Primary productivity and nitrogen, carbon, and biomass distribution in a dense *Myrica gale* stand

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Aboveground vascular vegetation was harvested in twenty 0.25-m^2 plots at the end of the growing season in a weakly minerotrophic, central Massachusetts peatland. The materials were separated by species and component and the *Myrica gale* fractions analyzed for N and C content. *Myrica gale* strongly dominated the site, contributing 66% of the total aboveground biomass and 74% of the main canopy leaf area. Its shoots had a mean density of 69 stems m^{-2} and mean height of 63 cm and reached a maximum age of 7 years. *Myrica gale* aboveground biomass was 604 g m^{-2} with stems contributing 75%, leaves 24%, and reproductive organs 2%. Similar patterns of biomass distribution have been reported in other peatland low shrubs. Aboveground net production was 392 g m^{-2} year^{-1} and total net production estimated to be 549 g m^{-2} year^{-1}. Nitrogen contents were higher than in other peatland shrubs and ranged from 0.94% in stems $\geq$ 3 years old to about 2.4% in leaves, nodules, and male flower buds. Carbon contents ranged from 50% in stems $\geq$ 3 years old to 56% in male flower buds. The N content of total annual net production was estimated to be 8.6 g m^{-2} and the C content 281 g m^{-2}. Nitrogen fixation provided 43% of the estimated annual N requirement.

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La végétation vasculaire épigée a été récoltée dans 20 parcelles de 0,25 m^2, à la fin de la saison de croissance, dans une tourbière légèrement minérotrophe du centre du Massachusetts. Le matériel récolté a été séparé selon les espèces et les parties composantes et la teneur en N et en C a été analysée dans les fractions consistant en *Myrica gale*. Cette espèce dominait le site, formant 66% de la biomasse épigée totale et 74% de la surface foliaire dans la principale strate foliaire. Ses pousses avaient une densité moyenne de 69 tiges m^{-2}, une hauteur moyenne de 63 cm et un âge maximum de 7 ans. La biomasse épigée de *Myrica gale* était de 604 g m^{-2}, les tiges contribuant 75% de la biomasse, les feuilles, 24% et les organes reproducteurs, 2%. Des patrons semblables de répartition de la biomasse ont été trouvés chez d'autres arbustes bas des tourbières. La production épigée nette était de 392 g m^{-2} année^{-1} et la production nette totale a été estimée à 549 g m^{-2} année^{-1}. La teneur en azote était plus élevée que dans d'autres arbustes des tourbières et elle variait de 0,94% dans les tiges âgées de 3 ans et plus, à environ 2,4% dans les feuilles, les nodules et les boutons floraux mâles. La teneur en carbone variait de 50% dans les tiges âgées de 3 ans et plus, à 56% dans les boutons floraux mâles. La teneur en azote de la production annuelle nette totale a été estimée à 8.6 g m^{-2} et la teneur en carbone, à 281 g m^{-2}. La fixation d'azote a fourni à environ 43% des besoins annuels estimés d'azote.

[Traduit par le journal]

Introduction

Myrica gale L. is an actinorhizal dinitrogen-fixing shrub commonly found in open peatlands and along shores of lakes and streams in northern North America and Europe. This deciduous low shrub is an ecological dominant in several plant associations within its extensive range (e.g., Abbayes and Hamant 1946; McVean and Ratcliffe 1962; Jeglum *et al.* 1974; Schwintzer 1978; Wells 1981; Wheeler 1980) and is capable of fixing substantial amounts of nitrogen (Schwintzer 1979).

Several aspects of nitrogen fixation by *Myrica gale* have been previously studied at a *Myrica gale* dominated site in a weakly minerotrophic peatland known as Tom Swamp in central Massachusetts (Schwintzer 1979; Schwintzer *et al.* 1982). These include the seasonal pattern of nitrogenase activity and nodule growth, shoot phenology, and nodule biomass. During 1978 and 1979 *Myrica gale* fixed about 3.5 g N m^{-2} year^{-1}, adding approximately five to six times the amount of N in bulk precipitation to the site.

