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Biomass and nutrient allocation of Tipularia discolor (Orchidaceae)

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Tipularia discolor (Orchidaceae) plants were sampled in a deciduous forest in Maryland to determine how biomass and nutrients were allocated to different plant structures during an annual cycle. Corms older than 1 year lose weight gradually during the year and most vegetative growth goes into current year corms. Leaves and sexual reproductive structures account, at peak biomass, for approximately 20% of the total plant biomass. The largest percentages of macronutrients (N, P, Mg, Ca, K) and micronutrients (Fe, Al, B, Sr, Mn, Zn, Cu, Pb) were found in corms 2 yr and older, and nutrient concentrations were also high in newly formed leaves and inflorescences. Analysis of the biomass and nutrient data suggest that translocation is important, but that it does not account for all of the uptake in new growth. Plants must, therefore, assimilate nutrients from the soil during periods of growth. The importance of large underground storage structures is discussed.

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Растения *Tipularia discolor* (Orchidaceae) собраны в листопадном лесу в Мэриленде для определения характера распределения биомассы и элементов питания в разных растительных структурах в течение годового цикла. Клубни старше одного года постепенно теряют вес, вегетативный рост преимущественно наблюдается в клубнях данного года. Листья и генеративные структуры при максимальной биомассе содержат примерно 20% от общей биомассы растений. Наибольший процент макроэлементов (N, P, Mg, Ca, K) и микроэлементов (Fe, Al, B, Sr, Mn, Zn, Cu, Pb) установлен в клубнях двухлетнего возраста и старше, концентрация элементов питания также высока в молодых листьях и соцветиях. Анализ данных по биомассе и элементам питани показал, что транслокация имеет важное значение, но она идет не за счет преимущественного вклада в молодые ткани. Растения могут таким образом, ассимилировать элементы питания из почвы в периоды роста. Обсуждается значение крупных подземных запасающих структур.

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1. Introduction

Patterns of biomass and nutrient allocation, although difficult to follow (Harper 1977), have been shown to vary both within and between species (Grime 1979, Abrahamson 1979, Muller 1979, Van Andel and Jager 1981, Gross and Soule 1981, Abrahamson and Caswell 1982, Soule and Werner 1981). Within limits, species of ephemeral habitats are able to vary patterns of resource (biomass) allocation in response to changing environmental conditions (Harper and Ogden 1970, Kawano and Hayashi 1977, Harper 1977, Lovett Doust 1980, Parrish and Bazzaz 1982), but biomass allocation patterns are not as elastic in species of more stable environments (Whigham 1974), even though some of the latter occupy microsuccessional sites within generally stable environments (Pitelka et al. 1980, Van Andel and Jager 1981). Biomass allocation has been studied in a number of herbaceous woodland perennials (Anderson and Loucks 1973, Whigham 1974, Van Andel and Vera 1977, Abrahamson 1979, Muller 1979, Van Andel and Jager 1981) and Kawano (1970, 1975, 1981, Kawano et al. 1976, 1982) has identified at least 16 distinct patterns of biomass allocation in Japanese woodland herbs. Kawano's work has clearly demonstrated the complexity of forest herb communities. A unifying conceptualization of the adaptive structure of woodland herb communities has been developed based on the identification of morphological and physiological guilds (Givnish 1982).

There have, however, been few studies of nutrient allocation in woodland perennial herbs despite the existence of a conceptual framework to describe allocation patterns (Kawano 1970, 1981, Sohn and Policansky 1977). The vernal dam hypothesis has also been proposed to described how woodland herbs may play an important role in the nutrient dynamics of forest ecosystems by retaining nutrients for a time (e.g. spring thaw) when they might otherwise be leached because woody plants are still dormant (Bormann and Likens 1979, Muller 1979, Blank et al. 1980, Yarie 1980).

It is difficult to assess patterns of nutrient allocation in perennial woodland herbs because most have comparatively large underground storage organs that are both difficult to age and, especially for rhizomatous species, difficult to assess patterns of translocation (Ashmun et al. 1982, Pitelka and Ashmun unpubl.). There are, however, several species of woodland herbs with morphological characteristics that seem suitable for studies of patterns of nutrient and biomass allocation (Muller 1979, Kawano et al. 1982). *Tipularia discolor* (Orchidaceae) is an example of this group because it generally produces 1 corm per year and the year-class corms remain separate except for a small piece of connecting tissue (Fig. 1). Corms persist for several years so it is possible to make comparisons between corms that differ in age. *Tipularia* also has distinct reproductive and vegetative phenophases (Whigham and McWethy 1980). Flowering occurs between late July and mid-August when the plants are leafless. Leaves develop in September and senesce by late June of the next year. In addition, only 1 yr old corms produce leaves and inflorescences, and plants only rarely produce more than 1 inflorescence and 1 leaf per year. The phenological separation of leaf development and senescence from inflorescence development and maturation enables one to separate the influences of development and senescence of vegetative and reproductive parts on nutrient allocation patterns.

