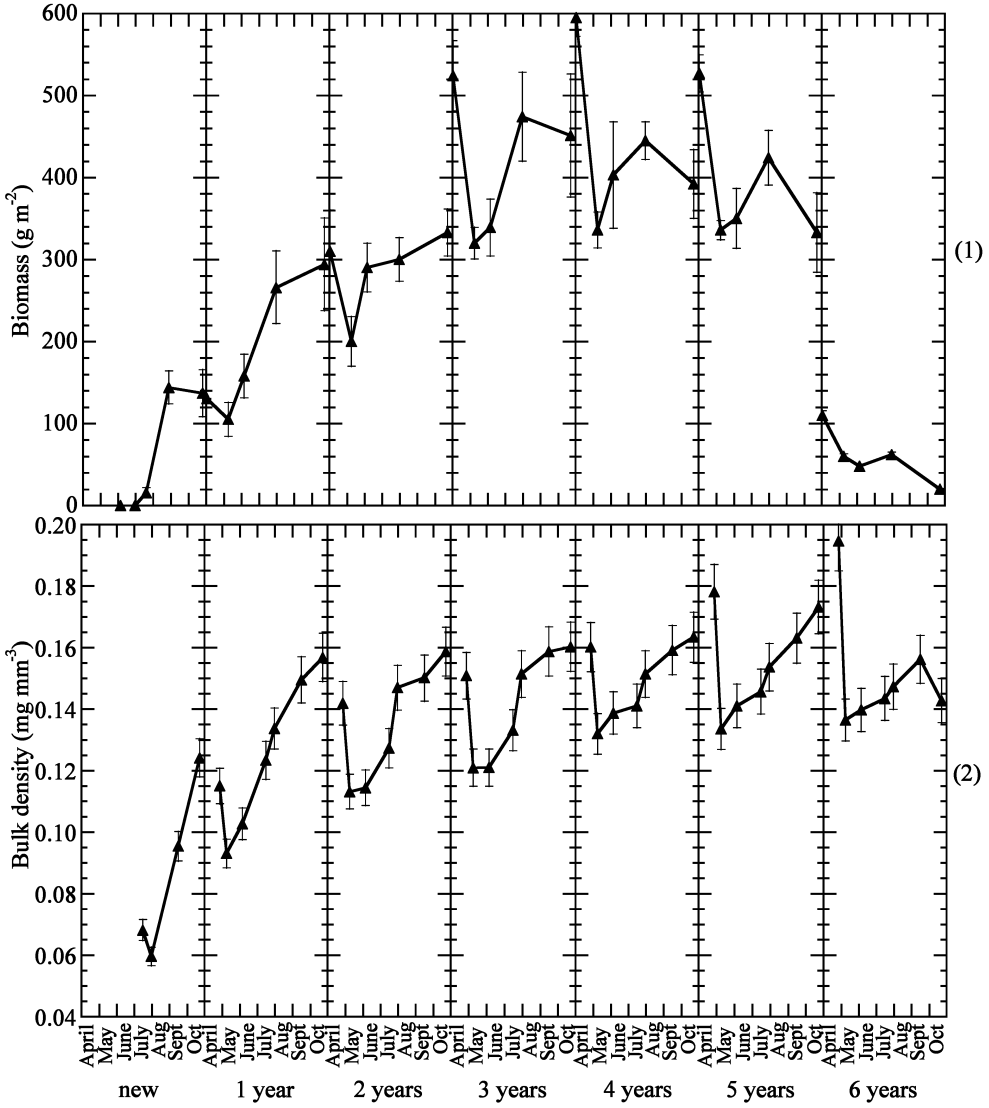

Figure 2. Seasonal variation of age-specific rhizome (1) biomass and (2) bulk density of *P. australis*. Bars indicate standard error for means.

the remobilization phase was positively and linearly correlated ($r = 0.97$, $P \leq 0.05$) with rhizome age (Figure 3a). One-year-old rhizome segments showed the lowest depletion rate of 0.0018 mg mm^{-3} d^{-1}, whereas the six-year-old rhizomes showed the highest depletion rate of 0.004 mg mm^{-3} d^{-1}, indicating a higher resource depletion with aging, during spring shoot growth.