In the present study I examined aboveground biomass and productivity of the previously studied *Myrica gale* stand to determine (*i*) basic structural characteristics of the stand, including stem age and length distribution and biomass distribution among stems, leaves, and reproductive organs; (*ii*) the fraction of the annual N requirement that is provided by nitrogen fixation; and (*iii*) annual net aboveground productivity compared with the productivity of other open peatlands.

Study area and methods

Study area

The study site is located in a weakly minerotrophic open peatland known as Tom Swamp in the Harvard University

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Forest at Petersham, MA. All observations were made in a 0.7-ha area designated "Open Mat" in an earlier study (Schwintzer 1979). The vegetation at this site is dominated by *Myrica gale* (mean cover 53%) and *Chamaedaphne calyculata* (12%). The ground layer consists primarily of *Sphagnum* spp. (35%) and leaf and woody litter. Further details including information on other studies in Tom Swamp are given by Schwintzer (1979).

Stand characteristics and aboveground biomass

All vascular biomass was clipped at ground level in twenty 0.25-m^2 circular plots randomly located along three widely spaced transects. The plots were harvested between 22 August and 13 September 1979 because growth was complete and most leaves did not yet show signs of senescence. However, some first-produced leaves had been shed (Schwintzer *et al.* 1982) and this loss was corrected for in the measurement of net primary production. There was almost no leaf loss by herbivory.

Myrica gale shoot density, length, and age distribution were determined by separating living *Myrica gale* shoots from other materials and determining the length and age of each. Shoot age was estimated from the number of annual rings in the basal xylem in conjunction with the number of groups of bud-scale scars.

Biomass distribution was determined by separating the materials from each plot into the components shown in Table 1. One-year-old stems were subdivided as vigorous (basal diameter > 0.8 mm) or weak (< 0.8 mm) because their radial growth rates appeared to differ. Stems ≥ 3 years old were grouped because they had similar radial growth rates. All living materials were dried to constant weight at 60°C in a forced-air oven to minimize loss of volatile nitrogen-containing compounds and weighed; the weights were corrected to weight at 100°C (Allen *et al.* 1976). Standing dead biomass was air dried for 6 months and weighed and the weights were corrected to weight at 100°C.

Specific leaf weight (milligrams per centimetre squared) and leaf area index (LAI, one leaf side) were determined for *Myrica gale* and *Chamaedaphne calyculata*. Specific leaf weight was obtained by taking random subsamples of fresh leaves equivalent to about 30 cm^2 each from six plots and determining their area and dry weight. Leaf area index was calculated from leaf dry weight and specific leaf weight.

Net primary production, N and C content

Aboveground net primary production by *Myrica gale* was obtained from standing biomass as follows. Leaf biomass for each individual plot was adjusted for leaf loss before harvest based on harvest date and leaf loss measured in litter buckets (C. R. Schwintzer, unpublished data). Stem production was calculated by multiplying stem dry weight of each stem component by the ratio of increase in xylem cross-sectional area during the current year to total xylem cross-sectional area. Cross-sectional increment was measured at midsegment in 70 stem segments of each component taken at random in groups of 10 in seven plots.

Total N and C were determined in random subsamples of each component from seven plots. Subsamples of materials dried at 60°C were ground to a homogeneous mixture and then further subsampled and weights corrected to weight at 100°C. Total N was determined by Kjeldahl digestion using selenium as catalyst and by analyzing the digest directly for ammonia by colorimetry in procedures slightly modified from those of Bergersen (1980). Carbon was determined by wet oxidation followed by titration as described by Allen *et al.* (1976).

TABLE 1. Standing aboveground vascular biomass (grams dry weight per metre squared) at the end of the growing season in a vigorous *Myrica gale* stand in central Massachusetts. Values are $\bar{x}$ ± SD; $N = 20$

Component	
Myrica gale	
Leaves	142±64
Stems	
Current	60±30
1 year old, vigorous	79±47
1 year old, weak	24±13
2 years old	112±51
≥3 years old	176±108
Male buds	6±9
Fruit	5±8
Dead	545±236
Chamaedaphne calyculata	
Leaves	54±55
Stems	263±290
Dead	108±161
Herbs[a]	22±24

[a]Primarily *Lysimachia terrestris* and *Carex* spp.