The primary purpose of this study was to determine and compare patterns of micronutrient, macronutrient, and biomass allocation in *Tipularia.* A second objective was to estimate whether the incorporation of nutrients into new growth was equal to, less than, or greater than the losses of nutrient from senescing and/or storage (e.g. corms) structures. In particular, nutrient gains and losses were compared for leaf development, leaf senescence, and inflorescence development phenophases. Finally, because there are few data on the storage and allocation of nutrients in woodland herbs (Newell 1982), all macronutrients, except sulfur, and a variety of essential micronutrients and nonessential trace elements were included in the study.

2. Materials and methods

Tipularia discolor is widespread throughout the North American deciduous forest biome (Braun 1950), where it and *Aplectrum hyemale* are the only orchids that produce leaves in the late summer (August and September) and are leafless during most of the summer (late May – late August) when sexual reproduction occurs (Whigham and McWethy 1980).

2.1. The study site

The study was conducted at the Smithsonian Institution's Chesapeake Bay Center for Environmental Studies (CBCES) near Annapolis, Maryland (Whigham and McWethy 1980). All plants were collected in a hardwood forest that is dominated by oaks (*Quercus alba, Q. falcata, Q. veluntina*), hickories (*Carya glabra, C. tomentosa*), tulip poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*). The forest has a well developed understory dominated by dogwood (*Cornus florida*), ironwood (*Carpinus caroliniana*), black haw (*Viburnum dentatum*), and spicebush (*Lindera benzoin*). Populations of *Tipularia* are distributed throughout the forest.

2.2. Methods

One hundred and twenty two *Tipularia* plants were collected on 9 dates between August 1977 and August 1978. Each plant was extracted from the soil, returned

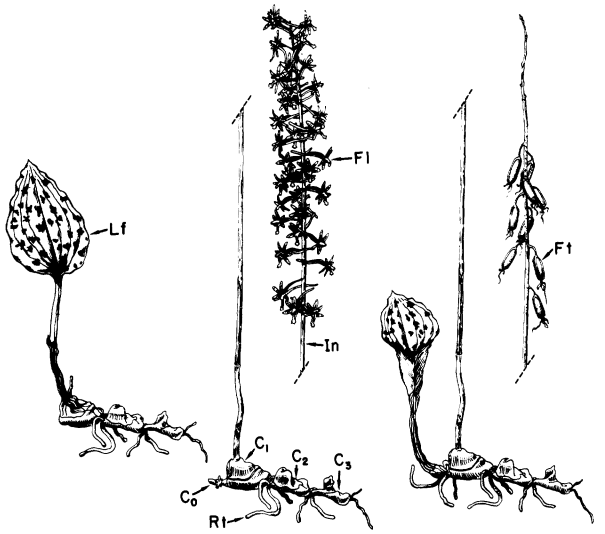

Fig. 1. Schematic representation of a one year growth cycle of *Tipularia discolor*. Between November and June plants consist of a mature leaf (Lf) attached to the current 1 yr corm and corms of various ages but usually including 1 (C1), 2 (C2) and 3 (C3) yr old corms. Roots (Rt) are attached to each corm. Sexual reproduction occurs in July and August with the production of an inflorescence (In) that contains numerous flowers (Fl). New corm (Co) growth is initiated then. Leaves (Lf) are formed on the new corm in September and fruits (Ft) mature with dehiscence occurring in late October to early November.

to the laboratory and washed to remove soil and organic matter. Each plant was dried at 60°C and dry weight determinations made for the following plant parts (Fig. 1): (1) leaves (Lf), (2) inflorescences (including peduncle (In), flowers (Fl), and/or fruits (Ft)), (3) new corms (Co), (4) one year old corms (C_1), (5) two year and older corms plus roots (C_2, C_3, etc., + Rt). While it was possible to determine the age of each corm it was not possible to determine the age of each plant because older corms wither and decompose. Following dry weight determinations, composite samples were prepared for chemical analyses by combining similar plant parts from each sampling date. The composite samples were then ground in a Wiley Mill and analyzed. Each composite sample was analyzed in triplicate for P, K, Mg, Ca, Fe, Cu, Al, Zn, B, Sr, Pb, and Mn. The analyses were performed on an Applied Research Laboratory (Bausch & Lomb) Model 137 individually coupled plasma emission spectrometer using procedures described in Dahlquist and Knoll (1978). Nitrogen analyses were performed in duplicate in our laboratory by digestion with sulfuric acid and peroxide followed by Nesslerization (Anon. 1976). The chemical data obtained represented an average concentration for each plant component on each sample date. Composite samples were thus analyzed to obtain an estimate of variability within the samples and not concentrations for individual plants. This procedure is similar to that described by Callaghan (1980) and is useful when the aim is to determine seasonal variations of average nutrient concentrations.

3. Observations

3.1. Structure of plants sampled

Of the plants sampled, only one did not produce any corm and the remainder produced at least one corm. Thirty plants produced two corms, and of that group, 4 produced 3 corms and 1 produced 4 corms. As indicated in the Introduction, corms persist for several years and it was possible to determine the pattern of corm longevity by examination of the ages of the corms on the 122 plants sampled. Most corms persist for at least 3 yr. One and two year old corms were present on 99.1% and 93.1%, respectively, of the plants sampled and 68% of the plants also had corms that were 3 yr old. Fewer corms persist beyond 3 yr as only 31.6% of the plants had 4, 9.5% had 5, and 0.8% had 6 yr old corms still attached.