Age dependency of rhizome reserve accumulation characteristics after spring depletion, were calculated in three stages, from May to August or September or October by determining the age-specific increment rates of ρ_{rhiz} (Figure 3b). It showed that the rate of increase in ρ_{rhiz} of different age categories of rhizomes during the accumulation phase was negatively and linearly correlated ($0.87 < r < 0.97$, $P \leq 0.05$) with rhizome age. Significant ($P \leq 0.05$) linear regressions of the rates of ρ_{rhiz} increase from May to August, May to September and May to October *vs.* rhizome age showed that the magnitude of the slope decreased as the period considered was longer. This was an indication of

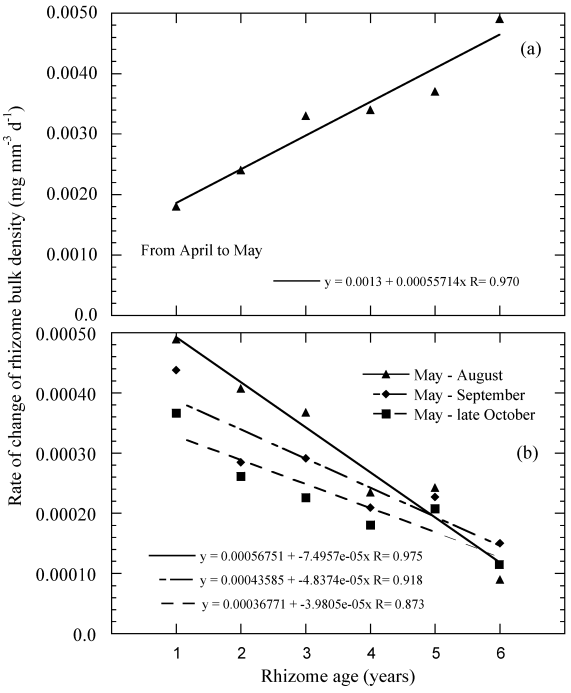

Figure 3. Rate of change of bulk density of *P. australis* rhizomes in different age categories (a) during the spring growth of shoots (from late April to early May) and (b) during late spring and summer (from May to August, May to September and May to October).

the slow down of reserve accumulation towards the end of the growing season, especially in younger rhizomes. One-year-old rhizomes showed the highest rate of ρ_{rhiz} increase, 0.00049, 0.00043 and 0.00037 mg mm^{-3} d^{-1} from May to August, May to September and May to late October, respectively. Percentage ρ_{rhiz} increases from May to late October were 66%, 33%, 31%, 21%, 22% and 14% in one- to six-year-old rhizomes, respectively. This seemed to suggest that after spring depletion in May, younger rhizome age categories accumulate greater amounts of reserves than their older counterparts; however, other factors may also be involved.

Discussion

Spring translocations of rhizomes

The plant's dependency on reserves for spring shoot growth is evident from the decrease in the mean total as well as age-specific rhizome biomass from April to May, and a corresponding decrease in ρ_{rhiz} of all age categories. However, a comparatively higher percentage reduction in ρ_{rhiz} of the older rhizomes occurred during this period compared with the younger rhizomes. This difference could be accounted for by three mechanisms, alone or in combination: (i) older rhizomes remobilize greater amounts of stored reserves for spring growth of shoots than younger rhizomes do; (ii) actual decrease in bulk density of young rhizomes is masked by an increase in their structural biomass, thereby making it appear as if the older rhizomes remobilize higher amounts for spring growth of shoots; and (iii) due to greater metabolic losses through respiration, associated with senescence and mortality in older rhizomes, a proportionally greater amount of stored reserves are spent on metabolic activities than in young rhizomes, resulting in the greater percentage reduction in ρ_{rhiz} observed in the older rhizome segments.

Of these three mechanisms, the second implies that young rhizomes grow in spring. Rhizome length per unit ground area or structural rhizome biomass per unit area (rhizome biomass, estimated by the three-point running median minus rhizome standing stock of TNC) was not measured in the present study. However, Graneli et al. (1992), using these techniques, did not observe any increase in rhizome length per unit area or structural biomass until June, likely corresponding with the end of the spring depletion of rhizomes, as shoot growth had begun in late April. These facts imply that rhizome growth does not occur during spring depletion of rhizomes. While his study ignored rhizome age, it was evident that the reduction in ρ_{rhiz} in younger rhizomes in spring was not masked by a rhizome growth; therefore, possibility (ii) can be eliminated.