Results

Stand characteristics and aboveground biomass

Myrica gale had a stem density of 69 ± 36 stems m^{-2} ($\bar{x}$ ± SD, $N = 20$) and stem height of 63.1 ± 21.7 cm ($\bar{x}$ ± SD, $N = 171$). Most stems (94%) were less than 5 years old and the oldest were 7 years old (Fig. 1A). Stem length increased rapidly with age during the first 3 years and then much more slowly. The oldest stems were tallest on average with a mean height of 81 cm (Fig. 1B). The tallest stem was 103 cm high.

The LAI of *Myrica gale* at harvest was 2.06 ± 0.93 ($\bar{x}$ ± SD; $N = 20$) and that of *Chamaedaphne calyculata*, the only other shrub with more than 1% cover, was 0.72 ± 0.74. Based on LAI, *Myrica gale* cover constitutes 74% of the total shrub cover. This compares favorably with 82% determined earlier in the season by visual estimate (Schwintzer 1979). The specific weight of the *Myrica gale* leaves was 7.16 ± 0.70 mg cm^{-2} ($\bar{x}$ ± SD; $N = 7$) and that of *Chamaedaphne calyculata* was 7.67 ± 0.56 mg cm^{-2}.

The aboveground vascular biomass (Table 1) was largely composed of *Myrica gale* (604 g m^{-2}) and *Chamaedaphne calyculata* (317 g m^{-2}). Herbs contributed only 22 g m^{-2}. Leaves made up 24% of *Myrica gale*

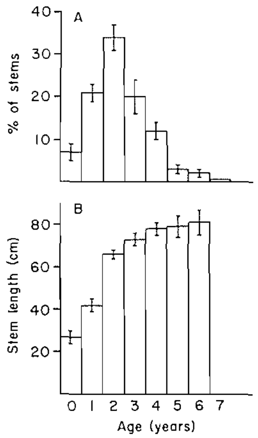

FIG. 1. (A) Age distribution of *Myrica gale* stems and (B) the relationship between stem length and age at the Tom Swamp site in late summer 1979. The stems were sampled in 0.25-m^2 plots (see text); $\bar{x} \pm$ SE, $N = 20$.

biomass and 17% of *Chamaedaphne calyculata*. There was also a large amount of standing dead biomass composed primarily of *Myrica gale* and *Chamaedaphne calyculata* stems in various states of decay.

Net primary production, N and C content

The percentage of stem xylem cross-sectional area produced during the current year decreased with increasing age (Table 2). The percentage produced during each of the first four seasons can be approximated by the calculated increment obtained by dividing 100 by the number of seasons of growth except in the case of 1-year weak stems. The fractional increment in 1-year weak stems was significantly smaller ($P < 0.001$) than in 1-year vigorous stems.

Nitrogen contents (Table 3) ranged from a high of about 2.4% in nodules, leaves, and male flower buds to a low of 0.94% in stems ≥ 3 years old. The N content of stems decreased with increasing age, but there was no significant difference ($P < 0.10$) in N or C content between 1-year-old weak and vigorous stems. Consequently the results for these two groups were combined. Carbon contents (Table 3) varied little, ranging from 56% in male flower buds to 50% in stems ≥ 3 years old.

TABLE 2. Percentage of stem xylem cross-sectional area produced during the current year

Age of stem segment	Measured ($\bar{x} \pm$ SD; $N = 70$)	Calculated
Current	100	100
1 year, vigorous[a]	55.1±14.1	50
1 year, weak[b]	39.5±14.3	50
2 years	35.7±11.6	33.3
≥3 years	23.9±12.3	
3 years		25

[a] Segments with a basal diameter > 0.8 mm.
[b] Segments with a basal diameter < 0.8 mm.

TABLE 3. Nitrogen and carbon content of *Myrica gale* fractions at the end of the growing season. Values are $\bar{x} \pm$ SD

Fraction	No. plots	%N	%C
Leaves	7	2.36±0.10	52.2±0.9
Stems, current	7	1.13±0.14	50.5±1.5
Stems, 1 year old	14	1.05±0.12	51.3±1.3
Stems, 2 years old	7	1.03±0.05	50.7±1.1
Stems ≥ 3 years old	7	0.94±0.04	50.1±1.0
Male buds	7	2.34±0.23	56.2±1.8
Fruit	4	2.15±0.18	54.5±1.3
Nodules	6[a]	2.40±0.30	—

[a] Number of 0.4- to 0.6-g samples.