3.2. Biomass allocation

Biomass data were analysed using an analysis of covariance to determine whether there were differences between components, temporal differences, and/or time-component interactions. In the analysis (Dixon et al. 1981), total plant weight was used as a covariate to

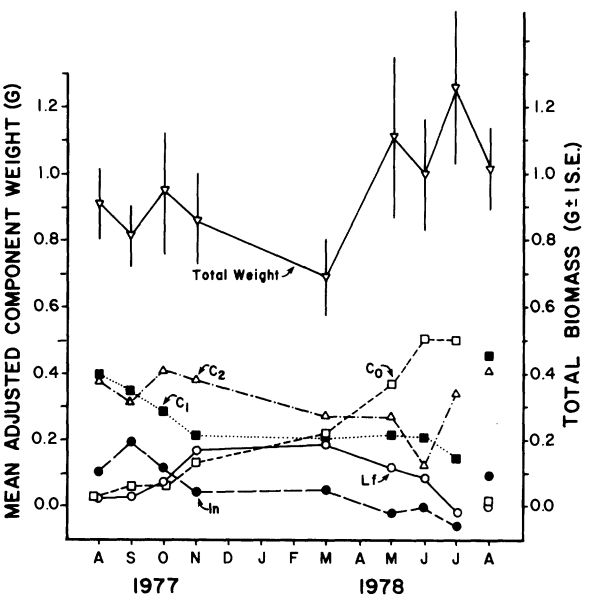

Fig. 2. Monthly total weights and adjusted mean weights for component parts of *T. discolor*. Refer to Fig. 1 legend for description of abbreviations. In this figure, C2 includes all 2 yr and older corms.

eliminate effects due to difference in the weights of individual plants. There were highly significant component ($F = 88.71$; $df = 4$; $p < 0.001$), time-component interactions ($F = 12.28$; $df = 32$; $P < 0.001$), and covariate ($F = 374.27$; $df = 1$; $P < 0.001$) effects while the overall effect due to time was not significant ($F = 0.04$; $df = 8$; $P < 1.000$). The significant covariate effect (total weight) was due, primarily, to the lower mean weights in September 1977 and March 1978 compared with July 1978 (Fig. 2). Adjusted weight values for component parts are also given in Fig. 2 and clearly indicate that there are seasonal trends for each component and interactions between components. The means plotted in Fig. 2 are adjusted for total plant weight and, thus, demonstrate temporal changes in component weights independent of differences in the total weight of plants. When inflorescence biomass increased between August and September, there were also slight increases in the biomass of new corms and decreases in the biomass of one and two year old corms. The average biomass of one year old corms declined almost 50% between August and November. During that same time period, inflorescence biomass declined to almost zero while leaf and new corm biomass each increased between 0.1 and 0.15 g. The average biomass of two year and older corms increased by 0.1 g between September and October. Biomass of leaves and 1 yr old corms changed very little between November and March but the two year and older corms decreased by almost 0.1 g and new corm biomass increased by almost the same amount. The period between March and May was characterized by a large increase, almost 0.2 g, in new shoot biomass and decline of almost 0.1 g in leaf biomass. The increase, between May and June, of almost 0.15 g in the biomass of new corms was offset by an equal decline in the biomass of two year and older corms. Leaf senescence continued between May and July and the growth of new corms stopped in June. Biomass of two year and older corms increased between June and July when there was a decrease in biomass of one year old corms.

Approximately equal percentages of biomass were found in corms older than 2 yr and in 1 yr old corms (Fig. 3). When combined and compared for the year, those components, accounted for between 40% and 90% of the total biomass. Corms accounted for the largest percentages of total biomass in August when new corms were only beginning to develop and when the inflorescences were the only non-corm component present. Percent biomass allocation to 1 yr and older corms declined gradually as new corms increased in size (Fig. 3). New corms matured throughout the year and accounted for increasingly larger percentages of the total biomass. The largest increases in actual weight (Fig. 2) and percentage weight (Fig. 3) of new corms occurred between May and July when leaves senesced.

Leaves began to develop in September and accounted for approximately 20% of the total plant biomass between November and March (Fig. 2). Inflorescences, which were present between late July and November (Whigham and McWethy 1980), never accounted for more than 20% of the total plant biomass.

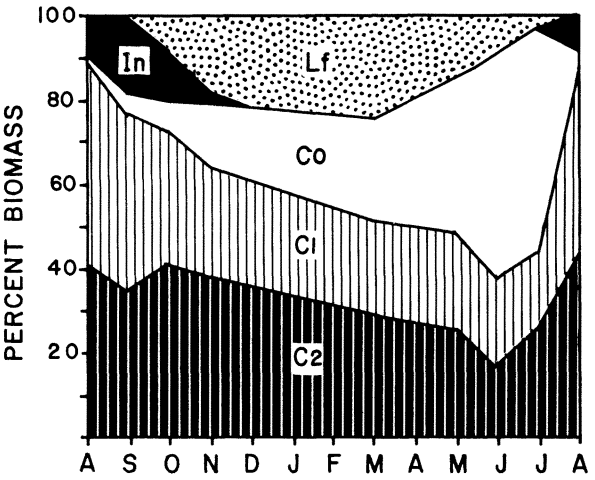

Fig. 3. Cumulative distribution (%) of biomass for component parts of *T. discolor*. Refer to Fig. 1 legend for description of abbreviations. In this figure, C2 includes all 2 yr and older corms.

