J. Aquat. Plant Manage. 31: 94-98

Rhizome Longevity in Two Floating-leaved Aquatic Macrophytes, *Nymphaea tetragona* and *Brasenia schreberi*

HIDENOBU KUNII[1]

ABSTRACT

Long-term observations on the fate and functioning of the underground parts in two floating-leaved macrophytes, *Nymphaea tetragona* Georgi and *Brasenia schreberi* J. F. Gmel., under field and seminatural conditions were carried out. While the individual tuberous rhizomes in *N. tetragona* never branched nor proliferated and persisted for a long time (>5 yr) at the suitable safe-site, runners in *B. schreberi* performed short-distance dispersal and more than 60% of the current-year rhizomes died off within a year in the field and their life expectancies averaged *ca.* 1.5 yr. It was also assumed that *N. tetragona* maintained an equilibrium rhizome volume by annual turnover of 20 to 30% of its mass.

Key words: biomass turnover, growth, underground part, water lily, water shield.

INTRODUCTION

The underground parts of aquatic macrophytes cannot be ignored because they form a large part of the biomass (Westlake 1982). They play an important role for the maintenance of populations, and many investigations on the production and biomass of helophytes have been made (Good *et al.* 1978, Whigham and Simpson 1978, Brinson *et al.* 1981, Westlake 1982, Sjörs 1991). However, there is still a general lack of information concerning the longevity and production of underground parts in floating-leaved macrophytes, except for particular species such as *Nuphar luteum* (L.) Sibth. & Smith (Twilley *et al.* 1985) and *Nymphoides peltata* (Gmel.) O. Kuntze (Van der Velde *et al.* 1979, Brock *et al.* 1983).

Nymphaea tetragona Georgi and *Brasenia schreberi* J. F. Gmel. are both perennial floating-leaved aquatic macrophytes and often occur together in irrigation ponds in Japan (Shimoda 1985, Kunii 1991). While *N. tetragona* has a short, erect tuberous rhizome, *B. schreberi* bears prostrate stoloniferous rhizomes (or runners). When these two species coexist within a single water body, *N. tetragona* usually occurs in shallower water than *B. schreberi*. Kunii and Aramaki (1987, 1992) have documented the life span of floating leaves of these macrophytes. However, it is clear that in order to understand the functioning of the plants within natural communities or to estimate true production, it is necessary to examine the persistence and growth of underground parts as well as aboveground parts (*cf.* Fitter 1987). Thus, the objective of the present study was to clarify the dynamics of underground parts in these two nymphaeid aquatic macrophytes.

[1]Department of Biology, Faculty of Science, Shimane University, Matsue 690, Japan. Current address: Research Center for Coastal Lagoon Environments, Shimane University, Matsue 690, Japan.

MATERIALS AND METHODS

Field observations. Field observations were made in two adjacent irrigation ponds (Engi-ike and Ryuzo-ike), located in Matsue, Shimane Prefecture, Japan (Kunii and Tsubaki 1987). To monitor the annual growth and longevity of rhizomes in *B. schreberi*, short shoots and tips and nodes of rhizomes were tagged with bamboo stakes. The short shoot is a part of the rhizome where the length of the internode is quite small (refer Figures 2 and 3 in Van der Velde *et al.* 1979). Marking was first done in December 1986 and the first observations were made in November 1987. After judging whether the marked parts were dead or alive, the length of the newly produced rhizome was measured. All growth beyond the stake, within the year, was regarded as annual growth. The marking and observations continued until November 1990 and 1991, respectively.

The individual rhizomes in *N. tetragona* were marked only once, in 1986, and their subsequent survival was determined by leaf development. Since the short rhizomes in *N. tetragona* were firmly rooted deep in the sediment, it was difficult under field conditions to excavate and examine their growth repeatedly without damaging them. Therefore, no effort was made to evaluate their annual growth.

