

Growth and Biomass Turnover of *Hydrocharis dubia* L. Cultured under Different Nutrient Conditions

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Abstract

Growth of a floating-leaved plant, *Hydrocharis dubia* L., was examined under varying nutrient conditions between 0.3 and 30 mgN l⁻¹ total inorganic nitrogen. *H. dubia* plants cultured under the most nutrient-rich condition showed the highest maximum ramet density (736 m⁻²), the highest maximum biomass (80.4 g dry weight m⁻²), and the highest total net production (185 g dry weight m⁻² in 82 days). Plants under nutrient-poor conditions had a relatively large proportion of root biomass and a small proportion of leaves with a long life span.

Compared with other floating-leaved and terrestrial plants, the maximum biomass of *H. dubia* was relatively small. This, and the rapid biomass turnover, was related to the short life span of leaves (13.2–18.7 days) and large biomass distribution to leaves.

Key words: Aquatic macrophyte; Biomass turnover; *Hydrocharis dubia*; Leaf life span; Nutrients.

Introduction

In eutrophic waters, aquatic plants grow vigorously and may play a significant role in removing nutrients from polluted water (Boyd, 1970). The effect of nutrient levels on the growth of aquatic plants has been well evaluated for free-floating plants (Sato and Kondo, 1981; Cary and Weerts, 1983; Reddy and Tucker, 1985) and emergent plants (Reddy and Porter, 1987; Wathugala et al., 1987), but little is known about floating-leaved plants. Most previous experiments on aquatic plants were only designed to evaluate plant ability for nutrient removal by measuring biomass yield and nutrient concentrations in plant tissues. There is also little information on the biological adaptation of aquatic plants to nutrient conditions, except for change in biomass distribution in response to nutrient levels (Gaudet, 1973; Cary and Weerts, 1983; Reddy and Porter, 1987).

Floating-leaved plants are characterized by a short leaf life span, which results in an extremely high rate of biomass turnover (Brock et al., 1983; Tsuchiya and Iwaki, 1983). Nutrient availability has been reported to affect the leaf life span of terrestrial plants (Shaver, 1981; Chabot and Hicks, 1982), but few data are available for aquatic plants. In the present study, therefore, the effects of nutrient availability on the growth characteristics of a floating-leaved plant, *Hydrocharis dubia* L., were evaluated under experimental conditions with special reference to leaf life span and biomass turnover.

Material and Methods

Plant material

H. dubia is a floating-leaved plant occurring widely in still waters in southern and eastern Asia (Cook and Luond, 1982). Stems of *H. dubia* are either contracted, bearing rosette leaves, or elongate-stoloniferous and leafless. The leaves, spirally arranged in a dense rosette, either float or occasionally emerge above the water surface. Adventitious roots with large and abundant root hairs are borne on leafy stems. The plant is usually rooted in the bottom sediment but occasionally hangs free in the water, i.e., free-floating. This species propagates vegetatively by elongation of stolons to form new rosette ramets, and overwinters in the form of hibernacula (known as winter buds or turions). Seeds are also formed, but little is known about sexual reproduction and establishment of seedlings. *H. dubia* may spread primarily by means of rapid clonal growth over the water surface, similar to most free-floating plants.

Culture of *H. dubia*

Ramets of *H. dubia* and sediment were collected in June 1982 from Tsuchiura-iri Bay in Lake Kasumigaura, 60 km northeast of Tokyo. The collected plants were precultured in a 100-l polyethylene stock tank with bottom sediment in the open on the campus of Tokyo Metropolitan University, Tokyo. Ten plants (7.43 g dry weight per ramet on average) were transplanted to each of thirty polyethylene planter pots (30 × 45 × 20 cm) on 26 July. The experiment was continued until all the plants had shed their leaves.

Each of the planter pots with no bottom sediment was filled with 20 l of Sato and Kondo (1981) culture solution (Table 1). Three levels of nutrient concentration were prepared. The nutrient levels were one (NL-1), ten (NL-10) and one hundred fold (NL-100) of the standard concentration. The most nutrient-rich solution (NL-100) contained about 30 mg l⁻¹ total inorganic nitrogen (TIN, including NO₂⁻, NO₃⁻ and NH₄-N) and 8 mg l⁻¹ PO₄-P. The solution was renewed every ten days. Nutrient concentrations in the solution before and after renewal were measured by the method of Strickland and Parsons (1968). Dissolved inorganic nitrogen and PO₄-P concentrations in NL-1 and -10 decreased by one order of magnitude over each ten-day period. There was little change in nutrient concentration in NL-100 throughout the experiment. Algal consumption of nutrients in the solution was assumed to be negligible.