The third mechanism requires that respiratory losses of older rhizomes account for a large part of rhizome mass loss during spring. The plausibility of this assumption can be estimated using the data from Cizkova and Bauer (1998) who measured respiration rates in different age categories of *P. australis* rhizomes in a stabilized reed stand in a littoral habitat near Trebon in Czech Republic. During a sampling made on 6th May 1997 (when shoots were 0.1–0.12 m high), they found that the respiration rates were positively related to rhizome age; their values being varied from 3.5–5.5 μmol

CO_2 g^{-1} dry wt h^{-1} for one- to four-year-old rhizome age categories, respectively. However, a reversed pattern was observed two weeks later on 23rd March 1997 (when shoots were 0.6–0.7 m high) and at all sampling dates later in the season. During this time the respiration rates were inversely related to rhizome age; their values being varied from 5.75–2.25 μmol CO_2 g^{-1} dry wt h^{-1} for one- to four-year-old rhizome age categories, respectively. Even though the growth phase, trophic status and other environmental factors that may alter the respiration rates might not exactly be similar between the two sites in Czech Republic and Japan, the approximate reduction in ρ_{rhiz} due to respiration was calculated for the period from 28th April 2000 (when shoots were 0.62 m high) to 10th May 2000 (when shoots were 1.2 m high), using the both spring respiration rates observed by Cizkova and Bauer (1998).

$$\rho_{rhiz} \text{ after one day's respiration losses (mg mm}^{-3}) = \rho_{rhiz} \text{ (mg mm}^{-3}) \times [1 - \text{respiration rate}] \text{ (mg mg}^{-1}\text{dry wt d}^{-1}) \quad (1)$$

The approximate reduction in ρ_{rhiz} due to respiration losses from April to May was calculated using equation 1. The approximate reduction in ρ_{rhiz} due to rhizome respiration (calculated using both respiration rates) as a ratio of the total reduction in ρ_{rhiz} in the corresponding period was 7–13% and 4–9% for one- and six-year-old rhizome segments, respectively (same rates of respiration as of four-year-old rhizomes were used to calculate the respiration losses of five- and six-year-old rhizomes). Therefore, the fraction of the reduction in ρ_{rhiz} that could be due to remobilization varied from 87–93% to 91–96% for one- to six-year-old rhizome segments, respectively. After accounting for the respiration losses, the reduction in ρ_{rhiz} due to possible remobilization was significantly different among the age categories: their values were positively related to rhizome age (one-way ANOVA; $df = 5$; $F = 4.45$; $P < 0.001$).

Obviously, the decrease in mean ρ_{rhiz} during the spring growth of shoots was somewhat greater than the value shown above as shoot growth began in early April. The present observations of the reduction in ρ_{rhiz} from April to May correspond to those of Graneli et al. (1992), who found a sharp decrease in TNC concentration from 41–45% in April to a minimum of 28–35% in early June. Further, water-soluble carbohydrates (WSC) concentration also displayed a similar pattern of variation during the same period. Therefore, the sharper spring drop in ρ_{rhiz} in older rhizomes cannot be attributed to possibility (iii). Therefore, the most likely reason for the higher percentage reduction in ρ_{rhiz} with increasing rhizome age was simply that older rhizomes remobilize greater amounts of stored reserves for spring growth of shoots than younger ones do.

Summer translocations of rhizomes

A 'reloading' of rhizomes from June onwards was indicated by increased ρ_{rhiz} of all age categories. A similar pattern of rising TNC was shown in *P. australis* rhizomes from Sweden (Graneli et al. 1992), Switzerland (Haldemann and Brandle 1986) and Canada (Thompson and Shay 1985).

The rate of increase in ρ_{rhiz} across the age categories from young to old decreased when the rates were calculated for longer periods. This cannot be explained with the same rationale, as were the rhizome dynamics of spring depletion. One possibility is that younger rhizomes accumulate higher amounts of stored reserves during this period. However, Graneli et al. (1992) in a study in Sweden, showed that an increase in rhizome length per unit area as well as in structural biomass of rhizomes began in June, after the spring depletion. Increase in structural biomass would likely result in the growth of rhizomes of younger age categories, such that the increase in ρ_{rhiz} in younger age categories would be an upper limit for the translocation of carbohydrates from shoots. Present results are insufficient to clarify this issue and require confirmation by future studies. However, it is most probable that during the early accumulation stages, while competing for the translocated reserves from the shoots, the younger rhizomes comparatively trap more reserves than the older ones. This means the younger rhizomes are being recharged at a quicker rate than the older ones, so that the older ones need to accumulate reserves to a greater extent towards the end of the growing season and/or the growth of younger rhizomes including new rhizomes, is a process mostly limited to the early summer period.

Conclusions

Proper understanding of ecophysiological mechanisms pertaining seasonal rhizome storage dynamics are of paramount importance in formulating management and conservation strategies of wetlands and aquatic habitats. In our study, we found that the rhizome reserves were lowest from May to June. Therefore, a harvest of above-ground biomass in May to June would be more effective in reducing the growth than a harvest in July to August or later, when rhizome reserves have already been replenished. However, the later may remove a larger shoot bound nutrient stock, still preserving a healthy stand for the subsequent years.

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