Myrica gale had an aboveground net primary production of 392 g dry weight m^{-2} $year^{-1}$ (Table 4), with stems contributing 50%, leaves 47%, and reproductive organs 3%. Total productivity was estimated to be 549 g dry weight m^{-2} $year^{-1}$ and to contain 8.56 g N and 281 g C. Although leaf production constituted only 34% of total production, it accounted for 51% of the total N content.

Discussion

Annual net production by *Myrica gale* at the Open Mat site in 1979 required about 8.6 g N m^{-2} (Table 4). During the same year *Myrica gale* fixed about 3.7 g N m^{-2} (Schwintzer *et al.* 1982) supplying approximately 43% of the annual requirement. The remaining 4.9 g N m^{-2} was obtained by redistribution within the plant (Sprent *et al.* 1978) and from the peat. Thus nitrogen fixation clearly made an important contribution to the nitrogen budget of *Myrica gale* at this site.

Both cover and biomass have been used as measures of ecological dominance. By either measure *Myrica gale* strongly dominated this site. It was responsible for 74% of the total shrub layer LAI, 66% of the total shrub biomass, and 64% of the total vascular biomass.

The Tom Swamp *Myrica gale* stand was similar in most respects to five Scottish stands (Sprent and Scott 1979). The similarities included aboveground biomass (604 g m^{-2} versus 301–580 g m^{-2} in Scotland), mean stem height (63 cm compared with 46–88 cm), and distribution of aerial biomass. Leaves accounted for 24% here and 21–24% in Scotland, while stems contributed 75% here and 76–79% in Scotland. Nitrogen contents were also similar in old stems (0.94–1.05% compared with 0.87–1.03% in Scotland) and August leaves (2.36% versus approximately 2.25%) but were somewhat higher here in nodules (2.40% versus 1.84–2.09%).

Plant growth in peatlands is often limited by N, P, and

TABLE 4. Primary productivity of a dense *Myrica gale* stand and the nitrogen and carbon contents of the biomass produced in 1979

	Net primary production, g dry weight m^{-2} $year^{-1}$	N, g m^{-2} $year^{-1}$	C, g m^{-2} $year^{-1}$
Leaves	185	4.37	97
Stems	196	2.06	99
Male buds and fruit	11	0.25	6
Total aboveground	392	6.68	202
Roots[a]	151	1.74	76
Nodules[b]	6	0.14	3
Total belowground	157	1.88	79
Overall total	549	8.56	281

[a] Estimated as follows: mean shoot/root ratio of *Myrica gale* growing on peat 10–35 cm above the water table = 2.31 (Schwintzer and Lancelle 1983); mean %N in *Myrica gale* roots = 1.15% (Sprent and Scott 1979); and %C = 50.6%, the mean for stems (Table 3).

[b] Estimated as follows: nodule biomass = 10.4 g m^{-2} (Schwintzer 1979) and annual production = 61% of nodule biomass (Schwintzer *et al.* 1982); %C = 50.6%, the mean for stems (Table 3), and %N = 2.4%.

TABLE 5. Distribution of aboveground biomass and current shoot biomass in leaf, stem, and reproductive tissue in common peatland low shrubs

	% of aboveground biomass[a]			% of current shoot biomass[b]		
Species	Leaf	Stem	Reproductive	Leaf	Stem	Reproductive
Chamaedaphne calyculata	21	78	1	63	30	6
Kalmia polifolia	11	88	1	53	19	26
Ledum groenlandicum	27	72	1	68	20	12
Myrica gale	24	75	2	67	29	5

[a] Values for *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Ledum groenlandicum* from data for the undisturbed plot from Sims and Stewart (1981); *Myrica gale* calculated from data in Table 1.

[b] Values for *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Ledum groenlandicum* are means for eight sites calculated from data for 1979 from Reader (1982); *Myrica gale* from data in Table 1.