The daily maximum water temperature ranged from 17 to 36°C during the experiment, and remained over 30°C in August.

Table 1. Mineral nutrient composition of the standard culture solution of Sato and Kondo (1981).

Chemicals (µg l ⁻¹)		Elements (µg l ⁻¹)	
NH ₄ H ₂ PO ₄	288	NH ₄ -N	35
KNO ₃	758	NO ₃ -N	245
MgSO ₄	1894	P	77
CaCl ₂ ·7H ₂ O	735	K	293
NaNO ₃	850	Mg	182
EDTA-Fe	180	Ca	200
H ₃ BO ₃	12	Fe	25
MnCl ₂ ·4H ₂ O	7	B	2
		Mn	2
		Na	230

Estimation of biomass, leaf life span and net production

Every twenty days from 26 July to 17 October, plants in one or two pots were harvested for each treatment. The plants were divided into component parts (lamina, petiole, stem, bud, root and turion). After measurement of leaf size (lamina length, petiole length and lamina area), they were dried at 70°C for two days to obtain the dry weights.

Leaves in three non-destructable pots for each treatment were marked with colored and numbered vinyl rings tied loosely around the petioles and the lengths of the laminae were measured at ten-day intervals. Since so many leaves were produced under the most nutrient-rich condition, each leaf census in NL-100 after late August was done for a single pot. The life span of a leaf was determined based on the dates of its appearance and death, the latter being the date when more than one-half of the lamina was lost.

Leaf biomass loss was estimated as the product of the mean leaf dry weight, measured on the nearest sampling date, and the number of leaves lost. Recovery of nutrients from senescent leaves was assumed to be negligible. Net production during a ten-day period was calculated as the sum of biomass increment and leaf loss, assuming that losses of other parts were negligible.

Results

Seasonal changes in ramet number, biomass and LAI

The growth in ramet number was exponential in the early growth stage (before mid-August) and then slowed down in all treatments (Fig. 1). The peak ramet density became higher with increasing nutrient level. In NL-100, ramets were continuously produced until September. The number of live ramets remained constant for a month after its peak in spite of the increase in dead ramets. In contrast, in NL-1 and NL-10, no new ramets were produced after attainment of the peak living ramet number.

The relationship between ramet dry weight and the sum of the square of leaf length was analysed by linear regression after logarithmic conversion. Figure 2 gives the relationship

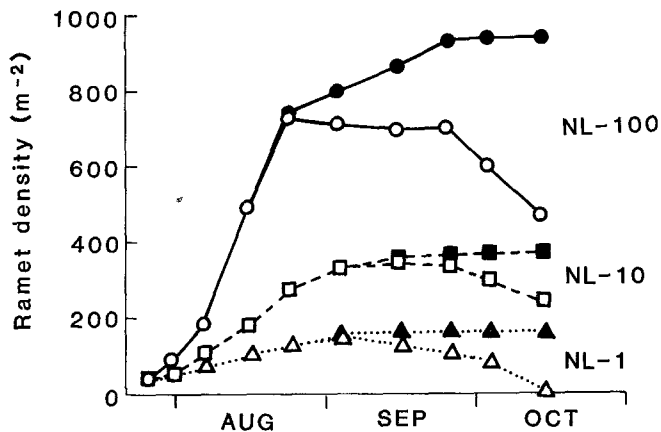


Fig. 1. Seasonal change in living ramet number (clear symbols) and the accumulated total ramet number (solid symbols) of *Hydrocharis dubia* cultured under different nutrient conditions: nutrient levels of NL-1 (Δ), NL-10 (\square) and NL-100 (\circ) correspond to about 0.3, 3 and 30 mgN l⁻¹ as total inorganic nitrogen, respectively.

obtained at harvest of the NL-100 pot on 16 August. Regression was performed for every treatment and harvest date (at twenty-day intervals). These regression equations were used for estimating ramet biomass from the length of leaves in unharvested pots.

Seasonal changes in biomass are shown in Fig. 3. The mean relative growth rates in terms of dry weight during the exponential growth stage in NL-1, NL-10 and NL-100 were 0.7, 4.9 and 9.1 % day⁻¹, respectively. Seasonal maximum biomasses in late August for NL-1, NL-10 and NL-100 were 20.3, 67.3 and 80.4 g dry weight m⁻², respectively.