3.3. Nutrient concentrations

Leaves and inflorescences had the highest concentrations for all macronutrients (Tabs 1 and 2) and temporal differences between components were particularly striking for N, P and K, all of which have been shown to be translocated or leached from senescing structures, particularly leaves (Staaf 1982). Leaf N averaged 3.28% in October and remained high until the leaves senesced in June when N concentrations declined from 1.62% to 0.85%. N concentrations were also high in inflorescences during the flowering period and, unlike leaves, N did not decline as the inflorescences matured. It seems likely that N remained high in the inflorescences because of the N requirement of developing seeds where it is stored, primarily, in the embryos (Evans and Sorger 1980). N content of new and 1 yr old corms was highest between August and October and declined between November and May suggesting N is translocated between storage organs and sinks (Lüttge and Higinbotham 1979). Except for low values in October (0.70%) and in June (1.89%), N in 2 yr and older corms showed no distinct temporal pattern and values were always higher than those measured in new and 1 yr old corms.

P, K, Mg and Ca concentrations were in the same order as N: leaves > inflorescences > 2 yr and older corms > new corms > 1 yr corms. There were no temporal trends for any of the macronutrients in 2 yr and older corms. Like N, P (0.67%) and K (2.70%) con-

Tab. 1. Concentrations (%) of macronutrients in *Tipularia*. All values are means (±1 standard error) of triplicate samples except for nitrogen which are means of duplicate samples. The duplicate nitrogen values never differed more than 5% from each other. The Inflorescence category includes flowers plus peduncles in August and fruits plus peduncles in September and October. A dash indicates plant parts were not present.

Plant part	Month							
	August	September	October	November	March	May	June	July
				Nitrogen				
Leaf	–	–	3.28	1.05	1.83	2.20	1.62	0.85
Inflorescence	1.25	1.09	1.38	–	–	–	–	–
New corm	0.87	0.77	0.80	0.67	0.58	0.45	0.70	0.89
1 yr corm	0.75	0.78	0.66	0.54	0.58	0.46	0.65	0.77
Older corms	0.92	1.06	0.70	0.93	1.09	0.86	1.89	1.00
				Phosphorus				
Leaf	–	–	0.67±0.00	0.34±0.00	0.34±0.00	0.27±0.00	0.27±0.00	0.10±0.00
Inflorescence	0.35±0.00	0.37±0.00	0.33±0.00	–	–	–	–	–
New corm	0.16±0.01	0.14±0.01	0.13±0.00	0.18±0.00	0.14±0.00	0.09±0.00	0.12±0.00	0.17±0.00
1 yr corm	0.18±0.01	0.14±0.01	0.09±0.00	0.07±0.00	0.09±0.00	0.09±0.00	0.11±0.00	0.15±0.00
Older corms	0.19±0.00	0.17±0.00	0.27±0.01	0.16±0.00	0.26±0.00	0.15±0.01	0.23±0.02	0.19±0.01
				Potassium				
Leaf	–	–	2.70±0.00	1.86±0.02	1.51±0.04	1.42±0.07	1.73±0.00	0.95±0.00
Inflorescence	1.44±0.03	1.75±0.03	1.62±0.02	–	–	–	–	–
New corm	0.72±0.04	0.73±0.03	0.54±0.00	0.91±0.00	0.74±0.02	0.42±0.03	0.42±0.03	0.79±0.04
1 yr corm	0.77±0.03	0.73±0.03	0.56±0.04	0.64±0.04	0.59±0.01	0.61±0.01	0.68±0.03	0.76±0.01
Older corms	0.92±0.03	1.04±0.01	1.43±0.05	1.14±0.07	1.40±0.09	0.96±0.03	1.30±0.03	0.98±0.01
				Magnesium				
Leaf	–	–	0.29±0.00	0.20±0.01	0.24±0.00	0.21±0.01	0.27±0.02	0.30±0.00
Inflorescence	0.14±0.00	0.15±0.01	0.17±0.00	–	–	–	–	–
New corm	0.11±0.00	0.12±0.01	0.12±0.00	0.10±0.02	0.12±0.00	0.07±0.00	0.07±0.01	0.11±0.00
1 yr corm	0.12±0.01	0.12±0.01	0.10±0.01	0.09±0.01	0.15±0.00	0.14±0.00	0.09±0.01	0.12±0.01
Older corm	0.16±0.00	0.18±0.01	0.21±0.00	0.20±0.01	0.28±0.03	0.21±0.01	0.24±0.01	0.17±0.01
				Calcium				
Leaf	–	–	0.44±0.00	0.49±0.00	0.38±0.00	0.54±0.02	0.96±0.01	1.42±0.05
Inflorescence	0.44±0.00	0.34±0.03	0.45±0.01	–	–	–	–	–
New corm	0.28±0.04	0.29±0.01	0.17±0.03	0.23±0.06	0.19±0.01	0.15±0.00	0.17±0.01	0.16±0.00
1 yr corm	0.32±0.04	0.29±0.01	0.23±0.02	0.23±0.15	0.19±0.00	0.23±0.01	0.23±0.02	0.23±0.05
Older corm	0.41±0.02	0.45±0.02	0.48±0.01	0.52±0.02	0.46±0.05	0.42±0.02	0.61±0.06	0.40±0.01

centrations were highest in new leaves and declined sharply in senescing leaves. Mg and Ca concentrations were also high in new leaves (Tab. 1) and concentrations of both nutrients increased in senescing leaves. Concentrations of immobile elements like Ca have been previously shown to increase in senescing structures (Guha and Mitchel 1966) primarily because they are tied up in cell walls.