Observations under seminatural conditions. To estimate the annual growth and/or loss of rhizomes in *N. tetragona*, many seeds were collected from Pond Ryuzo-ike during October 1986. In April 1987, 96 seedlings were planted outdoors in a tall cylindrical pot (70 cm in height). After a year, the 33 surviving plants were transplanted in two containers (60 cm in width by 40 cm in length by 30 cm in height in 10 cm of sediment taken from Pond Engi-ike) and then placed into an outdoor concrete pond (1.5 m deep). All plants were freely grown during the growth period and excavated annually during the resting period (late December to early March). Rhizome length from the lowest part to the upper part where buds sprouted and diameter (thickness) at the uppermost position where the roots developed were measured using a micrometer.

The growth and/or loss of rhizomes in *B. schreberi* was also monitored under the same seminatural conditions as described above. Thirty shoot apices (winter buds) were taken from Pond Engi-ike in 1987, marked individually, and planted in two containers (the same as described above). All rhizomes were uprooted during the resting period and current-year elongation of runners was measured. The newly produced runners were marked by loosely coiling flexible, thin wires around them and then buried again.

These observations under seminatural conditions are still ongoing.

RESULTS AND DISCUSSION

More than 60% of the current-year rhizomes of *B. schreberi* died off within 1 yr (Figure 1). No short shoots or nodes lived longer than 3 yr. Life expectancy of rhizomes (including apex, short shoot and node) averaged *ca.* 1.5 yr. Similar results were obtained from the plants grown under seminatural conditions (Figure 2): 49.2% and 46.3%, respectively, of the new runners produced in 1988 and 1989 survived until the end of the next growing seasons. No 2-yr old runners were found.

Figure 2 also shows that most of the runners in *B. schreberi* are the current ones, younger than a year, and only 29.6% and 29.0% are those of the previous years, 1989 and 1990, respectively. Thus mean runner age can be estimated as 1.3 yr both in 1989 and in 1990. The total length increased gradually through 1989 (21.6 m/m^2) and 1990 (24.3 m/m^2). These values compare with the maximum value in total length obtained from the natural habitat (18.5 m/m^2, unpublished data). However, the total suddenly dropped to the minimum value (4.6 m/m^2) in 1991. This phenomenon may reflect the detrimental effect of the continuous culture within a restricted place.

It is probable that the plants with smaller rhizomes in *N. tetragona* cultivated under seminatural conditions died earlier than those with larger ones (Figure 3). The plants seemed to have established stable states 4 to 5 yr after germination when the rhizomes became thick. In addition, field observation on

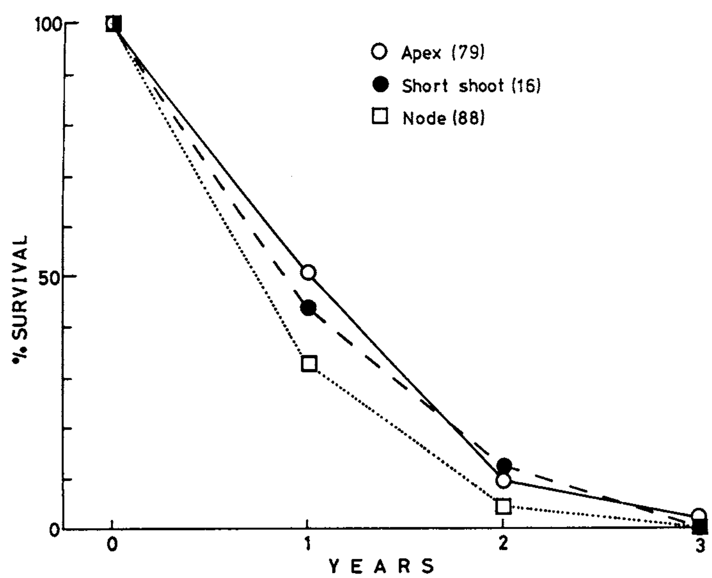

Figure 1. Time trend in percent survival of each organ of *B. schreberi* in the irrigation ponds. Results are shown as percent of the total marked in 1987 and 1988. Marked and observed numbers are shown in parentheses.