More than 50% of the biomass was distributed to the leaf (lamina plus petiole) for all treatments during the period before marked turion formation (Fig. 4). In late August, when the peak biomass was observed, the proportion of root biomass was largest in NL-1 and smallest in NL-100, while that of leaf biomass was largest in NL-100 and smallest in NL-1.

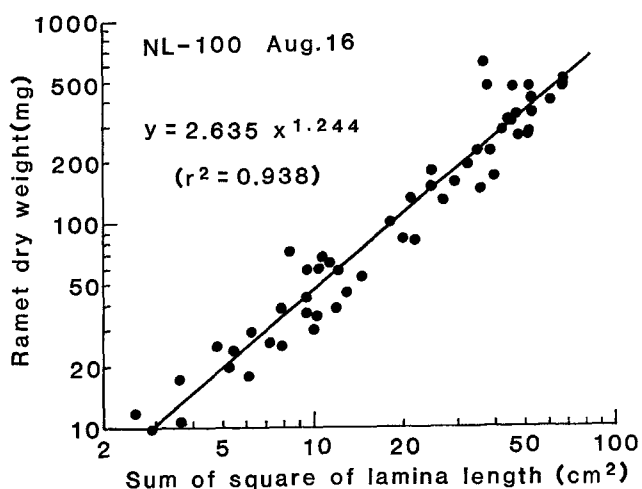


Fig. 2. An example of the relationship between sum of the square of lamina length and ramet dry weight of *Hydrocharis dubia*. The data obtained on 16 August in NL-100 are shown.

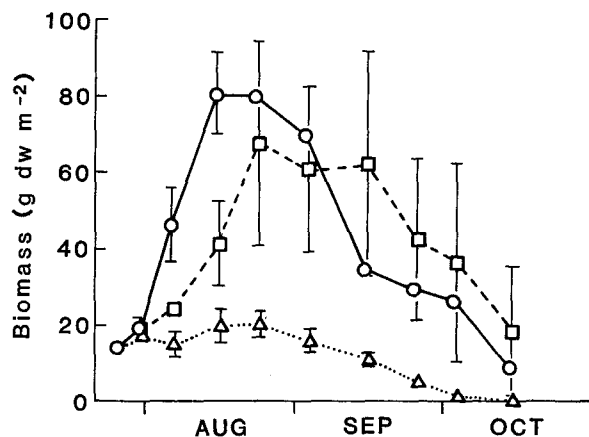


Fig. 3. Seasonal change in biomass of *Hydrocharis dubia* cultured under different nutrient conditions: NL-1 (Δ), NL-10 (\square) and NL-100 (\circ). Vertical bars represent standard deviations ($n = 3$). Values for NL-100 after late August are based on measurement for a single pot.

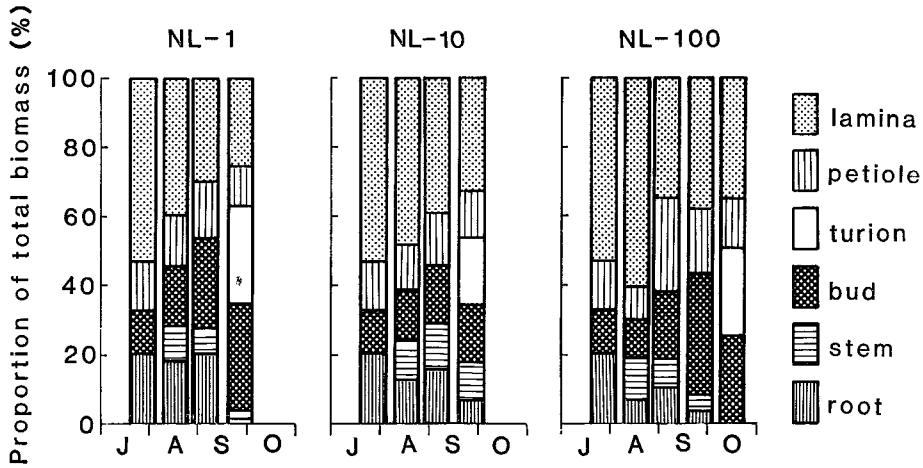


Fig. 4. Seasonal change in percentage of total biomass distributed to various component parts (lamina, petiole, turion, bud, stem and root) for *Hydrocharis dubia* cultured under different nutrient conditions.