Micronutrient concentrations were more variable than concentrations of macronutrients (Tab. 2) and seasonal patterns were difficult to discern because they are only used in very small quantities for various metabolic functions (Gaugh 1972). All micronutrient concentrations were high in 2 yr and older corms. There was a tendency for Fe and Al to increase between new and 1 yr old corms but none of the other micronutrients had any temporal pattern between those two components. Micronutrient concentrations were high in new leaves and inflorescences and all had a tendency to increase late in the leaf year (June and July) suggesting that they were not translocated or leached from senescing leaves. The data for the micronutrients suggest that they are stored throughout the plant in quantities sufficiently large enough to mask any clear patterns of translocation.

3.4. Nutrient allocation

Macronutrient allocation patterns are shown in Fig. 4. Between approximately 30% and 50% of the macronutrients were stored in 2 yr and older corms and there was a general trend for the percentages to de-

Tab. 2. Concentrations (μg g^{-1}) of micronutrients in *Tipularia*. All values are means (±1 standard error) of triplicate samples. The inflorescence category included flowers plus peduncle in August and fruits plus peduncle in September and October. A dash indicates plant parts were not present, asterisks indicate that 1 (*), 2 (**), or 3 (***) of the samples had concentrations greater than the maximum detectable. In the latter instance, standard errors were not calculated.

Plant part	Month							
	August	September	October	November	March	May	June	July
					Iron			
Leaf	–	–	293±50	312±58	736±58	393±17	448±36	934±40
Inflorescence	278±6	734±56	292±20	–	–	–	–	–
New corm	315±5	418±56	293±5	308±38	250±33	147±13	131±13	78±6
1 yr corm	420±181	418±56	312±110	514±104	638±88	522±37	356±98	167±33
Older corm	1264±69	2000***	961±107	1989**	1595**	1576±98	2000***	604±49
					Copper			
Leaf	–	–	42±3	13±1	8±0	10±1	12±1	10±1
Inflorescence	85±1	14±1	16±1	–	–	–	–	–
New corm	6±1	5±1	8±1	7±0	4±0	3±0	5±0	5±0
1 yr corm	5±0	5±1	5±1	4±1	4±1	4±1	6±1	9±2
Older corm	27±1	20±1	71±2	17±1	23±1	21±2	43±2	18±1
					Aluminum			
Leaf	–	–	208±11	288±48	48±23	276±26	389±41	709±47
Inflorescence	202±8	274±54	268±5	–	–	–	–	–
New corm	239±14	249±14	316±42	296±8	202±16	81±16	119±21	60±1
1 yr corm	341±38	249±14	305±74	511±92	526±92	404±22	253±59	138±30
Older corm	1002±68	1371±1	1186±46	1978**	1559**	1369±73	1994***	534±18
					Zinc			
Leaf	–	–	86±1	46±1	50±1	52±2	74±0	75±0
Inflorescence	34±0	39±6	53±1	–	–	–	–	–
New corm	30±1	36±1	23±1	26±1	24±0	14±0	15±1	26±0
1 yr corm	31±3	36±1	32±3	24±2	37±1	29±0	31±1	30±2
Older corm	47±2	64±3	90±1	54±3	77±8	55±2	75±17	55±1
					Boron			
Leaf	–	–	94±18	74±30	120±0	88±3	211±40	88±2
Inflorescence	67±1	44±3	41±1	–	–	–	–	–
New corm	12±1	21±1	11±0	14±1	13±1	7±0	13±3	10±0
1 yr corm	14±2	21±2	14±3	13±2	17±2	12±0	15±2	16±2
Older corm	24±1	34±2	49±1	54±3	77±8	55±2	75±17	55±18
					Strontium			
Leaf	–	–	33±0	27±0	42±1	29±1	49±3	109±1
Inflorescence	23±0	18±1	50±0	–	–	–	–	–
New corm	19±0	21±1	26±0	22±0	31±0	11±0	13±1	24±1
1 yr corm	25±3	21±1	36±3	21±2	36±1	23±0	19±2	30±2
Older corm	31±2	36±1	64±1	45±2	77±7	39±2	48±5	44±1
					Lead			
Leaf	–	–	7±0	9±2	13±1	15±0	24±0	33±0
Inflorescence	14±0	5±2	7±1	–	–	–	–	–
New corm	4±1	6±0	5±1	3±1	3±1	2±1	2±1	2±0
1 yr corm	4±1	6±0	5±1	5±1	4±1	4±1	5±1	2±0
Older corm	9±1	15±1	17±1	12±1	14±1	13±1	14±4	7±2
					Manganese			
Leaf	–	–	155±12	12±3	90±1	207±8	395±16	366±10
Inflorescence	46±0	75±4	107±3	–	–	–	–	–
New corm	23±1	51±2	29±2	33±1	18±1	22±1	20±1	16±0
1 yr corm	20±4	51±2	50±8	29±3	24±1	40±0	31±1	25±3
Older corm	51±3	101±2	162±2	107±12	77±16	116±5	154±26	39±1