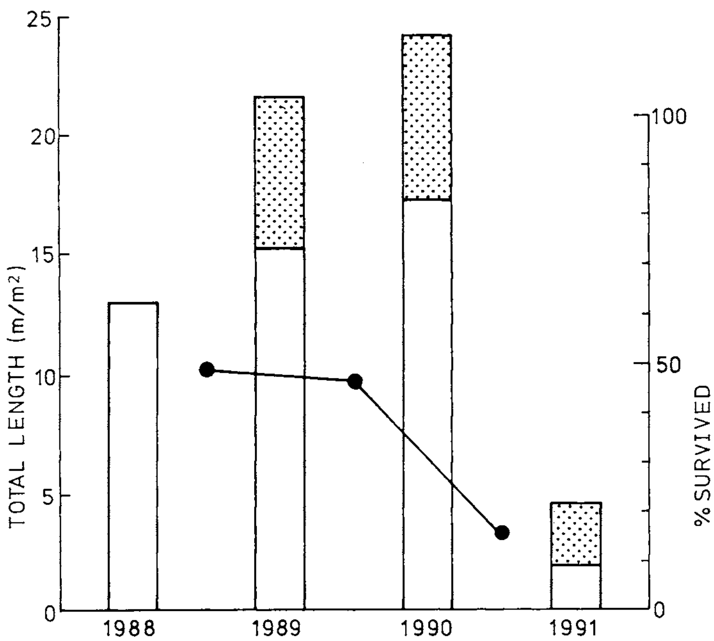

Figure 2. Temporal changes in total length of rhizomes of *B. schreberi* grown under seminatural conditions. Open and hatched columns indicate current year and previous year rhizomes, respectively. Percentage survival (in terms of length) of previous year rhizomes is shown as solid circles connected by solid lines. The results are shown as a total of two pots.

the survival of *N. tetragona* rhizomes showed that the rhizomes marked in 1986 were all still alive in 1991. These facts suggest that the rhizomes persist for a long time once they become larger than some critical size (*cf.* Heslop-Harrison 1955).

Annual growth of *N. tetragona* rhizome is shown in Figure 4. Because the rhizome shape is considered to be cylindrical, rhizome volume can be computed from length and diameter. The rhizomes attained their peak mean size in 1990 (26.2 ± 5.9 mm in length and 17.8 ± 3.5 mm in diameter) and then slightly decreased. It must be noted here that a recognizable necromass was found in 1991. The basal part of the rhizome was blackish and often without roots. The mean rhizome length in 1991 was 30.6 ± 8.3 mm and 23.4 ± 5.6 mm with and without necromass, respectively. Although there was a significant difference in diameter (F-test, $0.01 < P < 0.05$), no significant differences were found in both length and volume between the rhizomes in 1991 (without necromass) and those from Pond Ryuzo-ike. These facts imply that there is an equilibrium rhizome volume and the thickened rhizome maintains this volume by annual turnover of 20% to 30% of its mass. Further study is needed to confirm this estimation.