The proportion of leaf biomass decreased with time in NL-1 and NL-10, but did not decrease in NL-100 since a great number of small ramets with a larger proportion of leaf biomass were produced from July to August.

Since the relationship between lamina length (l , mm) and leaf area (S , mm²) of *H. dubia* was expressed by a single regression equation, $S = 0.0143 l^{2.02}$ ($r^2 = 0.917$, $n = 870$), the leaf area of unharvested plants was calculated from this equation based on data for lamina length. Seasonal trends of LAI thus calculated were similar to those of biomass (Fig. 5). Growth in leaf area was highest in NL-100, with a maximum LAI of 2.1 m² m⁻².

Turion formation was marked after late September (Fig. 4). The frequency distribution of turion dry weight is shown in Fig. 6. Plants in NL-10 produced the largest number of turions with the largest mean dry weight (41.2 mg). Although plants in NL-100 had the

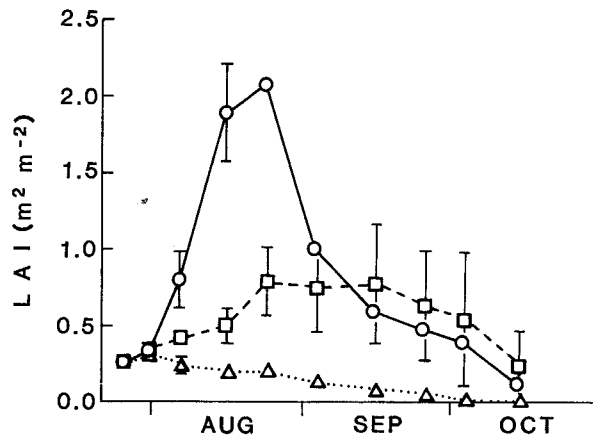


Fig. 5. Seasonal change in leaf area index (LAI) of *Hydrocharis dubia* cultured under different nutrient conditions: NL-1 (Δ), NL-10 (\square) and NL-100 (\circ). Vertical bars represent standard deviations ($n = 3$). Values for NL-100 after late August are based on measurement for a single pot.

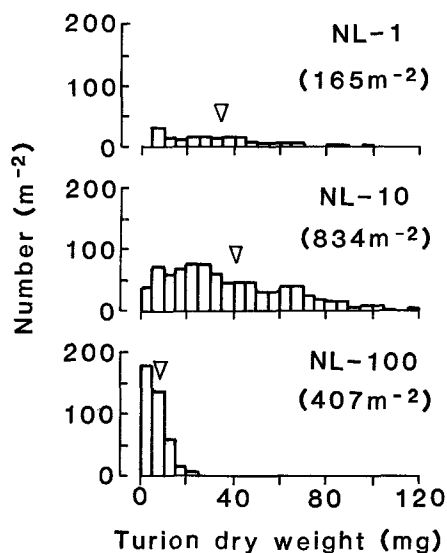


Fig. 6. Frequency distribution of turion dry weight of *Hydrocharis dubia* cultured under different nutrient conditions. NL-1 (upper), NL-10 (middle) and NL-100 (bottom). Turions that had sunk to the bottom of pots were collected in November when all vegetative parts had disappeared. Values in parentheses indicate total turion number. Triangles indicate the mean dry weight of a turion.

largest maximum biomass, the mean dry weight of their turions was the smallest (8.6 mg). Thus, turion biomass was largest in NL-10 (34.4 g dry weight m^{-2}) and smallest in NL-100 (3.5 g dry weight m^{-2}).

Leaf life span and net production

A ramet usually had 1–3 living leaves and produced 1–2 new leaves in ten days. Leaf life span did not show any marked seasonal change, but was affected by nutrient condition (Fig. 7). The mean life span of leaves in NL-100 (13.2 ± 4.7 days) was much shorter than that of leaves in NL-1 (18.2 ± 6.4 days) or NL-10 (18.7 ± 6.3 days). The leaf lamina began to etiolate 2–4 days before its death, but the petiole still persisted for a further 7–9 days.

Figure 8 shows seasonal changes in biomass and accumulated losses of lamina and petiole. Due to the short life span of leaves, accumulated losses in NL-1, NL-10 and NL-100 during the period up to late August reached 80%, 56% and 110% of the maximum biomass, respectively. Net production for each ten-day period was calculated as the sum of biomass increment and losses of lamina and petiole during the period. The maximum rates of net production occurred in mid-August, being 1.1, 3.1 and 6.5 g dry weight $m^{-2} day^{-1}$ for NL-1, NL-10 and NL-100, respectively. Leaves of total net production during the experimental period (82 days) were 40, 130 and 185 g dry weight m^{-2} for NL-1, NL-10 and NL-100, respectively.