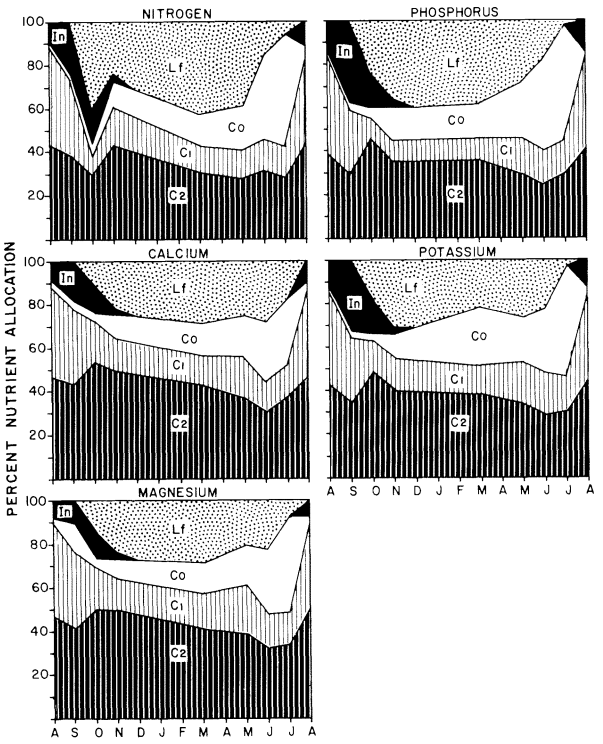

Fig. 4. Macronutrient allocation patterns for *T. discolor*. Refer to Fig. 1 legend for description of abbreviations. In this figure, C2 includes all 2 yr and older corms.

crease between November and May. One year old corms accounted for most of the remaining nutrients during the leafless months of August and September. The percentages of macronutrients in one year corms decreased to approximately 10–15% by October because nutrients were apparently being allocated to inflorescences and initiation of new corm growth (Figs 2 and 3). The percentages of macronutrients in 1 yr old corms remained constant throughout the remainder of the annual cycle.

Inflorescences accounted for between 10 and 40% of the total macronutrient standing stock in September demonstrating the large metabolic demands of reproductive organs. P and K were particularly enriched (see also Tab. 1) in the inflorescences while N, Ca, and Mg changed little except between October and November when fruit development was completed.

Leaves were also important sinks for several micronutrients (Fig. 5). Fifty percent of the B, required for carbohydrate transport (Evans and Sorger 1980), was found in leaves by November. Approximately 30% of the Pb and 40% of the Mn, a constituent of the chlorophyll molecule, were also concentrated in the leaves. Leaves accounted for smaller percentages of Fe (20%), Cu (20%), Al (15%), Zn (25%), and Sr (20%).

Compared with macronutrients, larger percentages of Fe (approximately 65%), Cu (approximately 66%), and Al (approximately 65%) were found in two year and older corms. The other micronutrients averaged approximately 50% in the two year and older corms. As with the macronutrients, there was a tendency for the percentages of micronutrients stored in older corms to decline throughout the year.

One year old corms contained approximately the same percentages of micronutrients (10–15%) as macronutrients. New corms accounted for increased percentages of micronutrients during the year but the increases between May and July, except for Zn, were not as striking for the macronutrients. Inflorescences, in general, contained smaller percentages of micronutrients than macronutrients although B and Cu were particularly enriched in August when inflorescences had matured and flowers had begun anthesis.

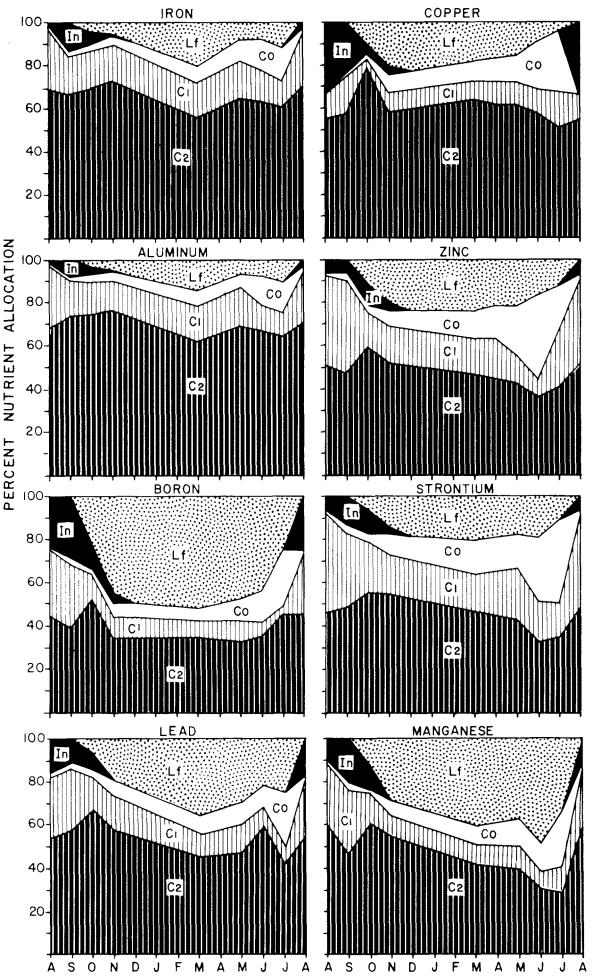

Fig. 5. Micronutrient allocation patterns for *T. discolor*. Refer to Fig. 1 legend for description of abbreviations. In this figure, C2 includes all 2 yr and older corms.

