# 1 Introduction

Bare sandbars have been reported to be declining throughout Japan. Damming of rivers over the past several decades has caused dramatic changes in discharge regimes of Japanese rivers. Reduced flow due to irrigation and regulated flow due to dams has reduced the number of flood events per year. When flood events are large enough to demobilize river bed, they can lead to the destruction of existing vegetation. As the frequency and magnitude of flood events decline, vegetation has longer periods to expand, and often intrudes into bare bar ecosystems. Established stands of vegetation can resist flow and increase sedimentation in the stand. Sedimentation of nutrients such as phosphorus (P) and nitrogen (N) can produce an excessive supply of nutrients similar to eutrophication, and thus result in a positive feedback system for the expansion of stands of vegetation. The encroachment of vegetation into bare bar ecosystems reduces habitat available to species adapted to bare areas.

*Phragmites* spp. inhabit nutrient-poor environments, and their growth rate responds to a broad range of nutrient conditions. Tylova-Munzarova *et al*. (2005) found that *P. australis* was less affected by low-N conditions than another wetland species *Glyceria maxima*. Meuleman *et al*. (2002) found that *P. australis* cultivated in a nutrient-rich infiltration wetland displayed higher biomass production and higher N concentrations than in a natural wetland. These findings suggest that current models of *Phragmites* spp. are insufficient to account for growth differences attributable to nutrient conditions. *P. japonica* is commonly found on sand-bed rivers with high hydraulic conductivity, and at a considerable distance from the river edge, suggesting limited access to water and nutrients. Even under conditions that may not be N-limited, the nitrogen concentration and growth rates of *Phragmites* spp. may differ. Therefore, models that include N-supply need to be developed.

# 2 Field observation

Field observations were conducted at the Yahagi River (description summarized from Mizoguchi (2005)), which stretches 117 km in the Southern Japanese Alps (Hiraya, Nagano). The river drains a 1830 km2 watershed including parts of Nagano, Gifu, and Aichi prefectures. There are 4.6 million people within the watershed, and 13.3 million people use the water. Tomoe River and Oto River are two of its major tributaries, and it branches off into Yahagifuru River before reaching Mikawa Bay. The slope is roughly 1/670 to 1/830 from the spring to the point 35 km from the mouth, and roughly 1/1100-1/2580 from the 35 km point to the mouth. From the spring to the 62 km point the river is like a mountain stream, then it flows in a riffle/pool structure until the 4.6 km point, where it widens into Mikawa Bay.

During the 1998 river census, 100 families and 522 species were recorded along the Yahagi. Grassland and woodland communities composed 62.1% and 28.6%of vegetated area, respectively. The lower reach included considerable coastal vegetation. Willow (*Salicacea* spp.) dominated much of the woodland of the middle segment. Among emergent vegetation, *Phragmites australis* were prolific in the lower segment, and *Phragmites japonica* were prolific in the middle and upper segments. Additionally, *Phragmites karka*, *Zizania latifolia*, and *Typha angustifolia* were recorded in smaller numbers. Riparian zones from the lower segment to the upper segment also included *Solidago altissima,* *Digitaria adscendens*, *Setaria faberi*, *Lespedeza juncea*, and *Artemisia* spp.

Table 2.1 Water quality data for the four observation locations V1, V2, V3, and B1 and the river, and soil nutrient content data for each observation location. Values are means for all observations. z is the depth of subsurface water referenced to ground level of B1 as datum, and y is the distance from subsurface water to the surface.



Fig. 2.1 The distribution of vegetation at the target bar in August 2004 (adapted from Mizoguchi 2005). The black dots indicate the observation locations.

Field observations were conducted at a sandbar 17 km upstream of Mikawa Bay. Fig. 2.1 shows the distribution of vegetation on the bar and the locations of observations. The stands of vegetation consisted chiefly of *Phragmites japonica* and *Phragmites karka*. Study locations were established in sections consisting only of *Phragmites japonica*. Willow and *Polygonum hydropiper* were scattered on bare sections of sand bar.

# 3 Hydroponics experiment

## 3.1 Methodology

On the morning of October 20, *P*. *japonica* were removed from the Yahagi river sandbar 17 km from Mikawa Bay. Plants were removed from the study site in groups by removing clods of soil containing the roots of shoot clusters. Root and rhizome structures were preserved as much as possible and placed in tubs with soil from the bar.