Turnover of biomass can be expressed as the ratio of total net production to seasonal maximum biomass (P/B_{max} ratio). The P/B_{max} ratio of *H. dubia* was as high as 2.0, 1.9 and 2.3 for NL-1, NL-10 and NL-100, respectively (Table 2). Compared with the maximum biomass and net production, the biomass turnover was little affected by nutrient level.

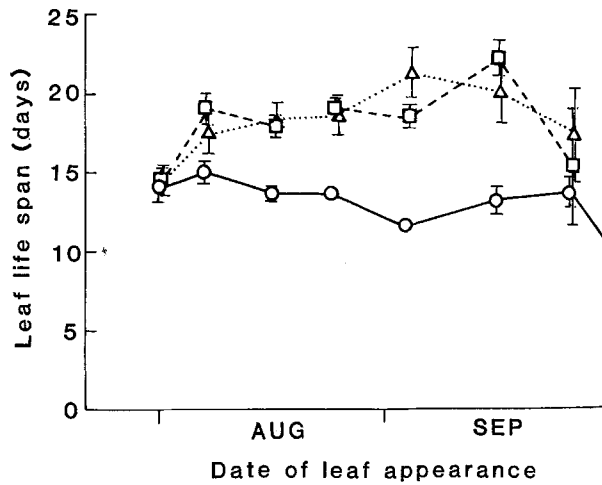


Fig. 7. Seasonal change in leaf life span of *Hydrocharis dubia* cultured under different nutrient conditions: NL-1 (Δ), NL-10 (\square) and NL-100 (\circ).

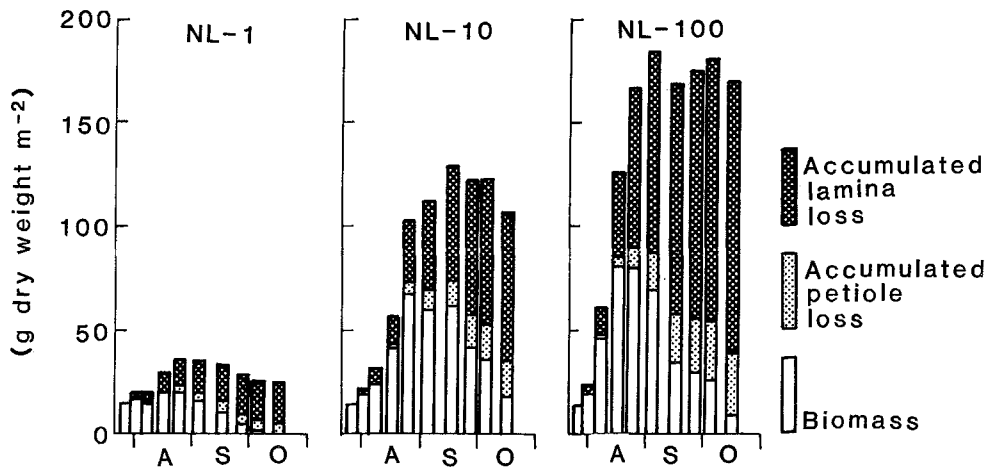


Fig. 8. Seasonal changes in biomass and accumulated losses of petiole and lamina of *Hydrocharis dubia* cultured under different nutrient conditions.

Table 2. Maximum biomass, accumulated net production and P/B_{max} ratio of *Hydrocharis dubia* cultured under different nutrient conditions.

Treatment	Initial TIN ¹ (mgN l ⁻¹)	Maximum biomass \pm SD ($n = 3$) (g dw m ⁻²)	Total net production ² (g dw m ⁻²)	P/B_{max} ratio ³
NL-1	0.3	20.3 \pm 3.1	40	2.0
NL-10	3	67.3 \pm 24.6	130	1.9
NL-100	30	80.4 \pm 9.4	185	2.3

¹Total inorganic nitrogen concentration in the culture solution.

²Total net production during the experimental period of 82 days.

³Estimated from net production divided by maximum biomass.

Discussion

Among the growth characteristics of *H. dubia* shown in the present study, a large biomass distribution to leaves and a short leaf life span were most remarkable.