4. Discussion

4.1. Biomass allocation

The amount of biomass allocated to belowground structures has been shown to vary widely among herbaceous woodland species. Abrahamson (1979) found that belowground/shoot organ ratios varied between 60 and 215 for all but three of the 16 woodland species he studied. Only *Geum canadense* and two spring ephemerals (*Erythronium americanum* and *Claytonia virginica* had ratios less than 50 (4, 10, and 7 respectively). Muller (1979) has shown that *Erythronium albidum* has belowground/aboveground ratios that vary from 2.5 for asexually reproductive individuals to 1.8 for nonreproductive individuals and 0.91 for sexually reproductive individuals. *Tipularia* belowground/aboveground ratios varied seasonally from a high of 35 in late June when the leaves were senescing to a low of 2.4 in November when leaf development was almost complete and when mature fruits had not yet dehisced. At the time of flowering the belowground/aboveground ratio averaged 4.0. The overall pattern of biomass allocation, for *Tipularia* therefore, is most similar to that exhibited by spring geophytic perennials (Kawano 1975, Kawano et al. 1982) even though *Tipularia* is phenologically very distinct from that group of plants.

4.2. Nutrient allocation

How do seasonal changes in the allocation of aboveground and belowground biomass relate to patterns of biomass and nutrient allocation between different plant parts? To date, several studies have shown how herbs of deciduous forests allocate biomass, (Kawano et al. 1976, 1982, Abrahamson 1979, Pitelka and Ashmun unpubl.) but few studies have considered nutrient allocation between component parts. Muller (1979) showed that a large amount of the annual net primary production is moved from parent plants into developing cormlets of *Erythronium albidum.* In *Erythronium,* however, the parent corm dies at the end of the growing season and it would be expected that most of the nutrients would be translocated to daughter corms. Kawano et al. (1982) has also found that most growth is restricted to the current year corms in the Japanese species *Erythronium japonicum.* In *Tipularia,* most of the annual increase in biomass and nutrients appear to be associated with developing corms (Figs 2–5). Using labelled carbon, Ashmun et al. (1982) have found similar results for *Aster acuminatus,* in which most of the labelled compounds were translocated to the newest portions of rhizomes. In contrast, the same authors found that photoassimilates were translocated throughout the underground system in *Clintonia borealis.* Newell (1982) also found that there was extensive translocation among shoots of *Viola blanda* that were connected by stolons. From the present study of *Tipularia,* it appears that macronutrients are more mobile than micronutrients (Figs 4 and 5) and that most of the annual variation is associated with the growth and senescence of leaves and inflorescences and the accumulation of nutrients in longer lived corms. Patterns of biomass and nutrient allocation have also been studied in several wetland herbaceous species (Klopatek 1978, Prentki et al. 1978, Bayley and Shibley 1978, Grace and Wetzel 1981). Plant parts older than 1 yr appear to be sites of nutrient storage and are only minimally related to seasonal allocation patterns even though they usually contained more than 50% of the total nutrient standing stock.

Abrahamson and Caswell (1982) have recently shown that biomass allocation patterns may not closely follow allocation patterns for nutrients. In contrast, allocation patterns of biomass and nutrients in *Tipularia* are rather similar. With the exception of a few species such as *Erythronium albidum* (Muller 1979), which allocate all of the stored resources into current year reproduction, the relationships between growth, senescence, leaching, translocation, and assimilation are complex (Pitelka and Ashmun unpubl.). Assimilation, a central part of the vernal dam hypothesis, should be more important than translocation if woodland herbs play an important role in ecosystem nutrient retention (Bormann and Likens 1979, Grigal and Ohman 1980, Blank et al. 1980, Muller 1980). In contrast, work with wetland macrophytes, plants of supposedly "leaky" ecosystems, suggest that translocation may be more important than assimilation (Klopatek 1978). The relationship between these factors was examined in *Tipularia* by combining mean monthly biomass and nutrient concentration data to compare the amounts of macronutrients that were assimilated into new growth or lost during senescence compared to the increase or decrease in older corms. Micronutrients demonstrated the same overall patterns as macronutrients. Three questions were asked in this analysis. First, were the nutrients allocated to inflorescences that develop during August equal to, greater than, or less than the nutrients translocated from senescing leaves? Tab. 3 (Part A) shows that, except for nitrogen, the decline in leaf macronutrients was less than the amounts allocated for inflorescences. The net differences may have been accounted for by assimilation and translocation, or probably a small amount of leaching, from other storage components. When all other component parts were included in the analysis (Tab. 3, Part B), new corms and 1 yr corms, in addition to inflorescences, showed increases in the amounts of all nutrients between June and September. The net result was that, except for Mg, total declines were less than total increases, suggesting that nutrient uptake from the litter and soil was required during the period of inflorescence development.