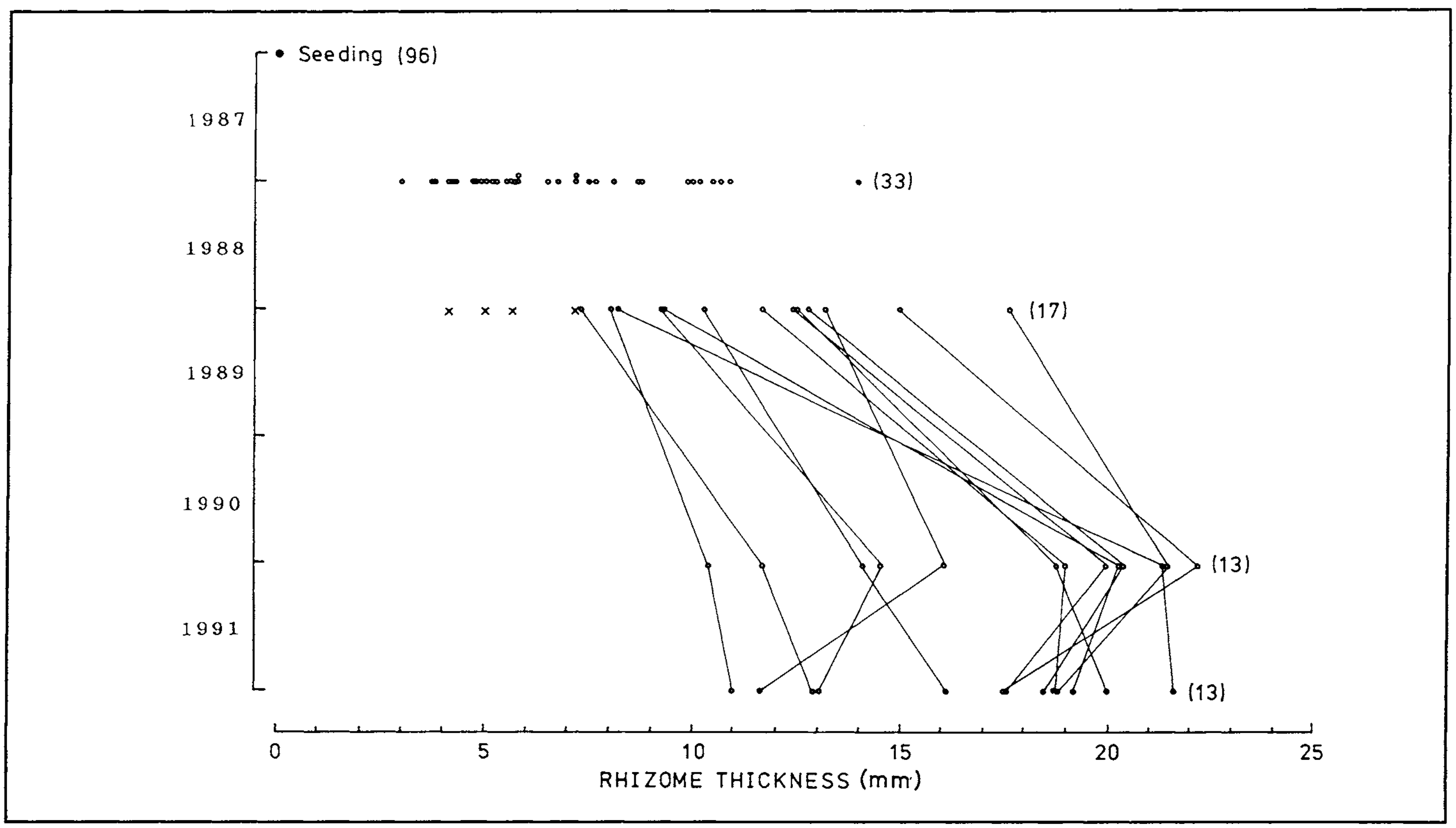

Figure 3. Temporal changes in rhizome thickness (diameter) of *N. tetragona* grown under seminatural conditions. Each rhizome was marked individually since December 1988. Figures in parentheses show number of surviving plants at each observation date.