Photo 3.1 Seed morphology of *Phragmites* spp.

The plants were separated into multi-shoot clusters of 65 to 123 g fresh weight. The roots were washed with a P-free detergent, and rinsed with tap water. Then the plants were placed in polyethylene jars containing 1 L of culture solution.

The culture solution was created by adding dibasic potassium phosphate (K2HPO4) and potassium nitrate (KNO3) to tap water. The culture solution contained 5.92 mg L-1 NO3-N, 4.62 mg L-1 PO4-P, 0 mg L -1 NH4-N, and 0 mg L-1 NO2-N. The N:P ratio was 1.73 mol N mol-1 P, so that P would not be a growth-limiting nutrient.

Plants were inserted into the culture solution at 22:00 October 20 and placed on the roof of a 3-story building at 0:00 October 21 to be exposed to natural weather conditions with little shade cover. Samples of 2-3 mL were taken at 8-hr intervals from 0:00 to 24:00 October 21. Weight was measured before and after each interval and before and after sampling so that nutrient uptake values could be adjusted by the amount of sample that was taken. Electroconductivity (EC), dissolved oxygen (DO), and pH were measured at the same time as sampling.

Transpiration was calculated by the weight change during each interval. Passive uptake was calculated as the product of mean concentration and weight change. Remaining uptake was considered active uptake. Water quality analysis was conducted with ion chromatography (TOA-DKK IA-200). Each sample was analyzed for NO3-N, NH4-N, NO2-N, and PO4-P. Values below 0.011 mg L-1 NO3-N, 0.039 mg L-1 NH4-N, 0.015 mg L-1 NO2-N, and 0.82 mg L-1 PO4-P are not detectable by the analyzer, and were recorded as 0.

Following the experiment, plants were dried for 2 hr at 105℃. Plants were divided into root, rhizome, stem, leaf, and panicle and weighed. Temperature and insolation data were obtained from the Nagoya observation station of the Japan Meteorological Agency.

## 3.2 Results and Discussions

Atmospheric temperature and insolation during the experiment are displayed in Fig. 3.1a. The corresponding temperature changes in culture solution are displayed in Fig. 3.1b. The recorded temperatures remain below the mean temperature for river water (27.4℃) for the observation period, because it is later in the season. The temperature of the culture solution increases during the day and declines at night. River water may follow a similar increase in temperature during the day.

Fig. 3.1 (a) Atmospheric temperature and insolation in Nagoya and (b) temperature of culture solution containing *P. japonica* on October 21.

Fig. 3.2 shows the passive and active uptake of NO3-N during the experiment. Proportion of passive uptake declines during the 24-hr period. Passive uptake for the whole day was only 1.5% of total uptake. Table 3.1 shows the nutrient concentrations at the beginning and end of the experiment. The final combined NO2-N and NH4-N concentration is only 6% of the total reduction in NO3-N concentration during the course of the experiment, so it is clear that NO3-N was not merely transformed to another N species. The 81.4% reduction in NO3-N was considerable greater than the 15.6% reduction in PO4-P uptake, so it can also be concluded that NO3-N uptake was not limited by P availability. Instead, acceleration in NO3-N uptake outpaced acceleration in PO4-P uptake.

Fig. 3.2 Passive and active uptake of NO3-N during 24-hr experiment on October 21.

Proportions are calculated on a mass basis.

The trends in DO and NO3-N uptake are linked in Fig. 3.4. Root respiration, as represented by DO consumption, was integrated from 0:00 for each of the shoot clusters and each interval. NO3-N uptake rate was normalized by NO3-N concentration and plotted against root respiration. The positive correlation of integrated respiration and concentration-normalized rate of active uptake demonstrates a respiration-mediated induction period. The stabilization of DO after 16:00 suggests that the induction period concluded in the 8:00-16:00 interval, which resulted in the high NO3-N uptake rates in the 16:00-24:00 interval.