The second analysis dealt with the period of leaf senescence (May–August) when new corms had the most rapid increase in weight (Fig. 2). Except for P, losses, assumed to be due primarily to translocation,

Tab. 3. Comparison of macronutrient changes in component parts of *Tipularia*. A plus (+) indicates a net increase and a negative (–) a decline during the time interval indicated. A net positive balance (+) indicates that translocation alone would not account for all of the gains. A net negative balance (–) indicates that translocation alone would account for all gains. All values are milligrams.

Part A. Comparison of gains in inflorescence between August and September and losses from senescing leaves between June and August

	Mg	Ca	N	P	K
Leaf	−214	−336	−3000	−369	−1802
Inflorescence	+267	+840	+2390	+669	+2750
Net	+ 53	+504	− 610	+300	+ 948

Part B. Similar to part A but including all components between June and September

New corm	+267	+869	+1600	+464	+1832
1 yr corm	+ 14	+ 36	+ 110	+113	+ 94
1 yr corm	+ 4	+536	+ 890	+197	+ 515
Older corm	−283	−359	− 550	−445	− 859
Leaf	−313	−805	−2720	−402	−2116
Inflorescence	+267	+840	+2390	+669	+2750
Net	− 44	+1117	+1720	+596	+2216

Part C. Similar to B except comparing the period May–August when leaf senesces and before inflorescences develops

New corm	+428	+595	+4120	+739	+3278
1 yr corm	+ 18	+327	+ 700	+169	+ 656
Older corm	−168	+ 43	+ 250	−491	−1729
Leaf	−232	− 55	−2250	−436	−1770
Net	+ 46	+910	+2820	− 19	+ 435

Part D. Comparison of gains and losses when leaf is developing (September–November)

New corm	+ 76	+285	+ 530	+347	+ 824
1 year corm	−206	−472	−1430	−309	−1068
Older corm	+444	+594	+ 270	+ 91	+1147
Leaf	+256	+627	+1340	+435	+2381
Inflorescence	−107	−147	− 570	−396	−1786
Net	+463	+887	+ 140	+168	+1498

from leaves and 2 yr and older corms did not account for the increases in nutrients in new and 1 yr old corms (Tab. 3, Part C). Particularly striking were the large nitrogen, phosphorus, and potassium requirements of new corms. Again, losses, assumed to be due primarily to translocation, did not appear to be sufficient to satisfy increased nutrient requirements, except for P, and uptake from the soil seemed necessary.

The third analysis dealt with the phase of growth between September and November, the period when leaves are developing. The question addressed was whether or not losses from other components could account for the nutrients found in the leaves. The analysis of gains and losses (Tab. 3, Part D) during that time interval suggested that 1 yr old corms and inflorescences lost macronutrients but that all others, especially leaf components, increased. The net effect was that losses apparently did not account for all of the growth needs and that uptake was necessary. All three analyses therefore provide support for the hypothesis that movement (translocation) and losses (leaching) are insufficient to account for all nutrient requirements during periods of rapid growth, and that this woodland perennial must assimilate substantial amounts of nutrients from the substrate. Benzing et al. (1983) have recently suggested that significant amounts of carbon, and probably nutrients, can be assimilated from the substrate by orchids that are leafless, or leafless for extended periods. Assimilation is effected through the mutualistic plant-fungus interaction. Additional data are required to determine the interplay between nutrient storage, translocation, leaching losses, and assimilation.

If the vernal dam hypothesis is true (Muller 1979, Blank et al. 1980), which suggests that most of the plant nutrients would be assimilated from the soil, why do most woodland perennials have such large belowground storage structures? This question is particularly interesting in light of this study which suggests that only small amounts of nutrients are lost, probably primarily due to translocation, from older storage structures compared with the amounts that are apparently moved from senescing structures to growing structures. Several roles have been suggested for belowground structures. Most obvious are the importance of perennial structures as sites of meristem protection during periods of climatic stress and as reserves for nutrients that are used during periods of growth and reproduction. Less emphasis has been given to the role that perennial structures might play in enabling plants to respond to predation (Pitelka and Ashmun unpubl.). Ashmun et al. (1982) found little or no translocation of carbon when they defoliated a woodland *Aster* while defoliation of one ramet of *Clintonia borealis* caused increased exportation of carbon from a connected ramet. Sohn and Policansky (1977) also found shifts in the allocation of resources when they artificially removed leaf tissue of *Podophyllum peltatum*, a species that apparently translocates large amounts of nutrients from belowground structures (Blank et al. 1980). In *Tipularia*, I have observed that plants can survive several successive years of complete leaf predation (Whigham, unpubl.). All of these results suggest that one purpose for maintenance of large belowground nutrient stores is to enable the plant to survive intense herbivory. These storage structures also may serve as important reserves for nutrients to be used during periods of rapid growth, and as sites where dor-

mant buds can survive periods of climatic stress (e.g., winter). The interplay among these, and possibly other, factors, remains unclear and awaits further research.

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