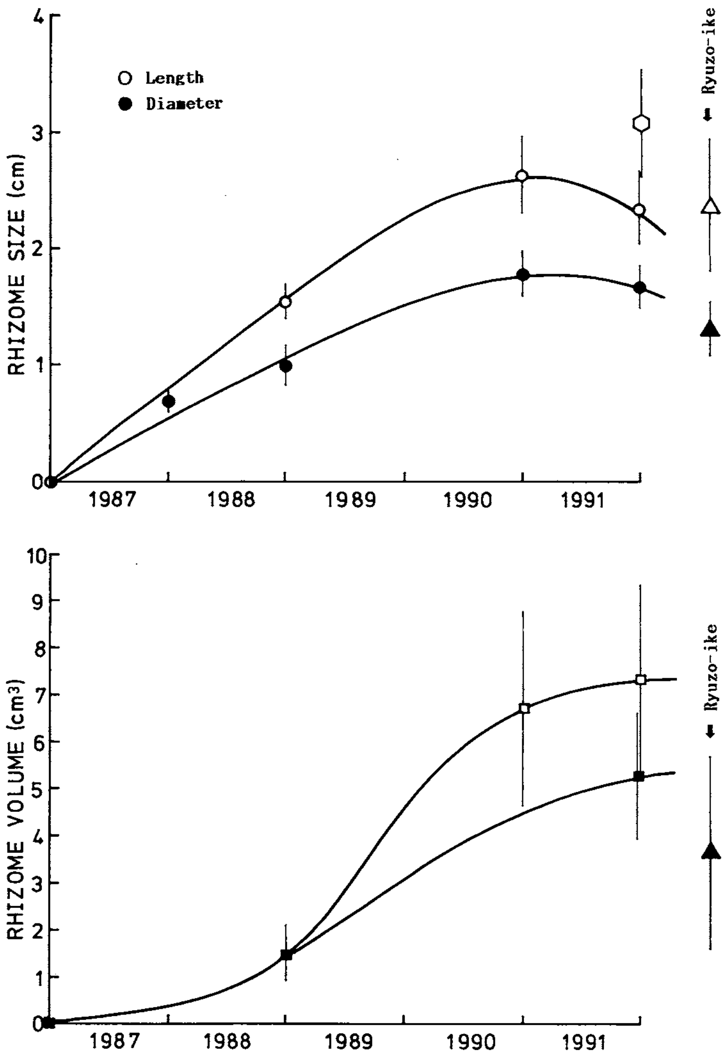

Figure 4. *Top*: Temporal changes in mean rhizome length (open circles) and diameter (solid circles) of *N. tetragona* grown under seminatural conditions. Open hexagon denotes mean rhizome length including decaying necromass and open and solid triangles show, respectively, length and diameter of rhizomes sampled from Pond Ryuzo-ike in 1985 (n = 7). *Bottom*: Temporal changes in mean rhizome volume with (open squares) and without (solid squares) necromass. Solid triangle shows mean volume of rhizomes sampled from Pond Ryuzo-ike. Vertical bars indicate 95% confidence intervals.

In general, rhizomes function as reproductive organs as well as storage organs. Short and erect tuberous rhizomes of *N. tetragona*, however, never branch nor proliferate, and only function as storage organs. They are buried at a relatively deeper site (3 to 5 cm below the sediment surface) and thus are protected from drought which often occurs in the shallow littoral zone. The plants, therefore, are enabled to persist for a long time at suitable sites and produce many seeds annually. Dispersion of this species thus depends entirely on seed. In contrast, rhizomes of *B. schreberi* act mainly as reproductive organs. The prostrate rhizomes or runners elongate just beneath/above the sediment and are suited for short-dispersal. Their longevity is quite short but they can seek the safe-sites successfully during the growing period. Shoot apices of this plant are also effective vegetative organs but somewhat less reliable than rhizomes (Adams 1969). Hard seeds seem to contribute little to the dispersal within a pond but they may allow between-pond long-distance dispersal or long periods of dormancy (Madsen 1991). The functioning of these species within natural communities will be discussed fully, coupled with information concerning the dynamics of aboveground parts in Kunii and Aramaki (1987, 1992).

ACKNOWLEDGMENTS

The author wishes to thank Tatsuhiko Shimada, Hiroshi Katsube and Kazuhiko Sakata for their assistance in the field. This research was financially supported in part by the Ministry of Education, Science and Culture, Japan (No. 63740361).

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