K (Moore and Bellamy 1974; Reader 1978*a*; Richardson *et al.* 1978). *Myrica gale* is unique among low peatland shrubs in its ability to fix nitrogen and it would be interesting to know whether this added N supply results in a different pattern of biomass distribution among stems, leaves, and reproductive organs than in other peatland shrubs. In particular greater biomass allocation to N-rich plant parts, i.e., leaves and reproductive organs, might be expected. The data in Table 5 show that this is apparently not the case. Allocation of total biomass and current shoot biomass to leaves and reproductive organs is among the higher values found but does not exceed them. It should be noted, however, that the other shrubs in Table 5 are all evergreen and retain their leaves for two growing seasons (Reader 1978*b*); thus the annual N investment in leaf production is much greater in *Myrica gale*. Moreover, *Myrica gale* leaves contain substantially more N (2.36%) than current-season *Chamaedaphne calyculata* leaves (1.71%; Richardson *et al.* 1978). The N content of *Kalmia polifolia* and *Ledum groenlandicum* is similar to that of *Chamaedaphne calyculata* (Reader 1978*b*). *Myrica gale* leaves also contain more N than the deciduous leaves of several *Salix* species (2.00%) and *Betula pumila* (1.87%) (Richardson *et al.* 1978). Because N content of *Myrica gale* (Sprent *et al.* 1978) and other peatland shrubs (Reader 1978*b*; Richardson *et al.* 1978) varies with the season, comparisons should be made at the same time of the year. The N contents compared here were all obtained in August. Nitrogen content also varies with the site, but in *Myrica gale* the degree of variation is limited since the values reported here and those at five sites in Scotland are similar (Sprent and Scott 1979). In addition to having a higher leaf N content than other peatland shrubs *Myrica gale* also has higher stem N contents. In August the N content of current stems was 1.13% in *Myrica gale* (Table 3) but only 0.71% to 0.90% in *Chamaedaphne calyculata*, *Salix* spp., and *Betula pumila* (Richardson *et al.* 1978). Thus although biomass allocation to stems, leaves, and reproductive organs is similar in *Myrica gale* and the three common peatland shrubs in Table 5, N use by *Myrica gale* is much greater because its leaves are deciduous and both leaves and stems have higher N contents.

Given the greater N use by *Myrica gale* and addition of biologically fixed N to the site via leaf and woody litter, greater productivity might be expected at this site than in peatlands containing little or no *Myrica gale*. Total aboveground vascular production at the Tom Swamp site was estimated to be 551 g m^{-2} $year^{-1}$, consisting of 392 g m^{-2} contributed by *Myrica gale* (Table 4), 22 g m^{-2} by herbs (Table 1), and 137 g m^{-2} by *Chamaedaphne calyculata* (estimated from the ratio of the leaf areas of *Chamaedaphne calyculata* and *Myrica gale* and *Myrica gale* productivity). In addition, mosses, primarily *Sphagnum* spp., had about 35% cover (Schwintzer 1979) and could add an additional 175 g m^{-2} $year^{-1}$ (based on the mean (5.0 g dm^{-2} $year^{-1}$) of the *Sphagnum* spp. growth rates summarized by Moore and Bellamy (1974) and 35% cover). The vascular productivity of the Tom Swamp site alone is greater than the total aboveground productivities of seven of nine peatlands with little or no *Myrica gale*, summarized by Reader (1978*a*), which ranged from 101 to 1026 g m^{-2} $year^{-1}$, but total productivity did not exceed the two highest values. Thus productivity at the Tom Swamp site is among the highest recorded for peatlands lacking *Myrica gale* but does not exceed it. The relative importance of the greater availability of N from N_2 fixation and other factors important in determining peatland productivity, especially heat sum, conductivity of the water, and depth to standing water (Reader 1982), cannot be determined from the available data.

Myrica gale and *Chamaedaphne calyculata*, the main canopy shrubs, apparently do not fully utilize the available light. Their combined LAI of 2.78 is well below the LAI of about 4.0 which results in maximum net production (Odum 1971) and the LAI of 4–6 found in temperate-zone forests (Whittaker 1975). Failure of these shrubs to develop a closed canopy on this relatively long-established site (Swan and Gill 1970) suggests that availability of one or more nutrients is limiting because water is in ample supply. Since N_2 fixation presumably provides adequate N, the nutrients most likely to be limiting are P, K, or both. Such limitation might explain why net productivity of this site dominated by *Myrica gale* was not higher.

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