H. dubia, a floating-leaved plant, needs only a few mechanically supporting parts. More than 50% of the biomass was distributed to leaves in the early growth stage (Fig. 4). Allocation of a larger proportion of resources to photosynthetic parts has a favorable effect on matter production and growth. The relationship between leafiness (i.e. a large leaf area ratio) and a high relative growth rate in terrestrial plants has been discussed using growth-analysis techniques by Watson (1952). Initial relative growth rates of *H. dubia* in NL-10 (4.9% day⁻¹) and NL-100 (9.1% day⁻¹) were as high as those of water hyacinth which grows extensively in tropical and subtropical waterways (Bock, 1969; Wooten and Dodd, 1976; Wolverton and McDonald, 1979; Oki, 1982; Reddy and DeBusk, 1984, 1985; Sale et al., 1985.)

In spite of the high initial relative growth rates, *H. dubia* sustains a remarkably smaller biomass (130 g dry weight m⁻² at maximum; Sastroutomo, 1982; Tsuchiya, 1986) than other floating-leaved and emergent plants (Whigham et al., 1978; Tsuchiya, 1986). Leaf life span in *H. dubia* ranged from 13 (NL-100) to 19 days (NL-1) in the present study and was 18.7 days for plants growing in a eutrophic lake, Lake Suwa (Tsuchiya, 1986). These values are smaller than those reported for other floating-leaved plants (Brock et al., 1983; Tsuchiya and Iwaki, 1983; Twilley et al., 1985; Kunii and Aramaki, 1987; Tsuchiya, 1988) and considerably smaller than those for other aquatic (Whigham et al., 1978; Westlake, 1982) and terrestrial plants (Jurik and Chabot, 1986).

Continuous leaf birth and loss contribute greatly to high biomass turnover. The P/B_{\max} ratio of *H. dubia* (about 2) is as high as those of other floating-leaved plants (Brock et al., 1983; Tsuchiya and Iwaki, 1983) and higher than those of most other aquatic plants (Westlake, 1982).

Nutrient level affects the growth of *H. dubia* in various ways. First, nutrient application increased the growth in both ramet number (Fig. 1) and biomass (Fig. 3). Vegetative growth was the most rapid in NL-100, of which the nitrogen level was about 30 mg N l⁻¹, or near the optimum level for other aquatic plants such as *Eichhornia crassipes* (Mart.) Solms. (Sato and Kondo, 1981; Oki, 1982), *Salvinia molesta* Mitchell (Cary and Weerts, 1983) and *Hydrocotyl umbellata* L. (Reddy and Tucker, 1985). However, the nutrient level in NL-100 was much higher than those observed in Lake Kasumigaura; the nitrogen levels of the open water and interstitial water in the sediment are similar to those in NL-1 and NL-10, respectively (Hosomi and Sudo, 1984; Aizaki et al., 1987). In Lake Kasumigaura, therefore, nutrients may limit the growth of *H. dubia*.

Second, nutrient level affects biomass distribution (Fig. 4). *H. dubia* plants growing under nutrient-poor conditions had a relatively large proportion of root biomass. This response to low nutrient conditions is advantageous for increasing nutrient acquisition. Such a change of biomass distribution is commonly observed in terrestrial plants (e.g. Fitter, 1986) and also in submerged (Best and Mantai, 1978) and emergent plants (Cary and Weerts, 1984; Reddy and Porter, 1987).

Third, nutrient level also affects leaf life span. Leaf life span in NL-1 and NL-10 was much longer than that in NL-100 (Fig. 7). Resources can be used efficiently by increasing leaf life span or by minimizing leaf turnover. The ecological significance of an increase in leaf life

span in nutrient-poor conditions has also been discussed for arctic evergreen plants in relation to evergreenness and resource storage (Shaver, 1981). Leaves of *H. dubia* seem to be of little importance for nutrient storage, since nutrients are easily available from the surrounding milieu and leaf senescence is extremely rapid in comparison with arctic evergreen plants. However, it is possible that leaves of lower productivity under nutrient-poorer conditions should persist longer in order to pay for the cost of their construction (Chabot and Hicks, 1982).

Finally, nutrient condition also affects reproduction. The optimum nutrient level for turion formation was lower than that for vegetative growth (Fig. 6). A smaller turion, such as that observed in NL-100, is considered to be less capable of establishment in spring (Scribailo and Posluszny, 1985). Further study on the nutrient dependence of seedling establishment and the success of propagation will be necessary.

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