Table 3.1 Original and final N and P concentrations of cultivation solution used in 24-hour experiment on October 21.

|  |  |  |
| --- | --- | --- |
|  | Concentration (mg L-1) | Molar concentration (mol L-1) |
| PO4-P | NH4-N | NO2-N | NO3-N | PO4-P | NH4-N | NO2-N | NO3-N |
| Original | 5.92 | 0.00 | 0.000 | 4.640 | 189 | 0 | 0 | 331 |
| Final | 4.99 | 0.07 | 0.162 | 0.861 | 158 | 5 | 12 | 61 |

# 4 Nutrient uptake model

## 4.1 Framework

Plants have been shown to regulate uptake based on demand. There is considerable support that amino acids down-regulate N uptake and carbohydrates up-regulate N uptake (Imsamde and Touraine, 1994). Both are translocated from the leaf to the roots by the phloem, indicating leaf-mediated demand regulation. Down-regulation resulting from satiety signals may be more common in most plants. However, in the current experiment a rapid and lengthy induction period and uptake beyond reasonable growth rate expectations indicate a nutrient deficiency. In other words, a starvation condition results in the absence of satiety signals, so upon exposure to NO3-N, plants uptake rapidly until satiety is signaled.

Because in the induction phase *Umax* changes rapidly, Michaelis-Menten kinetics are not sufficient in modeling demand-mediated uptake. Michaelis-Menten kinetics include neither time nor demand variables. Mankin and Finn (1994) proposed a demand model of nutrient uptake:

 (4.1)

where *Un* is nutrient uptake, *Dn* is nutrient demand, and *Xn* is luxury consumption or storage depletion. When plants draw on stores of nutrients (storage depletion), *Xn* is negative; and when plants store excess nutrients (luxury consumption), *Xn* is positive.

## 4.2 Nutrient uptake computation

A computation was performed to estimate potential growth at the investigated stands. All uptake was assumed to take place during flood, at the rate found in the experiment. The following equation was used:

PAGB  (4.2)

where PAGB is potential above-ground biomass (kg m-2); *y* is 1 when the root zone is saturated (water level at Iwadu>0.65 m) and 0 when the root zone is not saturated (water level≤0.65); *n* is N requirements for biomass production (8 g N kg-1 dry wt); *Bs* is mean biomass in stands on November 2 (1.95 kg m-2); *Be* is mean above-ground biomass in experiment (18.2 g dry wt); and *Ue* is mean rate of N uptake during experiment (151 g N kg-1 hr-1). The computation was conducted from January 1 to December 31, 2005 at 1 hr intervals. The results were compared to the mean biomass for all three observation locations.

The uptake rates obtained in the experiment only provide a rough estimation of uptake rates. The induction period only occurs on the first day of saturation, which indicates that uptake rates on days following induction may be greater. On the other hand, uptake may slow after plants down-regulate. These two tendencies may have balanced each other. Nonetheless, uptake rates for a longer period of time are not known. There also may be some uptake during dry periods. Because plants are still living and photosynthesizing, there must be at least enough water to sustain them, and some passive nutrient uptake associated with it. Additionally, there is the possibility that some nitrogen is lost to denitrification.

The existence of luxury uptake and storage depletion cycles implies that plants must have sufficient capacity to store nutrients. During nutrient deficiency, it is known that plants favor root growth more than during nutrient sufficiency (Sands and Smethurst, 1995). Over several years of starvation cycles, plants may develop roots sufficiently to provide for luxury uptake during saturation periods. Lipson *et al*. (1996) found luxury uptake and nutrient storage in large root structures in an alpine herb that may otherwise have been nutrient limited. Therefore, root and rhizome infrastructure sufficient to maintain growth during the season may have been developed in previous seasons in the *P. japonica* in this study. This would justify the constant root and rhizome biomass assumed in the computation.

# 5 Conclusion

Both a field study and a hydroponics experiment were conducted at stands of *Phragmites japonica* at a sand-bed river. The field study demonstrated periods of dehydrated and saturated conditions in the root zone. The experiment established rates of uptake, and suggested a starvation state in the plants. It is proposed that luxury consumption of N occurs during periods of soil saturation, and storage depletion occurs during dehydration periods. A water level that caused saturation of the root zone was estimated, and potential above-ground biomass was computed assuming that uptake occurs only during submersion of roots. A close fit of field data and computation results supports the concept of luxury consumption and storage depletion cycles.

The results suggest that water level in river controls N availability of *P. japonica* in floodplain of sand-bed river. Because *P. japonica* is a common pioneer reed in sand-bed river, its expansion or contraction can change the balance of vegetated and bare bar on river. In rivers, such as the study site, where flow regimes have been altered by the construction of dams and other human activities, management of discharge may significantly effect the N limitations of *P. japonica*. To develop complete models that predict growth of *P. japonica* in floodplain of sand-bed rivers, it is necessary to determine the rate of growth at different plant N concentrations.

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